# *Atoll islands as ecosystem replicates: Organization of biodiversity and environmental impact of different human land uses*

DISSERTATION

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***Sebastian Steibl***

aus *Pegnitz*

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Acting director: Prof. Dr. Hans Keppler

Doctoral committee:

Prof. Dr. Christian Laforsch (reviewer)
Prof. Dr. Heike Feldhaar (reviewer)
Prof. Dr. Gerhard Gebauer (chairman)
Prof. Dr. Stefan Schuster

(additional reviewer: Prof. Dr. Manuel Steinbauer)

*“Islands are havens and breeding grounds for the unique and anomalous.*
*They are natural laboratories of extravagant evolutionary experimentation.”*
- D. Quammen, The Song of the Dodo, 1996

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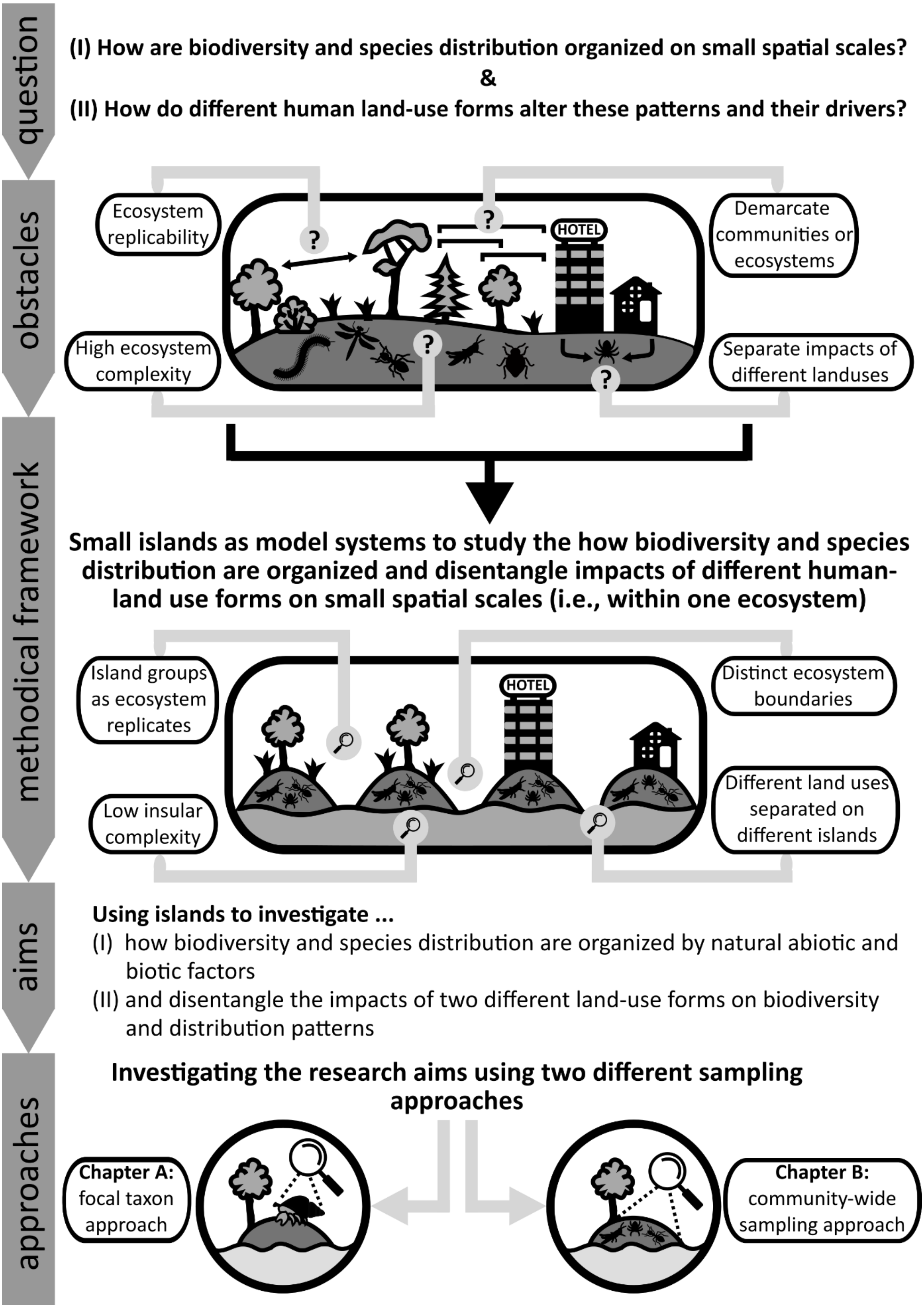
# I. Graphical Abstract



question

**(I) How are biodiversity and species distribution organized on small spatial scales?**
**&**
**(II) How do different human land-use forms alter these patterns and their drivers?**

obstacles

Ecosystem replicability

High ecosystem complexity

Demarcate communities or ecosystems

Separate impacts of different landuses

methodical framework

**Small islands as model systems to study the how biodiversity and species distribution are organized and disentangle impacts of different human-land use forms on small spatial scales (i.e., within one ecosystem)**

Island groups as ecosystem replicates

Low insular complexity

Distinct ecosystem boundaries

Different land uses separated on different islands

aims

**Using islands to investigate ...**

(I) how biodiversity and species distribution are organized by natural abiotic and biotic factors

(II) and disentangle the impacts of two different land-use forms on biodiversity and distribution patterns

approaches

**Investigating the research aims using two different sampling approaches**

**Chapter A:** focal taxon approach

**Chapter B:** community-wide sampling approach

# II. German Summary

Die Verteilung der Biodiversität unseres Planeten folgt bestimmten Mustern. Auf globaler Ebene sind diese Muster durch nur wenige Umweltfaktoren erklärbar, da sie primär Längen- und Höhengraden folgen. Auf kleinerer räumlicher Ebene werden die Verteilungsmuster jedoch schwieriger greifbar, da eine Vielzahl unterschiedlicher Faktoren gleichzeitig das Auftreten verschiedener Arten beeinflussen. Ein grundlegendes Ziel der Ökologie ist es daher zu verstehen, wie die Verteilung von Arten innerhalb von Ökosystemen organisiert ist. Dies bekommt vor allem hinsichtlich der fortschreitenden Veränderung der Natur durch den Menschen zusätzliche Relevanz, da der weltweit schwerwiegendste Verursacher für Biodiversitätsverlust Landnutzung ist, welche Veränderungen vor allem auf lokaler Ebene (d.h. in einzelnen Ökosystemen/ Habitaten) vorantreibt. Dabei bedingen verschiedenste Landnutzungsformen die Umwandlung von natürlichen Ökosystemen in anthropogen modifiziertes und degradiertes Land. Viele Studien konnten bereits den Rückgang von Biodiversität als Folge verschiedener Landnutzungsformen charakterisieren.

Trotz der detaillierten Beschreibung des Art- oder Biomasserückgangs durch menschliche Aktivitäten fehlt ein tieferes Verständnis über die zugrundeliegenden Mechanismen, welche Veränderungen in der Biodiversitätsverteilung verursachen. Um zu verstehen, wie menschliche Landnutzung die Biodiversitätsverteilung innerhalb von Ökosystemen verändert, ist es jedoch zunächst entscheidend zu verstehen, wie Biodiversität und Artverteilung in ungestörten Ökosystemen durch abiotische und biotische Faktoren organisiert wird. Erst dann kann auch ein tiefergreifendes Verständnis darüber generiert werden, wie menschliche Aktivitäten Biodiversitätsverlust durch Veränderung der natürlichen Verteilungsmuster verursachen.

Empirische Forschung, welche genau diese Verteilungsmuster auf Ökosystemebene identifizieren soll, ist jedoch in der Regel schwer umsetzbar. Dies liegt vor allem an der hohen Komplexität natürlicher Ökosysteme, der notwendigen artifiziellen Eingrenzung des zu untersuchenden Systems, und der schwer umzusetzenden Replikation ganzer Ökosysteme bei der Durchführung von Studien auf Ökosystemebene. Kleine Inseln können jedoch aufgrund ihrer geringen Komplexität, klaren Abgrenzung und Replizierbarkeit ein geeignetes Modellsystem sein, um die genannten Limitationen für Untersuchungen auf Ökosystemebene zu umgehen.

Das Ziel dieser Doktorarbeit ist daher, mithilfe des Modellsystems Insel zu untersuchen, wie Biodiversität und Artverteilung in Ökosystemen organisiert ist, und welchen Einfluss menschliche Landnutzungsformen auf eben diese haben. Dabei wählte ich ein zweistufiges methodisches Vorgehen. Im ersten Teil meiner Doktorarbeit bearbeitete ich die Fragestellungen auf einer *„focal taxon“*-Ebene, im zweiten Teil auf *„community“*-Ebene. Die Untersuchung der einzelnen Fragestellungen auf zwei unterschiedlichen Betrachtungsebenen erlaubte mir dabei einen detaillierteren Einblick in die zugrundeliegenden, relevanten Faktoren, da beide Untersuchungsebenen unterschiedliche methodische Vorteile bieten.

Im ersten Teil identifizierte ich die entscheidenden abiotischen Faktoren, welche die Verteilungsmuster des gewählten Beispielorganismus, Landeinsiedlerkrebse (Gattung *Coenobita*), auf Inseln bedingen und zeigte ferner, dass Konkurrenz um Ressourcen kein entscheidender Faktor für dessen räumliche Verteilung ist, sondern intrinsische Mechanismen die Koexistenz zweier Arten durch Ressourcenaufteilung stabilisieren. Durch die Untersuchung des Beispielorganismus auf Inseln, welche entweder nur touristisch („tourist island“) oder ausschließlich als Siedlungsraum durch die einheimische Bevölkerung genutzt werden („local islands“), konnten die ökologischen Folgen zweier verschiedener Landnutzungsformen räumlich klar voneinander getrennt untersucht werden. Dabei zeige ich, dass zwei unterschiedliche Landnutzungsformen gegenläufige Effekte auf denselben Organismus haben können.

Weil Studien, welche ökologische Phänomene nur anhand eines Beispielorganismus untersuchen, schwer auf gesamte Ökosysteme verallgemeinerbar sind, bearbeitete ich im zweiten Teil meiner Doktorarbeit die genannten Fragestellungen auf einer „*community*“-Ebene, in dem ich die bodenassoziierte Fauna (Kapitel B.1-B.3 und B.5-B.6), bzw. die Avifauna (Kapitel B.4) betrachtete. Hier konnte ich zeigen, dass die Biodiversitätsverteilung der bodenassoziierten Invertebraten-fauna auf natürlichen Inselökosystemen in Kompartimenten organisiert ist, sowohl in Bezug auf die ökologische Nischenbesetzung als auch in Bezug auf das Nahrungsnetz. Die jeweiligen Kompartimente umfassen dabei taxonomisch nahverwandte Arten und spiegeln die Habitate der untersuchten Inseln wider (z.B. separates Strand- und Inlandnahrungsnetz). Die Organisation der Biodiversitätsverteilung in Kompartimenten wird dabei vermutlich primär durch die relativen Produktivitätsgradienten zwischen den einzelnen Kompartimenten stabilisiert und nicht durch Randeffekte zwischen den einzelnen Kompartimenten. Auch die Verteilungsmuster größerer und mobilerer Wirbeltierarten, d.h. Vögel, stellen keine relevanten Verbindungen zwischen den Kompartimenten dar, sondern stabilisieren diese vermutlich zusätzlich. Weiter konnte ich zeigen, dass die beiden untersuchten menschlichen Landnutzungsformen, Tourismus und dauerhafte Besiedlung, einen negativen Einfluss auf die Biodiversität der untersuchten Inseln haben. Die Faktoren, welche diesen Biodiversitätsverlust bedingen, variieren jedoch zwischen den beiden Landnutzungsformen. Abschließend zeige ich, dass die trophischen Nischen der untersuchten Organismen unter menschlicher Landnutzung teilweise stark verändert werden, was Hinweise darauf geben könnte, ob ein Taxon negativ durch die beiden Landnutzungsformen beeinflusst wird oder nicht.

Meine Doktorarbeit präsentiert eine neue Herangehensweise, um zu untersuchen, wie Biodiversität und Artverteilung auf Ökosystemebene organisiert sind, indem Inseln als Modellsystem verwendet werden. Die Funde zweier Tierarten, welche bis dato noch nicht auf den untersuchten Inseln nachgewiesen wurden, unterstreicht dabei das breite Spektrum an möglichen Erkenntnisgewinn bei der Verwendung von Inseln als Modellsystem für die Biodiversitätsforschung.

# III. English Summary

Biodiversity on our planet follows defined patterns. On a global scale, these patterns are organized by few parameters, like latitude and elevation. On a local scale, the organization of biodiversity becomes less predictable as various factors simultaneously determine species' diversity and distribution. Understanding how biodiversity and species distribution are organized on small spatial scales (i.e., within ecosystems or habitats) is fundamental to ecological research. This relevance stems from the ongoing global change. The increasing necessity for understanding how biodiversity and species distribution is organized exists because the most prevalent threat for biodiversity worldwide is land conversion, which acts primarily on a local scale (i.e., within ecosystems or habitats).

Various land uses drive the conversion of former pristine ecosystems into modified and degraded land. A plethora of research has described the loss of habitat area or species richness following different human land uses. However, few studies reach beyond merely describing species losses and investigated the underlying mechanisms by which human activities alter the organization biodiversity and distribution. For a thorough understanding of how different human land uses impact the organization of biodiversity within ecosystems, it is first necessary understand how natural abiotic and biotic factors organize and drive biodiversity and distribution in natural systems free of any direct human disturbance before investigating any human-driven changes.

Empirical research aiming to analyse the organization of biodiversity and distribution in ecosystems is often hindered by the overall ecosystem complexity and difficulty of demarcating and replicating communities or ecosystems. In this PhD thesis, I introduce a methodical framework that uses small insular ecosystems for investigating how biotic, abiotic, and anthropogenic factors drive biodiversity and distribution. The small sizes and clear boundaries of islands, together with the possibility to use groups of islands as ecosystem replicates, pose an elegant solution to the abovementioned limitations.

This PhD thesis uses this insular framework as a model system to study how natural biotic and abiotic factors drive the organization of biodiversity and disentangle the impacts of different human land uses by investigating islands that hold only one specific type of human land use. For this, I consulted a two-step approach. In the first chapter of this PhD thesis, I used a focal taxon approach, while in the second chapter, I used a community-wide sampling approach. Analysing how abiotic, biotic, and anthropogenic factors drive biodiversity and distribution on two ecological levels enabled a more thorough understanding of the relevant factors, as both sampling approaches each bring their methodical advantages.

In chapter A, I identified the key natural abiotic drivers for the distribution patterns of the investigated focal taxon, terrestrial hermit crabs (genus *Coenobita*), and show which physical conditions predominantly influence its distribution. At the same time, interspecific competition does not drive its biodiversity and distribution patterns. Instead, intrinsic mechanisms of resource partitioning stabilize co-occurrence. The investigation of the focal taxon's biodiversity and distribution patterns on islands used either solely for touristic purposes ('tourist islands') or as permanent settlings by the local population ('local islands') disentangled the environmental impact of two different human land uses. I demonstrate that

two forms of human land use can impact different aspects of the same taxon in the same overall region.

Single-taxon-approaches are limited in their generalizability and give less insight than community-wide analyses. Hence, chapter B focused on the ground-associated faunal community of the investigated insular ecosystem (section B.1-B.4 and B.5-B.6) and the avifauna (section B.4). I demonstrate that the biodiversity and distribution patterns of the ground-associated insular community are organized in a compartmentalized way, both concerning habitat niche occupation and trophic niche occupation. Closely related species cluster within the overall niche space and form compartments attributable to distinct insular habitats (e.g., a beach food web compartment and an inland food web compartment). I show that this compartmentalized organization is not occurring due to an overall depauperate insular fauna, but likely stabilized by relative productivity gradients between compartments. More mobile bird taxa likely also form no relevant link between the distinct compartments of the ground-associated infauna. I further show that both investigated forms of human land use have a negative impact on the insular biodiversity patterns. However, the drivers for the observed losses differ between the two land uses. Ultimately, I show that both land uses are related, at least partly, to significant shifts in the trophic niche occupation of the impacted species, which might indicate a species' susceptibility to land-use-driven abundance declines.

By using islands as the methodical framework to study how biodiversity and species distribution is organized on a local scale and how human land uses alter these patterns, this PhD thesis paves the way for future research in community and disturbance ecology. The novelty of this insular approach is further emphasized by the presentation of two species newly recorded in the investigated insular region in the final chapter of my thesis. This underlines the broad spectrum of possible scientific insights that islands as model systems offer for biodiversity research.

# IV. General Introduction

Biodiversity on our planet follows distinct and observable patterns (Hamilton, 2005). Understanding what causes and drives these patterns is among the most fundamental objectives of modern ecological research (Sutherland et al., 2013). On a global scale, a growing body of empirical research and modelling approaches has already generated a thorough understanding of how biodiversity is organized (Kerr, 2001). Globally, biodiversity increases towards the tropics, decreases towards the poles, and increases when shifting from high elevations towards sea level (Fernández et al., 2009; Rohde, 1999; Whittaker et al., 2001). Several studies were also able to identify the major drivers behind these observable global biodiversity and distribution patterns. Temperature, environmental stability, light availability, and environmental predictability are all linked to higher rates in biotic processes and interactions and are thus the key drivers for the broad latitudinal and elevational patterns in the organization of biodiversity and species distribution on a global scale (Peters et al., 2016; Rohde, 1999; Whittaker et al., 2001). These drivers of global biodiversity and distribution patterns are consistent at high organizational levels and allow predicting biodiversity for taxonomically broad communities spanning over different phylogenetic groups (Gagné et al., 2020; Tittensor et al., 2010).

However, when shifting from global to local scales, i.e., when investigating how biodiversity and distribution are organized within single ecosystems or habitats, matters complicate. Downscaling from global to regional and local scales suspends the clear and uniform global patterns in biodiversity organization, and instead, less readily predictable patterns emerge (Astorga et al., 2003). Ecologists can observe and measure biodiversity and distribution within ecosystems in terms of species richness and biomass. However, our understanding of the drivers behind the observable patterns on a local scale is still limited (Adams et al., 2020; Gagné et al., 2020; Urban et al., 2020). Our overall limited understanding persists because, on smaller spatial scales, multiple different biotic and abiotic factors are simultaneously driving the organization of biodiversity and species distribution. On the one hand, biodiversity and distribution on local scales are organized and driven by taxon-specific resource requirements, their adaptations to the environment, and the positive and negative interactions and associations among co-occurring taxa (Fernández et al., 2009; Peters et al., 2016; Whittaker et al., 2001). On the other hand, biodiversity and distribution on local scales are also organized and driven by various environmental factors and gradients, which themselves become more finespun and diverse at smaller spatial scales (Armonies and Reise, 2000; Huston, 1979; Shmida and Wilson, 1985). Taken together, this results in less predictable biodiversity and distribution patterns on a local scale, i.e., within single ecosystems or habitats (Marquet et al., 2004).

However, thoroughly understanding how biodiversity and species distribution is organized on a local scale would be essential in the light of human-driven global change. This necessity exists because the most prevalent of the five major human pressures for biodiversity (habitat change, overexploitation, pollution, the introduction of invasive alien species, climate change (Hall, 2010)) is human-driven habitat change, which alters the organization of biodiversity predominantly on a local scale (Habel et al., 2019). Due to the increasing human land demands worldwide, anthropogenic habitat change has by now affected biodiversity in all of the world's ecosystems, across all latitudes and elevational zonations (Jantz et al., 2015; Sala et al., 2000; Sloan et al., 2014; Venter et al., 2016). This is caused by the growing human land demands for food production, pasture land, soil resources, tourist development, and urbanization (Hall, 2010; Sanderson et al., 2002; Venter et al., 2016). The negative environmental impacts of these different human land uses have been reported across all major taxonomic groups and communities, from protists and fungi to plants and animals (Hooper et al., 2012; Tscharntke et al., 2008).

Although numerous studies and modelling approaches investigated the impacts of different human land uses on biodiversity, few studies reach beyond the point of describing losses in habitat area or species richness due to a given form of human land use. To comprehensively understand the consequences of different human land uses, it is also pivotal to investigate the underlying mechanisms through which the organization of biodiversity and distribution is changed (Takemoto and Kajihara, 2016; Valiente-Banuet et al., 2015). For a thorough understanding of how different human land uses impact biodiversity and species distribution, it is further necessary to acknowledge that the different forms of human land use likely have different impacts within the same system or on the same taxa (Durán et al., 2020; Lucrezi et al., 2009; Welch, 1982). For empirical research on anthropogenic disturbance, this means that it is necessary to develop a framework where the environmental impacts of different human land uses can be isolated and investigated separately to ensure that no synergistic or antagonistic interactions occur (Raiter et al., 2014; Tekin et al., 2020). Only this will generate an in-depth understanding of the severity and variety of different impacts caused by the different land-use forms simultaneously present in most urbanized areas. It will also be necessary to generate a basic *a priori* understanding on how biodiversity and species distribution are organized in the absence of human activities, as a reference to enable direct comparisons between disturbed and undisturbed systems (Mitsch and Day Jr., 2004).

Therefore, the two main objectives for modern ecological and environmental research on human land-use-driven biodiversity loss build on one another.

First, we need to understand how biodiversity and species distribution are organized within ecosystems on different ecological levels (i.e., species, communities, ecosystems) in the absence of direct human disturbances (Sutherland et al., 2013).

Second, we need to understand how human land uses alter biodiversity and species distribution at different ecological levels (i.e., species, communities, ecosystems) and how these impacts vary between the different forms of human land use (Purvis and Hector, 2000). Thoroughly understanding what form of human land use is responsible for which environmental changes within one system is ultimately the key for developing more efficient conservation actions tailored to counteract the impacts of different human land uses more specifically.

However, empirical research aiming to investigate these two objectives is confronted with different obstacles (Fig. 1).

The first major limitation to empirically investigate how biodiversity and species distribution are organized in whole communities or ecosystems is the overwhelming complexity of most natural systems (Carpenter, 1990). While field studies that comprise only a few exemplified species or assemblages of closely related taxa are relatively easy to conduct, studies that aim to incorporate the whole community of an ecosystem are more challenging to realise (Peters et al., 2016). This is due to the overall high diversity and spatial complexity of most natural ecosystems, which often exceed the capacity and feasibility of field sampling and subsequent statistical analyses (Wisz et al., 2013).

The second major limitation is a lack of distinct natural barriers of most ecosystems towards adjoining communities or ecosystems (Carpenter, 1996; Hoffmann and Blows, 1994; Tracy and Brussard, 1994). The absence of natural demarcations in most natural systems requires either using experimental ecosystems (mesocosms) or introducing artificial barriers in the sampling design. However, introducing any artificial barrier can result in underestimating possible effects of cross-ecosystem energy fluxes at the transition zones (or ecotones), making it difficult to extrapolate data collected from enclosures to natural systems (Carpenter, 1996).

The third major limitation to empirically investigate how biodiversity and species distribution are organized on higher ecological levels (i.e., communities or ecosystems) is the difficulty of replication (Carpenter, 1990; Lemoine et al., 2016). While small natural ecosystems, like ponds or rock pools, can reasonably easily be treated and used as replicates (Clark, 1999), the replication of larger natural systems, especially in the terrestrial environment, is more difficult to realise (Schindler, 1998). This is due to the necessity to first identify and consider possible differences and unique properties of similar systems before treating them as ecosystem replicates (Carpenter et al., 1995). Although neighbouring ecosystems might appear similar, the organization of biodiversity and species distribution within them can differ markedly, which prohibits treating them as true replicates of the same ecosystem type (Fraser et al., 2020; Simberloff, 1998; Underwood, 1990).

The major limitation to investigate and compare the impacts of different anthropogenic disturbances on biodiversity is the difficulty of separating the environmental impacts of different human activities, which are typically simultaneously present in an urban environment (Durán et al., 2020; Lucrezi et al., 2009). Common approaches to describe the impacts of human activities on species, communities, or ecosystems are to compare sites that exhibit anthropogenic disturbance with sites free of any direct and permanent anthropogenic disturbance, for example, in national parks or marine reserves (Benedetti-Cecchi et al., 2001; Huijbers et al., 2013; Noriega et al., 2012). This approach allows generating a general insight into the ecological consequences of human land use compared to undisturbed reference sites. However, several forms of human land use are often simultaneously present in most urbanized regions, which likely impact or alter different aspects of the affected system’s biodiversity and species distribution (Lucrezi et al., 2009; Welch, 1982). Therefore, such approaches do not allow to gain insight into the extent to which the environmental impacts vary between different human land uses and which land-use form poses the most severe threat to biodiversity within a particular system.

To circumvent the abovementioned limitations for empirical investigations on the organization of biodiversity and species distribution and anthropogenic disturbance, insular ecosystems might offer an elegant solution (Carpenter et al., 1995; Losos and Ricklefs, 2009) (Fig. 1). Small and remote oceanic islands have lower biodiversity than continental systems due to their overall small size, isolation, and low habitat complexity

(MacArthur and Wilson, 1967, 1963; Thaman, 2008). Incorporating the whole insular community in field studies that investigate how biodiversity and species distribution are organized within ecosystems should be more easily achievable and feasible than in more complex continental counterparts. Furthermore, insular ecosystems have a distinct and natural habitat barrier towards the adjoining system, i.e., the marine environment, in the form of coasts and shorelines (Losos and Ricklefs, 2009; Wardle and Zackrisson, 2005). This clear ecosystem demarcation offers the opportunity to conduct experiments in spatially well-defined, natural systems without the necessity to introduce any artificial barrier. Additionally, groups of islands within the same region, e.g., islands in one atoll, can function as natural ecosystem replicates. Their spatial proximity, their shared natural history, and their similar sizes generally allow treating them as true replicates of the same ecosystem type (Anderson and Polis, 1998; Losos and Ricklefs, 2009). Ultimately, islands could also offer an elegant solution to disentangle the environmental impacts of different human disturbances. When different land uses occur on different islands, it should be possible to isolate single human land uses on the different insular ecosystems. A comparison with uninhabited islands free of

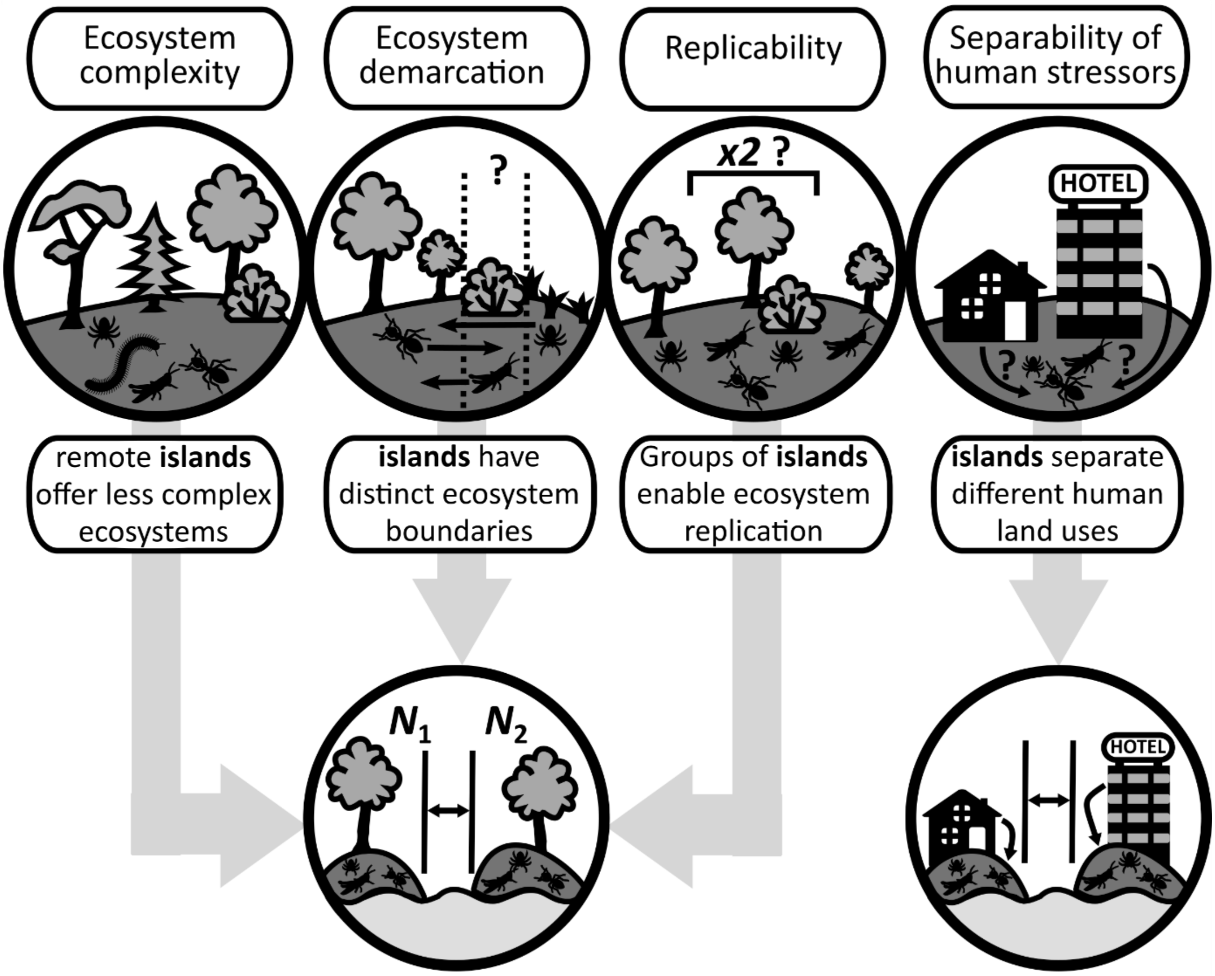


**Figure 1: Insular systems are possible solutions to overcome four major limitations for empirical studies on how biodiversity and species distribution is organized on small spatial scales (i.e., within ecosystems) and on the environmental impact of different human activities on these patterns.**

any direct and permanent land-use-associated disturbance should also enable comparing the organization of biodiversity and species distribution between disturbed and undisturbed systems.

Consequently, the advantage of using islands as a methodical framework to study ecological processes has been proclaimed repeatedly in ecological research, from as early as Darwin's work on the Galápagos Islands, and researchers continued to use islands to unravel fundamental ecological mechanisms in nutrient dynamics, colonization, adaptive radiation, or behavioural adaptation, to name but a few (Losos et al., 1998; Losos and Ricklefs, 2009; Piovia-Scott et al., 2011; Pringle et al., 2019).

Using islands as model systems to study how biodiversity and species distribution are organized in ecosystems and to disentangle the environmental impacts of different forms of human land use has not been realized so far. However, islands' general properties and characteristics suggest that they might also be ideal models to answer these open research questions.

Therefore, in this PhD thesis, I used small islands as methodical framework and model systems to study (I) how biodiversity and species distribution are organized in undisturbed insular systems and (II) to disentangle the impacts of different human land uses on insular systems with anthropogenic development. In a two-step process, I first identified how the main biotic and abiotic factors drive the organization of biodiversity and species distribution on uninhabited islands free of any direct and permanent human land use. Second, I investigated and disentangled the impact of two different forms of human land use on these patterns by investigating islands that display only one type of human land use.

The main goals of this work were to demonstrate

1. how biodiversity and species distribution are organized on undisturbed insular ecosystems by natural environmental factors and ecological interactions, and
2. how these identified biodiversity and distribution patterns are impacted by two different forms of human land use.

In this PhD thesis, I addressed these objectives using two separate study approaches. In the first part of this PhD thesis (**chapter A**), I investigated the two research questions using a focal-taxon study approach. In the second part of this PhD thesis (**chapter B**), I investigated the two research questions using a community-wide study approach. Chapter B of this PhD thesis thereby focuses primarily on the ground-associated infauna community, as they form the most diverse subset of the insular community on the investigated remote oceanic islands (Hogarth et al., 1998; Platia, 2015; Sunil, 2012; Taiti, 2014). Furthermore, the ground-associated faunal community is more easily accessible for sampling than, e.g., canopy-dwelling taxa.

Using different ecological levels allowed generating a more in-depth insight into the investigated research questions. Single-species and multispecies approaches offer different opportunities and advantages when studying ecological processes and anthropogenic impact (Kinzey and Punt, 2009). Using a focal taxon approach allows rapid assessments of human impacts and better opportunities to analyse interspecific competition or species-specific resource usage. A community-wide sampling approach allows generating a deeper understanding of the fundamental drivers of how biodiversity and species distribution are organized within ecosystems and offers more thorough estimates on how human activities impact whole communities (Clark, 1999; Kinzey and Punt, 2009; Simberloff, 1998; Tracy and Brussard, 1994).

Bringing together the results based on the focal taxa- and community-wide study approaches allowed thoroughly examining and discussing how natural and anthropogenic factors drive the organization of biodiversity and species distribution on small spatial scales.

The islands used as a methodical framework lay in the Republic of the Maldives, Indian Ocean (Fig. 2). The key advantage of using the Maldivian archipelago as a study site is that their islands do not offer much space for multiple land uses to be present on the same island. Instead, different land uses are distributed over the different islands in each atoll, resulting in a mosaic of land uses with islands used either exclusively for tourism or as permanent settling by the local population (Fallati et al., 2017). At the same time, many islands remain uninhabited, thus serving as reference systems free of any human land-use-associated disturbance. Additionally, the Maldivian islands share the same geo-evolutionary history, are of the same age, are all similarly sized, and have the same overall morphology (i.e., sand-dominated, without any rocky elevations) (Anderson and Shimal, 2020).

Together, these factors rendered the Maldivian islands an ideal and probably worldwide unique study site to be used as a methodical framework for investigating the organization of biodiversity and species distribution on small spatial scales. Importantly for conservation, the Maldivian islands are part of an ecoregion characterized by a rare and almost entirely unprotected habitat type, i.e., tropical moist forest, and thus considered part of a global biodiversity hotspot (Gillespie et al., 2012).

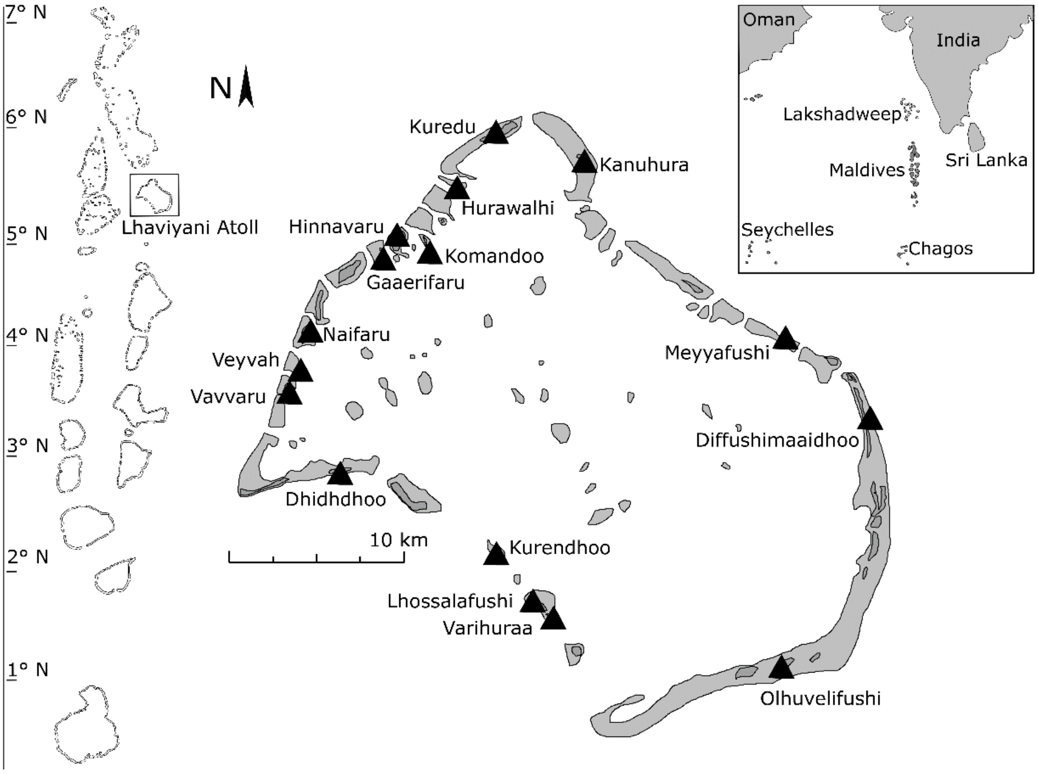


**Figure 2: Study area. Location of the Maldives within the Indian Ocean (top right), location of the Lhaviyani (Faadhippolhu) atoll within the Republic of Maldives (left), and distribution of the investigated islands within the Lhaviyani atoll (centre). Light grey areas in the atoll map indicate the spatial extension of the coral reefs. Dark grey areas indicate the spatial extension of the islands' landmasses.**

# V. Synopsis

## Chapter A. Using a focal taxon approach to investigate how biodiversity and distribution is organized and to disentangle the environmental impacts of different land uses

Chapter A of this PhD thesis uses a focal taxon approach as the level of investigation to study how biodiversity and distribution are organized on a local scale, and to disentangle the impact of different human land uses. Single taxon approaches allow more rapid assessments than community-wide approaches, and specific biotic interactions, like competition, occur mainly between taxa but rarely on a community level (Gilpin, 1994; Kinzey and Punt, 2009). Therefore, it was first necessary to find an adequate focal taxon that also acts as a reliable indicator for anthropogenic disturbance (Goodsell et al., 2009). A major review about faunal indicator taxa identified the key criteria that render a given species a good focal taxon for anthropogenic disturbance and ecosystem health. Among the most relevant criteria, which a candidate taxon has to comply, are (I) a clear taxonomy, (II) a well-studied biology and life-history, (III) known tolerance levels to anthropogenic stress, (IV) an established correlation to ecosystem change, (V) a cosmopolitan distribution, (VI) limited mobility, (VII) its functionality over a range of stress levels, (VIII) showing low variability, (IX) being a specialist, and (X) being easy to find and measure (Hilty and Merenlender, 2000). Because it is rather challenging to identify any single species that fulfils all abovementioned criteria, an elegant and standard solution is to select the focal taxon on a higher taxonomic level, e.g., on a genus or subfamily level (Hilty and Merenlender, 2000; Kerr et al., 2000; Simberloff, 1998). Besides adhering to the abovementioned criteria, it was further necessary that the focal taxon for the study approach in chapter A of this PhD thesis was common on the Maldivian islands, as the general framework of this thesis was built around these insular ecosystems. Therefore, I chose terrestrial hermit crabs (Decapoda: Anomura: genus *Coenobita*) as a focal taxon because a plethora of ecological, zoological, and zoogeographical studies suggested that they fulfil most of the abovementioned postulated criteria, and they are, at the same time, common inhabitants of most tropical to subtropical coastal and insular systems.

All terrestrial hermit crab species belong to the genus *Coenobita* (Latreille, 1829), which comprises 16 species in total (Lemaitre and McLaughlin, 2019). Their taxonomy has been thoroughly investigated and revised in the literature, and many identification keys exist that allow easy and fast recognition of the different species in the field (Hogarth et al., 1998; McLaughlin, 1983; McLaughlin et al., 2010; Naderloo, 2017). Terrestrial hermit crabs, like their marine counterparts, are commonly known for their conspicuous behaviour to utilize gastropod shells in order to protect their uncalcified abdomen against desiccation, predation, and mechanical stress from wave action. Partly due to this conspicuous behaviour, they are among the most well-studied decapods, and many aspects of their biology and life-history have been thoroughly described, including shell utilization (Abrams, 1978), locomotion (Herreid and Full, 1986; Osorno et al., 1998), olfaction (Small and Thacker, 1994; Szabo, 2012), water balance (Gross, 1964), ontogeny (Brodie, 1999; Hamasaki et al., 2015; Hsu and Soong, 2017; Taylor, 1988), moulting (Greenaway, 2003), feeding activities (Barnes, 1997a, 1997b; Page and Willason, 1983), mating behaviour (Gusev and Zabotin, 2007), migration (Barnes, 1997a; Nieves-Rivera and Williams, 2003; Vannini, 1976), visual abilities (Ping et al., 2015), and respiration (McMahon and Burggren, 1979). In addition to their well-established biology and life-history, terrestrial hermit crabs are known to be susceptible to anthropogenic change (Chan et al., 2010; Nigro et al., 2017). Thus, earlier studies suggested that they might be suitable indicators for human-driven biodiversity changes (Brook et al., 2009; Cardoso et al., 2016).

To thoroughly measure and describe anthropogenic biodiversity changes for any given taxon, it is first necessary to assess the natural variations in its diversity and distribution (de Graaf et al., 2004). These natural drivers can be categorized broadly in abiotic environmental factors and biotic interactions (Jackson et al., 2001).

Small insular ecosystems, which were consulted as the general framework of this PhD thesis, are generally an abiotic/ physically controlled environment because the proportionally large coastal environment, relative to the total island area, is predominantly shaped by tidal times, temperature (correlated with the course of a day), wind, wave action, and beach morphology (McLachlan, 2001; McLachlan et al., 1993). This physical control means that, especially for the beach-dwelling terrestrial hermit crabs used as a focal taxon in chapter A of this PhD thesis, it is crucial to assess first the role of abiotic environmental factors in organizing and shaping their distribution patterns before measuring any anthropogenic impacts.

To partly withstand the harsh environmental conditions encountered in the coastal habitat, terrestrial hermit crabs utilize gastropod shells as protection (Vance, 1972a). Therefore, the availability of empty and suitable gastropod shells poses a major limiting resource for their occurrence, over which they are in constant apparent inter- and intraspecific competition (Barnes and de Grave, 2000; Vance, 1972b). At the same time, terrestrial hermit crabs are not considered limited by any other resource under natural conditions, leaving shell resource competition the only relevant biotic interaction that possibly drives their diversity and distribution patterns (Abrams, 1980).

Therefore, I investigated in chapter A of this PhD thesis how the major abiotic factors, i.e., daytime, tidal time, and overall beach morphology (**section A.1**), and the competition over the limiting shell resource (**section A.2**) influence the organization of the natural diversity and distribution of the consulted focal taxon. After assessing its natural variation and the natural drivers for the observed distribution patterns, I then disentangled and analysed how two different human land uses alter its diversity and distribution (**section A.3**; Fig. 3). Bringing together the findings of the biotic, abiotic, and anthropogenic factors influencing the organization of the diversity and distribution of terrestrial hermit crabs enabled a rapid assessment of this PhD thesis's key objectives at a low taxonomic, i.e., genus, level.

Using terrestrial hermit crabs (genus *Coenobita*) as focal taxon allowed me to revert to a well-studied and common organism, suitable as an indicator for anthropogenic stress. Their worldwide distribution in the tropical and sub-tropical environment further renders the results obtained in chapter A of this PhD thesis relevant for a wide range of coastal and insular ecosystems.

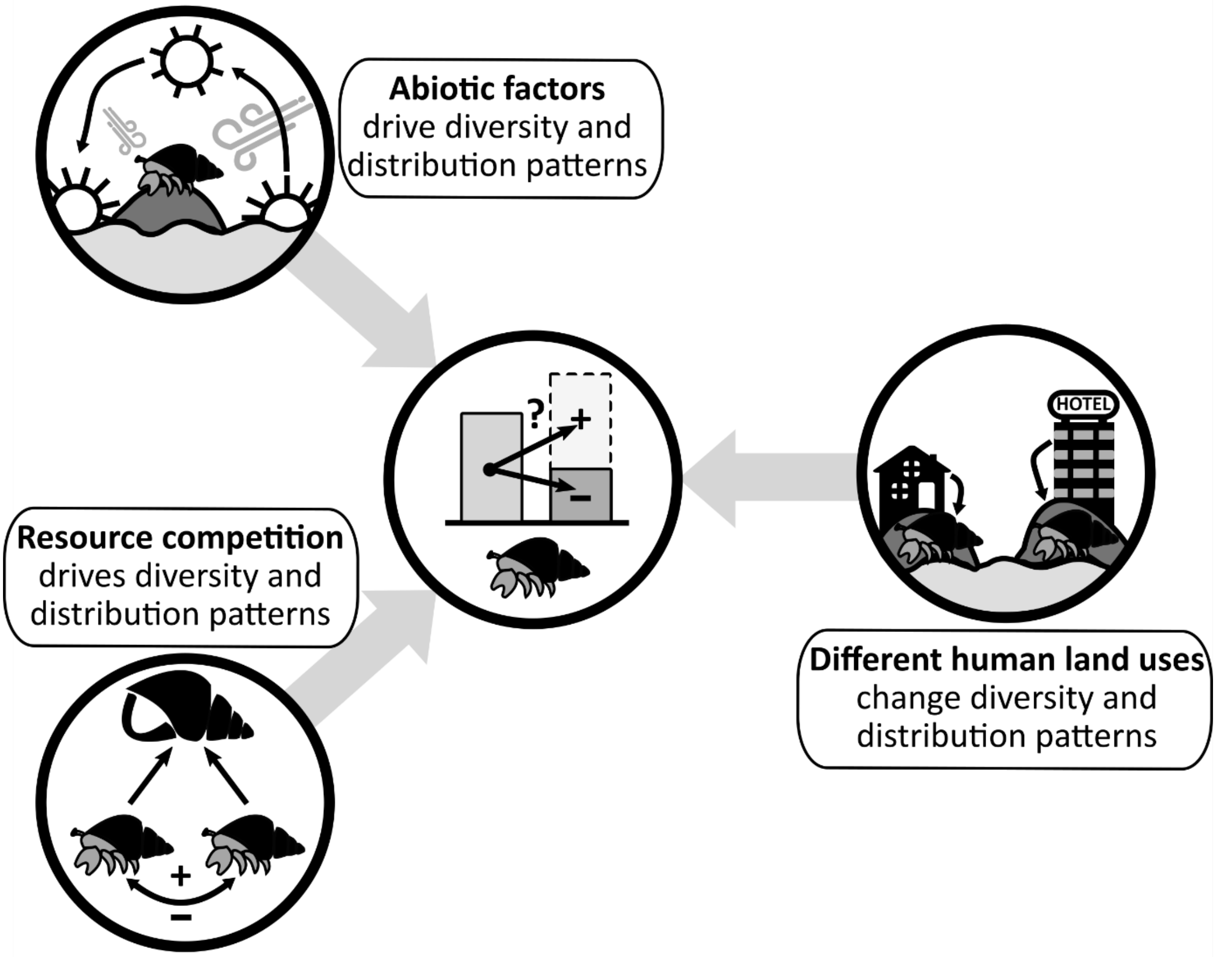


**Figure 3: Abiotic factors, biotic interactions, and different human land uses all influence the organization of the diversity and distribution of coenobitid hermit crabs. To thoroughly understand how different human land uses impact their diversity and distribution patterns, it is necessary to first investigate how natural abiotic and biotic factors shape the diversity and distribution of their populations under the absence of any land-use-associated disturbance.**

## Section A.1: Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*)

Originally published as:

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Coastal ecosystems, especially sandy beaches, are among the harshest terrestrial environments on the planet. They are predominantly controlled by physical forces, such as wave action, UV radiation, temperature, tidal regime, and by habitat morphology (McLachlan, 2001; Short, 1996). Therefore, the diversity and distribution of beach-dwelling organisms are mainly organized and dictated by the gradients and dynamics in these physical factors, whereas biotic interactions play only a minor role (Jaramillo and McLachlan, 1993).

This physical control has led to various morphological and behavioural adaptations of the beach fauna, which enable them to withstand these environmental conditions (McLachlan et al., 1993). Most beach-dwelling organisms display a clear orientation along the physical gradients and show circadian activity patterns to avoid unfavourable environmental conditions, like specific tidal regimes, swash climates, or high sun exposure during the day (Scapini, 2014).

To investigate how environmental factors drive the focal taxon's diversity and distribution, it was therefore primarily relevant to study the role of daytime and tidal time as the dominant forces in shaping their populations. Terrestrial hermit crabs are well-known for utilizing empty gastropod shells as protection against harsh environmental conditions. However, comparably little is known if and how physical factors also influence terrestrial hermit crabs' temporal and spatial distribution patterns (Greenaway, 2003).

Here, I hypothesized and demonstrated that daytime, tidal time, and habitat morphology (i.e., the beach's structural complexity) significantly drive the distribution of terrestrial hermit crabs in space and time. They became virtually absent from the beach surface during midday, probably to avoid desiccation from high sun exposure, while their occurrence peaked either in the morning or late afternoon, further depending on the tidal regime. During falling tides, their diurnal occurrence was peaking, likely because food is more readily available (Page and Willason, 1983), while the increased risk of displacement by waves during rising tides resulted in reduced occurrences (Branch and Cherry, 1985). Furthermore, the beach morphology, i.e., the beach's structural complexity (ranging from fine sand to predominantly rock-covered beaches), shapes the terrestrial hermit crabs' spatial distribution. More heterogeneous habitats (sandy beaches interspersed with small fragments or larger rocks) showed higher abundances than homogeneous beaches, likely because food and shells accumulate more abundantly in these heterogeneous habitats (Orr et al., 2005).

In conclusion, this study adds to our understanding of how the dominant abiotic factors of insular beach habitats drive the distribution patterns of the investigated focal taxon, terrestrial hermit crabs.

## Section A.2: Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species

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Besides the prominent role of abiotic factors in shaping species' distribution, biodiversity and distribution can also be organized by competition of co-occurring species over shared resources (D'Amen et al., 2018). When consumption or utilization modifies the availability of a limiting resource, it results in contrasting consequences for the abundances of competing species (i.e., one species increasing, one species decreasing in numbers), thereby influencing the overall spatial distribution pattern (Boulangeat et al., 2012). Inferring whether the organization of diversity and distribution is driven by competition over a shared resource requires experimentally examining the apparent competition over the respective resource (Connor and Simberloff, 1983).

However, empirically investigating resource competition in natural populations is generally hindered because most species are not limited by one resource only, but rather by several different resources (Vance, 1972b). However, the selected focal taxon in chapter A of this PhD thesis marks a rare exception to this rule. Under natural conditions, hermit crabs are only limited by the availability of empty gastropod shells, while, e.g., food availability does not limit their populations (Abrams, 1980; Fotheringham, 1976). This makes co-occurring species of hermit crabs ideal for studying whether competition influences the organization of their diversity and distribution or whether they have evolved mechanisms of shell resource partitioning that enable stable coexistence.

In this project, I investigated the shell utilization patterns of the two co-occurring hermit crab species, *Coenobita rugosus* and *C. perlatus*, on 11 separate insular populations and conducted shell selection experiments and morphometric analysis of their only limiting resource. I hypothesized and demonstrated that the two co-occurring species utilized distinct subsets of the available shell resource in natural populations. These distinct resource utilization patterns arise out of contrasting intrinsic preferences towards different shell morphometrics, i.e., one species preferring globose and heavy shells, the other preferring narrow and light-weighted shells.

This suggests that the investigated focal taxon's diversity and distribution patterns are not driven by interspecific resource competition with co-occurring species. Instead, the two hermit crab species have evolved contrasting intrinsic preferences towards different subsets of their limiting resource that enable a stable coexistence under natural conditions, rendering their distribution patterns independent of interspecific competitive exclusion.

As the preferred shell morphometrics of the two species either benefit clutch size or mechanical protection, these contrasting shell preferences might further indicate that the two species have evolved different strategies to respond to their environment's selective pressures by either maximizing reproductive output or protection against predation.

## Section A.3: Disentangling the environmental impact of different human disturbances: a case study on islands

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Steibl, S., & Laforsch, C. (2019) Disentangling the environmental impact of different human disturbances: a case study on islands. *Scientific Reports, 9*: 13712.

After having established how biodiversity and distribution of the investigated focal taxon are organized under natural conditions, i.e., mainly driven by habitat configuration and tidal time (**section A.1**), while interspecific competition does not influence their populations (**section A.2**), the third project in chapter A aimed to disentangle and assess the impacts of different human land uses on their diversity and distribution.

Most approaches that aim to investigate the impact of human land uses on the environment are realized by comparing populations in an urbanized area with populations in remote, undisturbed sites, such as national parks or marine reserves (Hereward et al., 2017; Huijbers et al., 2013). This approach allows assessing the environmental impact of overall human presence. However, it offers only limited insight, which of the many different forms of human land uses simultaneously present in most urbanized area has which ecological consequence (Defeo et al., 2009).

Among the most detrimental forms of land use for global biodiversity are habitat conversion for urban development and tourism (Hall, 2010). Urban development and tourism land use are related to an overall biodiversity loss, but whether they act similarly or alter different aspects of the natural ecosystem processes remains mostly unknown (Gössling, 2002).

Investigating islands that were either used solely for touristic purposes ("tourist islands") or urban developed by the local population and used as permanent settlings ("local islands") allowed spatially disentangling the environmental impacts of these two land use forms. Additionally, investigating uninhabited islands exempt from any direct and permanent human land use further allowed a direct comparison between disturbed and undisturbed sites.

Here, I hypothesized and showed that tourism and permanent settling have contrasting effects on the diversity and distribution patterns of the investigated focal taxon, terrestrial hermit crabs. Their densities were, compared to the undisturbed reference, only significantly reduced on tourist islands. On local islands, however, the body size was significantly reduced compared to tourist islands. The investigation of the underlying habitat configuration, shell resource, and food availability offered explanations for these contrasting patterns. On tourist islands, practices like beach cleaning, which alter the habitat configuration and remove washed-up detritus (Kelly, 2014), are likely driving the observed biodiversity loss. On local islands, the use of hermit crabs as fishing bait by the local fishermen (Thaman et al., 2010) could be a size-selective driver for the observed reduced body sizes.

Overall, this study demonstrates that two different human land uses, tourism and permanent settling, can have contrasting impacts on the same taxon. Effective conservation action must thus specifically consider the form of human land use and its associated changes to the environment.

# Chapter B. Using a community-wide sampling approach to investigate how biodiversity and distribution is organized and to disentangle the environmental impacts of different land uses

The study approach in chapter A of this PhD thesis allowed a first rapid assessment of how biodiversity and species distribution are organized on insular systems by using a focal taxon. Furthermore, it gave the first proof-of-concept for the applicability of the chosen insular framework for studying the organization of biodiversity and distribution and disentangling the different human land uses' environmental impacts.

However, the primary criticism for the study of anthropogenic disturbance using just one or few focal taxa as proxy for the overall ecosystem status is the limited generalizability of such findings for the whole species community or the whole ecosystem (Goodsell et al., 2009; Simberloff, 1998). Therefore, the concurrent dearth of and the necessity for community-wide studies has been a major and long-proclaimed issue in basic and applied environmental research (Clark, 1999; Hilty and Merenlender, 2000). The overall shortage of community-wide study approaches that incorporate all taxa from different phylogenetic backgrounds can be mainly ascribed to the exceeding complexity of natural communities and ecosystems for empirical research (Carpenter, 1990; Wisz et al., 2013; Peters et al., 2016; see **General Introduction**, p. 10 et seqq., for a detailed discussion). Despite the difficulty of realizing community-wide empirical studies in natural ecosystems, there exists a large body of theoretical work and concepts to describe how biodiversity and distribution are organized on small spatial scales (Heams et al., 2015).

The most widely accepted concept to describe the organization of biodiversity and species distribution in ecosystems is the ecological niche concept, originally postulated by G.E. Hutchinson in 1957 and, since then, updated continuously following advances in empirical and theoretical research (e.g., Holt, 2009; Hutchinson, 1978, 1957; Newsome et al., 2007; Soberón, 2007). In its original and fundamental form, the ecological niche of a species describes the *n*-dimensional hypervolume that comprises all biological, chemical, and physical parameters of a heterogeneous environment, in which this species can persist indefinitely. An important necessary difference is thereby made between the fundamental niche, i.e., the environmental conditions under which a species theoretically can live and reproduce in under the absence of other species, and the narrower realized niche. The realized niche describes only the set of conditions that a species occupies within a larger set of species (Alley, 1982). Using the ecological niche concept, it is possible to describe the major natural drivers for biodiversity and distribution patterns. These drivers comprise habitat configuration, expressed as habitat niche occupation, and food web dynamics, expressed as trophic niche occupation (Soberón, 2007). By studying shifts or changes in habitat or trophic niche occupation following anthropogenic disturbance, it is possible to gain insights into the mechanisms that ultimately cause human-driven biodiversity loss (Nigro et al., 2017; Tilman, 1999). As already described in Chapter A, it is crucial to first establish niche occupation under the absence of anthropogenic disturbance as a baseline of a natural *status quo* before investigating possible human-driven changes in habitat or trophic niche occupation (de Graaf et al., 2004).

Therefore, chapter B of this PhD thesis aimed to investigate first how habitat niche occupation (**section B.1**) and trophic niche occupation (**section B.2**) are driving biodiversity and distribution patterns under the absence of direct and permanent human land use. Ecotonal processes and the phenomena of increased or reduced biodiversity at the transition zone of habitats, can further influence niche occupation and, thus, the organization of biodiversity and species distribution in ecosystems (Kark, 2013; Kark and van Rensburg, 2006). Therefore, I further investigated the role of ecotonal processes in driving or stabilizing the observed biodiversity and distribution patterns of the studied insular community (**section B.3**). The focus of these three research projects was thereby concentrated on the ground-associated faunal community, as it constitutes the majority of insular biodiversity in the investigated study system, the Maldivian archipelago and it is more easily accessible for sampling than, e.g., canopy-dwelling species (Hogarth et al., 1998; Kevan and Kevan, 1995; Platia, 2015; Sunil, 2012; Taiti, 2014). However, next to the ground-associated faunal community, the avifauna is a relatively diverse and abundant part of the overall insular community in the investigated Maldivian system, which likely influences the diversity and distribution of the ground-associated fauna, e.g., via trophic interactions (Anderson and Shimal, 2020). Other than the investigated ground-associated faunal community (**section B.1-B.3**), the bird community is known to be strongly influenced by seasons in their diversity and distribution (Alerstam, 1993; Newton, 2011; Somveille et al., 2013). Therefore, I investigated how seasonal change, tidal regime, and habitat configuration drive the bird community's overall biodiversity and distribution patterns. Further, I examined whether the observed avian diversity and distribution patterns can be related to those observed in the ground-associated infauna community (**section B.4**).

After having established how biodiversity and species distribution of the investigated insular community are organized under natural conditions free of any land-use-associated human disturbance, I used the same insular setup as already described in section A.3 to investigate how two forms of human land use alter the biodiversity and distribution patterns and overall habitat configuration (**section B.5**) and the trophic niche occupation of the investigated ground-associated insular community (**section B.6**; Fig. 4).

The examination of habitat niche and trophic niche occupation under the absence and presence of different human land uses enabled a thorough understanding of how biodiversity and species distribution are organized and impacted on a community level. Studying the faunal communities on small insular ecosystems allowed gaining relevant insights into the drivers of biodiversity and distribution patterning on a community level and uncovering and disentangling the mechanisms by which different human land uses alter these patterns.

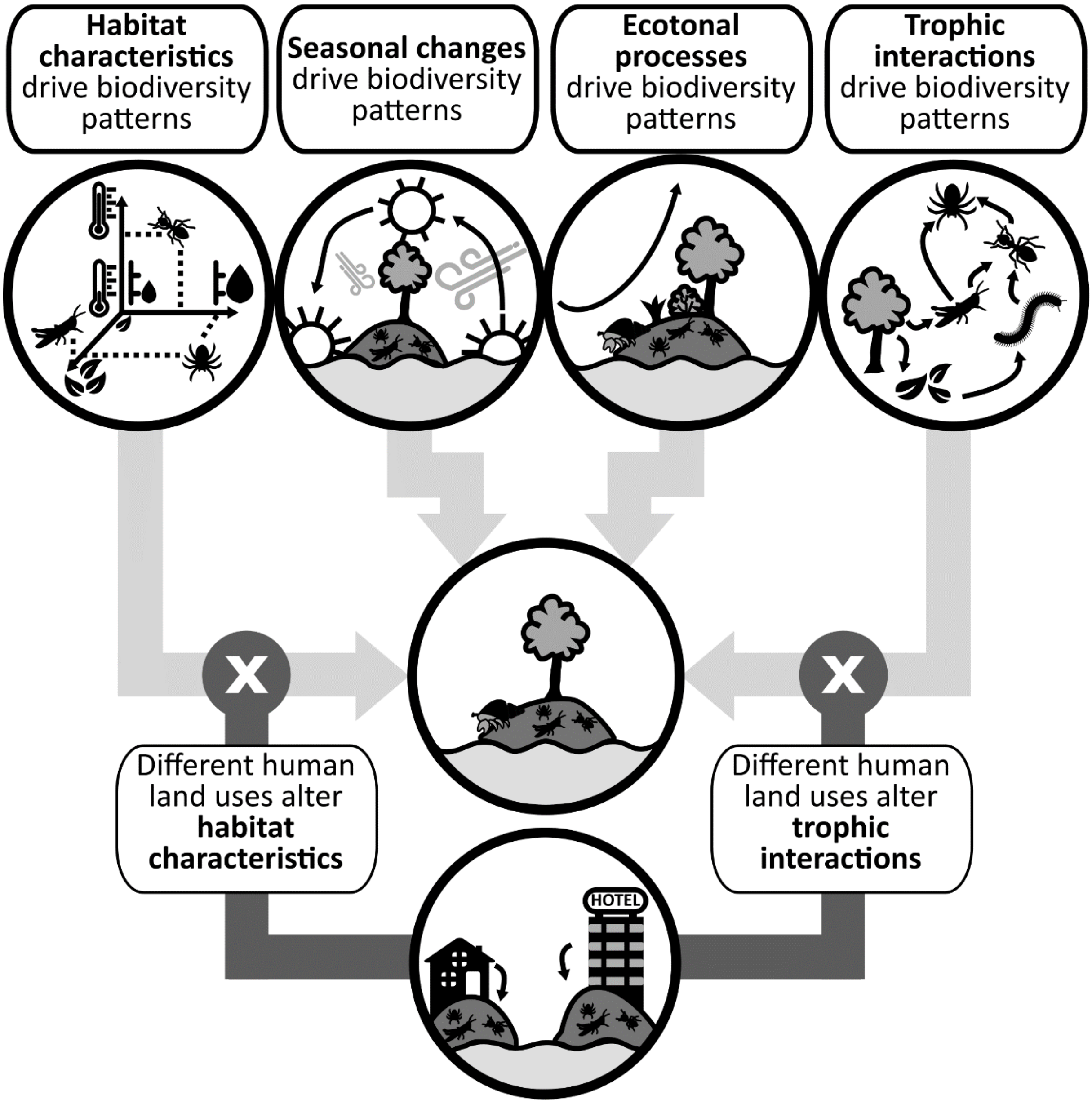

**Figure 4: Habitat niche occupation, seasonal changes, ecotonal processes, and trophic niche occupation are natural drivers that organize and influence the biodiversity and distribution of faunal communities on small spatial scales (i.e., within ecosytems). Human land uses can impact the biodiversity and distribution patterns by altering habitat characteristics or trophic nice occupation.**

## Section B.1: Compartmentalized organization of ecological niche occupation in insular invertebrate communities

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The habitat's environmental conditions are key drivers for organizing the diversity and distribution in natural systems (Kadmon and Allouche, 2007; Melo-Merino et al., 2020). Each species occupies a distinct combination of environmental factors, resulting in species-specific realized ecological niches and clear distribution patterns (Hutchinson, 1978, 1957). Studying niche occupation shows how environmental conditions have driven species differentiation to facilitate coexistence and, thus, organize biodiversity and distribution. Such mechanisms have been demonstrated in various closely related taxa, like spiders (Entling et al., 2007) or crustaceans (Lastra et al., 2009), to name but a few. However, there has been so far no empirical study approach that investigated niche occupation on a community level. Hence, it is unknown how niche occupation organizes the diversity and distribution of an entire faunal community.

By investigating niche occupation of the ground-associated invertebrate fauna of small tropical islands, I hypothesized and showed that, also on a community level, each taxon occupies its own distinct realized ecological niche in the overall available insular niche space. However, the occupied niches are not spread homogeneously over the total niche space. Instead, niche occupation of the ground-associated insular infauna community is organized in distinct niche compartments. These compartments are attributable to the different insular habitats (e.g., beach, grassland, dense forest), where species with similar niches cluster, while other areas of the niche space remain unoccupied. Each compartment comprises taxonomically distinct groups of taxa, e.g., all crustaceans form one niche compartment, suggesting that their shared evolutionary history resulted in similar niche occupation patterns, a postulated principle termed niche conservatism (Wiens et al., 2010).

The overall compartmentalized architecture of ecosystems has already been demonstrated for food webs (Pringle & Fox-Dobbs, 2008; Rezende et al., 2009, **section B.2**) and pollination networks (Olesen et al., 2007). This work suggests that habitat niche occupation might also be organized in a compartmentalized way. As niche occupation drives the overall diversity and distribution patterns in ecosystems (Soberón, 2007), the found compartmentalized structure reflects the overall organization of biodiversity and distribution of the ground-associated insular invertebrate community. Species do not spread evenly along environmental gradients but rather cluster in their niche occupation around certain environmental conditions. Therefore, these clusters or compartments result in a heterogeneous organization of biodiversity and species distribution on a local scale, with areas of increased and reduced biodiversity (Schluter and Pennell, 2017).

This compartmentalization in niche occupation could be related to the observed compartmentalization of food webs or pollination networks, as species interact more strongly with species within their niche cluster, resulting in segregated clusters (McCann et al., 2005).

## Section B.2: Allochthonous resources are less important for faunal communities on highly productive, small tropical islands

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Steibl, S., Sigl, R., Blaha, S., Drescher, S., Gebauer, G., Gürkal, E., Hüftlein, F., Satzger, A., Schwarzer, M., Seidenath, D., Welfenbach, J., Zinser, R.S., & Laforsch, C. (2021) Allochthonous resources are less important for faunal communities on highly productive, small tropical islands. *Ecology and Evolution, 11*: 13128-13138.

Besides ecological niche occupation, the occupation of a species' trophic niche is also relevant for organizing biodiversity and distribution in ecosystems (Shmida and Wilson, 1985). The spatial variability of resources is reflected in its consumers' distribution, diversity, and biomass, often resulting in aggregations where resources are abundant (Cardinale et al., 2006). This phenomenon has been well studied on desert islands with little *in situ* terrestrial primary (i.e., autochthonous) production (Anderson and Walsh, 2013; Anderson and Polis, 1999, 1998; Noy-Meir, 1980). In these low-productive systems, the whole insular fauna becomes dependent on the nutrient input at the beach (i.e., allochthonous resources), and they occupy trophic niches that are characterized by high proportions of marine resources. This dependency on allochthonous input and trophic niche occupation has far-reaching consequences for the organization of biodiversity and distribution on these desert islands, as the whole insular fauna concentrates in areas of allochthonous marine input (Noy-Meir, 1980; Rose and Polis, 1998).

On insular systems with elevated *in situ* primary production, this pattern should suspend, as sufficient autochthonous production of the insular vegetation should provide additional resources inland (Marczak et al., 2007; Subalusky and Post, 2019). So far, this was demonstrated for ant and spider taxa on a temperate island, where only specimens close to the shore were subsidized by allochthonous input. Further inland, the primary vegetation formed the major basal carbon source, allowing ants and spiders to disperse further landwards than under the absence of autochthonous production (Bergamino et al., 2012; Paetzold et al., 2008).

This project aimed investigated the role of allochthonous and autochthonous resources in driving trophic niche occupation and, thus, biodiversity and distribution of the ground-associated insular community. Using stable isotope analysis as a state-of-the-art tool to investigate trophic niche occupation and food web structure (Layman et al., 2012, 2007), I hypothesized and showed that a sufficient *in situ* primary production on the studied islands results in an overall limited important of marine subsidies for consumer trophic niches. Only the strict-beach dwelling taxa, i.e., crustaceans, are dependent on marine subsidies and remained at the shoreline. Most hexapods, arachnids, and diplopods built up primarily on autochthonous resources and remained inland.

The resulting bipartite architecture of the insular food web might be related to the compartmentalized organization of the ecological niche occupation (**section B.1**). Conclusively, this study demonstrates how resource availability influences trophic niche distribution and contributes towards a better understanding of biodiversity and species distribution on small spatial scales.

## Section B.3: Diversity patterns and community structure of the ground-associated macrofauna along the beach-inland transition zone of small tropical islands

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Steibl, S., Sigl, R., Bräumer, P.E., Clauß, V., Goddemeier, S., Hamisch, S., Lücker, D., Reiprich, L., Stegmann, L., Voigt, N., Laforsch, C. (2021) Diversity patterns and community structure of the ground-associated macrofauna along the beach-inland transition zone of small tropical islands. *Diversity, 13*(377): 1-12.

After demonstrating an overall compartmentalized organization of the ground-associated insular infauna community, this project aimed to establish what stabilizes this organization of the ecological and trophic niches. The two most distinct identified compartments in the investigated system were formed by the beach fauna and the inland fauna (**section B.1**), both with their separate food web (**section B.2**). To investigate what stabilizes the organization of the biota that form these compartments, this projected aimed to investigate the transition zone between the beach and inland.

Transition zones (or ecotones) are dynamic environments between two adjoining systems whose inhabitants are relevant for linking two adjoining habitats, e.g., via trophic transfers (Kark and van Rensburg, 2006). This process is often carried out by so-termed ecotonal species, i.e., species that have specifically adapted to the transition zone's dynamic environmental conditions (Kark, 2013). Therefore, the presence or absence of ecotonal taxa might explain the observed compartmentalized community organization of the investigated insular ecosystems.

This project analysed the biodiversity and distribution patterns along the transition zone between the inland and beach habitats. I hypothesized that there exists an overall absence of taxa in the transition zone, as this might explain why beach and inland food web remain largely separated with little energy transfer occurring between both compartments (**section B.1** and **B.2**).

I found that most ground-associated invertebrate taxa occurred only on either side of the transition zone and rarely, if at all, crossed the ecotone, probably because they are specifically adapted to the environmental conditions and resource availability of either the beach or the inland (Greenaway, 2003; Romanuk and Levings, 2003). However, non-web-building spiders were commonly observed on both sides of the transition zone. This suggests that an absence of ecotonal species is not responsible for the observed bipartite organization of the ground-associated insular invertebrate community in distinct beach and inland compartments.

At the same time, neither an increased nor decreased species richness and diversity in the transition zone was observed. Increased diversity commonly occurs in ecotonal habitats due to the overlapping distribution ranges of species occurring on either side of the transition zone and due to the presence of a diverse and specifically adapted ecotonal fauna (Kark, 2013). The absence of any ecotonal edge effect might be related to the overall remoteness, small size, and young age of the investigated insular system, which (yet) hindered the establishment and evolution of a diverse ecotonal fauna (Naylor, 2015).

## Section B.4: The importance of the Maldives as wintering ground for migratory birds of the Central Asian flyway

Originally published as:

FORKTAIL
Journal of Asian Ornithology

Steibl., S., & Laforsch, C. (2021) The importance of the Maldives as wintering ground for migratory birds of the Central Asian flyway. *Journal of Asian Ornithology, 37*: 80-87.

By now, this PhD thesis has established that the biodiversity and distribution of ground-associated insular infauna communities are organized in a compartmentalized way, both concerning ecological niche (**section B.1**) and trophic niche occupation (**section B.2**) and that an absence of ecotonal taxa is not responsible for this compartmentalized organization (**section B.3**). Project B.4 aimed to assess if the biodiversity and distribution of larger and more mobile vertebrate taxa can be related to the observed invertebrate community's compartmentalized organization and to identify drivers for the biodiversity and distribution patterns of the vertebrate community.

With only two species of flying fox, two species of amphibians, and five species of reptiles, the Maldivian vertebrate fauna is fairly depauperate. To some extent, birds form the only relevant exception to this phenomenon. While only 13 to 16 species of birds regularly and commonly breed on at least some islands, most of the 194 recorded bird species are migratory (Anderson and Shimal, 2020). Those species breed in the northern Palearctic realm and annually return to India and Sri Lanka for overwintering (Feare and High, 1977). While the role of the wetlands in the Indian subcontinent for migratory birds has been well documented, it is mostly unknown to what extent birds use the Indian Ocean islands as non-breeding grounds and how they disperse in the insular environment (Mundkur et al., 2017; Szabo and Mundkur, 2017). Previous bird recordings from the Indian Ocean islands rely on accidental sightings and single reports.

This project is the first-ever systematic survey of the avifauna on a Maldivian island, conducted during two consecutive wintering seasons. Bird taxa that were so far considered rare or uncommon in the Maldives (Anderson and Shimal, 2020) were commonly recorded in this study, suggesting that the Maldivian islands are of greater importance for migratory birds than previously known.

The occurrence of most bird species was not driven by the tidal regime, suggesting that they find sufficient food throughout the whole tidal cycle and tide-synchronized movements are unnecessary (Granadeiro et al., 2006). Habitat type significantly influenced the avian diversity and distribution patterns. While bird diversity in the beach habitat was overall high, few species were found inland, and almost no species occurred in both habitats.

This distribution pattern adds relevant information to the described compartmentalized organization of the ground-associated insular invertebrate community. It suggests that birds likely do not link the different ecological niche (**section B.1**) or food web compartments (**section B.2**) of the insular invertebrate community. Instead, the birds' restricted distribution patterns to either beach or inland might stabilize the invertebrate community's overall compartmentalized organization, as cross-habitat energy transfer from birds (e.g., through guano or predation) probably occurs only to a small proportion.

## Section B.5: Tourism and urban development as drivers for invertebrate diversity loss on tropical islands

Originally published as:

Steibl, S., Franke, J., & Laforsch, C. (2021) Tourism and urban development as drivers for invertebrate diversity loss on tropical islands. *Royal Society Open Science, 8*(10): 210411.

After having establishe how the ground-associated faunal community's biodiversity and distribution is organized on uninhabited islands, project B.5 aimed to assess and disentangle how different human land uses alter the observed biodiversity. For this project, I used the same overall framework as in section A.3, i.e., investigating and comparing urban developed islands used as permanent settlings by the local population ('local islands') with islands used solely for touristic purposes ('tourist islands'). Tourism and urban development for permanent settling are, globally, among the most prevalent land-use-associated threats for biodiversity (Hall, 2010).

Combining close-range sampling of the overall species richness and diversity of the ground-associated community with satellite-based remote sensing analysis of the overall habitat configuration enabled investigating also possible drivers of the observed human-driven changes in biodiversity and species distribution. I hypothesized that biodiversity and land use/ cover on tourist and local islands are significantly altered compared to uninhabited islands. The focal taxon approach in chapter A of this PhD thesis (**section A.3**) already showed that hermit crab species are negatively impacted by the investigated human land uses. The community-wide sampling approach in chapter B now indicated that the whole ground-associated invertebrate biodiversity is significantly impoverished on tourist and local islands. Compared to uninhabited islands as an undisturbed reference system, diversity and species richness on tourist and local islands were reduced by 50 to 80%. Remote-sensing-based analysis of the insular land use/ cover changes suggested that on local islands, habitat fragmentation due to road constructions and an overall reduction in vegetation cover are the primary drivers for the observed biodiversity loss. However, on tourist islands, large-scale land use/ cover changes could not be linked to the observed biodiversity loss, suggesting that other factors, like pesticide application, are the predominant drivers of invertebrate loss under this land-use form.

The magnitude of the invertebrate biodiversity loss on tourist and local islands is, in its dimension, comparable to that following agricultural land use in many industrialized countries (Hallmann et al., 2017). Therefore, both forms of human land use pose a major threat to the fragile and unique fauna of the Maldivian tropical islands, which are also considered part of a global biodiversity hotspot (Gillespie et al., 2012).

These findings underline that the growing tourist industry and continuing urban development on tropical atoll islands pose a severe and major threat to the unique terrestrial insular biodiversity (Saeed and Annandale, 1999). At the same time, it also demonstrates that the mechanisms through which tourism and permanent settling drive biodiversity losses differ markedly between these two land-use forms.

## Section B.6: Impacts on trophic niches and food web properties of invertebrate communities vary between different human land uses

Originally published as:

Steibl, S., Gebauer, G. & Laforsch, C. Impacts on trophic niches and food web properties of invertebrate communities vary between different human land uses. *in preparation*

The overall negative impact of human land use on species richness and diversity has long been established and well-described for numerous systems (Brown, 1997; Newbold et al., 2016; Habel et al., 2019; **section A.3** and **B.5**). Recently, the focus shifted from merely describing biomass and taxa losses towards investigating human-driven changes to fundamental ecological interactions. This aids in revealing the underlying factors responsible for the observable changes in biodiversity and distribution patterns following human activities (Takemoto and Kajihara, 2016; Valiente-Banuet et al., 2015).

Trophic interactions and trophic niche occupation are known to be impacted and altered by anthropogenic disturbances, and case studies on single taxa have demonstrated the variety of different possible responses to various disturbances (e.g., Barrett et al., 2005; Sobocinski, Cordell & Simenstad, 2010; Pringle et al., 2019). Responses to human disturbances comprise shifts in the trophic niche due to changes in resource availability, broadening of the trophic niche due to increased omnivory, apparent trophic upgrading due to anthropogenic nitrogen enrichment, or trophic downgrading due to truncated food webs (Estes et al., 2011; Penick et al., 2015). All these mechanisms have been observed in isolated case studies using single taxa. However, community-wide measures of human-driven changes to trophic niche structure of different species and following different land uses are lacking.

Using the overall insular framework as introduced in section A.3 and B.5 and the stable isotope approach as in section B.2, this project hypothesized and demonstrated that the trophic niches of the ground-associated insular invertebrate community are significantly shifted on tourist and local islands. However, the direction and magnitude of trophic shift and abundance change vary between the different species and depend on the type of land use. Several key food web properties, which are expressed and summarised as Layman metrics (Layman et al., 2007a, Layman et al., 2007b), were significantly altered under tourism and/ or urban land use.

These findings offer the first direct evidence that land-use impacts on food webs are context-dependent. As oceanic islands harbor a disproportionately high number of endangered species, it further indicates the cascading, long-term, and yet unpredictable changes to island ecosystems following human land use on islands.

# Chapter C. First records of species from the Maldives

The islands of the Maldivian archipelago, which constituted the PhD thesis's methodological framework, form a remote chain of atolls in the Indian Ocean, roughly 500 km south of the Indian subcontinent. The 26 atolls of the Maldives comprise more than 1,100 small islands, spanning from latitudes of 8° North over the equator to 1° South (Naylor, 2015) (Fig. 2). Due to this vast spatial extension and the islets' overall scattered distribution, comprehensive studies on the terrestrial fauna are challenging to conduct, and species new to this region are continuously recorded. While some terrestrial faunal groups on the Maldives, including hermit crabs (Hogarth et al., 1998), isopods (Taiti, 2014), orthopterans (Kevan and Kevan, 1995), spiders (Sunil, 2012), or birds (Anderson and Shimal, 2020) have received some attention from taxonomists and zoologists, other taxa have been completely neglected and never reported from the Maldives. Nevertheless, even the abovementioned and relatively well-studied biota are far from comprehensively reported, and novel species records can still be made from the Maldives.

During the fieldwork of this PhD thesis, I came across two species that have thus far not been recorded on the Maldives (Fig. 5). The discovery of both species, i.e., a wolf spider (**section C.1**) and a diplopod species (**section C.2**), has broader implications for our understanding of island colonization, animal dispersal, and conservation. Therefore, I reported these findings in the scientific literature to make the discoveries publicly available for taxonomists, zoologists, and conservationists worldwide.

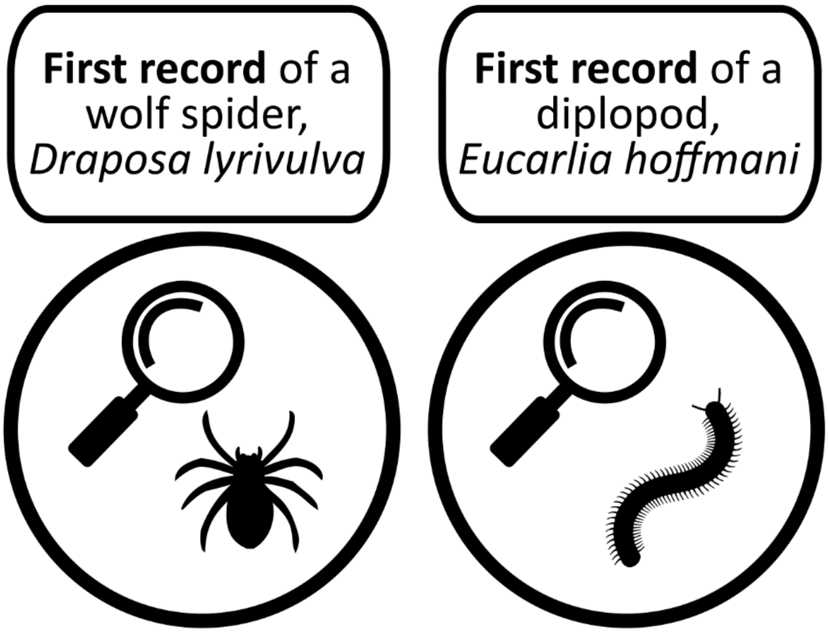

**Figure 5: During the field work of this PhD thesis, two invertebrate species, the wolf spider *Draposa lyrivulva* and the spirobolid diplopod *Eucarlia hoffmani,* have been found and identified, which have so far not been known to occur on the Maldivian archipelago.**

## Section C.1: First record of a wolf spider, *Draposa lyrivulva* (Bösenberg & Strand 1906) (Araneae: Lycosidae), from the Maldivian islands, Indian Ocean

Originally published as:

Steibl, S., Ballarin, F., Nadolny, A.A., Laforsch, C. (2020) First record of a wolf spider, *Draposa lyrivulva* (Bösenberg & Strand 1906) (Araneae: Lycosidae), from the Maldivian islands, Indian Ocean. *Acta Arachnologica, 69*(2): 61-65.

Wolf spiders (Araneae: Lycosidae) are a common and worldwide distributed family of spiders with more than 2,400 described species that are usually related to grassland or other open habitats (Jocqué and Alderweireldt, 2005). Their aerial dispersal abilities allowed wolf spiders to colonize all continents (except Antarctica) and most major geo-regions of the planet (Richter, 1970). Besides their wide distribution on the mainland, their dispersal strategy enabled them to conquer and inhabit remote island groups, like Micronesia or the Marshall Islands in the Pacific Ocean (Framenau et al., 2009). Nevertheless, in one vast region, the Indian Ocean, there have been until now no confirmed reports of any wolf spider species (Sunil, 2012).

During the field sampling of this PhD thesis, I noted a conspicuous and abundant wolf spider occurring on most investigated islands in the transition zone between beach and inland, where the first pioneering plants formed the supralittoral vegetation. Although Sunil (2012) published a thorough overview of the Maldives' spider fauna, this wolf spider species was not included in his spider species' inventory from the Maldives.

The correct identification of spiders requires a thorough examination of the copulatory organs (Poy et al., 2019). The copulatory bulb of male spiders is a highly modified part of the pedipalp that functions as a secondary sexual organ by taking up sperm from the primary sexual organ and transferring it into the female epigyne, thereby coupling mechanically like a key and a lock (Eberhard and Huber, 2010). This highly complex and specialized copula with the associated copulatory organs is species-specific. Therefore, examinations of the sexual organs allow identifying and distinguishing different species of spiders reliably.

The microscopic examination of the male pedipalp and the female epigyne of several collected specimens of the so-far unidentified wolf spider from the investigated Maldivian islands identified this species as *Draposa lyrivulva* (Bösenberg and Strand, 1906). This species belongs to the recently established genus *Draposa* (formerly *Pardosa*) and has, until now, only been known from mainland India, Pakistan, and Sri Lanka (Kronestedt, 2010). Reporting this species as a common inhabitant on several islands of the Maldivian archipelago extends its known occurrence range about 500 km further south. It further underlines the ability and relevance of aerial dispersal for the distribution of wolf spiders (Richter, 1970). Even though it remains unknown whether *D. lyrivulva* originally colonized the Maldivian islands naturally via aerial dispersal from India or the Lakshadweep, or has been introduced by human settlers, its abundant occurrence on most investigated islands shows that this species is adapted to colonize and spread easily between different habitat patches or islands via its aerial dispersal abilities.

## Section C.2: First record of the spirobolid *Eucarlia hoffmani* Golovatch & Korsós, 1992 (Diplopoda: Spirobolida: Pachybolidae) from the Maldives, Indian Ocean

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Journal of the Working Group of German-speaking Myriapodologists

Steibl, S., Spelda, J., & Laforsch, C. (2020) First record of the spirobolid *Eucarlia hoffmani* Golovatch & Korsós, 1992 (Diplopoda: Spirobolida: Pachybolidae) from the Maldives, Indian Ocean. *Schubartiana, 9*: 7-11.

With about 12,000 described species, millipedes are the third most species-rich class of arthropods, following arachnids (100,000 described species) and insects (900,000 described species) (Golovatch and Kime, 2009). Millipedes are detritivores and play a key role in most terrestrial ecosystems for nutrient cycling by fragmenting leaf litter, thus making nutrients more readily available for soil microbes (Snyder and Hendrix, 2008). Their faecal products are rich in minerals and a vital mineral source for plants and plant-associated microbes, comparable to that of earthworms (Dangerfield and Milner, 1996). Despite their pivotal role and global distribution in most terrestrial ecosystems, there has not been any confirmed species report of a millipede from the Maldivian archipelago.

During the fieldwork of this PhD thesis, I noted the presence of a common and highly abundant millipede within the leaf litter and detritus below the dense tropical insular tree and shrub vegetation.

The correct identification of most millipede species is only possible using adult males, as the decisive criteria for identification are the gonopods, i.e., the secondary external genitalia (Blower, 1985). However, this is hindered by the fact that males often cannot be recognized externally, and in some millipede species, they occur on the surface only for a limited time throughout the year (Dangerfield et al., 1992; Telford and Dangerfield, 1993). The dearth of males in natural populations commonly leads to type series and zoological museum collections that predominantly contain juveniles and females but almost entirely lack any adult male (Golovatch and Korsós, 1992).

Due to the extensive collection of millipedes on different islands in the investigated Maldivian atoll, I was able to find one male among the collected specimen that allowed correct identification to species level. The gonopod's microscopic examination identified this specimen as *Eucarlia hoffmani* (Spirobolida: Pachybolidae), a species thus far only reported from one atoll in the Seychellean archipelago (Golovatch and Korsós, 1992).

The finding of *E. hoffmani* as a presumably common and widespread millipede on different islands in the Maldivian archipelago is of further relevance for applied conservation efforts. It was up to now listed as "ENDANGERED" on the IUCN Red List$^{\mathrm{TM}}$, due to its presumed restricted spatial distribution only on the Farquhar Atoll in the Seychelles (Gerlach, 2014). By reporting this species from the Maldives, I show that its range extension is much larger than previously considered, rendering its current IUCN Red List$^{\mathrm{TM}}$ status open for debate, and suggesting a possible reassessment of its global risk status due to its apparently much broader distribution pattern.

# VI. Author Contributions

The whole idea of my PhD project and the concepts and designs of all studies within this PhD project were developed by myself and in consultation with my supervisor, Prof. Dr. Christian Laforsch (Department of Animal Ecology, University of Bayreuth, Germany). I acquired the funding for the PhD itself and for the, in total, four field research stays on the Maldives to conduct the field work by successfully applying for funding at the "Max Weber-Programm" scholarship (fieldwork 2017 during my Master's thesis) and the "Studienstiftung des deutschen Volkes" scholarship (fieldworks 2018-2019). I organized, planned, and conducted the research stays on the Maldives and initiated the contact to the various NGOs and institutions involved in the realization of this PhD project. I conducted all field samplings, the statistical analyses of all research projects, and was the leading and first author in the writing process of all projects. The stable isotope analyses (**sections B.2** and **B.6**) were done by Prof. Dr. Gerhard Gebauer in the laboratory for stable isotope biogeochemistry (BayCEER, University of Bayreuth, Germany). Field sampling of the projects **B.4** and **B.6** were conducted within the framework of the M.Sc. course "Marine Ecology" 2018 and 2019 at the university of Bayreuth. For these two projects, I conducted the field sampling together with the participating students (all listed as co-authors in the manuscripts) and, additionally, had the task of project supervision and administration by planning, organizing, and conducting the 12-day field stays for the M.Sc. classes. The remote sensing analysis (**section B.5**) was conducted by Dr. Jonas Franke (RSS GmbH, Munich, Germany). The identification of the two species reported for the first time from the Maldivian archipelago (**sections C.1** and **C.2**) was done by the taxonomists Dr. Jörg Spelda (SNSB-ZSM, Bavarian State Collection of Zoology, Munich, Germany), Dr. Francesco Ballarin (Systematic Zoology Laboratory, Tokyo Metropolitan University, Japan), and Dr. Anton A. Nadolny (A.O. Kovalevsky Institute of Biology of the Southern Seas, Sevastopol, Russia), all listed as co-authors in the respective publications.

A detailed overview of my own contributions, as well as my co-authors' contributions, to each publication following the standardized CRediT taxonomy (Contributor Roles Taxonomy, http://credit.niso.org/; access: 01/02/2021) reads as follows:

Steibl, S., & Laforsch, C. (2019) Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*). *Estuarine, Coastal and Shelf Science, 231:* 106482.

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Funding Acquisition.

**Co-author contributions:**

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., & Laforsch, C. (2020) Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species. *BMC Ecology, 20*(1): 1-9.

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Funding Acquisition.

**Co-author contributions:**

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., & Laforsch, C. (2019) Disentangling the environmental impact of different human disturbances: a case study on islands. *Scientific Reports, 9:* 13712.

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Funding Acquisition.

**Co-author contributions:**

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., & Laforsch, C. (2021) Compartmentalized organization of ecological niche occupation in insular invertebrate communities. *Ecology and Evolution, 11*(1): 471-480.

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Funding Acquisition.

**Co-author contributions:**

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., Sigl, R., Blaha, S., Drescher, S., Gebauer, G., Gürkal, E., Hüftlein, F., Satzger, A., Schwarzer, M., Seidenath, D., Welfenbach, J., Zinser, R.S., & Laforsch, C. (2021) Allochthonous resources are less important for faunal communities on highly productive, small tropical islands. *Ecology and Evolution, 11*: 13128-13138.

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Supervision, Project Administration, Funding Acquisition.

**Co-author contributions:**

S.B., S.D., E.G., F.H., A.S., M.S., D.S., J.W., R.S.Z.: Investigation, Writing – Original Draft.

R.S., C.L.: Conceptualization, Investigation, Writing – Review & Editing, Supervision, Project Administration.

G.G.: Conceptualization, Methodology, Formal Analysis, Writing – Review & Editing.

Steibl, S., Sigl, R., Bräumer, P.E., Clauß, V., Goddemeier, S., Hamisch, S., Lücker, D., Reiprich, L., Stegmann, L., Voigt, N., Laforsch, C. (2021) Diversity patterns and community structure of the ground-associated macrofauna along the beach-inland transition zone of small tropical islands. *Diversity, 13*(377): 1-12.

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Supervision, Project administration, Funding Acquisition.

**Co-author contributions:**

P.E.B., V.C., S.G., S.H., D.L., L.R., L.S., N.V.: Investigation, Writing – Original Draft.

R.S., C.L.: Conceptualization, Investigation, Writing – Review & Editing, Supervision, Project Administration.

Steibl., S., & Laforsch, C. (2021) The importance of the Maldives as wintering ground for migratory birds of the Central Asian flyway. *Journal of Asian Ornithology, 37*: 80-87.

**Own contributions:** Conceptualization, Methodology, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Supervision, Project administration, Funding Acquisition.

**Co-author contributions:**

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., Franke, J., & Laforsch, C. (2021) Tourism and urban development as drivers for invertebrate diversity loss on tropical islands. *Royal Society Open Science, 8*(10): 210411.

**Own contributions:** Conceptualization, Methodology, Writing – Original Draft, Writing –

Review & Editing, Data Visualization, Supervision, Project administration, Funding Acquisition.

**Co-author contributions:**

J.F.: Methodology, Writing – Review & Editing.

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., Gebauer, G. & Laforsch, C. Impacts on trophic niches and food web properties of invertebrate communities vary between different human land uses. *in preparation*

**Own contributions:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Funding Acquisition.

**Co-author contributions:**

G.G.: Conceptualization, Methodology, Formal Analysis, Writing – Review & Editing.

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., Spelda, J., Laforsch, C. (2020) First record of the spirobolid *Eucarlia hoffmani* (Golovatch & Korsós 1992) (Diplopoda, Spirobolida, Pachybolidae) from the Maldives, Indian Ocean. *Schubartiana, 9*: 7-11.

**Own contributions:** Conceptualization, Methodology, Writing – Original Draft, Writing – Review & Editing, Data Visualization, Supervision, Project administration, Funding Acquisition.

**Co-author contributions:**

J.S.: Methodology, Formal Analysis. Writing – Review & Editing.

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

Steibl, S., Ballarin, F., Nadolny, A. A., Laforsch, C. (2020) First record of the wolf spider *Draposa lyrivulva* (Bösenberg & Strand 1906) (Araneae: Lycosidae) from the Maldives, Indian Ocean. *Acta Arachnologica, 69*(2): 61-65.

**Own contributions:** Conceptualization, Methodology, Writing – Original draft, Writing – Review & Editing, Data Visualization, Supervision, Project administration, Funding Acquisition.

**Co-author contributions:**

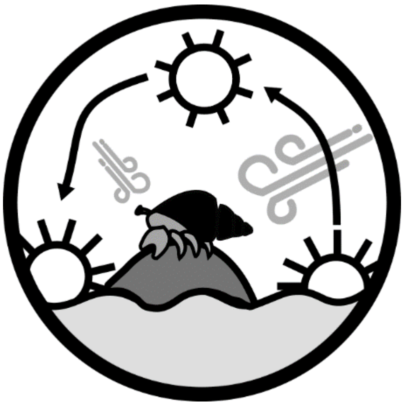
F.B., A.A.N.: Methodology, Formal Analysis, Writing – Review & Editing.

C.L.: Conceptualization, Writing – Review & Editing, Supervision.

# VII. Main Research

## A. Using a focal taxon approach to investigate how biodiversity and distribution is organized and to disentangle the environmental impacts of different land uses

**A.1** Steibl, S., & Laforsch, C. (2019) Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*). *Estuarine, Coastal and Shelf Science, 231*: 106482.



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# Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*)

Sebastian Steibl, Christian Laforsch *

*Department of Animal Ecology I, University of Bayreuth, Universitaetsstr. 30, D-95440, Bayreuth, Germany*

A R T I C L E I N F O

*Keywords:*
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*Coenobita perlatus*
*Coenobita rugosus*
circadian rhythms
Habitat selection

A B S T R A C T

The beach environment is extremely dynamic in space and time. Abiotic factors like tides, sun exposure or sediment structure are defining the ecology of the beach-associated fauna. Among the most common beach-dwelling organisms of tropical and subtropical shores are the hermit crabs of the genus *Coenobita* (Latreille, 1829) (Decapoda: Anomura). They utilize gastropod shells to protect against predators, to avoid desiccation and disruption by wave action and further show behavioural adaptations, like burrowing in the substratum to withstand the abiotic stressors of coasts. Little is known, however, if the abiotic factors of the beach habitat influence the daytime activity and habitat preferences. We therefore analysed the changes in abundance during daytime, at different tidal times and in different coastal habitats in a community of two sympatric *Coenobita* species, *C. rugosus* and *C. perlatus*. We hypothesized that habitat, daytime and tidal time influenced the overall abundance. Here, we showed that hermit crabs became largely absent during midday, while their highest diurnal activity laid in the 2 h before low tide until absolute low tide. Structurally more complex beach types were preferred over pure fine sand or rock beaches. These behaviours and preferences of the investigated hermit crabs are adaptive as they aid in avoiding desiccation, while becoming most active when food availability is highest during low tide. Heterogenous beach habitats are probably favoured over homogenous sandy beaches, because accumulation of marine debris, a major food source, is increased. This emphasizes how physically controlled the distribution of beach-dwelling organisms is and demonstrates how abiotic stressors can become major drivers for behavioural adaptations in beach crustaceans.

## 1. Introduction

Beaches are among the most dynamic terrestrial habitats (Defeo and McLachlan, 2005). They are shaped by the temporal and spatial variations in tidal regime, wave climate, sun exposure, heat and different sediment types (Short, 1996). The combination of these parameters causes a wide range of morphodynamic beach types and physically structures the beach macrofauna (McLachlan, 1990; Noy-Meir, 1980). Fine sand beaches have the overall lowest species diversity, while a higher substrate complexity is linked to a greater species diversity and also to higher abundance of organisms (Hendrickx, 1996; Leite et al., 1998). These variations in the overall species richness, density and abundance between different beach communities are thereby caused by the individual responses of the beach-dwelling taxa to the physical parameters (McLachlan and Dorvlo, 2005).

To adapt to the variable beach environment, beach-dwelling organisms have evolved various behavioural and physiological mechanisms to withstand the selective pressure of the physical factors they experience on the beach habitat (McLachlan et al., 1993). The orientation and navigation along physical gradients towards beneficial or away from disadvantageous conditions in the beach environment is widespread in many beach-associated organisms (Felicita, 2014): A circadian rhythm with either diurnal, nocturnal or crepuscular activity peaks aids in avoiding unfavourable conditions, e.g. heat during the day or predation pressure during night (Barnes, 1997a; Dahl, 1953). The synchronisation of activity patterns to the tidal regime always keeps the animals in an area with optimal feeding conditions and decreases the risk of displacement by heavy wave action (Branch and Cherry, 1985; McLachlan et al., 1979). Similarly, many beach-associated crustaceans synchronise their movement to the intensity of wave action to stay in the zone of greatest water movement, where food availability is maximised (Dahl, 1953).

A common and ubiquitous organism in the tropic and sub-tropic coastal habitats are the terrestrial hermit crabs (Decapoda: Anomura:

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* Corresponding author.
*E-mail addresses:* sebastian.steibl@uni-bayreuth.de (S. Steibl), christian.laforsch@uni-bayreuth.de (C. Laforsch).

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*Coenobitidae*). They belong to the genus *Coenobita* (Latreille, 1829) and comprise 25 species (Lemaitre and McLaughlin, 2019a). Besides predation, coenobitid hermit crabs utilize gastropod shells to minimize evaporation and the risk of desiccation in order to persist in the beach environment (Gross, 1964). They furthermore display behavioural adaptations to withstand the unfavourable and harsh physical conditions of the beach environment (Greenaway, 2003). During the day, they burrow themselves to avoid direct sun, dehydration and an increase in body temperature, making them mainly active at night and during dawn (Barnes, 2001; Vannini, 1976). Vertical movement with tidal times on the beach habitat is displayed to avoid displacement during feeding on washed-up material at the drift line (Vannini, 1976). Because organic debris, like seagrass or algae, is the main food source for coenobitid crabs, they accumulate and cluster in areas of the beach environment, where the amount of detritus is high (Ince et al., 2007; Page and Willason, 1982).

Although previous studies report clustering behaviour in coenobitid hermit crabs and suggest an overall night-active life habit that follows the tidal regime, many of the physical parameters shaping the temporal and spatial distribution of coenobitid hermit crabs in the beach environment are not thoroughly understood. Page and Willason (1982) reported for example that the coenobitid hermit crab *C. rugosus* (Lemaitre and McLaughlin, 2019) are commonly found during day and night, while other studies attribute a strict nocturnal activity to *C. rugosus* (Gross, 1964; Grubb, 1971; Vannini, 1976). Barnes (1997) observed no dependence of the activity of *C. rugosus* on tidal activity, while other studies suggest a strong influence of the tidal regime on coenobitid abundance (Hazlett, 1981). Additionally, little is known if and how the beach habitat type itself shapes the spatial distribution of coenobitid hermit crabs.

The aim of this study was therefore, to investigate how habitat characteristics together with daytime and tidal time influence the distribution of coenobitid hermit crabs in space and time. In the first experiment, the spatial distribution of hermit crab abundance on different types of beach habitats, ranging from a fine sand beach to a predominantly rock-covered beach, was measured. In a second experiment, samplings from sunrise to sunset with changing tidal times were carried out in the same plot to identify when the highest and lowest abundances of hermit crabs occur throughout a day.

## 2. Material and methods

The investigated hermit crab community in the studied system comprised two species, *Coenobita rugosus* and *C. perlatus* (Lemaitre and Mclaughlin, 2019). The two species occurred in a fairly constant ratio of 8:1 (*C. rugosus* - *C. perlatus*) throughout the whole investigated atoll (unpublished results). The mean body size (measured as shield length) of the hermit crabs in the investigated system was $0.62 \pm 0.19$ cm (mean ± SD) for *C. rugosus* and $0.61 \pm 0.21$ cm for *C. perlatus* (unpublished results).

### 2.1. Habitat preferences of a coenobitid hermit crab community

Sampling was carried out on 07/02/17 and 08/02/17 during falling tides between 7:17 am and 12:42 pm on Naifaru Island, Lhaviyani Atoll, Republic of Maldives (Fig. S1). The spatial variability of hermit crab distribution was recorded by assigning the beach into four categories: (1) fine sand (FS), (2) fine sand with small fragments (SF), (3) fine sand with larger rocks (LR) and (4) predominantly rock-covered beach (RC) (Fig. S2). Each of the four beach types was replicated six times by sampling different locations along the whole shoreline of the investigated island ($N = 6$; Fig. S1C). The investigated plots measured 10 m along the current drift line and 2 m landwards, measured from the current drift. Each plot was measured once and the total number of hermit crabs within each plot was recorded. For statistical analysis, hermit crab density of the hermit crab community per plot, i.e. 20 $m^2$, was calculated. Differences in the hermit crab density between the four beach habitat types were statistically compared using Kruskal-Wallis test and Dunn-Bonferroni post-hoc tests with Bonferroni corrections in R 3.3.0.

### 2.2. Daytime activity of a coenobitid hermit crab community

Sampling was carried out on nine days in the time between 12/01/17 and 05/02/17 on Naifaru Island, Lhaviyani Atoll, Republic of Maldives (Table 1). The temporal variability of the hermit crab distribution was investigated in a single plot that comprised fine sand and fine sand with small fragments habitats. The plot was 25 m long (measured along the drift line) and 2 m wide (measured perpendicular to the drift line). The vertical position of the plot was adjusted hourly to assure that the plot always covered the first 2 m landwards from the current drift line. The exact start and end position of the plot was marked using GPS (eTrex Vista® Cx, Garmin Ltd., Schaffhausen, Switzerland). All hermit crabs in the plot were counted every hour from sunrise to sunset with the exact hourly sampling times adjusted for every sampling day individually, based on the time of absolute low tide event for that day. For example, when absolute low tide occurred at 8:36 (e.g. sampling day six), sampling was conducted at 6:36, 7:36, 8:36, etc. (Tab. 1). To analyse the temporal variation in abundance, the mean abundance for each sampling during falling tides (i.e. the hourly measured abundance from 2 h before low tide until absolute low tide) and during rising tides (i.e. the hourly measured abundance in the first 3 h after absolute low tide) was calculated and statistically compared using a non-parametric Kruskal-Wallis test.

## 3. Results

### 3.1. Habitat preferences of a coenobitid hermit crab community

Hermit crab density differed significantly between the four beach habitats (Kruskal-Wallis: $df = 3$, $\chi^2 = 17.739$, $P < 0.001$; Fig. 1). Density was significantly higher in the 'fine sand with small fragments' beach habitat than in the 'fine sand' habitat (Kruskal-Dunn post-hoc: $P = 0.006$) and in the 'predominantly rock-covered' habitat (Kruskal-Dunn post-hoc: $P = 0.007$). Density was significantly lower in the 'fine sand' habitat than in the 'fine sand with larger rocks' habitat (Kruskal-Dunn post-hoc: $P = 0.050$). Hermit crab density did not differ between the 'fine sand' habitat and the 'predominantly rock-covered' habitat (Kruskal-Dunn post-hoc: $P = 1.000$) and the 'fine sand with larger rocks' habitat (Kruskal-Dunn post-hoc: $P = 0.057$). The density did not differ between the 'fine sand with larger rocks' habitat and the 'fine sand with small fragments' habitat (Kruskal-Dunn post-hoc: $P = 1.000$).

### 3.2. Daytime activity of a coenobitid hermit crab community

The abundance of *C. rugosus* and *C. perlatus* varied throughout the day (Fig. 2). Independently of the low tide event of each sampling day,

**Table 1**
Tidal events, sunrise and sunset for the nine sampling days on Naifaru, Republic of Maldives. Low tide events in bold mark the time to which each sampling day was adjusted.

| date | sunrise | sunset | high tide | low tide |
|---|---|---|---|---|
| 12/01/17 | 6:20 | 18:09 | 0:27, 11:26 | **6:34**, 17:58 |
| 23/01/17 | 6:22 | 18:14 | 23:17 | **15:04** |
| 24/01/17 | 6:22 | 18:14 | 8:51 | 5:54, **16:05** |
| 25/01/17 | 6:22 | 18:15 | 10:08 | 6:09, **16:50** |
| 26/01/17 | 6:22 | 18:15 | 0:15, 11:01 | **6:29**, 17:31 |
| 31/01/17 | 6:23 | 18:16 | 2:19, 14:15 | **8:36**, 20:14 |
| 01/02/17 | 6:23 | 18:17 | 2:42, 14:58 | **9:05**, 20:47 |
| 02/02/17 | 6:23 | 18:17 | 3:07, 15:45 | **9:40**, 21:20 |
| 05/02/17 | 6:23 | 18:17 | 4:28, 19:59 | **12:05** |

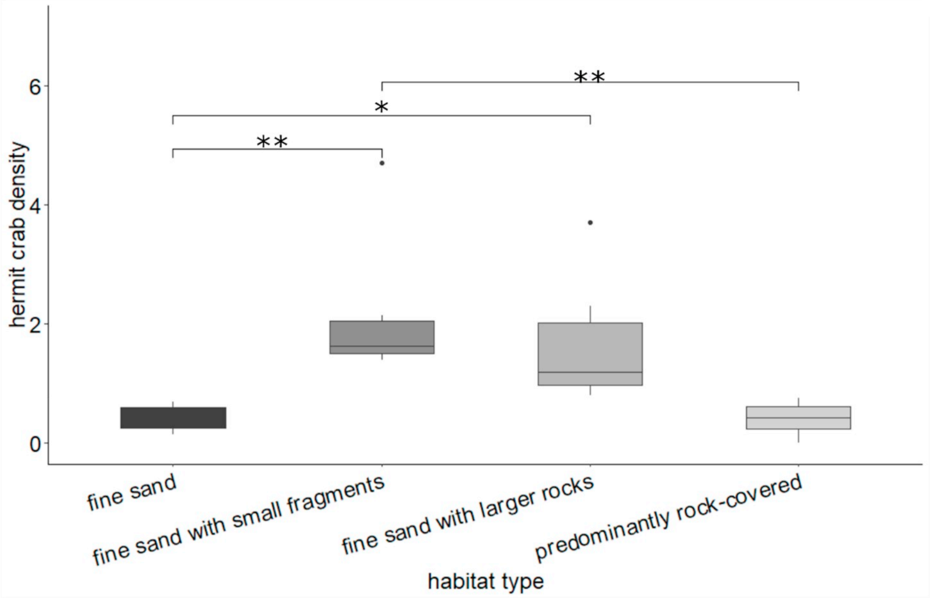

**Fig. 1.** Mean hermit crab density per 20 m$^2$ of the beach community of hermit crabs *Coenobita rugosus* and *C. perlatus* in the four different beach habitat types. *$P < 0.05$; **$P < 0.01$ (Kruskal-Wallis: $\chi^2 = 17.739$).

the first abundance minimum always occurred around midday. A second abundance minimum appeared in the late afternoon, shortly before sunset (between 18:09 and 18:17). The abundance maximum of each sampling day occurred either in the morning or in the afternoon and laid in the 2 h before low tide until absolute low tide. Only on one sampling day, where low tide occurred directly at midday (12:05), the abundance maximum occurred 4 h earlier (08:05). A diurnal abundance maximum was never observed after absolute low tide during rising tides. The abundance of hermit crabs was significantly higher during falling tides than during rising tides (Kruskal-Wallis: $\chi^2 = 19.000$, $P < 0.001$; Fig. 3).

## 4. Discussion

The results of the present study showed that coenobitid hermit crabs are strongly influenced in their diurnal activity by the structural habitat characteristics, day time, and tidal time. On the same island, significant variations in the abundance between different beach types demonstrated that coenobitid hermit crabs are more abundant in a more structured and complex habitat. At the same time, the abundance is highest before absolute low tide, while activity is, independently of tidal time, always decreased around midday.

Diurnal activity of coenobitid hermit crabs is influenced by variations in humidity (de Wilde, 1973). As coenobitid crabs normally

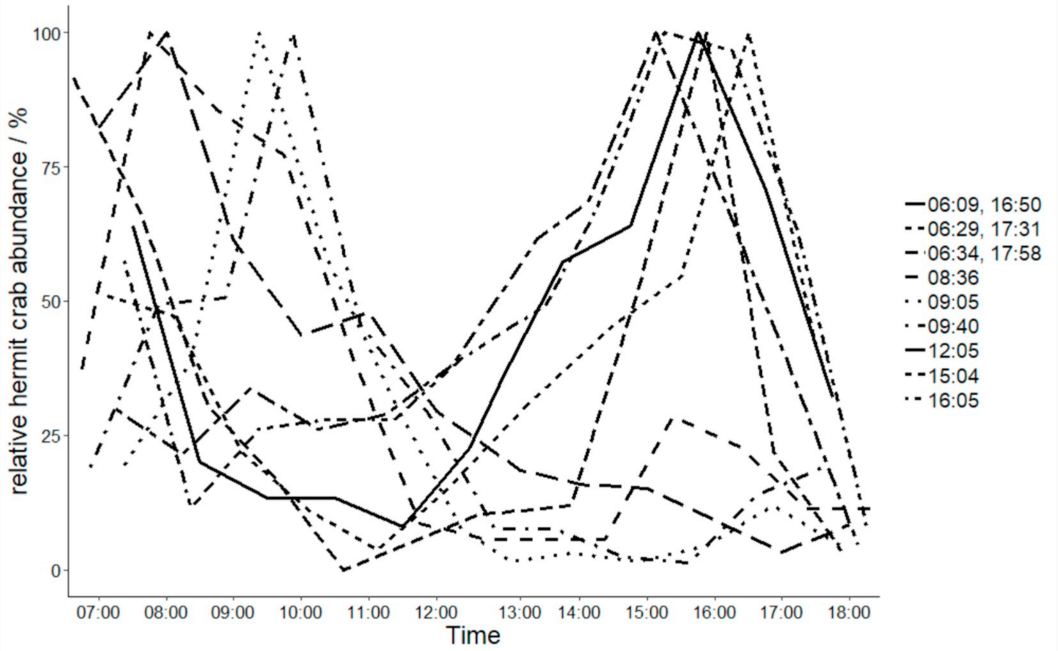

**Fig. 2.** Daytime activity of a coenobitid hermit crab community. Each line represents an individual sampling day ($N = 9$), measured hourly from sunrise to sunset. For each sampling day, the abundance was calculated relative to the daily maximum. The low tide event for each sampling day is given on the legend to the right (see also tab. 1 for low and high tide events).

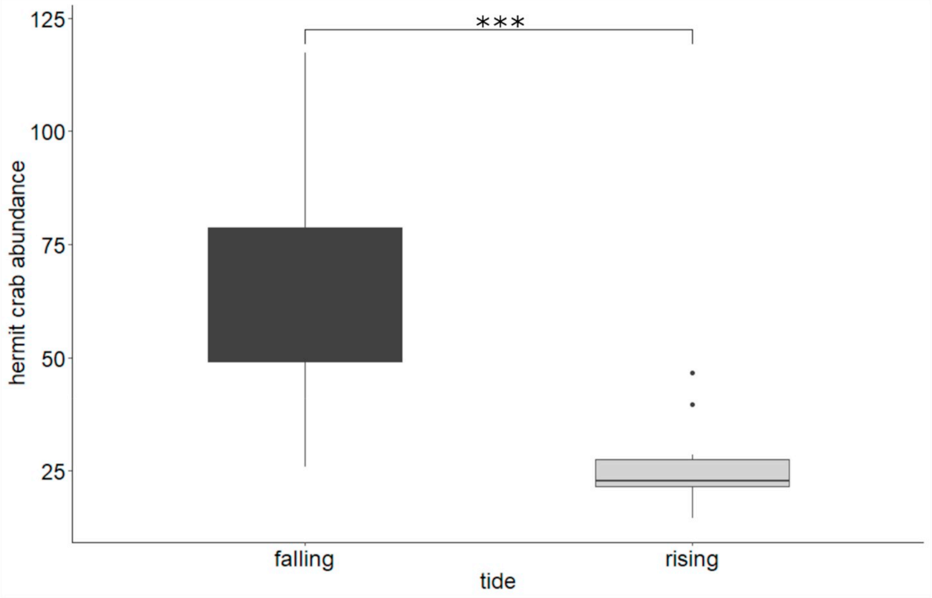

**Fig. 3.** Mean abundance of the beach community of hermit crabs *Coenobita rugosus* and *C. perlatus* during falling and rising tides ($N = 10$). ***$P < 0.001$ (Kruskal-Wallis, $\chi^2 = 19.000$).

burrow themselves during the day to avoid desiccation and to gain water from the sand, the relative high humidity in the tropical Maldives of about 80% in average (Mahlia and Iqbal, 2010) could explain the increased activity during day in the present study, as the necessity to avoid the daily heat is reduced (Vannini, 1975). In concordance with Barnes (1997), an overall abundance low was observed around midday, independently of the tidal regime, probably to avoid desiccation at the hottest time of the day.

A dependency on the tidal regime of coenobitid hermit crabs was nevertheless shown by Vannini (1976), Grubb (1971) and Hazlett (1981), although only observed at night. In contrast, Barnes (1997) observed no dependence on tidal times in *C. rugosus*. Unlike the aforementioned studies, the present study showed that there also exists a dependence on tides during daytime activity. This suggests that spatial and temporal variations in coenobitid hermit crab activity arise out of a combination of an endogenous circatidal and circadian rhythm component (Barnwell, 1966).

Synchronising activity to the tides is adaptive for coenobitid hermit crabs, as the risk of being displaced by wave action is diminished during falling tides and around absolute low tide (Branch and Cherry, 1985). Coenobitid hermit crabs are feeding on washed-up organic material at the drift line, thereby exposing themselves to the risk of being caught by waves (Barnes, 1997b; Page and Willason, 1983). During rising tides and at high tide, this risk of displacement is strongly increased (Felicita, 2014), which explains the measured abundance decline after low tide events in the present study. The overall input of accumulated washed-up organic material on the beaches is also influenced by the tidal regime (Marsden, 1991). An activity pattern, synchronised to falling tides, is also shown in many other beach-dwelling organisms, which wait until conditions become favourable to emerge for feeding (Gibson, 2003).

The overall high abundance of coenobitid crabs during day (in average 27 individuals with peaks of 119 coenobitid crabs in the plot, i. e. per 50 $m^2$) are contradictory to most studies suggesting a nocturnal activity, but an inactivity during day (Gross, 1964; Grubb, 1971; Page and Willason, 1982; Vannini, 1976). The reasons for the observed diurnal activity pattern in the present study might arise out of a sampling procedure with an overall higher temporal resolution, as the hermit crabs were counted every hour, while e.g. Page and Willason (1982) only sampled every 4 h, thereby reducing the possibility to capture diurnal variations in the abundances. Vannini (1976) and Grubb (1971) observed abundance peaks of *C. rugosus* between one to 2 h before sunset, while in present study the abundance was high in the late afternoon (around 16:00), but then halved every hour until it reached a minimum around sunset. *C. rugosus,* however, was observed to be nocturnal in some studies (Hazlett, 1981), while others have observed similar activities at night and day (Page and Willason, 1982). This could indicate differences in the circadian activity patterns, depending on the geographical location or physiological condition of the animals (Metcalfe and Steele, 2001; Metcalfe et al., 1998; Page and Willason, 1982).

Besides the changing physical conditions over the course of a day, the habitat itself also had a great influence on the activity of beach-dwelling coenobitid crabs. The significantly higher abundance in the ‘fine sand with small fragments’ and ‘fine sand with larger rock’ habitats compared to the less heterogenous ‘fine sand’ and ‘rock-covered’ habitats might result from a greater food availability in these structurally more complex and heterogenous beach habitat types (Hsu et al., 2018; Jaramillo et al., 2006; Moore et al., 2001; Orr et al., 2005). An artificial increase in the amount of rocks, logs, coconut husks and other detritus on the same beach location was shown to double the hermit crab abundance within one day (Page and Willason, 1982). The coral fragments and rocks in the investigated beach habitats in the present study may facilitate that a higher amount of organic material is detained from being rapidly flushed away by the waves (Orr et al., 2005). Hence, these structurally more complex habitats are likely favoured by the coenobitid hermit crabs as overall food availability is increased (Dugan et al., 2003; Ince et al., 2007; Jaramillo et al., 2006). Besides the increased food availability, it is also likely that more empty gastropod shells, which get washed ashore, accumulate in these more heterogeneous beach habitat types or get translocated into this habitat by foraging hermit crabs (Bell, 2009). As gastropod shells are the limiting resource for hermit crab populations, areas, where shell accumulation is increased, could show increased hermit crab abundance (Vance, 1972).

The results of the present study demonstrate, how the physical parameters of the beach environment shape the diurnal and spatial distribution of coenobitid hermit crabs. This shows that besides their shell utilization behaviour, hermit crabs display further behavioural responses to withstand the environmental conditions of beaches. This study thereby confirms that the harsh abiotic factors of beaches are major drivers for behavioural adaptations in beach-dwelling organisms (Felicita, 2014).

## Contributors

S.S. and C.L. developed the study design. S.S. performed field sampling and statistical analysis. S.S. and C.L. wrote the manuscript and agreed to the submission of the final version of the manuscript.

## Declaration of competing interest

None.

## Acknowledgements

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106482.

## References

Barnes, D.K.A., 2001. Hermit crabs, humans and Mozambique mangroves. Afr. J. Ecol. 39, 241–248.

Barnes, D.K.A., 1997. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: distribution, abundance and activity. Mar. Ecol. Prog. Ser. 154, 133–142. https://doi.org/10.3354/meps206171.

Barnes, D.K.A., 1997. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: a novel and locally important food source. Mar. Ecol. Prog. Ser. 161, 299–302. https://doi.org/10.3354/meps154133.

Barnwell, F.H., 1966. Daily and tidal patterns of activity in individual fiddler crab (genus *Uca*) from the Woods Hole Region. Biol. Bull. 130, 1–17.

Bell, J.J., 2009. Hitching a ride on a hermit crabs home: movement of gastropod shells inhabited by hermit crabs. Estuar. Coast Shelf Sci. 85, 173–178. https://doi.org/10.1016/j.ecss.2009.07.026.

Branch, G.M., Cherry, M.I., 1985. Activity rhythms of the pulmonate limpet *Siphonaria capensis* Q. & G. as an adaptation to osmotic stress, predation and wave action. J. Exp. Mar. Biol. Ecol. 87, 153–168.

Dahl, E., 1953. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos 4, 1–27.

de Wilde, P.A.W.J., 1973. On the ecology of *Coenobita clypeatus* in Curacao. Stud. Fauna Curaçao other Caribb. Island, 44, pp. 1–138.

Defeo, O., McLachlan, A., 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. Mar. Ecol. Prog. Ser. 295, 1–20. https://doi.org/10.3354/meps295001.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar. Coast Shelf Sci. 58, 25–40. https://doi.org/10.1016/S0272-7714(03)00045-3.

Felicita, S., 2014. Behaviour of mobile macrofauna is a key factor in beach ecology as response to rapid environmental changes. Estuar. Coast Shelf Sci. 150, 1–9. https://doi.org/10.1016/j.ecss.2013.11.001.

Gibson, R.N., 2003. Go with the flow: tidal migration in marine animals. Hydrobiologia 503, 153–161.

Greenaway, P., 2003. Terrestrial adaptations in the Anomura (Crustacea: Decapoda). Mem. Mus. Vic. 60, 13–26.

Gross, W.J., 1964. Water balance in anomuran land crabs on a dry atoll. Biol. Bull. 126, 54–68.

Grubb, P., 1971. Ecology of terrestrial decapod crustaceans on Aldabra. Philos. Trans. R. Soc. Lond. B Biol. Sci. 260, 411–416.

Hazlett, B.A., 1981. The behavioral ecology of hermit crabs. Annu. Rev. Ecol. Systemat. 12, 1–22. https://doi.org/10.1146/annurev.es.12.110181.000245.

Hendrickx, M.E., 1996. Habitats and biodiversity of decapod crustaceans in the SE Gulf of California. México. Rev. Biol. Trop. 44, 603–617.

Hsu, C.-H., Otte, M.L., Liu, C.-C., Chou, J.-Y., Fang, W.-T., 2018. What are the sympatric mechanisms for three species of terrestrial hermit crab (*Coenobita rugosus, C. brevimanus*, and *C. cavipes*) in coastal forests? PLoS One 13, e0207640.

Ince, R., Hyndes, G.A., Lavery, P.S., Vanderklift, M.A., 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Estuar. Coast Shelf Sci. 74, 77–86. https://doi.org/10.1016/j.ecss.2007.03.029.

Jaramillo, E., de la Huz, R., Duarte, C., Contreras, H., 2006. Algal wrack deposits and macroinfaunal arthropods on sandy beaches of the Chilean coast. Rev. Chil. Hist. Nat. 79, 337–351. https://doi.org/10.4067/S0716-078X2006000300006.

Latreille, P.A., 1829. Les Crustacés, les Arachnides et les Insectes, distribués en familles naturelles, ouvrage formant les tomes 4 et 5 de celui de M. le Baron Cuvier sur le Règne animal (deuxième édition). Déterville.

Leite, F.P.P., Turra, A., Gandolfi, S.M., 1998. Hermit crabs (Crustacea: Decapoda: Anomura), gastropod shells and environmental structure: their relationship in southeastern Brazil. J. Nat. Hist. 32, 1599–1608. https://doi.org/10.1080/00222939800771131.

Lemaitre, R., Mclaughlin, P.A., 2019. World Paguroidea & Lomisoidea Database. *Coenobita perlatus* H. Milne Edwards, 1837. World Regist, Mar. Species.

Lemaitre, R., McLaughlin, P.A., 2019. World Paguroidea & Lomisoidea Database. Coenobita Latreille, 1829. World Regist, Mar. Species.

Lemaitre, R., McLaughlin, P.A., 2019. World Paguroidea & Lomisoidea Database. *Coenobita rugosus* H. Milne Edwards, 1837. World Regist, Mar. Species.

Mahlia, T.M.I., Iqbal, A., 2010. Cost benefits analysis and emission reductions of optimum thickness and air gaps for selected insulation materials for building walls in Maldives. Energy 35, 2242–2250. https://doi.org/10.1016/j.energy.2010.02.011.

Marsden, I.D., 1991. Kelp-sandhopper interactions on a sand beach in New Zealand. I. drift composition and distribution. J. Exp. Mar. Biol. Ecol. 152, 61–74. https://doi.org/10.1016/0022-0981(91)90135-J.

McLachlan, A., 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. J. Coast. Res. 6, 57–71. https://doi.org/10.2307/4297644.

McLachlan, A., Dorvlo, A., 2005. Global patterns in sandy beach macrobenthic communities. J. Coast. Res. 21, 674–687. https://doi.org/10.21121/03-0114.1.

McLachlan, A., Jaramillo, E., Donn, T.E., Wessels, F., 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. J. Coast. Res. Special Is 27–38. https://doi.org/10.2307/25735721.

McLachlan, A., Wooldridge, T., van der Horst, G., 1979. Tidal movements of the macrofauna on an exposed sandy beach in South Africa. J.Zool.,Lond. 187, 433–442.

Metcalfe, N.B., Steele, G.I., 2001. Changing nutritional status causes a shift in the balance of nocturnal to diurnal activity in European Minnows. Funct. Ecol. 15, 304–309. https://doi.org/10.1046/j.1365-2435.2001.00527.x.

Metcalfe, N.H., Fraser, N.H.C., Burns, M.D., 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. Proc. R. Soc. Biol. Sci. 265, 1503–1507. https://doi.org/10.1098/rspb.1998.0464.

Moore, S.L., Gregorio, D., Carreon, M., Weisberg, S.B., Leecaster, M.K., 2001. Composition and distribution of beach debirs in Orange County, California. Mar. Pollut. Bull. 42, 241–245.

Noy-Meir, I., 1980. Structure and function of desert ecosystems. Isr. J. Bot. 28, 1–19.

Orr, M., Zimmer, M., Jelinski, D.E., Mews, M., 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86, 1496–1507.

Page, H.M., Willason, S.W., 1983. Feeding activity patterns and carrion removal by terrestrial hermit crabs at Enewetak Attol, Marshall Islands. Pac. Sci. 37, 151–155.

Page, H.M., Willason, S.W., 1982. Distribution patterns of terrestrial hermit crabs at Enewetak Atoll, Marshall Islands. Pac. Sci. 36, 107–117.

Short, A.D., 1996. The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. Rev. Chil. Hist. Nat. 69, 589–604.

Vance, R.R., 1972. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53, 1062–1074.

Vannini, M., 1976. Researches on the coast of Somalia. The shore and the dune of Sar Uanle 7. Field observations on the periodical transdunal migrations of the hermit crab *Coenobita rugosus* Milne Edwards. Monit. Zool. Ital. 7, 145–185.

Vannini, M., 1975. Researches on the coast of Somalia. The shore and the dune of Sar Uanle 5. Description and rhythmicity of digging behaviour in *Coenobita rugosus* Milne Edwards. Monit. Zool. Ital. Suppl. 13, 233–242. https://doi.org/10.1080/03749444.1987.10736729.

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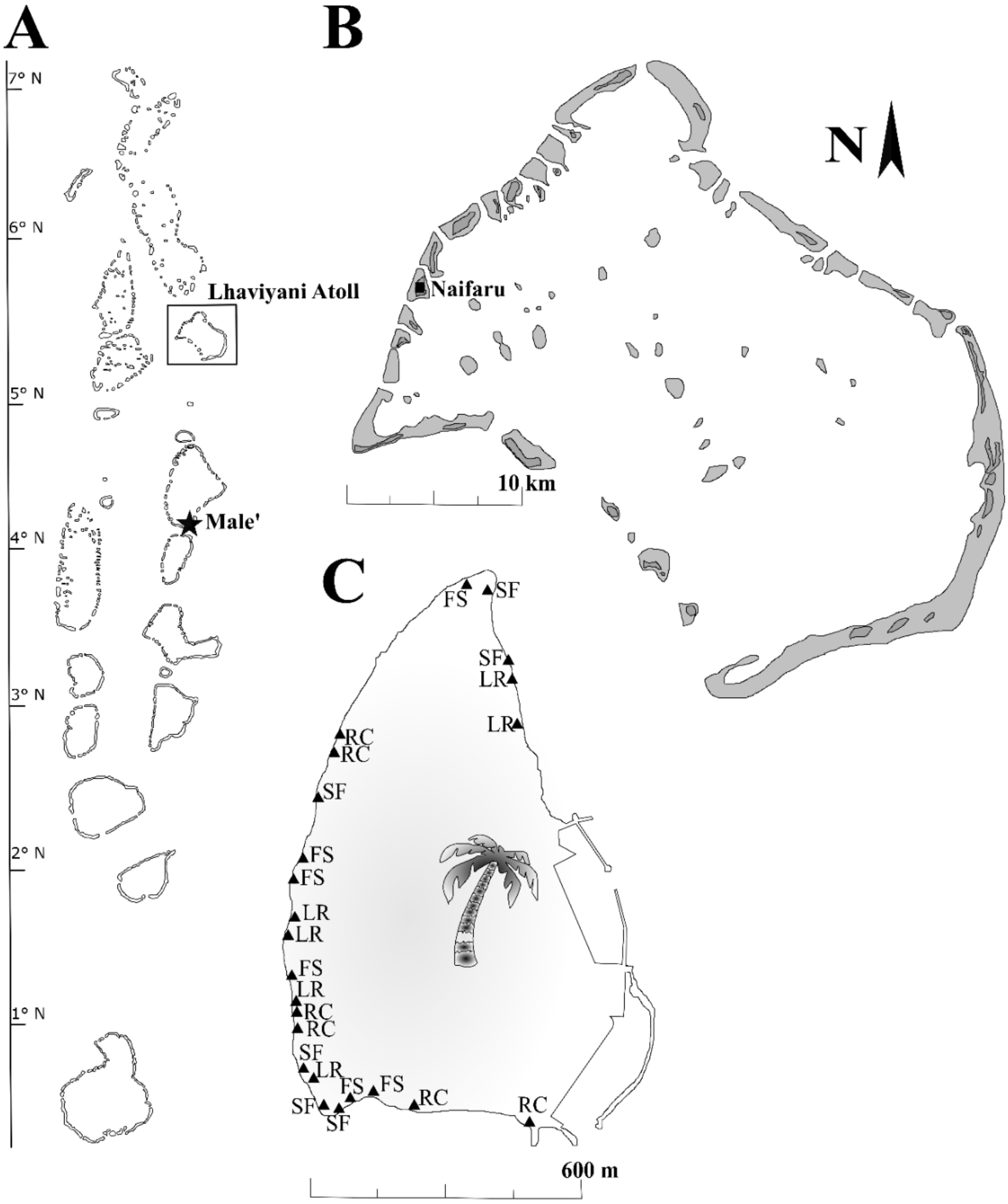
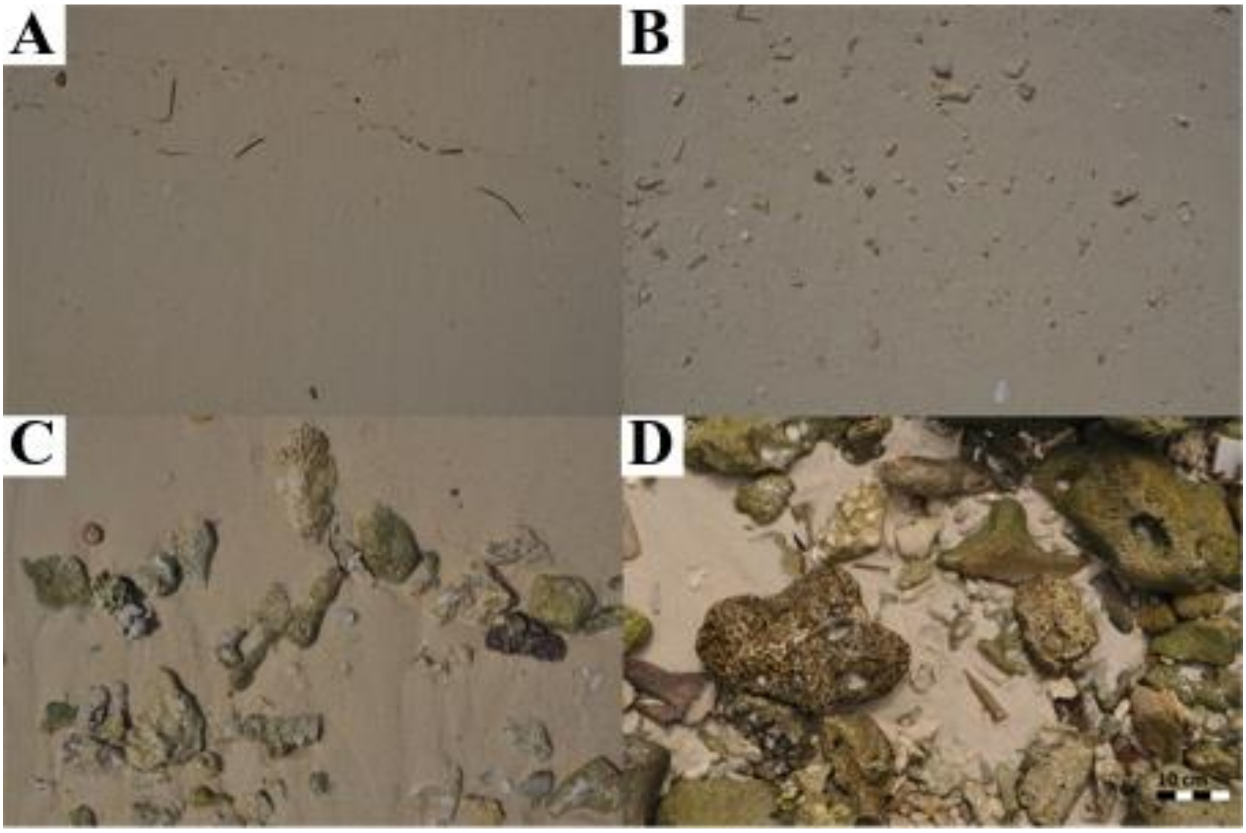
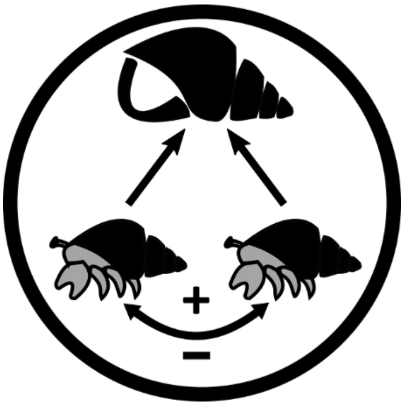


**Supplementary figure A.1-S1.** Map of the study area and the distribution of plots. Location of the Lhaviyani Atoll within the Republic of Maldives (**A**). Location of the investigated island, Naifaru, within the Lhaviyani Atoll (**B**). Distribution of the sampled plots with the four investigated beach types on the investigated island, Naifaru (**C**). FS, fine sand; SF, fine sand with small fragments; LR, fine sand with larger rocks; RC, predominantly rock-covered.



**Supplementary figure A.1-S2.** The four beach categories present on the shoreline of the investigated tropic island: ‘fine sand’ beach habitat (**A**). ‘Fine sand with small fragments’ habitat (**B**). ‘Fine sand with larger rocks’ habitat (**C**). ‘predominantly rock-covered’ beach habitat (**D**).

**A.2** Steibl, S., & Laforsch, C. (2020) Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species. *BMC Ecology, 20*(1): 1-9.



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RESEARCH ARTICLE Open Access

# Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species

Sebastian Steibl and Christian Laforsch*

**Abstract**

**Background:** Coexistence is enabled by ecological differentiation of the co-occurring species. One possible mechanism thereby is resource partitioning, where each species utilizes a distinct subset of the most limited resource. This resource partitioning is difficult to investigate using empirical research in nature, as only few species are primarily limited by solely one resource, rather than a combination of multiple factors. One exception are the shell-dwelling hermit crabs, which are known to be limited under natural conditions and in suitable habitats primarily by the availability of gastropod shells. In the present study, we used two co-occurring terrestrial hermit crab species, *Coenobita rugosus* and *C. perlatus*, to investigate how resource partitioning is realized in nature and whether it could be a driver of coexistence.

**Results:** Field sampling of eleven separated hermit crab populations showed that the two co-occurring hermit crab species inhabit the same beach habitat but utilize a distinct subset of the shell resource. Preference experiments and principal component analysis of the shell morphometric data thereby revealed that the observed utilization patterns arise out of different intrinsic preferences towards two distinct shell shapes. While *C. rugosus* displayed a preference towards a short and globose shell morphology, *C. perlatus* showed preferences towards an elongated shell morphology with narrow aperture.

**Conclusion:** The two terrestrial hermit crab species occur in the same habitat but have evolved different preferences towards distinct subsets of the limiting shell resource. Resource partitioning might therefore be the main driver of their ecological differentiation, which ultimately allowed these co-occurring species to coexist in their environment. As the preferred shell morphology of *C. rugosus* maximizes reproductive output at the expense of protection, while the preferred shell morphology of *C. perlatus* maximizes protection against predation at the expense of reproductive output, shell resource partitioning might reflect different strategies to respond to the same set of selective pressures occurring in beach habitats. This work offers empirical support for the competitive exclusion principle-hypothesis and demonstrates that hermit crabs are an ideal model organism to investigate resource partitioning in natural populations.

**Keywords:** *Coenobita perlatus*, *Coenobita rugosus*, Coexistence, Competitive exclusion principle, Shell utilization, Resource partitioning

## Background

Throughout all ecosystems, species can be found that are closely related to each other, occupy the same trophic level within the food web and share the same habitat, thus fulfilling similar ecological roles for the ecosystem [1]. When two or more species overlap to a certain degree in their biology and share a common and essential resource

*Correspondence: christian.laforsch@uni-bayreuth.de
Department Animal Ecology I, University of Bayreuth and BayCEER, Universitaetsstr. 30, 95440 Bayreuth, Germany

that is limited in supply, these species experience competition [2, 3]. This interspecific competition can occur in two forms, either via direct interference competition (i.e. fighting over resources) or via indirect exploitative competition (i.e. consumption of resources by one species makes it unavailable for second species). In ecological research, evidence for competition between two species can be provided by comparing which resources are used and which are intrinsically preferred [4].

When investigating resource utilization between co-occurring species, studies have shown that some animals that presumably compete over the same resource, actually partition the resource [5, 6]. According to the competitive exclusion principle, this resource partitioning, as a form of ecological differentiation between species, can thereby be the mechanism that allows co-occurring species to coexist in the same environment [7]. This coexistence can only be realized when each species uses a discrete subset of the limiting resource, which differs qualitatively from those of the co-occurring species [8, 9]. This premise for resource partitioning is described in the concept of limiting similarity, which states that there needs to be a limit to how similar two species can be to each other in order to stably coexist, rather than compete [5].

Such theoretical hypotheses are difficult to test using empirical research, as most animals in nature are not limited by only a single resource, but rather by a multitude of abiotic and biotic factors [10]. There exist, however, some co-occurring species, where enough evidence has been collected to suggest that they are indeed primarily limited by only one resource. Shell-dwelling hermit crabs are limited under natural conditions and in suitable habitats only by the availability of the shell resource, while food and habitat are not considered as a limiting factor [10–13]. Therefore, they appear to be suitable model organisms to investigate competition theory in empirical research.

Hermit crabs (Superfamily: Paguroidea) are characterized by an uncalcified and reduced abdomen, which they protect by utilizing mainly gastropod shells [14, 15]. As a well-fitting shell optimizes growth and maximizes clutch size [16], offers protection against predators and mechanical disruption [17, 18], and decreases the risk of desiccation in the intertidal and terrestrial species [19], hermit crabs are under constant pressure to find a well-fitting shell. The availability of empty and well-fitting shells thereby depends on the gastropod population and their mortality and hence is the limiting resource of hermit crab populations [10, 14, 20].

Co-occurring species of hermit crabs experience direct interference competition by fighting over shells in a highly ritualized behaviour and indirect exploitative competition, as the utilization of an empty shell makes it unavailable for other individuals [11, 13, 14, 21–23]. This competition can force hermit crabs to utilize shells outside their optimal fit range, resulting in a reduced fitness [10, 20, 24]. A number of studies, however, were able to demonstrate, that, contrary to the proposed shell competition, at least some co-occurring hermit crab species partition the shell resource [10, 25–27]. In these studies, the utilized gastropod shells and their morphometric parameters (e.g. size, weight) of co-occurring hermit crab species in the field were investigated and compared. It was thereby shown that co-occurring hermit crabs utilize indeed shells of different gastropod species or with different shell parameters [8, 25], although other studies suggested that the observed differences in shell utilization arise not out of different preferences [11, 21]. Therefore, it is discussed whether shell resource partitioning is indeed the mechanism of coexistence in co-occurring hermit crab species [10, 23].

One major limitation of many research approaches that investigate shell resource partitioning in hermit crabs is that the proposed preferences are based on the species identities of the gastropod shells [e.g. 20, 26]. The utilization of different shell species depends on the gastropod communities in the particular habitat and gastropod species vary between different regions [19, 24, 28, 29]. Proposing that co-occurring hermit crab species partition the shell resource by preferring different shell species is an uninformative and not universally applicable approach, because the available set of utilizable gastropod species varies between regions and does not reflect the actual preference of a hermit crab species, i.e. the same hermit crab species can prefer two completely different shell species in two different populations but in both cases select for the same morphological shell parameters.

A better approach is the comparison of preferences for different shell parameters. Determining the shell partitioning mechanism based on single shell parameters, however, is restricted, as the various shell variables are all highly intercorrelated, making it impossible to characterize a single parameter on which preferences could be based upon [30]. Using morphometric data, it was demonstrated that co-occurring hermit crab species have distinct preferences towards e.g. large shells or narrow apertures [25].

To deepen our understanding of resource partitioning as a possible driver of coexistence using empirical research on hermit crabs, it would be essential to incorporate (I) a large-scale sampling effort to pool data of multiple distinct hermit crab and gastropod populations, (II) a comparison between shell utilization patterns in the natural habitat and the intrinsic preferences towards distinct subsets of the resource and (III) a statistical analysis of the overall morphology of the different subsets of the resources, rather than a single parameter-approach.

The present study complies with the three abovementioned criteria by conducting an atoll-wide sampling that covered eleven distinct hermit crab and gastropod populations and by comparing the field data with laboratory shell preference experiments. A principal component analysis (PCA) of the shell morphometrics was then applied to compare the decisive criteria of the shell morphology between the co-occurring species. As research organisms to test competition theory, the only terrestrial hermit crab genus, *Coenobita*, was chosen, because it has already been established that the two co-occurring hermit crab species in the investigated system, *C. rugosus* and *C. perlatus*, are both primarily beach associated and unspecialized detritus feeders with no clear food preferences [31–33]. They are therefore an ideal system to test for the effect of the shell resource on coexistence, because other potentially limiting factors can be excluded upfront. The overall shell utilization in land hermit crabs has received only limited research focus in comparison to their well-studied marine counterparts [34, 35]. As terrestrial hermit crabs are restricted to one island, they inhabit and obtain the shell resource only from the surrounding coastal water [19]. Therefore, sampling multiple islands covers distinct hermit crab and gastropod populations and decreases the effect of predominant species in one island ecosystem.

## Results

### Field data

Of the 876 collected hermit crabs, 700 were identified as *C. rugosus* and 176 as *C. perlatus.* The proportion of *C. rugosus* and *C. perlatus* varied significantly between the eleven investigated islands (F = 6.2536, *df* = 10, p < 0.001). On nine out of the eleven investigated islands within the Atoll, the mean proportion of *C. rugosus* was 86.47 ± 11.64%. On one island however, only 37.05% of the collected crabs were identified as *C. rugosus*, while 62.95% were *C. perlatus*. On another island, *C. perlatus* was completely absent from the investigated plots. The proportion of *C. rugosus* (80.28 ± 7.10%) and *C. perlatus* (19.72 ± 7.10%) was not significantly different between the four investigated beach habitat types (F = 1.9196, *df* = 3, p = 0.147). The collected *C. rugosus* and *C. perlatus* had a carapace length of 6.50 ± 2.23 mm and 6.46 ± 2.71 mm, respectively. The mean carapace length of the two species did not differ statistically (Wilcoxon W = 56,344, p = 0.291). The collected *C. rugosus* inhabited gastropod shells of 90 different species (in 21 different families), while the collected *C. perlatus* inhabited gastropod shells of 41 different species (in 14 different families; see Additional file 1: Table S1). The shell species diversity index, i.e. the diversity of shell species inhabited by the two investigated hermit crab species, of *C. rugosus* was H = 3.644 and of *C. perlatus* H = 3.039. The niche width in respect to utilizable shell species was therefore B = 23.870 for *C. rugosus* and B = 12.869 for *C. perlatus* (Table 1).

The proportional utilization of the investigated shell types differed significantly between *C. rugosus* and *C. perlatus* (Table 1). Proportionally more *C. rugosus* inhabited naticid shells than *C. perlatus* (p = 0.003), while proportionally more *C. perlatus* inhabited cerithiid (p < 0.001) and strombid shells (p < 0.001). No differences were found in the number of inhabited nassariid shells between *C. rugosus* and *C. perlatus* (p = 0.237; Table 1).

### Shell preference experiments

The mean carapace length of the 150 tested *C. rugosus* was 6.25 ± 1.43 mm and of the 150 tested *C. perlatus* 6.42 ± 1.42 mm (mean ± standard deviation). The size of the tested hermit crab in the laboratory experiment did not differ statistically between the two species (Wilcoxon W = 12,207, p = 0.199).

The two terrestrial hermit crabs *C. rugosus* and *C. perlatus* had significantly different shell preferences for the tested gastropod shells (Table 1, Additional file 2: Table S2). *C. perlatus* selected strombid shells significantly more often than *C. rugosus* (p < 0.001) and *C.*

**Table 1 Comparison of the shell utilization and preferences of the two co-occurring hermit crab species**

| | *Coenobita rugosus* | *Coenobita perlatus* |
|---|---|---|
| Utilized gastropod shells | 90 species (21 families) | 41 species (14 families) |
| Cerithiid shells utilized | 13.90% | 32.06% (***) |
| Cerithiid shells selected | 54.67% | 56.00% |
| Nassariid shells utilized | 28.78% | 18.49% |
| Nassariid shells selected | 64.00% | 65.33% |
| Naticid shells utilized | 14.09% | 4.22% (***) |
| Naticid shells selected | 56.00% | 20.00% (***) |
| Strombid shells utilized | 12.77% | 39.52% (***) |
| Strombid shells selected | 25.33% | 58.67% (***) |
| Shell diversity Shannon H | 3.644 | 3.039 |
| Niche width B in respect to shell species | 23.870 | 12.869 |

Asterisks (***p < 0.001) indicate significant differences in the proportional utilization or selection of the respective shell type between the two hermit crab species, *C. rugosus* and *C. perlatus* *rugosus* selected naticid significantly more often than *C. perlatus* ($p < 0.001$). No differences existed for the number of selected cerithiid ($p = 1.000$) and nassariid shells ($p = 1.000$) between the two hermit crab species.

### Morphometric analysis of gastropod shells

The five investigated morphometric parameters (shell length, shell width, aperture length, aperture width, shell weight) of the utilized gastropod shells differed significantly between the four investigated gastropod shell types ($F = 71.505$, $df = 3$, $p < 0.001$) and between the two hermit crab species ($F = 16.080$, $df = 1$, $p < 0.001$).

The first three principal components of the PCA, comparing the morphometric parameters, explained 96.47% of the total variance and were therefore used for further analysis (Fig. 1). Principal component 1 (PC1) correlates with all five morphometric parameters, suggesting that all five parameters vary together. PC2 is primarily a measure for shell length (correlation 0.784) and aperture width (correlation −0.526) and can be viewed as an overall descriptor of the shell shape with high values of PC1 indicating an elongated and narrow shell shape, while low values of PC2 indicate a short and bulbous shell shape. PC3 negatively correlates with aperture length (correlation −0.851) and can be viewed as a measure of how elongated the shell aperture is Table 2.

The four gastropod shell types differed significantly in PC1 ($F = 60.96$, $df = 3$, $p < 0.001$), PC2 ($F = 548.1$, $df = 3$, $p < 0.001$) and PC3 ($F = 307.8$, $df = 3$, $p < 0.001$). Tukey HSD post hoc test indicated significant differences in PC1 between all pairwise comparisons ($p < 0.001$), apart from nassariid-cerithiid ($p = 0.997$) and strombid-naticid shells ($p = 0.999$). PC2 was significantly different in all pairwise comparisons ($p < 0.001$ in all comparisons). PC3 was significantly different in all comparisons ($p < 0.001$), apart from one non-significant difference in the pairwise comparison of nassariid and cerithiid shells ($p = 0.051$; Table 2).

All three principal components of the shell parameters differed significantly between the two hermit crab species (PC1: $F = 9.819.3$, $df = 1$, $p = 0.001$; PC2: $F = 57.01$, $df = 1$, $p < 0.001$; PC3: $F = 92.14$ $df = 1$, $p < 0.001$; Additional file 3: Fig. S1).

## Discussion

According to the competitive exclusion principle, ecological differentiation is the premise for coexistence in co-occurring species [7]. This ecological differentiation can be realized by partitioning the limiting resource between two species [9]. In the present study, the utilization of the limiting resource of two co-occurring hermit crab species was investigated to study the relevance of resource partitioning as a driver of coexistence. In natural populations,

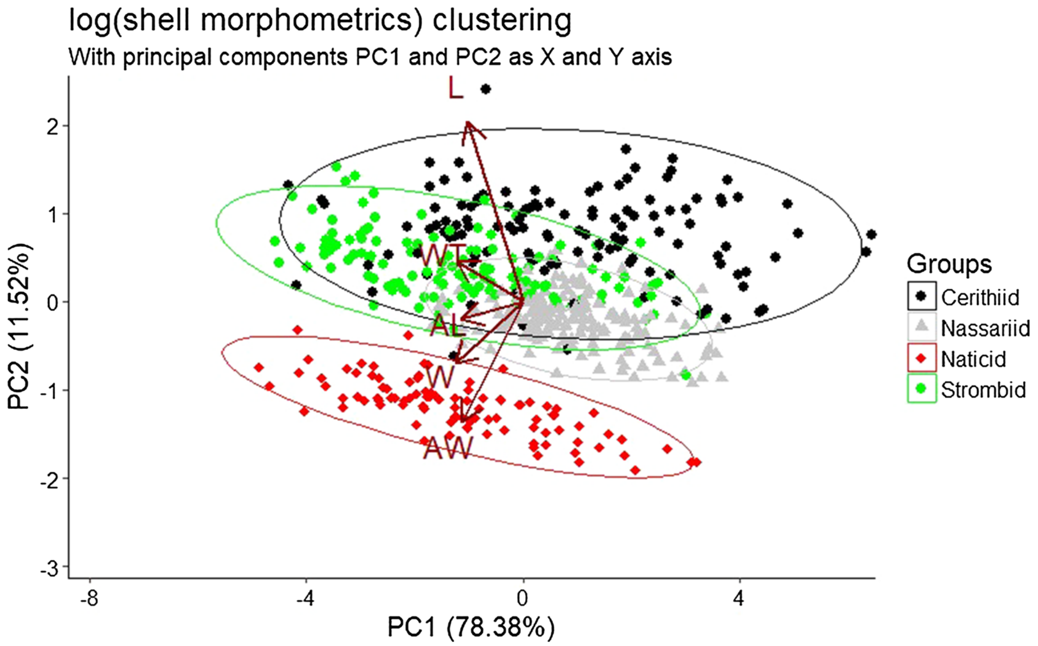

**Fig. 1** The shell morphology of the four most utilized gastropod shell types. The principal component analysis is based on the five log-transformed morphometric parameters (*AL* aperture length, *AW* aperture width, *L* length, *W* width, *WT* weight). Each data point represents a single shell, colours resemble the different shell types

**Table 2 Comparison of the shell morphology of the four most utilized gastropod shell types and the two hermit crab species**

| | PC 1 | PC 2 | PC 3 |
|---|---|---|---|
| Shell length | − 0.396 | 0.784 | 0.080 |
| Shell width | − 0.485 | − 0.265 | 0.016 |
| Aperture length | − 0.438 | − 0.078 | − 0.851 |
| Aperture width | − 0.437 | − 0.526 | 0.362 |
| Shell weight | − 0.472 | 0.174 | 0.370 |
| Shell thickness | − 0.329 | − 0.804 | 0.046 |
| Cerithiid shells | 0.874 (A) | 0.765 (A) | 0.372 (A) |
| Nassariid shells | 0.839 (A) | − 0.200 (B) | 0.268 (A) |
| Naticid shells | − 1.198 (B) | − 1.189 (C) | 0.056 (B) |
| Strombid shells | − 1.195 (B) | 0.384 (D) | − 0.791 (C) |
| *Coenobita rugosus* | 0.151 (A) | − 0.134 (A) | 0.046 (A) |
| *Coenobita perlatus* | − 0.479 (B) | 0.424 (B) | − 0.146 (B) |

Principal components (PC) of the PCA are based on five morphometric parameters of the four utilized gastropod shell types. Significant differences between the mean PC values for each shell type are indicated by different letters behind the PC value, same letters indicate no statistical difference between the PC values of the respective shell types

the two co-occurring hermit crabs *C. rugosus* and *C. perlatus* utilized different gastropod shell species. These differences in the shell utilization of the two hermit crab species arise out of different preferences towards different shell types. Together with the morphometric analysis, the presented data suggest that the two hermit crab species are not in competition over the limited shell resource but have evolved different preferences towards distinct subsets of the shell resource, which ultimately could enable both species to coexist in their habitat.

Coexistence of co-occurring marine hermit crabs has been suggested to arise out of a combination of resource and habitat partitioning [10, 14]. Terrestrial hermit crabs are more restricted in their habitat choice, as especially small islands offer only little heterogeneity in the beach environment [36–39]. Although *C. perlatus* was overall less abundant than *C. rugosus*, there relative proportions did not differ between the four present beach habitat types. As both species are known to be primarily beach-associated and rarely occurring in the densely vegetated inland [40–44], the high overlap of both species in the beach habitats suggests that habitat partitioning is not a driver of coexistence in these two species.

Partitioning of or competition over the food resource can also be excluded as a driver for coexistence, as previous studies demonstrated that *C. rugosus* and *C. perlatus* are both unspecific detritus feeders with no clear food preference [32, 43] and not limited by food availability [10, 14, 22].

As habitat and food resource partitioning appears to play a minor role for *C. rugosus* and *C. perlatus*, the possible mechanism for coexistence might arise out of shell resource partitioning. The morphometric analysis of the utilized shells in the field suggests that *C. rugosus* utilizes shells with a small and globose morphology, while *C. perlatus* utilizes shells with a large, elongated and narrow morphology. These utilization patterns arise indeed out of different intrinsic preferences towards the respective shell morphology, as *C. rugosus* selected for the short and globose naticid shells, while C. *perlatus* selected for the large and elongated strombid shells in the laboratory experiments. The determined preferences towards a certain shell morphology lay in concordance with previous studies, which reported *C. rugosus* to utilize mainly Muricidae, Neritidae or Turbinidae shells, which also have a globose morphology, and *C. perlatus* to utilize mainly the elongated cerithiid shells [35, 40, 43–45]. This overall similarity further underlines that not the shell species itself is the decisive criteria in the shell selection process, but rather the overall morphology of the present shell, described by the principal components of the morphometric data. The utilized shells found in the natural populations were overall fairly eroded and showed no striking variations in colour or ornamentation but appeared rather uniform pale and smooth, independent of the gastropod species. Therefore, preferences towards certain shell colours or ornamental features like spines can be excluded as further decisive factors in shell selection of the investigated hermit crab species. As gastropod communities vary between different regions, the adaptive mechanism in shell selection behaviour is therefore not the evolution of preferences towards species (although at least one hermit crab species is known utilizing only one shell species, *Calcinus seurati* [14, 20]), but rather of preferences towards certain shell morphologies [46].

The two investigated hermit crab species apparently have evolved different shell preferences towards distinct subsets of the shell resource. These intrinsic preferences could hint towards differing strategies of the two hermit crab species to respond to the same overall selective pressures [47, 48]. Heavy and elongated shells with a narrow aperture, like the strombid shells, offer optimal protection against desiccation and predation, but limit clutch size and increase energy expenditure during locomotion due to a reduced internal volume and increased weight [8, 16, 20, 25]. Light-weight and voluminous shells, like the naticid shells, allow a greater dispersal and are advantageous for burrowing, but cannot retain water efficiently and offer less protection against predation [27, 40, 49]. As different shell preferences might represent different strategies to respond to selective pressures from the same environment, *C. perlatus* might has evolved a strategy to reduce desiccation- and predation-related mortality at the expense of an increased energy expenditure and limited clutch size [48]. *C. rugosus* has evolved a strategy to maximize reproductive output at the expense of an increased susceptibility for desiccation and predation.

Further research is needed to test, whether the observed shell resource partitioning in the two co-occurring hermit crab species is the cause or the effect of the proposed ecological differentiation in respect to their life-history strategy and if the utilization of different subsets of the shell resource can even be a driver of speciation in hermit crabs.

In either way, it is shown that the utilization of distinct subsets of the limiting resource can drive ecological differentiation, which then ultimately enables two species to coexist [7, 9]. It is thereby demonstrated that co-occurring hermit crabs are indeed suitable model organisms to empirically investigate competition and coexistence theory, as their limitation by primarily one resource offers controllable and empirically testable conditions for investigating natural and intrinsic behaviour of resource partitioning.

## Conclusion

Overall, our research investigated the mechanism of resource partitioning as a driver of coexistence and demonstrated that two co-occurring species of terrestrial hermit crabs have evolved intrinsic preferences towards distinct subsets of the shell resource, which attenuates interspecific competition over the limiting resource in natural populations. As the preferred shell morphologies of the two hermit crab species either maximize reproductive output or minimize predation risk, the two hermit crab species might have evolved different strategies to respond to the overall selective pressures in their natural habitat.

These findings offer empirical support for theoretical hypotheses on competition theory and mechanisms of coexistence in ecology. By discussing different life-history strategies, associated with the observed resource partitioning, the presented model system using hermit crabs can form the basis for future research on mechanisms of coexistence and speciation.

## Methods

### Field data

Hermit crabs were collected on the beaches of eleven coral islands, distributed over the Lhaviyani (Faadhippolhu) Atoll, Republic of Maldives. Sampling was carried out between 03/02/2017 and 10/03/2017, always in the time from 2 h before low tide until absolute low tide. On each island, hermit crabs were collected in six plots with 10 m length (measured along the current drift line) and 2 m width (measured perpendicular to the current drift line). The habitat structure of each plot was assigned in four different beach habitat types: (1) fine sand beach, (2) fine sand beach interspersed with small coral and rock fragments, (3) fine sand beach interspersed with larger boulders and (4) predominantly rock-covered beach. The collected hermit crabs were transferred to the laboratory and removed from their shell by carefully heating the apex of the shell above an open flame. This is a standard procedure when investigating hermit crabs and leaves the animal without injuries [27, 49]. Afterwards, the hermit crab and their corresponding shell were photographed on millimetre paper (Nikon D5000 mounted with Nikon AF-S Nikkor 18–105 mm, 1:3.5–5.6, Nikon Corp., Tokyo, Japan.) and identified using identification keys [50–54]. The weight of the shell was measured using a fine scale (TS-300 300 g × 0.01 g, G&G GmbH, Neuss, Germany).

The carapace length of the hermit crabs and the morphometric parameters of their corresponding shell were determined using ImageJ 1.49b (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997–2015). Shell length was measured from the shell's apex to the siphonal notch—if present—or otherwise to the lower end of the aperture. Shell width was measured perpendicular to the longitudinal axis of the shell at the broadest section. Shell aperture length was measured from the anterior to the posterior canal of the aperture and aperture width was measured perpendicular to the aperture length between the outer lip and the columellar fold at the broadest section.

Statistical analysis was performed using R 3.5.1. [55] Differences in the number of shells utilized for a given shell species between *C. rugosus* and *C. perlatus* were tested for the four most abundant gastropod families in the plots, i.e. strombid shells (246 specimen), nassariid shells (196 specimen), cerithiid shells (166 specimen) and naticid shells (141 specimen; Fig. 2). Statistical comparison in the number of utilized shells of each of the four shell types between the two collected hermit crab species were analysed using Fisher's exact test [56]. Levels of significance were adjusted using Bonferroni–Holm-correction. The relative abundance of the two hermit crab species was calculated and statistically compared between the four investigated beach habitat type and between the eleven investigated coral islands using non-parametric multivariate analysis (PERMANOVA) with 999 permutations, implemented in the vegan package of R [57]. The diversity of shell species occupied by the two hermit crab species was calculated using the Shannon-Index H. Based on the number of inhabited shells from the two hermit crab species, the niche breadth (B) with respect to shell species inhabited was calculated using

$$B = \frac{1}{\sum (p_i^2)}$$

where $p_i$ is the proportion of crabs (*C. rugosus* or *C. perlatus*) found in shells of the gastropod species I [13]. The sizes of the two sampled hermit crab species were statistically compared using Wilcoxon test.

**Fig. 2** The two co-occurring hermit crab species and the four most commonly utilized gastropod shell types. On the top, the two tested hermit crab species, *Coenobita rugosus* (**a**) and *C. perlatus* (**b**) and below the four different shell types utilized, i.e. nassariid (**c**; here depicted: *Nassarius variciferus*), naticid (**d**; here depicted *Polinices mammilla*), cerithiid (**e**; here depicted *Rhinoclavis aspera*) and strombid shells (**f**; here depicted *Gibberulus gibberulus*)

### Shell preference experiments

150 hermit crabs of each of the two species *C. rugosus* and *C. perlatus* and 150 cerithiid, nassariid, naticid and strombid shells were collected on the beaches of Naifaru, Lhaviyani (Faadhippolhu) Atoll, Republic of Maldives from 16/03 to 20/03/2017. The collected hermit crabs were transferred into the laboratory and removed from their shell. After removing the crab out of its shell, the carapace length was measured using a ruler and the size of the crab with its corresponding shell was noted.

One hermit crab (without its shell) of a given size was then transferred into a 45-cm diameter test arena, filled 2 cm with sand from the adjacent beaches, and left to acclimatise for 5 min. After acclimatisation, two of the four tested shell types, were placed next to each other on a random place inside the test arena with the aperture facing upwards. For each tested hermit crab of a given size, two empty gastropod shells were presented that were formerly inhabited by a hermit crab with the same size of the one tested in the arena (e.g. a 1 cm-sized hermit crab was offered two shells that were formerly inhabited by 1 cm-sized crabs). This procedure was conducted to ensure that both presented shells were principally utilizable for the tested hermit crab of a given size. For *C. rugosus* and *C. perlatus* each combination of two shell species (strombid vs. naticid, strombid vs. nassariid, strombid vs. cerithiid, naticid vs. nassariid, naticid vs. cerithiid, nassariid vs. cerithiid) was tested 25 times ($n = 25$). One hour after presenting the two empty gastropod shells, the utilized shell type was noted and the hermit crab together with both shells transferred back to its original habitat. If no shell had been utilized by the tested hermit crab after 1 h, the experiment was terminated and the crab, as well as both shells, excluded from the experiment and transferred back to the original habitat.

The carapace lengths between the two tested hermit crab species was statistically compared using the Wilcoxon test. Preferences for the investigated shell species, between the two hermit crab species were analysed using Fisher's exact test. Levels of significance were adjusted using Bonferroni–Holm-correction.

### Morphometric analysis of gastropod shells

Differences in the five morphometric parameters between the four different gastropod types and the two hermit crab species were compared using non-parametric multivariate analysis (PERMANOVA) with 999 permutations. One principal component analysis (PCA) was performed with log-transformed values of the five morphometric parameters. Statistical differences between the principal components of the four shell types and the two hermit crab species were analysed using ANOVA and Tukey HSD post hoc tests.

## Supplementary information

**Supplementary information** accompanies this paper at https://doi.org/10.1186/s12898-019-0268-2.

**Additional file 1: Table S1.** Gastropod species utilized by the two co-occurring hermit crab species, *C. rugosus* and *C. perlatus*, in natural populations ($N = 11$).

**Additional file 2: Table S2.** Outcome of the two-choice preference experiments. Each combination of shells was tested 25 times ($N = 25$).

**Additional file 3: Fig. S1.** Shell partitioning of the two hermit crab species. PCA calculation based on the five investigated morphometric parameters of their utilized gastropod shells. (AL: aperture length, AW: aperture width, L: length, W: width, WT: weight). Each data point represents a single shell, colours resemble the two co-occurring hermit crab species (black: *C. perlatus*, grey: *C. rugosus*).

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**Authors' contributions**
SS and CL designed the study. SS conducted the field sampling and the laboratory experiments; SS analysed the data. SS and CL wrote the manuscript. Both authors read and approved the final manuscript.

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**Availability of data and materials**
The datasets generated during this study are available from the corresponding author on reasonable request.

**Ethics approval and consent to participate**
The study was carried in accordance with the Ministry of Fisheries and Agriculture, Male', Republic of Maldives (research permit no.: (OTHR)30-D/INDIV/2017/122) and complied the fundamental principles of the Basel declaration for research in animals. The investigated species are not at risk of extinction or considered as endangered species by IUCN. No permissions other than the research permit were required from the landowners in order to sample the hermit crabs.

**Consent for publication**
Not applicable.

**Competing interests**
The authors declare that they have no competing interests.

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### References

1. Barnes DKA. Local, regional and global patterns of resource use in ecology: hermit crabs and gastropod shells as an example. Mar Ecol Prog Ser. 2003;246:211–23.
2. Birch LC. The meanings of competition. Am Nat. 1957;91:5–18.
3. Klomp H. The concepts "similar ecology" and "competition" in animal ecology. Arch Neerl Zool. 1961;14:90–102.

4. Abrams P. Shell selection and utilization in a terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards). Oecologia. 1978;34:239–53.
5. Roughgarden J. Resource partitioning among competing species—a coevolutionary approach. Theor Popul Biol. 1976;9:388–424.
6. Schoener TW. Resource partitioning in ecological communities. Science (80-). 1974;185:27–39.
7. Hardin G. The competitive exclusion principle. Science (80-). 1960;131:1292–7.
8. Gherardi F, Nardone F. The question of coexistence in hermit crabs: population ecology of a tropical intertidal assemblage. Crustaceana. 1997;70:608–29.
9. MacArthur R, Levins R. Competition, habitat selection, and character displacement in a patchy environment. PNAS. 1964;51:1207–10.
10. Vance RR. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology. 1972;53:1062–74.
11. Abrams PA. Resource partitioning and interspecific competition in a tropical hermit crab community. Oecologia. 1980;46:365–79.
12. Fotheringham N. Hermit crab shells as a limiting resource (Decapoda, Paguridea). Crustaceana. 1976;31:193–9.
13. Hazlett BA. Interspecific shell fighting in three sympatric species of hermit crabs in Hawaii. Pac Sci. 1970;24:472–82.
14. Hazlett BA. The behavioral ecology of hermit crabs. Annu Rev Ecol Syst. 1981;12:1–22.
15. Kavita J. Spatial and temporal variations in population dynamics of few key rocky intertidal macrofauna at tourism influenced intertidal shorelines. Saurashtra University; 2010.
16. Bertness MD. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana. 1981;40:197–205.
17. Borjesson DL, Szelistowski WA. Shell selection, utilization and predation in the hermit crab *Clibanarius panamensis* stimpson in a tropical mangrove estuary. J Exp Mar Biol Ecol. 1989;133:213–28.
18. Vance RR. The role of shell adequacy in behavioral interactions involving hermit crabs. Ecology. 1972;53:1075–83.
19. Völker L. Zur Gehäusewahl des Land-Einsiedlerkrebses *Coenobita scaevola* Forskal vom Roten Meer. J Exp Mar Biol Ecol. 1967;1:168–90.
20. Reese ES. Behavioral adaptations of intertidal hermit crabs. Am Sci. 1969;9:343–55.
21. Bach C, Hazlett BA, Rittschof D. Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. Ecology. 1976;57:579–86.
22. Childress JR. Behavioral ecology and fitness theory in a tropical hermit crab. Ecology. 1972;53:960–4.
23. Grant WC, Ulmer KM. Shell selection and aggressive behavior in two sympatric species of hermit crabs. Biol Bull. 1974;146:32–43. https://doi.org/10.2307/1540395.
24. Scully EP. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. J Exp Mar Biol Ecol. 1979;37:139–52.
25. Bertness MD. Shell preference and utilization patterns in littoral hermit crabs of the bay of Panama. J Exp Mar Biol Ecol. 1980;48:1–16.
26. Gherardi F, McLaughlin PA. Shallow-water hermit crabs (Crustacea: Decapoda: Anomura: Paguridea) from Mauritius and Rodrigues Islands, with the description of a new species of Calcinus. Raffles Bull Zool. 1994;42:613–56.
27. Reddy T, Biseswar R. Patterns of shell utilization in two sympatric species of hermit crabs from the Natal Coast (Decapoda, Anomura, Diogenidae). Crustaceana. 1993;65:13–24.
28. Blackstone NW. The effects of shell size and shape on growth and form in the hermit crab *Pagurus longicarpus*. Biol Bull. 1985;168:75–90.
29. Wilber TPJ, Herrnkind W. Rate of new shell acquisition by hermit crabs in a salt marsh habitat. J Crustac Biol. 1982;2:588–92.
30. Mitchell KA. Shell selection in the hermit crab *Pagurus bernhardus*. Mar Biol. 1976;35:335–43.
31. Hsu C-H, Soong K. Mechanisms causing size differences of the land hermit crab *Coenobita rugosus* among eco-islands in Southern Taiwan. PLoS ONE. 2017;12:e0174319. https://doi.org/10.1371/journal.pone.0174319.
32. Nigro KM, Hathaway SA, Wegmann AS, Miller-ter Kuile A, Fisher RN, Young HS. Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication. Restor Ecol. 2017;25:1015–25.
33. Page HM, Willason SW. Distribution patterns of terrestrial hermit crabs at Enewetak Atoll, Marshall Islands. Pac Sci. 1982;36:107–17. http://scholarspace.manoa.hawaii.edu/handle/10125/412.
34. Sallam WS, Mantelatto FL, Hanafy MH. Shell utilization by the land hermit crab *Coenobita scaevola* (Anomura, Coenobitidae) from Wadi El-Gemal, Red Sea. Belgian J Zool. 2008;138:13–9.
35. Willason SW, Page HM. Patterns of shell resource utilization by terrestrial hermit crabs at Enewetak Atoll, Marhsall Islands. Pac Sci. 1983;37:157–64.
36. Greenaway P. Terrestrial adaptations in the Anomura (Crustacea: Decapoda). Mem Mus Vic. 2003;60:13–26.
37. Kadmon R, Allouche O. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. Am Nat. 2007;170:443–54. https://doi.org/10.1086/519853.
38. McMahon BR, Burggren WW. Respiration and adaptation to the terrestrial habitat in the land hermit crab *Coenobita clypeatus*. J Exp Biol. 1979;79:265–81.
39. Morrison LW, Spiller DA. Land hermit crab (*Coenobita clypeatus*) densities and patterns of gastropod shell use on small Bahamian islands. J Biogeogr. 2006;33:314–22.
40. Barnes DKA. Hermit crabs, humans and Mozambique mangroves. Afr J Ecol. 2001;39:241–8.
41. Burggren WW, McMahon BR. Biology of the land crabs. Cambridge: Cambridge University Press; 1988.
42. Gross WJ. Water balance in anomuran land crabs on a dry atoll. Biol Bull. 1964;126:54–68.
43. Hsu C-H, Otte ML, Liu C-C, Chou J-Y, Fang W-T. What are the sympatric mechanisms for three species of terrestrial hermit crab (*Coenobita rugosus, C. brevimanus,* and *C. cavipes*) in coastal forests ? PLoS ONE. 2018;13:e0207640.
44. Vannini M. Researches on the coast of Somalia. The shore and the dune of Sar Uanle 10. Sandy beach decapods. Monit Zool Ital. 1976;8:255–86.
45. Barnes DKA. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: shell characteristics and utilisation. Mar Ecol Prog Ser. 1999;183:241–51.
46. Lively CM. A graphical model for shell-species selection by hermit crabs. Ecology. 1988;69:1233–8.
47. Bertness MD. Conflicting advantages in resource utilization: the hermit crab housing dilemma. Am Nat. 1981;118:432–7.
48. Conover MR. The importance of various shell characteristics to the shell-selection behavior of hermit crabs. J Exp Mar Biol Ecol. 1978;32:131–42.
49. Bertness MD. Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. Ecology. 1981;62:411–25. https://doi.org/10.2307/1936715.
50. Abbott RT, Dance SP. Compendium of seashells. New York: E.P. Dutton Inc.; 1983.
51. Bosch DT, Dance SP, Moolenbeek RG, Oliver PG. Seashells of Eastern Arabia. Dubai: Motivate Publishing; 1995.
52. Hogarth P, Gherardi F, McLaughlin PA. Hermit crabs (Crustacea Decapoda Anomura) of the Maldives with the description of a new species of *Catapagurus* A. Milne Edwards 1880. Trop Zool. 1998;11:149–75. https://doi.org/10.1080/03946975.1998.10539358.
53. Okutani T. Marine mollusks in Japan. Tokyo: Tokai University Press; 2000.
54. Steger J, Jambura PL, Mähnert B, Zuschin M. Diversity, size frequency distribution and trophic structure of the macromollusc fauna of Vavvaru Island (Faadhippolhu Atoll, northern Maldives). Ann des naturhistorischen Museums Wien. 2017;119:17–54.
55. Team R. R: a language and environment for statistical computing. 2013. https://www.r-project.org/.
56. Fisher RA. The logic of inductive inference. J R Stat Soc. 1935;98:39–82.
57. Oksanen J. Multivariate analysis of ecological communities in R: vegan tutorial. R Doc. 2015:43.

## Publisher's Note

**Supporting information published as supplementary material for:**

Steibl, S., & Laforsch, C. (2020) Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species. *BMC Ecology, 20*(1): 1-9.

**Supplementary table A.2-S1:** Gastropod species utilized by the two co-occurring hermit crab species, *C. rugosus* and *C. perlatus*, in natural populations (*N* = 11).

| Gastropod species | *Coenobita rugosus* | *Coenobita perlatus* |
|---|---|---|
| *Angaria rugosa* | 1 | 0 |
| *Bursa bufonia* | 4 | 0 |
| *Canarium labiatum* | 4 | 0 |
| *Canarium mutabile* | 22 | 13 |
| *Casmaria erinaceus* | 4 | 0 |
| *Casmaria ponderosa* | 5 | 0 |
| *Cerithium columna* | 27 | 19 |
| *Cerithium echinatum* | 1 | 2 |
| *Cerithium nesioticum* | 1 | 0 |
| *Cerithium nodulosum* | 13 | 0 |
| *Cerithium punctatum* | 1 | 0 |
| *Cerithium rostratum* | 5 | 2 |
| *Chicoreus* cf. *axicornis* | 2 | 0 |
| *Chicoreus* cf. *brunneus* | 1 | 1 |
| *Clypeomorus* cf. *irrorata* | 2 | 0 |
| *Columbella sp.* | 1 | 0 |
| *Coralliophila erosa* | 24 | 1 |
| *Coralliophila violacea* | 1 | 0 |
| *Cymatium gemmatum* | 1 | 0 |
| *Cymatium hepaticum* | 0 | 2 |
| *Cymatium labiosum* | 5 | 0 |
| *Cymatium mundum* | 6 | 1 |
| *Cymatium nicobarium* | 15 | 7 |
| *Drupa ricinus* | 3 | 0 |
| *Drupa rubusidaeus* | 2 | 2 |
| *Drupella* cf. *margariticola* | 29 | 6 |
| *Drupella cornus* | 13 | 4 |
| *Drupella fragum* | 1 | 0 |
| *Drupina lobata* | 4 | 2 |
| *Euplica turturina* | 1 | 0 |
| *Gibberulus gibberulus* | 51 | 36 |
| *Gutturnium muricinum* | 4 | 1 |
| *Gyrineum bituberculare* | 1 | 0 |

**Supplementary table A.2-S1** (continued)

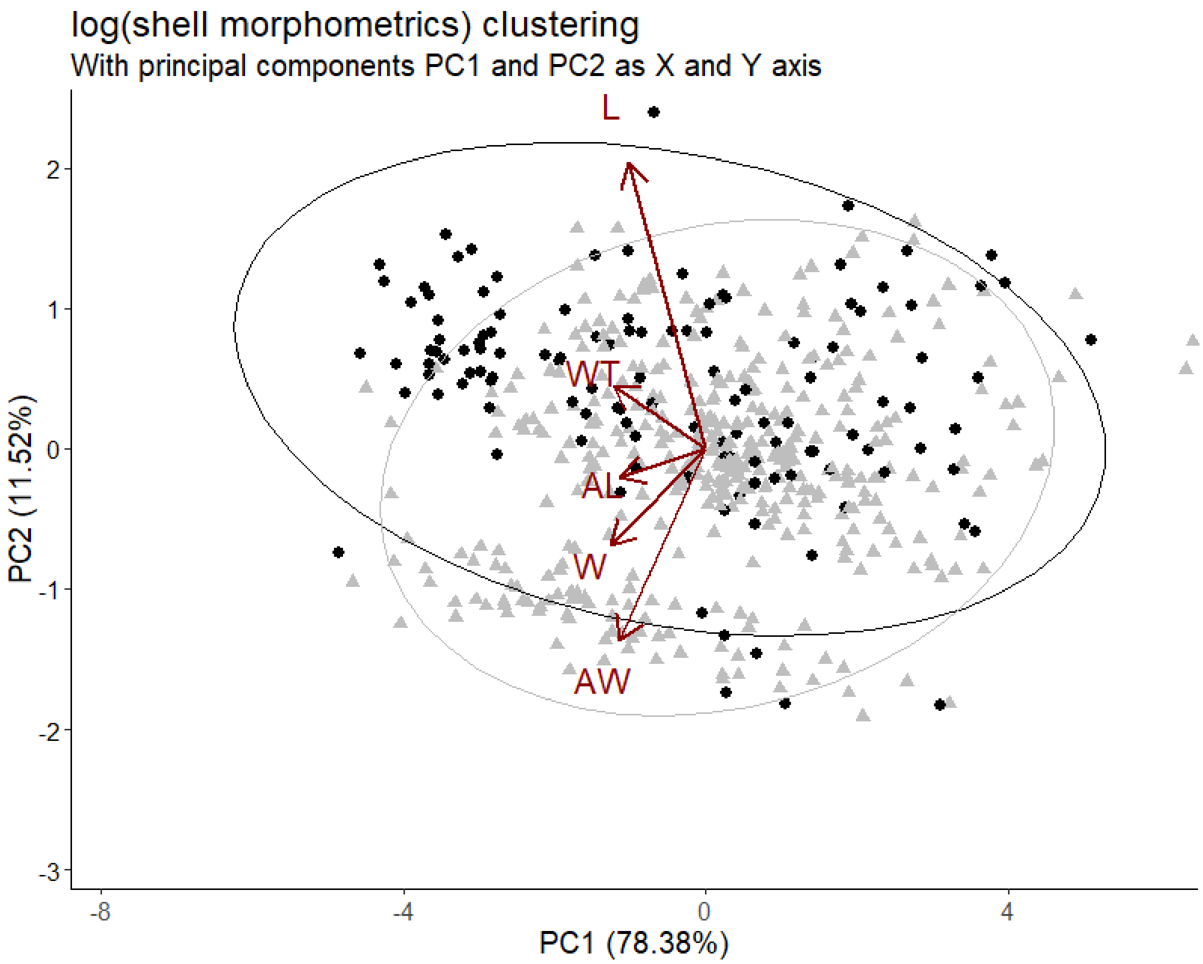
| | | |
|---|---|---|
| *Gyrineum gyrinum* | 1 | 0 |
| *Gyrineum natator* | 1 | 0 |
| *Harpa amouretta* | 1 | 1 |
| *Hemipolygona* cf. *bonnieae* | 3 | 0 |
| *Latirus polygonus* | 3 | 0 |
| *Littoraria undulata* | 4 | 1 |
| *Malea pomum* | 1 | 1 |
| *Mammilla melanostoma* | 6 | 0 |
| *Mammilla simiae* | 1 | 0 |
| *Mancinella alouina* | 7 | 0 |
| *Mancinella echinata* | 18 | 1 |
| *Mancinella echinulata* | 1 | 0 |
| *Modulus tectum* | 24 | 2 |
| *Monoplex aquatile* | 19 | 5 |
| *Monoplex* cf. *parthenopeus* | 3 | 1 |
| *Morula aspera* | 1 | 0 |
| *Myurella affinis* | 10 | 3 |
| *Nassa francolina* | 2 | 0 |
| *Nassarius* cf. *reeveanus* | 4 | 0 |
| *Nassarius distortus* | 13 | 2 |
| *Nassarius echinatus* | 24 | 6 |
| *Nassarius granifer* | 73 | 11 |
| *Nassarius horridus* | 28 | 6 |
| *Nassarius papillosus* | 7 | 0 |
| *Nassarius sp.* | 0 | 1 |
| *Nassarius variciferus* | 3 | 1 |
| *Natica vitellus* | 0 | 1 |
| *Neothais marginatra* | 1 | 0 |
| *Nerita albicilla* | 1 | 0 |
| *Nerita costata* | 7 | 1 |
| *Nerita plicata* | 0 | 1 |
| *Nerita polita* | 9 | 0 |
| *Notocochlis gualtieriana* | 1 | 0 |
| *Oxymeris felina* | 1 | 0 |
| *Oxymeris maculata* | 2 | 1 |
| *Peristernia nassatula* | 5 | 0 |
| *Peristernia ustulata* | 1 | 1 |
| *Pleuroploca* cf. *trapezium* | 2 | 0 |
| *Polinices mammilla* | 74 | 6 |
| *Polinices melanostomoides* | 1 | 0 |
| *Pollia rawsoni* | 1 | 0 |

**Supplementary table A.2-S1** (continued).

| | | |
|---|---|---|
| *Psilaxis radiatus* | 1 | 0 |
| *Rhinoclavis articulata* | 7 | 1 |
| *Rhinoclavis aspera* | 9 | 5 |
| *Rhinoclavis kochi* | 2 | 0 |
| *Rhinoclavis sinensis* | 13 | 12 |
| *Semiricinula tissoti* | 2 | 0 |
| *Tectonatica violacea* | 1 | 0 |
| *Thais sp.* | 0 | 1 |
| *Thalessa* cf. *aculeata* | 1 | 0 |
| *Thalessa virgata* | 2 | 0 |
| *Tonna allium* | 2 | 0 |
| *Tonna perdix* | 1 | 1 |
| *Trochus* cf. *kochii* | 1 | 0 |
| *Turbo argyrostomus* | 10 | 0 |
| *Turbo petholatus* | 1 | 0 |
| *Turridrupa cincta* | 1 | 1 |
| *Turris crispa* | 2 | 0 |
| *Turritriton labiosus* | 2 | 0 |
| *Vanikoro cancellata* | 1 | 0 |
| *Vexilla vexillum* | 1 | 0 |
| *Vitularia sp.* | 1 | 0 |

**Supplementary table A.2-S2: Outcome of the two-choice preference experiments.** Each combination of shells was tested 25 times (*N* = 25).

| **Pairwise comparison** | ***Coenobita rugosus*** | ***Coenobita perlatus*** |
|---|---|---|
| nassariid – naticid | 16 – 9 | 23 – 2 |
| nassariid – strombid | 18 – 7 | 13 – 12 |
| nassariid - cerithiid | 14 – 11 | 13 – 12 |
| naticid – strombid | 18 – 7 | 7 – 18 |
| naticid – cerithiid | 15 – 10 | 6 – 19 |
| cerithiid – strombid | 20 – 5 | 11 – 14 |



**Supplementary figure A.2-S1: Shell partitioning of the two hermit crab species**. PCA calculation based on the five investigated morphometric parameters of their utilized gastropod shells. (AL: aperture length, AW: aperture width, L: length, W: width, WT: weight). Each data point represents a single shell, colours resemble the two co-occurring hermit crab species (black: *C. perlatus*, grey: *C. rugosus*)

**A.3** Steibl, S., & Laforsch, C. (2019) Disentangling the environmental impact of different human disturbances: a case study on islands. *Scientific Reports, 9:* 13712.

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# Disentangling the environmental impact of different human disturbances: a case study on islands

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Sebastian Steibl & Christian Laforsch

**Coastal ecosystems suffer substantially from the worldwide population growth and its increasing land demands. A common approach to investigate anthropogenic disturbance in coastal ecosystems is to compare urbanized areas with unaffected control sites. However, the question remains whether different types of anthropogenic disturbance that are elements of an urbanized area have the same impact on beach ecosystems. By investigating small islands that are utilized for tourism, inhabited by the local population, or remained completely uninhabited, we disentangled different anthropogenic disturbances and analysed their impacts on hermit crabs as indicator species. We observed a negative impact on abundance on tourist islands and a negative impact on body size on local islands. In comparison to the uninhabited reference, both disturbances had an overall negative impact. As both forms of disturbance also impacted the underlying food resource and habitat availability differently, we propose that the findings from our study approach are valid for most obligate beach species in the same system. This demonstrates that in urbanized areas, the coastal ecosystem is not always impacted identically, which emphasizes the importance of considering the particular type of anthropogenic disturbance when planning conservation action in urbanized areas.**

Our planet faces an ever increasing number of environmental problems caused by the growth of the human population and its land demands[1]. One ecosystem that suffers substantially from population growth are coasts. Between 50% and 75% of the world's population live close to coasts[2], thereby intensifying the anthropogenic impacts on this fragile environment. Globally, sand-dominated beaches comprise 75% of the ice-free coastline[3] – and in addition to their inherent ecological value, they form a crucial component of the travel and tourism industries worldwide[4].

Many ecological studies try to identify factors that impact sandy beach ecosystems for the development of conservation measures[5]. Disruption of sand transport by coastal protection structures, sewage pollution, beach nourishment, tourism, beach cleaning, bait collecting and fishing have previously been characterized as anthropogenic disturbances with negative consequences for the beach ecosystem[3]. Under the assumption that these human activities lead to similar ecological consequences and due to the difficulty of a distinct spatial separation of single elements, a common approach to evaluate human disturbances for beach ecosystems is the comparison between urbanized areas and remote, unaffected control sites[6–8]. However, it remains unclear whether various types of anthropogenic disturbances within urbanized areas (e.g. permanent settlements, infrastructure, tourist facilities, etc.) actually have similar impacts on the environment[9]. If not, then current conservation efforts might be improvable by developing strategies that are more specifically tailored to counteract the environmental degradation of the distinct human disturbance.

To investigate this question, the present study was conducted on small coral islands which were either (I) inhabited by the local population, (II) accommodating a tourist facility, or (III) completely uninhabited. This approach guaranteed a distinct spatial separation of two different anthropogenic disturbances and enabled a comparison to ecosystems with no permanent and direct human impact.

University of Bayreuth and BayCEER, Department Animal Ecology I, Universitaetsstr. 30, D-95440, Bayreuth, Germany. Correspondence and requests for materials should be addressed to C.L. (email: christian.laforsch@uni-bayreuth.de)

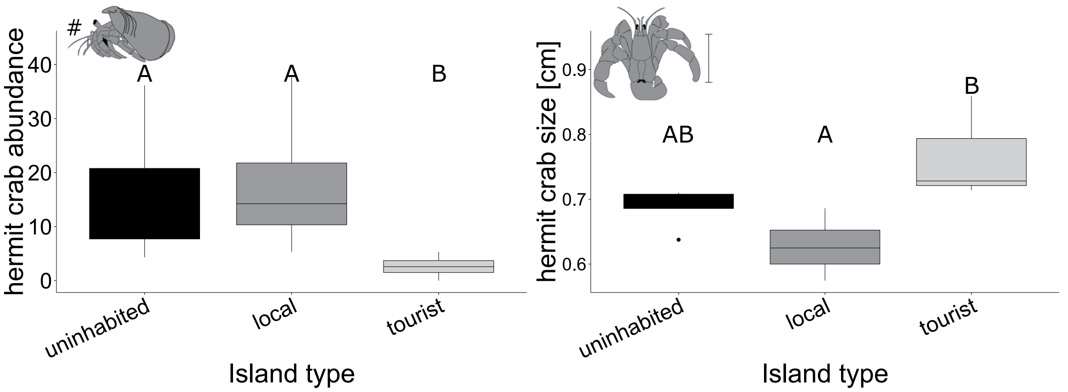

**Figure 1.** Anthropogenic impact on the abundance and size of hermit crabs. Hermit crab abundance (left) and hermit crab size (right) compared between uninhabited, local and tourist islands ($N = 4$). Significant differences between island types are indicated by different letters.

A terrestrial hermit crab community comprising two species (*Coenobita rugosus* and *C. perlatus*) was chosen as an indicator to investigate human disturbances[10]. Terrestrial hermit crabs are a crucial component in beach ecosystems that link the marine and the terrestrial food web[11]. As adult terrestrial hermit crabs are restricted to the beaches, populations on small coral islands – like most beach-associated macrofauna – cannot avoid human stressors by migration[10]. Consequently, they can be considered representative of a large number of beach-associated taxa for the purpose of examining anthropogenic disturbances.

## Results

### Impact of different human disturbance on the abundance and size of hermit crabs.

The studied organisms belonged to the only terrestrial genus of hermit crabs, *Coenobita*, and comprised *C. rugosus* and *C. perlatus*. Significant differences in the abundance and size of the investigated hermit crabs were observed between uninhabited, local and tourist islands (Fig. 1). Island type had a significant effect on the hermit crab abundance within the investigated plots (ANOVA: $N = 4$, $df = 2$, $F = 28.997$, $P < 0.001$). Significantly fewer hermit crabs were present in the plots on tourist islands than on uninhabited ($P < 0.001$) and local islands ($P < 0.001$). The abundance within the plots did not differ between uninhabited (16.25 ± 7.03 mean ± standard error) and local islands (17.87 ± 6.98; $P = 0.692$), although the availability of suitable habitats was significantly reduced on local islands, which might ultimately result in a reduced island population size on the local islands as well (see results section (c)). Furthermore, island type had a significant effect on the hermit crab size (ANOVA: $N = 4$, $df = 2$, $F = 5.764$, $P = 0.028$). On local islands, the investigated hermit crabs were significantly smaller compared to tourist islands ($P = 0.022$). No significant differences were observed between the size of hermit crabs on uninhabited (0.68 ± 0.01 cm) and on local islands (0.62 ± 0.02 cm; $P = 0.292$), nor between uninhabited and tourist islands (0.76 ± 0.04 cm; $P = 0.201$).

To elicit potential reasons for the differences in hermit crab abundance and size between the three island types, food availability, beach habitat structure and empty shell resource were investigated using NMDS (Fig. 2). The three island types differed significantly in resource and habitat (PERMANOVA: $N = 4$, $df = 2$, $F = 4.770$, $P = 0.004$). For a more detailed analysis, each parameter was further investigated specifically.

### Impact of different human disturbances on the food resource of hermit crabs.

Island type had no significant effect on the amount of organic material per m² on the beach (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 4.653$, $P = 0.097$), but calculated means suggest a non-significant tendency towards fewer organic material on tourist islands (1.14 ± 0.28 g), compared to uninhabited islands (4.63 ± 1.09 g) and local islands (2.85 ± 1.19 g).

### Impact of different human disturbances on the beach habitat structure.

The composition of the beach habitat (for categorization see methods section and Fig. S1) varied significantly between the three island types (Fig. 3): the proportion of the fine sand beach habitat on the total island's circumference was significantly different between the three island types (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 7.565$, $P = 0.022$), with a significantly higher proportion of fine sand beach on tourist islands than on local islands ($P = 0.018$). Additionally, the proportion of artificial shoreline (Kruskal-Wallis: $N = 4$, $\chi^2 = 8.459$, $P = 0.014$) and vegetation-covered beach (Kruskal-Wallis: $N = 4$, $\chi^2 = 7.461$, $P = 0.024$) was significantly altered, with a significantly higher proportion of artificial shoreline on local islands than on uninhabited islands ($P = 0.013$) and significantly fewer vegetation-covered beach on tourist islands than on uninhabited islands ($P = 0.026$). No significant differences were observed in the proportion of "fine sand with small fragments" habitat (Kruskal-Wallis: $N = 4$, $\chi^2 = 0.115$, $P = 0.944$), "fine sand with larger rock" habitat (Kruskal-Wallis: $N = 4$, $\chi^2 = 4.832$, $P = 0.089$) and "predominantly rock-covered beach" habitat (Kruskal-Wallis: $N = 4$, $\chi^2 = 5.434$, $P = 0.066$). The adjacent shore composition did not differ significantly between the three island types (Kruskal-Wallis: Seagrass: $N = 4$, $\chi^2 = 0.927$, $P = 0.629$, Seagrass and Sand: $N = 4$, $\chi^2 = 1.457$, $P = 0.483$, Sand: $N = 4$, $\chi^2 = 0.731$, $P = 0.694$, Sand and Rock: $N = 4$, $\chi^2 = 2.457$, $P = 0.293$, Rock: $N = 4$, $\chi^2 = 4.352$, $P = 0.114$).

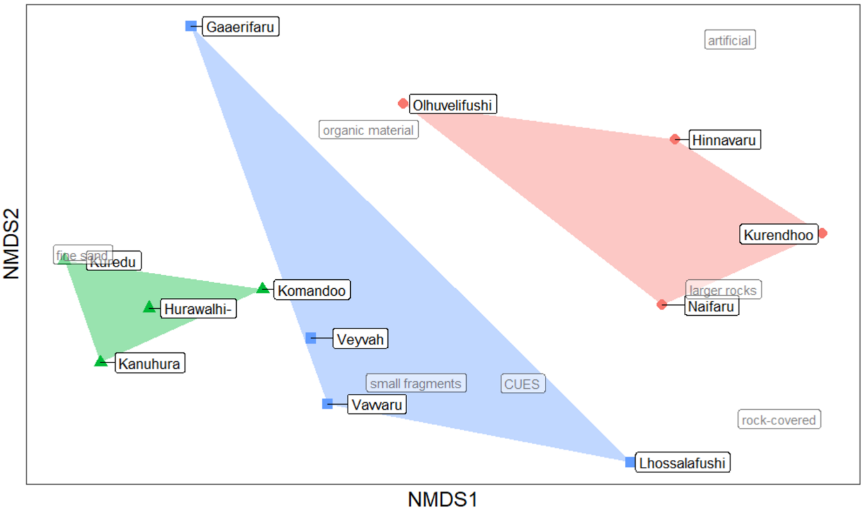

**Figure 2.** Distinctness of the three investigated island types. NMDS ordination of the investigated islands (blue squares and blue cluster area: uninhabited islands, red circles and red cluster area: local islands, green triangles and green cluster area: tourist islands) is based on the three resource and habitat parameters that influence hermit crab abundance and size (food, shell and habitat availability)). NMDS ordination thereby groups points, i.e. islands, with similar values closer together. Spatial proximity of a data point, i.e. an island, to one of the investigated parameters shows that the island is described by high values in the respective parameter.

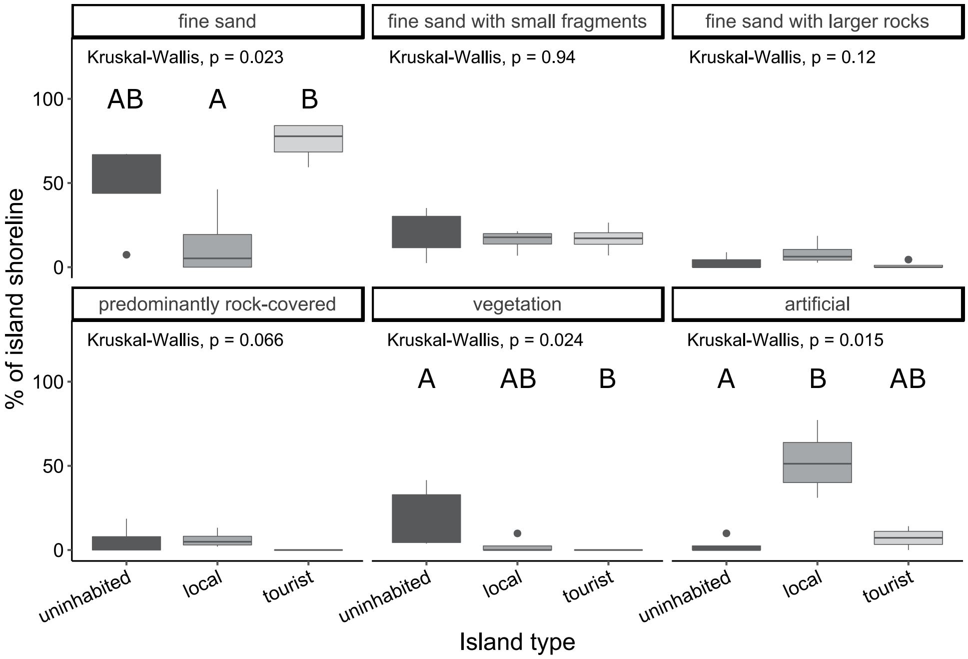

**Figure 3.** Beach habitat composition of the three island types. Proportions of each of the six categorized beach types on the three investigated island types ($N = 4$). Significant differences in the pairwise comparisons between island types are indicated by different letters.

The investigated beach habitat types had a significant effect on the hermit crab abundance (crossed fixed-factor ANOVA island type x habitat type: $N = 4$, $df = 3$, $F = 5.969$, $P = 0.001$), but beach type and island type did not interact significantly ($N = 4$, $df = 5$, $F = 0.427$, $P = 0.827$). When considering the abundance of hermit crabs in only one of the four investigated beach habitat types, island type still had a significant effect on the hermit crab abundance: the abundance of hermit crabs in the "fine sand beach" habitat differed significantly between the three island types (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 15.920$, $P < 0.001$), with significantly fewer hermit crabs in the fine sand habitat of tourist islands than in that of uninhabited islands ($P < 0.001$) and of local islands ($P = 0.035$). Island type had also a significant effect on the abundance of hermit crabs in the "fine sand with small fragments beach" habitat (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 12.501$, $P = 0.001$) with significantly fewer hermit crabs in this habitat type on tourist islands than in uninhabited islands ($P = 0.007$) and local islands ($P = 0.007$).

**Impact of different human disturbances on the shell resource of hermit crabs.** Island type had a significant effect on the overall abundance of empty shells (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 7.130$, $P = 0.028$) and on the crab-per-utilizable-empty-shell (CUES)-ratio (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 7.730$, $P = 0.020$). This CUES-ratio can be understood as a measure for the intensity of competition over the shell resource. Higher values of this ratio indicate a more severe competition, while values closer to 1 indicate that for each hermit crab a potential utilizable empty shell is readily available. The CUES-ratio was significantly smaller on tourist islands than on uninhabited islands ($P = 0.024$). On uninhabited islands, on average 10 hermit crabs competed over one shell, while on local islands only 6 hermit crabs competed over one shell. For each hermit crab on a tourist island existed on average one utilizable empty shell. Island type had a significant effect on the abundance of non-utilizable empty shells (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 6.545$, $P = 0.037$): significantly more non-utilizable empty shells were found on local islands than on uninhabited islands $P = 0.046$) and on tourist islands ($P = 0.046$), while the number of non-utilizable empty shells did not differ statistically between uninhabited and tourist islands ($P = 0.922$). To investigate the reasons for the hermit crab size differences, the shell parameter that most strongly determines hermit crab size, i.e. the aperture area of the shell (Spearman: $R^2 = 0.861$, $P < 0.001$), was analysed. The aperture area of utilized shells did not differ significantly between the three island types (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 5.303$, $P = 0.070$). The aperture area of utilizable empty shells did not differ between the three island types (Kruskal-Wallis: $N = 4$, $df = 2$, $\chi^2 = 3.803$, $P = 0.149$).

## Discussion

Numerous studies have demonstrated that coastal ecosystems are substantially altered or degraded in urbanized areas[6–8]. Due to spatial proximity, different anthropogenic disturbances impact beach ecosystems simultaneously in those areas. It is therefore difficult to disentangle the environmental impacts of different disturbances and investigate with certainty whether ecosystems respond differently to different disturbances[9]. We investigated this issue by studying small coral islands, where different anthropogenic disturbances are spatially separated. The results from our novel study approach show that these disturbances are having clear but distinct impacts on the investigated terrestrial hermit crabs. These findings, based on our study approach, should be transferable to a large number of beach-dwelling taxa, as food and habitat availability generally limit species distribution and population size[12,13].

On tourist islands, hermit crabs were significantly less abundant and significantly larger than on local islands. Compared to the uninhabited reference system, the abundance was negatively impacted on tourist islands, but did not differ compared to local islands. However, the overall population size on local islands should be considered reduced, as the availability of suitable habitats has been reduced by harbours and coastal protection structures. Therefore, different elements of urbanized areas, i.e. permanent settling or tourism, can have distinct environmental impacts on beach ecosystems.

Food, habitat availability and empty shell abundance are limiting resources for hermit crabs and might offer reasons for the observed differences between the two different land uses[12,14]. The tendency towards less organic material on tourist islands ($1.14 \pm 0.31\,\mathrm{g/m^2}$) compared to local islands ($4.26 \pm 3.43\,\mathrm{g/m^2}$) and the uninhabited reference ($4.88 \pm 1.84\,\mathrm{g/m^2}$) could be explained by beach grooming measurements, which were performed on all four studied resort islands up to four times per day (personal communication). Beach grooming is a common practice around tourist facilities and aims to remove washed-up organic material and debris from the beaches[9]. It causes a reduced food availability for the affected beach fauna, which can result in decreased population densities[15]. In concordance, on average only three hermit crabs per plot were found on the groomed beaches of the tourist islands, compared to 16 hermit crabs on average on uninhabited islands. The beach fauna on the tourist islands might also experience a higher mortality from the cleaning process, either when getting accidentally removed together with the algal material (personal observation) or when being mechanically crushed in the cleaning process, as already demonstrated for ghost crabs[16]. Hence, we hypothesize that beach cleaning is one reason for the significantly decreased abundance on islands with tourist facilities. As beach cleaning was not performed on local islands, hermit crab abundance in suitable habitats remained unaffected (average 18 hermit crabs per plot), although beaches are also used by the local population for recreational activities.

Apart from the overall availability of organic material, the beach habitat structure needs to be considered when investigating the population structure of the beach fauna[17]: compared to the structurally more complex beach habitat types, the fine sand beaches had a significantly reduced hermit crab abundance on all three island types. On tourist islands, this fine sand beach habitat accounted for 75 ± 12% of the total circumference. However, the higher proportion of the more sparsely inhabited fine sand beach cannot be held solely responsible for the reduced hermit crab abundance on tourist islands. Less than one hermit crab per plot was collected in the fine sand beach habitat of tourist islands, while on average eleven hermit crabs were present in the fine sand beach habitat on uninhabited islands. Therefore, disturbances associated with tourist facilities are probably responsible for the reduced abundance on the fine sand beaches of tourist islands. Beach nourishment, a technique where sand gets extracted from the adjacent benthic zone and deposited on the existing shoreline to extend the sandy beaches desired by tourists, is often performed to an extent where the whole natural beach shoreline becomes artificially altered to unvegetated sandy beaches[18]. This measurement can reduce the population size of the whole beach fauna[10,19,20] – especially when the beach-associated vegetation is completely removed, many beach taxa can become completely absent[10,18]. Therefore, we hypothesize that the removal of beach-associated vegetation, together with the removal of organic material caused by beach grooming and nourishment, are the main drivers for the reduced hermit crab abundance on the islands with tourist facilities.

The shoreline of local islands was differently altered and affected than that of tourist islands: the shoreline of local islands was 53 ± 21% artificially obstructed in form of concrete walls, either for harbour sites or to stabilize reclaimed land. Hence, on average only about half of the local islands shoreline formed a soft-bottom beach habitat suitable for beach-associated organisms[21]. Although the abundance in the investigated plots on local islands were similar to those on uninhabited islands, local islands as a whole, with their extensive artificial shorelines, must be considered as degraded coastal ecosystems with reduced and fragmented beach habitats[22]. In conclusion, this suggests that the total hermit crab population size of a complete local island is on average 50% smaller than the overall population size of uninhabited islands, as the constructions on local islands caused the shoreline to become widely uninhabitable for these organisms[23]. However, the hermit crab abundance within suitable beach habitats did not differ between uninhabited and local islands. This demonstrates that beach-dwelling organisms can occur in densely populated areas in the same high abundance as they do on uninhabited islands, as long as the beach habitat itself remains intact and not altered by human activities.

Besides food availability and habitat structure, shell availability is the most limiting resource for hermit crabs, as they are dependent on the input of empty gastropod shells from the adjacent coastal waters[24]. Therefore, analysing patterns in the shell resource might offer further explanations for the observed differences between the different island types.

The number of non-utilizable empty shells, like cones or cowries, can be considered as a proxy for the overall shell input of an island as these shells accumulate on the beaches without getting removed or utilized by hermit crabs[25]. The number of non-utilizable empty shells did not differ between uninhabited and tourist islands, suggesting that the overall input of the shell resource was similar on both island types. Taken together with the significantly reduced CUES-ratio on tourist islands (on average, one utilizable empty shell per hermit crab was available), neither a diminished shell input, nor high competition over the shell resource, are responsible for the significantly decreased population densities on tourist islands. A sufficient number of empty shells can result in a strong growth of a hermit crab population in a natural system[24]. This suggests that, based on the availability of the shell resource, populations on the tourist islands would have the potential to further grow, but are probably limited due to beach grooming or removal of vegetation.

On local islands however, the number of non-utilizable empty shells was on average four times higher than on uninhabited islands. Harvesting of gastropods for consumption has been shown to provide a surplus of empty gastropod shells for hermit crab populations and might be responsible for the overall increase in shells on local islands[26]. Furthermore, an overall higher gastropod population density in the adjacent coastal waters might be an additional reason for the increased empty shell abundance. This might stem from a greater food supply resulting from wastewater release[27]. This effect only occurred on the local islands, as sewage and other municipal waste is released mostly untreated into the coastal water, while tourist resorts collect the effluents in septic tanks, thereby minimizing nutrient enrichment of the adjacent waters[28].

The higher abundance of empty gastropod shells on local island beaches is beneficial for the hermit crab populations, as the limiting resource becomes largely available[29]. This is also shown by a decreased CUES-ratio on local islands, suggesting a reduced competition over the shell resource compared to the uninhabited reference. This could explain at least partially why the hermit crab abundance within the investigated plots remained unaffected on the local islands in the present study.

Although the abundance within the investigated plots was not affected negatively, the mean body size on local islands was decreased compared to tourist islands. The body size of a hermit crab correlated with the aperture area of its utilized shell. Therefore, analysing the aperture area of the utilizable empty shells might provide an explanation for the reduced body size on local islands, as the size of the aperture limits growth[30]. However, the aperture areas of both the utilized shells and the utilizable empty shells did not differ significantly between the three island types. This suggests that a lack of larger empty shells is not the main driver for the reduced body size in hermit crabs on local islands, as enough large-sized shells were available, potentially allowing the hermit crabs on the local islands to further grow. Therefore, we hypothesize that human activities on the local islands are responsible for the reduced body size: beach-dwelling decapod crustaceans, like *C. perlatus*, are widely used as fishing bait by the local fishermen[31]. They may select for bigger specimen, as they are easier to find and more suitable as fishing bait[32]. A size-selective harvesting could result in smaller body sizes on local islands, compared to uninhabited and tourist islands, where harvesting is absent[33]. A comparable human-driven size selection is already known in commercial gastropod and fish species, where intensive harvesting and fishing resulted in a shift towards smaller body size due to overexploitation of the larger-sized specimen[34,35]. In comparison, hermit crabs were significantly larger on tourist islands. This can be linked to the reduced abundance on these islands, as a smaller population size decreases intraspecific competition, which ultimately can enable organisms to grow larger[11].

Our study reveals that two elements of urbanized areas have different environmental impacts. Abundance was negatively impacted on tourist islands, whereas body size was negatively impacted on local islands. Although the abundance within the investigated plots was unaffected on local islands, it is negatively impacted on a larger scale, as about half of the shoreline consists of concrete walls for harbour sites and coastal protection and is therefore uninhabitable for all beach-dwelling organisms.

Here, it is demonstrated that the environment is not always impacted identically by the different elements of an urbanized area, but rather that the type of anthropogenic disturbance is decisive for the ecological consequence. At the same time, organisms can maintain the same population size in densely populated areas as in uninhabited ecosystems, as long as certain habitat characteristics remain unaffected. Our novel approach using small islands thereby ensured that the observed environmental impacts are attributable to only one element of an urbanized area, namely tourism or permanent settlement.

The implications of this study are beneficial for environmental protection measures, as it demonstrates the importance of disentangling various types of disturbance that stem from urbanized areas and to consider each element specifically when developing management strategies for conservation[36]. In practical terms this could mean that the prime measurement for tourist facilities is to reduce beach grooming and leave seagrass and other allochthonous material as a food resource for the beach fauna. The prime measurement for permanently colonized land on the other hand would be to minimize the obstruction of the shoreline by concrete structures and implement some regulations that leave parts of the shoreline as natural sandy beaches. These two proposed management implications to counteract two different forms of land use underline how important it is to disentangle anthropogenic disturbances. A greater understanding of how specific human actions lead to certain environmental responses, will enable us to better curtail these stressors and counteract the global loss of biodiversity and ecosystems[37].

## Methods

The research was conducted under the permission of the Ministry of Fisheries and Agriculture (Male', Maldives), permit number: (OTHR)30-D/INDIV/2017/122 and in accordance with the given guidelines and regulations.

Sampling was carried out on 12 small coral islands, all located within the Lhaviyani (Faadhippolhu) Atoll, Republic of Maldives (see Fig. S2). The islands were assigned into three categories: (I) islands that were inhabited solely by the local Maldivian population (local islands), (II) islands with a tourist resort (tourist island) and (III) islands with no permanent direct human disturbance (uninhabited islands) (see Table S1 and Fig. S3). Note that Vavvaru island is strictly speaking not a completely uninhabited island but was a former marine biology field station (Korallionlab). However, the station has closed and during its active time only inhabited three to five staff members and occasionally guest researchers. Sampling of the island's beaches was carried out from 03/02/2017 to 10/03/2017, always within 2 hours before low tide until low tide. The whole island's beachline and the adjacent shore were mapped with GPS (eTrex Vista® Cx, Garmin Ltd., Schaffhausen, Switzerland) by assigning it in the following habitat categories: artificial, vegetation-covered (i.e. inaccessible beach, covered fully by shrub vegetation), predominantly rock-covered beach, fine sand with larger rocks, fine sand with small fragments and fine sand beach for the beachline (see Fig. S1) and seagrass, seagrass & sand, sand, sand & rock, rock for the adjacent shore. The percentage of each habitat on the total circumference of each island was calculated.

Each beach was sampled in the abovementioned beach habitat types, distributed randomly over the natural shoreline of the island. The vegetation-covered beach habitat and artificial shorelines were excluded from the sampling due to their inaccessibility. To minimize a biased selection of the sampled part of the beach, the location of the plot was chosen from a distance of minimum 15 m, so that the present hermit crabs could not have been seen in advance. The sampling plots were chosen to guarantee that each present beach habitat type was sampled at least once. Additionally, the two dominant habitat types (i.e. highest percentage of the islands circumference) of every island were sampled in a second plot. When one habitat type was not present on an island or covered less than 10 m in length (i.e. the plot size), an additional plot within the dominant habitat type was sampled, resulting in a total of six plots per island.

Each plot was 10 m long and 2 m wide, measured landwards from the present drift line using a folding rule and a measuring tape. The position of every plot was documented using GPS. All hermit crabs and all empty shells within the plot were counted, collected and stored in a plastic bucket for further analysis.

To assess the amount of potential food, the organic debris in four 0.5 m × 0.5 m sub-plots (resulting in 1 $m^2$ per plot in total) within each plot was collected using forceps and stored in a plastic bag. The four sub-plots were positioned at equal distances in a diagonal manner within the plot (0 m, 3.3 m, 6.6 m and 10 m along the plot length and at distances of 1.5 m, 1.0 m, 0.5 m and 0 m from the drift line; Fig. S4). The wet weight of the organic material per plot was measured using a fine scale (TS-300 300 g × 0.01 g, G&G GmbH, Neuss, Germany).

Hermit crabs were removed from their shell by carefully heating the apex of the shell above an open flame. This is a standard procedure to remove hermit crabs from their shells and leaves the animal without injuries[38,39]. Hermit crabs were photographed on millimetre paper (Nikon D5000 mounted with Nikon AF-S Nikkor 18–105 mm, 1:3.5–5.6, Nikon Corp., Tokyo, Japan).

All shells (utilized and empty) were photographed on millimetre paper and identified using morphological identification keys[40–43]. All empty shells were assigned in two categories: (I) empty shells belonging to a gastropod species that was found to be utilized by a hermit crab and therefore considered being in general utilizable, and (II) empty shells belonging to a gastropod species, which was never found to be utilized by a hermit crab (mainly cone or cowrie shells) and therefore considered to be generally not utilizable by the investigated hermit crab species. Non-utilizable empty shells, like cowrie or cone shells, accumulate on the beaches without being ever utilized or transferred over longer distances by hermit crabs or any other beach inhabitant[25,44] and can therefore be used as a proxy for the overall shell input on the beaches.

After this procedure, the hermit crabs were transferred into a plastic bucket together with their removed shell and left to recover before being transferred back to their original beach habitat.

The size of the hermit crabs and their corresponding shell was determined using ImageJ 1.49b (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997–2015) by measuring the carapace length of the hermit crab, and the length and width of the aperture area of each shell.

The statistical analysis was carried out using R 3.5.1, extended with the "vegan" package for multivariate ecological analysis[45]. Prior to statistical analysis, abundance data was Tukey-transformed (lambda = 0.375) to meet the assumptions of normality and variance homogeneity. Where assumptions for parametric testing were violated, non-parametric Kruskal-Wallis tests were conducted. To test for differences in hermit crab abundance between the three island types (uninhabited, local, tourist islands) and account for the different habitat types on each island, univariate ANOVA with crossed fixed factors (island type x habitat type) was performed and pairwise comparisons were calculated using TukeyHSD post-hoc tests ($N = 4$). The influence of human land use on hermit crab size was analysed by calculating the mean body size for each island and statistically compare it between the three island types ($N = 4$) using ANOVA and TukeyHSD post-hoc tests. To investigate how the two different forms of human land use influence the underlying resources of hermit crabs, a non-metric multidimensional scaling (NMDS) was performed. First, the parameters "empty shell abundance", "organic material" and the proportion of the four different beach habitat types were rescaled between 0 and 1 for Bray-Curtis dissimilarity matrix calculation. Then, NMDS ordination was calculated using $k = 2$ dimensions. To test for differences in resource availability between the three island types based on the NMDS, a PERMANOVA was calculated (Bray-Curtis, 4999 permutations). Additionally, Kruskal-Wallis tests with Dunn post-hoc tests and Bonferroni corrections were performed to compare the underlying resources (i.e. organic material [g/m²], empty shell abundance, and proportion of each beach habitat type) separately between the three island types ($N = 4$). The abundance of hermit crabs within the "fine sand with larger rocks"- and the "predominantly rock-covered"-beach habitat were not compared individually between the three island types, as the "fine sand with larger rocks"-habitat occurred only on 50% of all investigated islands and the predominantly rock-covered beach was overall absent on tourist islands. To further investigate reasons for the differences in hermit crab size between the three island types, the shell parameter that correlated best with hermit crab size was identified using Spearman rank correlation test. The aperture area of the shell showed a high correlation with hermit crab body size ($R^2 = 0.861$, $P < 0.001$) and was subsequently compared for utilized and utilizable empty shells between the three island types using Kruskal-Wallis tests.

The datasets generated during this study are available from the corresponding author on reasonable request.

## References

1. Osenberg, C. W. & Schmitt, R. J. In *Detecting ecological impacts: Concepts and applications in coastal habitats* (eds Osenberg, C. W. & Schmitt, R. J.) 83–108 (Academic Press, 1996).
2. Roberts, C. M. & Hawkins, J. P. Extinction risk in the sea. *Trends Ecol. Evol.* **14**, 241–246 (1999).
3. Brown, A. C. & McLachlan, A. Sandy shore ecosystems and the threats facing them: Some predictions for the year 2025. *Environ. Conserv.* **29**, 62–77 (2002).
4. Houston, J. R. The economic value of beaches — a 2008. *update. Shore & Beach* **81**, 3–11 (2008).
5. Lercari, D. & Defeo, O. Variation of a sandy beach macrobenthic community along a human-induced environmental gradient. *Estuar. Coast. Shelf Sci.* **58**, 17–24 (2003).
6. Benedetti-Cecchi, L. *et al*. Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* **214**, 137–150 (2001).
7. Huijbers, C. M., Schlacher, T. A., Schoeman, D. S., Weston, M. A. & Connolly, R. M. Urbanisation alters processing of marine carrion on sandy beaches. *Landsc. Urban Plan.* **119**, 1–8 (2013).
8. Hereward, H. F. R., Gentle, L. K., Ray, N. D. & Sluka, R. D. Ghost crab burrow density at Watamu Marine National Park: An indicator of the impact of urbanisation and associated disturbance? *African J. Mar. Sci.* **39**, 129–133 (2017).
9. Defeo, O. *et al*. Threats to sandy beach ecosystems: a review. *Estuar. Coast. Shelf Sci.* **81**, 1–12 (2009).
10. Brook, S., Grant, A. & Bell, D. Can land crabs be used as a rapid ecosystem evaluation tool? A test using distribution and abundance of several genera from the Seychelles. *Acta Oecologica* **35**, 711–719 (2009).
11. Morrison, L. W. & Spiller, D. A. Land hermit crab (*Coenobita clypeatus*) densities and patterns of gastropod shell use on small Bahamian islands. *J. Biogeogr.* **33**, 314–322 (2006).
12. Orr, M., Zimmer, M., Jelinski, D. E. & Mews, M. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. *Ecology* **86**, 1496–1507 (2005).
13. Barboza, F. R. & Defeo, O. Global diversity patterns in sandy beach macrofauna: a biogeographic analysis. *Sci. Rep.* **5**, 1–9 (2015).
14. Fotheringham, N. Hermit crab shells as a limiting resource (Decapoda, Paguridea). *Crustaceana* **31**, 193–199 (1976).
15. Belovsky, G. E. & Slade, J. B. Dynamics of two Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition. *Oecologia* **101**, 383–396 (1995).
16. Noriega, R., Schlacher, T. A. & Smeuninx, B. Reductions in ghost crab populations reflect urbanization of beaches and dunes. *J. Coast. Res.* **28**, 123–131 (2012).
17. Lohrer, A. M., Fukui, Y., Wada, K. & Whitlatch, R. B. Structural complexity and vertical zonation of intertidal crabs, with focus on habitat requirements of the invasive asian shore crab, *Hemigrapsus sanguineus* (de Haan). *J. Exp. Mar. Bio. Ecol.* **244**, 203–217 (2000).
18. Schlacher, T. A. *et al*. Human threats to sandy beaches: A meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuar. Coast. Shelf Sci.* **169**, 56–73 (2016).
19. Davenport, J. & Davenport, J. L. The impact of tourism and personal leisure transport on coastal environments: a review. *Estuar. Coast. Shelf Sci.* **67**, 280–292 (2006).
20. Gheskiere, T., Vincx, M., Weslawski, J. M., Scapini, F. & Degraer, S. Meiofauna as descriptor of tourism-induced changes at sandy beaches. *Mar. Environ. Res.* **60**, 245–265 (2005).
21. Page, H. M. & Willason, S. W. Distribution patterns of terrestrial hermit crabs at Enewetak Atoll, Marshall Islands. *Pacific Sci.* **36**, 107–117 (1982).
22. Airoldi, L. *et al*. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coast. Eng.* **52**, 1073–1087 (2005).
23. Reese, E. S. Behavioral adaptations of intertidal hermit crabs. *Am. Sci.* **9**, 343–355 (1969).
24. Vance, R. R. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. *Ecology* **53**, 1062–1074 (1972).
25. Szabo, K. Terrestrial hermit crabs (Anomura: Coenobitidae) as taphonomic agents in circum-tropical coastal sites. *J. Archaelogical Sci.* **39**, 931–941 (2012).
26. Barnes, D. K. A., Corrie, A., Whittington, M., Carvalho, M. A. & Gell, F. Coastal shellfish resource use in the Quirimba archipelago, Mozambique. *J. Shellfish Res.* **17**, 51–58 (1998).
27. Cabral-Oliveira, J., Mendes, S., Maranhão, P. & Pardal, M. A. Effects of sewage pollution on the structure of rocky shore macroinvertebrate assemblages. *Hydrobiologia* **726**, 271–283 (2014).
28. Saeed, S. & Annandale, D. Tourism and the management of environmental impacts in the Republic of Maldives. *J. Policy Stud.* **7**, 81–88 (1999).
29. Scully, E. P. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. *J. Exp. Mar. Biol. Ecol* **37**, 139–152 (1979).
30. Hazlett, B. A. The behavioral ecology of hermit crabs. *Annu. Rev. Ecol. Syst.* **12**, 1–22 (1981).
31. Thaman, R. R., Puia, T., Tongabaea, W., Namona, A. & Fong, T. Marine biodiversity and ethnobiodiversity of Bellona (Mungiki) Island, Solomon Islands. *Singap. J. Trop. Geogr.* **31**, 70–84 (2010).
32. Fenberg, P. B. & Roy, K. Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Mol. Ecol.* **17**, 209–220 (2008).
33. Hsu, C.-H. & Soong, K. Mechanisms causing size differences of the land hermit crab *Coenobita rugosus* among eco-islands in Southern Taiwan. *PLoS One* **12**, e0174319 (2017).
34. Garcia, S. M. *et al*. Reconsidering the consequences of selective fisheries. *Science (80-.).* **335**, 1045–1048 (2012).
35. Roy, K., Collins, A. G., Becker, B. J., Begovic, E. & Engle, J. M. Anthropogenic impacts and historical decline in body size of rocky intertidal gastropods in southern California. *Ecol. Lett.* **6**, 205–211 (2003).
36. Roome, N. Developing environmental management strategies. *Bus. Strateg. Environ.* **1**, 11–24 (1992).
37. Odum, E. P. The strategy of ecosystem development. *Science (80-.).* **164**, 262–270 (1969).

38. Reddy, T. & Biseswar, R. Patterns of shell utilization in two sympatric species of hermit crabs from the Natal Coast (Decapoda, Anomura, Diogenidae). *Crustaceana* **65**, 13–24 (1993).
39. Bertness, M. D. Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. *Ecology* **62**, 411–425 (1981).
40. Bosch, D. T., Dance, S. P., Moolenbeek, R. G. & Oliver, P. G. *Seashells of Eastern Arabia*. (Motivate Publishing, 1995).
41. Abbott, R. T. & Dance, S. P. *Compendium of Seashells*. (E.P. Dutton Inc., 1983).
42. Okutani, T. *Marine Mollusks in Japan*. (Tokai University Press, 2000).
43. Steger, J., Jambura, P. L., Mähnert, B. & Zuschin, M. Diversity, size frequency distribution and trophic structure of the macromollusc fauna of Vavvaru Island (Faadhippolhu Atoll, northern Maldives). *Ann. des naturhistorischen Museums Wien* **119**, 17–54 (2017).
44. Völker, L. Zur Gehäusewahl des Land-Einsiedlerkrebses *Coenobita scaevola* Forskal vom Roten Meer. *J. Exp. Mar. Bio. Ecol.* **1**, 168–190 (1967).
45. Oksanen, J. Multivariate analysis of ecological communities in R: vegan tutorial. *R Doc*. **43** (2015).

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## Author Contributions

S.S. and C.L. designed the study. S.S. conducted the field sampling and the data analysis. S.S. and C.L. wrote the manuscript. Both authors read and approved the final manuscript.

## Additional Information

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**Supporting information published as supplementary material for:**

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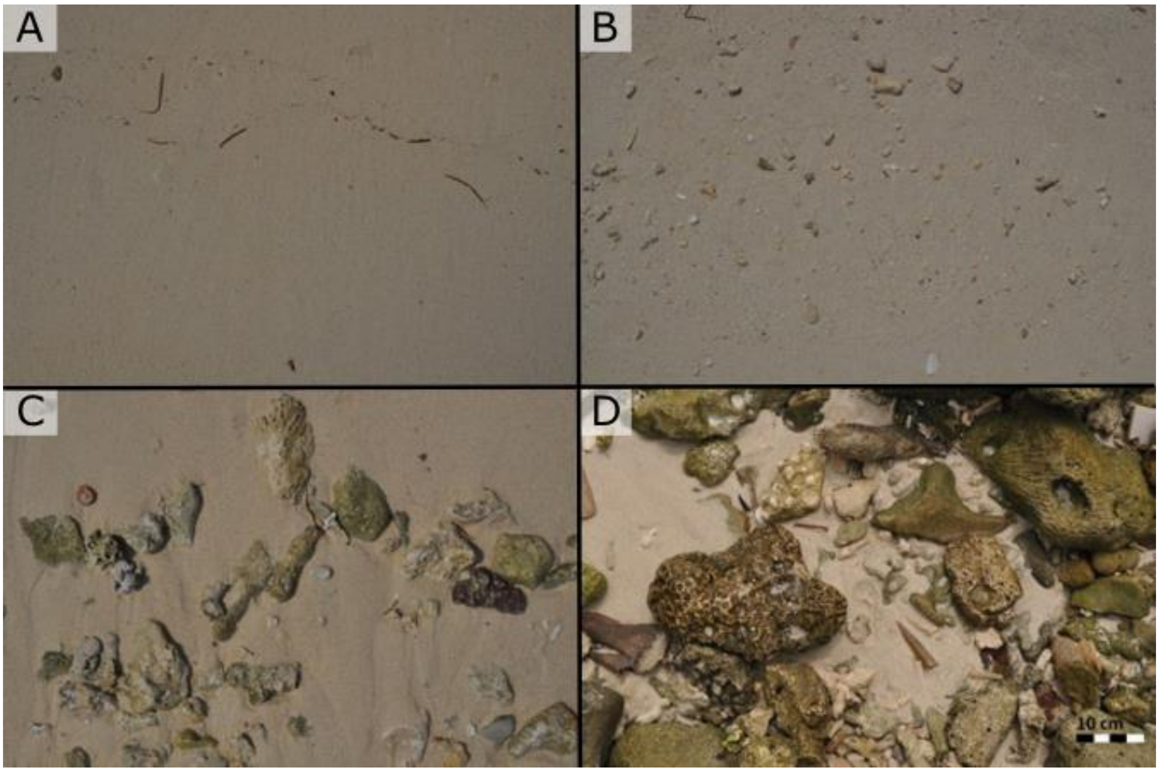
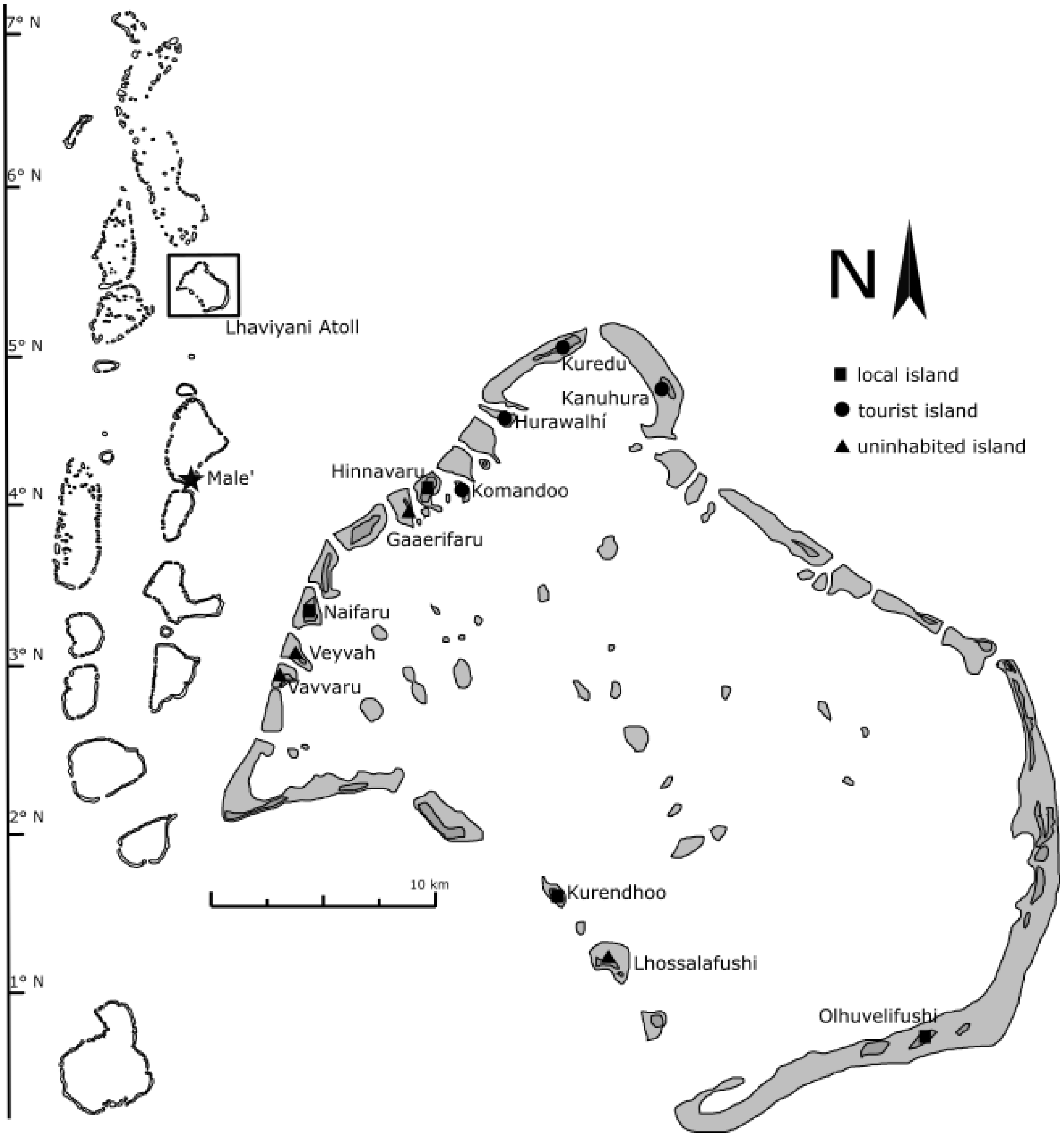
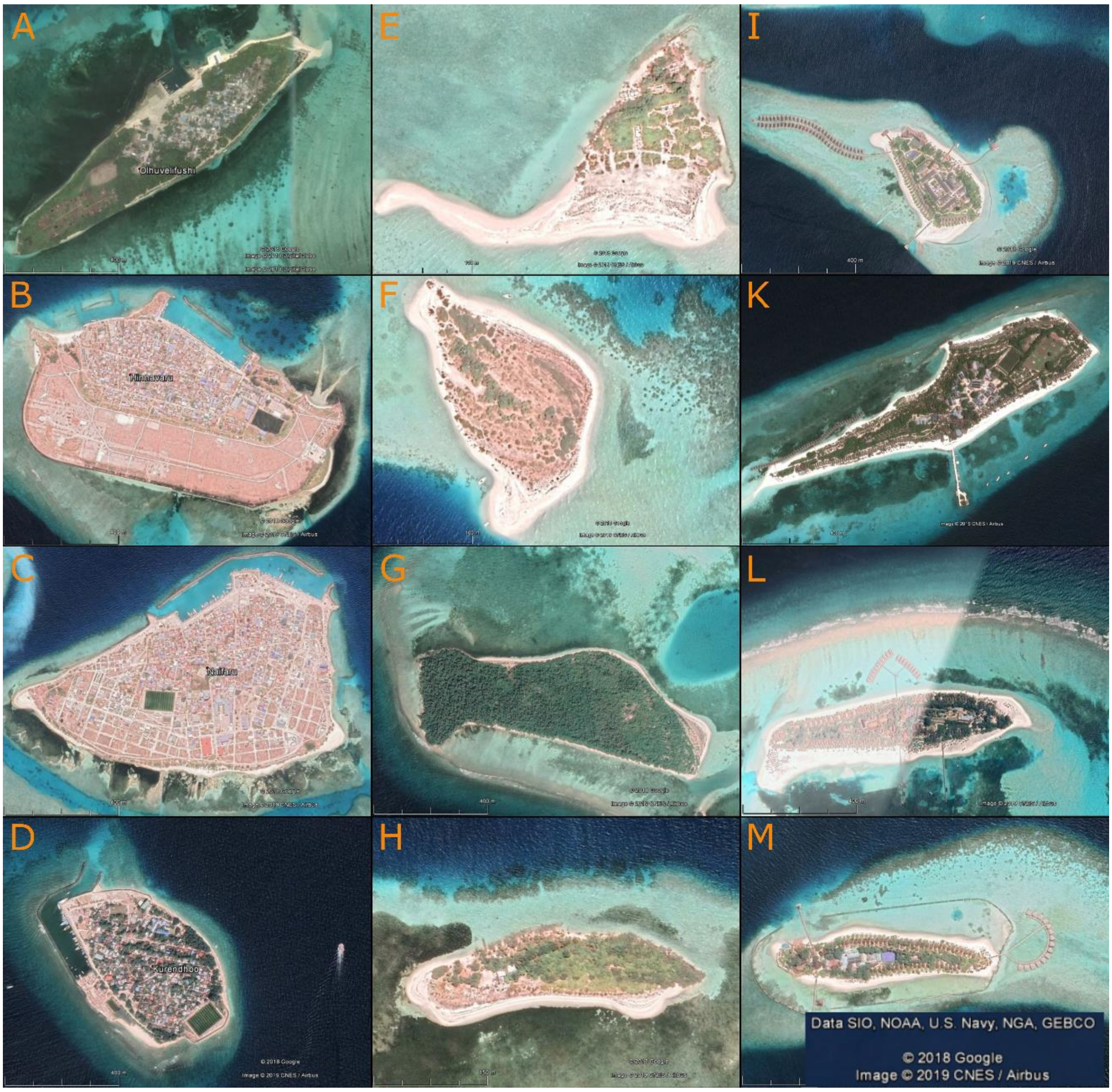


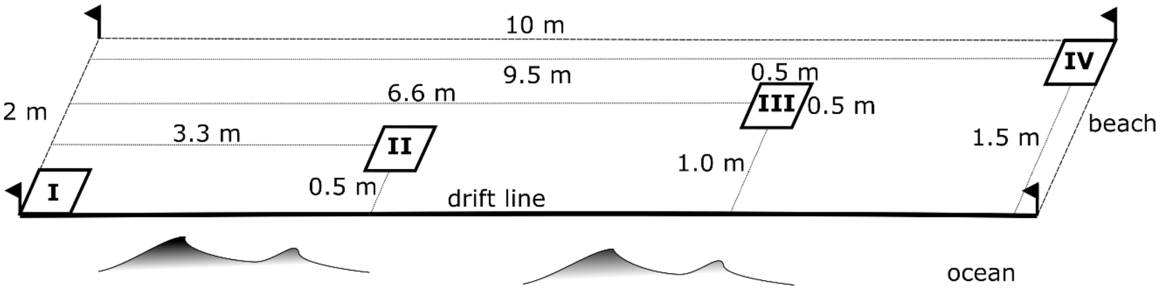
**Supplementary figure A.3-S1:** Categorized types of beaches: (1) fine sand, (2) fine sand with small fragments (3) fine sand with larger rocks, (4) predominantly rock-covered.



**Supplementary figure A.3-S2:** Location of the Lhaviyani Atoll within the Republic of Maldives shown on the left side. Detail view of the Lhaviyani Atoll with all sampled islands is shown on the right. Local islands are indicated with a square, tourist islands with a circle and uninhabited islands with a triangle (see also supplementary table A.3-S1).



**Supplementary figure A.3-S3:** Satellite images (obtained from Google Earth 7.1.5.1557; Map data: Google, CNES / Airbus 2019) of the twelve investigated islands: A-D (left column) local islands, E-H (central column) uninhabited islands, I-M (right column) tourist islands. Note that islands are not to scale. Local islands (A-D) are overall characterized by a high degree of impervious surface (such as roads, houses, harbour, etc.) and a reduced vegetation cover, except for A, where the western side of the local island was agricultural land. Tourist islands (I-M) also have housing sites (guest bungalows, restaurants, swimming pools etc.), but at the same time an overall higher degree of intact vegetation.



**Supplementary figure A.3-S4:** Schematic illustration of the sampling procedure. Each plot measured 10x2 m and was positioned along the drift line. Within each plot, all hermit crabs and empty shells were collected. To assess the amount of washed-up organic material, four sub-plots (I-IV), measuring 0.5x0.5 m each, were positioned at 0 m, 3.3 m, 6.6 m, and 9.5 m along the shoreline and 0 m, 0.5 m, 1.0 m and 1.5 m perpendicular to the shoreline.

**Supplementary table A.3-S1:** Name, type and circumference of the sampled islands, as well as the dates when sampling was conducted. All islands are located in the Lhaviyani Atoll, Republic of Maldives (see supplementary figure A.3-S2).

| Island type | Island name | Circumference | Sampling date, time of low tide |
|---|---|---|---|
| Tourist island | Kuredu | 3616 m | 04/02/2017 11:04 |
| | Hurawalhí | 1186 m | 17/02/2017 09:59 |
| | Kanuhura | 2182 m | 09/03/2017 16:12 |
| | Komandoo | 1072 m | 05/03/2017 10:24 |
| Local island | Naifaru | 3312 m | 03/02/2017 10:18 |
| | Hinnavaru | 3277 m | 19/02/2017 11:06 |
| | Olhuvelifushi | 2913 m | 08/03/2017 14:42 |
| | Kurendhoo | 1888 m | 07/03/2017 12:44 |
| Uninhabited island | Veyvah | 775 m | 18/02/2017 10:30 |
| | Vavvaru | 922 m | 06/02/2017 13:22 |
| | Gaaerifaru | 853 m | 06/03/2017 11:19 |
| | Lhossalafushi | 2480 m | 10/03/2017 17:09 |

# B. Using a community-wide study approach to investigate how biodiversity and distribution is organized and to disentangle the environmental impacts of different land uses

Ecology and Evolution

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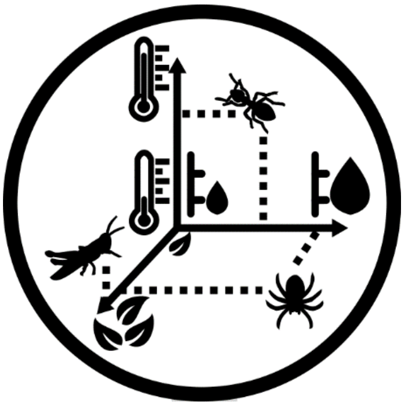

ORIGINAL RESEARCH

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# Compartmentalized organization of ecological niche occupation in insular invertebrate communities

**Sebastian Steibl** | **Christian Laforsch**

Department of Animal Ecology and BayCEER, University of Bayreuth, Bayreuth, Germany

**Correspondence**
Christian Laforsch, Department of Animal Ecology and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany.
Email: christian.laforsch@uni-bayreuth.de

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## Abstract

Understanding the mechanisms of species distribution within ecosystems is a fundamental question of ecological research. The current worldwide changes and loss of habitats associated with a decline in species richness render this topic a key element for developing mitigation strategies. Ecological niche theory is a widely accepted concept to describe species distribution along environmental gradients where each taxon occupies its own distinct set of environmental parameters, that is, its niche. Niche occupation has been described in empirical studies for different closely related taxa, like ant, ungulate, or skink species, just to name a few. However, how species assemblages of whole ecosystems across multiple taxa are structured and organized has not been investigated thoroughly, although considering all taxa of a community would be essential when analyzing realized niches. Here, we investigated the organization of niche occupation and species distribution for the whole ground-associated invertebrate community of small tropical insular ecosystems. By correlating environmental conditions with species occurrences using partial canonical correspondence analysis (pCCA), we demonstrated that the ground-associated invertebrate community does not spread evenly across the overall niche space, but instead is compartmentalized in four distinct clusters: crustacean and gastropod taxa occurred in one cluster, attributable to the beach habitat, whereas hexapods and spider taxa occurred in three distinct inland clusters, attributable to distinct inland habitats, that is, grassland, open forest, and dense forest. Within the clusters, co-occurrence pattern analysis suggested only a few negative interactions between the different taxa. By studying ground-associated insular invertebrate communities, we have shown that species distribution and niche occupation can be, similar to food webs, organized in a compartmentalized way. The compartmentalization of the niche space might thereby be a mechanism to increase ecosystem resilience, as disturbances cascade more slowly throughout the ecosystem.

KEYWORDS
ecological community, habitat, insular ecosystem, modularity, Niche clustering, niche segregation, species assemblage

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## 1 | INTRODUCTION

The central goal of ecology is to understand species interactions with the biotic and abiotic environment. In the light of growing human land demands, it becomes increasingly relevant to predict species' interactions and responses to the accelerating environmental changes (Holt, 2009). Therefore, understanding species distribution and the role of environmental variability is considered to be among the most urgent and fundamental goals for ecological research (Sutherland et al., 2013). Characterizing those factors that shape animals' distribution in a given ecosystem will ultimately protect the habitat features necessary for a species' persistence (Broennimann et al., 2012).

One of the most widely accepted concepts to describe species distribution in the environment is niche theory, originally postulated by Hutchinson in 1957 and continuously updated and extended following recent empirical research and modeling. Hutchinson (1957) stated that species distribute in the environment according to their ecological niche. A species' ecological niche is defined as the n-dimensional hypervolume that comprises all biological, chemical, and physical parameters of a heterogeneous environment in which a species can exist indefinitely. Differentiations are made between the fundamental niche of a species, which is the set of environmental conditions in which a species theoretically can live and reproduce in, and the much narrower realized niche, which contains the set of conditions that a species occupies, including its biological interactions with other species. The axes in this abstract model niche space correspond to the environmental factors that influence the organisms' performance and incorporate, in general, habitat, diet, and time (Holt, 2009; Kiszka et al., 2011).

The gradient of each environmental factor in a given ecosystem is the key determinant of niche occupation and ecosystem organization. As species distribute along the environmental gradients of an ecosystem according to their specific niche optimum, heterogeneous ecosystems have more available niche space (Schwilk & Ackerly, 2005). They can, therefore, carry an overall higher number of species (Chesson & Warner, 1981; Harner & Harper, 1976; Kadmon & Allouche, 2007). High diversity and abundance of species mean that the distance between the niche optima of different species along a fixed environmental gradient decreases, which results in an even spacing of species across the heterogeneous environment (D'Andrea & Ostling, 2016; Schwilk & Ackerly, 2005).

Simultaneously, for low-diversity systems, an increase in niche space due to heterogeneity results in potentially empty niche space allowing for more variation in the spacing of species (D'Andrea & Ostling, 2016). Especially when suitable conditions occur within a larger set of less favorable conditions, this can result in the formation of species aggregations or clusters (Fox, 1981). These clusters in niche space are formed by species that require similar environmental conditions, that is, similar niche optima, while species with different niche optima are organized in different clusters with little to no overlap (Goodman, 2007).

However, studying niche occupation and cluster formation in natural ecosystems is challenging (Darmon et al., 2012). Empirical studies have mainly focused on closely related taxa, like ants (Goldstein, 1975), dolphins (Kiszka et al., 2011), spiders (Entling et al., 2007), skinks (Goodman, 2007), ungulates (Darmon et al., 2012), scorpions (Goodman & Esposito, 2020), or peracarid crustaceans (Lastra et al., 2009), just to name a few. This gives relevant insight into the mechanisms of coexistence and differentiation between closely related taxa but generates only a limited understanding of the organization and architecture of whole faunal communities within an ecosystem. As the realized niches of species within ecosystems depend on the interactions with all other co-occurring taxa (Hutchinson, 1957), including all taxa of a given ecosystem would be essential when investigating the architecture of niches and their occupation in ecosystems.

Empirically, this can best be achieved in simple communities as they occur on islands (MacArthur & Wilson, 1967). The key advantage of insular ecosystems is that ecological processes can be observed more comprehensively than on continental, mainland ecosystems (Goldstein, 1975). Additionally, the overall smaller size, distinct boundaries formed by the adjacent ocean, and reduced species richness allow us to observe and interpret the patterns of niche occupation better and include multiple taxa (Losos & Ricklefs, 2009; MacArthur et al., 1972).

Here, we used small tropical insular ecosystems to investigate the organization of niche occupation and species distribution of the whole ground-associated faunal community. Because in the investigated system, the Maldivian archipelago, vertebrate taxa are virtually absent (except for only locally common sea birds, two species of flying foxes, two species of amphibians, and five species of reptiles), the study focused on the ground-associated invertebrate community. We hypothesized that different small tropical islands in the same region provide the overall same ecological niche space for the present ground-associated invertebrate taxa and that these taxa cluster in distinct niche patches due to the overall low diversity. We examined the relevant environmental gradients for the distribution patterns and tested whether co-occurrence patterns appear within the identified patterns indicating mechanisms of niche partitioning or competitive exclusion.

## 2 | METHODS

### 2.1 | Field sampling

All sampling was carried out between 21 February 2019 and 4 April 2019, sampling one island per day on six uninhabited tropical islands in the Lhaviyani (Faadhippolhu) Atoll, the Republic of Maldives (Figure 1). The island sizes were estimated using GPS by walking along the shoreline of each island (Garmin eTrex Vista Cx; Garmin International Inc., Olathe, USA). The six islands' circumferences were as follows: Dhidhdhoo: 2,400 m, Gaaerifaru: 862 m, Lhossalafushi: 2,610 m, Varihuraa: 645 m, Vavvaru: 855 m, and Veyvah: 706 m.

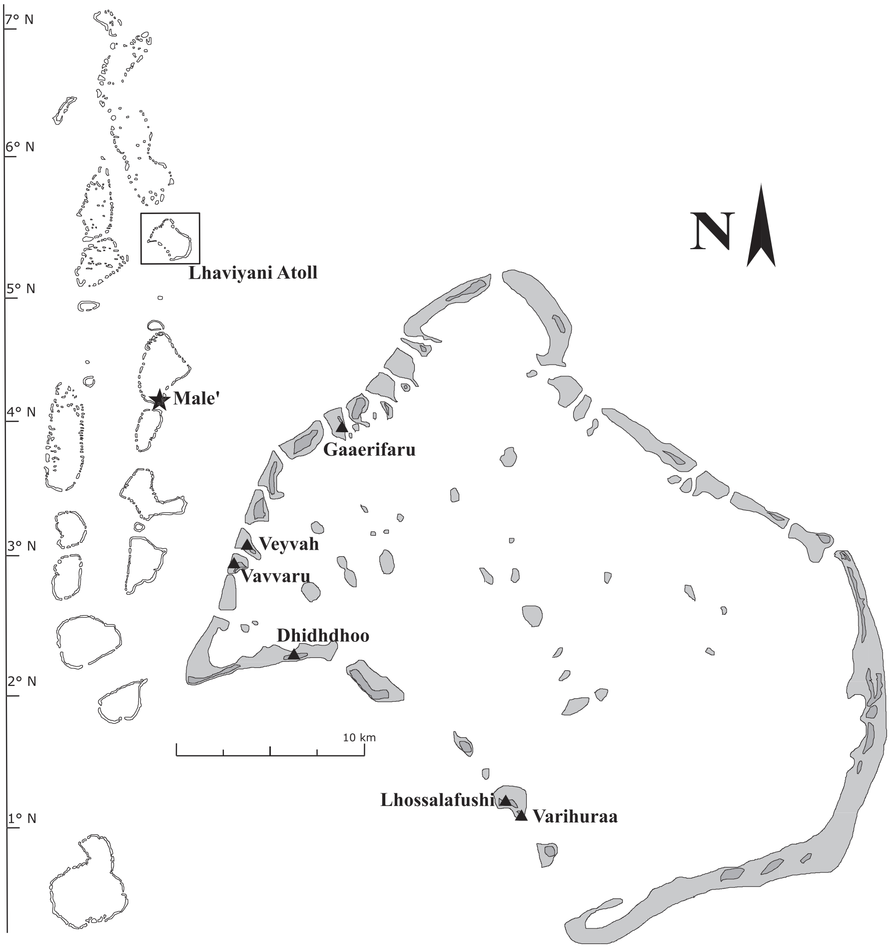


**FIGURE 1** Position of the Lhaviyani (Faadhippolhu) atoll within the Republic of the Maldives (left) and location of the sampled islands, Dhidhdhoo, Gaaerifaru, Lhossalafushi, Varihuraa, Vavvaru, and Veyvah (right). Dark gray indicates land masses, and light gray around the islands indicates the spatial extensions of the lagoons and reefs surrounding each coral island. Note that Lhossalafushi and Varihuraa are two separate islands that do not share any land bridge but have the same outer coral reef

For each sampling day, the weather conditions and the tidal range, that is, the height difference between current water level and neap tide [m], were noted. On each island, 20 1 x 1 m-plots were distributed randomly over the whole island area by placing a grid over each island's map and randomly selecting 20 sampling grids ($N = 20$). On each plot, a picture from a height of 1.80 m downwards and a picture facing skywards was taken to estimate vegetation coverage (D5000, Nikon Corp.). The exact location was marked using GPS, and the sampling time was noted. All present and visible day-active ground-associated invertebrate taxa in the plot were identified to the lowest possible taxonomic level (species or genus) using available identification literature and counted. Interstitial and soil-associated invertebrate taxa were not included in the sampling. Ghost crab abundance (*Ocyode cordimana*) was measured by counting the number of burrows within each plot (Rodrigues et al., 2016). Afterward, all debris and detritus present in the plot were collected, assigned to either of the two categories "seagrass" (i.e., leaves of *Caulerpa spp.*, *Posidonia spp.*, *Syringodium spp.*, *Thalassia spp.*), or "terrestrial" (i.e., leaves of autochthonous terrestrial plants and small deadwood), and weighed on-site using a fine scale (NTP2K 2,000 ± 0.1 g, Nohlex GmbH, Buchholz, Germany). The soil temperature was measured on the four edges of the plot at a depth of 1.4 cm using a digital precision thermometer (P300W 0–100 ± 0.5°C, Dostmann electronic GmbH, Wertheim-Reicholzheim, Germany) and averaged for each plot. The distance of the center of each plot to the nearest shoreline was measured. A soil sample from each plot was taken by scraping off the top 3 cm layer in a 10 × 10 cm area at each of the plot's four corners using a metal shovel. The soil samples were weighed and dried until no further weight reduction. When fully dried, the soil samples were weighed again and the delta value, that is, the soil water percentage, of each plot calculated. The fully dried soil samples were fractionated through a sieve combination, the weight in each fraction (6.3, 2, 0.63, 0.1 mm) was measured, and the mean grain size calculated from the proportional weights in each fraction was recorded. The percentage of grass/herb, shrub, and tree coverage was measured for each plot using ImageJ 1.49b (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997–2015).

## 2.2 | Statistical analysis

All statistical analyses were carried out using R 3.5.3 (R Core Team, 2018) extended with the "vegan" package (Anderson, 2001).

### 2.2.1 | Similarity of overall niche space (NMDS)

The islands' overall ecological niche space was compared between the investigated islands ($N = 6$) using nonmetric multidimensional scaling (NMDS). NMDS is a robust ordination technique used to compare differences in parameter compositions among multiple sites (Oksanen, 2015). Prior to NMDS analysis, the investigated physical parameters (soil temperature [°C], soil grain size [mm], seagrass detritus amount [g], terrestrial detritus amount [g], soil water content [%], grass & herb coverage [%], shrub coverage [%], tree coverage [%]) were rescaled between 0 and 1. The output of the $k = 2$ dimension NMDS representation showed high regression between ordination distances and community dissimilarities ($R^2 = 0.964$). To statistically test for differences in the physical parameter set between the investigated islands, nonparametric multivariate analysis of variances (PERMANOVA) with post hoc testing using Bray–Curtis dissimilarity indices and 4,999 permutations was performed.

### 2.2.2 | Species distribution in the niche space (pCCA)

NMDS and PERMANOVA testing indicated that the investigated islands generally provide the overall same ecological niche space ($p > .05$ for all but one pairwise comparison; see also results section). The obtained physical parameters and species abundance matrices (plot × species) were pooled over the six islands for subsequent partial canonical correspondence analysis (pCCA). This was further necessary, as calculating a separate pCCA for each island would not allow for any comparability between the islands as the loadings of the pCCA axes differ between each analysis (and hence island). The pCCA treats the physical parameter data matrix as the predictor and the plot x species abundance matrix as the response in multivariate multiple regression, where the gradient axes are constrained as linear combinations of the environmental variables (Ter Braak, 1987). An advantage of pCCA is that the effect of specific, redundant environmental parameters can be excluded, thereby allowing us to merely investigate the effects of those physical parameters that are of primary interest while controlling for other spatial between-island differences, for example, distance between systems (Reiskind et al., 2017). Abundance data were log + 1 transformed to dampen effects of dominant or very rare taxa. A pCCA was run with the plot x species abundance matrix as the response, the rescaled physical parameters (soil temperature, soil grain size, seagrass detritus amount, terrestrial detritus amount, soil water content, grass & herb coverage, shrub coverage, tree coverage, distance to the nearest shore, tidal range, rescaled to range between zero and one) as predictor variables and the spatial data (longitudinal and latitudinal position of each plot; obtained from GPS) as the conditioning variables. Variance inflation factors (VIF), which indicate collinearity between predictor variables, scored VIF < 4 for all predictors, thus showing no problematic redundancy in the variable set. Permutation tests for constrained correspondence analysis (999 permutations) were performed to test whether the pCCA model, the physical parameters (predictor variables), and the pCCA axes significantly explain the variance in the plot x species abundance matrix (response variables).

### 2.2.3 | Cluster formation within the niche space (Cluster analysis)

Permutation tests suggested that CCA1 and CCA2 significantly explain variance in the plot × species abundance matrix ($p < .05$; see also results section). Therefore, scores from the first two CCAs were used for subsequent analysis. Cluster analysis was performed using scores of CCA1 and CCA2 of each taxon to test for any underlying compartmentalized structure in niche occupation. NbClust method, which uses 30 different indices for determining the most likely number of clusters *K*, was conducted (Charrad et al., 2014). To test, whether the clusters differ statistically in their pCCA scores, we calculated the mean pCCA1 and mean pCCA2 score of each cluster by averaging all taxa scores assigned to the particular cluster. The mean pCCA scores were statistically compared between the identified clusters using ANOVA with TukeyHSD post hoc testing.

### 2.2.4 | Co-Occurrence pattern analysis

The abundance data matrix was subsequently subset into the identified clusters. For each of the clusters, an additional pCCA following the same procedure as described above was performed. To investigate patterns of co-occurrence within the identified clusters, we used the "cooccur" package (Griffith et al., 2016). Before analysis, the abundance data matrices of the identified clusters were transformed into presence–absence matrices. For all taxa pairs in each of the identified clusters, the "cooccur()" function produces probabilities of co-occurrence, which are greater or less than those observed in the sampling. To enumerate all possible species combinations within the investigated clusters, the implemented threshold that allows us to investigate only the most important associations (i.e., remove those species pairs expected to share less than one site) was used. The output of the analysis is distribution-free, and the probabilities can be considered as p-values, which indicate whether two taxa are significantly negatively or positively associated with their occurrence (for details on calculations refer to Griffith et al. (2016)).

## 3 | RESULTS

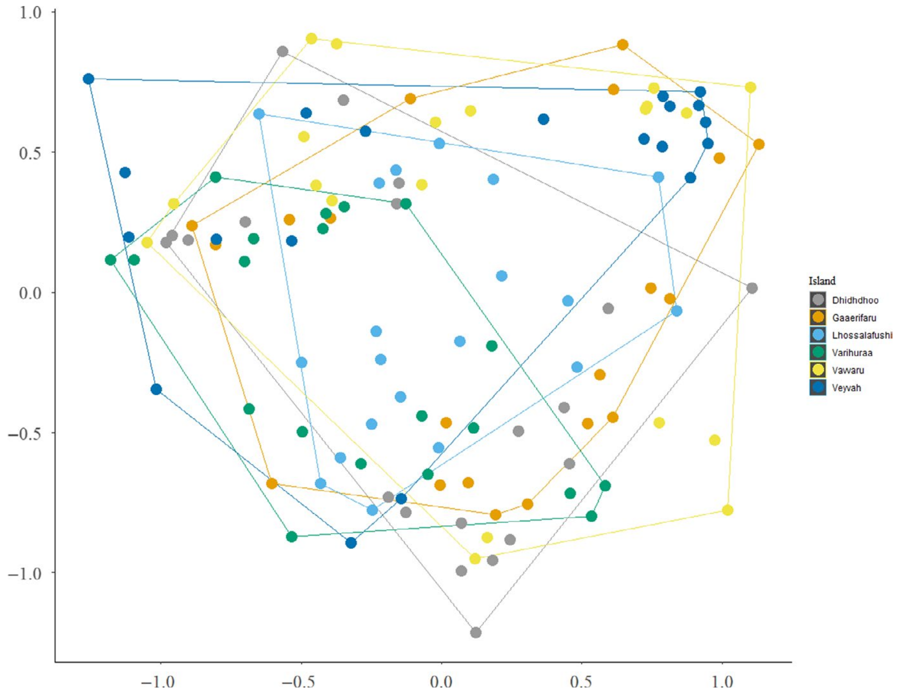
### 3.1 | Comparison of overall niche space of the investigated insular ecosystems

Overall, the six investigated tropical islands provided, in general, the same physical parameters (PERMANOVA: all pairwise comparisons $p > .05$, except Veyvah – Lhossalafushi: $F = 8.408$, $p = .015$) (Figure 2).

### 3.2 | Species distribution along the environmental parameters and cluster formation

The pCCA output revealed that the investigated physical parameters explained a significant amount of variation in the ground-associated invertebrate community (permutational test for constrained correspondence analysis: $F = 1.990$, $p < .001$) (Figure 3; for an overview of all identified taxa refer to appendix Table S1). After controlling for spatial covariables, the investigated physical parameters explained 16.06% of the overall variation in the species distribution.

**FIGURE 2** Ecological niche space provided by the investigated uninhabited coral islands ($N = 6$). Calculation of the NMDS representation of the niche space is based on normalized values for the following parameters: soil temperature, soil grain size, seagrass detritus amount, terrestrial detritus amount, soil water content, grass & herb coverage, shrub coverage, tree coverage. Each data point represents one plot ($N = 20$ per island), and different colors indicate different islands. The spatial proximity of any two data points in the NMDS representation indicates the similarity of the two plots



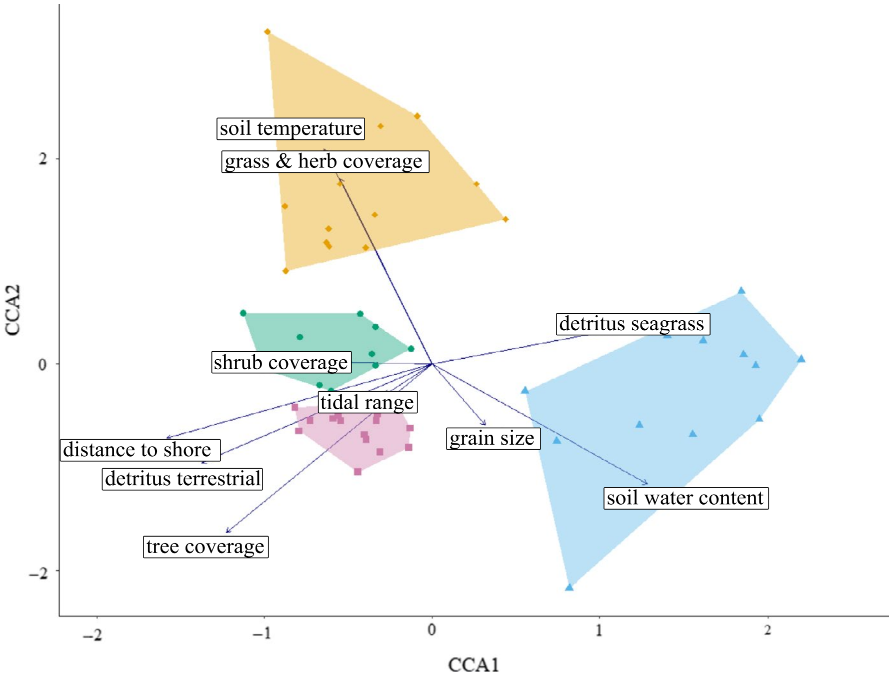


**FIGURE 3** CCA representation of the species distribution within the ecological niche space of the investigated uninhabited islands (CCA model: $F = 1.990$, $p = .001$; for details on model performance refer to Table 1). Each data point represents a single taxon within the ecological niche space, and different colors and hulls indicate the cluster assignments (NbClust method. blue: beach cluster, yellow: grassland cluster, green: open forest cluster, purple: dense forest cluster; see also Table S1 for detailed taxa identities of each cluster). The spatial proximity of any data point to a physical parameter vector indicates that this parameter influences the distribution/occurrence of the particular taxon. The vectors of physical parameters that point in the same direction indicate a positive correlation between them, and vectors that point in the opposite direction indicate a negative correlation between them

Permutational tests suggested that the first two CCAs significantly explained species distribution (CCA1: $F = 6.209$, $p < .001$; CCA2: $F = 3.298$, $p = .035$; Table 1). CCA1 thereby accounted for 31.20% of the total explained variance (eigenvalue: 0.695) and CCA2 for 16.58% (eigenvalue: 0.369). Most obtained physical parameters thereby significantly explained species distribution (Table 1).

Cluster analysis revealed that the present taxa do not spread homogenously over the provided niche space, but rather that $K = 4$ clusters occur within the niche space of the investigated islands. The four identified clusters differed significantly in their mean CCA scores (Table 2). Cluster 1, which comprises most crustacean and all molluscan taxa present on the investigated islands, showed a significantly higher mean score in CCA1 than clusters 2, 3, and 4, which comprised all hexapod and insect taxa (Tukey HSD: $p < .001$ for all pairwise comparisons). CCA1 is represented by high soil water and seagrass detritus amounts, proximity to the shoreline, as well as low tree coverage and terrestrial detritus amounts. Therefore, cluster 1 could be attributed to the beach habitat and considered the "beach cluster," as those taxa occurred in proximity to the shore and where seagrass was abundant. Cluster 4 showed a significantly higher mean score in CCA2 than clusters 1–3 (Tukey HSD: $p < .001$ for all pairwise comparisons). CCA2 is represented by high soil temperature and grass/herb coverage scores, as well as low soil water content and tree coverage. Therefore, cluster 4 can be attributed to the grassland habitat and considered the "grassland cluster," as those taxa occurred in dry areas with high grass coverage. Cluster 2 and 3 are both distinct by having low scores in CCA1 (Tukey HSD: $p = .999$), that is, occurring preferably in areas with high tree coverage and terrestrial detritus and being further inland. Cluster 2 had a significantly higher score in CCA2 than cluster 3 (Tukey HSD: $p = .004$), suggesting that taxa in cluster 2 occurred in forested areas with understory grass & herb vegetation, while taxa in cluster 3 occurred in the inland with denser tree coverage and no understory vegetation. Therefore, cluster 2 can be attributed to the open and dense forest habitats and considered the "open forest cluster" and cluster 3 the "dense forest cluster."

**TABLE 1** Summary of the pCCA output and statistical testing of the physical parameters (predictor variables) and CCA axes based on permutational tests (999 permutations)

| | Explained variance | *F*-Value | *p*-Value |
|---|---|---|---|
| Overall CCA model | - | 1.990 | .001*** |
| Tidal range | - | 1.396 | .047* |
| Shore distance | - | 3.200 | <.001*** |
| Soil temperature | - | 3.028 | <.001*** |
| Detritus seagrass | - | 1.110 | .312 |
| Detritus terrestrial | - | 2.553 | .003** |
| Soil water content | - | 2.197 | .002** |
| Grain size | - | 1.719 | .101 |
| Grass herb coverage | - | 1.814 | .030 * |
| Shrub coverage | - | 0.955 | .487 |
| Tree coverage | - | 1.923 | .005** |
| CCA1 | 31.20% | 6.209 | <.001*** |
| CCA2 | 16.58% | 3.298 | .035* |
| CCA3 | 12.02% | 2.392 | .202 |
| CCA4 | 10.04% | 1.998 | .353 |
| CCA5 | 7.51% | 1.496 | .764 |
| CCA6 | 6.43% | 1.281 | .880 |
| CCA7 | 6.19% | 1.233 | .821 |
| CCA8 | 4.64% | 0.924 | .968 |
| CCA9 | 3.24% | 0.645 | .993 |
| CCA10 | 2.11% | 0.420 | .982 |

*Note:* Asterisks indicate significance levels *0.05; **0.01; ***0.001.

**TABLE 2** The relative contribution of the investigated physical parameters (predictor variables) to CCAs and mean (± *SD*) CCA1 and CCA2 score for the four identified clusters

| | CCA1 | CCA2 |
|---|---|---|
| Tidal range | −0.112 | −0.113 |
| Shore distance | **−0.631** | −0.263 |
| Soil temperature | −0.239 | **0.820** |
| Seagrass detritus | **0.435** | 0.131 |
| Terrestrial detritus | **−0.551** | −0.352 |
| Soil water content | **0.497** | **−0.455** |
| Soil grain size | 0.122 | −0.239 |
| Grass/ herb coverage | −0.206 | **0.726** |
| Shrub coverage | −0.248 | −0.032 |
| Tree coverage | **−0.500** | **−0.605** |
| Cluster 1 (beach cluster) | 1.753 ± 0.613 (B) | −0.461 ± 1.212(AB) |
| Cluster 2 (open forest cluster) | −0.611 ± 0.376 (A) | 0.408 ± 0.320 (B) |
| Cluster 3 (dense forest cluster) | −0.601 ± 0.282 (A) | −0.878 ± 0.352 (A) |
| Cluster 4 (grassland cluster) | −0.484 ± 0.507 (A) | 2.862 ± 1.206 (C) |

*Note:* Scores in bold identify the main predictors for the respective CCA axes. Different letters after the CCA scores of the four clusters indicate significant differences in the CCAs in the pairwise comparisons of the clusters (ANOVA, Tukey HSD).

## 3.3 | Co-occurrence analysis within the identified niche compartments

To investigate differences within the four identified clusters, pCCA was performed for each cluster. The physical parameters were no longer able to describe variations in the distribution within the cluster 2, that is, "open forest cluster" ($F = 1.023$, $p = .429$), cluster 3, that is, "dense forest cluster" ($F = 0.936$, $p = .569$), and cluster 4, that is, "grassland cluster" ($F = 1.174$, $p = .162$). For cluster 1, that is, "beach cluster" the physical parameters significantly explained variations in species abundance ($F = 2.026$, $p = .006$). Permutational tests, however, suggested that none of the CCA niche axes could explain species distribution (CCA1: $F = 6.942$, $p = .076$; CCA2: $F = 5.573$, $p = .119$; CCA3: $F = 2.957$, $p = .523$; CCA4: $F = 2.332$, $p = .657$).

Analysis of the co-occurrence patterns for each of the four identified clusters suggests that significantly negative associations between species pairs occur in cluster 1 ("beach cluster"), in cluster 2 ("open forest cluster"), and cluster 3 ("dense forest cluster") (Table 3, Figure 4). A significant positive association was identified between species pairs in cluster 3 ("dense forest cluster"), that is, a cockroach (*Balta sp.*), woodlice (*Cubaris sp.*), and a carpenter spider (*Crassopriza lyoni*), as well as a beetle species (*Elasmolomus pallens*) and a bug (*Dysdercus cingulatus*) (Figure 4c). No significant positive or negative association between any taxon pair was found in cluster 4 ("grassland cluster").

## 4 | DISCUSSION

Most previous empirical studies on niche occupation focused on closely related taxa and did not explicitly consider the entire community. Here, we studied the structure and occupation of the ecological niche space of the entire ground-associated invertebrate community on small tropical atoll islands in the Indo-Pacific. Analysis of the occupied ecological niche space suggested that the investigated taxa

**TABLE 3** Summary of the co-occurrence analysis of taxa within the four identified clusters

| | Cluster 1 (Beach) | Cluster 2 (Open Forest) | Cluster 3 (Dense Forest) | Cluster 4 (Grassland) |
|---|---|---|---|---|
| Positive associations | 0 | 0 | 3 | 0 |
| Negative associations | 16 | 5 | 28 | 0 |
| Random associations | 75 | 61 | 122 | 78 |
| Nonrandom associations | 18.7% | 7.6% | 20.3% | 0% |

*Note:* Associations were determined as "random" when pairs did not differ significantly from the expected number of co-occurrences and deviated <10% of the total number of sites.

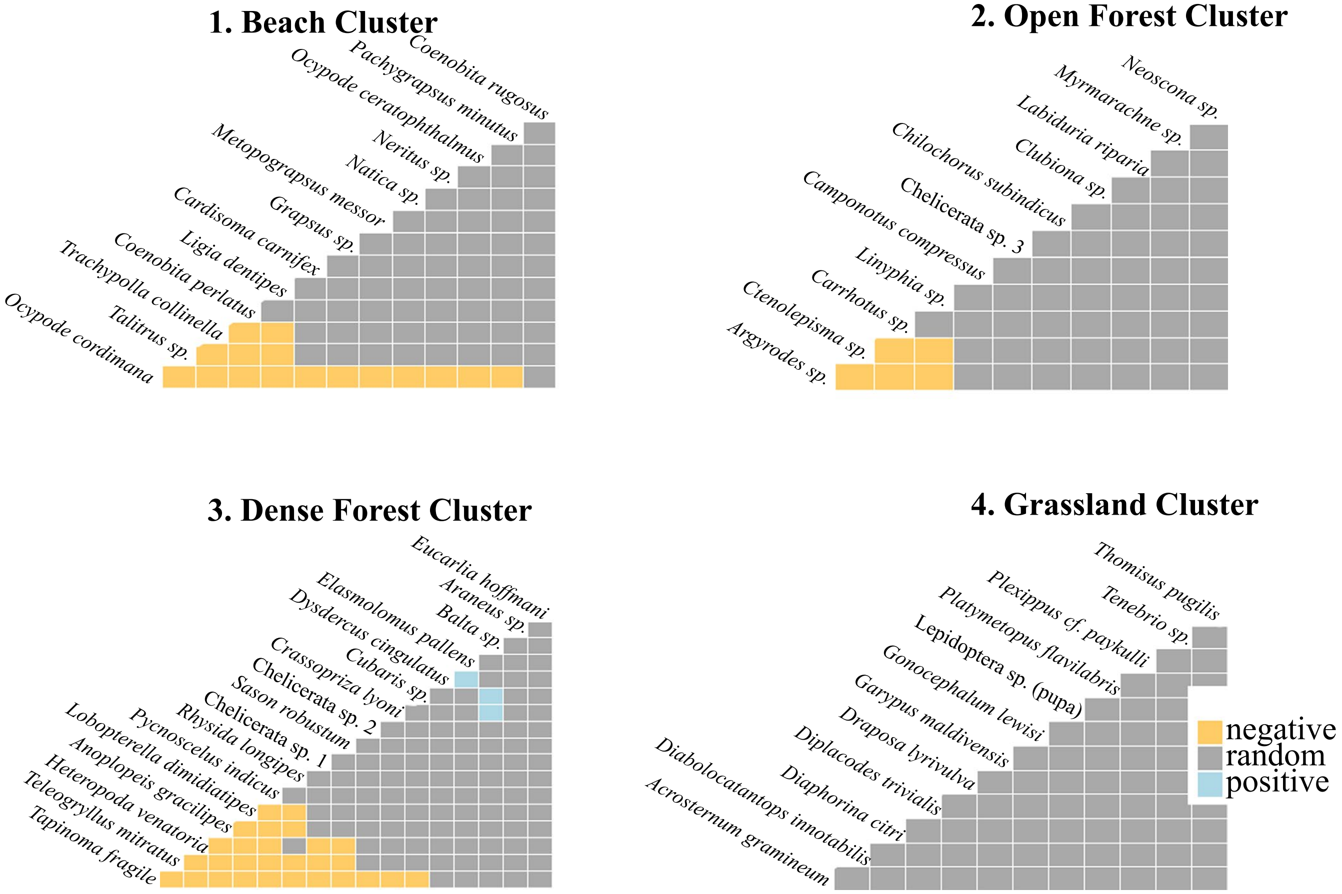


**FIGURE 4** Co-occurrence pattern analysis within the four identified clusters 1–4 (see also Table S1). Negative association, that is, occurrence of taxon 1 excludes taxon 2, between two taxa pairs indicated by yellow rectangles, positive co-occurrence, that is, occurrence of taxon 1 favors occurrence of taxon 2, indicated by blue rectangles and random co-occurrence, that is, no significant positive or negative association between two taxa, by gray rectangles

do not spread evenly over the provided niche space, but instead aggregated in four distinct clusters within the overall niche space, attributable to habitats within the low-lying atoll insular ecosystem, that is, beach, grassland, open forest, and dense forest. The majority (~85%) of all associations between taxa pairs within each cluster showed no negative interactions, indicating that neither mechanisms of competitive exclusion nor contrasting habitat preferences dominate the interactions within the clusters. In contrast, only a few taxa appear to be positively or negatively associated with one another.

Abiotic (i.e., tidal range, shore distance, soil temperature, soil water content) and biotic (i.e., terrestrial detritus, grass & herb coverage, tree coverage) parameters significantly influenced the distribution of the ground-associated invertebrate community on the investigated low-lying atoll islands in the Indo-Pacific. The same set of parameters influenced animals' occurrences across multiple taxa, demonstrating that the factors and mechanisms that cause niche occupation and differentiation are consistent not only within closely related taxa as shown, for instance, in spiders (Entling et al., 2007), ungulates (Darmon et al., 2012), or dolphins (Kiszka et al., 2011) but also across species assemblages of whole insular invertebrate communities. Although a high proportion of variation in species occurrence remained unexplained in the conducted pCCA model in this study, the investigated environmental parameters were able to significantly explain species distribution over a wide range of unrelated taxa and indicate clustering mechanisms within the available niche space. Our data indicate that the major environmental parameters (e.g., temperature, humidity, vegetation cover, etc.) only contribute to a small proportion of the overall occurrence patterns of faunal communities, that is, roughly 16%. Trophic relationships, inter- and intraspecific competition, or pure stochasticity could, therefore, be equally or even more relevant determinants of insular invertebrate community assemblages than environmental parameters.

According to Hutchinsons (1957) original postulations on ecological niches, the present study confirmed that niche differences are essential in structuring the occurrence of closely related taxa and whole invertebrate communities. Faunal communities on remote and low-lying tropical atolls islands are dependent on various physical and chemical parameters, type of vegetation cover, and distance to the shoreline. However, the analyzed taxa did not spread evenly across the overall ecological niche space, but instead aggregated in four distinct clusters, that is, beach, grassland, open forest, and dense forest. This clustering into distinct habitats might be a crucial mechanism that allows coexistence, even in small and remote insular ecosystems with overall limited space (Chesson, 2000; Goodman, 2007). The clustering could further be favored by the overall low diversity in these remote and low-lying atoll insular ecosystems because low-diversity systems offer relatively more available niche space to each species (D'Andrea & Ostling, 2016; Fox, 1981).

A conspicuous feature of the clustering within the niche space in our study is that most identified crustacean and all molluscan taxa occurred exclusively in the beach cluster, whereas most hexapods and all spider taxa only occurred in the three inland clusters, that is, grassland, open forest, and dense forest. Both observations might be caused by niche conservatism, where the realized ecological niches of related taxa remain similar due to only a slow evolution of niche occupation and differentiation (Peterson et al., 1999; Wiens et al., 2010). As beach-associated crustaceans colonized the terrestrial environment from the adjacent ocean and are still closely associated to the shoreline in parts of their life cycle, for example, for reproduction, many of their adaptations, for example, returning to the shore for spawning, are conserved across different taxa (Bliss & Mantel, 1968; Greenaway, 2003; Harzsch et al., 2011; Taylor, 1988). For hexapod and spider taxa in the inland clusters, adaptations to terrestrial life in the inland might hinder distribution and differentiation into the beach habitat, as conditions require specific adaptations to withstand, for example, heat, high soil water content, or soil salinity on the beaches (Defeo & McLachlan, 2005). Therefore, niche conservatism might explain why closely related taxa clustered within the niche space and did not spread randomly over all four clusters.

Within each of the four identified clusters, the respective taxa overlapped in their occurrence and co-occurrence pattern analysis within each cluster indicated that the majority of taxa (85% of all pairwise comparisons) co-occur without any negative associations, like competitive exclusion or contrasting habitat preferences (Griffith et al., 2016). Co-occurrence can be achieved when resources are abundant and not limiting (Darmon et al., 2012; Fox, 1981). In the investigated tropical insular ecosystem in the Indo-Pacific, sufficient resource availability inland is ensured by the high annual precipitation that enhances primary production and biomass (Gischler et al., 2014; Rosenzweig, 1968). On the beach, allochthonous subsidies from the adjacent ocean provide a constant and reliable nutrient input for the beach-dwelling taxa (Paetzold et al., 2008; Stapp & Polis, 2003). In the open forest cluster, most of the co-occurring taxa with neither positive nor negative associations to any other taxa where predatory spiders (*Myrmarachne sp.*, *Clubiona sp.*, *Neoscona sp.*, *Linyphia sp. Carrhotus sp.*, and one unidentified spider species "Chelicerata sp. 3"). When the abundance of their herbivorous prey taxa is sufficiently high, different spiders can overlap in their occurrences without apparent interspecific competition or competitive exclusion (Chesson, 2000).

Negative coassociations were observed within the open forest (7% of all pairwise associations), dense forest (18% of all pairwise associations), and the beach cluster (17% of all pairwise associations). For example, in the beach cluster, the presence of the predatory ghost crab *O. cordimana*, a known predator of other crustaceans like *Coenobita spp.*, excluded other beach-associated organisms from the plots, as they avoid this predatory crab (Burggren & McMahon, 1988; Pringle et al., 2019). In the dense forest cluster, the ant *Tapinoma fragile* excluded several hexapods, including predatory spider taxa, a phenomenon already demonstrated in controlled manipulation experiments for other ant species (Mestre et al., 2016).

The combination of ecological niche and co-occurrence pattern analysis for the investigation of species distribution within tropical atoll insular ecosystems of the Indo-Pacific region revealed multiple mechanisms and levels of organization and structuring (Fox, 1981):

Within the insular habitats, the different taxa co-occur and this co-occurrence is likely stabilized via a high availability of resources or a fine-scale niche differentiation not detectable in the current sampling approach, for example, differences in shell resource use of the two present hermit crab species (Chesson & Warner, 1981; Darmon et al., 2012; Steibl & Laforsch, 2020). The overall distribution of species within the insular ecosystem is, however, organized in a compartmentalized way. Comparable compartmentalization has already been established for pollination networks or food webs, where compartmentalization increases overall ecosystem resilience, as disturbances spread more slowly throughout the system and between different compartments (Bastolla et al., 2009; Olesen et al., 2007; Pimm & Lawton, 1980; Tylianakis et al., 2010). Similarly, compartmentalization of niche space might be a mechanism that enhances the resilience of the ground-associated invertebrate community, as, for example, environmental changes in vegetation cover or seagrass deposition only affect single compartments of the insular ecosystem rather than the whole community.

As the basic mechanisms of ecological organization are in general transferable from simple, that is, insular, to more complex, that is, mainland terrestrial, ecosystems (Goldstein, 1975), we suggest that our results on the organization and architecture of niche space on atoll insular ecosystems of the Indo-Pacific region could be transferable to a wider range of terrestrial insular or mainland ecosystems. As a compartmentalized architecture is known to increase ecosystem resilience (Olesen et al., 2007), it is conceivable that niche compartmentalization might also be a more widespread phenomenon that benefits the stability of different ecosystems than previously thought.

Our findings have further important implications for ecosystem conservation. It would be relevant in future impact assessments to first identify the clusters in niche occupation of a given ecosystem and to develop specifically tailored protective measurements to conserve each cluster with its unique assembly of species. Only in this way can a conservation action plan guarantee the overall stability and protection of all organisms in an ecosystem rather than protecting just some compartments of the faunal community.

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## CONFLICT OF INTEREST

The authors declare no conflicting interests.

## AUTHOR CONTRIBUTION

**Sebastian Steibl:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Christian Laforsch:** Data curation (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing-review & editing (equal).

## DATA AVAILABILITY STATEMENT

Raw data and statistical code can be accessed via Dryad Digital Repository (https://doi.org/10.5061/dryad.63xsj3v18).

## ORCID

*Sebastian Steibl* https://orcid.org/0000-0003-4819-8581
*Christian Laforsch* https://orcid.org/0000-0002-5889-4647

## REFERENCES

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46.

Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, *458*, 1018–1020. https://doi.org/10.1038/nature07950

Bliss, D. E., & Mantel, L. H. (1968). Adaptations of crustaceans to land: A summary and analysis of new findings. *American Zoologist*, *8*, 673–685. https://doi.org/10.1093/icb/8.3.673

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H., & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Burggren, W. W., & McMahon, B. R. (1988). *Biology of the land crabs*. Page (W. W. Burggren, & B. R. McMahon, Eds.). Cambridge University Press.

Charrad, M., Ghazzali, N., Boiteau, V., & Niknafs, A. (2014). NbClust : An R package for determining the relevant number of clusters in a data set. *Journal of Statistical Software*, *61*, 1–36.

Chesson, P. L. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chesson, P. L., & Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, *117*, 923–943. https://doi.org/10.1086/283778

D'Andrea, R., & Ostling, A. (2016). Challenges in linking trait patterns to niche differentiation. *Oikos*, *125*, 1369–1385. https://doi.org/10.1111/oik.02979

Darmon, G., Calenge, C., Loison, A., Jullien, J.-M., Maillard, D., & Lopez, J.-F. (2012). Spatial distribution and habitat selection in coexisting species of mountain ungulates. *Ecography*, *35*, 44–53. https://doi.org/10.1111/j.1600-0587.2011.06664.x

Defeo, O., & McLachlan, A. (2005). Patterns, processes and regulatory mechanisms in sandy beach macrofauna: A multi-scale analysis. *Marine Ecology Progress Series*, *295*, 1–20. https://doi.org/10.3354/meps295001

Entling, W., Schmidt, M. H., Bacher, S., Brandl, R., & Nentwig, W. (2007). Niche properties of Central European spiders: Shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography*, *16*, 440–448. https://doi.org/10.1111/j.1466-8238.2006.00305.x

Fox, B. J. (1981). Niche parameters and species richness. *Ecology*, *62*, 1415–1425. https://doi.org/10.2307/1941497

Gischler, E., Storz, D., & Schmitt, D. (2014). Sizes, shapes, and patterns of coral reefs in the Maldives, Indian Ocean: The influence of wind, storms, and precipitation on a major tropical carbonate platform. *Carbonates and Evaporites*, *29*, 73–87. https://doi.org/10.1007/s13146-013-0176-z

Goldstein, E. L. (1975). Island biogeography of ants. *Evolution*, *29*, 750–762. https://doi.org/10.1111/j.1558-5646.1975.tb00869.x

Goodman, A., & Esposito, L. (2020). Niche partitioning in congeneric scorpions. *Invertebrate Biology*, *139*(1), 1–9. https://doi.org/10.1111/ivb.12280

Goodman, B. A. (2007). Microhabitat separation and niche overlap among five assemblages of tropical skinks. *Australian Journal of Zoology*, *55*, 15. https://doi.org/10.1071/ZO06066

Greenaway, P. (2003). Terrestrial adaptations in the Anomura (Crustacea: Decapoda). *Memoirs of Museum Victoria*, *60*, 13–26.

Griffith, D. M., Veech, J. A., & Marsh, C. J. (2016). cooccur: Probabilistic species co-occurrence analysis in R. *Journal of Statistical Software*, *69*, 1–17.

Harner, R. F., & Harper, K. T. (1976). The role of area, heterogeneity, and favorability in plant species diversity of Pinyon-Juniper ecosystems. *Ecology*, *57*, 1254–1263. https://doi.org/10.2307/1935049

Harzsch, S., Rieger, V., Krieger, J., Seefluth, F., Strausfeld, N. J., & Hansson, B. S. (2011). Transition from marine to terrestrial ecologies: Changes in olfactory and tritocerebral neuropils in land-living isopods. *Arthropod Structure & Development*, *40*, 244–257. https://doi.org/10.1016/j.asd.2011.03.002

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, *106*, 19659–19665. https://doi.org/10.1073/pnas.0905137106

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Kadmon, R., & Allouche, O. (2007). Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: A unification of island biogeography and niche theory. *The American Naturalist*, *170*, 443–454. https://doi.org/10.1086/519853

Kiszka, J., Simon-Bouhet, B., Martinez, L., Pusineri, C., Richard, P., & Ridoux, V. (2011). Ecological niche segregation within a community of sympatric dolphins around a tropical island. *Marine Ecology Progress Series*, *433*, 273–288. https://doi.org/10.3354/meps09165

Lastra, M., Schlacher, T. A., & Olabarria, C. (2009). Niche segregation in sandy beach animals: An analysis with surface-active peracarid crustaceans on the Atlantic coast of Spain. *Marine Biology*, *157*, 613–625. https://doi.org/10.1007/s00227-009-1346-3

Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, *457*, 830–836. https://doi.org/10.1038/nature07893

MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, *53*, 330–342. https://doi.org/10.2307/1934090

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.

Mestre, L., Piñol, J., Barrientos, J. A., & Espadaler, X. (2016). Differential ant exclusion from canopies shows contrasting top-down effects on community structure. *Oecologia*, *180*, 193–203. https://doi.org/10.1007/s00442-015-3442-z

Oksanen, J. (2015). Multivariate analysis of ecological communities in R: vegan tutorial. R documentation:43

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Paetzold, A., Lee, M., & Post, D. M. (2008). Marine resource flows to terrestrial arthropod predators on a temperate island: The role of subsidies between systems of similar productivity. *Oecologia*, *157*, 653–659. https://doi.org/10.1007/s00442-008-1098-7

Peterson, A. T., Soberón, J., & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, *285*, 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Pimm, S. L., & Lawton, J. H. (1980). Are food webs divided into compartments? *Journal of Animal Ecology*, *49*, 879–898. https://doi.org/10.2307/4233

Pringle, R. M., Kartzinel, T. R., Palmer, T. M., Thurman, T. J., Fox-Dobbs, K., Xu, C. C. Y., Hutchinson, M. C., Coverdale, T. C., Daskin, J. H., Evangelista, D. A., Gotanda, K. M., A. Man in 't Veld, N., Wegener, J. E., Kolbe, J. J., Schoener, T. W., Spiller, D. A., Losos, J. B., & Barrett, R. D. H. (2019). Predator-induced collapse of niche structure and species coexistence. *Nature*, *570*, 58–64. https://doi.org/10.1038/s41586-019-1264-6

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reiskind, M. H., Griffin, R. H., Janairo, M. S., & Hopperstad, K. A. (2017). Mosquitoes of field and forest: The scale of habitat segregation in a diverse mosquito assemblage. *Medical and Veterinary Entomology*, *31*, 44–54.

Rodrigues, E., Freitas, R., Delgado, N. de C., & Soares-Gomes, A. (2016). Distribution patterns of the ghost crab *Ocypode cursor* on sandy beaches of a tropical island in the Cabo Verde archipelago, Eastern Central Atlantic. *African Journal of Marine Science*, *38*, 181–188.

Rosenzweig, M. L. (1968). Net primary productivity of terrestrial communities: Prediction from climatological data. *The American Naturalist*, *102*, 67–74. https://doi.org/10.1086/282523

Schwilk, D. W., & Ackerly, D. D. (2005). Limiting similarity and functional diversity along environmental gradients. *Ecology Letters*, *8*, 272–281. https://doi.org/10.1111/j.1461-0248.2004.00720.x

Stapp, P., & Polis, G. A. (2003). Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia*, *134*, 496–504. https://doi.org/10.1007/s00442-002-1146-7

Steibl, S., & Laforsch, C. (2020). Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species. *BMC Ecology*, *20*. https://doi.org/10.1186/s12898-019-0268-2

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., … Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*, 58–67. https://doi.org/10.1111/1365-2745.12025

Taylor, E. W. (1988). A functional analysis of the shift from gill- to lung-breathing during the evolution of land crabs (Crustacea, Decapoda). *Biological Journal of the Linnean Society*, *34*, 229–247. https://doi.org/10.1111/j.1095-8312.1988.tb01961.x

Ter Braak, C. J. F. (1987). The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio*, *69*, 69–77. https://doi.org/10.1007/BF00038688

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*, 2270–2279. https://doi.org/10.1016/j.biocon.2009.12.004

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Jonathan Davies, T., Grytnes, J.-A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*, 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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**Supplementary table B.1-S1:** Overview of all identified taxa and their assignment in the clusters of the given niche space. One lepidopteran pupa (Lepidoptera sp.) found in one plot on one island and three different spider species (Chelicerata sp. 1: found in three plots on two islands; Chelicerata sp. 2: found in one plot on one island; and Chelicerata sp. 3: found in one plot on one island) could not be identified to genus/species level because they were all sub-adult or juvenile specimens and were included as Lepidoptera sp. and Chelicerata sp. 1 – 3.

| Cluster | Taxon |
|---|---|
| 1 (“beach cluster”) | *Cardisoma carnifex* |
| | *Coenobita perlatus* |
| | *Coenobita rugosus* |
| | *Grapsus sp.* |
| | *Ligia dentipes* |
| | *Metopograpsus messor* |
| | *Natica sp.* |
| | *Neritus sp.* |
| | *Ocypode ceratophthalmus* |
| | *Ocypode cordimana* |
| | *Pachygrapsus minutus* |
| | *Talitrus sp.* |
| | *Trachyopella collinella* |
| 2 (“open forest cluster”) | *Argyrodes sp.* |
| | *Camponotus compressus* |
| | *Carrhotus sp.* |
| | Chelicerata sp. 3 |
| | *Chilochorus subindicus* |
| | *Clubiona sp.* |
| | *Ctenolepisma sp.* |
| | *Labiduria riparia* |
| | *Linyphia sp.* |
| | *Myrmarachne sp.* |
| | *Neoscona sp.* |
| 3 (“dense forest cluster”) | *Anoplolepis gracilipes* |
| | *Araneus sp.* |
| | *Balta sp.* |
| | Chelicerata sp. 1 |
| | Chelicerata sp. 2 |

**Supplementary table B.1-S1** (continued).

| | |
|---|---|
| | *Crassopriza lyoni* |
| | *Cubaris sp.* |
| | *Dysdercus cingulatus* |
| | *Elasmolomus pallens* |
| | *Eucarlia hofmanni* |
| | *Heteropoda venatoria* |
| | *Lobopterella dimidiatipes* |
| | *Pycnoscelus indicus* |
| | *Rhysida longipes* |
| | *Sason robustum* |
| | *Tapinoma fragile* |
| | *Teleogryllus mitratus* |
| 4 (“grassland cluster”) | *Acrosternum gramineum* |
| | *Diabolocatantops innotabilis* |
| | *Diaphorina citri* |
| | *Diplacodes trivalis* |
| | *Draposa lyrivulva* |
| | *Garypus maldivensis* |
| | *Gonocephalum lewisi* |
| | Lepidoptera sp. (pupa) |
| | *Platymetopus flavilabris* |
| | *Plexippus cf. paykulli* |
| | *Tenebrio sp.* |
| | *Thomisus pugilis* |

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**B.2** Steibl, S., Sigl, R., Blaha, S., Drescher, S., Gebauer, G., Gürkal, E., Hüftlein, F., Satzger, A., Schwarzer, M., Seidenath, D., Welfenbach, J., Zinser, R.S., & Laforsch, C. (2021) Allochthonous resources are less important for faunal communities on highly productive, small tropical islands. *Ecology and Evolution*, 11: 13128-13138.

ORIGINAL RESEARCH

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# Allochthonous resources are less important for faunal communities on highly productive, small tropical islands

**Sebastian Steibl**[1] | **Robert Sigl**[1] | **Sanja Blaha**[1] | **Sophia Drescher**[1] | **Gerhard Gebauer**[2] | **Elif Gürkal**[1] | **Frederic Hüftlein**[1] | **Anna Satzger**[1] | **Michael Schwarzer**[1] | **Dimitri Seidenath**[1] | **Jana Welfenbach**[1] | **Raphael S. Zinser**[1] | **Christian Laforsch**[1]

[1] Department Animal Ecology I and BayCEER, University of Bayreuth, Bayreuth, Germany

[2] BayCEER—Laboratory of Isotope Biogeochemistry, University of Bayreuth, Bayreuth, Germany

**Correspondence**
Christian Laforsch, Department of Animal Ecology and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany.
Email: Christian.laforsch@uni-bayreuth.de

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## Abstract

Ecosystems are interconnected by energy fluxes that provide resources for the inhabiting organisms along the transition zone. Especially where in situ resources are scarce, ecosystems can become highly dependent on external resources. The dependency on external input becomes less pronounced in systems with elevated in situ production, where only consumer species close to the site of external input remain subsidized, whereas species distant to the input site rely on the in situ production of the ecosystem. It is largely unclear though if this pattern is consistent over different consumer species and trophic levels in one ecosystem, and whether consumer species that occur both proximate to and at a distance from the input site differ in their dependency on external resource inputs between sites. Using stable isotope analysis, we investigated the dependency on external marine input for common ground-associated consumer taxa on small tropical islands with high in situ production. We show that marine input is only relevant for strict beach-dwelling taxa, while the terrestrial vegetation is the main carbon source for inland-dwelling taxa. Consumer species that occurred both close (beach) and distant (inland) to the site of marine input showed similar proportions of marine input in their diets. This supports earlier findings that the relevance of external resources becomes limited to species close to the input site in systems with sufficient in situ production. However, it also indicates that the relevance of external input is also species-dependent, as consumers occurring close and distant to the input site depended equally strong or weak on marine input.

KEYWORDS
beach wrack, food web, marine subsidies, stable isotope analysis

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Sebastian Steibl and Robert Sigl are shared first-authorship.

# 1 | INTRODUCTION

Even when separated by distinct borders, ecosystems rarely function without interconnection to each other (Barrett et al., 2005). Cross-ecosystem energy transfer is often crucial for animals and plants occurring in adjacent systems (Richardson & Wipfli, 2016). This external resource input into recipient ecosystems, commonly referred to as allochthonous input, can occur via biotic factors, when organisms forage and actively move between adjacent ecosystems (Bouchard & Bjorndal, 2000; Hilderbrand et al., 1999), or via abiotic factors, when wind, currents, or runoff passively transport resources from one ecosystem into another (Gauthier et al., 2011; Jansson et al., 2000; Richardson & Sato, 2015).

Numerous studies demonstrated the importance of this allochthonous input in different systems and taxa, for example, between forests and freshwater systems (Helfield & Naiman, 2001; Nakano & Murakami, 2001), the canopy and understory (Pringle & Fox-Dobbs, 2008), benthic and pelagic zones (Renaud et al., 2015), or marine and coastal systems (Dugan et al., 2003). The allochthonous input thereby subsidizes the recipient system and can result in significant increases in the overall biomass production and species abundance (Gounand et al., 2018; Polis & Hurd, 1996; Subalusky & Post, 2019).

These subsidization effects are suggested to become more pronounced with an increasing ratio of allochthonous-to-autochthonous resources (Marczak et al., 2007). This is particularly well documented for different arid or desert insular ecosystems, which offer only few in situ basal resources, compared to the highly productive adjacent oceans. Here, the allochthonous input, either in the form of beach wrack or as guano, is considered to be crucial for the stability of the whole insular food web (Polis et al., 1997). In these systems, various taxa, such as spiders, mice, or scorpions, depend on allochthonous input or its consumers (Anderson & Polis, 1998; Gauthier et al., 2011; Polis & Hurd, 1996). In these low-productive insular ecosystems, the allochthonous input benefitted all investigated organisms, as even those who primarily occurred inland return to the coast to forage on allochthonous marine input (Anderson & Polis, 1999; Stapp et al., 1999).

However, when two systems have only shallow productivity gradients and the ratio between allochthonous-to-autochthonous resources is low, the overall dependency on subsidies becomes limited to consumer species close to the site of allochthonous input (Marczak et al., 2007). It is largely unclear if this pattern is consistent among different consumer species and different trophic levels within one ecosystem. When the relevance of allochthonous input becomes limited to consumers close to the site of resource input (Muehlbauer et al., 2014; Paetzold et al., 2008), then consumer species with a broad distribution range that occur close to as well as at a distance to the site of allochthonous input might differ in their dependency on allochthonous input.

In this study, we evaluate the importance of allochthonous input for common ground-associated consumer species on highly productive tropical islands. We sampled common terrestrial insular animal taxa, comprising different trophic guilds, that occurred either close to the site of allochthonous input, that is, the beach, or at distance, that is, the inland, or throughout the entire island, that is, in both habitats. The study was carried out on four islands in the Lhaviyani Atoll, Republic of Maldives. These islands receive high amounts of annual rainfall and are classified as tropical moist forests (Gillespie et al., 2012). Most allochthonous input on these islands is deposited passively in the form of washed-up seagrass and marine carrion, while seabirds or other high-dispersal foragers that usually are the main depositor of allochthonous nutrients on oceanic islands are virtually absent (Anderson & Polis, 1999). We hypothesized that, due to the investigated islands' high autochthonous production, allochthonous marine input is only a relevant subsidy for ground-associated consumer species close to the beach, while those taxa occurring inland mainly rely on autochthonous production. To evaluate the relevance of allochthonous marine inputs for consumers in systems with high in situ production, we used stable isotope mixing models based on carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) signatures to calculate the relative proportion of diet derived from allochthonous marine resources for each consumer taxon.

# 2 | MATERIAL AND METHODS

## 2.1 | Sampling location

Oceanic islands can be considered as discrete community assemblages, with oceans acting as barriers (Leibold et al., 2004; Mehranvar & Jackson, 2001). Multiple uninhabited islands of an atoll can thereby be treated as repetitive units (Steibl & Laforsch, 2019a). We investigated four small uninhabited islands in the Lhaviyani atoll (Republic of the Maldives), namely Dhidhdhoo, Gaaerifaru, Vavvaru, and Veyvah, ($N = 4$). We determined the islands' sizes by walking along the shoreline of each island using GPS (Garmin eTrex Vista Cx; Garmin International Inc., Olathe, USA). The circumferences and areas of the four islands were 2,400 m and 116,537 $m^2$ for Dhidhdhoo; 862 m and 29,081 $m^2$ for Gaaerifaru; 855 m and 29,629 $m^2$ for Vavvaru; and 706 m and 28,456 $m^2$ for Veyvah. We conducted sampling between 26/05/2018 and 29/05/2018, sampling one island per day between 9:00 a.m. and 3:00 p.m. As the investigated islands lie in the tropics close to the equator with stable temperatures and wind conditions throughout the year, they show only little seasonal variation in primary production compared to more temperate systems (Clark et al., 2001), suggesting that variation in primary production should be minimal.

## 2.2 | Sampling of allochthonous and autochthonous resources

To quantify the amount of standing stock at the shoreline and collect basal resources on the beach, we positioned five 10-m transects randomly along each islands' high tide drift line. In each 10 m-transect, we placed four subplots (0.5 × 0.5 m) at the zero-, three-, six-, and nine-meter markings along the coastline and collected all organic material in the top 2 cm layer of the drift line. We categorized the collected material as either seagrass, marine carrion (i.e., washed-up dead sea urchins and fish), or terrestrial debris. Undefined debris was excluded from further analysis as it accounted for only 0–0.2 $g/m^2$ (Table 1). We weighed larger material on-site using a scale (Etekcity EL11, Etekcity Corp.) and smaller material in the laboratory using a fine scale (TS-300, G&G GmbH). We took five tissue samples from each resource category per island, transferred the samples to 1.5-ml Eppendorf safe-lock tubes (Eppendorf AG), and stored them at −20°C in a freezer until further processing.

To sample terrestrial plant material, we collected five leaves from the dominant plant species that occurred on all four investigated islands (*Calophyllum inophyllum*, *Cassytha filiformis*, *Cyperus dubius*, *Launaea sarmentosa*, *Pandanus tectorius*, *Pemphis acidula*, *Scaevola taccada*, *Sesuvium portulacastrum*, *Suriana maritima*, *Tournefortia argentea*, *Wollastonia biflora*). We stored the leaves in paper bags and dried them at room temperature until further processing.

## 2.3 | Consumer sampling

To investigate differences in marine subsidization between beach and inland consumer species on small tropical islands, we defined the beach habitat as ranging from the drift line up to the first 10 m of pioneer plant cover landwards, and the inland habitat as starting at a minimum 20 m away from beach and having shrub or tree vegetation. We obtained tissue samples from insects and spiders by collecting whole animals with insect nets (mesh size 1 mm). We obtained tissue samples from decapod crustaceans by grabbing the third walking leg of a crab with forceps and cutting it above the second tibia segment. This procedure has minimal impact on the crustaceans as the removed segments will be regenerated within the next molts (Kuris & Mager, 1975; Skinner, 1985; Skinner & Graham, 1970). We obtained tissue samples from the common house gecko, *Hemidactylus frenatus*, by grabbing its tail with forceps until caudal autotomy, that is, shedding of its tail, was initiated. Where possible, we collected five tissue samples per taxon in both habitats and on each island. If an investigated taxon was found in only one habitat, we collected five tissue samples only in the occupied habitat on each island. Because the Maldivian atolls are overall scarce in terrestrial taxa, especially vertebrates, compared to continental tropical ecosystems (Thaman, 2008), we could include all relevant and abundant macroinvertebrate and vertebrate groups that commonly occur on the investigated islands. We only excluded flying insect taxa, that is, moths, day-active Lepidopterans, and Apidae, from the sampling as they are known pollinators that are obligatory herbivores and feed on plant pollen or nectar. We grouped the collected euarthropod taxa into the following taxonomic groups: Amphipoda (sandhoppers), Blattodea (cockroaches), Caelifera (locusts), Arachnida (spiders), Curculionidae (weevils), Formicidae (ants), Gryllidae (crickets), Spirobolida (millipedes), and Tenebrionidae (darkling beetles). We identified all decapods except *Grapsus* sp. (shore crab) to species level. We found and collected amphipods, Tenebrionidae, *Grapsus* sp., *Metopograpsus messor* (grapsid crab), *Ocypode ceratophthalmus*, and *O. cordimana* (both ghost crabs), if present on the investigated islands, only in the beach habitat. We found and collected Curculionidae, *Hemidactylus frenatus* (house gecko), and *Geograpsus grayii* (shore crab), if present on the investigated islands, only in the inland habitat. We found and collected Spirobolida, Caelifera, Blattodea, *Coenobita perlatus*, *C. rugosus* (two terrestrial hermit crab species), Formicidae, Gryllidae, and Arachnida, if present on the investigated islands, in the beach and inland habitat (Table 2). We sampled most species on all investigated islands, except for Gryllidae and *O. ceratophthalmus* (only Dhidhdhoo), Curculionidae (only Vavvaru), and Tenebrionidae (only Vavvaru and Dhidhdhoo). As all investigated taxa are ground-associated, they cannot migrate between the islands. Therefore, their isotope signature can be considered as an integration of their diet obtained only from the investigated island, hence minimizing any mismatch between baseline and consumer data. We stored all collected consumer samples in 1.5-ml Eppendorf safe-lock tubes at −20°C until further processing.

## 2.4 | Stable isotope analysis

In the laboratory, we lyophilized all samples in a drying oven (Memmert GmbH + Co. KG, Schwabach, Germany) at 110°C for 48 hr and homogenized the dried samples using a ball mill (Retsch MM 400, Haan, Germany) at 30 Hz for 90 s. As recent findings suggest that acidification to remove inorganic carbon from samples of shoreline species for stable isotope analysis has no relevant effect

**TABLE 1** Allochthonous and autochthonous resource input on the beaches

| Island | Seagrass [$g/m^2$] | Marine carrion [$g/m^2$] | Terrestrial material [$g/m^2$] | Undefined debris [$g/m^2$] | Total beach wrack [$g/m^2$] |
|---|---|---|---|---|---|
| Dhidhdhoo | 18.2 ± 8.6 | 0.0 ± 0 | 62.6 ± 8.7 | 0.1 ± 0.1 | 80.6 ± 15.8 |
| Gaaerifaru | 740.1 ± 213.7 | 0.0 ± 0 | 694.5 ± 625.6 | 0.0 ± 0.0 | 1,434.6 ± 569.4 |
| Vavvaru | 13.9 ± 8.4 | 0.0 ± 0 | 487.3 ± 215.1 | 0.1 ± 0.1 | 501.3 ± 211.6 |
| Veyvah | 4.4 ± 1.31 | 8.0 ± 7.6 | 556.7 ± 349.9 | 0.2 ± 0.2 | 569.3 ± 348.1 |

*Notes:* Amount of the different types of allochthonous input and accumulating terrestrial debris along the drift line for each of the four investigated islands (*N* = 4; mean ± standard error).

**TABLE 2** Isotope signature of the four basal resources

| | Allochthonous resources | | Autochthonous resources | |
|---|---|---|---|---|
| **Island** | **Seagrass** | **Marine carrion** | **Terrestrial debris** | **Plant material** |
| Dhidhdhoo | $\delta^{13}C = -9.5 \pm 3.0$‰<br>$\delta^{15}N = 2.9 \pm 0.9$‰ | – | $\delta^{13}C = -27.5 \pm 1.6$‰<br>$\delta^{15}N = -1.7 \pm 2.3$‰ | $\delta^{13}C = -24.3 \pm 6.8$‰<br>$\delta^{15}N = 1.0 \pm 2.9$‰ |
| Gaaerifaru | $\delta^{13}C = -6.7 \pm 0.7$‰<br>$\delta^{15}N = 4.1 \pm 1.9$‰ | – | $\delta^{13}C = -28.8 \pm 2.4$‰<br>$\delta^{15}N = 1.5 \pm 1.2$‰ | $\delta^{13}C = -24.7 \pm 6.8$‰<br>$\delta^{15}N = 0.2 \pm 3.0$‰ |
| Vavvaru | $\delta^{13}C = -8.1 \pm 1.8$‰<br>$\delta^{15}N = 3.0 \pm 0.5$‰ | – | $\delta^{13}C = -28.2 \pm 2.0$‰<br>$\delta^{15}N = -2.8 \pm 1.3$‰ | $\delta^{13}C = -24.1 \pm 6.8$‰<br>$\delta^{15}N = -1.0 \pm 4.1$‰ |
| Veyvah | $\delta^{13}C = -9.8 \pm 1.3$‰<br>$\delta^{15}N = 2.0 \pm 1.1$‰ | $\delta^{13}C = -4.7 \pm 2.8$‰<br>$\delta^{15}N = 3.8 \pm 0.6$‰ | $\delta^{13}C = -28.1 \pm 0.7$‰<br>$\delta^{15}N = -3.0 \pm 1.2$‰ | $\delta^{13}C = -24.8 \pm 6.4$‰<br>$\delta^{15}N = -0.9 \pm 3.1$ ‰ |
| Average | $\delta^{13}C = -8.6 \pm 2.1$‰<br>$\delta^{15}N = 2.9 \pm 1.2$‰ | – | $\delta^{13}C = -28.1 \pm 0.7$‰<br>$\delta^{15}N = -3.0 \pm 1.2$‰ | $\delta^{13}C = -24.5 \pm 6.7$‰<br>$\delta^{15}N = -0.2 \pm 3.3$‰ |

*Notes:* For each island, the mean ± *SD* isotope signature is presented ($N = 5$ per island). As the isotope signatures did not differ significantly between the four investigated islands (PERMANOVA: $F = 2.257$, $df = 3$, $p = .056$), the average isotope signature was calculated over the four islands and used as baseline resource values in the Bayesian mixing models.

on carbon isotope values, we analyzed the collected consumer tissue samples without acidification treatment (Pires-Teixeira et al., 2020).

We measured the relative nitrogen and carbon isotope natural abundances of the tissue samples in a dual element analysis with an elemental analyzer (Carlo Erba Instruments 1108), coupled to a continuous flow isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany) via a ConFlo III open-split interface (Thermo Fisher Scientific). Measured relative isotope abundances are denoted as $\delta$ values using ($R_{sample}/R_{standard}$–1) × 1,000 [‰], with $R_{sample}$ and $R_{standard}$ being the ratios of the heavy to light isotope of the sample and the standard, respectively. We calibrated standard gases with respect to international standards ($CO_2$ vs. V-PDB, $N_2$ vs. $N_2$ in the air) with the reference substances CH6, CO8, and NBS18 for carbon isotopes and N1 and N2 for nitrogen isotopes, provided by the International Atomic Energy Agency, Vienna, Austria (Bidartondo et al., 2004). We corrected the obtained $\delta^{13}C$ values for their lipid content following the method described by Post et al. (2007) using linear regression equations to adjust the $\delta^{13}C$ based on C:N ratios for terrestrial animals and relative carbon content for plant material with carbon content <40%, respectively. The corrected isotope signatures for each consumer are presented in Table S1.

## 2.5 | Statistical analysis

We performed all statistical analysis using R 3.5.1 (R Core Team, 2018) extended with the "vegan" (Oksanen, 2015) and "simmr" packages (Parnell et al., 2010, 2013).

Prior to running the mixing models, we compared the isotope signature ($\delta^{13}C$ and $\delta^{15}N$) of the four sampled basal resources (seagrass, marine carrion, terrestrial debris, terrestrial plant material) and the consumer species between the four investigated islands to test whether the four islands must be treated separately, or data can be combined using nonparametric PERMANOVA (4,999 permutations, Bray-Curtis distance matrix). The isotope signatures of the basal resources did not differ significantly between the four investigated islands ($F = 2.25$, $df = 3$, $p > .05$) and were consequently averaged over the four investigated islands for the mixing model. The isotope signatures of the consumers differed significantly between species ($F = 43.16$, $df = 16$, $p < .001$) and between the four investigated islands ($F = 10.64$, $df = 3$, $p < .001$). Therefore, we treated the consumer species from each island separately in the mixing models.

For herbivorous and detritivorous consumers, we used trophic enrichment factors (TEFs) for terrestrial consumers without acidification treatment of +0.5 ± 0.17‰ for $^{13}C$ and +2.4 ± 0.24‰ for $^{15}N$ (McCutchan et al., 2005). For omnivorous and carnivorous consumers, we doubled the TEF and calculated the variability using $(2 \times SD^2)^{0.5}$ following the method described in Neres-Lima et al. (2016) and Neves et al. (2021).

We run two separate Bayesian mixing models for herbivorous + detritivorous and for omnivorous + carnivorous consumers, respectively, using "simmr" version 0.4.5 to infer the relative contributions of the different allochthonous (seagrass, marine carrion) and autochthonous (terrestrial plant material, terrestrial detritus) resources for the consumer species in the beach and inland habitat on the four investigated islands. Prior to running the Bayesian mixing models, we visually inspected the data on whether the consumer species fall within the isotope polygon of the resources (Smith et al., 2013). Isotope signatures of Spirobolida, Curculionidae, Caelifera, and Blattodea fell outside the source polygon, and these consumers were thus excluded from the Bayesian mixing models. The Markov Chain Monte Carlo chains for both models were run with 1,000,000 iterations, discarding the first 500,000 runs. We tested the models' convergences using Gelman-Rubin diagnostics, and all MCMC runs showed acceptable model convergence (Gelman-Rubin values between 1.00 and 1.02). As the aim of this study was to compare the relevance of allochthonous versus autochthonous resources for consumer species of tropical islands and the Bayesian mixing model indicted overall high correlation in the isotope signature between seagrass and marine carrion, and between plant material and terrestrial debris, we applied the posterior combining function on the two source pairs and grouped them in

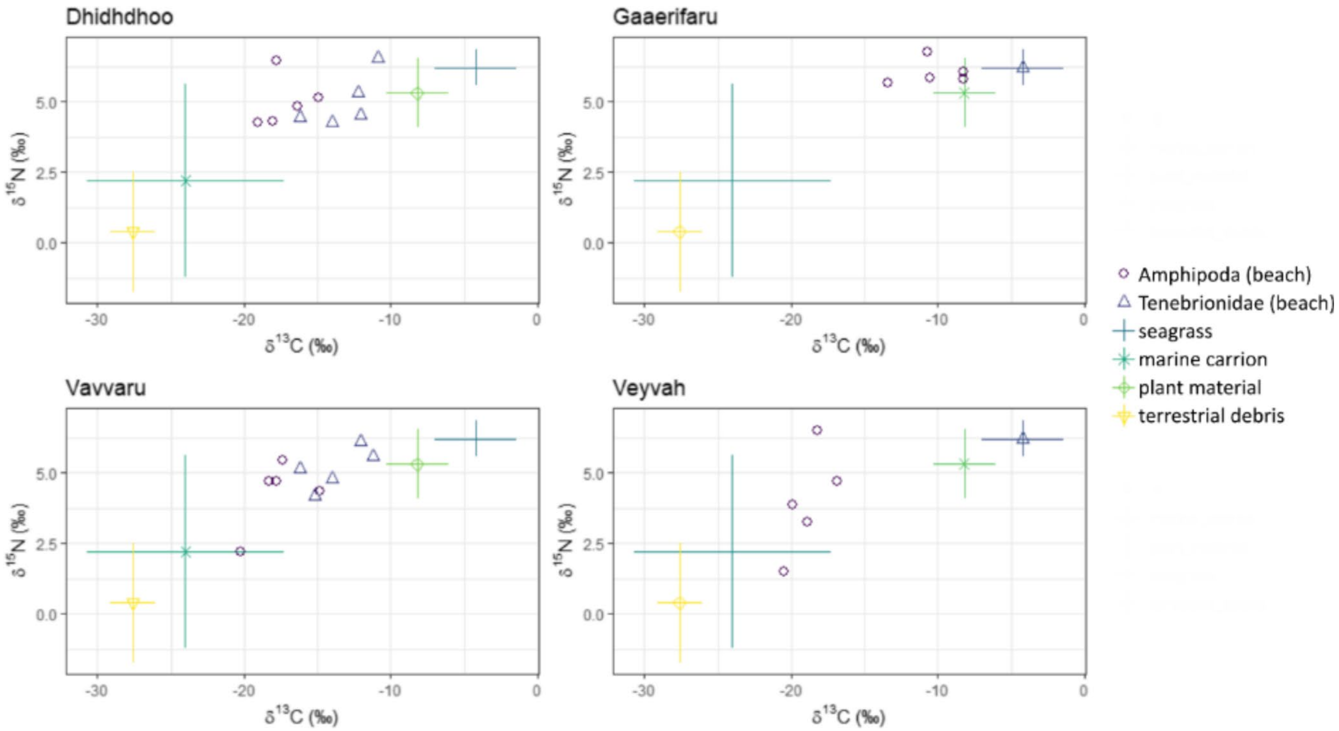

**FIGURE 1** Isotope biplot for the primary consumers on the four investigated islands. The isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) are plotted for each primary consumer, that is, herbivores and detritivores, together with the mean isotope signature of the four basal resources from the four investigated islands ($N = 5$). Isospace plots have been corrected assuming 1 trophic enrichment factors (TEFs) for primary consumers, following the method described in Neres-Lima et al. (2016) and Neves et al. (2021). Vertical and horizontal error bars indicate mean ± standard deviations of the four investigated basal resources

allochthonous and autochthonous resources, respectively. To test for differences in the relevance of allochthonous input for consumer species among habitats, we calculated the probabilities that the posterior probability of the relative contribution of allochthonous resources of each consumer was indeed greater than the relative contribution of autochthonous resources between beach and inland habitat. We assumed a significantly higher contribution of allochthonous resources in one habitat for probabilities >0.95. To further test for differences in contribution of allochthonous resources to the diets of the investigated consumers between species and between habitats, we extracted the estimated mean contributions of allochthonous resources for each consumer from the Bayesian mixing model. We compared the arcsin-transformed relative contributions (Shapiro test for normality: $W = 0.997$, $p = 0.380$; Levene test for homoscedasticity: $F = 0.943$, $p = 0.535$) between species and habitat as explanatory variables using ANOVA with Tukey HSD post hoc testing and Bonferroni *p*-value correction.

## 3 | RESULTS

### 3.1 | Quantification of allochthonous standing stock on the beach

The amount of allochthonous and autochthonous standing stock per $m^2$ along the beach shoreline of the four investigated island ecosystems ranged between 18–740 $g/m^2$ allochthonous material and 62–695 $g/m^2$ autochthonous material (Table 1).

### 3.2 | Differences in isotope signature between islands and consumer species

The isotope signature ($\delta^{13}C$ and $\delta^{15}N$) of each of the four basal resources, that is, seagrass, marine carrion, terrestrial debris, and plant material, did not differ significantly between the four investigated islands (PERMANOVA: $F = 2.257$, $df = 3$, $p = .056$, Table 2). The isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of the investigated consumers differed significantly between species (PERMANOVA: $F = 43.160$, $df = 16$, $p < .001$) and between the four investigated islands ($F = 10.638$, $df = 3$, $p < .001$), and the difference in isotope signature between species varied between the four investigated islands (interaction effect: $F = 2.251$, $df = 33$, $p < .001$).

### 3.3 | Proportion of allochthonous resources in the diet of consumer species

The isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of the different primary and secondary consumers on the four investigated islands ranged over the entire isotope source polygons formed by the four basal resources (Figures 1 and 2). The results from the Bayesian mixing

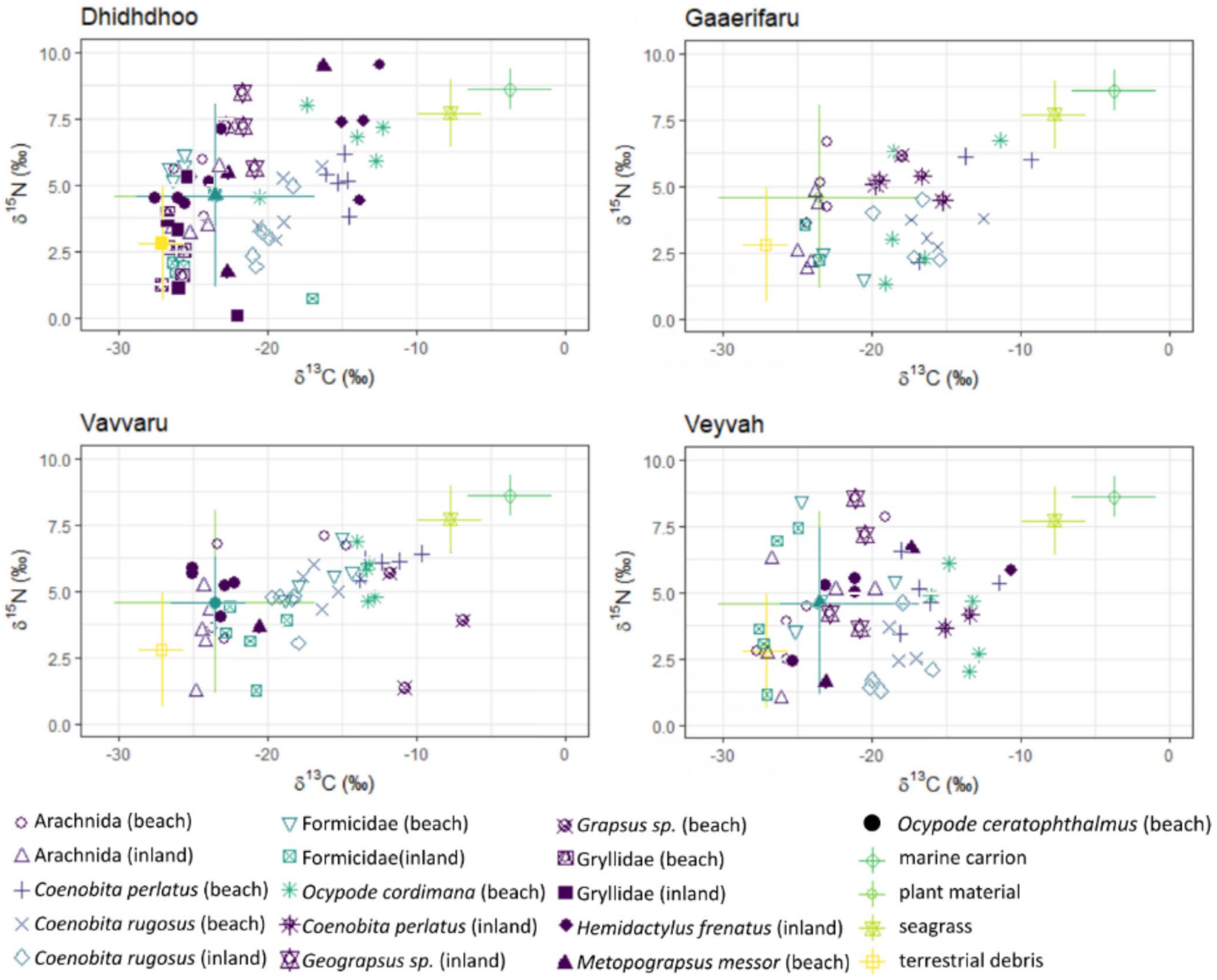

**FIGURE 2** Isotope biplot for the secondary consumers on the four investigated islands. The isotope signatures ($\delta^{13}$C and $\delta^{15}$N) are plotted for each secondary consumer, that is, omnivores and carnivores, together with the mean isotope signature of the four basal resources from the four investigated islands ($N = 5$). Isospace plots have been corrected assuming 2 trophic enrichment factors (TEFs) for secondary consumers, following the method described in Neres-Lima et al. (2016) and Neves et al. (2021). Vertical and horizontal error bars indicate mean ± standard deviations of the four investigated basal resources

models showed a great variability in the relative contribution of allochthonous resources (i.e., seagrass and marine carrion combined) among invertebrate consumer species but an overall consistency within species sampled in the beach and inland habitat, that is, either a high or a low proportion in both habitats (Table 3, Table S2). Only for Formicidae on two of the four investigated islands, the probability, that the estimated relative contribution of allochthonous resources to their diet is indeed greater in those specimens sampled at the beach than in those found inland, was >95%.

The relative contribution of allochthonous resources differed significantly between the different species (ANOVA: $F = 15.581$, $df = 12$, $p < .001$), but was not significantly different between habitats ($F = 3.578$, $df = 1$, $p = .066$), and the differences in relative contribution of allochthonous resources between the different species was not dependent on sampling location (interaction term species*habitat: $F = 0.732$, $df = 0.575$). Therefore, we must reject our initial hypothesis that consumer species on the beach have a consistently higher relative contribution of allochthonous resources in their diet than inland species. Instead, the contribution of allochthonous resources differed between consumer species, but not between the two insular habitats.

On the one hand, consumer species that were found only in the beach habitat did show consistently higher relative contributions of allochthonous resources to their diet than consumer species sampled only in the inland (Tukey HSD: $p < .05$ for all pairwise comparisons; Figure 3). The mean contribution of allochthonous resources was >40% for all consumers that occurred exclusively on the beach, except *M. messor* (Table 3, Table S2). However, on the other hand, those consumer species that occurred in both habitats exhibited a less clear, bipartite pattern (Figure 3). The two hermit crab species, *C. rugosus* and *C. perlatus*, showed consistently greater relative contributions of allochthonous resources to their diets (>40%) in the

**TABLE 3** Relative contributions of allochthonous resources to the diets of invertebrate consumers on the four investigated islands

| Species | Habitat | Dhidhdhoo | Gaaerifaru | Vavvaru | Veyvah |
|---|---|---|---|---|---|
| Amphipoda | Beach | 59.4 ± 5.6% | 85.4 ± 4.3% | 54.2 ± 7.1% | 49.4 ± 7.2% |
| Tenebrionidae | Beach | 74.8 ± 6.3% | – | 72.6 ± 5.9% | – |
| Arachnida | Beach | 18.5 ± 6.2% | 23.4 ± 6.2% | 34.4 ± 10.9% | 18.3 ± 8.3% |
|  | Inland | 15.9 ± 6.3% | 17.0 ± 5.6% | 16.6 ± 5.3% | 18.4 ± 8.6% |
| *Coenobita perlatus* | Beach | 63.7 ± 8.4% | 56.7 ± 19.4% | 73.2 ± 10.0% | 50.8 ± 12.9% |
|  | Inland | – | 44.1 ± 11.7% | – | 54.4 ± 19.6% |
| *Coenobita rugosus* | Beach | 41.9 ± 10.4% | 36.5 ± 17.1% | 56.3 ± 9.9% | 44.4 ± 12.2% |
|  | Inland | 38.6 ± 9.0% | 48.1 ± 13.9% | 45.6 ± 8.9% | 44.3 ± 10.5% |
| Formicidae | Beach | 12.9 ± 5.2% | 36.1 ± 17.3% | 54.4 ± 9.2% | 32.8 ± 14.2% |
|  | Inland | 17.2 ± 9.8% | 29.8 ± 17.5% | 30.6 ± 9.3% (*) | 10.6 ± 5.9% (*) |
| *Geograpsus* sp. | Inland | 32.4 ± 6.5% | – | 35.3 ± 8.0% | – |
| *Grapsus* sp. | Beach | – | 47.5 ± 11.4% | 67.0 ± 22.3% | 53.3 ± 19.4% |
| Gryllidae | Beach | 7.6 ± 3.8% | – | – | – |
|  | Inland | 12.9 ± 6.2% | – | – | – |
| *H. frenatus* | Inland | 17.1 ± 6.0% | – | 23.1 ± 5.0% | 24.9 ± 8.2% |
| *M. messor* | Beach | 38.6 ± 15.0% | – | 27.2 ± 10.1% | 41.0 ± 18.3% |
| *O. ceratophthalmus* | Beach | 70.5 ± 7.2% | – | – | 68.4 ± 18.0% |
| *O. cordimana* | Beach | 57.8 ± 10.5% | 48.4 ± 13.9% | 71.8 ± 7.4% | 68.0 ± 9.1% |

*Notes:* The contribution of allochthonous resources (a posteriori combination of seagrass and marine carrion) was estimated for each consumer species on each of the four investigated tropical islands individually using Bayesian mixing models. Values present mean ± standard deviation of relative contribution of allochthonous resources. Asterisks indicate >95% probability that the estimated relative contribution of allochthonous material to the diet of the consumer is indeed greater in the beach than the inland habitat (only for Formicidae on Vavvaru and Veyvah).

inland and beach habitat than Arachnida, Formicidae, and Gryllidae from both habitats (Tukey HSD: $p < .05$ for all pairwise comparisons). Arachnida, Formicidae, and Gryllidae sampled at the beach and in the insular interior showed consistently low contributions (<25%) of allochthonous resources to their diet in both habitats.

## 4 | DISCUSSION

Earlier research on the importance of allochthonous input has proposed an overall high dependency of insular food webs on marine input when donor and recipient systems differ markedly in their productivity (Fukami et al., 2006; Gauthier et al., 2011; Ince et al., 2007; Piovia-Scott et al., 2011; Polis & Hurd, 1995; Spiller et al., 2010). The present study, conducted on islands with high terrestrial in situ production, partly supports the hypothesis that marine subsidies become only relevant for strict beach-dwelling animal taxa that are close to the site of allochthonous input, while species occurring only inland primarily consume resources derived from the in situ primary production (Paetzold et al., 2008). However, we also show that consumer species with broader distribution ranges, that is, occurring both at the beach and inland, showed no difference in allochthonous subsidization between habitats. Instead, the proportion of allochthonous resources to the diets were either consistently high in both habitats (in the case of the terrestrial hermit crabs, *C. rugosus*, and *C. perlatus*), or consistently low (in the case of Formicidae, Gryllidae, and Arachnida), suggesting that relevance of allochthonous subsidization is also species-dependent.

The primary carbon source for species on insular ecosystems can originate from the terrestrial vegetation (autochthonous resources) or the standing stock of deposited marine material along the beaches (allochthonous resources) (Barrett et al., 2005). In the present study, only strict beach-dwelling taxa consumed high amounts of allochthonous material, while relying only to a smaller proportion on terrestrial-derived resources. Although leaf litter was quantitatively more available than marine input in the standing stock of deposited material on the beaches, allochthonous resources strongly subsidized the strict beach-dwelling taxa. As algal carbon is more easily digestible due to its lower structural stability than leaf litter, it is probably the preferred resource for beach-dwelling detritivores (Marcarelli et al., 2011). The beach-dwelling consumer species might additionally be restricted to beaches, because the environmental conditions or food availability further inland are unsuitable (Steibl et al., 2021). For example, low-density sediment, required for burrowing, solidifies further landwards, therefore offering no opportunity to hide for strict beach dwellers (Burggren & McMahon, 1988; Rodrigues et al., 2016; da Rosa & Borzone, 2008; Steibl & Laforsch, 2019b).

On the other hand, the strictly inland-dwelling taxa showed only small proportions of allochthonous resources in their diet. It suggests

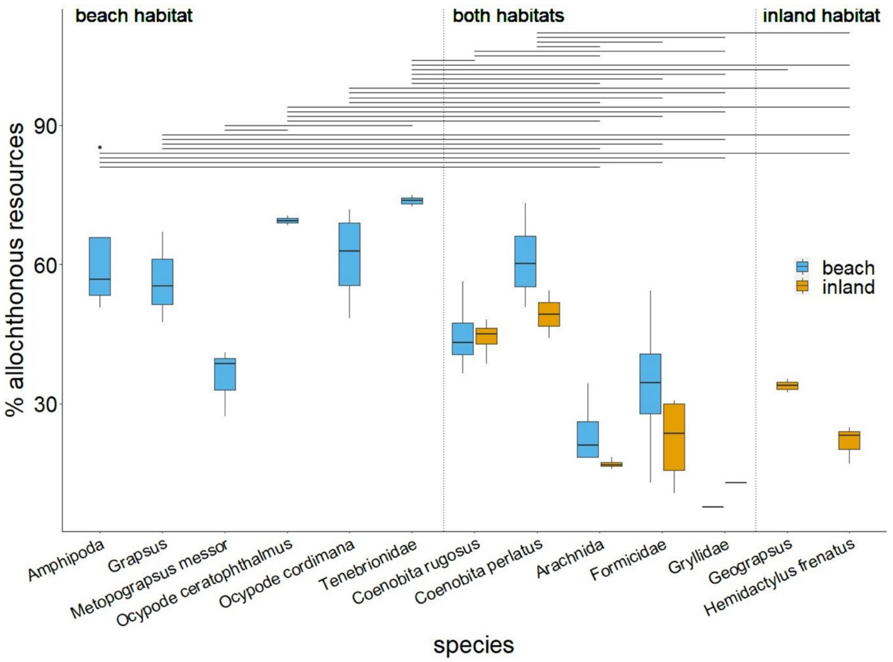

**FIGURE 3** Contribution of allochthonous resources to the diet of insular invertebrates found in the beach, the inland, or in both habitats of tropical islands. The proportion of allochthonous resources, that is, seagrass and marine carrion, in the diet of common insular invertebrate consumer species occurring in the beach (blue), the inland (orange) or in both habitats was estimated based on $\delta^{13}$C and $\delta^{15}$N stable isotope ratios using Bayesian mixing models. For each consumer, the mean ± *SD* relative dietary contribution is presented based on the estimates from $N = 4$ investigated islands. Statistical differences (ANOVA, Tukey HSD post hoc test: $p < .05$) in the relative contribution between different consumer species are indicated by significance bars. The relative contribution of allochthonous resources did not differ significantly between habitats in species occurring in both habitats ($F = 0.732$, $df = 4$, $p = .575$)

that these consumer species mainly rely on resources derived from the terrestrial in situ primary production and do not actively forage for allochthonous resources, probably because they cannot withstand the beach environment's physical conditions and therefore do not disperse into the beach habitat while foraging (McLachlan et al., 1993; Steibl & Laforsch, 2021).

*Coenobita rugosus* and *C. perlatus* were strongly subsidized by allochthonous resources and were found on the beach and the inland due to their ability and tendency to disperse landwards (Page & Willason, 1982). The consistently high contribution of allochthonous resources to their diet in both habitats suggests that terrestrial hermit crabs in the investigated insular system disperse landwards to seek shelter, but return to the shore to feed on allochthonous material (Hsu et al., 2018). The apparent movement of hermit crabs between the beach and inland might, however, be an important indirect subsidy for terrestrial plants or coprophagous inland consumers, when hermit crabs disperse landwards and release marine-derived nutrients in the insular interior via defecation (Green et al., 1997; Schmitz et al., 2018).

Predatory spiders (Arachnida), omnivorous ants (Formicidae), and omnivorous crickets (Gryllidae) also commonly occurred on the beach and in the inland. However, these consumer species all had isotope signatures which suggest that they rely primarily on resources derived from autochthonous sources, even though they disperse further into the beach habitat (Colombini et al., 2011). Here, they might utilize the washed-up detritus originating from terrestrial primary production, for example, coconuts. In this line, predatory spiders may also follow their prey, for example, ants, to the beach, which would then explain their “autochthonous” isotope signature and their occurrence in the beach habitat (Almquist, 1973). The estimated low contribution of allochthonous resources to the diet of spiders collected on the beaches suggests that they do not disperse to the beach to prey on the beach-dwelling taxa subsidized by allochthonous resources.

These results are contrasting earlier findings from low-productive insular ecosystems, in which all investigated insular consumers strongly depended on marine input (Polis & Hurd, 1996). Other than these desert islands, the Maldivian islands at focus in the present study are located in a tropical region with high annual precipitation (2,013 mm in the investigated atoll of this study vs. 59 mm on the investigated desert islands in the studies of Polis & Hurd, 1996), which strongly enhances in situ primary production (Gischler et al., 2014; Rosenzweig, 1968). The high autochthonous production of the tropical moist forests might be sufficient to allow most taxa to become independent of allochthonous input, while only the strict beach-dwelling species remain dependent on allochthonous subsidies (Gillespie et al., 2012). Another noteworthy feature that might further result in the overall low dependency of the inland-associated consumer species on allochthonous input is that no seabirds roosted or bred on the investigated islands. One of the most relevant links between allochthonous material and insular food webs is guano (Anderson & Polis, 1999; Croll et al., 2005; Fukami et al., 2006; Young et al., 2010). Where bird colonies occur on islands, they introduce large amounts of marine resources on islands and, other than the passive deposition of seagrass at the shoreline, can transport these nutrients far inland. As seabirds were virtually absent in the investigated system, or rested solely at the beach and never inland, the effects of marine subsidies were thus limited only to the direct input of seagrass and other wrack onto the beach habitat, making it primarily available to the beach-dwelling consumer species.

Overall, we show that small tropical islands with high autochthonous production depend only partly on allochthonous subsidies. Taken together with previous findings of a strong dependency on allochthonous subsidies in low-productive desert or tundra islands (Croll et al., 2005; Gauthier et al., 2011; Stapp & Polis, 2003), our study comprising multiple animal taxa supports the hypothesis that the relevance of allochthonous resources becomes limited to an edge effect when in situ production is sufficient (Paetzold et al., 2008). Where the donor and recipient ecosystems differ significantly in their productivity and the ratio of allochthonous-to-autochthonous resources is high, the recipient ecosystem becomes more dependent on allochthonous input (Marczak et al., 2007; Polis et al., 1997). Vice versa, this means that when the inland vegetation provides sufficient resources relative to the marine input, beaches can become sinks for allochthonous input from the adjacent oceans and are no longer links between ocean and inland. However, we also show that the depen-dency on allochthonous resources is to some extent also species- dependent, as those consumer species that occurred throughout the whole island did not switch their diet toward allochthonous resources when closer to the site of allochthonous nutrient input. Besides the ratio of allochthonous-to-autochthonous material in a system, this suggests that the trophic niches of its consumer species further influence the dependency of a system on subsidization.

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## CONFLICT OF INTEREST

The authors declare not conflicting interests.

## AUTHOR CONTRIBUTION

**Sebastian Steibl:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Robert Sigl:** Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing-original draft (equal); Writing-review & editing (equal). **Sanja Blaha:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Sophia Drescher:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Gerhard Gebauer:** Conceptualization (equal); Formal analysis (equal); Methodology (equal); Project administration (equal); Resources (equal); Validation (equal); Writing-original draft (equal); Writing-review & editing (equal). **Elif Gürkal:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Frederic Hüftlein:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Anna Satzger:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Michael Schwarzer:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Dimitri Seidenath:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Jana Welfenbach:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Raphael S. Zinser:** Investigation (equal); Methodology (equal); Writing-original draft (equal). **Christian Laforsch:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing-original draft (equal); Writing-review & editing (equal).

## DATA AVAILABILITY STATEMENT

All raw data and statistical codes can be accessed under Dryad Data repository https://doi.org/10.5061/dryad.5x69p8d1k.

## ORCID

*Sebastian Steibl* https://orcid.org/0000-0003-4819-8581

## REFERENCES

Almquist, S. (1973). Spider associations in coastal sand dunes. *Oikos*, *24*, 444–457. https://doi.org/10.2307/3543821

Anderson, W. B., & Polis, G. A. (1998). Marine subsidies of island communities in the gulf of California: Evidence from stable carbon and nitrogen isotopes. *Oikos*, *81*, 75–80. https://doi.org/10.2307/3546469

Anderson, W. B., & Polis, G. A. (1999). Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, *118*, 324–332. https://doi.org/10.1007/s004420050733

Barrett, K., Anderson, W. B., Wait, D. A., Grismer, L. L., Polis, G. A., & Rose, M. D. (2005). Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos*, *1*, 145–153. https://doi.org/10.1111/j.0030-1299.2005.13728.x

Bidartondo, M. I., Burghardt, B., Gebauer, G., Bruns, T. D., & Read, D. J. (2004). Changing partners in the dark: Isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 1799–1806. https://doi.org/10.1098/rspb.2004.2807

Bouchard, S. S., & Bjorndal, K. A. (2000). Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology*, *81*, 2305–2313. https://doi.org/10.1890/0012-9658(2000)081[2305:STABTO]2.0.CO;2

Burggren, W. W., & McMahon, B. R. (Eds.) (1988). *Biology of the land crabs*. Cambridge University Press.

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., & Holland, E. A. (2001). Net primary production in tropical forests: An evaluation and synthesis of existing field data.

*Ecological Applications*, *11*, 371–384. https://doi.org/10.1890/1051-0761(2001)011[0371:NPPITF]2.0.CO;2

Colombini, I., Brilli, M., Fallaci, M., Gagnarli, E., & Chelazzi, L. (2011). Food webs of a sandy beach macroinvertebrate community using stable isotopes analysis. *Acta Oecologica*, *37*, 422–432. https://doi.org/10.1016/j.actao.2011.05.010

Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, *307*, 1959–1961. https://doi.org/10.1126/science.1108485

da Rosa, L. C., & Borzone, C. A. (2008). Spatial distribution of the *Ocypode quadrata* (Crustacea: Ocypodidae) along estuarine environments in the Paranaguá Bay Complex, southern Brazil. *Revista Brasileira De Zoologia*, *25*, 383–388. https://doi.org/10.1590/S0101-81752008000300001

Dugan, J. E., Hubbard, D. M., McCrary, M. D., & Pierson, M. O. (2003). The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal and Shelf Science*, *58*, 25–40. https://doi.org/10.1016/S0272-7714(03)00045-3

Fukami, T., Wardle, D. A., Bellingham, P. J., Mulder, C. P. H., Towns, D. R., Yeates, G. W., Bonner, K. I., Durrett, M. S., Grant-Hoffman, M. N., & Williamson, W. M. (2006). Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters*, *9*, 1299–1307. https://doi.org/10.1111/j.1461-0248.2006.00983.x

Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., Legagneux, P., & Cadieux, M.-C. (2011). The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. *Écoscience*, *18*, 223–235. https://doi.org/10.2980/18-3-3453

Gillespie, T. W., Lipkin, B., Sullivan, L., Benowitz, D. R., Pau, S., & Keppel, G. (2012). The rarest and least protected forests in biodiversity hotspots. *Biodiversity and Conservation*, *21*, 3597–3611. https://doi.org/10.1007/s10531-012-0384-1

Gischler, E., Storz, D., & Schmitt, D. (2014). Sizes, shapes, and patterns of coral reefs in the Maldives, Indian Ocean: The influence of wind, storms, and precipitation on a major tropical carbonate platform. *Carbonates and Evaporites*, *29*, 73–87. https://doi.org/10.1007/s13146-013-0176-z

Gounand, I., Little, C. J., Harvey, E., & Altermatt, F. (2018). Cross-ecosystem carbon flows connecting ecosystems worldwide. *Nature Communications*, *9*(1), 1–8.

Green, P. T., O'Dowd, D. J., & Lake, P. S. (1997). Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. *Ecology*, *78*, 2474–2486. https://doi.org/10.1890/0012-9658(1997)078[2474:COSRBL]2.0.CO;2

Helfield, J. M., & Naiman, R. J. (2001). Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology*, *82*, 2403–2409. https://doi.org/10.1890/0012-9658(2001)082[2403:EOSDNO]2.0.CO;2

Hilderbrand, G. V., Hanley, T. A., Robbins, C. T., Schwartz, C. C., & Robbins, C. T. (1999). Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia*, *121*, 546–550. https://doi.org/10.1007/s004420050961

Hsu, C.-H., Otte, M. L., Liu, C.-C., Chou, J.-Y., & Fang, W.-T. 2018. What are the sympatric mechanisms for three species of terrestrial hermit crab (*Coenobita rugosus*, *C. brevimanus*, and *C. cavipes*) in coastal forests? *PLoS One 13*:e0207640.

Ince, R., Hyndes, G. A., Lavery, P. S., & Vanderklift, M. A. (2007). Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. *Estuarine, Coastal and Shelf Science*, *74*, 77–86. https://doi.org/10.1016/j.ecss.2007.03.029

Jansson, M., Bergström, A.-K., Blomqvist, P., & Drakare, S. (2000). Allochthonous organic carbon and phytoplankton/ bacterioplankton production relationships in lakes. *Ecology*, *81*, 3250–3255. https://doi.org/10.1890/0012-9658(2000)081[3250:AOCAPB]2.0.CO;2

Kuris, A. M., & Mager, M. (1975). Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. *Journal of Experimental Zoology*, *193*, 353–359. https://doi.org/10.1002/jez.1401930311

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Marcarelli, A. M., Baxter, C. V., Mineau, M. M., & Hall, R. O. (2011). Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, *92*, 1215–1225. https://doi.org/10.1890/10-2240.1

Marczak, L. B., Thompson, R. M., & Richardson, J. S. (2007). Meta-analysis: Trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology*, *88*, 140–148. https://doi.org/10.1890/0012-9658(2007)88[140:MTLHAP]2.0.CO;2

McCutchan, J. H., Lewis, W. M., Kendall, C., & McGrath, C. C. (2005). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, *111*, 416.

McLachlan, A., Jaramillo, E., Donn, T. E., & Wessels, F. (1993). Sandy beach macrofauna communities and their control by the physical environment: A geographical comparison. *Journal of Coastal Research*, *15*, 27–38.

Mehranvar, L., & Jackson, D. A. (2001). History and taxonomy: Their roles in the core-satellite hypothesis. *Oecologia*, *127*, 131–142. https://doi.org/10.1007/s004420000574

Muehlbauer, J. D., Collins, S. F., Doyle, M. W., & Tockner, K. (2014). How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. *Ecology*, *95*, 44–55. https://doi.org/10.1890/12-1628.1

Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 166–170. https://doi.org/10.1073/pnas.98.1.166

Neres-Lima, V., Brito, E. F., Krsulović, F. A. M., Detweiler, A. M., Hershey, A. E., & Moulton, T. P. (2016). High importance of autochthonous basal food source for the food web of a Brazilian tropical stream regardless of shading. *International Review of Hydrobiology*, *101*, 132–142. https://doi.org/10.1002/iroh.201601851

Neves, M. P., Kratina, P., Delariva, R. L., Jones, J. I., & Fialho, C. B. (2021). Seasonal feeding plasticity can facilitate coexistence of dominant omnivores in Neotropical streams. *Reviews in Fish Biology and Fisheries*, *31*, 417–432. https://doi.org/10.1007/s11160-021-09648-w

Oksanen, J. (2015). Multivariate analysis of ecological communities in R: vegan tutorial. R documentation:43.

Paetzold, A., Lee, M., & Post, D. M. (2008). Marine resource flows to terrestrial arthropod predators on a temperate island: The role of subsidies between systems of similar productivity. *Oecologia*, *157*, 653–659. https://doi.org/10.1007/s00442-008-1098-7

Page, H. M., & Willason, S. W. (1982). Distribution patterns of terrestrial hermit crabs at Enewetak Atoll, Marshall Islands. *Pacific Science*, *36*, 107–117.

Parnell, A. C., Inger, R., Bearhop, S., & Jackson, A. L. (2010). Source partitioning using stable isotopes: Coping with too much variation. *PLoS One*, *5*, 1–5. https://doi.org/10.1371/journal.pone.0009672

Parnell, A. C., Phillips, D. L., Bearhop, S., Semmens, B. X., Ward, E. J., Moore, J. W., Jackson, A. L., Grey, J., Kelly, D. J., & Inger, R. (2013). Bayesian stable isotope mixing models. *Environmetrics*, *24*, 387–399. https://doi.org/10.1002/env.2221

Piovia-Scott, J., Spiller, D. A., & Schoener, T. W. (2011). Effects of experimental seaweed deposition on lizard and ant predation in an island food web. *Science*, *331*, 461–463. https://doi.org/10.1126/science.1200282

Pires-Teixeira, L. M., Neres-Lima, V., & Creed, J. C. (2020). Is acidification of samples for isotopic analysis of carbon and nitrogen necessary for shoreline marine species? *Marine and Freshwater Research*, *72*, 256–262.

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, *28*, 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

Polis, G. A., & Hurd, S. D. (1995). Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 4382–4386. https://doi.org/10.1073/pnas.92.10.4382

Polis, G. A., & Hurd, S. D. (1996). Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*, *147*, 396–423. https://doi.org/10.1086/285858

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montaña, C. G. (2007). Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*, 179–189. https://doi.org/10.1007/s00442-006-0630-x

Pringle, R. M., & Fox-Dobbs, K. (2008). Coupling of canopy and understory food webs by ground-dwelling predators. *Ecology Letters*, *11*, 1328–1337. https://doi.org/10.1111/j.1461-0248.2008.01252.x

R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Renaud, P. E., Løkken, T. S., Jørgensen, L. L., Berge, J., & Johnson, B. J. (2015). Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Frontiers in Marine Science*, *2*, 1–15. https://doi.org/10.3389/fmars.2015.00031

Richardson, J. S., & Sato, T. (2015). Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology*, *8*, 406–415. https://doi.org/10.1002/eco.1488

Richardson, J. S., & Wipfli, M. S. (2016). Getting quantitative about consequences of cross-ecosystem resource subsidies on recipient consumers. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1609–1615. https://doi.org/10.1139/cjfas-2016-0242

Rodrigues, E., Freitas, R., Delgado, N. D. C., & Soares-Gomes, A. (2016). Distribution patterns of the ghost crab *Ocypode cursor* on sandy beaches of a tropical island in the Cabo Verde archipelago, Eastern Central Atlantic. *African Journal of Marine Science*, *38*, 181–188.

Rosenzweig, M. L. (1968). Net primary productivity of terrestrial communities: Prediction from climatological data. *The American Naturalist*, *102*, 67–74. https://doi.org/10.1086/282523

Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., & Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon cycle. *Science 362*:eaar3213.

Skinner, D. M. (1985). Molting and regeneration. In D. E. Bliss, & L. H. Mantel (Eds.), *The biology of Crustacea*, *9* (pp. 43–146). Academic Press.

Skinner, D. M., & Graham, D. E. (1970). Molting in land crabs: Stimulation by leg removal. *Science*, *169*, 383–385. https://doi.org/10.1126/science.169.3943.383

Smith, J. A., Mazumder, D., Suthers, I. M., & Taylor, M. D. (2013). To fit or not to fit: Evaluating stable isotope mixing models using simulated mixing polygons. *Methods in Ecology and Evolution*, *4*, 612–618. https://doi.org/10.1111/2041-210X.12048

Spiller, D. A., Piovia-Scott, J., Wright, A. N., Yang, L. H., Takimoto, G., Schoener, T. W., & Iwata, T. (2010). Marine subsidies have multiple effects on coastal food webs. *Ecology*, *91*, 1424–1434. https://doi.org/10.1890/09-0715.1

Stapp, P., & Polis, G. A. (2003). Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia*, *134*, 496–504. https://doi.org/10.1007/s00442-002-1146-7

Stapp, P., Polis, G. A., & Sánchez Piñero, F. (1999). Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature*, *401*, 1997–1999.

Steibl, S., & Laforsch, C. (2019a). Disentangling the environmental impact of different human disturbances: A case study on islands. *Scientific Reports*, *9*, 13712.

Steibl, S., & Laforsch, C. (2019b). Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*). *Estuarine, Coastal and Shelf Science*, *231*, 106482. https://doi.org/10.1016/j.ecss.2019.106482

Steibl, S., & Laforsch, C. (2021). Compartmentalized organization of ecological niche occupation in insular invertebrate communities. *Ecology and Evolution*, *11*, 471–480. https://doi.org/10.1002/ece3.7067

Steibl, S., Sigl, R., Bräumer, P. E., Clauß, V., Goddemeier, S., Hamisch, S., Lücker, D., Reiprich, L., Stegmann, L., Voigt, N., & Laforsch, C. (2021). Diversity patterns and community structure of the ground-associated macrofauna along the beach-inland transition zone of small tropical islands. *Diversity*, *13*(8), 377. https://doi.org/10.3390/d13080377.

Subalusky, A. L., & Post, D. M. (2019). Context dependency of animal resource subsidies. *Biological Reviews*, *94*, 517–538. https://doi.org/10.1111/brv.12465

Thaman, R. R. (2008). Atolls - the “biodiversity cool spots” vs “hot spots”: A critical new focus for research and conservation. *Micronesica*, *40*, 33–61.

Young, H. S., McCauley, D. J., Dunbar, R. B., & Dirzo, R. (2010). Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 2072–2077. https://doi.org/10.1073/pnas.0914169107

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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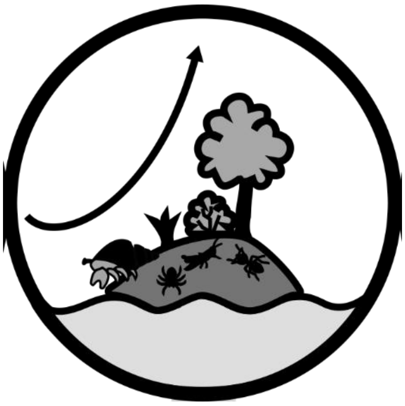
**Supplementary table B.2-S1: Stable isotope raw data of the investigated insular consumer species.** For each consumer species at each of the two sampling locations (beach, inland) and each of the four investigated islands, the mean ± SE $\delta^{13}C$ and $\delta^{15}N$ values are presented (*N* = 5 per consumer species).

| | **Dhidhdhoo** | | **Gaaerifaru** | | **Vavvaru** | | **Veyvah** | |
|---|---|---|---|---|---|---|---|---|
| **Species** | **$\delta^{13}C$** | **$\delta^{15}N$** | **$\delta^{13}C$** | **$\delta^{15}N$** | **$\delta^{13}C$** | **$\delta^{15}N$** | **$\delta^{13}C$** | **$\delta^{15}N$** |
| Amphipoda (beach) | -15.6 ± 0.7 | 5.0 ± 0.4 | -8.9 ± 0.8 | 6.0 ± 0.2 | -16.2 ± 0.7 | 4.3 ± 0.5 | -14.8 ± 0.9 | 4.0 ± 0.8 |
| Arachnida (beach) | -24.2 ± 0.5 | 5.2 ± 0.5 | -22.6 ± 0.5 | 4.9 ± 0.7 | -19.4 ± 1.8 | 5.5 ± 0.9 | -23.6 ± 1.3 | 4.3 ± 1.0 |
| Arachnida (inland) | -24.1 ± 0.8 | 3.9 ± 0.6 | -23.5 ± 0.2 | 3.1 ± 0.6 | -23.5 ± 0.3 | 3.5 ± 0.7 | -24.0 ± 1.4 | 4.0 ± 1.0 |
| Blattodea (beach) | -23.8 ± 2.0 | -0.2 ± 0.1 | -23.5 ± 0.9 | 1.6 ± 1.1 | -22.8 ± 0.4 | -2.0 ± 0.6 | -26.5 ± 0.5 | 0.0 ± 0.8 |
| Blattodea (inland) | - | - | -24.4 ± 0.2 | -0.3 ± 0.8 | -22.8 ± 0.5 | 1.1 ± 1.5 | -24.6 ± 0.6 | 1.0 ± 0.7 |
| Caelifera (beach) | -24.7 ± 1.5 | 3.6 ± 0.2 | -16.6 ± 2.5 | 1.7 ± 0.5 | -22.6 ± 0.5 | 1.5 ± 1.0 | -19.4 ± 2.5 | 1.4 ± 0.8 |
| Caelifera (inland) | -19.3 ± 4.0 | -0.2 ± 0.5 | - | - | - | - | -12.6 ± 0.9 | 0.6 ± 0.6 |
| *Coenobita perlatus* (beach) | -6.5 ± 1.9 | 5.1 ± 0.4 | -7.6 ± 2.8 | 4.8 ± 1.3 | -6.8 ± 0.8 | 6.1 ± 0.2 | -12.8 ± 1.4 | 5.0 ± 0.5 |
| *Coenobita perlatus* (inland) | - | - | -11.2 ± 0.9 | 5.0 ± 0.2 | - | - | -10.1 ± 0.8 | 3.9 ± 0.3 |
| *Coenobita rugosus* (beach) | -14.4 ± 0.9 | 4.2 ± 0.5 | -12.5 ± 3.0 | 2.6 ± 0.7 | -10.5 ± 0.6 | 5.3 ± 0.3 | -13.6 ± 0.9 | 3.0 ± 0.3 |
| *Coenobita rugosus* (inland) | -14.7 ± 0.3 | 3.1 ± 0.5 | -12.2 ± 1.4 | 3.3 ± 0.6 | -13.3 ± 1.1 | 4.4 ± 0.3 | -14.0 ± 0.9 | 2.2 ± 0.6 |
| Curculionidea (beach) | - | - | - | - | -23.2 ± 0.2 | -1.5 ± 0.7 | - | - |
| Formicidae (beach) | -22.6 ± 0.6 | 4.4 ± 1.3 | -20.3 ± 1.3 | 2.0 ± 0.5 | -14.3 ± 0.7 | 5.7 ± 0.4 | -21.0 ± 2.1 | 5.8 ± 1.4 |
| Formicidae (inland) | -22.2 ± 1.6 | 1.8 ± 0.3 | -20.4 ± 0.2 | 2.9 ± 0.7 | -18.5 ± 1.0 | 3.2 ± 0.5 | -24.0 ± 0.6 | 4.4 ± 1.2 |
| *Geograpsus* (inland) | -20.7 ± 0.4 | 6.6 ± 0.7 | - | - | - | - | 19.0 ± 0.8 | 5.9 ± 1.2 |
| *Grapsus* (beach) | - | - | - | - | -8.0 ± 1.4 | 3.6 ± 1.3 | -12.7 ± 0.9 | 5.2 ± 0.6 |
| Gryllidae (beach) | -25.5 ± 0.4 | 2.4 ± 0.5 | - | - | - | - | - | - |
| Gryllidae (inland) | -24.4 ± 1.1 | 2.7 ± 0.9 | - | - | - | - | - | - |
| *Hemidactylus frenatus* (inland) | -22.9 ± 0.7 | 5.1 ± 0.5 | - | - | -20.0 ± 1.1 | 5.2 ± 0.3 | -22.4 ± 1.0 | 4.6 ± 0.7 |
| *Metopograpsus messor* (beach) | -18.8 ± 2.1 | 5.5 ± 2.2 | - | - | - | - | -17.6 ± 4.1 | 4.1 ± 2.5 |
| *Ocypode ceratophthalmus* (beach) | -11.2 ± 0.3 | 7.2 ± 1.1 | - | - | - | - | | |
| *Ocypode cordimana* (beach) | -14.1 ± 1.5 | 6.5 ± 0.6 | -14.7 ± 1.6 | 3.9 ± 1.1 | -12.0 ± 0.3 | 5.6 ± 0.4 | -11.4 ± 1.0 | 4.1 ± 0.8 |
| Spirobolida (beach) | -19.9 ± 0.3 | 0.7 ± 1.3 | -17.0 ± 0.5 | -1.8 ± 0.5 | -19.1 ± 0.2 | -2.8 ± 0.4 | -22.4 ± 0.2 | -2.4 ± 0.4 |
| Spirobolida (inland) | -20.1 ± 0.2 | -1.8 ± 0.2 | -16.6 ± 0.6 | -2.0 ± 0.5 | -19.4 ± 0.2 | -2.6 ± 0.4 | -20.6 ± 0.4 | -3.3 ± 0.5 |
| Tenebrionidae (beach) | -11.7 ± 0.9 | 5.0 ± 0.4 | - | - | -12.6 ± 0.9 | 5.1 ± 0.3 | - | - |

**Supplementary table B.2-S2: Quantiles of the estimated relative contributions of allochthonous resources.** For each species and for each of the four investigated islands, the 2.5%, 50% (i.e., the mode), and 97.5% of the estimated relative contributions of allochthonous resources to the consumers' diet based on Bayesian stable isotope mixing model ($\delta^{13}C$ and $\delta^{15}N$) is presented. Consumer species that fell outside the resource polygon were removed from the model and are thus not included in this table (see methods section).

| | **Dhidhdhoo** | | | **Gaaerifaru** | | | **Vavvaru** | | | **Veyvah** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **2.5%** | **50%** | **97.5%** | **2.5%** | **50%** | **97.5%** | **2.5%** | **50%** | **97.5%** | **2.5%** | **50%** | **97.5%** |
| Amphipoda (beach) | 46.8% | 59.7% | 69.6% | 76.2% | 85.5% | 92.9% | 38.5% | 54.9% | 66.8% | 32.9% | 50.2% | 61.5% |
| Tenebrionidae (beach) | 60.7% | 75.6% | 85.6% | - | - | - | 58.8% | 73.1% | 82.5% | - | - | - |
| Arachnida (beach) | 8.2% | 18.0% | 32.0% | 11.5% | 23.3% | 36.4% | 13.9% | 34.6% | 56.4% | 5.5% | 17.2% | 37.3% |
| Arachnida (inland) | 6.1% | 15.3% | 30.0% | 6.5% | 17.0% | 27.5% | 6.9% | 16.6% | 27.4% | 5.7% | 17.0% | 38.9% |
| *Coenobita perlatus* (beach) | 39.1% | 65.7% | 74.1% | 15.0% | 61.4% | 86.5% | 44.7% | 75.7% | 85.8% | 21.4% | 53.2% | 70.4% |
| *Coenobita perlatus* (inland) | - | - | - | 18.5% | 45.5% | 63.4% | - | - | - | 12.7% | 58.8% | 84.7% |
| *Coenobita rugosus* (beach) | 17.0% | 43.9% | 57.0% | 6.5% | 36.5% | 70.0% | 29.6% | 58.4% | 69.7% | 13.5% | 47.1% | 62.6% |
| *Coenobita rugosus* (inland) | 15.0% | 40.7% | 51.3% | 14.0% | 51.2% | 68.6% | 21.4% | 47.9% | 57.5% | 16.3% | 46.6% | 58.9% |
| Formicidae (beach) | 4.5% | 12.4% | 24.7% | 8.8% | 34.2% | 76.6% | 33.0% | 55.9% | 68.6% | 10.3% | 31.0% | 67.1% |
| Formicidae (inland) | 3.5% | 15.7% | 41.2% | 7.1% | 25.5% | 74.9% | 10.8% | 31.9% | 46.1% | 3.1% | 9.5% | 25.1% |
| *Geograpsus* (inland) | 19.6% | 32.3% | 45.2% | - | - | - | - | - | - | 18.0% | 35.8% | 49.9% |
| *Grapsus* (beach) | - | - | - | 19.9% | 48.8% | 65.8% | 14.3% | 75.4% | 92.6% | 14.8% | 59.4% | 85.0% |
| Gryllidae (beach) | 2.4% | 7.0% | 16.2% | - | - | - | - | - | - | - | - | - |
| Gryllidae (inland) | 4.0% | 12.1% | 26.9% | - | - | - | - | - | - | - | - | - |
| *Hemidactylus frenatus* (inland) | 7.0% | 16.5% | 30.7% | - | - | - | 13.7% | 23.0% | 33.0% | 10.5% | 24.6% | 42.4% |
| *Metopograpsus messor* (beach) | 11.3.% | 37.9% | 72.1% | - | - | - | 8.2% | 26.9% | 47.1% | 9.9% | 39.3% | 81.7% |
| *Ocypode ceratophthalmus* (beach) | 52.5% | 71.6% | 81.7% | - | - | - | - | - | - | 25.2% | 73.6% | 92.1% |
| *Ocypode cordimana* (beach) | 35.8% | 58.6% | 76.8% | 15.6% | 50.7% | 70.5% | 50.1% | 73.3% | 81.3% | 40.5% | 70.1% | 79.1% |

**B.3** Steibl, S., Sigl, R., Bräumer, P.E., Clauß, V., Goddemeier, S., Hamisch, S., Lücker, D., Reiprich, L., Stegmann, L., Voigt, N., Laforsch, C. (2021) Diversity patterns and community structure of the ground-associated macrofauna along the beach-inland transition zone of small tropical islands. *Diversity*, 13(377): 1-12.



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# Diversity Patterns and Community Structure of the Ground-Associated Macrofauna along the Beach-Inland Transition Zone of Small Tropical Islands

**Sebastian Steibl †, Robert Sigl †, Paul E. Bräumer, Victoria Clauß, Simon Goddemeier, Stephan Hamisch, Darleen Lücker, Lisa Reiprich, Lucas Stegmann, Nora Voigt and Christian Laforsch ***

Department of Animal Ecology and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany; sebastian.steibl@uni-bayreuth.de (S.S.); robert.sigl@uni-bayreuth.de (R.S.); paul.e.braeumer@uni-bayreuth.de (P.E.B.); victoria.clauss@uni-bayreuth.de (V.C.); simon.goddemeier@freenet.de (S.G.); stephan.hamisch@uni-bayreuth.de (S.H.); darleen.luecker@uni-bayreuth.de (D.L.); lisa.reiprich@uni-bayreuth.de (L.R.); lucas.stegmann@gmail.com (L.S.); nora.voigt@uni-bayreuth.de (N.V.)
* Correspondence: Christian.Laforsch@uni-bayreuth.de
† Shared first-authorship.

**Abstract:** Biodiversity follows distinct and observable patterns. Where two systems meet, biodiversity is often increased, due to overlapping occurrence ranges and the presence of specialized species that can tolerate the dynamic conditions of the transition zone. One of the most pronounced transition zones occurs at shores, where oceans and terrestrial habitat collide, forming the shore–inland transition zone. The relevance of this transition zone in shaping a system's community structure is particularly pronounced on small islands due to their high shore-to-inland-area ratio. However, the community structure of insular faunas along this transition zone is unknown. Here, we investigated the diversity patterns along the beach–inland transition zone of small islands and tested the hypothesis that species diversity increases toward the transition zone where beach and interior habitat meet. By measuring environmental parameters, resource availability, and ground-associated macrofauna diversity along transects running across the beach–inland transition zone, we show that a gradual change in species composition from beach to the inland exists, but neither taxa richness, diversity, nor overall abundance changed significantly. These findings offer important insights into insular community structure at the transition zone from sea to land that are relevant to better understand the dynamic and unique characteristics of insular ecosystems.

**Keywords:** atoll; edge effect; insular ecosystem; species richness; zonation

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## 1. Introduction

Understanding the drivers for species distribution and biodiversity patterns at different spatial scales is among the fundamental goals of ecological research [1]. On a global scale, biodiversity changes with elevation and latitude [2]. The main factors shaping these global diversity gradients are temperature, habitat heterogeneity, and area, coupled with environmental stability, predictability, and productivity [3]. With some exceptions (e.g., in marine gastropods in the Southern Hemisphere [4]), these environmental factors allow for the prediction of overall species richness on large spatial scales in the terrestrial and aquatic environment [5]. On smaller spatial scales, however, a given environmental parameter does not determine the occurrence of all species in the same way. Instead, different taxa adapt and respond differently to the same environmental parameter, resulting in idiosyncratic diversity patterns [6].

Shifting from global to local scales, variations in more fine-scale environmental abiotic and biotic interactions become the predominant factors influencing species distribution and, thus, biodiversity patterns [2,5]. The fine-scale gradients determining species composition and diversity within ecosystems or habitats can comprise, among others, distance to a site of constant nutrient input, distance to competing conspecifics or species, chemical gradients like oxygen availability or pH, or gradual exposure to physical factors like wind or wave action [7–10].

When these abiotic or biotic gradients change rapidly on small spatial scales, transition zones between distinct communities or habitats can occur with a unique set and combination of environmental characteristics [11,12]. These transition zones can often show patterns of increased species richness, diversity, and biomass. The increased biodiversity in transition zones can be the result of overlapping distribution ranges from species occurring on either side of the transition zone. Additionally, transition zones often harbor an additional set of species that are specifically adapted to tolerate the rapidly changing environmental gradients at the transition zone, which increases the total biodiversity in the transition zone, relative to the two adjoining habitats [11,13,14].

These effects of increased diversity and species turnover in the transition zone become more pronounced when the two adjacent ecosystems are more dissimilar [15], as demonstrated, for example, in bird communities [16], tropical dung beetle species [17], or grassland arthropods [18]. The dissimilarity is thereby expressed in terms of contrasting abiotic environmental conditions, habitat quality, or vegetation structure.

Shores are among the most drastic transition zones between two highly dissimilar ecosystems (i.e., ocean and land) [19]. The most common inter- and supratidal habitats of shores are beaches, which are predominantly shaped by the ocean [20]. Beach-associated species are thereby primarily controlled by physical factors like wave climate, high salinity, or sun exposure, especially on exposed beach types, like sandy beaches [10]. However, within a short distance, the environmental conditions and habitat structure change significantly with the beginning of the first pioneering plants and increasing vegetation cover [21]. Along the shifting environmental parameters between the beach and inland system, a distinct transition zone occurs. In this beach–inland transition zone, diversity patterns of plants change significantly [22], peaking at intermediate positions [23]. Whether the same patterns along the beach–inland transition zone are also present in faunal communities has not been explicitly tested.

Understanding the faunal community structure along beach–inland transition zones is particularly important for insular ecosystems (i.e., the ecosystem on a land mass that is completely surrounded by water), as their high shore-to-inland-area ratio renders this zone a dominant component of islands, especially compared to continental shores [19]. As island beaches are also regions of high external nutrient input that can form a relevant energy source for insular consumer species [24–26], understanding the faunal community structure along their beach–inland transition zone is relevant to identify how marine nutrient inputs can propagate from the beach further inland.

Therefore, this study aimed to investigate how the ground-associated macrofauna community, resource availability in the form of seagrass and terrestrial detritus, and environmental parameters change along the beach–inland transition zone of small tropical islands. We hypothesized that species diversity, species richness, and abundance gradually increase toward the edge at which the beach and inland habitat meet. We further hypothesized that the ecological gradients change rapidly along the beach–inland transition zone. To test our hypotheses, we measured environmental parameters and ground-associated macrofauna diversity along transects running from the drift line at the beach into the island interior in 0.5 m intervals and tested for differences in environmental parameters and diversity indices along the gradient.

## 2. Materials and Methods

### 2.1. Study Site and Site Conditions

The field study was carried out on remote, low-lying tropical atoll islands of the Maldives in the Indian Ocean. Two uninhabited islands, Veyvah (N5.425284, E73.361301) and Dhidhdhoo (N5.376454, E73.383118) (Lhaviyani/Faadhippolhu atoll) were investigated (for a map of the study site refer to [27]). Sampling was performed on 13 September 2019 between 11:45 to 15:00 on Veyvah (conditions: air temperature: 32 °C, wind speed: 2.4 m/s (avg. 1 min), wind direction: SSW, weather conditions: clouded, partly sunny), on 14 September 2019 between 11:15 to 16:45 on Dhidhdhoo (conditions: air temperature: 31 °C, wind speed: 1.1 m/s, wind direction: SSW, weather conditions: sunny with clouds) and on 15 September 2019 between 10:30 to 12:45 on Veyvah (conditions: air temperature: 33 °C, wind speed: 0.7 m/s, wind direction: SSW, weather conditions: sunny). The field surveying was covered by the legal permit of the Atoll Marine Center field station (10-A/2000/31).

### *2.2. Sampling Preparation*

Sampling on both islands was carried out on the accessible beachlines (i.e., exposed sandy beaches not covered by (mangrove) vegetation). These beachlines were mapped using GPS (Garmin GPSMAP 62st, Garmin International Inc., Olathe, KS, USA) and six transects per islands were uniformly distributed along the accessible beachline in a perpendicular orientation to the drift line. The first and last transect were always positioned at 10 m away from the outer edges of the mapped accessible beachline, with the four remaining transects evenly distributed along the remaining space in between. The beginning of the primary vegetation (predominantly *Cyperus dubius*, *Launaea sarmentosa*, *Ipomoea spp.*, and *Sphagneticoa trilobata*) was chosen as the starting point of each transect. Starting from this point, 5.5 m landward and seaward were defined as one transect line. Every transect comprised a total of ten 1 × 1 m plots, four positioned seaward toward the drift line, and four positioned landward in the opposite direction, each equally spaced 0.5 m apart and terminating with an additional inland and beach reference plot, respectively. The beach and inland reference plots did not adhere to the regular 0.5 m spacing and were positioned directly on the drift line and further inland under the dense interior insular vegetation, respectively (see Supplementary Figure S1 for schematic drawing of the sampling design).

### *2.3. Sampling Procedure*

Sampling started from the beach reference plot toward the inland. Each plot was sampled only once following the same sampling procedure. First, a picture of each plot was taken from the top view to measure vegetation cover (Tevion DC-14, Supra, Kaiserslautern, Germany; Panasonic Lumix DMC-FT5, Panasonic, Kadoma, Japan; Galaxy A5 (2017) – SM-A520F, Samsung, Seoul, South Korea). Next, the plot was scanned for organisms. To detect species that might be hidden beneath vegetation, debris, or human waste, any material obstructing the view of the observers was carefully removed while scanning for hidden or buried organisms. Species were counted and identified up to the lowest possible taxonomic level and subsequently released in their original habitat. Plot temperature was measured in the four corners and in the center by inserting a soil thermometer 1 cm deep into the ground and averaging the five values for each plot (P300W 0-100°C ± 0.5°C, Dostmann electronic GmbH, Wertheim-Reicholzheim, Germany). Detritus was collected and classified into two categories (i.e., terrestrial (leaves, branches, deadwood) and marine (seagrass, marine carrion)). The wet mass of the collected detritus per plot was weighed on site using a digital scale (NTP2K 2000 g ± 0.1 g, Nohlex GmbH, Buchholz, Germany). Percentage of grass/herb and shrub coverage per plot was measured using ImageJ 1.49b (Rasband, W.S., ImageJ, U.S. National Institutes of Health, Bethesda, MD, USA, http://imagej.nih.gov/ij/, 1997–2015, accessed on 1 October 2019).

### *2.4. Statistical Analysis*

Statistical analysis was carried out using R 3.5.3 extended with the "vegan" and "hillR" packages for multivariate data analysis and calculation of Hill numbers, respectively [28–30]. The measured environmental parameters (i.e., soil surface temperature, marine detritus, terrestrial detritus, grass/herb coverage, shrub coverage) were compared between the two investigated islands using permutational multivariate analysis of variance

(PERMANOVA) with Bray–Curtis dissimilarity indices and 4999 permutations. For each island, the environmental parameters of the beach–inland transition zone were analyzed using principal component analysis (PCA). The first three principal components (PCs) explained 70.07% of the total inertia and were used for subsequent statistical testing. One-way analysis of variances (ANOVAs) with Tukey HSD post-hoc testing and Bonferroni $p$-value correction were performed to statistically compare the first three principal components (PC1 to PC3). Taxa richness (Hill number $q = 0$), exponential Shannon–Wiener (Hill number $q = 1$), the inverse of Simpson's concentration index (Hill number $q = 2$), Berger–Parker index (Hill number $q = 3$), and total number of individuals were calculated for each plot of the transect line ($N = 6$ per island). The different values for the parameter $q$ of the Hill number quantifies how much rare species are discounted in the calculation of the diversity index. A hill number with $q = 0$ is simply the number of species, while $q = 1$ weighs species in proportion to their frequency. Hill numbers with $q = 2$ and $q = 3$ add more weight on the more abundant species, while discounting rare ones [31]. Higher values for the $q = 3$ Hill number (Berger–Parker index) thus indicate that the most common species dominate (i.e., a lower evenness). The diversity indices were statistically compared between the transects of each island using the non-parametric Kruskal–Wallis test with Bonferroni $p$-value correction for multiple testing, as data did not meet the assumptions for parametric testing. For each taxon, the average occurrence range (i.e., distribution maximum ± standard variation) along the beach–inland transition zone was obtained from the mean taxa's abundances for each plot of the transect ($N = 6$ for each island). Differences in average occurrence ranges were statistically compared between the two islands using Monte Carlo-simulations (100,000 runs) and Bonferroni $p$-value corrections.

## 3. Results

Overall, the environmental parameters along the beach–inland transition zones differed significantly between the two investigated islands (PERMANOVA: F = 6.537, df = 1, $p = 0.0016$). Consequently, the two islands were treated separately for all subsequent statistical analysis. Scores in PC1 correlated negatively with soil temperature, amount of standing stock of terrestrial detritus per m$^2$, and grass/herb coverage. Within the beach–inland transition zone of each island, the PC1 scores differed significantly between the plots on Dhidhdhoo (one-way ANOVA: F = 24.840, df = 9, $p < 0.001$) and on Veyvah (F = 4.637, df = 9, $p < 0.001$; for loadings of the PCs and pairwise comparisons see Table 1 and Figure 1). Scores in PC2 correlated negatively with grass/herb coverage and positively with shrub coverage. PC2 scores did not differ significantly between the plots on Dhidhdhoo (F = 0.443, df = 9, $p = 0.904$) and on Veyvah (F = 1.93, df = 9, $p = 0.072$; Figure 1B). Scores in PC3 correlated positively with the amount of seagrass standing stock per m$^2$. PC3 scores differed significantly between the plots on Dhidhdhoo (F = 3.382, df = 9, $p = 0.003$), but not between the plots on Veyvah (F = 0.634, df = 9, $p = 0.762$; Figure 1C).

**Table 1. Loadings of the PCA analysis for the environmental parameters.** Bold values indicate major contributions of an environmental parameter to the principal component. The first three PCs explained in total 70.07% of the total inertia.

| Environmental Parameters | PC1 | PC2 | PC3 |
|---|---|---|---|
| Explained variance | 26.86% | 22.29% | 20.92% |
| Temperature | **−0.701** | −0.133 | 0.410 |
| Marine detritus | 0.261 | 0.022 | **0.904** |
| Terrestrial detritus | **−0.605** | 0.368 | 0.128 |
| Grass/ herb coverage | **−0.576** | **−0.608** | −0.160 |
| Shrub coverage | −0.288 | **0.769** | −0.122 |

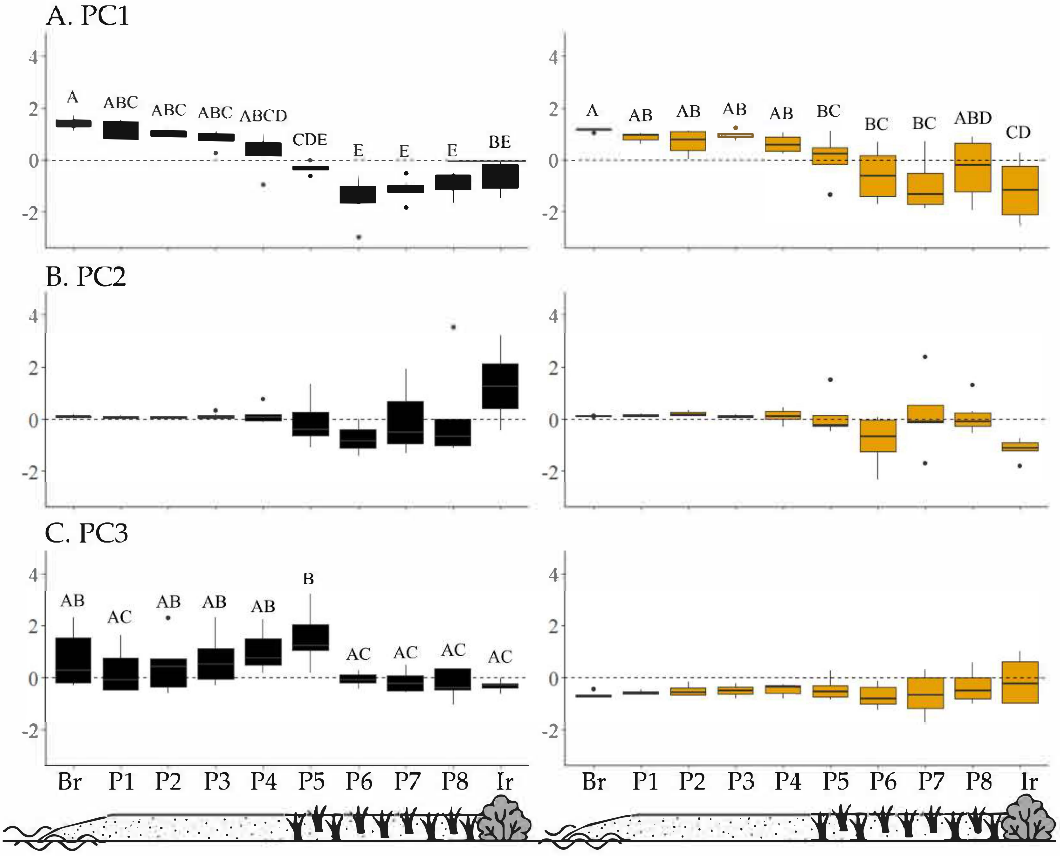

**Figure 1. Principal components scores along the beach–inland transition zone.** Boxplot representation for the mean PC1–PC3 scores of the beach–inland transition zones. Br: Beach reference plot; P1–P8: plot 1 to plot 8, with the first pioneering plants of the supralittoral vegetation starting between plot 4 and plot 5; Ir: Inland reference plot) of the two investigated islands (black: Dhidhdhoo, orange: Veyvah; *N* = 6 per island). For the loadings of the PCs, refer to Table 1. Significant differences in the PC scores of the plots of the two islands were detected for PC1—Dhidhdhoo ($p < 0.001$) and Veyvah ($p < 0.001$) and PC3—Dhidhdhoo ($p = 0.003$). Different letters indicate significant differences ($p < 0.05$) in the pairwise comparisons of the single plots (Tukey HSD post-hoc testing), same letters indicate no significant difference in PC score ($p > 0.05$).

Taxa richness (Hill number $q = 0$) along the beach–inland transition zone neither differed significantly between the two investigated islands ($X^2 = 0.978$, df = 1, $p = 1.000$) nor between the plots of the transects on Dhidhdhoo ($X^2 = 11.666$, df = 9, $p = 1.000$) and Veyvah ($X^2 = 22.185$, df = 9, $p = 0.125$; Figure 2A). Exponential Shannon–Wiener $H'$ (Hill number $q = 1$) neither differed significantly between the two investigated islands ($X^2 = 0.035$, df = 1, $p = 1.000$), nor between the plots of the transects on Dhidhdhoo ($X^2 = 7.865$, df = 9, $p = 1.000$) and Veyvah ($X^2 = 20.481$, df = 9, $p = 0.228$; Figure 2B). The inverse Simpson Index (Hill number $q = 2$) neither differed significantly between the two investigated islands ($X^2 = 2.433$, df = 1, $p = 1.000$) nor between the plots of the transects on Dhidhdhoo ($X^2 = 7.104$, df = 9, $p = 1$) and Veyvah ($X^2 = 15.949$, df = 9, $p = 1.000$; Figure 2C). The Berger–Parker index (Hill number $q = 3$) neither differed significantly between the two investigated islands ($X^2 = 2.978$, df = 1, $p = 1.000$), nor between the plots of the transects on Dhidhdhoo ($X^2 = 6.735$, df = 9, $p = 1.000$) and Veyvah ($X^2 = 15.708$, df = 9, $p = 1.000$; Figure 2D). The total number of individuals per plot neither differed significantly between the two investigated islands ($X^2 = 5.720$, df = 1, $p = 0252$), nor between the plots of the transects of Dhidhdhoo ($X^2 = 16.024$, df = 9, $p = 0.998$) and Veyvah ($X^2 = 21.296$, df = 1, $p = 0.171$; Figure 2E).

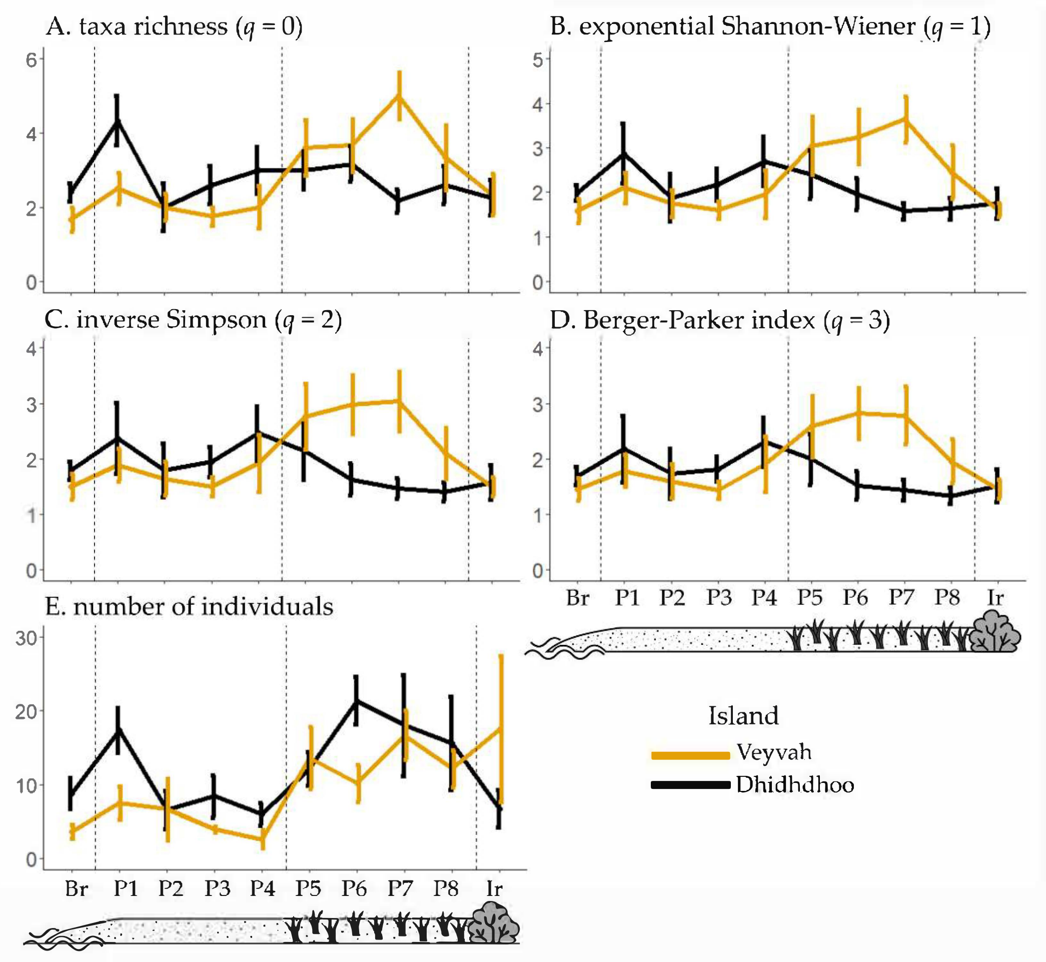

**Figure 2. Change in the biodiversity parameters along the beach–inland transition zone.** For each plot along the beach–inland transition zone (Br: Beach reference plot; P1–P8: plot 1 to plot 8, with the first pioneering plants of the supralittoral vegetation starting between plot 4 and plot 5; Ir: Inland reference plot), the mean ± standard error of the four biodiversity parameters (based on Hill number $q = 0$, $q = 1$, $q = 2$, and $q = 3$) and of the total number of individuals are presented ($N = 6$ per island). The two colors indicate the two different islands (black: Dhidhdhoo, orange: Veyvah). (**A**) Number of taxa per plot, (**B**) Exponential Shannon–Wiener $H'$, puts species richness in proportion to their abundance. (**C**) Inverse Simpson, gives abundant species more weight and discounts for rarer ones. (**D**) Berger–Parker index, weighs also for more abundant species. (**E**) Total number of individuals per plot. None of the calculated diversity indices differed significantly between the two islands (Kruskal–Wallis: $p > 0.05$) or between the different plots within each island ($p > 0.05$).

The calculated mean occurrences of the species along the beach–inland transition zone (Figure 3) did not differ significantly between the two investigated islands (Monte Carlo simulation: $p > 0.05$ for all comparisons). The summarized taxa richness into phylogenetic groups (crustaceans, insects, spiders, other, i.e., one chilopod, one reptile, one pseudoscorpion taxa) changed from predominantly crustaceans in the beach habitat to insect- and spider-dominated in the supralittoral vegetated inland habitat (Figure 4).

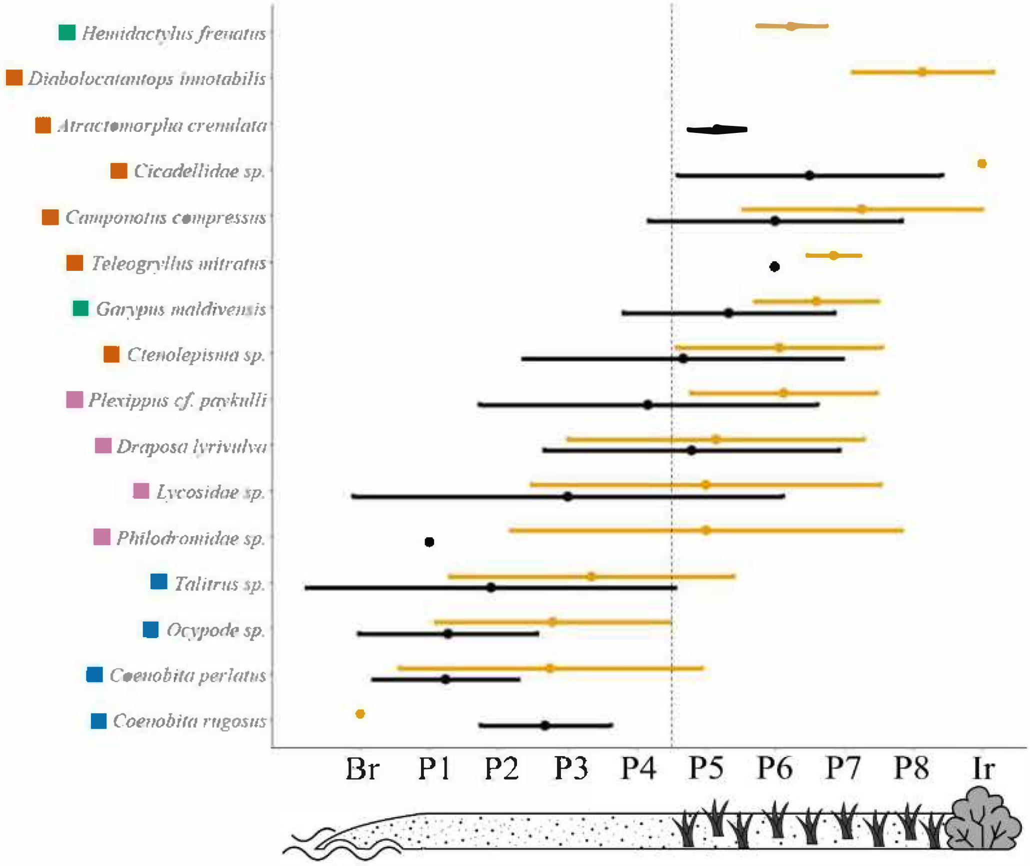

**Figure 3. Mean occurrence range of the macrofauna in the beach–inland transition zone.** Circles indicate the mean occurrence maximum for each taxon, error bars the occurrence range (i.e., mean ± standard deviation; $N = 6$ per island) at the beach–inland transition zone (Br: Beach reference plot; P1–P8: plot 1 to plot 8, with the first pioneering plants of the supralittoral vegetation starting between plot 4 and plot 5, indicated by the dashed vertical line; Ir: Inland reference plot). The five taxa that were sampled only once during the field sampling were excluded from this analysis and graphical representation. The coloration of the plotted bars indicates the two different islands (black: Dhidhdhoo, orange: Veyvah). The colors before the species names indicate the broader taxonomic grouping (blue: crustaceans, brown: insects, purple: spiders, green: other, see also Figure 4).

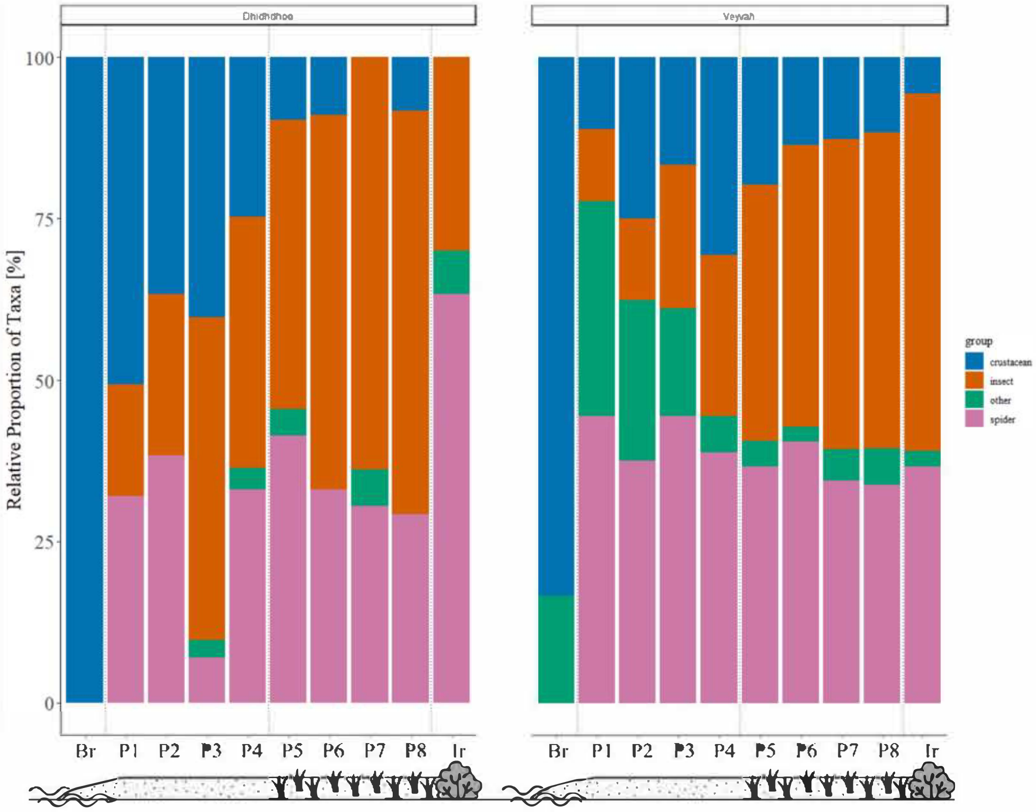

**Figure 4. Relative proportion of phylogenetic groups to the overall taxa richness along beach–inland transition zone.** The deconstructed mean taxa richness into phylogenetic groups (blue: crustaceans, brown: insects, purple: spiders, green: other) along the beach–inland transition zone (Br: Beach reference plot; P1–P8: plot 1 to plot 8, with the first pioneering plants of the supralittoral vegetation starting between plot 4 and plot 5, indicated by the dashed vertical line; Ir: Inland reference plot) changed from crustacean-dominated close to the drift line to insect- and spider-dominated in the supralittoral vegetation on Dhidhdhoo (**left**) and Veyvah (**right**; *N* = 6).

## 4. Discussion

This study investigated the environmental parameters and the diversity pattern of the ground-associated macrofauna community along the beach–inland transition zone of small and remote tropical atoll islands. We show that the environmental parameters gradually changed from beach to inland. Along this environmental gradient, different ground-associated species occupy different sections with a smooth trend for increasing terrestriality in the type of fauna present (i.e., more insect and spider taxa, fewer crustaceans when shifting along the transition zone from beach to insular interior) as the environmental conditions become less shaped by the harsh beach conditions.

Generally, both islands matched the conditions of reflective microtidal beaches [32,33]. Even though one island (Dhidhdhoo) showed a rapid change (i.e., significant changes in environmental parameters within 0.5 m) at the area of the first pioneer plants in the transition zone and the second island (Veyvah) displayed a more gentle gradient, the general patterns of the environmental gradients were similar on both atoll islands [34]. Terrestrial detritus, which forms the dietary basis for most taxa on the inland, on islands with sufficient in situ primary production [24], along with soil temperature and vegetation coverage increased from the beach to the inland on both islands, displaying the expected patterns also known from continental beach systems [35,36]. The amount of available marine detritus, which forms the dietary basis for most beach-dwelling taxa [37], was generally higher on the beach on Veyvah. In contrast, on Dhidhdhoo, it peaked at the edge toward the inland habitat where the first pioneer plants appear (Figure 1C). Here, pioneering supralittoral vegetation at the upper margin of the beach might act as a barrier holding back seagrass and other marine detritus that gets washed ashore during high tide or storm events, resulting in its highest availability not directly at the drift line, but at the margin of the inland habitat [38].

Despite the apparent gradient in environmental conditions from the drift line at the beach across the beach–inland transition zone and into the interior insular vegetation, the ground-associated fauna's overall richness, abundance, and diversity did not change significantly across the investigated transition zone on a species/genus level. However, summarizing the overall species distribution into larger taxonomic groups revealed that the ground-associated macrofauna community is changing completely along the beach–inland transition zone, albeit the diversity indices did not change significantly (Figures 3 and 4). This species turnover is in line with earlier findings that showed comparable turns in community composition in other highly dissimilar adjoining ecosystems [16,17].

Crustaceans (*Coenobita spp., Ocypode sp., Pachygrapsus minutus, Talitrus sp.*) dominated the beach environment and rarely—if at all—were observed dispersing over the margin of the beach across the transition zone into the vegetated supralittoral habitat. The gradually increasing soil temperature, which also indicates decreased soil moisture and salinity [36,39], toward the upper margin of the beach and the beach–inland transition zone likely forms a natural dispersal barrier for the beach-associated crustacean taxa, which depend on, for example, fine-grained, moist soil for burrowing [27,40]. Although terrestrial hermit crabs, *Coenobita spp.*, are known to disperse further landward into densely vegetated mangrove or forest habitats [41–43], these results indicate that they do not reside in large numbers in the sparsely vegetated beach–inland transition zone, at least during the day, probably to avoid desiccation [44]. On the other hand, hexapods and their common predator, the house gecko *Hemidactylus frenatus*, were recorded rarely—if at all—on the beach side of the transition zone. Their natural dispersal range seaward might be limited by available supralittoral vegetation, which offers a heterogeneous microenvironment and serves as a shelter, and food and nutrient supply [45]. The absence of primary production and terrestrial detritus further seaward might additionally deter the herbivorous and detritivorous taxa from dispersing further into the beach side of the transition zone beyond the line of first pioneering plants [46]. This bipartite distribution pattern of crustaceans (beach) and hexapods (inland), following their natural dispersal limits along the beach–inland transition zone, would also partly explain why energy fluxes between beach and inland communities on small islands with sufficient primary production are limited [24].

Although the dispersal ranges of crustaceans and hexapods only marginally overlapped around the beach–inland transition zone, a third group of taxa was found on both sides of the transition zone: non-web-building spiders (Lycosidae, Philodromidae, Salticidae). Since vegetation structure and prey availability determine the distribution of spiders [47], it is likely that the observed wolf-, jumping-, and running-spider taxa are all adapted specifically to sparse vegetation structure, like as occurred along the beach–inland transition zone in the studied system [48]. Jumping-, wolf-, and running-spiders can be fairly thermotolerant [48], allowing them to withstand the dynamic environmental conditions at the beach–inland transition zone. They are not dependent on vegetation as they do not build webs for hunting prey [47] and thus can advance further into the beach environment for foraging than other predators [49,50]. Therefore, other than the initial hypothesis, the beach–inland transition zone of small tropical islands is not an area of elevated species diversity where beach and inland taxa overlap, but instead, is primarily occupied by non-web building spiders. Their occurrence between the beach and inland fauna results in the observed consistent total taxa richness when shifting across the beach–inland transition zone on the investigated small tropical insular system.

A noteworthy feature of the observed biodiversity patterns across the beach–inland transition zone is the remoteness of the investigated system, the Maldivian archipelago in the Indo-Pacific. Many studies in various continental systems identified transition zones as regions with increased biodiversity due to overlapping distribution ranges of species and additional specialists that are adapted to tolerate the rapidly changing environmental gradients [11,12]. This pattern could not be observed in the present system. The overall remoteness of the Maldivian islands coupled with their small island sizes allows only a limited number of taxa to reach and successfully colonize these islands [51–53]. Furthermore, the absence of any transition-zone-specialists could be caused by the highly dynamic character of these small atoll islands, which display constant changes in their insular morphology [54,55]. When systems are dynamic in space and time, transition zones and ecosystem boundaries become less diverse with fewer specifically adapted taxa present than in more stable ecosystems [56]. Additionally, due to the Maldivian islands' overall young geological age (although the archipelago itself is about 55 million years old, the present Maldivian islands started forming ca. 3000 years ago after being fully submersed during the last glacial period), processes of speciation and adaptive radiation to tolerate the environmental conditions of the beach–inland transition zone might have not (yet) taken place. These factors probably result in a paucity of endemic and specialist taxa in the beach–inland transition zone of the investigated remote atoll islands compared to continental systems [54,57]. Taking the factors above together could explain why neither a highly diverse beach and inland fauna, nor any changes in taxa richness or abundance along the transition zone were observed. Instead, an overall low but consistent taxa richness across the beach–inland transition zone in the investigated system was recorded, albeit the macrofauna community composition changed completely along the transition zone.

## 5. Conclusions

The present study shows how taxa richness and diversity of the ground-associated macrofauna on remote tropical atoll islands in the Indo-Pacific are structured along the environmental gradients of the beach–inland transition zone. While the relevant environmental gradients that determine the biodiversity patterns of the beach and supralittoral communities have already been investigated on global to regional scales [58], this study demonstrated how the biodiversity of the beach and supralittoral macrofauna is structured on a small spatial scale. In light of globally accelerating habitat conversion, especially drastic in the coastal environment [59], these findings also provide new and relevant insights into community dynamics and diversity patterns of the coastal- and supralittoral-associated macrofauna.

**Supplementary Materials:** The following supplementary figures are available online at https://www.mdpi.com/article/10.3390/d13080377/s1, Figure S1: Scheme of sampling transects and plots.

**Author Contributions:** Conceptualization, S.S., R.S. and C.L.; Methodology, S.S., R.S., and C.L.; Validation, S.S., R.S. and C.L.; Formal analysis, S.S.; Investigation, S.S., R.S., P.E.B., V.C., S.G., S.H., D.L., L.R., L.S., N.V. and C.L.; Resources, C.L.; Data curation, S.S.; Writing—original draft preparation, S.S., R.S., P.E.B., V.C., S.G., S.H., D.L., L.R., L.S., N.V. and C.L.; Writing—review and editing, S.S., R.S. and C.L.; Visualization, S.S.; Supervision, S.S., R.S. and C.L.; Project administration, S.S., R.S. and C.L. All authors have read and agreed to the published version of the manuscript.

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## References

1. Sutherland, W.J.; Freckleton, R.P.; Godfray, H.C.J.; Beissinger, S.R.; Benton, T.; Cameron, D.D.; Carmel, Y.; Coomes, D.A.; Coulson, T.; Emmerson, M.C.; et al. Identification of 100 fundamental ecological questions. *J. Ecol.* **2013**, *101*, 58–67. [CrossRef]
2. Willis, K.J.; Whittaker, R.J. Species diversity—Scale matters. *Science* **2002**, *295*, 1245–1248. [CrossRef]
3. Rohde, K. Latitudinal gradients in species diversity and Rapoport's rule revisited: A review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* **1999**, *22*, 593–613. [CrossRef]
4. Valdovinos, C.; Navarrete, S.A.; Marquet, P.A. Mollusk species diversity in the Southeastern Pacific: Why are there more species towards the pole? *Ecography* **2003**, *26*, 139–144. [CrossRef]
5. Whittaker, R.J.; Willis, K.J.; Field, R. Scale and species richness: Towards a general, hierarchical theory of species diversity. *J. Biogeogr.* **2001**, *28*, 453–470. [CrossRef]
6. Astorga, A.; Fernández, M.; Boschi, E.E.; Lagos, N. Two oceans, two taxa and one mode of development: Latitudinal diversity patterns of South American crabs and test for possible causal processes. *Ecol. Lett.* **2003**, *6*, 420–427. [CrossRef]
7. Mittelbach, G.G.; Steiner, C.F.; Scheiner, S.M.; Gross, K.L.; Reynolds, H.L.; Waide, R.B.; Willig, M.R.; Dodson, S.I.; Gough, L. What is the observed relationship between species richness and productivity? *Ecology* **2001**, *82*, 2381–2396. [CrossRef]
8. Terborgh, J.; Weske, J.S. The role of ecotones in the distribution of Andean birds. *Ecology* **1975**, *56*, 562–576. [CrossRef]
9. Armonies, W.; Reise, K. Faunal diversity across a sandy shore. *Mar. Ecol. Prog. Ser.* **2000**, *196*, 49–57. [CrossRef]
10. McLachlan, A.; Jaramillo, E.; Donn, T.E.; Wessels, F. Sandy beach macrofauna communities and their control by the physical environment: A geographical comparison. *J. Coast. Res.* **1993**, *15*, 27–38. [CrossRef]
11. Kark, S. Ecotones and ecological gradients. In *Ecological Systems: Selected Entries from the Encyclopedia of Sustainability Science and Technology*; Leemans, R., Ed.; Springer Science & Business Media: New York, NY, USA, 2013; pp. 147–160. ISBN 9781441908513.
12. Kark, S.; van Rensburg, B.J. Ecotones: Marginal or central areas of transition? *Isr. J. Ecol. Evol.* **2006**, *52*, 29–53. [CrossRef]
13. Schilthuizen, M. Ecotone: Speciation-prone. *Trends Ecol. Evol.* **2000**, *15*, 130–131. [CrossRef]
14. Kolasa, J.; Zalewski, M. Notes on ecotone attributes and functions. *Importance Aquat. Ecotones Freshw. Fish* **1995**, *303*, 1–7. [CrossRef]
15. Angelstam, P. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* **1986**, *47*, 365–373. [CrossRef]
16. Reino, L.; Beja, P.; Osborne, P.E.; Morgado, R.; Fabião, A.; Rotenberry, J.T. Distance to edges, edge contrast and landscape fragmentation: Interactions affecting farmland birds around forest plantations. *Biol. Conserv.* **2009**, *142*, 824–838. [CrossRef]
17. Peyras, M.; Vespa, N.I.; Bellocq, M.I.; Zurita, G.A. Quantifying edge effects: The role of habitat contrast and species specialization. *J. Insect Conserv.* **2013**, *17*, 807–820. [CrossRef]
18. Yekwayo, I.; Pryke, J.S.; Roets, F.; Samways, M.J. Responses of ground living arthropods to landscape contrast and context in a forest-grassland mosaic. *Biodivers. Conserv.* **2017**, *26*, 631–651. [CrossRef]
19. Gillis, J.R. Not continents in miniature: Islands as ecotones. *Isl. Stud. J.* **2014**, *9*, 155–166.
20. McLachlan, A. Coastal beach ecosystems. *Encycl. Biodivers.* **2001**, *1*, 741–751. [CrossRef]
21. Fenu, G.; Carboni, M.; Acosta, A.T.R.; Bacchetta, G. Environmental factors influencing coastal vegetation pattern: New insights from the Mediterranean basin. *Folia Geobot.* **2013**, *48*, 493–508. [CrossRef]
22. Torca, M.; Campos, J.A.; Herrera, M. Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. *Estuar. Coast. Shelf Sci.* **2019**, *218*, 39–47. [CrossRef]
23. Fenu, G.; Cogoni, D.; Ferrara, C.; Pinna, M.S.; Bacchetta, G. Relationships between coastal sand dune properties and plant community distribution: The case of Is Arenas (Sardinia). *Plant Biosyst.* **2012**, *146*, 586–602. [CrossRef]
24. Paetzold, A.; Lee, M.; Post, D.M. Marine resource flows to terrestrial arthropod predators on a temperate island: The role of subsidies between systems of similar productivity. *Oecologia* **2008**, *157*, 653–659. [CrossRef] [PubMed]
25. Ince, R.; Hyndes, G.A.; Lavery, P.S.; Vanderklift, M.A. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. *Estuar. Coast. Shelf Sci.* **2007**, *74*, 77–86. [CrossRef]
26. Polis, G.A.; Hurd, S.D. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* **1996**, *147*, 396–423. [CrossRef]
27. Steibl, S.; Laforsch, C. Compartmentalized organization of ecological niche occupation in insular invertebrate communities. *Ecol. Evol.* **2021**, *11*, 471–480. [CrossRef]
28. Oksanen, J. Multivariate analysis of ecological communities in R: Vegan tutorial. *R Package Version* **2011**, *1*, 1–43. [CrossRef]
29. Team, R.C. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2018.
30. Li, D. hillR: Taxonomic, functional, and phylogenetic diversity and similarity through Hill Numbers. *J. Open Source Softw.* **2018**, *3*, 1041. [CrossRef]
31. Chao, A.; Gotelli, N.J.; Hsieh, T.C.; Sander, E.L.; Ma, K.H.; Colwell, R.K.; Ellison, A.M. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* **2014**, *84*, 45–67. [CrossRef]
32. McArdle, S.B.; McLachlan, A. Sand beach ecology: Swash features relevant to the macrofauna. *J. Coast. Res.* **1992**, *8*, 398–407.
33. Defeo, O.; McLachlan, A. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: A multi-scale analysis. *Mar. Ecol. Prog. Ser.* **2005**, *295*, 1–20. [CrossRef]
34. Woodroffe, C.D. Reef-island topography and the vulnerability of atolls to sea-level rise. *Glob. Planet. Chang.* **2008**, *62*, 77–96. [CrossRef]

35. Colombini, I.; Chelazzi, L. Influence of marine allochthonous input on sandy beach communities. *Oceanogr. Mar. Biol. Annu. Rev.* **2003**, *41*, 115–159.
36. Harrison, S.J.; Morrison, P. Temperatures in a sandy beach under strong solar heating: Patara beach, Turkey. *Estuar. Coast. Shelf Sci.* **1993**, *37*, 89–97. [CrossRef]
37. Dugan, J.E.; Hubbard, D.M.; McCrary, M.D.; Pierson, M.O. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuar. Coast. Shelf Sci.* **2003**, *58*, 25–40. [CrossRef]
38. Feagin, R.A.; Furman, M.; Salgado, K.; Martinez, M.L.; Innocenti, R.A.; Eubanks, K.; Figlus, J.; Huff, T.P.; Sigren, J.; Silva, R. The role of beach and sand dune vegetation in mediating wave run up erosion. *Estuar. Coast. Shelf Sci.* **2019**, *219*, 97–106. [CrossRef]
39. Barboza, F.R.; Gómez, J.; Lercari, D.; Defeo, O. Disentangling diversity patterns in sandy beaches along environmental gradients. *PLoS ONE* **2012**, *7*, e40468. [CrossRef]
40. Scapini, F. Behaviour of mobile macrofauna is a key factor in beach ecology as response to rapid environmental changes. *Estuar. Coast. Shelf Sci.* **2014**, *150*, 36–44. [CrossRef]
41. Page, H.M.; Willason, S.W. Distribution patterns of terrestrial hermit crabs at Enewetak Atoll, Marshall Islands. *Pac. Sci.* **1982**, *36*, 107–117.
42. Hamasaki, K.; Fujikawa, S.; Sanda, T.; Tsuru, T.; Kitada, S. Distributions of land hermit crabs (Decapoda: Coenobitidae) on the coast of the tidal lagoon, Nagura Amparu, on Ishigakijima Island, Japan. *Biogeography* **2017**, *19*, 142–149.
43. Barnes, R.S.K.; Smith, D.J.; Barnes, D.K.A.; Gerlach, J. Variation in the distribution of supralittoral vegetation around an atoll cay: Desroches (Amirante Islands, Seychelles). *Atoll Res. Bull.* **2008**, *565*, 1–6. [CrossRef]
44. Steibl, S.; Laforsch, C. Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*). *Estuar. Coast. Shelf Sci.* **2019**, *231*, 106482. [CrossRef]
45. Romanuk, T.N.; Levings, C.D. Associations between arthropods and the supralittoral ecotone: Dependence of aquatic and terrestrial taxa on riparian vegetation. *Environ. Entomol.* **2003**, *32*, 1343–1353. [CrossRef]
46. Colombini, I.; Brilli, M.; Fallaci, M.; Gagnarli, E.; Chelazzi, L. Food webs of a sandy beach macroinvertebrate community using stable isotopes analysis. *Acta Oecol.* **2011**, *37*, 422–432. [CrossRef]
47. Uetz, G.W. Habitat structure and spider foraging. In *Habitat Structure: The Physical Arrangements of Objects in Space*; Bell, S.S., McCoy, E.D., Mushinsky, H.R., Eds.; Springer: Dordrecht, The Netherlands, 1991; pp. 325–348.
48. Almquist, S. Thermal tolerances and preferences of some dune-living spiders. *Oikos* **1970**, *21*, 230–235. [CrossRef]
49. Lowrie, D.C. The ecological succession of spiders of the Chicago Area Dunes. *Ecology* **1948**, *29*, 334–351. [CrossRef]
50. Almquist, S. Spider associations in coastal sand dunes. *Oikos* **1973**, *24*, 444–457. [CrossRef]
51. MacArthur, R.H.; Wilson, E.O. *The Theory of Island Biogeography*; Princeton University Press: Princeton, NJ, USA, 1967.
52. Whittaker, R.J.; Triantis, K.A.; Ladle, R.J. A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* **2008**, *35*, 977–994. [CrossRef]
53. Thaman, R.R. Atolls—The "biodiversity cool spots" vs "hot spots": A critical new focus for research and conservation. *Micronesica* **2008**, *40*, 33–61.
54. Kench, P.S.; McLean, R.F.; Nichol, S.L. New model of reef-island evolution: Maldives, Indian Ocean. *Geology* **2005**, *33*, 145–148. [CrossRef]
55. Kench, P.S.; Ford, M.R.; Owen, S.D. Patterns of island change and persistence offer alternate adaptation pathways for atoll nations. *Nat. Commun.* **2018**, *9*, 605. [CrossRef] [PubMed]
56. Delcourt, P.A.; Delcourt, H.R. Ecotone dynamics in space and time. In *Landscape Boundaries*; Hansen, A.J., di Castri, F., Eds.; Springer: Berlin/Heidelberg, Germany, 1992; pp. 19–54.
57. Losos, J.B.; Ricklefs, R.E. Adaptation and diversification on islands. *Nature* **2009**, *457*, 830–836. [CrossRef] [PubMed]
58. Barboza, F.R.; Defeo, O. Global diversity patterns in sandy beach macrofauna: A biogeographic analysis. *Sci. Rep.* **2015**, *5*, 14515. [CrossRef]
59. Martínez, M.L.; Intralawan, A.; Vázquez, G.; Pérez-Maqueo, O.; Sutton, P.; Landgrave, R. The coasts of our world: Ecological, economic and social importance. *Ecol. Econ.* **2007**, *63*, 254–272. [CrossRef]

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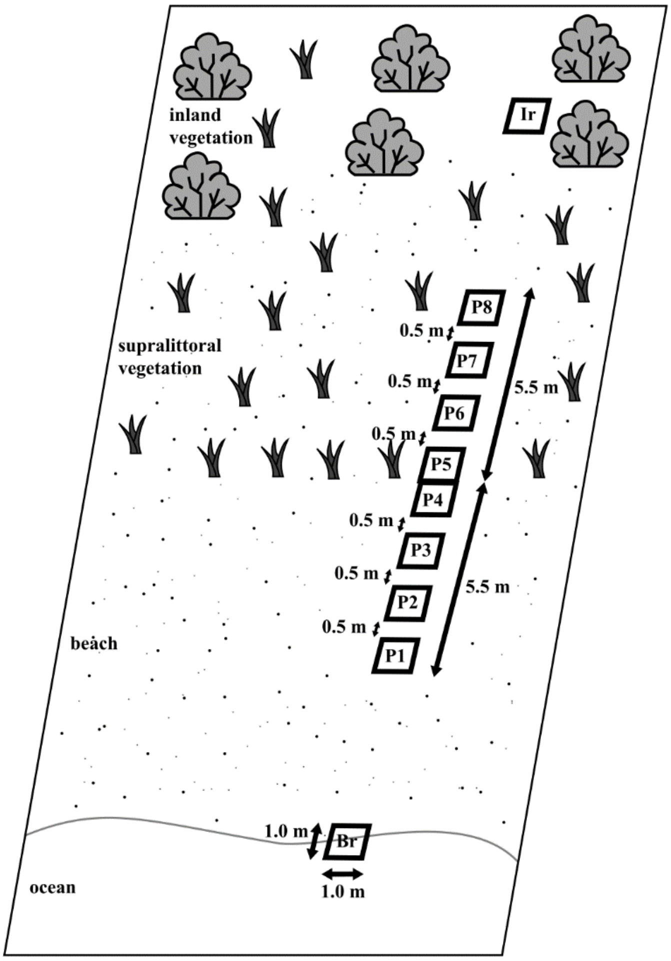
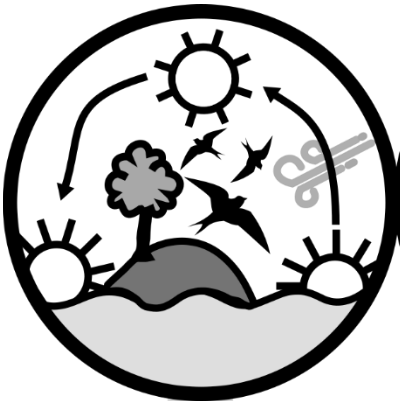


**Supplementary figure B.3-S1: Scheme of sampling transects and plots.** Six transects per island were distributed homogeneously across the accessible beachline of each of the two investigated islands and ten plots per transect positioned perpendicular to the drift line along the beach-inland transition zone. The first plot was positioned directly at the drift line (Br: beach reference plot). The eight plots spanning across the beach-inland transition zone were arranged in a way that the first pioneering plants of the supralittoral vegetation started to occur always between plot 4 (P4) and plot 5 (P5), resulting in four plots at the beach (P1 to P4) and four plots at the supralittoral inland habitat (P5 to P8). The last plot was positioned further in the inland habitat, where shrubs and trees occurred (Ir: inland reference plot).

**B.4** Steibl., S., & Laforsch, C. (2021) The importance of the Maldives as wintering ground for migratory birds of the Central Asian flyway. *Journal of Asian Ornithology*, 37: 80-87.



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# The importance of the Maldives as a wintering ground for migratory birds of the Central Asian flyway

SEBASTIAN STEIBL & CHRISTIAN LAFORSCH

**Among the world's major migratory corridors, research on the Central/South Asian flyways is comparably underrepresented, and little is known about the bird communities of the islands in the Indian Ocean and their relevance for bird migration. Here, we present the first systematic study of a migratory bird assemblage on an island in the Maldives based on data collected over two consecutive non-breeding seasons, using field transect counts conducted on a daily basis. We recorded a total of 22 bird species (11% of all documented species from the Maldives), of which 40% were long-distance migratory species. Most migratory species were waders (Charadriiformes: Charadriidae and Scolopacidae) and were only observed on the narrow sandy beaches which they use as stopover and foraging sites. The inland and urban habitats of the surveyed Maldivian island were only inhabited by resident Maldivian breeding birds. By regularly observing bird species that were thus far considered rare or uncommon, we suggest that certain migratory species more commonly occur on the coralline islands of the Maldives than previously considered, albeit not in large numbers. As many migratory species on the Central Asian flyway are in decline or already globally threatened, our study provides relevant preliminary information about the occurrence of migratory birds on remote islands in the Indian Ocean which will be relevant to future cross-national conservation actions.**

## INTRODUCTION

The annual migration of birds is one of the world's largest movements of biomass (Alerstam 1993). Around 20% of all extant bird species (an estimated 1,855 species) are migratory, meaning that they show annual cyclical movements between their breeding and non-breeding grounds (Kirby *et al.* 2008, Runge *et al.* 2015). The distances that migratory birds cover range from only a few (short-distance migration) to several thousand (long-distance migration) kilometres, thereby crossing whole continents and oceans (Newton 2011). The phenomenon of bird migration is largely synchronised to seasonal changes, as arrivals in the breeding grounds are timed with the return of more favourable conditions for breeding, e.g. the Arctic summer, and the urge to breed and fledge before less favourable conditions return (Alerstam & Lindström 1990, Marra *et al.* 2005).

Recent advances in bird survey and monitoring techniques (e.g. geolocation, satellite-tagging) have broadly extended our understanding of bird migration. It is now well established that the annual routes of migratory birds follow distinct corridors and can therefore be grouped into broad flyways that are often used in a similar way by different species (Boere & Stroud 2006, Kranstauber *et al.* 2015). Flyways are the ranges of migratory bird species through which they move annually between breeding and non-breeding seasons (Boere & Stroud 2006). They can be broadly summed up to, in total, eight global flyways: the East Atlantic, the Mediterranean/Black Sea, the West Asian/African, the Central/South Asian, the Australasian Flyway, and three American/Neotropical flyways (Davidson & Stroud 2016).

The Central Asian flyway is the shortest, as it does not cross the equator. A total of 182 species have been identified to migrate between their temperate to subarctic breeding grounds in Russia and their subtropical to tropical non-breeding grounds on the Indian subcontinent (Szabo & Mundkur 2017). The wetlands of southern India and Sri Lanka mark the endpoint for many wintering species on the Central Asian flyway. Hosting up to one million shorebirds within a single lagoon in some instances, several of these wetlands are of high importance for the annual migration of many species along this flyway (Wijesundara *et al.* 2017). Compared to the other flyways, however, the movement and distribution of migratory bird species along the Central Asian flyway has only recently gained increased scientific attention, and our knowledge about certain aspects within this flyway is still relatively limited (Szabo & Mundkur 2017, Balachandran *et al.* 2018).

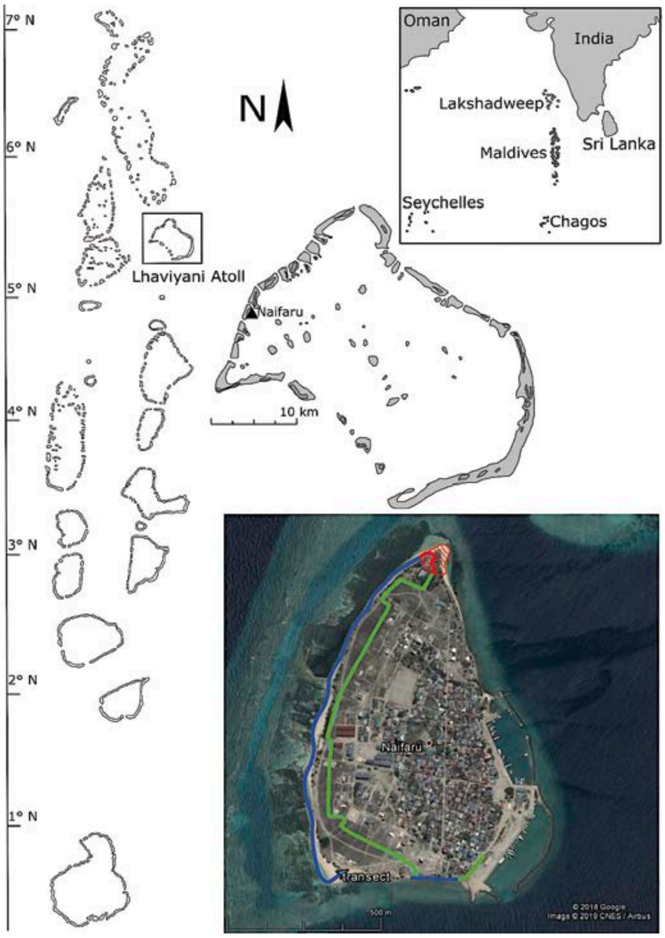
In particular, the role and significance of the smaller island groups in the Indian Ocean south of Sri Lanka (Lakshadweep, Maldives and Chagos) for migratory birds in the Central Asian flyway have been implied but rarely quantified. Only a few studies exist for this area and these cover only short observational periods or rely mainly on incidental bird sightings (Bailey 1967, Feare & High 1977, Anderson & Baldock 2001, Anderson 2007, Anderson & Shimal 2020). It has been argued that the landmasses offered by the Indian Ocean islands provide a critical 'safety net' for birds that fail to make landfall in south India (Penny 1971). However, so far, no systematic surveys have been conducted to demonstrate this. As many of the migratory species in the Central Asian flyway are in decline or already globally threatened, a quantitative and systematic analysis of migratory bird distributions on these islands and their relevance will be crucial to improve the current conservation actions of birds following the Central Asian flyway (Currie *et al.* 2005, Mundkur *et al.* 2017).

This study therefore aimed to investigate if and to what extent a tropical Maldivian island in the Indian Ocean serves as a non-breeding ground for migratory birds. We quantified the bird community on one Maldivian island over two consecutive winters, in February to April 2019 and January 2020. Our study is thereby the first quantitative and systematic analysis of birds in this archipelago. We recorded the abundance of all resident and migratory species along a transect covering the predominant natural and anthropogenic habitats (inland, coast, waste incineration area) of a typical inhabited Maldivian island on a daily basis between February and April 2019 and in January 2020.

## METHODS

Bird abundance and diversity were investigated on Naifaru Island, Lhaviyani (Faadhippolhu) Atoll, Republic of Maldives (Figure 1). The island has approximately 5,000 inhabitants and a total area of 0.553 km$^2$. Most of the island's area, especially the eastern coastline, is covered with buildings, streets and a harbour with vertical concrete walls and sea defence structures. The western part of the island is reclaimed land with grassy vegetation (predominantly *Cyperus dubius, Launaea sarmentosa* and *Dactyloctenium aegyptium*). The island's western coast has a natural shoreline with sandy beaches, interspersed by a rock-covered shoreline and seagrass meadows offshore, as well as a band of dense tropical shrubland and trees. The northern tip of the island holds the local waste incineration area. Due to these land cover characteristics of the island, only the

**Figure 1**. Location of the investigated island and transect. The top right inset shows the location of the Maldives within the Indian Ocean, the left shows the location of the Lhaviyani (Faadhippolhu) atoll within the Republic of Maldives, the central shows the location of Naifaru, the investigated island, within the atoll, and the inset satellite image shows the transect through the island, with colours indicating the three different investigated insular habitats (blue: beach; green: inland; red: waste incineration area). Satellite image obtained from Google Earth 7.1.5.1557; Map data: Google, CNES / Airbus 2019.



grassland, the western shoreline and the northern waste incineration area ('waste tip') were investigated, while the urbanised central and eastern parts of the island were excluded from our fieldwork (Figure 1). The natural beaches and the surrounding band of shrub and tree vegetation on the island of our investigation, Naifaru, are considered to be typical and representative of the overall habitat conditions of most Maldivian islands (Figure 2).

The transect for surveying the present bird species was marked using GPS (Garmin eTrex Vista Cx; Garmin International Inc., Olathe, Kansas, USA). The transect measured in total 3,190 m. To further distinguish between the different natural and anthropogenic habitats on the investigated island, the transect was separated into three broad habitat categories: (I) coastline transect, i.e. 'beach', (II) inland transect, i.e. 'inland' and (III) local waste incineration area, i.e. 'waste tip' (Figures 1 & 2).

The whole island transect was walked daily between 3 February and 30 April 2019 and between 4 and 26 January 2020, resulting in 96 sampling days in total. The survey along the transect started each day with sunrise, between 05h54 and 06h23 (for an overview of the sunrise times for each sampling day, refer to Appendix 1). The transect was walked at the same pace, i.e. within 50 minutes, and always in the same direction. All bird species observed in a range of a maximum of 25 m left and right of the transect were recorded and counted separately for each of the three habitats. As the Maldivian islands' beaches are commonly narrow, microtidal beaches without any large tidal flats that are completely exposed at any point of the tidal cycle (Kench & Brander 2006), all birds present can be recorded using these transect dimensions (Figure 2). Tidal times and current tide level, ranging from 0 m (neap tide) to 0.77 m (spring tide), were recorded for each sampling day (Table A1). One observer (SS) made all observations using 8–15x42 binoculars and Grimmett *et al*. (2014) as a field guide for identification.

Statistical analysis was carried out using R 3.5.3 (R Core Team 2018). The relative abundance of each species in the three habitats (beach, inland, waste tip) was statistically compared using non-parametric Kruskal-Wallis tests and Dunn-Bonferroni post hoc tests with a p-value correction. To investigate the possible drivers that can explain the presence or absence of wader species, we analysed the influence of tidal times on the occurrence of the recorded bird species. Therefore, we only used the occurrence data of the 11 bird species that occurred significantly more often along the beach than in the inland or at the waste tip, as sufficient data points were needed for correlation analysis (Table 1). Linear regression was performed to investigate the correlation between tide level and abundance and between tide level and overall species richness in the beach habitat. The overall abundance of each bird species, i.e. abundance in all three habitat categories taken together, during the first sampling year (3 February–30 April 2019) was plotted and regression curves fitted using local weighted polynomial regression (LOESS) with 95% confidence intervals and span of $\alpha = 0.75$. This type of regression analysis was used as it allows models to represent more complex relationships through 'local' approximations for the investigated sampling period, rather than trying to fit a simple linear regression throughout the whole sampling period, which might not adequately represent the changes in daily abundances over the investigated time.

## RESULTS

Throughout the investigated months and the two consecutive years, a total of 22 species (19 genera, 9 families) were recorded on Naifaru. The occurrence of the observed species varied between the three different habitats and between the two years (Table 1). Twenty-one bird species were recorded during the 2019 sampling period and 9 species in January 2020. Three of the 11 bird species that occurred significantly more often in the beach habitat than in the other two insular habitats (Green-backed Heron *Butorides striata,* Lesser Sandplover *Charadrius mongolus*, Common Sandpiper *Actitis hypoleucos*) showed a significant correlation between their abundance and the tide level (Table 2). Overall bird species richness in the beach habitat did not correlate significantly with tide level ($R^2 = 0.043$, $t = -2.310$, $P = 0.231$). The occurrence of the recorded bird species further varied throughout the three-month sampling period in 2019 (Figures 3 & A1). Some species, especially residents such as House Crow *Corvus splendens* and Grey Heron *Ardea cinerea*, showed fairly consistent daily abundances during the sampling period. Others, especially waders such as Greater Sandplover *Charadrius leschenaultii*, Sanderling *Calidris alba* and Common Greenshank *Tringa nebularia*, were temporally limited in their occurrence and/or decreased in abundance over the observation period.

## DISCUSSION

The southern endpoint of the Central Asian flyway comprises the wetlands of south India, Sri Lanka and adjacent islands in the Indian Ocean (Szabo & Mundkur 2017). While the occurrence and distribution of migratory bird species in the former regions have been systematically documented (e.g. Kannan & Pandiyan 2012,

**Figure 2**. Study site. **A**) the surveyed beach habitat on Naifaru is typical and representative of most Maldivian islands' beaches. The microtidal beaches have an overall narrow and reflective morphology without any tidal flats or coastal wetlands that fall dry during low tide. The beaches are demarcated oceanward by the waterline and increase fairly rapidly in water depth toward the lagoon and coral reefs; landward, the beaches are demarcated by a small band of pioneering plants (predominantly *Cyperus* spp., *Dactyloctenia* spp.), immediately followed by dense shrub and tree vegetation (predominantly *Suriana maritima, Scaevola taccada, Tournefortia argentea, Pandanus* spp.). **B**) the surveyed inland habitat is characterised by grassland vegetation (front) and a band of dense shrub and tree vegetation towards the shoreline (background, left).

Mundkur *et al.* 2017, Wijesundara *et al.* 2017), we are unaware of any systematic long-term observations on the distribution of migratory birds on any Indian Ocean island. By systematically surveying the bird community on one Maldivian island, our findings provide first deeper insights into the avifaunal community composition on these remote low-lying atoll islands during the northern hemispheric winter. We demonstrated that a small set of shorebird species used a Maldivian island as a wintering site, albeit not occurring in large numbers. The absence of any larger and more diverse flocks of shorebirds likely stems from the overall morphology and geography of the low-lying Maldivian atoll islands, which have steep and narrow beaches without any tidal flats or extensive wetlands that can support high bird abundances or more specialised taxa, together with their overall remoteness and isolation in the Indian Ocean, roughly 500 km off the Indian subcontinent (Figure 1).

Almost 40% of the recorded bird species were migratory waders with pan-Palearctic (Kentish Plover *Charadrius alexandrinus*, Ruddy Turnstone *Arenaria interpres,* Sanderling, Common Greenshank, Common Sandpiper), west and central Palearctic (Whimbrel *Numenius phaeopus*), central Palearctic (Lesser and Greater Sandplovers) or central and east Palearctic (Grey Plover *Pluvialis squatarola*) breeding ranges (Feare & High 1977). Some of these species are also fairly common on other Indian Ocean islands, such as the Seychelles (Feare & High 1977) and the Chagos Archipelago (Bourne 1971, Hutson 1975). However, they have been recorded only in relatively small numbers in mainland India or Sri Lanka during the Asian waterbird census: 1–55 Greater Sandplovers recorded annually on Sri Lanka and 21–393 Whimbrel recorded annually in India (Kannan & Pandiyan 2012, Mundkur *et al.* 2017, Wijesundara *et al.* 2017). Our systematic observations suggest that Maldivian islands such as Naifaru are probably more frequently used as a non-breeding ground by multiple wader species, albeit not in large numbers, than previously thought as, for example, the Sanderling was observed fairly regularly, with up to seven individuals per day between March and April 2019. Sanderling had been considered a rare to uncommon visitor, with only five confirmed observations in the Maldives between 2001 and 2007 (Anderson 2007, Anderson & Shimal 2020).

Only one wader species, the Common Sandpiper, was recorded daily on the surveyed island, while all other species showed daily fluctuations in their occurrence (Figures 3 & A1). These daily fluctuations suggests that most recorded waders may not remain on one island throughout the whole non-breeding season but rather disperse widely to forage between the numerous neighbouring

**Table 1. Occurrence of bird species in different island habitats and years. For each species, the proportional occurrence (i.e. on how many of the 96 sampling days was a given species recorded?) in percent and mean daily abundance (mean ± SD) in each of the three investigated island habitats (beach, inland, waste tip) is listed. Different letters in brackets indicate significant differences in mean daily abundance between the three island habitats for each species (Kruskal-test, Dunn Bonferroni post hoc testing; $P < 0.05$), the same letters indicate no significant differences ($P > 0.05$). Additionally, the number of days with observations for each species in the two sampling periods (February–April 2019, January 2020) is presented.**

| | Island habitat | | | Year | |
|---|---|---|---|---|---|
| **Species** | **beach** | **inland** | **waste tip** | **2019** | **2020** |
| Little Swift *Apus affinis* | 0% (0 ± 0) [A] | 4% (0.06 ± 0.34) [B] | 0% (0 ± 0) [A] | 4 | 0 |
| Unidentified swift *Apus* sp. | 0% (0 ± 0) [A] | 1% (0.01 ± 0.10) [A] | 0% (0 ± 0) [A] | 1 | 0 |
| Asian Koel *Eudynamys scolopaceus* | 0% (0 ± 0) [A] | 45% (0.53 ± 0.64) [B] | 0% (0 ± 0) [A] | 41 | 2 |
| White-breasted Waterhen *Amaurornis phoenicurus* | 14% (0.14 ± 0.38) [A] | 9% (0.09 ± 0.29) [A] | 0% (0 ± 0) [B] | 22 | 0 |
| Green-backed Heron *Butorides striata* | 85% (2.03 ± 1.37) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 64 | 18 |
| Indian Pond-heron *Ardeola grayii* | 17% (0.16 ± 0.37) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 16 | 0 |
| Cattle Egret *Bubulcus ibis* | 39% (0.48 ± 0.68) [A] | 17% (0.28 ± 0.73) [B] | 69% (2.16 ± 1.78) [C] | 71 | 0 |
| Grey Heron *Ardea cinerea* | 96% (2.61 ± 1.20) [A] | 3% (0.03 ± 0.17) [B] | 0% (0 ± 0) [B] | 73 | 20 |
| Grey Plover *Pluvialis squatarola* | 1% (0.01 + 0.10) [A] | 0% (0 ± 0) [A] | 0% (0 ± 0) [A] | 1 | 0 |
| Kentish Plover *Charadrius alexandrinus* | 2% (0.02 ± 0.14) [A] | 0% (0 ± 0) [A] | 0% (0 ± 0) [A] | 2 | 0 |
| Lesser Sandplover *Charadrius mongolus* | 53% (0.88 ± 1.05) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 44 | 7 |
| Greater Sandplover *Charadrius leschenaultii* | 34% (0.46 ± 0.76) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 33 | 0 |
| Whimbrel *Numenius phaeopus* | 7% (0.09 ± 0.35) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 7 | 0 |
| Ruddy Turnstone *Arenaria interpres* | 13% (0.19 ± 0.57) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 12 | 0 |
| Sanderling *Calidris alba* | 32% (0.72 ± 1.36) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 25 | 6 |
| Common Sandpiper *Actitis hypoleucos* | 100% (10.23 ± 3.03) [A] | 34% (0.39 ± 0.64) [B] | 1% (0.01 ± 0.10) [C] | 76 | 20 |
| Common Greenshank *Tringa nebularia* | 20% (0.19 ± 0.40) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 19 | 0 |
| Black-naped Tern *Sterna sumatrana* | 4% (0.16 ± 0.86) [A] | 0% (0 ± 0) [B] | 0% (0 ± 0) [B] | 4 | 0 |
| Lesser Crested Tern *Thalasseus bengalensis* | 1% (0.01 ± 0.10) [A] | 0% (0 ± 0) [A] | 0% (0 ± 0) [A] | 0 | 1 |
| Greater Crested Tern *Thalasseus bergii* | 1% (0.01 ± 0.10) [A] | 0% (0 ± 0) [A] | 0% (0 ± 0) [A] | 1 | 0 |
| Brown Shrike *Lanius cristatus* | 0 (0 ± 0) [A] | 19% (0.18 ± 0.39) [B] | 0% (0 ± 0) [A] | 18 | 0 |
| House Crow *Corvus splendens* | 99% (9.52 ± 7.14) [A] | 100% (22.7 ± 6.64) [B] | 100% (48.5 ± 23.27) [C] | 76 | 20 |
| Barn Swallow *Hirundo rustica* | 6% (0.07 ± 0.29) [A] | 3% (0.04 ± 0.24) [AB] | 0% (0 ± 0) [B] | 5 | 3 |
| Species richness | 19 | 9 | 3 | 21 | 9 |
| Overall abundance | 28.10 ± 8.15 | 24.40 ± 6.75 | 50.76 ± 23.80 | 35.9 ± 20.21 | 28.3 ± 11.22 |

islands in the atoll (Penny 1971, Johnson 1979). The occurrence of most wader species was not influenced by the tidal regime, suggesting that they do not follow the tidal-dependent occurrence of beach macroinvertebrates (Steibl & Laforsch 2019). It is more likely that human disturbances from the local population trigger these inner-atoll movements, given that people regularly use the beaches for recreational and fishing activities (Davidson & Rothwell 1993). However, another possible explanation for the fluctuations could be that the species reside further south, e.g. in the southern Maldives or the Chagos Archipelago, and used the investigated island for stopovers on their migration to their breeding grounds in the northern latitudes (Penny 1971). As we recorded the abundance over different months in the two study years, the differences in observation between 2019 and 2020 might indicate that many of the observed species winter even further south and only transit through the central/northern Maldivian atolls in their spring migration.

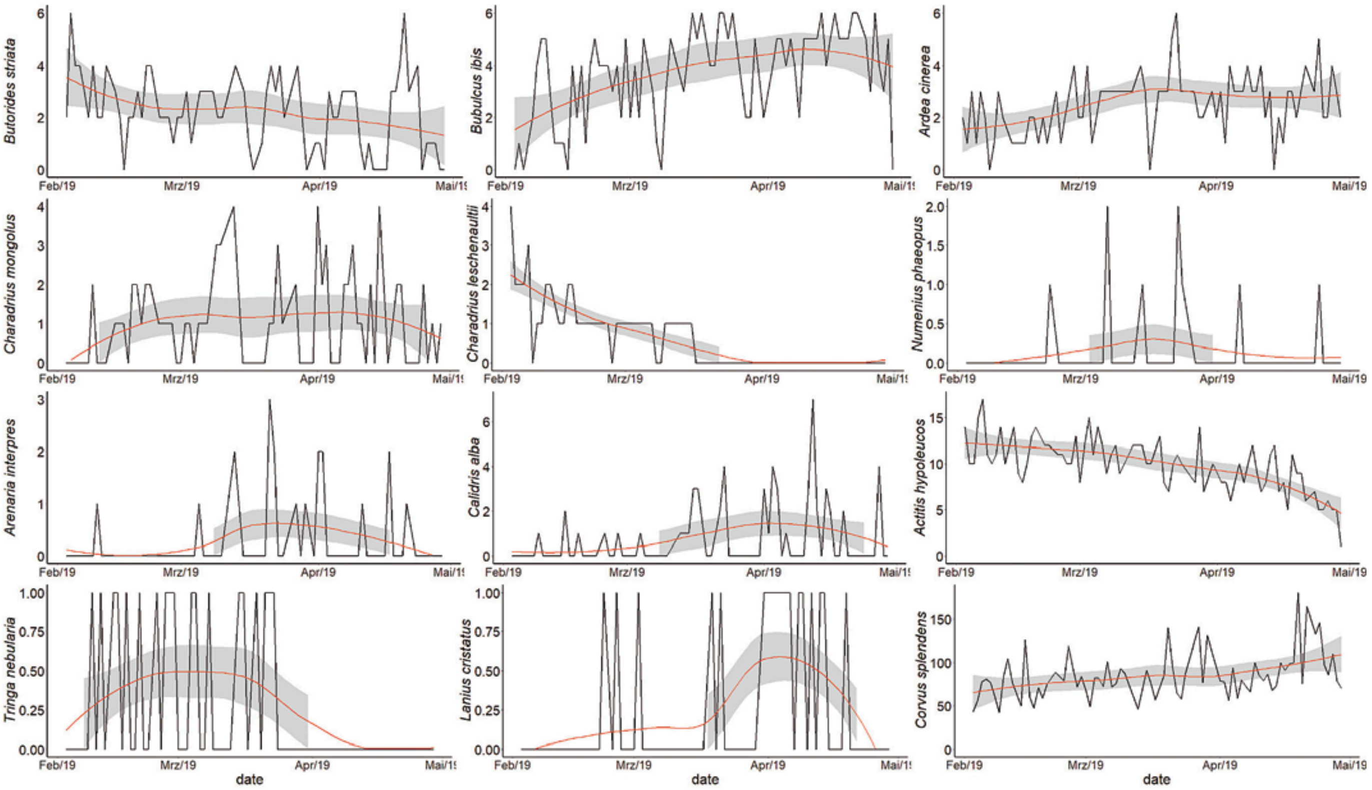
Apart from the non-breeding waders, Little Swift *Apus affinis*, Barn Swallow *Hirundo rustica* and Brown Shrike *Lanius cristatus* were the only migratory landbirds recorded on Naifaru. For the Brown Shrike, fewer than 10 confirmed observations exist from the whole Maldives, rendering this species being listed as 'uncommon' in the 2020 Maldivian bird atlas (Anderson & Shimal 2020). We recorded this species 18 times between February and April 2019, suggesting that this shrike could occur more regularly as a winter visitor to the Maldives than previously thought (Grimmett *et al.* 2014, Anderson & Shimal 2020). However, further systematic surveying on more islands and different atolls would be necessary to establish whether the observation of the Brown Shrike on Naifaru was an accidental recording of an influx of an otherwise vagrant, or if greater numbers of this species use the Maldivian islets as a non-breeding ground during the northern hemispheric winter.

Besides the migratory species, we recorded eight resident breeding birds on Naifaru island. By far the most common resident was the House Crow, which was particularly abundant around the waste incineration area. This clustered occurrence underlines that food wastes are relevant anthropogenic food resources for this species (Wilson *et al.* 2015). Reducing the amount of unregulated garbage disposal and better recycling systems for biodegradable

**Table 2. Correlation analysis between species occurrence and tidal range. Using linear regression models, the correlation between tide level and the occurrence of those bird species that were significantly more often recorded in the beach habitat than in the other insular habitats (Table 1) was calculated and *P*-values were corrected for multiple testing using Bonferroni correction. The abundance of three out of the 11 considered species correlated significantly with tide level (indicated by asterisks: *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).**

| Species | $R^2$ | t-value | p-value |
|---|---|---|---|
| Green-backed Heron *Butorides striata* | 0.155 | -4.301 | < 0.001 (***) |
| Indian Pond-heron *Ardeola grayii* | 0.040 | -2.382 | 0.134 |
| Grey Heron *Ardea cinerea* | 0.020 | -1.723 | 0.409 |
| Lesser Sandplover *Charadrius mongolus* | 0.069 | -2.855 | 0.047 (*) |
| Greater Sandplover *Charadrius leschenaultii* | 0.021 | 1.759 | 0.409 |
| Whimbrel *Numenius phaeopus* | 0.043 | -2.305 | 0.140 |
| Ruddy Turnstone *Arenaria interpres* | 0.052 | -2.496 | 0.114 |
| Sanderling *Calidris alba* | -0.006 | -0.594 | 1.000 |
| Common Sandpiper *Actitis hypoleucos* | 0.104 | 3.481 | 0.007 (**) |
| Common Greenshank *Tringa nebularia* | -0.010 | 0.054 | 1.000 |
| Black-naped Tern *Sterna sumatrana* | 0.014 | -1.547 | 0.409 |

**Figure 3**. Temporal variation in bird species abundance on a remote Indian Ocean island. For the 12 most common bird species on Naifaru, the daily abundance of individuals is plotted over the three-month sampling period from 3 February 2019 to 30 April 2019. Smoothing of the abundance curves was estimated by fitting local weighted polynomial regression (LOESS); a grey area around curves indicates 95% confidence intervals. For the abundance plots of the remaining, more rarely observed bird species during this survey, see Figure A1.



waste might be critical to local government policies that aim to contain the number of House Crows on the local islands (Ash & Shafeeg 1994).

Ecologically, the overall variation in bird abundance and species richness between the three investigated natural and anthropogenic habitats further suggests that birds mediate little cross-habitat energy and biomass transfer on the small Maldivian islands (Barrett *et al.* 2005, Steibl *et al.* 2021). Wader and egret species that feed on marine resources along the beach did not disperse inland and are thus likely not subsidising the different interior insular habitat compartments with their guano to any considerable extent (Anderson & Polis 1999, Young *et al.* 2010, Steibl & Laforsch 2021). Other than on larger tropical islands, most Maldivian islands lack widespread inland nesting seabirds such as petrels, shearwaters or storm-petrels, and thus the subsidising effects of sea- and shorebirds for the insular interior might play a less significant role than on other island systems (Ash & Shafeeg 1994, Fukami *et al.* 2006).

Overall, our first systematic investigation of a bird community on one Maldivian island over two non-breeding seasons gives relevant insights into the avifaunal community composition and the occurrence of migratory bird species on these remote Indian Ocean islands. Approximately 11% (22 out of 194) of all confirmed bird species recorded in the Maldives (including vagrants and rarities) were found on the investigated island during the sampling periods (Anderson & Shimal 2020). Species considered 'rare' or 'uncommon', such as Sanderling and Brown Shrike, have been regularly observed in this first ever systematic sampling of the islands' avifauna, even by surveying the bird assemblage on just one Maldivian island (Anderson & Shimal 2020). The regular observations of bird species considered uncommon on the Maldives underline our overall incomplete understanding of the role of these Indian Ocean islands as a non-breeding ground for migratory birds of the Central Asian flyway. As the Maldivian archipelago consists of more than 1,200 islands, most bearing similar habitat conditions to the one investigated in this study, it is likely that the overall relevance of the Maldivian islands as an extended endpoint of the Central Asian flyway might have been underestimated (Gischler *et al.* 2014). Large-scale and systematic surveying of migratory and resident bird species in all of the Maldives' 26 atolls will be necessary to understand the significance of these remote Indian Ocean islands for bird migration more thoroughly. Until then, our survey on one Maldivian island offers the first systematically documented insights into the avifaunal community of these islets and their possible relevance for bird migration. Thoroughly understanding the Indian Ocean islands' relevance for birds will ultimately help establish improved conservation measures to protect migratory birds of the Central Asian flyway more completely.

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## REFERENCES

Alerstam, T. (1993) *Bird migration*. Cambridge, UK: Cambridge University Press.

Alerstam, T. & Lindström, Å. (1990) Optimal bird migration: the relative importance of time, energy, and safety. Pp.331–351 in E. Gwinner (ed.) *Bird migration*. Berlin Heidelberg: Springer Verlag.

Anderson, R.C. (2007) New records of birds from the Maldives. *Forktail* 23: 135–144.

Anderson, R.C. & Baldock, M. (2001) New records of birds from the Maldives, with notes on other species. *Forktail* 17: 67–74.

Anderson, W.B. & Polis, G.A. (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* 118: 324–332.

Anderson, R.C. & Shimal, M. (2020) A checklist of birds of the Maldives. *Indian Bird Monographs* 3: 1–56.

Ash, J.S. & Shafeeg, A. (1994) Birds of the Maldive Islands, Indian Ocean. *Forktail* 10: 3–32.

Bailey, R.S. (1967) Migrant waders in the Indian Ocean. *Ibis* 109: 437–439.

Balachandran, S., Katti, T. & Manakadan, R. (2018) *Indian bird migration atlas*. Mumbai: Bombay Natural History Society & Oxford University Press.

Barrett, K., Anderson, W.B., Wait, D.A., Grismer, L.L., Polis, G.A. & Rose, M.D. (2005) Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos* 1: 145–153.

Boere, G.C. & Stroud, D.A. (2006) The flyway concept: what it is and what it isn't. Pp.40–47 in G.C. Boere, C.A. Galbraith & D.A. Stroud (eds.) *Waterbirds around the world*. Edinburgh: The Stationery Office.

Bourne, W. (1971) The birds of the Chagos group, Indian Ocean. *Atoll Res. Bull.* 149: 175–207.

Currie, D., Wunderle, J.M. Jr., Ewert, D.N., Anderson, M.R., Davis, A. & Turner, J. (2005) Habitat distribution of birds wintering in central Andros, the Bahamas: implications for management. *Caribeean J. Sci.* 41: 75–87.

Davidson, N.C. & Rothwell, P.I. (1993) Human disturbance to waterfowl on estuaries: the conservation and coastal management implications of current knowledge. *Wader Study Gr. Bull.* 68: 97–105.

Davidson, N.C. & Stroud, D.A. (2016) Waterbird flyways and history of international cooperation for waterbird conservation. Pp.1–8 in C.M. Finlayson (ed.) *The Wetland Book*. Dordrecht: Springer.

Feare, C.J. & High, J. (1977) Migrant shorebirds in the Seychelles. *Ibis* 119: 323–338.

Fukami, T., Wardle, D.A., Bellingham, P.J., Mulder, C.P.H., Towns, D.R., Yeates, G.W., Bonner, K.I., Durrett, M.S., Grant-Hoffman, M.N. & Williamson, W.M. (2006) Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Lett.* 9: 1299–1307.

Gischler, E., Storz, D. & Schmitt, D. (2014) Sizes, shapes, and patterns of coral reefs in the Maldives, Indian Ocean: the influence of wind, storms, and precipitation on a major tropical carbonate platform. *Carbonates and Evaporites* 29: 73–87.

Grimmett, R., Inskipp, C. & Inskipp, T. (2014) *Birds of the Indian subcontinent*. London: Bloomsbury.

Hutson, A.M. (1975) Observations on the birds of Diego Garcia, Chagos archipelago, with notes on other vertebrates. *Atoll Res. Bull.* 1–25.

Johnson, O.W. (1979) Biology of shorebirds summering on Enewetak Atoll. *Stud. Avian Biol.* 2: 193–205.

Kannan, V. & Pandiyan, J. (2012) Shorebirds (Charadriidae) of Pulicat Lake, India with special reference to conservation. *World J. Zool.* 7: 178–191.

Kench, P.S. & Brander, R.W. (2006) Response of reef island shorelines to seasonal climate oscillations: South Maalhosmadulu atoll, Maldives. *J. Geophys. Res.* 111: 1–12.

Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R., O'Sullivan, J., Tucker, G.M. & Newton, I. (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conserv. Int.* 18: 49–73.

Kranstauber, B., Weinzierl, R., Wikelski, M. & Safi, K. (2015) Global aerial flyways allow efficient travelling. *Ecol. Lett.* 18: 1338–1345.

Marra, P.P., Francis, C.M., Mulvihill, R.S. & Moore, F.R. (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142: 307–315.

Mundkur, T., Langendoen, T. & Watkins, D. (2017) *The Asian waterbird census 2008–2015: results of coordinated counts in Asia and Australasia*. Ede: Wetlands International.

Newton, I. (2011) The ecology of bird migration patterns. *BOU Proc*. 1–3.

Penny, M.J. (1971) Migrant waders at Aldabra, September 1967 – March 1968. *Philos. Trans. R. Soc. London. B, Biol. Sci*. 260: 549–559.

R Core Team (2018) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015) Protected areas and global conservation of migratory birds. *Science* 350: 1255–1258.

Steibl, S. & Laforsch, C. (2019) Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*). *Estuar. Coast. Shelf Sci.* 231: 106482.

Steibl, S. & Laforsch, C. (2021) Compartmentalized organization of ecological niche occupation in insular invertebrate communities. *Ecol. Evol*. 11(1): 471–480.

Steibl, S., Sigl, R. *et al.* (2021) Allochthonous resources are less important for faunal communities on highly productive, small tropical islands. *Ecol. Evol.* 11(19): 13128–13138. Available at https://doi.org/10.1002/ece3.8035.

Szabo, J.K. & Mundkur, T. (2017) Conserving wetlands for migratory waterbirds in South Asia. Pp.1–587 in B.A.K. Prusty (ed.) *Wetland science: perspectives from South Asia*. Springer.

Wijesundara, C.S., Warakagoda, D., Sirivardana, U., Chathuranga, D., Hettiarachchi, T., Perera, N., Rajkumar, P., Wanniarachchi, S. & Weerakoon, G. (2017) Diversity and conservation of waterbirds in the northern avifaunal region of Sri Lanka. *Ceylon J. Sci.* 46: 143.

Wilson, R.F., Sarim, D. & Rahman, S. (2015) Factors influencing the distribution of the invasive house crow (*Corvus splendens*) in rural and urban landscapes. *Urban Ecosyst.* 18: 1389–1400.

Young, H.S., McCauley, D.J., Dunbar, R.B. & Dirzo, R. (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proc. Natl. Acad. Sci. U.S.A.* 107: 2072–2077.

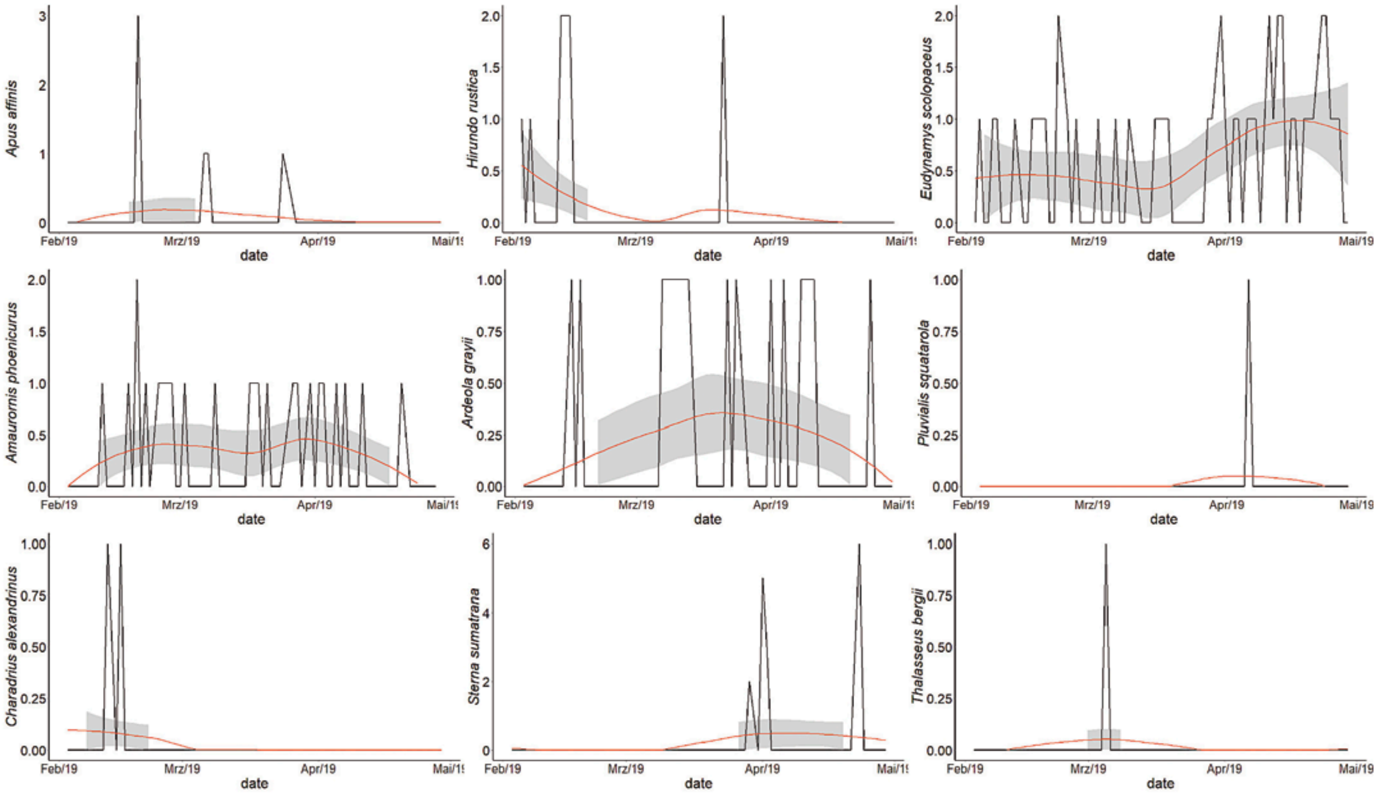
***Sebastian Steibl & Christian Laforsch****, Department of Animal Ecology 1 and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany. Email (corresponding author): sebastian.steibl@uni-bayreuth.de*

**Appendix 1.** Metadata for the sampling period. For each sampling day, the sunrise (i.e. sampling start time), low and high tide events and the current tide level at the start of sampling are listed.

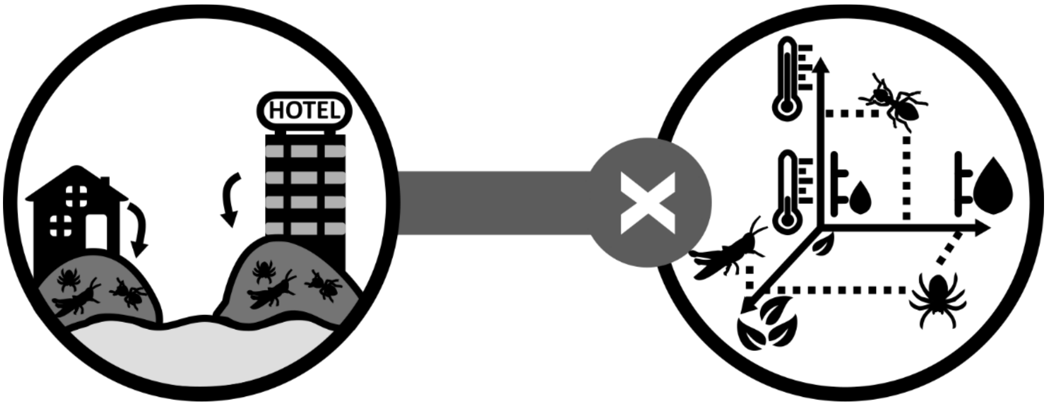
| Date | Sunrise | Low tides | High tides | Tide level at sampling start (m) |
|---|---|---|---|---|
| 03/02/2019 | 06h23 | 06h45 (0.46 m), 17h47 (0.16 m) | 00h27 (0.91 m), 11h25 (0.66 m) | 0.48 |
| 04/02/2019 | 06h23 | 07h08 (0.42 m), 18h21 (0.13 m) | 00h53 (0.95 m), 12h05 (0.69 m) | 0.49 |
| 05/02/2019 | 06h23 | 07h31 (0.38 m), 18h52 (0.13 m) | 01h18 (0.97 m), 12h41 (0.72 m) | 0.48 |
| 06/02/2019 | 06h23 | 07h55 (0.34 m), 19h22 (0.14 m) | 01h41 (0.98 m), 13h16 (0.75 m) | 0.50 |
| 07/02/2019 | 06h23 | 08h19 (0.30 m), 19h50 (0.17 m) | 02h04 (0.98 m), 13h49 (0.76 m) | 0.51 |
| 08/02/2019 | 06h23 | 08h45 (0.28 m), 20h18 (0.21 m) | 02h26 (0.97 m), 14h23 (0.76 m) | 0.54 |
| 09/02/2019 | 06h23 | 09h10 (0.26 m), 20h44 (0.27 m) | 02h47 (0.99 m), 14h58 (0.75 m) | 0.58 |
| 10/02/2019 | 06h23 | 09h36 (0.25 m), 21h11 (0.34 m) | 03h06 (0.91 m), 15h34 (0.73 m) | 0.58 |
| 11/02/2019 | 06h22 | 10h03 (0.24 m), 21h39 (0.42 m) | 03h25 (0.87 m), 16h16 (0.71 m) | 0.59 |
| 12/02/2019 | 06h22 | 10h34 (0.24 m), 22h09 (0.51 m) | 03h41 (0.82 m), 17h12 (0.69 m) | 0.60 |
| 14/02/2019 | 06h22 | 12h13 (0.25 m) | 04h40 (0.73 m), 21h28 (0.71 m) | 0.62 |
| 15/02/2019 | 06h22 | 02h04 (0.69 m), 13h42 (0.24 m) | 03h16 (0.69 m), 22h52 (0.80 m) | 0.56 |
| 16/02/2019 | 06h22 | 15h17 (0.20 m) | 23h30 (0.88 m) | 0.57 |
| 17/02/2019 | 06h21 | 06h03 (0.56 m), 16h28 (0.14 m) | 09h24 (0.61 m) | 0.56 |
| 18/02/2019 | 06h21 | 06h17 (0.48 m), 17h24 (0.09 m) | 00h01 (0.94 m), 10h51 (0.68 m) | 0.48 |
| 19/02/2019 | 06h21 | 06h42 (0.39 m), 18h12 (0.07 m) | 00h31 (0.99 m), 11h52 (0.76 m) | 0.43 |
| 20/02/2019 | 06h21 | 07h11 (0.30 m), 18h55 (0.08 m) | 01h00 (1.02 m), 12h44 (0.83 m) | 0.41 |
| 21/02/2019 | 06h21 | 07h42 (0.21 m), 19h36 (0.12 m) | 01h29 (1.03 m), 13h32 (0.88 m) | 0.39 |
| 22/02/2019 | 06h20 | 08h16 (0.14 m), 20h15 (0.19 m) | 01h58 (1.02 m), 14h18 (0.14 m) | 0.42 |
| 24/02/2019 | 06h20 | 09h27 (0.10 m), 21h29 (0.36 m) | 02h54 (0.95 m), 15h51 (0.84 m) | 0.50 |
| 25/02/2019 | 06h19 | 10h04 (0.13 m), 22h06 (0.46 m) | 03h21 (0.89 m), 16h41 (0.79 m) | 0.55 |
| 26/02/2019 | 06h19 | 10h44 (0.18 m), 22h46 (0.54 m) | 03h47 (0.82 m), 17h41 (0.73 m) | 0.59 |
| 27/02/2019 | 06h19 | 11h31 (0.25 m), 23h55 (0.62 m) | 04h08 (0.75 m), 19h19 (0.69 m) | 0.61 |
| 28/02/2019 | 06h18 | 12h41 (0.31 m) | 04h15 (0.67 m), 21h59 (0.71 m) | 0.58 |
| 01/03/2019 | 06h18 | 14h34 (0.33 m) | 23h07 (0.77 m) | 0.51 |
| 02/03/2019 | 06h18 | 06h13 (0.53 m), 16h05 (0.31 m) | 09h16 (0.56 m), 23h40 (0.82 m) | 0.53 |
| 03/03/2019 | 06h17 | 06h13 (0.48 m), 17h00 (0.27 m) | 10h46 (0.60 m) | 0.48 |
| 04/03/2019 | 06h17 | 06h27 (0.42 m), 17h39 (0.23 m) | 00h06 (0.86 m), 11h32 (0.66 m) | 0.41 |
| 05/03/2019 | 06h17 | 06h44 (0.37 m), 18h12 (0.20 m) | 00h29 (0.90 m), 12h08 (0.72 m) | 0.41 |
| 06/03/2019 | 06h16 | 07h03 (0.31 m), 18h43 (0.19 m) | 00h50 (0.92 m), 12h40 (0.77 m) | 0.40 |
| 07/03/2019 | 06h16 | 07h23 (0.26 m), 19h12 (0.20 m) | 01h11 (0.94 m), 13h11 (0.81 m) | 0.39 |
| 08/03/2019 | 06h16 | 07h45 (0.22 m), 19h40 (0.22 m) | 01h31 (0.94 m), 13h42 (0.84 m) | 0.40 |
| 09/03/2019 | 06h15 | 08h07 (0.19 m), 20h07 (0.26 m) | 01h51 (0.93 m), 14h13 (0.86 m) | 0.36 |
| 10/03/2019 | 06h15 | 08h30 (0.17 m), 20h34 (0.31 m) | 02h10 (0.90 m), 14h44 (0.86 m) | 0.43 |
| 13/03/2019 | 06h14 | 09h47 (0.17 m), 22h02 (0.52 m) | 02h47 (0.80 m), 16h41 (0.78 m) | 0.49 |
| 15/03/2019 | 06h13 | 11h15 (0.24 m) | 03h24 (0.71 m), 20h01 (0.72 m) | 0.48 |
| 16/03/2019 | 06h12 | 12h48 (0.28 m) | 22h07 (0.77 m) | 0.48 |
| 17/03/2019 | 06h12 | 14h55 (0.28 m) | 22h54 (0.84 m) | 0.53 |
| 19/03/2019 | 06h11 | 05h46 (0.39 m), 17h19 (0.20 m) | 11h08 (0.72 m), 23h58 (0.92 m) | 0.42 |
| 20/03/2019 | 06h10 | 06h12 (0.29 m), 18h07 (0.18 m) | 12h01 (0.82 m) | 0.29 |
| 21/03/2019 | 06h10 | 06h41 (0.18 m), 18h49 (0.19 m) | 00h27 (0.95 m), 12h47 (0.91 m) | 0.23 |
| 22/03/2019 | 06h10 | 07h12 (0.09 m), 19h28 (0.22 m) | 00h55 (0.96 m), 13h29 (0.96 m) | 0.24 |
| 23/03/2019 | 06h09 | 07h44 (0.04 m), 20h06 (0.27 m) | 01h24 (0.95 m), 14h10 (0.98 m) | 0.27 |
| 24/03/2019 | 06h09 | 08h17 (0.02 m), 20h42 (0.33 m) | 01h52 (0.93 m), 14h50 (0.97 m) | 0.31 |
| 27/03/2019 | 06h07 | 09h55 (0.17 m), 22h33 (0.53 m) | 03h11 (0.77 m), 16h57 (0.79 m) | 0.51 |
| 28/03/2019 | 06h07 | 10h31 (0.26 m), 23h40 (0.59 m) | 03h31 (0.70 m), 18h03 (0.72 m) | 0.54 |
| 29/03/2019 | 06h06 | 11h19 (0.34 m) | 03h34 (0.63 m), 20h17 (0.70 m) | 0.54 |
| 31/03/2019 | 06h05 | 05h40 (0.49 m), 15h35 (0.40 m) | 09h45 (0.54 m), 22h54 (0.77 m) | 0.50 |
| 01/04/2019 | 06h05 | 05h37 (0.43 m), 16h40 (0.36 m) | 10h53 (0.61 m), 23h22 (0.81 m) | 0.45 |
| 02/04/2019 | 06h04 | 05h49 (0.37 m), 17h22 (0.32 m) | 11h30 (0.69 m), 23h46 (0.84 m) | 0.38 |
| 03/04/2019 | 06h04 | 06h05 (0.31 m), 17h56 (0.29 m) | 12h01 (0.76 m) | 0.31 |
| 04/04/2019 | 06h04 | 06h24 (0.24 m), 18h28 (0.28 m) | 00h08 (0.86 m), 12h31 (0.83 m) | 0.29 |
| 05/04/2019 | 06h03 | 06h44 (0.19 m), 18h58 (0.28 m) | 00h29 (0.86 m), 13h00 (0.88 m) | 0.26 |
| 06/04/2019 | 06h03 | 07h05 (0.14 m), 19h27 (0.29 m) | 00h50 (0.86 m), 13h29 (0.92 m) | 0.27 |
| 07/04/2019 | 06h02 | 07h27 (0.11 m), 19h56 (0.32 m) | 01h11 (0.85 m), 13h59 (0.95 m) | 0.27 |
| 08/04/2019 | 06h02 | 07h51 (0.09 m), 20h26 (0.36 m) | 01h31 (0.84 m), 14h30 (0.95 m) | 0.30 |
| 09/04/2019 | 06h01 | 08h16 (0.08 m), 20h56 (0.41 m) | 01h52 (0.81 m), 15h03 (0.94 m) | 0.34 |
| 10/04/2019 | 06h01 | 08h44 (0.09 m), 21h29 (0.47 m) | 02h12 (0.78 m), 15h40 (0.90 m) | 0.37 |
| 11/04/2019 | 06h01 | 09h15 (0.13 m), 22h09 (0.53 m) | 02h32 (0.75 m), 16h25 (0.85 m) | 0.44 |
| 12/04/2019 | 06h00 | 09h52 (0.18 m), 23h12 (0.59 m) | 02h52 (0.71 m), 17h25 (0.80 m) | 0.47 |
| 13/04/2019 | 06h00 | 10h43 (0.25m) | 03h13 (0.66 m), 19h00 (0.76 m) | 0.42 |
| 14/04/2019 | 05h59 | 02h51 (0.59 m), 12h16 (0.34 m) | 03h13 (0.59 m), 20h51 (0.76 m) | 0.46 |
| 15/04/2019 | 05h59 | 04h12 (0.50 m), 14h39 (0.37 m) | 08h25 (0.56 m), 21h56 (0.79 m) | 0.52 |
| 16/04/2019 | 05h59 | 04h37 (0.40 m), 16h11 (0.35 m) | 10h19 (0.66 m), 22h38 (0.82 m) | 0.47 |
| 17/04/2019 | 05h58 | 05h06 (0.28 m), 17h11 (0.32 m) | 11h16 (0.78 m), 23h13 (0.85 m) | 0.35 |

| Date | Sunrise | Low tides | High tides | Tide level at sampling start (m) |
|---|---|---|---|---|
| 18/04/2019 | 05h58 | 05h36 (0.18 m), 17h59 (0.31 m) | 12h01 (0.89 m), 23h46 (0.86 m) | 0.22 |
| 19/04/2019 | 05h57 | 06h07 (0.08 m), 18h41 (0.31 m) | 12h42 (0.97 m) | 0.12 |
| 20/04/2019 | 05h57 | 06h39 (0.02 m), 19h19 (0.32 m) | 00h17 (0.87 m), 13h20 (1.02 m) | 0.12 |
| 21/04/2019 | 05h57 | 07h12 (-0.01 m), 19h56 (0.34 m) | 00h48 (0.86 m), 13h57 (1.03 m) | 0.15 |
| 23/04/2019 | 05h56 | 08h15 (0.04 m), 21h07 (0.42 m) | 01h48 (0.81 m), 15h09 (0.97 m) | 0.31 |
| 24/04/2019 | 05h56 | 08h46 (0.10 m), 21h44 (0.46 m) | 02h17 (0.77 m), 15h45 (0.91 m) | 0.40 |
| 25/04/2019 | 05h55 | 09h17 (0.18 m), 22h30 (0.50 m) | 02h44 (0.71 m), 16h26 (0.84 m) | 0.46 |
| 26/04/2019 | 05h55 | 09h48 (0.27 m), 23h44 (0.54 m) | 03h09 (0.65 m), 17h16 (0.78 m) | 0.48 |
| 27/04/2019 | 05h55 | 10h24 (0.35 m) | 03h31 (0.59 m), 18h33 (0.73 m) | 0.50 |
| 28/04/2019 | 05h54 | 11h33 (0.43 m) | 20h20 (0.72 m) | 0.53 |
| 29/04/2019 | 05h54 | 04h19 (0.46 m), 14h27 (0.47 m) | 09h42 (0.54 m), 21h32 (0.73 m) | 0.48 |
| 06/01/2020 | 06h17 | 03h26 (0.63 m), 15h00 (0.25 m) | 06h37 (0.65 m), 23h09 (0.79 m) | 0.65 |
| 07/01/2020 | 06h18 | 05h20 (0.60 m), 15h48 (0.20 m) | 08h06 (0.62 m), 23h41 (0.87 m) | 0.61 |
| 08/01/2020 | 06h18 | 06h02 (0.57 m), 16h32 (0.14 m) | 09h25 (0.62 m) | 0.57 |
| 09/01/2020 | 06h18 | 06h31 (0.53 m), 17h13 (0.08 m) | 00h12 (0.94 m), 10h24 (0.64 m) | 0.54 |
| 10/01/2020 | 06h18 | 06h58 (0.50 m), 17h52 (0.03 m) | 00h43 (1.00 m), 11h13 (0.67 m) | 0.56 |
| 11/01/2020 | 06h19 | 07h26 (0.47 m), 18h31 (0.01 m) | 01h13 (1.03 m), 11h59 (0.70 m) | 0.57 |
| 12/01/2020 | 06h19 | 07h56 (0.43 m), 19h10 (0.01 m) | 01h44 (1.05 m), 12h45 (0.73 m) | 0.58 |
| 15/01/2020 | 06h20 | 09h40 (0.29 m), 21h07 (0.23 m) | 03h15 (1.00 m), 15h15 (0.73 m) | 0.67 |
| 16/01/2020 | 06h21 | 10h22 (0.25 m), 21h49 (0.34 m) | 03h44 (0.96 m), 16h17 (0.70 m) | 0.68 |
| 17/01/2020 | 06h21 | 11h10 (0.22 m), 22h56 (0.47 m) | 04h14 (0.90 m), 17h33 (0.68 m) | 0.70 |
| 18/01/2020 | 06h21 | 12h06 (0.21 m), 23h44 (0.58 m) | 04h46 (0.84 m), 19h18 (0.68 m) | 0.71 |
| 19/01/2020 | 06h21 | 13h13 (0.20 m) | 05h21 (0.77 m), 21h23 (0.73 m) | 0.70 |
| 20/01/2020 | 06h21 | 02h07 (0.65 m), 14h27 (0.19 m) | 06h10 (0.70 m), 22h44 (0.81 m) | 0.69 |
| 21/01/2020 | 06h22 | 04h47 (0.62 m), 15h37 (0.16 m) | 07h45 (0.65 m), 23h33 (0.88 m) | 0.64 |
| 22/01/2020 | 06h22 | 05h50 (0.56 m), 16h36 (0.13 m) | 09h31 (0.64 m) | 0.57 |
| 23/01/2020 | 06h22 | 06h27 (0.51 m), 17h24 (0.11 m) | 00h10 (0.93 m), 10h44 (0.65 m) | 0.52 |
| 24/01/2020 | 06h22 | 06h58 (0.46 m), 18h05 (0.09 m) | 00h43 (0.97 m), 11h38 (0.68 m) | 0.50 |
| 25/01/2020 | 06h22 | 07h26 (0.46 m), 18h41 (0.09 m) | 01h13 (0.99 m), 12h22 (0.71 m) | 0.56 |
| 26/01/2020 | 06h23 | 07h54 (0.38 m), 19h14 (0.10 m) | 01h40 (1.00 m), 13h02 (0.73 m) | 0.52 |
| 27/01/2020 | 06h23 | 08h21 (0.34 m), 19h45 (0.14 m) | 02h06 (1.00 m), 13h39 (0.74 m) | 0.54 |

**Figure A1.** Variation in daily occurrence of the remaining, more rarely observed bird species. The daily abundance of individuals is plotted over the three-month sampling period from 3 February 2019 to 3 April 2019. Smoothing of the abundance curves was estimated by fitting local weighted polynomial regression (LOESS), a grey area around curves indicates 95% confidence intervals. The Lesser Crested Tern was excluded from this analysis, as it was observed on only one occasion in the second year of observation, on 26 January 2020.



**B.5** Steibl, S., Franke, J., & Laforsch, C. (2021) Tourism and urban development as drivers for invertebrate diversity loss on tropical islands. *Royal Society Open Science*, 8(10): 210411.



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**Author for correspondence:**
Christian Laforsch
e-mail: christian.laforsch@uni-bayreuth.de

# Tourism and urban development as drivers for invertebrate diversity loss on tropical islands

Sebastian Steibl[1], Jonas Franke[2] and Christian Laforsch[1]

[1]Department of Animal Ecology I and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany
[2]Remote Sensing Solutions (RSS) GmbH, Dingolfingerstr. 9, D-81673 Munich, Germany

SS, 0000-0003-4819-8581; CL, 0000-0002-5889-4647

Oceanic islands harbour a disproportionately high number of endemic and threatened species. Rapidly growing human populations and tourism are posing an increasing threat to island biota, yet the ecological consequences of these human land uses on small oceanic island systems have not been quantified. Here, we investigated and compared the impact of tourism and urban island development on ground-associated invertebrate biodiversity and habitat composition on oceanic islands. To disentangle tourism and urban land uses, we investigated Indo-Pacific atoll islands, which either exhibit only tourism or urban development, or remain uninhabited. Within the investigated system, we show that species richness, abundance and Shannon diversity of the investigated invertebrate community are significantly decreased under tourism and urban land use, relative to uninhabited islands. Remote-sensing-based spatial data suggest that habitat fragmentation and a reduction in vegetation density are having significant effects on biodiversity on urban islands, whereas land use/cover changes could not be linked to the documented biodiversity loss on tourist islands. This offers the first direct evidence for a major terrestrial invertebrate loss on remote oceanic atoll islands due to different human land uses with yet unforeseeable long-term consequences for the stability and resilience of oceanic island ecosystems.

## 1. Introduction

The growing human population and its increasing land and resource demands have altered the whole biosphere and caused a major impact on ecosystems worldwide [1,2]. Globally, the human-driven loss of ecosystems reduced the average species

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abundance by 88% compared with its value before human impact [3] and within the foreseeable future, between 33 and 66% of all species worldwide may probably disappear [4]. However, the rate of biodiversity loss differs markedly between different systems [5]. Oceanic islands exhibit one of the fastest rates in human-driven biodiversity loss [6]. At the same time, they harbour about 20% of all species, and 50% of all endangered species, despite constituting only 2.5% of the Earth's surface [7]. Understanding the human impacts on oceanic island ecosystems is thus of particular significance for monitoring and counteracting the global biodiversity loss [8].

Biological invasions and resource exploitation have been long regarded as the principal drivers of biodiversity loss on oceanic islands [9,10]. With the growing economic development of most island states, increasing human land demands and land use-related system modifications are predicted to become predominant threats to island biodiversity in the future [7]. Land use on oceanic islands is primarily driven by urban development, due to rapidly growing human populations [11,12]. With limited agricultural land available, tourism often constitutes the biggest and fastest-growing economic sector for island states, thus further driving human land consumption and modifications on oceanic islands [13,14].

Other than urbanization with its large-scale infrastructure and city development, tourism land use includes a series of system modifications, like the development of tourism infrastructure, golf courses, landscape gardening and other leisure-related activities that generally differ from urban developed areas [15–17]. Frequently, tourism land use can overburden local waste-management leading to pollution of surrounding ecosystems [18]. Increasing transportation and leisure activities are leading to direct disturbances for native biota, like nesting birds, in tourism-developed areas [19]. While the environmental impacts of pollution, transportation or individual leisure activities under tourism land use have been demonstrated on mainland and marine systems [19–22], the impact of tourism on oceanic island biodiversity has not been investigated, despite constituting a major and increasing form of land consumption on these island systems ([20,22,23], but see [24]).

In this study, we disentangled the environmental impacts of tourism and urban land use on oceanic islands. We achieved a clear spatial separation of these two different forms of human land use by investigating small atoll islands that either harbour only tourist facilities, or are inhabited by the local communities, or remained completely uninhabited [20]. We focused on the ground-associated invertebrate community, as it commonly forms the most diverse and abundant species group on small oceanic islands and carries out various ecological functions critical for the stability and resilience of island ecosystems [23,25,26]. We combined *in situ* sampling of the ground-associated invertebrate community with island-wide geospatial information derived from very-high-resolution satellite data. We tested for differences in diversity indices and in land use/land cover (LULC) between uninhabited islands as control sites free of permanent human land use, and islands under tourism or urban land use. We then tested if LULC changes (i.e. reduction in overall available habitat area, reduction in vegetation density and increase in habitat fragmentation) on tourist and urban islands can be linked to the observed differences in biodiversity, relative to uninhabited islands.

## 2. Methods

Field sampling was carried out in the Lhaviyani (Faadhippolhu) atoll, Republic of Maldives, from 1 February to 26 March 2019. In total, 12 islands were sampled: four uninhabited islands free of any direct and permanent human land use (uninhabited islands), four resort islands used for international tourism (tourist islands) and four islands permanently inhabited by the local Maldivian population. The inhabited islands had total human populations of *ca* 800–5000. Due to their small total area, this results in extremely high population densities (3000–8000 inhabitants km$^{-2}$), comparable or even exceeding those of many metropolitan continental urban areas. Therefore, these inhabited islands meet the criteria of most common definitions of urban areas and were referred to as 'urban islands' [27] (for a map of the study site see [20]). The average island size of each island type was uninhabited islands: 4.91 ± 4.36 ha, urban islands: 40.31 ± 17.85 ha and tourist islands: 18.38 ± 15.85 ha (mean ± s.d.).

On each island, 20 1 × 1 m plots were distributed over the island area using a grid scheme and randomly picking 20 sampling grids. If a plot was positioned in an inaccessible area (e.g. cemetery on urban island, private guest area on tourist island), the plot position was moved for 2 m until the plot lay in an area where it could be sampled. The position of each plot was marked using GPS (Garmin Ltd, Schaffhausen, Switzerland).

Ground-associated macroinvertebrates in each plot were counted and identified to the lowest possible taxonomic level, i.e. species or genus level. One beetle (*Carabidae* sp.) and three spider taxa (*Chelicerata* sp. 1, *Chelicerata* sp. 2, *Theridiidae* sp.) could not been identified to a lower taxonomic level and were treated as four unidentified morphospecies. Ghost crab (*Ocypode cordimana*) abundance was measured by counting the number of burrows within each plot, a standard procedure for estimating their population size [28].

For the remote sensing-based analysis of the landscape parameters, very-high-resolution SkySat data (Planet Labs Inc., San Francisco, USA) were acquired in April 2020. SkySat acquires data with a spatial resolution of 1 m with four spectral bands (visible red, green, blue, near-infrared). The SkySat data were used for LULC mapping and for assessing the vegetation fraction of the investigated islands. An object-based image classification was applied to the SkySat imagery using eCognition (Trimble, Germany). The classification scheme considered the classes infrastructure, water bungalow/jetty/wavebreakers, bare soil/sand, tree cover, shrub and grass/sparse vegetation. The final LULC statistics per island were generated using ArcMap (ESRI, Redlands, USA), excluding the class 'water bungalow/jetty/wavebreaker', since these features are not located on the islands. To evaluate the accuracy of the LULC map, standard procedures for accuracy assessment were followed [29]. Stratified random sampling, using the land cover classes, was chosen for the sampling of the 396 reference locations. This ensured that a minimum number of observations could be randomly placed in each land cover class, while a minimum distance between reference points of 50 m applied. These reference points were manually categorized by an independent image interpreter who was not involved in the classification task. The SkySat imagery and Google Earth data were used for interpreting LULC. The comparison of the classification to the reference data showed an overall accuracy of 88%. The fragmentation of LULC classes was analysed using the fragmentation tool of SAGA-GIS (SAGA User Group Association, Hamburg, Germany) [24,30]. For each island, the defined LULCs were reclassified into three classes. All classes referring to natural vegetation (tree + shrubs + grass/sparse vegetation) were aggregated to 'vegetation area', all infrastructure were aggregated into the class 'other land cover' and the bare soil/sand class was kept as is. The activity in settlement areas (infrastructure) influence fragmentation and must therefore be incorporated. To assess the fragmentation for both natural habitat types, i.e. vegetated areas and bare soil/sand areas, two fragmentation analyses were conducted separately by changing the primary input class. The fragmentation tool first derives two parameters from the aggregated land covers, a density index and a connectivity index [31]. These indices are then used by the fragmentation tool to create the output, which are five fragmentation classes for each island: 'Core', if density = 100%; 'Perforated', if density greater than 60% and density is greater than connectivity; 'Edge', if density greater than 60% and density is less than connectivity; 'Transitional', if density is between 40 and 60%; 'Patch', if density is less than 40%. The percentage area of the 'Core' areas per island was used as the main parameter to assess the influence of habitat fragmentation on biodiversity.

The vegetation cover fraction per 1 m pixel was derived by a partial unmixing method, the mixture tuned matched filtering (MTMF) using the software ENVI/IDL (Harris Geospatial Solutions, Broomfield, USA). MTMF combines parts of a linear spectral mixing model with a matched filter (MF) model and estimates subpixel target abundance [32,33]. MF assesses the spectral signature of a pixel for good matches to the end-member spectrum while suppressing background spectra. An MF score of 1.0 is a perfect match and background material (unknown end-members) is centred around zero [33,34]. For the MTMF, an end-member was used representing a pure vegetation spectrum that was then applied to all data for estimating the vegetation cover fraction in per cent per 1 m pixel. The statistics (mean and s.d.) of the vegetation cover fraction per island were derived using ArcMap (figure 1).

Statistical analysis was done using R v. 4.0.4 [35], extended with the packages 'vegan' for community data analysis [36], 'hillR' for calculating diversity indices based on the Hill numbers [37], 'lme4' for fitting linear mixed-effect models [31], 'emmeans' to estimate marginal means for generalized linear models [38] and 'lavaan' package for path analysis [39]. Effect of island type on the investigated invertebrate community composition was tested using non-parametric permutational analysis of variance (PERMANOVA), based on a Bray–Curtis-dissimilarity matrix and 4999 permutations. Diversity indices were calculated for each plot using the Hill numbers $q = 0$ and $q = 1$. The first Hill number corresponds to species richness and gives no weight to the relative abundances, whereas $q = 1$ corresponds to the exponential Shannon index and weighs species richness by relative abundance [40]. Hill numbers $q > 1$ were not generated, as plot-wise species richness on tourist and urban islands was often zero, which does not permit calculation of Hill numbers $q > 1$. Total accumulated species abundance was calculated as the sum of all invertebrates per plot. To test for the effect of island type

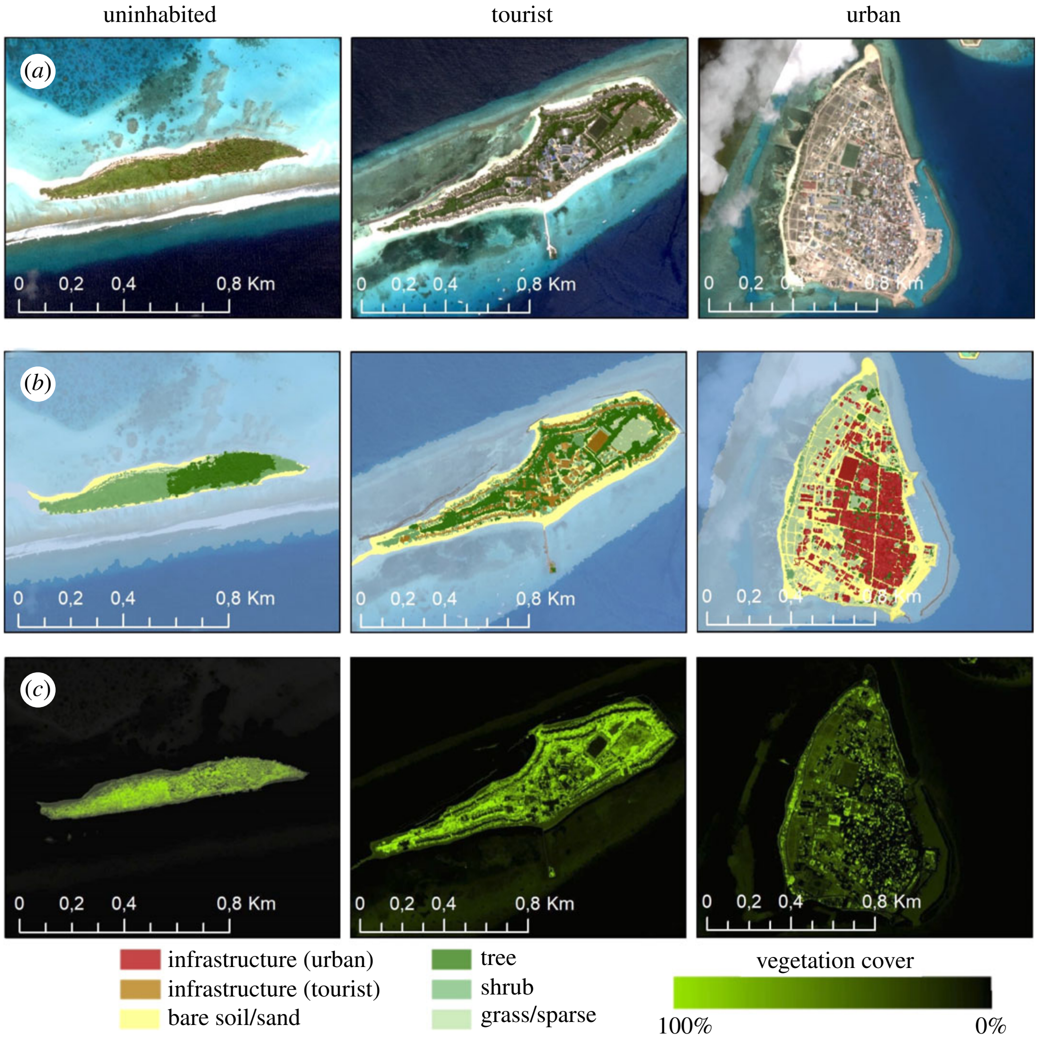

**Figure 1.** Remote-sensing analysis of the landscape parameters. Example images of each island type (uninhabited, tourist and urban) of (*a*) SkySat satellite images, (*b*) land use/land cover classification and (*c*) vegetation cover fraction.

on species richness (Hill number $q = 0$), exponential Shannon diversity (Hill number $q = 1$) and total species abundance, linear regression (ANOVA) using nested generalized linear mixed-effect models with Poisson distribution (for count data) and Gamma distribution (for Shannon diversity) with Tukey HSD *post hoc* testing and 'holm' $p$-value correction were applied. Island size was fitted as a random effect to account for species–area relationships. LULC composition was compared between island types using PERMANOVA. A principal component analysis (PCA) was used as a dimension reduction technique and to account for correlations between different LULCs. The first three principal components (PCs) accounted for 93.54% of the total inertia and were statistically compared between island types using ANOVA and Tukey HSD *post hoc* testing. To generate estimates of the effect of habitat area reduction, vegetation density reduction, fragmentation of the inner insular vegetation and fragmentation of the bare soil/beach habitat on the mean diversity per island, two separate path analysis models were run for the island-wide mean species richness and exponential Shannon diversity (Hill number $q = 0$ and $q = 1$, respectively). The path analysis model showed acceptable fits on the three measures, $\chi^2$ (0.475, d.f. = 2, $p = 0.789$), CFI (1.000) and RMSEA (0.000) for Shannon diversity and taxa richness for the data from the urban islands. However, the model showed no acceptable fits on the three measures, $\chi^2$ (8.141, d.f. = 2, $p = 0.017$), CFI (0.811) and RMSEA (0.620) for Shannon diversity and taxa richness for the data from tourist islands and were thus not further investigated and reported. The overall regression coefficients $R^2$ of the path analysis models were 79.5% and 76.3% for Shannon diversity and richness, respectively. No significant covariances were estimated to occur between the four explanatory variables ($p > 0.05$).

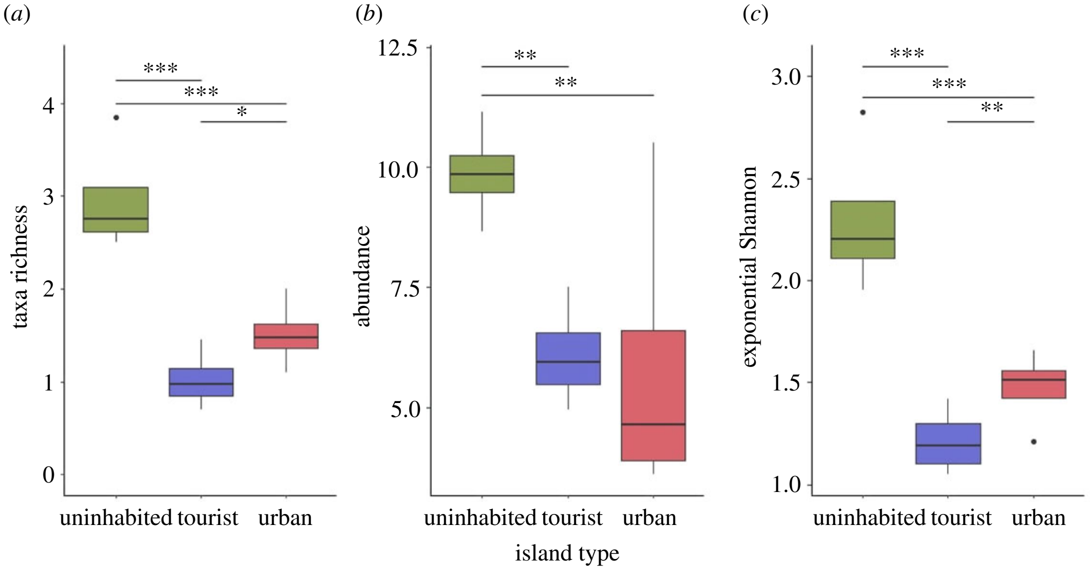

**Figure 2.** Effect of island type on the richness, accumulated abundance and diversity of ground-associated invertebrate communities on tropical islands. Plot-wise taxa richness (*a*), total accumulated species abundance (*b*) and exponential Shannon diversity (*c*) were significantly lower under tourism and urban land uses, compared with uninhabited islands free of permanent human land uses (GLMM: $^{***}p < 0.001$, $^{**}p < 0.01$ and $^{*}p < 0.05$). Plotted for graphical presentation were the mean values for each island ($N = 4$ islands per island type).

# 3. Results

In total, 43 different ground-associated invertebrate taxa were recorded on the investigated uninhabited islands, 31 different taxa on urban islands and 16 different taxa on tourist islands (see electronic supplementary material for an overview of all taxa). The composition of the investigated invertebrate community differed significantly between island types (PERMANOVA: $F = 3.089$, d.f. = 2, $p = 0.001$). Community composition was significantly different on tourist islands, compared with uninhabited (*post hoc*: $p = 0.003$) and urban islands ($p = 0.022$), but community composition did not differ statistically between urban and uninhabited islands ($p = 0.062$).

Island type had a significant effect on the species richness (GLMM: $\chi^2 = 53.558$, d.f. = 2, $p < 0.001$), plot-wise accumulated total species abundance ($\chi^2 = 16.116$, d.f. = 2, $p < 0.001$) and the diversity (exponential Shannon D index) ($\chi^2 = 66.706$, d.f. = 2, $p < 0.001$) of the investigated ground-associated invertebrate communities (figure 2 and table 1). Species richness (Hill number $q = 0$) was significantly smaller on tourist (*post hoc*: $z = 6.899$, $p < 0.001$) and urban islands ($z = 4.782$, $p < 0.001$), compared with uninhabited islands. The negative effect on species richness was thereby larger under tourist land use (Cohen $d = 1.061$) than under urban land use (Cohen $d = 0.672$), relative to uninhabited islands, and species richness further differed significantly between tourist and urban islands (*post hoc*: $z = -2.341$, $p = 0.019$; Cohen $d = -0.389$). Total accumulated species abundance was also significantly smaller on tourist ($z = 3.546$, $p = 0.001$) and urban islands ($z = 0.724$, $p = 0.002$), compared with uninhabited islands. Total accumulated species abundance was not significantly different between urban and tourist islands ($z = -0.053$, $p = 0.806$). Exponential Shannon diversity (Hill number $q = 1$) was significantly smaller on tourist ($z = -8.078$, $p < 0.001$) and urban islands ($z = -5.082$, $p < 0.001$), compared with uninhabited islands. Exponential Shannon diversity was also significantly smaller on tourist islands than on urban islands ($z = 2.996$, $p = 0.003$).

The overall island habitat composition derived from the LULC data differed significantly between the three island types (PERMANOVA: $F = 2.952$, d.f. = 2, $p = 0.013$), yet *post hoc* testing could not identify any significant pairwise differences between island types ($p > 0.05$). Dimensionality reduction using PCA was applied to detect differences and inter-correlations in LULC, fragmentation and vegetation density. The first three PCs explained 93.54% of the total variance in LULC cover (figure 3 and table 2). PC1 is a measure for shrub and tree coverage, as well as vegetation density. Although mean PC1 values for each island type suggest higher shrub and tree cover and overall vegetation cover on uninhabited islands than on tourist and urban islands, PC1 scores were not statistically different between island types (ANOVA: $F = 0.316$, d.f. = 2, $p = 0.737$). PC2 is a measure for bare soil/sand and grass coverage,

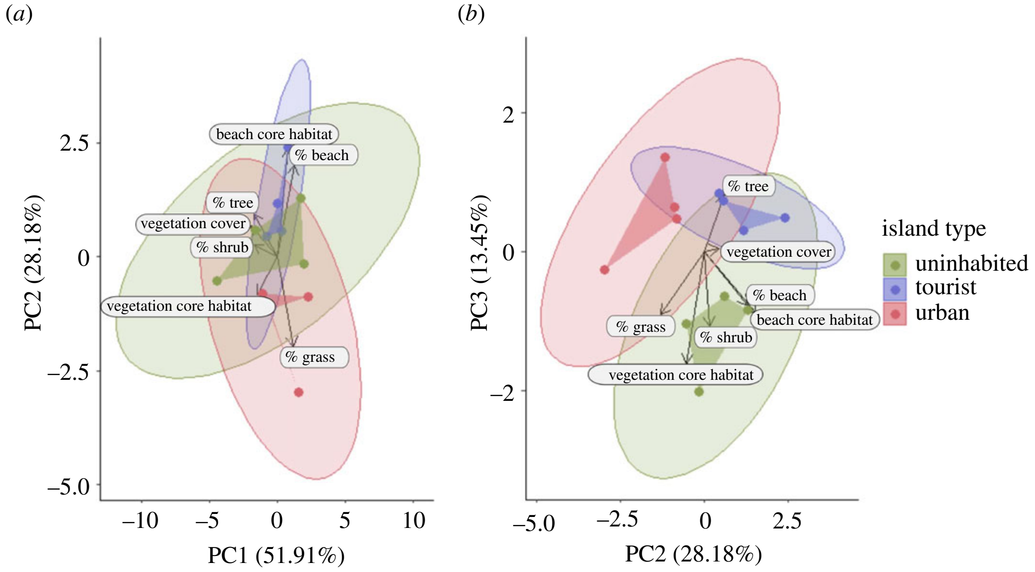

**Figure 3.** PCA of the LULC data and system modifications on the three investigated island types. Each data point denotes the PC values of one island ($N = 4$ islands per island type). The standard ellipses for each island type are assuming multivariate *t*-distributions. For loadings of PCs refer to table 2. (*a*) PC1 and PC2 bi-plot; (*b*) PC2 and PC3 bi-plot. All three PCs together explain 93.54% of total variance.

**Table 1.** Diversity metrics and LULC data for the three island types. For the three island types, the mean ± s.d. of the diversity metrics and the relative proportion of each LULC to the total island area is presented ($N = 4$). Core vegetation and core bare soil/sand of the LULC data measure the area of core habitat, with larger values indicating greater connectedness and lower values higher fragmentation of the inner vegetation and bare soil/sand habitat, respectively.

| | island type | | |
|---|---|---|---|
| parameter | uninhabited | tourist | urban |
| richness | 3.0 ± 0.6 | 1.0 ± 0.1 | 1.5 ± 0.2 |
| accumulated abundance | 9.9 ± 3.5 | 6.1 ± 5.2 | 5.9 ± 6.0 |
| exponential Shannon | 2.3 ± 0.4 | 1.2 ± 0.2 | 1.5 ± 0.2 |
| bare soil/sand | 33.9 ± 15.3% | 34.6 ± 6.5% | 22.5 ± 8.3% |
| grass/sparse vegetation | 20.9 ± 14.0% | 8.9 ± 4.2% | 22.5 ± 8.3% |
| shrub vegetation | 25.4 ± 14.8% | 14.3 ± 5.4% | 9.7 ± 6.5% |
| tree vegetation | 19.8 ± 15.0% | 23.9 ± 6.2% | 15.7 ± 12.7% |
| infrastructure | 0% | 18.3 ± 3.9% | 22.4 ± 10.1% |
| core vegetation habitat | 41.6 ± 23.6% | 12.2 ± 5.6% | 20.8 ± 14.0% |
| core bare soil/sand habitat | 17.6 ± 9.8% | 18.7 ± 7.6% | 4.5 ± 2.3% |
| vegetation cover | 37.5 ± 16.9% | 36.2 ± 5.9% | 27.6 ± 13.2% |

as well as fragmentation of the bare soil/sand habitat. PC2 scores differed significantly between island types ($F = 8.453$, d.f. = 2, $p = 0.009$). Urban islands had significantly lower PC2 values than tourist islands ($p = 0.007$) and lower scores than uninhabited islands at the margin of statistical significance ($p = 0.057$), indicating higher grass coverage and lower bare soil/sand coverage with increased fragmentation on urban islands. PC2 scores did not differ between uninhabited and tourist islands ($p = 0.420$). PC3 is a measure of shrub coverage and the fragmentation of the island vegetation. PC3 scores differed significantly between island types ($F = 13.330$, d.f. = 2, $P = 0.002$). Uninhabited islands had significantly lower PC3 scores than tourist ($p = 0.004$) and urban islands ($p = 0.004$), suggesting higher shrub

**Table 2.** PCA of the LULC remote-sensing data for the three investigated island types. The first three PCs explained a total cumulative variance of 93.54% and were chosen for subsequent statistical testing. Loadings of each PC indicate relationship with the given LULC parameter. Italicized values (threshold greater than 0.4 or less than −0.4) suggest a clear positive or negative correlation (e.g. PC2 is positively correlated with sand cover and negatively correlated with grass cover. Higher PC2 values thus correspond to higher sand cover and lower grass cover of an island). Mean ± s.d. of PC1–PC3 score for the three island types are presented below ($N = 4$). Different letters behind values indicate significant differences in the PC between island types (ANOVA: $p < 0.05$); same letters indicate no statistical difference ($p > 0.05$).

| parameter | PC1 | PC2 | PC3 |
|---|---|---|---|
| explained variance | 51.91% | 28.18% | 13.45% |
| sand coverage | 0.322 | *0.508* | −0.300 |
| grass coverage | 0.293 | *−0.498* | −0.352 |
| shrub coverage | *−0.442* | 0.065 | *−0.417* |
| tree coverage | *−0.437* | 0.239 | 0.318 |
| vegetation density | *−0.492* | 0.172 | 0.018 |
| core vegetation habitat | −0.374 | −0.210 | *−0.626* |
| core sand habitat | 0.204 | *0.598* | −0.346 |
| uninhabited islands | $-0.61 \pm 3.06^{A}$ | $0.30 \pm 0.81^{AB}$ | $-1.14 \pm 0.61^{A}$ |
| tourist islands | $0.08 \pm 0.66^{A}$ | $1.15 \pm 0.90^{A}$ | $0.59 \pm 0.24^{B}$ |
| urban islands | $0.53 \pm 1.62^{A}$ | $-1.45 \pm 1.03^{B}$ | $0.55 \pm 0.66^{B}$ |

coverage and less fragmented inner vegetation on uninhabited islands. PC3 scores were not statistically different between tourist and urban islands ($p = 0.995$).

A reduction of available natural habitat could not be correlated to mean invertebrate Shannon diversity ($Z = 1.953$, $p > 0.05$) and mean taxa richness ($Z = 1.961$, $p > 0.05$) on urban islands, but vegetation density reduction ($Z = -2.362$, $p = 0.018$; $Z = -2.315$, $p = 0.021$), fragmentation of the inner vegetation habitat ($Z = -2.279$, $p = 0.023$; $Z = -2.363$, $p = 0.018$) and fragmentation of the bare soil/beach habitat ($Z = -3.070$, $p = 0.002$; $Z = -2.797$, $p = 0.005$) had a significant negative effect on average diversity and richness on urban islands, respectively. The model for tourist islands was not able to estimate any direct relationship between the diversity indices and the explanatory LULC variables.

# 4. Discussion

We disentangled and directly compared the impact of two predominant human land use forms on oceanic islands, i.e. tourism and urban development, on the ground-associated invertebrate communities. On islands with tourism or urban land use, species richness, accumulated abundance and diversity of the investigated island invertebrate community were significantly smaller than on uninhabited islands. Remote-sensing data suggest that habitat fragmentation and the spatial extension of sparse grass vegetation are significantly higher on urban islands, compared with uninhabited islands, and have significant effects on the measured biodiversity, whereas biodiversity loss on islands under tourism land use could not be correlated to LULC data.

Human land uses can drive biodiversity losses by modifying natural habitats and whole ecosystems [41]. Modifications comprise habitat quality loss, habitat fragmentation, loss of natural vegetation cover and density [42,43], and habitat area loss (i.e. a loss in the amount of habitat). As biodiversity is positively correlated with habitat size [44], a loss of suitable natural habitat area is probably a relevant driver for the observed biodiversity loss following both island types as, on average, 18% of the available island area on tourist islands and 22% of urban islands were covered by housing sites and/or infrastructure.

The relative proportion of sparse grassland vegetation was higher on urban islands than on uninhabited and tourist islands. In accordance, a reduction of overall vegetation cover was suggested to have a significant effect on invertebrate biodiversity on islands under urban development. Here, land reclamation and the creation of new construction sites for future settlements are probably the drivers for the overall reduced vegetation cover [45,46]. As vegetation density and cover are positively associated with invertebrate biodiversity, its extensive reduction could be one possible explanation for the observed biodiversity loss on the islands under urban land use [47–49]. Generalist taxa, e.g. ants, might still find enough suitable ecological niches to persist in this urbanized environment, but ground-associated specialist taxa, which require specific habitat conditions, probably became locally extinct [50–52]. This effect of niche degradation might be even more relevant for the tree- or shrub-associated taxa that entirely lost their habitat due to the removal of tree and shrub vegetation on urban developed islands [53]. In contrast with the urban development on the permanently inhabited islands, tourist facilities are interested in keeping much of the natural forest and shrub vegetation intact to conserve the image of a 'tropical paradise' for their guests [46]. Therefore, a reduced vegetation cover is probably not a relevant driver for biodiversity loss around tourist facilities, underlined by overall similar vegetation cover on tourist and uninhabited islands (36% versus 38%, respectively, table 1).

Fragmentation of the beach and inland vegetation was higher under urban land use than on the other two island types. Further, the fragmentation was estimated to have a significant effect on the measured biodiversity on urban islands. Habitat fragmentation is probably driven by infrastructure development, resulting in a more patchy environment with more habitat edges [42,43]. Besides roads as drivers of fragmentation of the islands' interior, the coastline's ongoing obstruction by harbour sites and coastal defence structures increases the fragmentation of the natural beachline on urban islands [20,46,54]. At a certain point where habitat patches become smaller than a critical threshold, species could become locally extinct [48,49,55]. On tourist islands, where neither large roads nor coastal defence structures are present that are fragmenting the inner vegetated habitat or beaches to a great extent, fragmentation is thus probably not a significant driver for the observed biodiversity loss. Nevertheless, the inner vegetation on tourist islands was more fragmented relative to uninhabited islands. Fragmentation under tourism land use is probably caused by landscape gardening around tourist facilities, where trees and flowers have been planted in a well-planned manner, resulting in small garden patches with small trails in between.

While LULC data could not be linked to the observed losses in ground-associated invertebrate diversity and taxa richness on tourist islands, another process is probably the critical driver for the impoverished invertebrate fauna under tourism land use. All investigated tourist islands applied insecticides around their facilities to diminish fly, mosquito, cockroach and bedbug populations on a weekly to daily basis (2019, personal communication). Therefore, we suggest that the large-scale application of pesticides, including S-bioallethrin, deltamethrin and many other pyrethroid substances as active ingredients (see also PestEx Maldives, Neeolafaru Magu, Male', Republic of Maldives; [18]) probably is responsible for the impoverished invertebrate communities on tourist islands. Although primarily applied to fight high mosquito abundances typical in the tropics [56,57], pyrethroid insecticides like deltamethrin attack the insects' sodium channels and are therefore not specific to single pest species but also impact non-target invertebrates [58,59]. Consequently, insecticide application probably causes a large-scale loss of many ground-associated invertebrate taxa and may therefore be, at least partly, responsible for the observed loss of ground-associated invertebrate taxa under tourism land use.

Remote oceanic islands contribute disproportionately to global biodiversity and harbour a great number of range-restricted and endangered species [4,60]. Due to their small size, these islands experience little agricultural land use, but as for many small island states, the tourist industry is among the biggest and fastest-growing economic sectors and a dominant driver for land consumption [61]. Assessing its ecological impacts is therefore essential to mitigate associated risks for the unique and often endemic flora and fauna of tropical islands around the globe.

Taken together, our findings underline the necessity to disentangle and directly compare different human land uses in order to understand their ecological consequences more comprehensively [20]. We demonstrate that conventional tourism land use and urban development can have severe impacts on the ground-associated invertebrate diversity on remote oceanic atoll islands. Although agriculture is currently considered the predominant driver of the worldwide species decline [62], it is crucial to investigate and consider all human land uses for obtaining a global impact assessment, especially in regions where land use types other than agriculture are predominant. Only by generating a holistic understanding of the different human pressures and their severity on the world's biomes will it be possible to effectively counteract the ongoing global biodiversity loss.

Data accessibility. All data (besides the original Planet satellite data) are stored in a public repository (Dryad) and can be accessed via https://datadryad.org/stash/dataset/doi:10.5061/dryad.kwh70rz31 [63].

Authors' contributions. S.S. and C.L. designed the study. J.F. conducted the remote-sensing analysis. S.S. carried out the fieldwork and data analysis. S.S., J.F. and C.L. wrote the manuscript. All authors gave final approval for publication.

Competing interests. The authors declare no competing interests.

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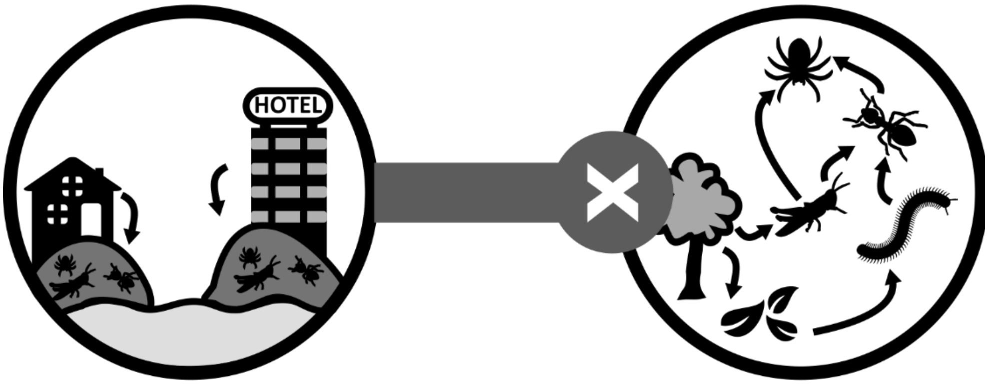
# References

1. Hooper DU *et al.* 2012 A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105–108. (doi:10.1038/nature11118)
2. Bradshaw CJA, Brook BW. 2014 Human population reduction is not a quick fix for environmental problems. *Proc. Natl Acad. Sci. USA* **111**, 16 610–16 615. (doi:10.1073/pnas.1410465111)
3. Newbold T *et al.* 2016 Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* **353**, 288–291. (doi:10.1126/science.aaf2201)
4. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. (doi:10.1038/35002501)
5. Waldron A, Miller DC, Redding D, Mooers A, Kuhn TS, Nibbelink N, Roberts JT, Tobias JA, Gittleman JL. 2017 Reductions in global biodiversity loss predicted from conservation spending. *Nature* **551**, 364–367. (doi:10.1038/nature24295)
6. Simberloff D. 2000 Extinction-proneness of island species: causes and management implications. *Raffles Bull. Zool.* **48**, 1–9.
7. Russell JC, Kueffer C. 2019 Island biodiversity in the Anthropocene. *Annu. Rev. Environ. Resour.* **44**, 31–60. (doi:10.1146/annurev-environ-101718-033245)
8. Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W. 2009 A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl Acad. Sci. USA* **106**, 9322–9327. (doi:10.1073/pnas.0810306106)
9. Russell JC, Meyer JY, Holmes ND, Pagad S. 2017 Invasive alien species on islands: impacts, distribution, interactions and management. *Environ. Conserv.* **44**, 359–370. (doi:10.1017/S0376892917000297)
10. Pearson DE. 2009 Biological invasions on oceanic islands: implications for island ecosystems and avifauna. In *Proc. 3rd Int. Symp. Migr. Birds Seabirds Danger Invasive Species Conserv. Isl. Ecosyst.*, pp. 3–16.
11. Haberkorn G. 2008 Pacific Islands population and development: facts, fictions and follies. *New Zeal. Popul. Rev.* **33/34**, 95–127.
12. Singh R, Swami NS, Prasad BC. 2014 Urbanization and economic growth: an empirical study of Pacific Island economies. *Scool Econ. Work. Pap.* **1**, 1–20.
13. Yang J, Ge Y, Ge Q, Xi J, Li X. 2016 Determinants of island tourism development: the example of Dachangshan Island. *Tour. Manag.* **55**, 261–271. (doi:10.1016/j.tourman.2016.03.001)
14. Tolkach D, Pratt S. 2019 Globalisation and cultural change in Pacific Island countries: the role of tourism. *Tour. Geogr.* **23**, 371–396. (doi:10.1080/14616688.2019.1625071)
15. Boavida-Portugal I, Rocha J, Ferreira CC. 2016 Exploring the impacts of future tourism development on land use/cover changes. *Appl. Geogr.* **77**, 82–91. (doi:10.1016/j.apgeog.2016.10.009)
16. Gössling S. 2002 Global environmental consequences of tourism. *Glob. Environ. Chang.* **12**, 283–302. (doi:10.1016/S0959-3780(02)00044-4)
17. Gössling S, Peeters P. 2015 Assessing tourism's global environmental impact 1900–2050. *J. Sustain. Tour.* **23**, 639–659. (doi:10.1080/09669582.2015.1008500)
18. DeGeorges A, Goreau TJ, Reilly B. 2010 Land-sourced pollution with an emphasis on domestic sewage: lessons from the Caribbean and implications for coastal development on Indian Ocean and Pacific coral reefs. *Sustainability* **2**, 2919–2949. (doi:10.3390/su2092919)
19. Davenport J, Davenport JL. 2006 The impact of tourism and personal leisure transport on coastal environments: a review. *Estuar. Coast. Shelf Sci.* **67**, 280–292. (doi:10.1016/j.ecss.2005.11.026)
20. Steibl S, Laforsch C. 2019 Disentangling the environmental impact of different human disturbances: a case study on islands. *Sci. Rep.* **9**, 1–8. (doi:10.1038/s41598-019-49555-6)
21. Kowalewski M, Domènech R, Martinell J. 2014 Vanishing clams on an Iberian beach: local consequences and global implications of accelerating loss of shells to tourism. *PLoS ONE* **9**, e83615. (doi:10.1371/journal.pone.0083615)
22. Hernández-Cordero AI, Hernández-Calvento L, Espino EP-C. 2017 Vegetation changes as an indicator of impact from tourist development in an arid transgressive coastal dune field. *Land use policy* **64**, 479–491. (doi:10.1016/j.landusepol.2017.03.026)
23. Prather CM *et al.* 2013 Invertebrates, ecosystem services and climate change. *Biol. Rev.* **88**, 327–348. (doi:10.1111/brv.12002)
24. Conrad O, Bechtel B, Bock M, Dietrich H, Fischer E, Gerlitz L, Wehberg J, Wichmann V, Analyses AG. 2015 System for automated geoscientific analyses (SAGA) v. 2.1.4. *Geosci. Model Dev. Discuss.* **8**, 2271–2312. (doi:10.5194/gmdd-8-2271-2015)
25. Green PT, O'Dowd DJ, Lake PS. 1997 Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. *Ecology* **78**, 2474–2486.
26. Green PT. 1997 Red crabs in rain forest on Christmas Island, Indian Ocean: activity patterns, density and biomass. *J. Trop. Ecol.* **13**, 17–38.
27. U.S. Census Bureau. 1994 The urban and rural classifications. *Geogr. Areas Ref. Man.* 1–24.
28. Hereward HFR, Gentle LK, Ray ND, Sluka RD. 2017 Ghost crab burrow density at Watamu Marine National Park: an indicator of the impact of urbanisation and associated disturbance? *Afr. J. Mar. Sci.* **39**, 129–133. (doi:10.2989/1814232X.2017.1305990)
29. Olofsson P, Foody GM, Stehman SV, Woodcock CE. 2013 Making better use of accuracy data in land change studies: estimating accuracy and area and quantifying uncertainty using stratified estimation. *Remote Sens. Environ.* **129**, 122–131. (doi:10.1016/j.rse.2012.10.031)
30. Riitters K, Wickham J, O'Neill R, Jones B, Smith E. 2000 Global-scale patterns of forest fragmentation. *Conserv. Ecol.* **4**, 1–33. (doi:10.5751/es-00209-040203)
31. Bates D, Mächler M, Bolker BM, Walker SC. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
32. Boardman JW, Kruse FA, Green RO. 1995 Mapping target signatures via partial unmixing of AVIRIS data. *Summ. JPL Airborne Earth Sci. Work* 3–6.
33. Mundt JT, Streutker DR, Glenn NF. 2007 *Partial unmixing of hyperspectral imagery: theory and methods*. In *Proc. of ASPRS Annual Conf., Tampa, FL*.
34. Mitchell JJ, Glenn NF. 2009 Subpixel abundance estimates in mixture-tuned matched filtering classifications of leafy spurge (*Euphorbia esula* L.). *Int. J. Remote Sens.* **30**, 6099–6119. (doi:10.1080/01431160902810620)
35. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
36. Oksanen J. 2015 Multivariate analysis of ecological communities in R: vegan tutorial. *R Doc.* **43**, 1–43. (doi:10.1016/0169-5347(88)90124-3)
37. Li D. 2018 hillR: taxonomic, functional, and phylogenetic diversity and similarity through Hill numbers. *J. Open Source Softw.* **3**, 1041. (doi:10.21105/joss.01041)

38. Searle SR, Speed FM, Milliken GA. 1980 Population marginal means in the linear model: an alternative to least squares means. *Am. Stat.* **34**, 216–221. (doi:10.1080/00031305.1980.10483031)
39. Rosseel Y. 2012 lavaan: an R package for structural equation modeling. *J. Stat. Softw.* **48**, 1–36. (doi:10.18637/jss.v048.i02)
40. Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014 Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* **84**, 45–67.
41. Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016 Biodiversity: the ravages of guns, nets and bulldozers. *Nature* **536**, 143–145. (doi:10.1038/536143a)
42. Rodríguez-Echeverry J, Echeverría C, Oyarzún C, Morales L. 2018 Impact of land-use change on biodiversity and ecosystem services in the Chilean temperate forests. *Landsc. Ecol.* **33**, 439–453. (doi:10.1007/s10980-018-0612-5)
43. Pardini R, Nichols E, Püttker T. 2018 Biodiversity response to habitat loss and fragmentation. *Ref. Modul. Earth Syst. Environ. Sci.* **3**, 1–11. (doi:10.1016/b978-0-12-409548-9.09824-9)
44. Triantis KA, Guilhaumon F, Whittaker RJ. 2012 The island species–area relationship: biology and statistics. *J. Biog.* **39**, 215–231. (doi:10.1111/j.1365-2699.2011.02652.x)
45. Dai L, Li S, Lewis BJ, Wu J, Yu D, Zhou W, Zhou L, Wu S. 2019 The influence of land use change on the spatial–temporal variability of habitat quality between 1990 and 2010 in Northeast China. *J. For. Res.* **30**, 2227–2236. (doi:10.1007/s11676-018-0771-x)
46. Fallati L, Savini A, Sterlacchini S, Galli P. 2017 Land use and land cover (LULC) of the Republic of the Maldives: first national map and LULC change analysis using remote-sensing data. *Environ. Monit. Assess.* **189**, 1–5. (doi:10.1007/s10661-017-6120-2)
47. Diehl E, Mader VL, Wolters V, Birkhofer K. 2013 Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia* **173**, 579–589. (doi:10.1007/s00442-013-2634-7)
48. Bazelet CS, Samways MJ. 2014 Habitat quality of grassland fragments affects dispersal ability of a mobile grasshopper, *Ornithacris cyanea* (Orthoptera: Acrididae). *Afr. Entomol.* **22**, 714–725. (doi:10.4001/003.022.0405)
49. Fleishman E, Ray C, Sjögren-Gulve P, Boggs CL, Murphy DD. 2002 Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conserv. Biol.* **16**, 706–716. (doi:10.1046/j.1523-1739.2002.00539.x)
50. Buczkowski G, Richmond DS. 2012 The effect of urbanization on ant abundance and diversity: a temporal examination of factors affecting biodiversity. *PLoS ONE* **7**, 22–25. (doi:10.1371/journal.pone.0041729)
51. McKinney ML. 2006 Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260. (doi:10.1016/j.biocon.2005.09.005)
52. Steibl S, Laforsch C. 2021 Compartmentalized organization of ecological niche occupation in insular invertebrate communities. *Ecol. Evol.* **11**, 471–480. (doi:10.1002/ece3.7067)
53. Sánchez-Bayo F, Wyckhuys KAG. 2019 Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* **232**, 8–27. (doi:10.1016/j.biocon.2019.01.020)
54. Duvat VKE, Magnan AK. 2019 Rapid human-driven undermining of atoll island capacity to adjust to ocean climate-related pressures. *Sci. Rep.* **9**, 1–16. (doi:10.1038/s41598-019-51468-3)
55. Fahrig L. 2003 Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)
56. Reiskind MH, Griffin RH, Janairo MS, Hopperstad KA. 2017 Mosquitoes of field and forest: the scale of habitat segregation in a diverse mosquito assemblage. *Med. Vet. Entomol.* **31**, 44–54. (doi:10.1111/mve.12193)
57. Greenway M, Dale P, Chapman H. 2003 An assessment of mosquito breeding and control in four surface flow wetlands in tropical-subtropical Australia. *Water Sci. Technol.* **48**, 249–256. (doi:10.2166/wst.2003.0330)
58. Laufer J, Roche M, Pelhate M, Elliott M, Janes NF, Sattelle DB. 1984 Pyrethroid insecticides: actions of deltamethrin and related compounds on insect axonal sodium channels. *J. Insect Physiol.* **30**, 341–349.
59. Smith TM, Stratton GW. 1986 Effects of synthetic pyrethroid insecticides on nontarget organisms. *Residue Rev.* **97**, 93–120. (doi:10.1007/978-1-4612-4934-4_4)
60. Myers N. 2003 Biodiversity hotspots revisited. *Bioscience* **53**, 916–917. (doi:10.1641/0006-3568(2003)053[0916:bhr]2.0.co;2)
61. Brandt JS, Buckley RC. 2018 A global systematic review of empirical evidence of ecotourism impacts on forests in biodiversity hotspots. *Curr. Opin. Environ. Sustain.* **32**, 112–118. (doi:10.1016/j.cosust.2018.04.004)
62. Habel JC *et al*. 2019 Final countdown for biodiversity hotspots. *Conserv. Lett.* **12**, e12668, 1–9. (doi:10.1111/conl.12668)
63. Steibl S, Franke J, Laforsch C. 2021 Data from: Tourism and urban development as drivers for invertebrate diversity loss on tropical islands. Dryad Digital Repository. (https://datadryad.org/stash/dataset/doi:10.5061/dryad.kwh70rz31)

**B.6** Steibl, S., Gebauer, G. & Laforsch, C. Impacts on trophic niches and food web properties of invertebrate communities vary between different human land uses. *in preparation*



## Title

Impacts on trophic niches and food web properties of invertebrate communities vary between different human land uses

## Authors and affiliations

Sebastian Steibl[1], Gerhard Gebauer[2], Christian Laforsch[1,*]

[1]: Department of Animal Ecology I and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany
[2]: BayCEER - Laboratory of Isotope Biogeochemistry, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany
*: corresponding author

## Abstract

Human activities have a major impact on global biodiversity. While the ecological consequences of human disturbance for species richness and abundance are well established, investigating the anthropogenic impacts on ecological processes, like trophic relationships, has only recently received broader scientific attention. Case studies investigating human impacts on trophic dynamics of different taxa demonstrated various possible ecological responses. However, studies that directly compare and disentangle the trophic responses of different taxa due to different forms of human impact are lacking. Therefore, we investigated whether trophic responses to anthropogenic disturbances are consistent between different taxa and whether they depend on the type of human disturbance. We analysed the trophic niches and population densities of eight invertebrate model taxa with different feeding strategies using stable isotope analysis. By studying small insular ecosystems that were either inhabited by the local population as permanent settlings, or used for international tourism, or remained completely uninhabited, we disentangled the impacts of two forms of human land use and directly compared it to undisturbed reference systems. We show that the impacts on trophic niche and population densities of the investigated invertebrate taxa vary between different taxa and depend on the type of human disturbance. The type of response further depends on whether a species is unable or able to shift in its dietary niche and hence show stable or reduced population densities. Disentangling the environmental impact of two forms of human land use on the trophic niche structure of multiple invertebrate taxa adds to our understanding of the complexity of ecological responses. The combination of trophic niche analysis and population density measurements helps to predict the risks for species losses in future global change scenarios.

## Keywords

anthropogenic disturbance, food web, island ecosystem, niche shift, stable isotope analysis, tourism, trophic niche

## Introduction

The growing human population causes major changes in the world's biomes. It has led to an increase of the human footprint, a measure for the anthropogenic impact on the environment, by 9% in just 15 years (Venter et al. 2016). The most severe impacts on ecosystems worldwide are habitat change, overexploitation, pollution, the introduction of invasive species, tourism, and climate change (Hall 2010). Thereby, human-driven habitat change is estimated to have by far the most severe environmental consequences (Habel et al. 2019). Due to anthropogenic habitat change, natural intact ecosystems will be reduced by 25 to 58% by 2100 (Jantz et al. 2015).

The loss of pristine ecosystems due to human land use inevitably leads to dramatic consequences for global biodiversity (Harrison and Bruna 1999). Between 33 to 66% of all vascular plant and vertebrate species are likely to disappear from the world's most species-rich and valuable ecoregions in the foreseeable future (Myers et al. 2000). Simultaneously, a major decline in invertebrate diversity, mostly insects, has been attributed to growing human land use (Hallmann et al. 2017). While many studies thoroughly reported these direct impacts of human land use on species richness and abundance, investigating and understanding the impacts of human land use on the underlying ecological processes in ecosystems has only recently gained broad scientific attention (Valiente-Banuet et al. 2015, Takemoto and Kajihara 2016).

A useful and well-established tool to investigate and understand how ecological processes respond to disturbances is the niche concept, initially proposed by Hutchinson in 1957 (Hutchinson 1957). A species' niche comprises all its interactions with the present biotic and abiotic environmental factors. The resulting n-dimensional niche space is organized in scenopoetic axes, represented by the habitat conditions in which a species occurs, and bionomic axes, represented by the available resources and its trophic position (Hutchinson 1978). By determining the ecological and trophic niches of species in pristine and disturbed environments, conclusions about the impacts of human land use on ecological processes, like niche occupation or trophic relationships, can be drawn.

The consequences of human land use for a species' ecological niche are often directly observable, e.g., when pristine ecosystems are converted into agricultural land, thereby completely altering or eliminating the necessary habitat conditions of a species to persist (Jantz et al. 2015, Valiente-Banuet et al. 2015). The consequences of human land use for a species' trophic niche, on the other hand, are generally more complex, cryptic, and difficult to analyse. One of the most established and elaborated tools to analyse trophic niches is stable isotope analysis (Layman et al. 2012). By combining the relative abundances of $^{13}C$ and $^{15}N$ in a species' tissue, its isotopic signal can be used as a quantitative indicator for its trophic niche (Marshall et al. 2019). The relative abundance of $^{13}C$ provides information about a species' basal food resource (e.g., marine or terrestrial primary production), whereas the relative abundance of $^{15}N$ provides information about the trophic position of a species in the food web (Peterson and Fry 1987).

Using stable isotope analysis, various case studies on different taxa and in different ecosystems have demonstrated how diverging anthropogenic disturbances on species' trophic niches can be (e.g., Barrett et al., 2005; Gauthier et al., 2011; Pringle et al., 2019; Sobocinski, Cordell, & Simenstad, 2010). Among the established responses to human disturbances are shifts in the trophic niche due to changing resource availability, a broadening in the trophic niche due to increased omnivory, apparent upward shifts due to anthropogenic $^{15}$N enrichment from fertilizers and sewage, or trophic downgrading due to changes in food chain length (Estes et al. 2011, Penick et al. 2015). These case studies investigating trophic niche shifts in single species provide relevant insights into the variety of possible trophic changes. Our understanding about the reasons for this variety of different responses to human disturbances is, however, still relatively limited, as studies that directly compare the impact of different forms of human disturbances and that cover multiple taxa with different taxonomic backgrounds are overall scarce.

In the present study, we analysed the impact of two different forms of human land use on the trophic niches of different invertebrate taxa. By investigating the population densities and trophic niche of invertebrate model taxa on islands that were either used by the local population for permanent settling, used for international tourism, or remained completely uninhabited, we disentangled the impacts of two forms of human land use on trophic niche structure and directly compared it to undisturbed systems (Steibl and Laforsch 2019). We selected eight common and widespread invertebrate taxa of tropical insular ecosystems with different feeding strategies (comprising crustacean, insect, millipede, and spider taxa) to analyse changes in trophic niche width, trophic niche position, and overall food web structure using stable isotope analysis. Using this system, we investigated whether the type of trophic response is consistent in all studied taxa, or depends on the type of human disturbance, or the particular species. Measuring resource availability and population densities allowed us to draw further conclusions about the reasons and consequences for changes in the trophic niche due to different forms of human land use.

## Material and Methods

### a) Field sampling

Field sampling was carried out between 01/02/2019 and 26/03/2019 on four uninhabited, four local, and four tourist islands in the Lhaviyani (Faadhippolhu) Atoll, the Republic of Maldives (Fig. S1). On each island, the amount of allochthonous (i.e., seagrass) and autochthonous (i.e., leaf litter material) resources and the density of the investigated invertebrate model taxa was measured. Ten 1x1 m²-plots were distributed randomly over the natural shoreline and ten 1x1 m²-plots over the inland area (20 plots per island). In each plot, allochthonous and autochthonous material was collected from the surface and weighed using a fine scale (NTP2K 2000 g ± 0.1 g, Nohlex GmbH, Buchholz, Germany). As model taxa for this study, eight different invertebrate species from different phylogenetic groups (Crustacea, Hexapoda, Chelicerata, Myriapoda) with different feeding strategies (omnivorous, carnivorous, detritivorous, herbivorous) and habitat preferences were selected (Tab. 1). The population densities of the eight selected taxa (*Coenobita rugosus, C. perlatus, Ocypode cordimana, Talitrus sp.,*

**Table 1: Investigated model taxa.** Overview of systematic classification and feeding strategies of the eight investigated model taxa in the present study.

| Phylum | Order | Species | Feeding guild |
|---|---|---|---|
| Crustacea | Amphipoda | *Talitrus sp.* (sandhopper) | detritivorous |
| Crustacea | Decapoda | *Coenobita perlatus* (hermit crab) | omnivorous |
| Crustacea | Decapoda | *Coenobita rugosus* (hermit crab) | omnivorous |
| Crustacea | Decapoda | *Ocypode cordimana* (ghost crab) | carnivorous |
| Hexapoda | Hymenoptera | *Camponotus compressus* (ant) | omnivorous |
| Hexapoda | Orthoptera | *Diabolocatantops innotabilis* (grasshopper) | herbivorous |
| Myriapoda | Spirobolida | *Eucarlia hoffmani* (millipede) | detritivorous |
| Chelicerata | Araneae | *Draposa lyrivulva* (wolf spider) | carnivorous |

*Camponotus compressus, Draposa lyrivulva, Eucarlia hoffmani, Diabolocatantops innotabilis*) per plot (i.e., per m²) and per island was noted. Five tissue samples from the selected invertebrate taxa were collected per island, if present on an island. Insects were caught using an insect net (mesh size 1 mm). Tissue samples from decapods were obtained by carefully grasping the right third walking leg with forceps, which initiated an autotomy reaction of the fixated leg and left the animal with minimal restraints, as they can regenerate the lost limb within the next moults (Skinner and Graham 1970, Skinner 1985). Additionally, five leave samples from the eight most common plant species, i.e., two tree species (*Calophyllum inophyllum, Pandanus odorifer*), two shrub species (*Scaevola taccada, Tournefortia argentea*), one herb species (*Launaea sarmentosa*), and three grass species (*Cyperus dubius, Dactyloctenium aegyptium, Panicum repens*) were collected per island, i.e., the autochthonous resources. Five tissue samples from accumulating seagrass *Posidonia sp.*, i.e., allochthonous resources, were collected along the shoreline on each island. All animal tissue and seagrass samples were stored in 1.5 ml Eppendorf safe-lock tubes (Eppendorf AG, Hamburg, Germany) at -20°C until further processing. Leave tissue samples from plants were dried at room temperature until no further weight reduction and stored in a desiccator filled with silica gel (Orange-Gel 123951000U, Grüssing GmbH, Filsum, Germany).

All collected samples were transferred to Germany, defrosted, and dried in a drying oven (Memmert GmbH + Co. KG, Schwabach, Germany) at 105°C for 48 hours. The dried samples were homogenized using ball mills (Cryomill and Retsch MM 400, Haan, Germany) at 30 Hz for 90 seconds, transferred into new 1.5 ml Eppendorf safe-lock tubes and stored in a desiccator filled with silica gel until stable isotope analysis.

### b) Stable isotope analysis

Relative nitrogen and carbon isotope natural abundances of the collected organisms were analysed in a dual element analysis with an elemental analyser (Carlo Erba Instruments 1108, Milano, Italy), coupled to a continuous flow isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany) with a ConFlo III open-split interface (Thermo Fisher Scientific, Bremen, Germany). The δ values denote the measured relative carbon and nitrogen isotope abundances and were calculated using (R $_{sample}$ / R $_{standard}$ – 1) x 1000 [‰], with R $_{sample}$ and R $_{standard}$ as the ratios of heavy to light isotope of the sample and the standard, respectively. Standard gases were calibrated with respect to given international standards ($CO_2$ vs. V-PDB and $N_2$ vs. $N_2$ in the air). Reference substances were CH6, CO8, and NBS18 for carbon and N1 and N2 for nitrogen isotopes, provided by the International Atomic Energy Agency, Vienna, Austria (Bidartondo et al. 2004). The obtained δ values of the investigated invertebrate taxa were not corrected for lipid content, as subsequent statistical analyses only compared within-species differences in $\delta^{13}C$ and $\delta^{15}N$, which showed consistent C:N ratios among same taxa, suggesting negligible intraspecific variation in lipid content (Post et al. 2007).

### c) Statistical analysis

Stable isotope data was analysed statistically using R 3.5.3, extended with the, "circular", "vegan" and "NbClust" packages for circular, multivariate data and cluster analysis (Charrad et al. 2014, Oksanen 2015). The amount of available autochthonous and allochthonous resources per m² and the density of each invertebrate taxon (individuals per m²) were statistically compared between the three island types using ANOVA (with island type as fixed and island as random effect) and TukeyHSD post-hoc testing with Bonferroni-Holm p-value correction. The plant $\delta^{13}C$ and $\delta^{15}N$ values were averaged for each island to obtain the mean isotopic signature of autochthonous production. To investigate differences in the invertebrate taxa's trophic niche widths between the three island types, the variation in $\delta^{13}C$ and $\delta^{15}N$ values were calculated for each invertebrate taxon and each island as the standard deviation of the five collected specimen per island (Bearhop et al. 2004). As *C. perlatus* and *D. innotabilis* were found only on one tourist island and *E. hoffmani* only on one local island, they were excluded from the statistical analysis of niche width. The standard deviations of $\delta^{13}C$ and $\delta^{15}N$ as an approximation of trophic niche width with respect to carbon and nitrogen sources, were then compared between the three island types using one-way ANOVA ($N = 4$). Changes in the trophic niche position (i.e., $\delta^{13}C$ and $\delta^{15}N$ combined) of the investigated invertebrate taxa were statistically analysed using a combination of circular and multivariate data analysis. Permutational multivariate analysis of variances (PERMANOVA) was conducted to compare the trophic niche position of each invertebrate taxon between the three islands: first, $\delta^{13}C$ and $\delta^{15}N$ values for each collected organism were rescaled between zero and one. Second, Bray-Curtis dissimilarity indices were calculated for the rescaled isotope values for each invertebrate taxon and, third, statistically compared between the three island types using PERMANOVA with 4999 permutations with island type as fixed and island as random effect and pairwise post-hoc testing ($N = 4$). To investigate the directionality of possible trophic niche shifts between undisturbed and disturbed system, circular statistical analysis was conducted following a previously reported method (Schmidt et al. 2007, Han et al. 2015). The trophic niche shift of a species from undisturbed (i.e., uninhabited island) to disturbed system (i.e., local or tourist island) is described by the magnitude of change r and the direction of change θ. The Euclidean vector of any taxon from the undisturbed system as the point of origin to the disturbed system with length r and direction θ is calculated using

$$r = \left[\left(\delta^{13}\mathrm{C}_{\mathrm{local/tourist}} - \delta^{13}\mathrm{C}_{\mathrm{uninhabited}}\right)^{2} + (\delta^{15}\mathrm{N}_{\mathrm{tourist}} - \delta^{15}\mathrm{N}_{\mathrm{uninhabited}})^{2}\right]^{1/2} \text{ and}$$

$$\theta = \arccos\left(\frac{\delta^{15}\mathrm{N}_{\mathrm{tourist}} - \delta^{15}\mathrm{N}_{\mathrm{uninhabited}}}{r}\right) \text{for } \delta^{13}\mathrm{C}_{\frac{\mathrm{local}}{\mathrm{tourist}}} - \delta^{13}\mathrm{C}_{\mathrm{uninhabited}} \geq 0, \text{or}$$

$$\theta = 2\pi * \arccos\left(\frac{\delta^{15}\mathrm{N}_{\mathrm{tourist}} - \delta^{15}\mathrm{N}_{\mathrm{uninhabited}}}{r}\right) \text{for } \delta^{13}\mathrm{C}_{\frac{\mathrm{local}}{\mathrm{tourist}}} - \delta^{13}\mathrm{C}_{\mathrm{uninhabited}} < 0.$$

The calculated direction θ was then corrected according to the mean trophic enrichment factors of $\delta^{13}C$ = 0.4‰ and $\delta^{15}N$ = 3.54‰ respectively (Inger et al. 2006), following the method described by Han et al., (2015).

Following this procedure, the magnitude and direction of change for each invertebrate taxon on each tourist and each local island was calculated. To analyse, whether the trophic niche of any given invertebrate taxon shifts uniformly circular or directional between undisturbed and disturbed system, Rayleigh's tests were performed. The null hypothesis of Rayleigh's test is that the direction of the vectors occurs in all directions and the alternative hypothesis states that the orientation of vectors is directional. For each invertebrate taxon, as well as the basal autochthonous and allochthonous resources, a Rayleigh's test was performed for local and tourist islands.

Under the assumption that insular food webs can be organized in clusters or compartments, depending on the relevance of allochthonous or autochthonous resources for each taxon (Paetzold et al. 2008), we investigated food web structure on the three island types using NbClust, a tool that combines 30 different measurements of cluster identification. Mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated for each invertebrate taxon on each island and rescaled to range between zero and one. Then, NbClust was conducted to obtain the most likely number of clusters *k* within the food web of each of the three island types (*N* = 4).

## Results

### a) Human impact on availability and isotopic signal of basal resources

The amount of autochthonous resources (g/m²) varied significantly between the three island types (ANOVA: *df* = 2, *F* = 7.591, *P* < 0.001) with significantly fewer autochthonous material per m² on local and tourist islands than on uninhabited islands (*P* = 0.001 and *P* = 0.005, respectively; Fig. 1A-B). The amount of allochthonous resources did not differ significantly between the three island types (ANOVA: *df* = 2, *F* = 0.869, *P* = 0.421). The $\delta^{13}C$ and $\delta^{15}N$ of autochthonous resources differed significantly between the three island types (PERMANOVA: *df* = 2, *F* = 6.641, *P* = 0.006; Fig. 1C). The isotopic signal of autochthonous resources on local islands was significantly different from that on tourist (*P* = 0.025) and uninhabited islands (*P* = 0.026). No significant differences were observed in the isotopic signal of autochthonous resources between uninhabited and tourist islands (*P* = 0.599). The $\delta^{13}C$ and $\delta^{15}N$ signal of allochthonous resources did not differ significantly between the three island types (PERMANOVA: *df* = 2, *F* = 1.536, *P* = 0.245). Circular analysis indicated significantly directional shifts in the isotopic signal of autochthonous material from uninhabited to local islands (*P* = 0.009). No significantly directional shifts were recorded from uninhabited to tourist islands

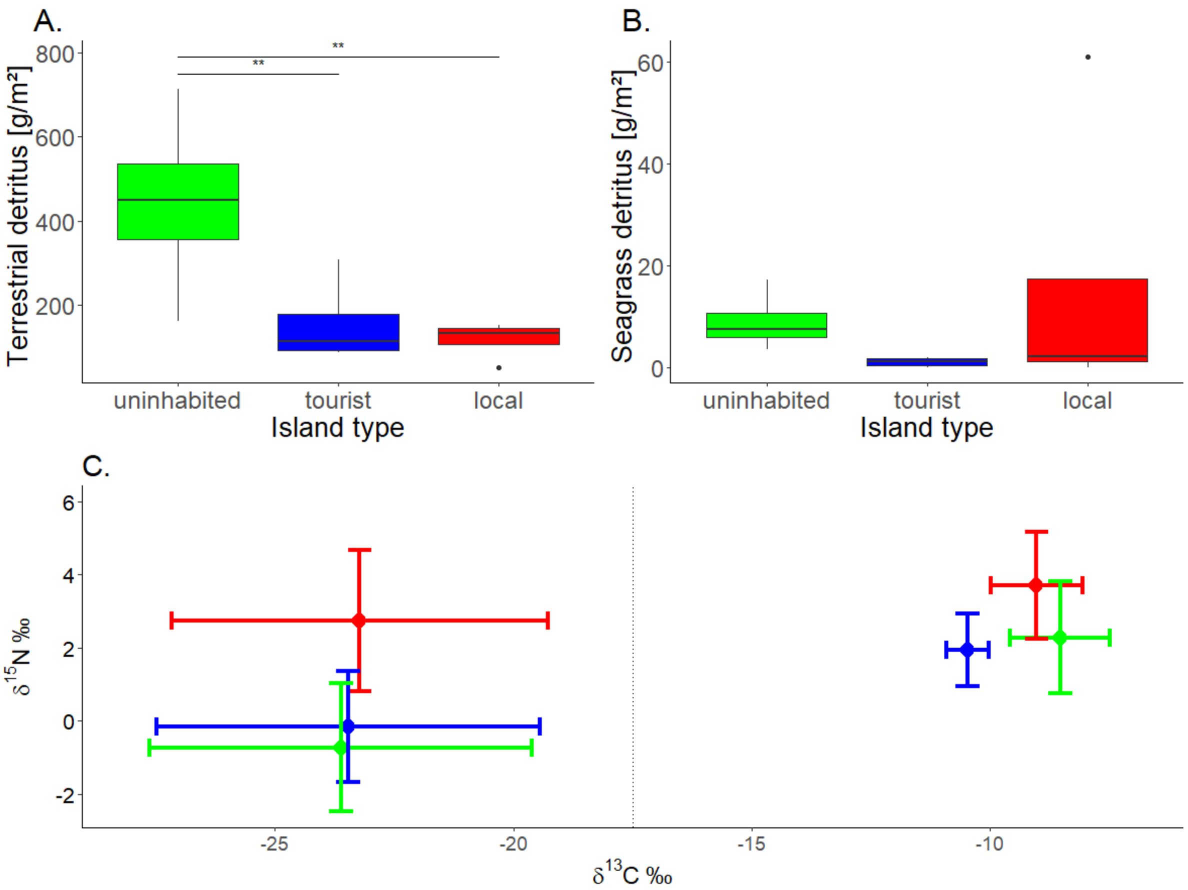


**Figure 1: Availability and isotopic signature of basal autochthonous and allochthonous resources.** The average amount of autochthonous (A) and allochthonous (B) resources on the three investigated island types (green: uninhabited, blue: tourist, red: local; N = 4). Brackets with asterisks indicate significant differences between pairwise comparisons (ANOVA: ** P < 0.001). The mean ± SE isotopic signature of autochthonous resources (C, left) differed significantly between the three island types (PERMANOVA: P = 0.006), the isotopic signature of allochthonous resources (C, right) showed no significant differences between the three island types (PERMANOVA: P = 0.599).

(*P* = 0.400) and for allochthonous material (uninhabited-local: *P* = 0.313, uninhabited-tourist: *P* = 0.062).

### b) Human impact on population density and trophic structure of invertebrate taxa

The population density of four out of the eight investigated invertebrate taxa (*C. perlatus, E. hoffmani, O. cordimana, D. lyrivulva*) differed significantly between the three island types (ANOVA: *df* = 2, *F* = 4.683, *P* = 0.010; *F* = 3.338, *P* = 0.037; *F* = 3.712, *P* = 0.025 and *F* = 3.184, *P* = 0.043, respectively; Fig. 2, Tab. 2). The population density of *C. perlatus* was significantly reduced on local and tourist islands compared to uninhabited islands (*P* = 0.047 and *P* = 0.012, respectively). The population density of *E. hoffmani* was significantly reduced on tourist islands compared to uninhabited islands (*P* = 0.041) but did not differ statistically between local and uninhabited islands (*P* = 0.120). Population density of *O. cordimana* was significantly reduced on tourist islands compared to uninhabited islands (*P* = 0.040), and a marked trend towards a reduced density on local islands compared to uninhabited islands (*P* = 0.062) was recorded. Population density of *D. lyrivulva* differed significantly between

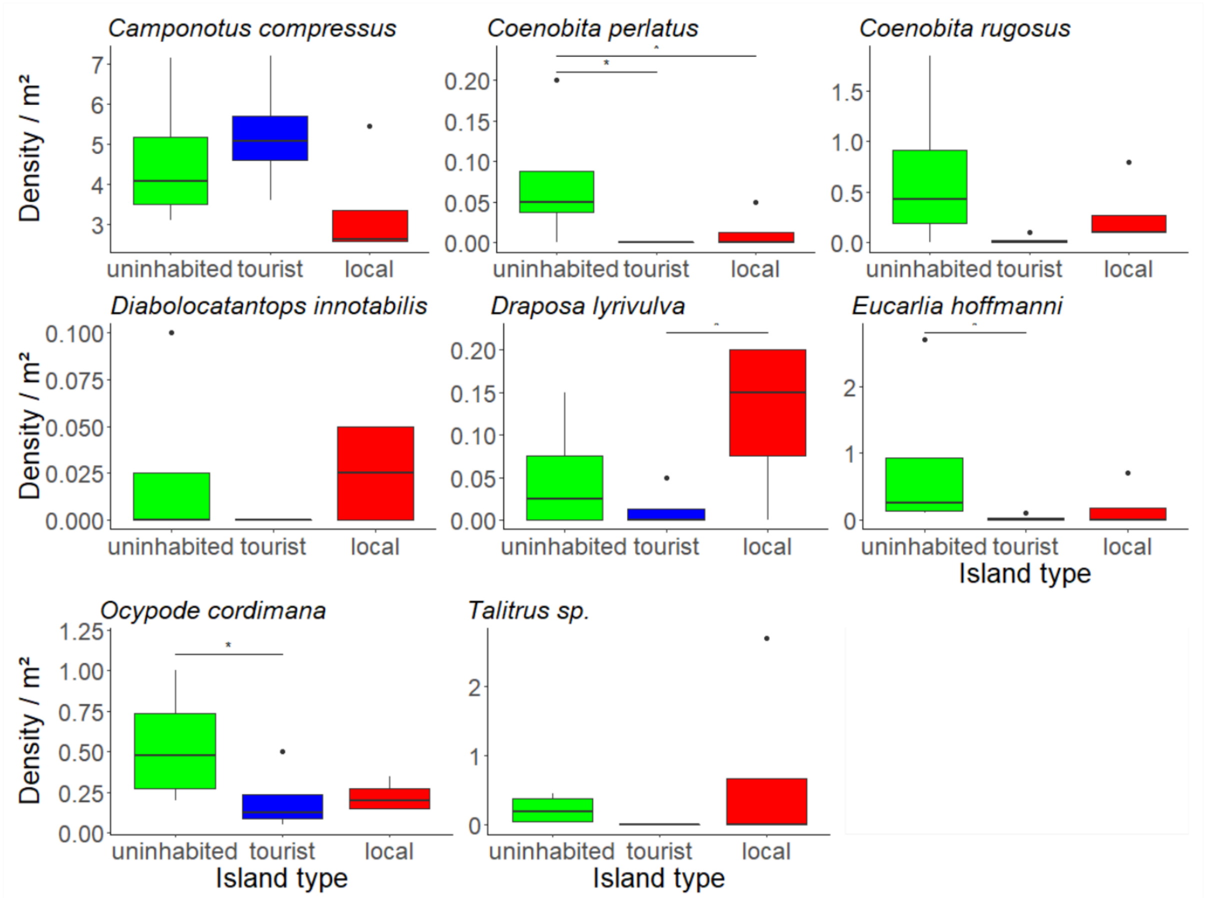


**Figure 2: Population densities of the investigated invertebrate taxa on the three different island types.** The mean ± SD population density per m² of each invertebrate taxon on the three island types (green: uninhabited, blue: tourist, red: local; N = 4). Significant differences in density indicated by asterisks (ANOVA: * P < 0.05, ** P < 0.01).

local and tourist islands (*P* = 0.036), but no statistical differences in density were observed between uninhabited and local or tourist islands (*P* = 0.226 and *P* = 0.687, respectively). The population densities of *C. rugosus*, *C. compressus, Talitrus sp.,* and *D. innotabilis* did not differ significantly between the three island types (*P* > 0.05 for all comparisons).

The trophic niche position of four out of the eight investigated invertebrate taxa (*C. perlatus, C. rugosus, C. compressus* and *D. lyrivulva)* differed significantly between the three island types (*F* = 8.194, *P* < 0.001; *F* = 16.450, *P* < 0.001; *F* = 18.348, *P* < 0.001 and *F* = 10.588, *P* < 0.001, respectively; Fig. 3, Table 2). The trophic niche position of *C. perlatus* on local islands differed significantly to that of uninhabited (*P* < 0.001) and tourist islands (*P* < 0.001), while only a marked trend for different trophic niche position was observed between uninhabited and tourist islands (*P* = 0.056). Trophic nice position of *C. rugosus* and *C. compressus* differed significantly between all pairwise comparisons of the three island types (*P* < 0.001 for all pairwise comparisons). Trophic niche position of *D. lyrivulva* on uninhabited islands differed significantly to that of local (*P* < 0.001) and tourist islands (*P* < 0.001), while no significant difference was observed between local and tourist islands (*P* = 0.342). The shifts in the trophic niche from undisturbed to disturbed (local or tourist island) system was thereby significantly directional for these four taxa

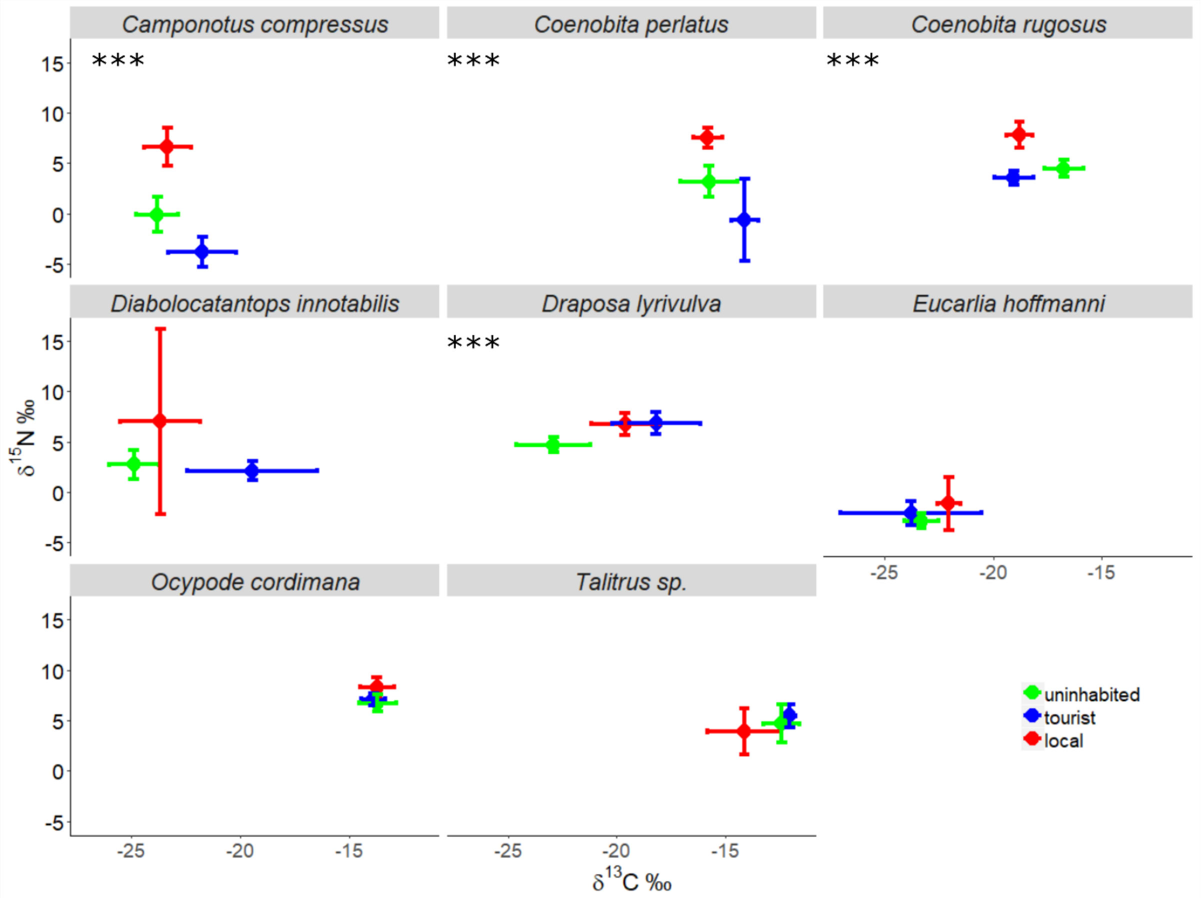


**Figure 3: Trophic niche positions of the investigated invertebrate taxa on the three island types.** Mean ± SE trophic niche position for carbon and nitrogen isotopes for the investigated invertebrate taxa calculated for each of the three island types (N = 4, green: uninhabited, blue: tourist, red: local islands). Significant differences in species' trophic niche positions between the three island types indicated by asterisks (PERMANOVA): *** P < 0.001

(Rayleigh: $P < 0.05$ for all comparisons). The trophic niche position of *Talitrus sp.* (ANOVA: $F = 1.449$, $P = 0.225$), *D. innotabilis* ($F = 2.218$, $P = 0.065$), *E. hoffmani* ($F = 0.532$, $P = 0.644$) and *O. cordimana* ($F = 1.348$, $P = 0.269$) did not differ significantly between the island types and no significantly directional shifts in trophic niche occurred from undisturbed to disturbed system (Rayleigh: $P > 0.05$ for all comparisons).

The trophic niche width with respect to carbon and nitrogen isotopes of any of the investigated invertebrate taxa did not differ significantly between the three island types ($P > 0.05$ for all comparisons; Fig. S2).

### c) Human impact on food web structure

Food webs of small tropical islands with high autochthonous production can be organized in two separate compartments (or clusters), where one comprises the part of the fauna that is strongly subsidized by allochthonous resources, and the second comprises the part of the fauna that mainly utilizes autochthonous resources (Steibl et al. 2021). This compartmentalized structure of the insular food web was confirmed for uninhabited islands in the present analysis ($K = 2$; Fig. 4A). On uninhabited islands, the first cluster comprised *C. perlatus*, *C. rugosus*, *O. cordimana,* and *Talitrus sp.*, i.e., the beach-dwelling taxa that are subsidized by allochthonous resources, and the second

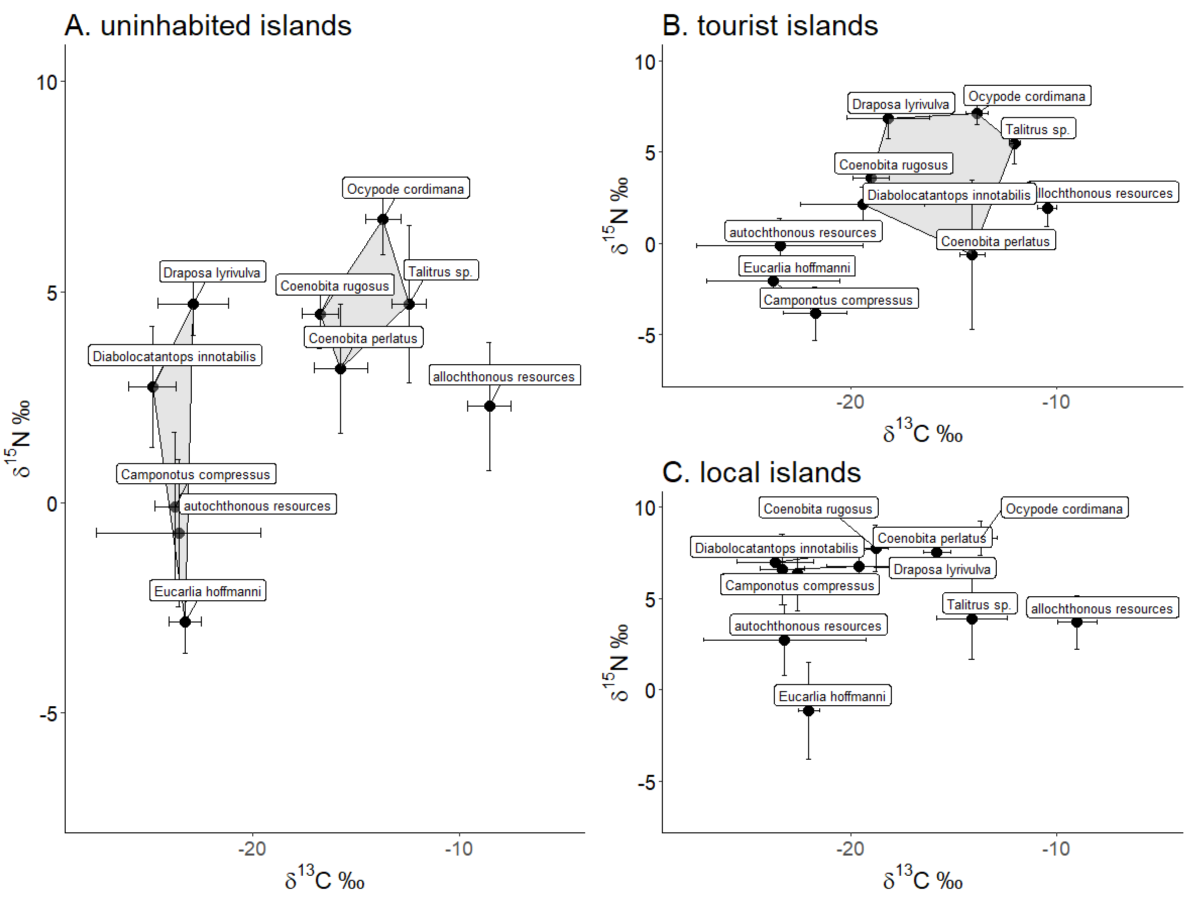


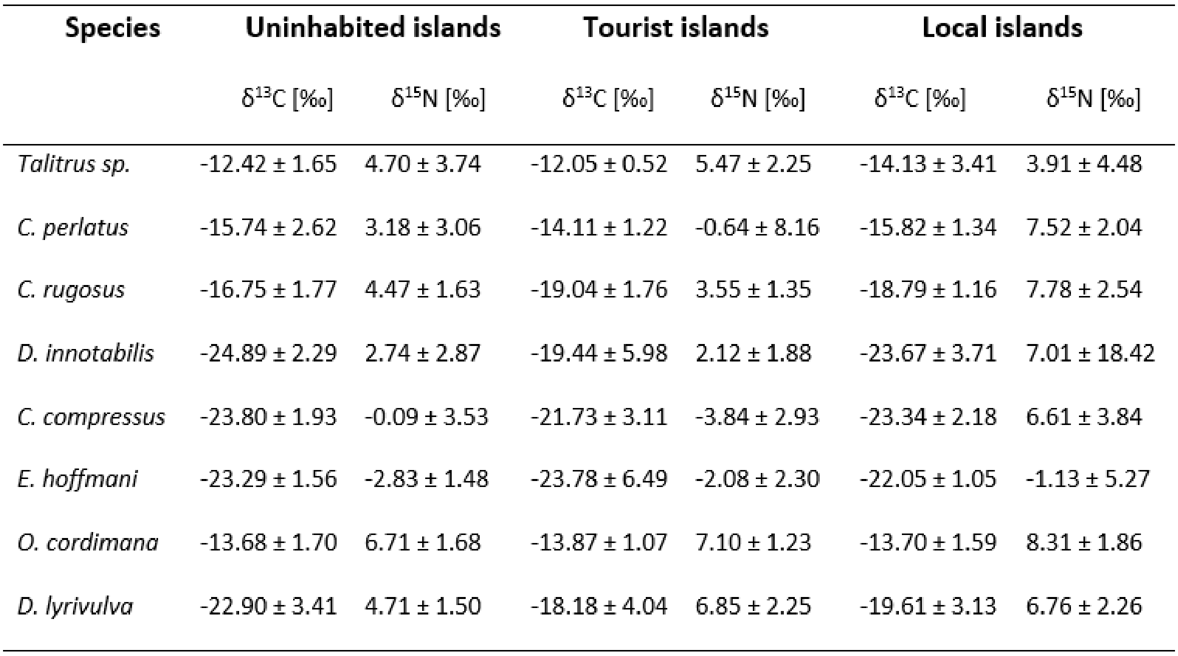
**Figure 4: Food web compartmentalization on uninhabited, local, and tourist islands.** For each species, and autochthonous and allochthonous resources, mean ± SE trophic niche position is presented (N = 4 per island type). Hulls around the investigated invertebrate taxa indicate the identified clusters (NbClust method).

cluster comprised *C. compressus*, *E. hoffmani*, *D. innotabilis,* and *D. lyrivulva,* i.e., the inland-dwelling taxa that primarily utilize autochthonous resources. For local and tourist islands, this compartmentalization could not be reproduced (Fig. 4B-C). On tourist islands, cluster analysis also suggested $K = 2$ as the most likely number of clusters in the food web, but *D. innotabilis* and *D. lyrivulva* clustered together with the beach-dwelling taxa, while only *C. compressus* and *E. hoffmani* formed a two-species cluster. On local islands, cluster analysis suggested $K = 6$ as the most likely number of clusters, thereby assigning each species in a distinct cluster, except for *D. innotabilis* and *C. compressus*, as well as *C. rugosus* and *D. lyrivulva*, which were assigned in two two-species clusters (Fig. S3).

## Discussion

Worldwide, human land use has drastic impacts on biodiversity (Habel et al. 2019). Compared to our profound knowledge about anthropogenic impacts on species richness and abundance, our understanding of the impacts on ecological processes, like trophic relationships, is still relatively limited (Takemoto and Kajihara 2016). Studies characterized possible ecological responses of trophic relationships to human disturbances for single taxa and specific impacts, but direct comparisons between

**Table. 2: Trophic niche positions between the three island types.** Mean ± SD δ$^{13}$C and δ$^{15}$N values for the investigated invertebrate taxa on the three island types (N = 4).



| Species | Uninhabited islands | | Tourist islands | | Local islands | |
|---|---|---|---|---|---|---|
| | δ$^{13}$C [‰] | δ$^{15}$N [‰] | δ$^{13}$C [‰] | δ$^{15}$N [‰] | δ$^{13}$C [‰] | δ$^{15}$N [‰] |
| *Talitrus sp.* | -12.42 ± 1.65 | 4.70 ± 3.74 | -12.05 ± 0.52 | 5.47 ± 2.25 | -14.13 ± 3.41 | 3.91 ± 4.48 |
| *C. perlatus* | -15.74 ± 2.62 | 3.18 ± 3.06 | -14.11 ± 1.22 | -0.64 ± 8.16 | -15.82 ± 1.34 | 7.52 ± 2.04 |
| *C. rugosus* | -16.75 ± 1.77 | 4.47 ± 1.63 | -19.04 ± 1.76 | 3.55 ± 1.35 | -18.79 ± 1.16 | 7.78 ± 2.54 |
| *D. innotabilis* | -24.89 ± 2.29 | 2.74 ± 2.87 | -19.44 ± 5.98 | 2.12 ± 1.88 | -23.67 ± 3.71 | 7.01 ± 18.42 |
| *C. compressus* | -23.80 ± 1.93 | -0.09 ± 3.53 | -21.73 ± 3.11 | -3.84 ± 2.93 | -23.34 ± 2.18 | 6.61 ± 3.84 |
| *E. hoffmani* | -23.29 ± 1.56 | -2.83 ± 1.48 | -23.78 ± 6.49 | -2.08 ± 2.30 | -22.05 ± 1.05 | -1.13 ± 5.27 |
| *O. cordimana* | -13.68 ± 1.70 | 6.71 ± 1.68 | -13.87 ± 1.07 | 7.10 ± 1.23 | -13.70 ± 1.59 | 8.31 ± 1.86 |
| *D. lyrivulva* | -22.90 ± 3.41 | 4.71 ± 1.50 | -18.18 ± 4.04 | 6.85 ± 2.25 | -19.61 ± 3.13 | 6.76 ± 2.26 |

different forms of disturbances and the response of various taxa are, thus far, lacking (Tylianakis et al. 2008). Here, we demonstrated that two forms of human land use, i.e., tourism and permanent settling, can have profoundly different impacts on the trophic structure and that different taxa can show different responses to the same human disturbance. Linking shifts in the trophic niche to differences in resource availability and species population densities between the investigated systems provided further insights into possible mechanisms for human-driven biodiversity loss.

When studying trophic dynamics and food web processes, considering the availability and isotopic signal of allochthonous and autochthonous material as the basal resources is crucial (Layman et al. 2012). For small insular ecosystems with high primary production, both resources form the foundation of distinct trophic pathways (Paetzold et al. 2008). The primary production inland supports several terrestrial primary consumers (e.g., millipedes, grasshoppers), which in turn are consumed by higher-order inland predators (e.g., spiders, lizards). The accumulation of allochthonous material in the form of seagrass and other beach detritus along the shoreline supports a diverse beach fauna, ranging from detritivorous and omnivorous scavengers (e.g., amphipods, hermit crabs) to higher-order shore predators (e.g., larger decapod crabs) (Spiller et al. 2010). Both investigated forms of human land use, tourism and permanent settling, significantly reduced available autochthonous material (Fig. 1A). On local islands, a loss in insular vegetation due to housing constructions and urban consolidation probably reduced the available plant detritus (Brunner and Cozens 2013). On tourist islands, much of the vegetation is left intact, but gardening activities and removal of leaf litter to conform with the standards of luxurious resort facilities might be causing a comparable reduction in autochthonous resources (Hernández-Cordero et al. 2017). At the same time, the two forms of human land use did not significantly alter the availability of allochthonous material along the beaches in the snapshot sampling of this study. However, earlier research in the same system suggested that beach cleaning and dredging, together with the active removal of seagrass beds around tourist facilities can reduce the amount of allochthonous material on the beaches (Daby 2003, Steibl and Laforsch 2019). The isotopic signal of autochthonous resources was significantly changed on local but not on tourist islands. On local islands, the isotopic signal of autochthonous material was significantly and directionally shifted towards an elevated $\delta^{15}N$ signal (Fig. 1C). Large-scale disposal of wastewater and food waste cause elevations of $\delta^{15}N$ around human facilities and might be the reason for the directional shift in $\delta^{15}N$ in autochthonous resources on local islands (Penick et al. 2015). The overall significantly directional shift towards higher $\delta^{15}N$ in the investigated invertebrate taxa on local islands further supports this hypothesis. However, on tourist islands the isotopic signal of autochthonous resources was not shifted towards higher $\delta^{15}N$ (Fig. 1C). Better wastewater treatment and filtering systems at the tourist facilities might explain why a significant elevation of $\delta^{15}N$, caused by large-scale disposal of waste, did not occur on tourist islands (Saeed and Annandale 1999).

The investigated taxa in this study showed markedly different responses in their trophic niche and population densities, and their response further depended on the type of human land use. Trophic niche width and trophic niche position of *Talitrus sp.*, a common detritivorous grazer on beach wrack along the shore, and *D. innotabilis*, a widespread herbivorous orthopteran of grassland, were not significantly altered on local and tourist islands. As *Talitrus sp.* consumes allochthonous material at the beach, its basal resource was neither changed in availability nor isotopic signature (Olabarria et al. 2009). Similarly, the consistent trophic position of *D. innotabilis* on uninhabited, local, and tourist islands could stem from a sufficient availability of grass and herbs at the transition zone from the beach to inland, even on islands with human land use (Kevan and Kevan 1995). For both species, the sufficient availability of their basal resource does not force any changes in their trophic niche, e.g. shifting to different resources or increasing their dietary spectra (Burdon et al. 2019). The densities of *Talitrus sp.* and *D. innotabilis* were also not significantly reduced on tourist or local islands. Therefore, these two taxa might represent parts of the ecosystem that are not impacted by local or tourist land use in their trophic structure and show population density changes.

*E. hoffmani*, a terrestrial detritivorous millipede on leaf litter, and *O. cordimana*, a predatory decapod crab on the beaches, also showed no significant changes in their trophic niche widths and trophic positions on local and tourist islands. However, other than *Talitrus sp.* and *D. innotabilis*, *E. hoffmani* and *O. cordimana* showed significantly reduced densities on tourist islands and a marked trend towards reduced densities on local islands. This reduction in abundance may be explained as both taxa, *E. hoffmani* and *O. cordimana*, are trophic niche specialists that cannot shift in their trophic position when their resources become reduced (Semenyuk et al. 2011). As *E. hoffmani* feeds on plant detritus in the inland, the significantly reduced availability of this autochthonous resource on local and tourist islands might explain its reduced densities on both island types. Similarly, the loss of a diverse beach fauna, commonly observed around tourist facilities, might cause a reduced prey availability for *O. cordimana*, which could explain its reduced population densities (Schlacher and Thompson 2012, Steibl and Laforsch 2019). Therefore, these two taxa might represent those parts of the ecosystem that, due to unknown evolutionary restraints, cannot respond to human-driven changes in resource availability by shifting or broadening their dietary spectra and, hence, declining in their population densities.

A different response was observed in the two investigated hermit crab species, *C. rugosus* and *C. perlatus*. Both taxa showed significant changes in their trophic niche position on local and tourist islands, compared to the uninhabited reference system. These trophic niche shifts were significantly directional for both taxa but occurred in different directions on local and on tourist islands. On local islands, the isotopic niches of both taxa were shifted towards higher $\delta^{15}N$ values. Similar to the elevated $\delta^{15}N$ signature of the basal resources on local islands, this elevation in $\delta^{15}N$ could be caused by the unregulated disposal of garbage and food waste along the beaches of local islands (Huijbers et al. 2013). Human waste and garbage generally show elevated $\delta^{15}N$ signals (Penick et al. 2015). The consumption of disposed human food by these opportunistic omnivores on the local islands might explain their significant and directional shift in their trophic niche (Barnes 1997). The surplus in food availability due to human waste disposal might also explain why hermit crab population densities were not significantly reduced on local islands (Steibl and Laforsch 2019). On tourist islands, however, the trophic niche of *C. rugosus* and *C. perlatus* shifted significantly different compared to uninhabited and local islands and, in the case of *C. rugosus*, also directionally towards lower $\delta^{15}N$ values. A significant decrease in $\delta^{15}N$ could indicate trophic downgrading and food chain truncation for these two invertebrate taxa on tourist islands (Estes et al. 2011). A lower prey or resource diversity is known to decrease overall trophic position, as predators shift towards the relatively more abundant primary consumers (Burdon et al. 2019). As the beach fauna can be drastically reduced in diversity around tourist facilities and accumulating seagrass and washed-up carcasses are actively removed (Steibl and Laforsch 2019), we hypothesize that this reduction in resource diversity could be one reason for the shifts in the trophic niche of these omnivorous taxa on tourist islands. Another noteworthy observation is that the trophic niche of *C. rugosus* shifted on both island types towards more negative $\delta^{13}C$ values (i.e., towards a higher proportion of autochthonous resources in their diet). In comparison, the trophic niche of *C. perlatus* shifted towards less negative $\delta^{13}C$ values (i.e., towards a higher proportion of allochthonous resources in their diet). These contrasting shifts might indicate that the two co-occurring species, which generally show similar dietary spectra, are forced to increased resource partitioning and differentiation due to human land use (Crowley et al. 2013).

The omnivorous ant, *C. compressus,* and the predatory wolf spider *D. lyrivulva* also showed significant changes in trophic niche position and directional trophic shifts on local and tourist islands. However, neither of these two taxa changed significantly in their population densities compared to the uninhabited reference (although *D. lyrivulva* showed significantly higher population densities on tourist islands than on local islands). These two taxa might therefore represent parts of the ecosystem that can be considered as trophic niche generalists, which can adapt to the human-driven changes in resource availability by shifting their dietary spectra towards resources that are still sufficiently available (Burdon et al. 2019). By being able to shift their diet, these taxa can maintain similar densities as on undisturbed systems and ultimately to persist the given anthropogenic disturbances (Gibb and Cunningham 2011).

Overall, by investigating trophic niche shifts of different invertebrate taxa in system with two different forms of human land use, we show that the specific trophic responses vary not only between the type of anthropogenic disturbance but also between different taxa in the same system. These findings add to the knowledge of the complexity and variety of trophic responses to human impact (Burdon et al. 2019). It further demonstrates how linking trophic niche shifts to resource availability and, at the same time, investigating changes in population densities might give insights into the reasons for species losses due to human activities. Analysing if and how different species respond in their trophic niche to disturbances might help assess a species' specific risk to either withstand human-driven changes or decline.

On an ecosystem scale, the trophic shifts of various taxa might add up to more far-reaching consequences for the whole food web and its resilience. The compartmentalized food web structure into two distinct clusters on the small uninhabited islands might increase overall ecosystem resilience, as disturbances propagate more slowly between the different clusters (Takemoto and Kajihara 2016). The investigated trophic shifts in the invertebrate taxa on local and tourist islands might have also led to significant changes in this compartmentalization, as species (e.g., *C. rugosus*) subsidized by allochthonous resources on uninhabited islands, appeared to become more dependent on autochthonous resources on disturbed islands. These apparent shifts on tourist and local islands might add further susceptibility to these systems, as disturbances (natural or anthropogenic) might propagate easier throughout the whole insular food web (Tylianakis et al. 2010).

Investigating how human disturbances directly impact species abundance and richness and influence ecological processes is relevant to more fully understand how human activities alter ecosystems (Tylianakis et al. 2008). A thorough understanding of species' interactions and niches might better predict which taxa are more and less susceptible to human disturbances (Purvis et al. 2000). Ultimately, it will help curtail the negative impacts of human land use and develop more effective conservation measurements.

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## References

Barnes, D. K. A. 1997. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: Mar. Ecol. Prog. Ser. 161: 299–302.

Barrett, K. et al. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. - Oikos 1: 145–153.

Bearhop, S. et al. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. - J. Anim. Ecol. 73: 1007–1012.

Bidartondo, M. I. et al. 2004. Changing partners in the dark: isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. - Proc. R. Soc. B Biol. Sci. 271: 1799–1806.

Brunner, J. and Cozens, P. 2013. “Where have all the trees gone?” Urban consolidation and the demise of urban vegetation: a case study from Western Australia. - Planning, Pract. Res. 28: 231–255.

Burdon, F. J. et al. 2019. Mechanisms of trophic niche compression: evidence from landscape disturbance. - J. Anim. Ecol. 89: 730–744.

Charrad, M. et al. 2014. NbClust : An R package for determining the relevant number of clusters in a data set. - J. Stat. Softw. 61: 1–36.

Crowley, B. E. et al. 2013. Stable isotopes document resource partitioning and effects of forest disturbance on sympatric cheirogaleid lemurs. - Naturwissenschaften 100: 943–956.

Daby, D. 2003. Effects of seagrass bed removal for tourism purposes in a Mauritian bay. - Environ. Pollut. 125: 313–324.

Estes, J. A. et al. 2011. Trophic downgrading of planet earth. - Science (80-. ). 333: 301–306.

Gauthier, G. et al. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. - Écoscience 18: 223–235.

Gibb, H. and Cunningham, S. A. 2011. Habitat contrasts reveal a shift in the trophic position of ant assemblages. - J. Anim. Ecol. 80: 119–127.

Habel, J. C. et al. 2019. Final countdown for biodiversity hotspots. - Conserv. Lett. e12668: 1–9.

Hall, C. M. 2010. Tourism and biodiversity: more significant than climate change? - J. Herit. Tour. 5: 253–266.

Hallmann, C. A. et al. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. - PLoS One 12: e0185809.

Han, E. et al. 2015. Stable isotope analysis of a newly established macrofaunal food web 1.5 years after the Hebei Spirit oil spill. - Mar. Pollut. Bull. 90: 167–180.

Harrison, S. P. and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: What do we know for sure? - Ecography (Cop.). 22: 225–232.

Hernández-Cordero, A. I. et al. 2017. Vegetation changes as an indicator of impact from tourist development in an arid transgressive coastal dune field. - Land use policy 64: 479–491.

Huijbers, C. M. et al. 2013. Urbanisation alters processing of marine carrion on sandy beaches. - Landsc. Urban Plan. 119: 1–8.

Hutchinson, G. E. 1957. Concluding remarks. - Cold Spring Harb. Symp. Quant. Biol. 22: 415–427.

Hutchinson, G. E. 1978. An introduction to population ecology. - New Haven.

Inger, R. et al. 2006. Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. - J. Anim. Ecol. 75: 1190–1200.

Jantz, S. M. et al. 2015. Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. - Conserv. Biol. 29: 1122–1131.

Kevan, D. K. M. and Kevan, P. G. 1995. A preliminary record of Orthopteroid insects of the Maldive Islands. - J. Orthoptera Res.

4: 223–236.

Layman, C. A. et al. 2012. Applying stable isotopes to examine food-web structure: An overview of analytical tools. - Biol. Rev. 87: 545–562.

Marshall, H. H. et al. 2019. Stable isotopes are quantitative indicators of trophic niche. - Ecol. Lett. 22: 1990–1992.

Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. - Nature 403: 853–858.

Oksanen, J. 2015. Multivariate analysis of ecological communities in R: vegan tutorial. - R Doc.: 43.

Olabarria, C. et al. 2009. Intraspecific diet shift in *Talitrus saltator* inhabiting exposed sandy beaches. - Estuar. Coast. Shelf Sci. 84: 282–288.

Paetzold, A. et al. 2008. Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. - Oecologia 157: 653–659.

Penick, C. A. et al. 2015. Stable isotopes reveal links between human food inputs and urban ant diets. - Proc. R. Soc. B Biol. Sci. 282: 20142608.

Peterson, B. J. and Fry, B. 1987. Stable isotopes in ecosystem studies. - Annu. Rev. Ecol. Syst. 18: 293–320.

Post, D. M. et al. 2007. Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. - Oecologia 152: 179–189.

Pringle, R. M. et al. 2019. Predator-induced collapse of niche structure and species coexistence. - Nature 570: 58–64.

Purvis, A. et al. 2000. Extinction. - BioEssays 22: 1123–1133.

Saeed, S. and Annandale, D. 1999. Tourism and the management of environmental impacts in the Republic of Maldives. - J. Policy Stud. 7: 81–88.

Schlacher, T. A. and Thompson, L. 2012. Beach recreation impacts benthic invertebrates on ocean-exposed sandy shores. - Biol. Conserv. 147: 123–132.

Schmidt, S. N. et al. 2007. Quantitative approaches to the analysis of stable isotope food web data. - Ecology 88: 2793–2802.

Semenyuk, I. et al. 2011. Structure of mandibles in relation to trophic niche differentiation in a tropical millipede community. - Int. J. Myriap. 6: 37–49.

Skinner, D. M. 1985. Molting and regeneration. - In: Bliss, D. E. and Mantel, L. H. (eds), The Biology of Crustacea, 9. Academic Press, pp. 43–146.

Skinner, D. M. and Graham, D. E. 1970. Molting in land crabs: Stimulation by leg removal. - Science (80-. ). 169: 383–385.

Sobocinski, K. L. et al. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget sound, Washington beaches. - Estuaries and Coasts 33: 699–711.

Spiller, D. A. et al. 2010. Marine subsidies have multiple effects on coastal food webs. - Ecology 91: 1424–1434.

Steibl, S. and Laforsch, C. 2019. Disentangling the environmental impact of different human disturbances: a case study on islands. - Sci. Rep.: 13712.

Takemoto, K. and Kajihara, K. 2016. Human impacts and climate change influence nestedness and modularity in food-web and mutualistic networks. - PLoS One 11: e0157929.

Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. - Ecol. Lett. 11: 1351–1363.

Tylianakis, J. M. et al. 2010. Conservation of species interaction networks. - Biol. Conserv. 143: 2270–2279.

Valiente-Banuet, A. et al. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. - Funct. Ecol. 29: 299–307.

Venter, O. et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. - Nat. Commun. 7: 1–11.

# C. First records of species from the Maldives

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**C.1** Steibl, S., Ballarin, F., Nadolny, A. A., Laforsch, C. (2020) First record of the wolf spider, *Draposa lyrivulva* (Bösenberg & Strand 1906) (Araneae: Lycosidae) from the Maldivian Islands, Indian Ocean. *Acta Arachnologica, 69*(2): 61-65.

*Acta Arachnologica*, 69 (2): 115–119, December 20, 2020

# First record of a wolf spider, *Draposa lyrivulva* (Bösenberg & Strand 1906) (Araneae: Lycosidae), from the Maldivian Islands, Indian Ocean

Sebastian Steibl[1*], Francesco Ballarin[2], Anton A. Nadolny[3] & Christian Laforsch[1]

[1] *Department of Animal Ecology and BayCEER, University of Bayreuth, Universitaetsstr. 30, D-95440 Bayreuth, Germany*
[2] *Systematic Zoology Laboratory, Department of Biological Sciences, Tokyo Metropolitan University, 1-1 Minami-Osawa, 192-0397 Tokyo, Japan*
[3] *A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Nakhimov Avenue 2, Sevastopol 299011*
*E-mail: sebastian.steibl@uni-bayreuth.de, *Corresponding author*

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**Abstract —** We report the first record of the wolf spider *Draposa lyrivulva* (Bösenberg & Strand 1906) outside its known distribution in Pakistan, India and the island of Sri Lanka on the remote tropical islands of the Maldives. It is the first species report of any Lycosidae from these islands. As this remote archipelago in the Indian Ocean lies about 500 km off the Indian subcontinent and comprises more than 1100 islands, the finding of *D. lyrivulva* as a common species there suggests that this spider could have colonized the islands either via aerial dispersal, rafting or has been introduced by humans.

**Key words —** coralline, Maldives, spider fauna, wolf spider

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## Introduction

Wolf spiders (Lycosidae Sundevall 1833) are a large family of spiders comprising more than 2400 species (World Spider Catalog 2020). They are abundant and usually related to grassland and other open habitats, where they are polyphagous predators on a multitude of prey species (Oelbermann & Scheu 2002; Jocqué & Alderweireldt 2005). Due to the ability of many Lycosidae species to aerial dispersal, they have colonized most temperate to tropical habitats worldwide (Richter 1970; Piacentini & Ramírez 2019).

Besides their continental distribution, different Lycosidae species have therefore already been reported from several remote oceanic islands, e.g. Micronesia or Marshall Islands in the Pacific Ocean (Framenau, Betty & Beatty 2009). However, in one major region within the Indian Ocean, the Maldivian archipelago, there are so far no confirmed species reports of Lycosidae. The Maldivian archipelago lies south of the Indian subcontinent and Sri Lanka in the Indian Ocean, spanning from latitudes of 8° North over the equator to 1° South. The Maldives comprise more than 1100 small coralline islands that are arranged in 26 atolls. These islands are not larger than one or two square kilometers (most even considerably smaller than one square kilometer) but because of their tropical environment, they support a variety of terrestrial invertebrate taxa (Hogarth *et al.* 1998; Sunil 2012; Taiti 2014).

Due to the scattered distribution and overall geography of the islands, comprehensive studies investigating the fauna on all 26 atolls (or the 1192 islands) are almost impossible to realize and therefore new species for this region are still reported regularly. The spider fauna of the Maldives has been reviewed in 2012 with 57 species from 35 genera and 17 families reported (Sunil 2012). Nevertheless, no Lycosidae species have been recorded so far from these islands, although Sunil (2012) reported the finding of two unidentified specimens termed *Pardosa* sp. 1 and 2.

Examining spider samples collected on numerous Maldivian islands, we noticed the presence of an unrecorded species belonging to the family Lycosidae. Here, we report for the first time the occurrence of the wolf spider *Draposa lyrivulva* (Bösenberg & Strand 1906) on the Maldives. This species belongs to the recently established genus *Draposa* Kronestedt 2010 and it has thus far only been recorded from continental India and Pakistan and the adjacent island of Sri Lanka (Kronestedt 2010).

## Materials and Methods

The sampling was carried out in the Lhaviyani (Faadhippolhu) and North Male' (Uthuruburi) Atoll in the central Maldives in January 2020 (Fig. 1). 15 islands in the Lhaviyani atoll and one island in the North Male' Atoll were investigated. On 15 out of the 16 investigated islands, specimens were found and collected. The collected spiders were

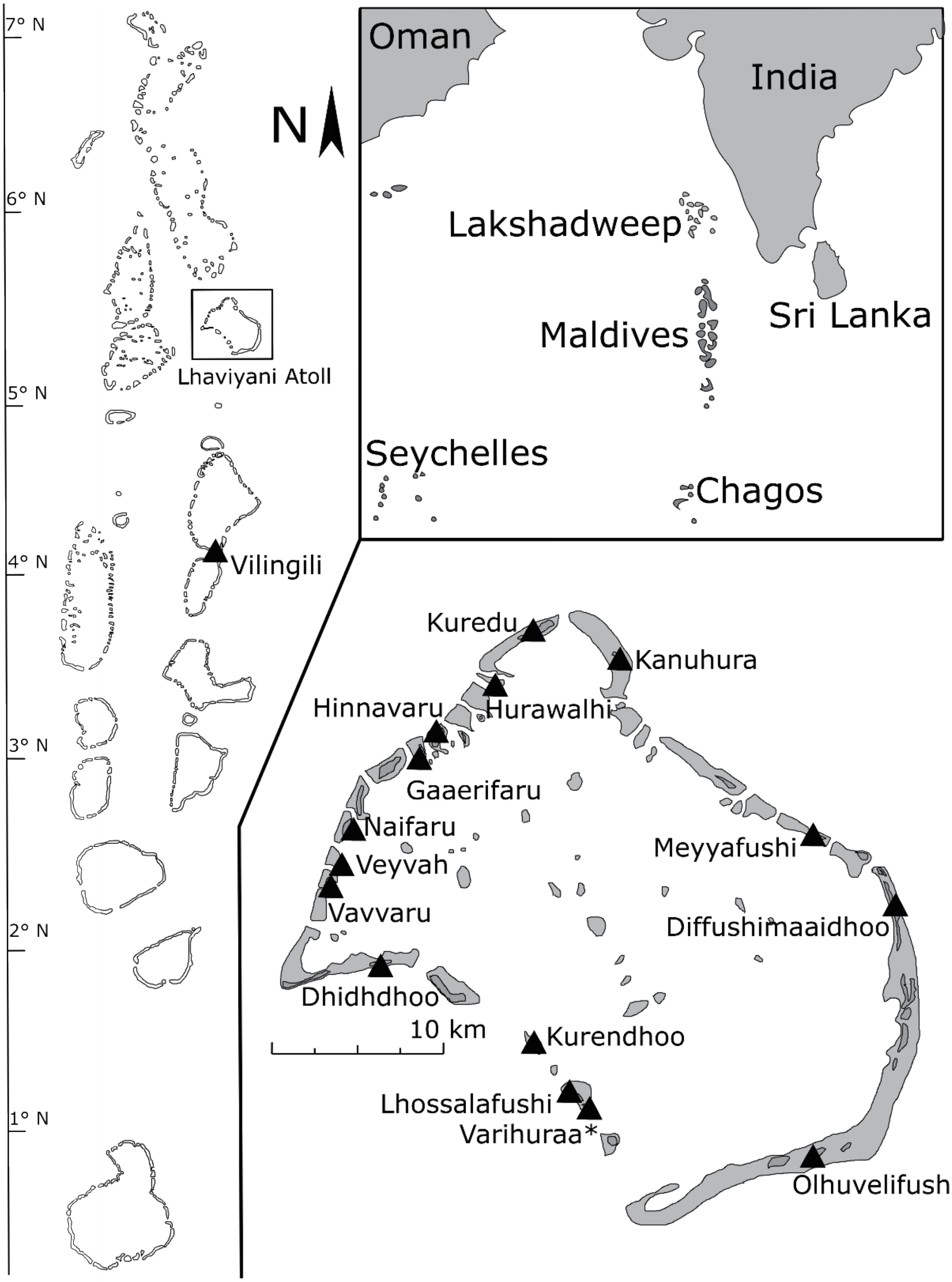

**Fig. 1.** Map of the study area (top right, location of Maldives within Indian Ocean; left, location of Lhaviyani Atoll within Republic of Maldives; bottom right, location of investigated islands within Lhaviyani Atoll), black triangles indicate islands that were investigated. Specimens of *Draposa lyrivulva* were found on all investigated islands, except for Varihuraa (indicated by asterisk).

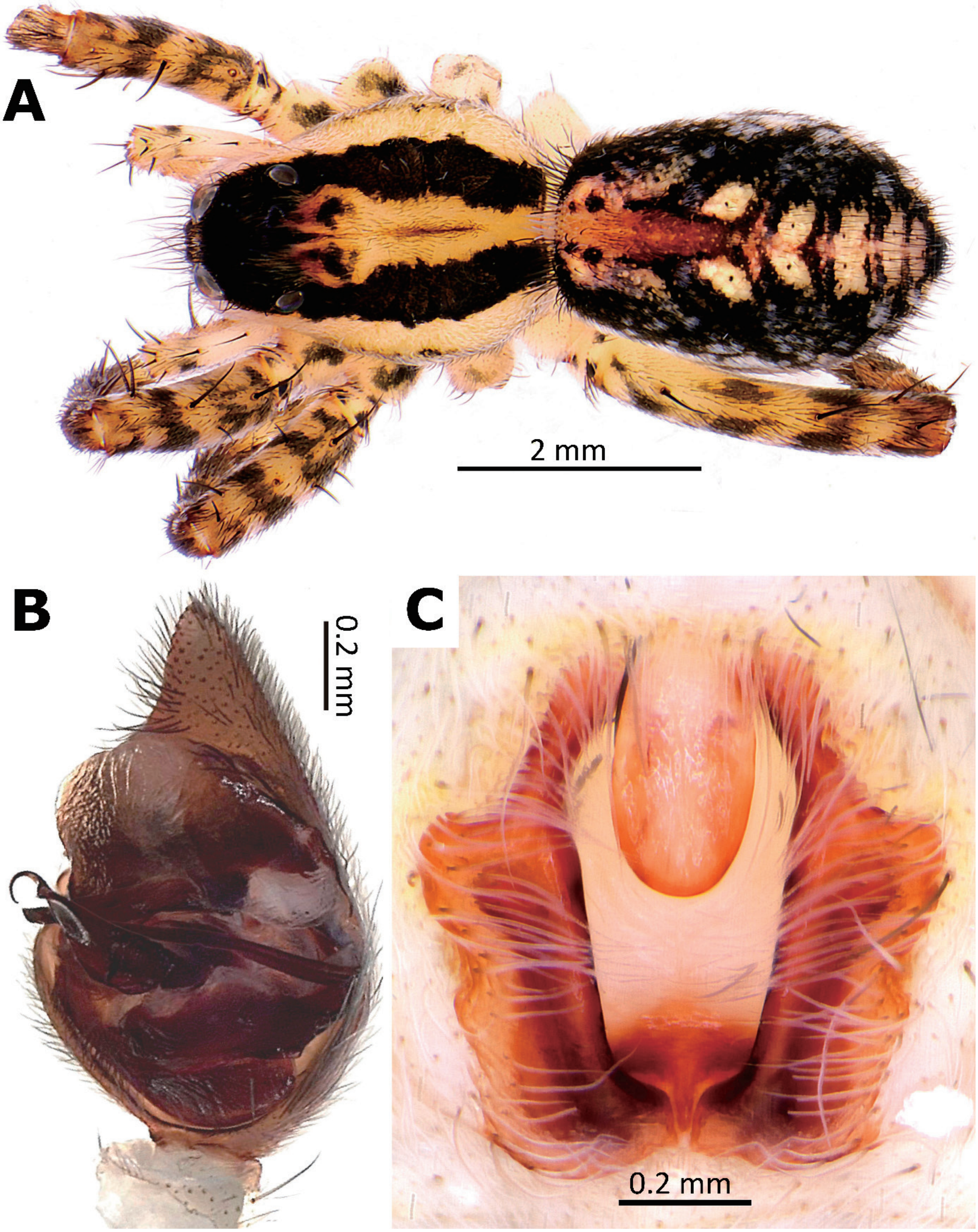

**Fig. 2.** Details of *Draposa lyrivulva* from Gaaerifaru Island, Maldives: A, female habitus; B, male palp, ventral view; C, epigyne, ventral view.

fixated in 98% ethanol and stored at 8°C in a freezer at the Department of Animal Ecology, University of Bayreuth, Germany (UBT). Morphology was examined using a Leica DVM6 (Leica Camera AG, Wetzlar, Germany) and a Nikon SMZ1270 stereomicroscope (Nikon Corp., Tokyo, Japan) and photographed with a Canon EOS Kiss x8i (Canon AG, Tokyo, Japan) and Leica Camera AG digital cameras attachments. Resulting photos were combined using the image stacking software Helicon Focus 6.7.1. Morphology of male palp and epigyne were compared to drawings from the recent revision of the genus *Draposa* (Kronestedt 2010). The nomenclature follows the World Spider Catalog (2020).

## Results and Discussion

### Family Lycosidae Sundevall 1833

### Genus *Draposa* Kronestedt 2010

### *Draposa lyrivulva* (Bösenberg & Strand 1906)

*Lycosa lyrivulva* Bösenberg & Strand 1906: 326 (♀)
*Pardosa leucopalpis* Tikader & Malhotra 1980: 349, figs 203–206 (♂♀).
*P. lyrivulva* Tanaka 1993: 176, fig 5 (♀).
*Draposa lyrivulva* Kronestedt 2010: 39, fig 5–6, 15–18, 24, 30, 33–41 (♂♀).
For the complete list of references see the World Spider Catalog 2020

**Material examined:**

Maldives, Lhaviyani (Faadhippolhu) Atoll: 1 ♂, 1 ♀, Naifaru Island, reclaimed area (5.44066, 73.363055), 6.I.2020; 1 ♂, Veyvah island, transition zone beach-inland (5.42463, 73.36138), 9.I.2020; 2 ♀, Vavvaru island transition zone beach-inland (5.41690, 73.35437), 10.I.2020; 1 ♀, Hinnavaru island, reclaimed area (5.49186, 73.41000), 11.I.2020; 4 ♂, 1 ♀, Gaaerifaru island, transition zone between beach and inland (5.48627, 73.403055), 12.I.2020; 1 ♀, Kuredu island, tourist area (5.54719, 73.46416), 13.I.2020; 1 ♀, Kanuhura island, tourist area (5.53516, 73.50472), 14.I.2020; 2 ♀, Kurendhoo island, reclaimed area (5.33313, 73.46194), 15.I.2020; 3 ♀, Dhidhdhoo island, transition zone beach-inland (5.37661, 73.38222), 16.I.2020; 4 ♀, Olhuvelifushi island, harbor area (5.27711, 73.60500), 19.I.2020; 3 ♀, Lhossalafushi island, transition zone beach-inland (5.30613, 73.48750), 26.I.2020; 2 ♀, Diffushimaaidhoo and Meyyafushi island, transition zone beach-inland (5.41138, 73.64416), 27.I.2020; 1 ♀, Hurawalhí island, tourist area (5.52191, 73.44138), 28.I.2020; 1 ♀, North Male' Atoll: Vilingili island, reclaimed area (4.17197, 73.48722), 29.I.2020, all specimen collected by S. Steibl (UBT)

**Description:** Habitus and copulatory organs as in Fig. 2A–C. For a detailed description of *D. lyrivulva* and the genus *Draposa,* refer to Bösenberg & Strand (1906) and Kronestedt (2010).

**Ecology:** The specimens were collected on pristine uninhabited islands, islands used for touristic purposes, and islands inhabited by the local Maldivian population. On all islands, the specimens were found in the transition zone between beach and inland, where the first pioneering plants (mainly *Cyperus dubius, Launaea sarmentosa, Dactyloctenium* spp.*, Cassytha filiformis*) occurred and in the reclaimed grass areas on the inhabited islands.

**Remarks on distribution:** *D. lyrivulva* has been described for the first time by Bösenberg & Strand in 1906 based on a single female from Saga Prefecture in Kyushu Island, Western Japan. Since then, this species has never been found in the type locality or in any other parts of Japan (Tanaka 1993). It is thus considered probably introduced in Japan or mislabeled (Kronestedt 2010). Other records of *D. lyrivulva* were reported so far only from continental India and Pakistan and adjacent Sri Lanka (World Spider Catalog 2020). Our findings extend the area of distribution of this species approximately 500 km to the South. Our data is the first confirmed report of a wolf spider species from the Maldives. In its extensive study on the Maldivian spider fauna, Sunil (2012) previously reported the finding of an unidentified Lycosidae (*Pardosa* sp.). Although unconfirmed, it is likely that his records refer to *D. lyrivulva.* The discovery of *D. lyrivulva* on several islands in the Maldivian archipelago shows that this species is widespread and a common resident on the islands off the Indian mainland in the Indian Ocean. As the genus *Draposa* is widespread in the Indomalayan region, it remains uncertain if this species colonized the Maldivian archipelago either naturally or artificially. We suggest that *D. lyrivulva* may have colonized the Maldivian archipelago either via aerial dispersal, rafting or it has been unintentionally introduced by human settlers

## Acknowledgments

We thank the NGOs 'Naifaru Juvenile' and 'Atoll Marine Centre' for providing infrastructure and accommodation during the field stay. Financial support for Sebastian Steibl from the scholarship 'Studienstiftung des deutschen Volkes' is gratefully acknowledged. We thank Mechthild Kredler for their help in preparing the pedipalps of the collected specimens. We are equally grateful to the two anonymous reviewers for their comments which helped to improve the manuscript. The work of A. A. Nadolny was carried out within the framework of the State research assignment of IBSS (AAAA-A18-118020890074-2)

## References

Bösenberg, W. & Strand, E. 1906. Japanische Spinnen. Abhandlungen Hrsg. von der Senckenbergischen Naturforschenden Gesellschaft, 30: 93–422.

Framenau, V. W., Berry, J. W., & Beatty, J. A. 2009. Wolf spiders of the Pacific region: the genus *Zoica* (Araneae, Lycosidae). J Arachnol. 37: 225–231.

Jocqué, R., & Alderweireldt, M. 2005. Lycosidae: the grassland spiders. Acta Zoologica Bulgarica, 1: 125–130.

Hogarth, P. J., Gherardi, F. & McLaughlin, P. A. 1998. Hermit crabs (Crustacea Decapoda Anomura) of the Maldives with the description of a new species of *Catapagurus* A. Milne Edwards 1880. Trop. Zool., 11: 149–175.

Kronestedt, T. 2010. *Draposa*, a new wolf spider genus from South and Southeast Asia (Araneae: Lycosidae). Zootaxa, 54: 31–54.

Oelbermann, K., & Scheu, S. 2002. Stable isotope enrichment ($\delta^{15}$N and $\delta^{13}$C) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): effects of prey quality. Oecologia, 130: 337–344.

Piacentini, L. N., & Ramírez, M. J. 2019. Hunting the wolf: a molecular phylogeny of the wolf spiders (Araneae, Lycosidae). Mol. Phyl. Evol., 136: 227–240.

Richter, C. J. J. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). Oecologia, 5: 200–214.

Sundevall, J. C. 1833. Svenska spindlarnes beskrifning. Fortsättning och slut. Kongl. Svenska Vet. Ak. Handl., 1832: 172-272.

Sunil, J. K. 2012. The spider fauna of Maldive islands in Indian Ocean (Araneae). Munis Entomol. Zool., 7: 424–431.

Taiti, S. 2014. The terrestrial Isopoda (Crustacea, Oniscidea) of the Maldives. Trop. Zool., 27: 9–33.

Tanaka, H. 1993. Lycosid spiders of Japan XII. The genus *Pardosa* C. L. Koch - *pullata*-group and *P. lyrivulva*. Acta Arachnol., 42: 173–179.

World Spider Catalog 2020. World Spider Catalog, Natural History Museum Bern, online at http://wsc.nmbe.ch, version 21.0, accessed on 01 June 2020.

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**C.2** Steibl, S., Spelda, J., Laforsch, C. (2020) First record of a spirobolid *Eucarlia hoffmani* (Golovatch & Korsós 1992) (Diplopoda, Spirobolida, Pachybolidae) from the Maldives, Indian Ocean. *Schubartiana, 9*: 7-11.

SCHUBARTIANA 9 (2020): 7-11

# First record of the spirobolid *Eucarlia hoffmani* Golovatch & Korsós, 1992 (Diplopoda: Spirobolida: Pachybolidae) from the Maldives, Indian Ocean

SEBASTIAN STEIBL[1]*, JÖRG SPELDA[2] and CHRISTIAN LAFORSCH[1]

[1] Department of Animal Ecology and BayCEER, University of Bayreuth, Universitätsstr. 30, 95440, Bayreuth, Germany, sebastian.steibl@uni-bayreuth.de

[2] SNSB-ZSM, Bavarian State Collection of Zoology, Münchhausenstr. 21, 81247 Munich, Germany

* Corresponding author: Sebastian Steibl

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**Abstract.** The remote Maldivian archipelago in the Indian Ocean has a diverse invertebrate fauna both underwater and on land. While some terrestrial classes, e.g. spiders, orthopterans, or decapods, have thoroughly been investigated and described on these coralline islands, others have been completely neglected. Although millipedes (Diplopoda) are important detritivores in almost all terrestrial ecosystems, they have until now never been reported from the Maldivian islands. Here, we report the finding of *Eucarlia hoffmani* Golovatch & Korsós, 1992 on one atoll of the Maldivian archipelago. This species has so far only been recorded from a single atoll between Madagascar and the Seychelles (Farquhar atoll) and therefore be considered as "endangered" by the IUCN red list. Our record of *E. hoffmani* on the Maldives suggests that the distribution of *E. hoffmani* is larger than previously known and that this species might, therefore, be less susceptible to possible extinction than considered.

**Keywords.** Archipelago, millipede, tropical island

## 1. Introduction

The Maldivian archipelago lies in the Indian Ocean, south of the Indian subcontinent, and the adjacent island of Sri Lanka. It consists of more than 1,100 small coralline islands that form a double chain of 26 atolls, spanning from latitudes of 8° North over the equator up to 1° South. The islands are mostly made up of sand, lack freshwater, and are on average not bigger than one square kilometre. The dominant habitat type on the islands is tropical moist forest, a forest type that is considered to be among the rarest and least protected of the world (GILLESPIE et al. 2012). Due to these moist forests and the overall tropical environment, the Maldivian islands have a diverse terrestrial invertebrate community (KEVAN & KEVAN 1995, HOGARTH et al. 1998, SUNIL 2012, TAITI 2014). While the occurrence and diversity of some terrestrial invertebrate groups on the Maldives have been thoroughly reported (e.g. spiders, orthopterans, isopods), others have never been investigated.

Millipedes (Diplopoda) are the third-largest class of terrestrial arthropods (following insects and arachnids) with more than 12,000 described species that have a relevant function as detritivores in most terrestrial ecosystems (GOLOVATCH & KIME 2009). Despite their key role as detritivores, they have never been investigated and reported from the Maldivian archipelago. Here, we report for the first time the record of a millipede (Diplopoda: Spirobolida) species found on Maldivian islands.

## 2. Material and Methods

We visited and investigated 14 coralline islands within the Lhaviyani (Faadhippolhu) Atoll, Republic of Maldives, between February to April 2019 (Fig. 1). The sampled islands were either pristine uninhabited islands, islands used for touristic purposes, or islands inhabited by the local Maldivian population. Millipedes were searched for by removing detritus and deadwood underneath shrub and tree vegetation on random locations on each investigated island. For microscopic investigations and identification, five millipedes from one island (Gaaerifaru) were hand-collected using forceps, fixated in 98 % ethanol and stored at 8° C in a freezer. The millipedes were identified based on the gonopods using given literature (GOLOVATCH & KORSÓS 1992) and are stored at the Bavarian State Collection of Zoology.

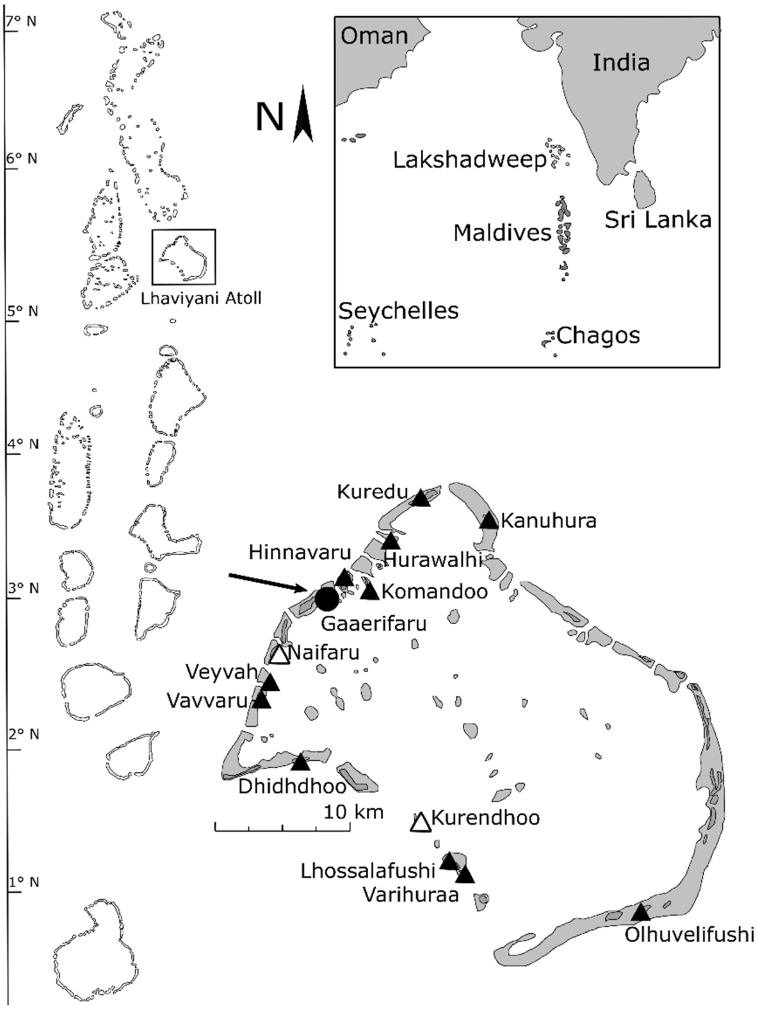

**Figure 1:** Study area. The Maldivian islands lie south of the Indian Subcontinent (top right). The Lhaviyani Atoll (left) with 14 investigated islands (bottom right) lies in the centre of the archipelago. Spirobolida spec. (observations on 11 islands) – black triangles; no millipedes (Naifaru and Kurendhoo) – white triangles; *Eucarlia hoffmani* Golovatch & Korsós, 1992 (1 male, 4 females on Gaaerifaru) – black circle and arrow.

## 3. Results and Discussion

On 11 islands of the 14 investigated (Fig. 1), Spirobolida spec. were observed, while only on two islands, Naifaru and Kurendhoo, no millipedes were found. On one island, Gaaerifaru, *Eucarlia hoffmani* Golovatch& Korsós, 1992 (1 male, Fig. 2; 4 females, Fig. 3) was found.

### *Eucarlia hoffmani* Golovatch & Korsós, 1992

**Material examined (Fig. 1, black circle):**

1 ♂ (ZSM-A20200002, 4 ♀♀ (ZSM-A20200001, ZSM-A20200003, ZSM-A20200004, ZSM-A20200005): Maldives, Lhaviyani (Faadhippolhu) Atoll, Gaaerifaru island, underneath detritus and deadwood in shrub and tree vegetation (5.4863°N, 73.4031°E), 26.II.2019.

### Spirobolida spec.

**Material observed (Fig. 1, black triangles):** Unidentified spirobolids underneath detritus and deadwood in shrub and tree vegetation: Maldives, Lhaviyani (Faadhipoolhu) Atoll, Kanuhura island (5.5338°N, 73.5058°E) 25.III.2019; Kuredu island (5.5474°N, 73.4608E) 14.III.2019; Hurawalhí island (5.5225°N, 73.4417°E) 18.III.2019; Komandoo island (5.4917°N, 73.4250°E) 26.III.2019; Hinnavaru island (5.4961°N, 37.4147°E) 05.III.2019; Vavvaru island (5.4181°N, 73.3544°E) 25.II.2019; Veyvah island (5.4255°N, 73.3608°E) 21.II.2019; Dhidhdhoo island (5.3755°N, 73.3792°E) 16.III.2019; Lhossalafushi island (5.3088°N, 73.4853°E) 07.IV.2019; Varihuraa island (5.3034°N, 73.4883°E) 11.IV.2019; Olhuvelifushi island (5.2779°N, 73.6047°E) 11.III.2019.

**Identification:** A detailed description of the morphology is given by Golovatch & Korsós (1992). An exact identification of most millipede species, especially in the tropics, is only possible with adult males, as the gonopod is the decisive identification criteria. However, adult males are often extremely rare or occur only during a limited time. For example, the type series of *E. hoffmani* consists of a single 1 adult male, 6 females, and 56 juveniles.

In *E. hoffmani* we face another problem already mentioned by Golovatch & Korsós (1992): Adult males in Spirobolida are often hardly recognizable externally, thus every specimen has to be checked carefully under a dissecting microscope for being an adult male with developed gonopods. Fortunately, there was one adult male among the collected material from the Maldivian Lhaviyani atoll that allowed the identification to species level based on the unique structure of the phallopod telopodite (Fig. 2). Because the other collected animals could not be identified to species level and specimens from the other investigated islands were not collected for microscopic analysis, we cannot exclude with certainty whether or not *E. hoffmani* is the only diplopod species, or if more than one Spirobolid species is present on the investigated islands.

The entire classification of the family Pachybolidae is still under discussion (Golovatch & Korsós 1992). With the alternative to unite all species from the East Indies in the genus *Trigoniulus*, Golovatch & Korsós (1992) decided to broaden the concept of the genus *Eucarlia* to incorporate several Seychellean pachybolids. However, the allocation of the Seychellean species of *Eucarlia* to this genus is only provisional until a thorough revision of the whole family (Golovatch & Korsós 1992).

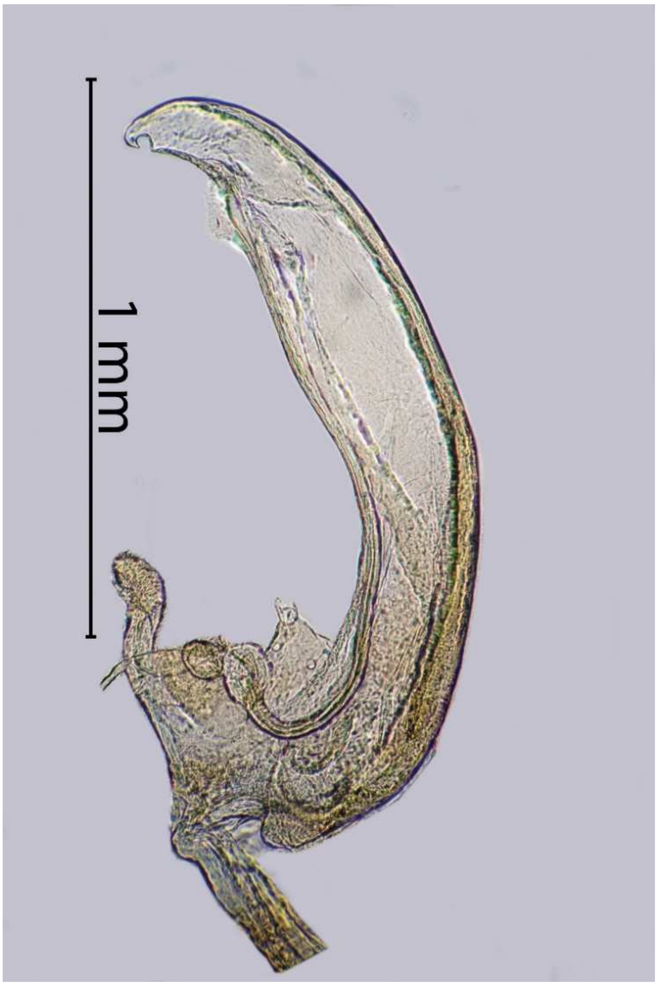

**Figure 2:** The phallopod telopodite of the collected male of *Eucarlia hoffmani*.

**Figure 3:** A female of *Eucarlia hoffmani.*

**Ecology:** The collected species aggregated under deadwood or leaf litter in the tropical moist forests of the coralline islands. The two islands, Naifaru and Kurendhoo (Fig. 1), where no spirobolids were found, are larger islands inhabited by the local population, where most of the pristine forest habitat has been removed.

**Distribution:** The species has previously only been recorded from the Farquhar atoll lying between Madagascar and the Seychelles (GOLOVATCH & KORSÓS 1992). Due to this very restricted distribution, it is listed as "Endangered" in the IUCN red list (GERLACH 2014). However, GOLOVATCH & KORSÓS (1992) already expressed their doubts about *Eucarlia hoffmanni* being a local endemic. The main evidence was the fact that all other millipede species recorded from Farquhar atoll are common species widespread due to human introduction. They supposed it to be an obvious introduced species and noted that "the source area of *E. hoffmani* sp. n. is still to be discovered" (GOLOVATCH & KORSÓS 1992). The records from the Maldives show that *E. hoffmani* has a much larger distribution than previously considered, and we suggest that its area might span over more island groups in the Indian Ocean. Nevertheless, all these young islands could not be the area of origin of this species. The family Pachybolidae is species-rich in the Indo-Australian region (ATTEMS 1914, CHAMBERLIN 1920). Considering the direction of sea currents together with our confirmation from the Maldives, *E. hoffmani* probably originates from one of the larger Indo-Australian islands, continental Asia or even Australia.

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## References

ATTEMS, C. (1914): Die indo-australischen Myriopoden. – Archiv für Naturgeschichte 80 (4): 1-398.

CHAMBERLIN, R.V. (1920): The Myriapoda of the Australian Region. – University of California Publications in Zoology 19 (12): 389-402.

GERLACH, J. (2014): *Eucarlia hoffmani*. – The IUCN Red List of Threatened Species e.T201475A2706786. doi: 10.2305/IUCN.UK.2014-1.RLTS.T201475A2706786.en

GILLESPIE, T.W.; LIPKIN, B.; SULLIVAN, L.; BENOWITZ, D.R.; PAU, S.; KEPPEL, G. (2012): The rarest and least protected forests in biodiversity hotspots. – Biodiversity Conservation 21: 3597-3611. doi: 10.1007/s10531-012-0384-1

GOLOVATCH, S.I.; KIME, R.D. (2009): Millipede (Diplopoda) distributions: a review. – Soil Organisms 81: 565-597.

GOLOVATCH, S.I.; KORSÓS, Z. (1992): Diplopoda collected by the Soviet zoological expedition to the Seychelles islands in 1984. – Acta Zoologica Hungarica 38: 1-31.

HOGARTH, P.J.; GHERARDI, F.; MCLAUGHLIN, P.A. (1998): Hermit crabs (Crustacea Decapoda Anomura) of the Maldives with the description of a new species of *Catapagurus* A. Milne Edwards 1880. – Tropical Zoology 11: 149-175. doi: 10.1080/03946975.1998.10539358

KEVAN, D.K.M.; KEVAN, P.G. (1995): A preliminary record of orthopteroid insects of the Maldive islands. – Journal of Orthoptera Research 4: 223-236.

SUNIL, J.K. (2012): The spider fauna of the Maldive islands in Indian Ocean (Araneae). – Munis Entomology & Zoology 7: 424-431.

TAITI, S. (2014): The terrestrial Isopoda (Crustacea, Oniscidea) of the Maldives. – Tropical Zoology 27: 9-33. doi: 10.1080/03946975.2014.894397

# VIII. Publication Record

## Record of all publications presented in this thesis:

Steibl, S., & Laforsch, C. (2019) Daytime activity and habitat preferences of two sympatric hermit crab species (Decapoda: Anomura: *Coenobita*). *Estuarine, Coastal and Shelf Science, 231:* 106482.

Steibl, S., & Laforsch, C. (2020) Shell resource partitioning as a mechanism of coexistence in two co-occurring terrestrial hermit crab species. *BMC Ecology, 20*(1): 1-9.

Steibl, S., & Laforsch, C. (2019) Disentangling the environmental impact of different human disturbances: a case study on islands. *Scientific Reports, 9:* 13712.

Steibl, S., & Laforsch, C. (2021) Compartmentalized organization of ecological niche occupation in insular invertebrate communities. *Ecology and Evolution, 11*(1): 471-480.

Steibl, S., Sigl, R., Blaha, S., Drescher, S., Gebauer, G., Gürkal, E., Hüftlein, F., Satzger, A.,Schwarzer, M., Seidenath, D., Welfenbach, J., Zinser, R.S., & Laforsch, C. (2021) Allochthonous resources are less important for faunal communities on highly productive, small tropical islands. *Ecology and Evolution, 11*: 13128-13138.

Steibl, S., Sigl, R., Bräumer, P.E., Clauß, V., Goddemeier, S., Hamisch, S., Lücker, D., Reiprich, L., Stegmann, L., Voigt, N., Laforsch, C. (2021) Diversity patterns and community structure of the ground-associated macrofauna along the beach-inland transition zone of small tropical islands. *Diversity, 13*(377): 1-12.

Steibl., S., & Laforsch, C. (2021) The importance of the Maldives as wintering ground for migratory birds of the Central Asian flyway. *Journal of Asian Ornithology, 37*: 80-87.

Steibl, S., Franke, J., & Laforsch, C. (2021) Tourism and urban development as drivers for invertebrate diversity loss on tropical islands. *Royal Society Open Science, 8*(10): 210411.

Steibl, S., Gebauer, G. & Laforsch, C. Impacts on trophic niches and food web properties of invertebrate communities vary between different human land uses. *in preparation*

Steibl, S., Ballarin, F., Nadolny, A. A., Laforsch, C. (2020) First record of the wolf spider *Draposa lyrivulva* (Bösenberg & Strand 1906) (Araneae: Lycosidae) from the Maldives, Indian Ocean. *Acta Arachnologica, 69*(2): 61-65.

Steibl, S., Spelda, J., Laforsch, C. (2020) First record of the spirobolid *Eucarlia hoffmani* (Golovatch & Korsós 1992) (Diplopoda, Spirobolida, Pachybolidae) from the Maldives, Indian Ocean. *Schubartiana, 9*: 7-11.

## Record of further own publications not used in this thesis:

Steibl, S. (2020) Terrestrial hermit crab populations in the Maldives: ecology, distribution and anthropogenic impact. *Springer Spektrum Verlag, Wiesbaden.*

Imhof, H.K., Sigl, R., Brauer, E., Feyl, S., Giesemann, P., Klink, S., Leupolz, K., Löder, M.G.J., Löschel, L., Missun, J., Muszynski, S., Ramsperger, A.F.R.M., Schrank, I., Speck, S., Steibl, S., Trotter, B., Winter, I., Laforsch, C. (2017) Spatial and temporal variation of macro-, meso- and microplastic abundance on a remote coral island of the Maldives, Indian Ocean. *Marine Pollution Bulletin, 116*(1-2): 340-347.

Sigl, R., Steibl, S., & Laforsch, C. (2016) The role of vision for navigation in the crown-of-thorns seastar, *Acanthaster planci. Scientific Reports, 6*(1)*:* 30834.

# IX. Conclusion

Understanding how biodiversity and species distribution are organized on different spatial scales is one of the key questions in modern ecological research (Sutherland et al., 2013). Identifying the relevant drivers and mechanisms that act on a local scale becomes a pressing issue under the light of global change: the most prevalent threat for global biodiversity is not climate change, which acts on a global level, but human-driven land conversion, which alters the organization of biodiversity and species distribution on a local scale, i.e. within ecosystems (Habel et al., 2019). Therefore, understanding how different forms of human land use alter the organization of biodiversity and species distribution is ultimately the key to more sustainable land use and conservation efforts that counteract and reverse the damages already done. This PhD thesis investigated how biodiversity and species distribution are organized by natural abiotic and biotic factors on a local scale and disentangled the environmental impacts of different human land uses using small insular ecosystems as a methodical framework.

In the first chapter of this PhD thesis, I demonstrate which abiotic factors are the key drivers for the investigated focal taxon's biodiversity and distribution and showed that intrinsic mechanisms of resource partitioning likely stabilize the diversity and distribution patterns of the investigated focal taxa. The two investigated forms of human land use (tourism and permanent settling) significantly impacted different aspects of the focal taxon (abundance or body size), demonstrating that two human land uses can have overall contrasting impacts on the same taxon within the same system.

As focal taxon approaches always lack the generalizability of community-wide approaches (Purvis and Hector, 2000), the second chapter of this PhD thesis shifted the level of investigation towards whole communities. I demonstrated that the ground-associated faunal community is organized in distinct compartments with respect to ecological and trophic niche occupation. The community-wide analysis of biodiversity and distribution patterns on islands used as permanent settlings or for tourism offered the first empirical evidence for a dramatic loss in tropical insular invertebrate taxa following touristic and urban development. This finding in itself is of major importance for conservation. It underlines how threatened even remote tropical insular systems have become due to the growing global tourist industry and the increasing human land demands (Gillespie et al., 2012; Hall, 2010). The investigation of the land-use-associated changes to trophic niche occupation further gave first indications why certain species are more susceptible to human land use than others, suggesting that the ability to dietary shifts might be a decisive adaptation of ground-associated invertebrate species to persist in an anthropogenically modified environment.

Bringing together the findings of the individual research projects can form the basis of further research on the basic architecture and organization of ecosystems. The results of this PhD thesis also offer relevant insight for applied global change ecology and conservation planning, as I demonstrated the necessity to disentangle different human land uses to assess the harmful effects of human activities on nature more comprehensively. To protect the native insular fauna most efficiently, it would be important to tailor any future conservation action specifically to the type of land use present, its associated activities and land use/ cover changes. Reducing pesticide application and intensive beach cleaning activities would be the key to sustaining biodiversity on the investigated tropical atoll islands used for tourism. On islands inhabited by the local population and developed as an urban environment, it would be primarily important to leave parts of the natural insular vegetation intact or establish protected areas with native insular vegetation, which can act as refugia for the islands' biota.

I can also conclude that the methodical framework of this PhD thesis, i.e., using islands as model systems for studying the organization of biodiversity on small spatial scales and for disentangling the impacts of different human land uses, is a suitable tool for future research in community and disturbance ecology. Empirical research aiming to investigate ecological organization on higher ecological levels (i.e., within communities or ecosystems) is often hindered by the overall complexity of most natural ecosystems, the difficulty of ecosystem or community demarcation, and the absence of suitable ecosystem replication (Carpenter, 1996, 1990; Carpenter and Turner, 2007). Therefore, groups of small islands have been used repeatedly to study ecological processes more comprehensively than on the mainland (Goldstein, 1975). The research and findings of this PhD thesis underline the suitability of islands as model systems for a wide range of open and fundamental questions in empirical ecological research (Sutherland et al., 2013).

The findings reported in this PhD thesis thus can pave the way for future research in community and disturbance ecology. The islands' simple communities, low habitat complexity, and clear demarcation, together with the possibility of replicating whole ecosystems, offer the perfect setting and conditions required to test fundamental ecological principles on different ecological levels empirically. The two species newly recorded from the investigated insular system in the last chapter of this PhD thesis further underline how understudied at least some remote insular systems still are in the 21st century. Conclusively, probably many species, as well as ecological processes and interactions new to science are likely to be discovered when studying insular ecosystems.

> *"Every island,* [at least] *to a child, is a treasure island."*
> - P.D. James, The Lighthouse, 2005.

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# XI. References

Abrams, P.A., 1980. Resource partitioning and interspecific competition in a tropical hermit crab community. Oecologia 46, 365–379.

Abrams, P.A., 1978. Shell selection and utilization in a terrestrial hermit crab, Coenobita compressus (H. Milne Edwards). Oecologia 34, 239–253.

Adams, B.J., Li, E., Bahlai, C.A., Meineke, E.K., McGlynn, T.P., Brown, B. V., 2020. Local- and landscape-scale variables shape insect diversity in an urban biodiversity hot spot. Ecol. Appl. 30, 1–14.

Alerstam, T., 1993. Bird migration. Cambridge University Press.

Alley, T.R., 1982. Competition theory, evolution, and the concept of an ecological niche. Acta Biotheor. 31, 165–179.

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol. Monogr. 83, 557–574. 1

Anderson, R.C., Shimal, M., 2020. A checklist of birds of the Maldives. Indian Birds Monogr. 3, 1–56.

Anderson, W.B., Polis, G.A., 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118, 324–332.

Anderson, W.B., Polis, G.A., 1998. Marine subsidies of island communities in the gulf of California: evidence from stable carbon and nitrogen isotopes. Oikos 81, 75–80.

Armonies, W., Reise, K., 2000. Faunal diversity across a sandy shore. Mar. Ecol. Prog. Ser. 196, 49–57.

Astorga, A., Fernández, M., Boschi, E.E., Lagos, N., 2003. Two oceans, two taxa and one mode of development: Latitudinal diversity patterns of South American crabs and test for possible causal processes. Ecol. Lett. 6, 420–427.

Barnes, D.K.A., 1997a. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: vertical migration (tree climbing). Mar. Ecol. Prog. Ser. 183, 233–240.

Barnes, D.K.A., 1997b. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: a novel and locally important food source. Mar. Ecol. Prog. Ser. 161, 299–302.

Barnes, D.K.A., de Grave, S., 2000. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: niche width and resource allocation. Mar. Ecol. Prog. Ser. 206, 171–179.

Barrett, K., Anderson, W.B., Wait, D.A., Grismer, L.L., Polis, G.A., Rose, M.D., 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. Oikos 1, 145–153.

Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. Mar. Ecol. Prog. Ser. 214, 137–150.

Bergamino, L., Lercari, D., Defeo, O., 2012. Terrestrial trophic subsidy in sandy beaches: Evidence from stable isotope analysis in organic matter sources and isopod *Excirolana armata*. Aquat. Biol. 14, 129–134.

Blower, J.G., 1985. Millipedes: Keys and notes for the identification of the species. The Linnean Society of London, London, Leiden, Köln, København.

Bösenberg, W., Strand, E., 1906. Japanische Spinnen. Abhandlungen Hrsg. von der Senckenbergischen Naturforschenden Gesellschaft 30, 93–422.

Boulangeat, I., Gravel, D., Thuiller, W., 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecol. Lett. 15, 584–593.

Branch, G.M., Cherry, M.I., 1985. Activity rhythms of the pulmonate limpet *Siphonaria capensis* Q. & G. as an adaptation to osmotic stress, predation and wave action. J. Exp. Mar. Biol. Ecol 87, 153–168.

Brodie, R.J., 1999. Ontogeny of shell-related behaviors and transition to land in the terrestrial hermit crab *Coenobita compressus* H. Milne Edwards. J. Exp. Mar. Bio. Ecol. 241, 67–80.

Brook, S., Grant, A., Bell, D., 2009. Can land crabs be used as a rapid ecosystem evaluation tool? A test using distribution and abundance of several genera from the Seychelles. Acta Oecologica 35, 711–719.

Brown, B.E., 1997. Disturbances to reefs in recent times, in: Birkeland, C. (Ed.), Life and Death of Coral Reefs. Chapman and Hall, New York, pp. 354–379.

Cardinale, B.J., Weis, J.J., Forbes, A.E., Tilmon, K.J., Ives, A.R., 2006. Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator-prey system. J. Anim. Ecol. 75, 497–505.

Cardoso, R.S., Barboza, C.A.M., Skinner, V.B., Cabrini, T.M.B., 2016. Crustaceans as ecological indicators of metropolitan sandy beaches health. Ecol. Indic. 62, 154–162.

Carpenter, S.R., 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77, 677–680.

Carpenter, S.R., 1990. Large-scale pertubations: opportunities for innovation. Ecology 71, 2038–2043.

Carpenter, S.R., Chisholm, S.W., Krebs, C.J., Schindler, D.W., Wright, R.F., 1995. Ecosystem experiments. Science. 269, 324–327.

Carpenter, S.R., Turner, M.G., 2007. A decade of ecosystems. Ecosystems 10, 519–522.

Chan, A.A.Y.-H., Giraldo-Perez, P., Smith, S., Blumstein, D.T., 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biol. Lett. 6, 458–61.

Clark, J.R., 1999. The ecosystem approach from a practical point of view. Conserv. Biol. 13, 679–681.

Connor, E.F., Simberloff, D., 1983. Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. Oikos 41, 455–465.

D’Amen, M., Mod, H.K., Gotelli, N.J., Guisan, A., 2018. Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. Ecography (Cop.). 41, 1233–1244.

Dangerfield, J.M., Milner, A.E., 1996. Millipede fecal pellet production in selected natural and managed habitats of Southern Africa: implications for litter dynamics. Biotropica 28, 113.

Dangerfield, J.M., Milner, A.E., Matthews, R., 1992. Seasonal activity patterns and behaviour of Juliform millipedes in South-Eastern Botswana. J. Trop. Ecol. 8, 451–464.

de Graaf, M., Machiels, M.A.M., Wudneh, T., Sibbing, F.A., 2004. Declining stocks of Lake Tana’s endemic Barbus species flock (Pisces, Cyprinidae): Natural variation or human impact? Biol. Conserv. 116, 277–287.

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J.E., Jones, A., Lastra, M., Scapini, F., 2009. Threats to sandy beach ecosystems: a review. Estuar. Coast. Shelf Sci. 81, 1–12.

Durán, A.P., Green, J.M.H., West, C.D., Visconti, P., Burgess, N.D., Virah-Sawmy, M., Balmford, A., 2020. A practical approach to measuring the biodiversity impacts of land conversion. Methods Ecol. Evol. 11, 910–921.

Eberhard, W.G., Huber, B.A., 2010. Spider genitalia, in: Leonard, J., Cordoba-AguilarA (Eds.), The Evolution of Primary Sexual Characters in Animals. Oxford University Press, New York, pp. 249–284.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R., Nentwig, W., 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Glob. Ecol. Biogeogr. 16, 440–448.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science. 333, 301–306.

Fallati, L., Savini, A., Sterlacchini, S., Galli, P., 2017. Land use and land cover (LULC) of the Republic of the Maldives: first national map and LULC change analysis using remote-sensing data. Environ. Monit. Assess. 189.

Feare, C.J., High, J., 1977. Migrant shorebirds in the Seychelles. Ibis (Lond. 1859). 119, 323–338.

Fernández, M., Astorga, A., Navarrete, S.A., Valdovinos, C., Marquet, P.A., 2009. Deconstructing latitudinal species richness patterns in the ocean: Does larval development hold the clue? Ecol. Lett. 12, 601–611.

Fotheringham, N., 1976. Hermit crab shells as a limiting resource (Decapoda, Paguridea). Crustaceana 31, 193–199.

Framenau, V.W., Berry, J.W., Beatty, J.A., 2009. Wolf spiders of the pacific region: The genus Zoica (Araneae, Lycosidae. J. Arachnol. 37, 225–231.

Fraser, H., Barnett, A., Parker, T.H., Fidler, F., 2020. The role of replication studies in ecology. Ecol. Evol. 10, 5197–5207.

Gagné, T.O., Reygondeau, G., Jenkins, C.N., Sexton, J.O., Bograd, S.J., Hazen, E.L., van Houtan, K.S., 2020. Towards a global understanding of the drivers of marine and terrestrial biodiversity. PLoS One 15, 1–17.

Gerlach, A., 2014. *Eucarlia hoffmani*. IUCN Red List Threat. Species 2307–8235.

Gillespie, T.W., Lipkin, B., Sullivan, L., Benowitz, D.R., Pau, S., Keppel, G., 2012. The rarest and least protected forests in biodiversity hotspots. Biodivers. Conserv. 21, 3597–3611.

Gilpin, M., 1994. Community-level competition: Asymmetrical dominance. Proc. Natl. Acad. Sci. U. S. A. 91, 3252–3254.

Goldstein, E.L., 1975. Island biogeography of ants. Evolution (N. Y). 29, 750–762.

Golovatch, S.I., Kime, R.D., 2009. Millipede (Diplopoda) distributions : A review. Soil Org. 81, 565–597.

Golovatch, S.I., Korsós, Z., 1992. Diplopoda collected by the Soviet zoological expedition to the Seychelles islands in 1984. Acta Zool. Hungarica 38, 1–31.

Goodsell, P.J., Underwood, A.J., Chapman, M.G., 2009. Evidence necessary for taxa to be reliable indicators of environmental conditions or impacts. Mar. Pollut. Bull. 58, 323–331.

Gössling, S., 2002. Global environmental consequences of tourism. Glob. Environ. Chang. 12, 283–302.

Granadeiro, J.P., Dias, M.P., Martins, R.C., Palmeirim, J.M., 2006. Variation in numbers and behaviour of waders during the tidal cycle: implications for the use of estuarine sediment flats. Acta Oecologica 29, 293–300.

Greenaway, P., 2003. Terrestrial adaptations in the Anomura (Crustacea: Decapoda). Mem. Museum Victoria 60, 13–26.

Gross, W.J., 1964. Water balance in anomuran land crabs on a dry atoll. Biol. Bull. 126, 54–68.

Gusev, O., Zabotin, Y., 2007. Observation of intersexuality in land hermit crabs (Anomura: Coenobitidae). J. Mar. Biol. Assoc. UK 87, 533–536.

Habel, J.C., Rasche, L., Schneider, U.A., Engler, J.O., Schmid, E., Rödder, D., Meyer, S.T., Trapp, N., Sos del Diego, R., Eggermont, H., Lens, L., Stork, N.E., 2019. Final countdown for biodiversity hotspots. Conserv. Lett. e12668, 1–9.

Hall, C.M., 2010. Tourism and biodiversity: more significant than climate change? J. Herit. Tour. 5, 253–266.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12, e0185809.

Hamasaki, K., Kato, S., Murakami, Y., Dan, S., Kitada, S., 2015. Larval growth, development and duration in terrestrial hermit crabs. Sex. Early Dev. Aquat. Org. 1, 93–107.

Hamilton, A.J., 2005. Species diversity or biodiversity? J. Environ. Manage. 75, 89–92.

Heams, T., Lecointre, G., Huneman, P., Silberstein, M., 2015. Handbook of evolutionary thinking in the sciences, Handbook of Evolutionary Thinking in the Sciences. Springer Science+Business Media, Dordrecht.

Hereward, H.F.R., Gentle, L.K., Ray, N.D., Sluka, R.D., 2017. Ghost crab burrow density at Watamu Marine National Park: An indicator of the impact of urbanisation and associated disturbance? African J. Mar. Sci. 39, 129–133.

Herreid, C.F., Full, R.J., 1986. Energetics of hermit crabs during locomotion: the cost of carrying a shell. J. Exp. Mar. Bio. Ecol. 120, 297–308.

Hilty, J., Merenlender, A., 2000. Faunal indicator taxa selection for monitoring ecosystem health. Biol. Conserv. 92, 185–197.

Hoffmann, A.A., Blows, M.W., 1994. Species borders: ecological and evolutionary perspectives. Trends Ecol. Evol. 9, 223–227.

Hogarth, P.J., Gherardi, F., McLaughlin, P.A., 1998. Hermit crabs (Crustacea Decapoda Anomura) of the Maldives with the description of a new species of Catapagurus A. Milne Edwards 1880. Trop. Zool. 11, 149–175.

Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proc. Natl. Acad. Sci. 106, 19659–19665.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105–108.

Hsu, C.-H., Soong, K., 2017. Mechanisms causing size differences of the land hermit crab *Coenobita rugosus* among eco-islands in Southern Taiwan. PLoS One 12, e0174319.

Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Weston, M.A., Connolly, R.M., 2013. Urbanisation alters processing of marine carrion on sandy beaches. Landsc. Urban Plan. 119, 1–8.

Huston, M., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.

Hutchinson, G.E., 1978. An introduction to population ecology. New Haven, New Haven.

Hutchinson, G.E., 1957. Concluding remarks, in: Cold Spring Harbor Symposia on Quantitative Biology. pp. 415–427.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D., 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. Can. J. Fish. Aquat. Sci. 58, 157–170.

James, P.D. 2005. The lighthouse. Faber & Faber publishing.

Jantz, S.M., Barker, B., Brooks, T.M., Chini, L.P., Huang, Q., Moore, R.M., Noel, J., Hurtt, G.C., 2015. Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. Conserv. Biol. 29, 1122–1131.

Jaramillo, E., McLachlan, A., 1993. Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. Estuar. Coast. Shelf Sci. 37, 615–624.

Jocqué, R., Alderweireldt, M., 2005. Lycosidae: the grassland spiders. Acta Zool. Bulg. 1, 125–130.

Kadmon, R., Allouche, O., 2007. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. Am. Nat. 170, 443–454.

Kark, S., 2013. Ecotones and ecological gradients, in: Leemans, R. (Ed.), Ecological Systems: Selected Entries from the Encyclopedia of Sustainability Science and Technology. Springer Science & Business Media, New York, pp. 147–160.

Kark, S., van Rensburg, B.J., 2006. Ecotones: marginal or central areas of transition? Isr. J. Ecol. Evol. 52, 29–53.

Kelly, J.F., 2014. Effects of human activities (raking, scraping, off-road vehicles) and natural resource protections on the spatial distribution of beach vegetation and related shoreline features in New Jersey. J. Coast. Conserv. 18, 383–398.

Kerr, J., 2001. Global biodiversity patterns: from description to understanding. Trends Ecol. Evol. 16, 424–425. https://doi.org/10.1016/S0169-5347(01)02226-1

Kerr, J.T., Sugar, A., Packer, L., 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. Conserv. Biol. 14, 1726–1734.

Kevan, D.K.M., Kevan, P.G., 1995. A preliminary record of Orthopteroid insects of the Maldive Islands. J. Orthoptera Res. 4, 223–236.

Kinzey, D., Punt, A.E., 2009. Multispecies and single-species models of fish population dynamics: comparing parameter estimates. Nat. Resour. Model. 22, 67–104.

Kronestedt, T., 2010. *Draposa*, a new wolf spider genus from South and Southeast Asia (Araneae: Lycosidae). Zootaxa 54, 31–54.

Lastra, M., Schlacher, T.A., Olabarria, C., 2009. Niche segregation in sandy beach animals: an analysis with surface-active peracarid crustaceans on the Atlantic coast of Spain. Mar. Biol. 157, 613–625.

Latreille, P.A., 1829. Les Crustacés, les Arachnides et les Insectes, distribués en familles naturelles, in: Cuvier, G. (Ed.), Le Règne Animal, Distribué d'après Son Organisation, Pour Servir de Base à l'histoire Naturelle Des Animaux et d'introduction à l'anatomie Comparée. pp. 1–584.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: An overview of analytical tools. Biol. Rev. 87, 545–562.

Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88, 42–48.

Lemaitre, R., McLaughlin, P.A., 2019. World Paguroidea & Lomisoidea database. Coenobita Latreille, 1829. World Regist. Mar. Species.

Lemoine, N.P., Hoffman, A., Felton, A.J., Baur, L., Chaves, F., Gray, J., Yu, Q., Smith, M.D., 2016. Underappreciated problems of low replication in ecological field studies. Ecology 97, 2554–2561.

Losos, J.B., Jackman, T.R., Larson, A., Queiroz, K. De, Rodrı, L., 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science (80-. ). 279, 2115–2118.

Losos, J.B., Ricklefs, R.E., 2009. Adaptation and diversification on islands. Nature 457, 830–836.

Lucrezi, S., Schlacher, T.A., Walker, S.J., 2009. Monitoring human impacts on sandy shore ecosystems: a test of ghost crabs (Ocypode spp.) as biological indicators on an urban beach. Environ. Monit. Assess. 152, 413–424.

Marczak, L.B., Thompson, R.M., Richardson, J.S., 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88, 140–148.

Marquet, P.A., Fernández, M., Navarrete, S.A., Valdovinos, C., 2004. Diversity emerging: toward a deconstruction of biodiversity patterns, in: Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland MA.

McCann, K.S., Rasmussen, J.B., Umbanhowar, J., 2005. The dynamics of spatially coupled food webs. Ecol. Lett. 8, 513–523.

McLachlan, A., 2001. Coastal beach ecosystems. Encycl. Biodivers. 1, 741–751.

McLachlan, A., Jaramillo, E., Donn, T.E., Wessels, F., 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. J. Coast. Res. Special Is, 27–38.

McLaughlin, P.A., 1983. Hermit crabs: are they really polyphyletic? J. Crustac. Biol. 3, 608–621.

McLaughlin, P.A., Komai, T., Lemaitre, R., Rahayu, D., 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part I –Lithodoidea, Lomisoidea and Paguroidea. Raffles Bull. Zool. 23, 5–107.

McMahon, B.R., Burggren, W.W., 1979. Respiration and adaptation to the terrestrial habitat in the land hermit crab *Coenobita clypeatus*. J. exp. Biol 79, 265–281.

Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecol. Modell. 415, 108837.

Mitsch, W.J., Day Jr., J.W., 2004. Thinking big with whole-ecosystem studies and ecosystem restoration - A legacy of H.T. Odum. Ecol. Modell. 178, 133–155.

Mundkur, T., Langendoen, T., Watkins, D., 2017. The Asian waterbird census 2008-2015: results of coordinated counts in Asia and Australasia. Wetlands International, Ede.

Naderloo, R., 2017. Atlas of crabs of the Persian Gulf. Springer, Teheran.

Naylor, A.K., 2015. Island morphology, reef resources, and development paths in the Maldives. Prog. Phys. Geogr. 39, 728–749.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science. 353, 291–288.

Newsome, S.D., del Rio, C.M., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436.

Newton, I., 2011. The ecology of bird migration patterns. BOU Proc. 1–3.

Nieves-Rivera, Á.M., Williams, E.H., 2003. Annual migrations and spawning of *Coenobita clypeatus* (Herbst) on Mona Island (Puerto Rico) and notes on inland crustaceans. Crustaceana 76, 547–558.

Nigro, K.M., Hathaway, S.A., Wegmann, A.S., Miller-ter Kuile, A., Fisher, R.N., Young, H.S., 2017. Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication. Restor. Ecol. 1–11.

Noriega, R., Schlacher, T.A., Smeuninx, B., 2012. Reductions in ghost crab populations reflect urbanization of beaches and dunes. J. Coast. Res. 28, 123–131.

Noy-Meir, I., 1980. Structure and function of desert ecosystems. Isr. J. Bot. 28, 1–19.

Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. Proc. Natl. Acad. Sci. U. S. A. 104, 19891–19896.

Orr, M., Zimmer, M., Jelinski, D.E., Mews, M., 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86, 1496–1507.

Osorno, J.-L., Fernández-Casillas, L., Rodríguez-Juárez, C., 1998. Are hermit crabs looking for light and large shells?: evidence from natural and field induced shell exchanges. J. Exp. Mar. Bio. Ecol. 222, 163–173.

Paetzold, A., Lee, M., Post, D.M., 2008. Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. Oecologia 157, 653–659.

Page, H.M., Willason, S.W., 1983. Feeding activity patterns and carrion removal by terrestrial hermit crabs at Enewetak Attol, Marshall Islands. Pacific Sci. 37, 151–155.

Penick, C.A., Savage, A.M., Dunn, R.R., 2015. Stable isotopes reveal links between human food inputs and urban ant diets. Proc. R. Soc. B Biol. Sci. 282, 20142608.

Peters, M.K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Mwangomo, E., Ngereza, C., Otte, I., Röder, J., Rutten, G., Schellenberger Costa, D., Tardanico, J., Zancolli, G., Deckert, J., Eardley, C.D., Peters, R.S., Rödel, M.O., Schleuning, M., Ssymank, A., Kakengi, V., Zhang, J., Böhning-Gaese, K., Brandl, R., Kalko, E.K.V., Kleyer, M., Nauss, T., Tschapka, M., Fischer, M., Steffan-Dewenter, I., 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nat. Commun. 7.

Ping, X., Lee, J.S., Garlick, D., Jiang, Z., Blaisdell, A.P., 2015. Behavioral evidence illuminating the visual abilities of the terrestrial Caribbean hermit crab *Coenobita clypeatus*. Behav. Processes 118, 47–58.

Piovia-Scott, J., Spiller, D.A., Schoener, T.W., 2011. Effects of experimental seaweed deposition on lizard and ant predation in an island food web. Science. 331, 461–463.

Platia, G., 2015. Contribution to the knowledge of the click beetles of the Maldives (Coleoptera: Elateridae). Bol. la S.E.A. 57, 182–184.

Poy, D., Ramírez, M.J., Michalik, P., Piacentini, L.N., 2019. Copulatory mechanics in the wolf spider Agalenocosa pirity reveals a hidden diversity of locking systems in Lycosidae (Araneae). J. Morphol. 281, 250–257.

Pringle, R.M., Fox-Dobbs, K., 2008. Coupling of canopy and understory food webs by ground-dwelling predators. Ecol. Lett. 11, 1328–1337.

Pringle, R.M., Kartzinel, T.R., Palmer, T.M., Thurman, T.J., Fox-Dobbs, K., Xu, C.C.Y., Hutchinson, M.C., Coverdale, T.C., Daskin, J.H., Evangelista, D.A., Gotanda, K.M., Man in ’t Veld, N.A., Wegener, J.E., Kolbe, J.J., Schoener, T.W., Spiller, D.A., Losos, J.B., Barrett, R.D.H., 2019. Predator-induced collapse of niche structure and species coexistence. Nature 570, 58–64.

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. Nature 405, 212–219.

Quammen, D. 1997. The song of the Dodo: Island biogeography in an age of extinction. Scribner publishing.

Raiter, K.G., Possingham, H.P., Prober, S.M., Hobbs, R.J., 2014. Under the radar: mitigating enigmatic ecological impacts. Trends Ecol. Evol. 29, 635–644.

Rezende, E.L., Albert, E.M., Fortuna, M.A., Bascompte, J., 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecol. Lett. 12, 779–788.

Richter, C.J.J., 1970. Aerial dispersal in relation to habitat in eight wolf spider species (Pardosa, Araneae, Lycosidae). Oecologia 5, 200–214.

Rohde, K., 1999. Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? Ecography (Cop.). 22, 593–613.

Romanuk, T.N., Levings, C.D., 2003. Associations between arthropods and the supralittoral ecotone: dependence of aquatic and terrestrial taxa on riparian vegetation. Environ. Entomol. 32, 1343–1353.

Rose, M.D., Polis, G.A., 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79, 998–1007.

Saeed, S., Annandale, D., 1999. Tourism and the management of environmental impacts in the Republic of Maldives. J. Policy Stud. 7, 81–88.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science. 287, 1770–1774.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A. V, Woolmer, G., 2002. The human footprint and the last of the wild. Bioscience 52, 891–904.

Scapini, F., 2014. Behaviour of mobile macrofauna is a key factor in beach ecology as response to rapid environmental changes. Estuar. Coast. Shelf Sci. 150, 1–9.

Schindler, D.W., 1998. Replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1, 323–334.

Schluter, D., Pennell, M.W., 2017. Speciation gradients and the distribution of biodiversity. Nature 546, 48–55.

Semenyuk, I., Tiunov, A. V, Golovatch, S.I., 2011. Structure of mandibles in relation to trophic niche differentiation in a tropical millipede community. Int. J. Myriap. 6, 37–49.

Shmida, A., Wilson, M. V, 1985. Biological determinants of species diversity. J. Biogeogr. 12, 1.

Short, A.D., 1996. The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. Rev. Chil. Hist. Nat. 69, 589–604.

Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. 83, 247–257.

Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L.A., Laurance, W.F., 2014. Remaining natural vegetation in the global biodiversity hotspots. Biol. Conserv. 177, 12–24.

Small, M.P., Thacker, R.W., 1994. Land hermit crabs use odors of dead conspecifics to locate shells. J. Exp. Mar. Bio. Ecol. 182, 169–182.

Snyder, B.A., Hendrix, P.F., 2008. Current and potential roles of soil macroinvertebrates (earthworms, millipedes, and isopods) in ecological restoration. Restor. Ecol. 16, 629–636.

Soberón, J., 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecol. Lett. 10, 1115–1123.

Sobocinski, K.L., Cordell, J.R., Simenstad, C.A., 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget sound, Washington beaches. Estuaries and Coasts 33, 699–711.

Somveille, M., Manica, A., Butchart, S.H.M., Rodrigues, A.S.L., 2013. Mapping global diversity patterns for migratory birds. PLoS One 8, e70907.

Subalusky, A.L., Post, D.M., 2019. Context dependency of animal resource subsidies. Biol. Rev. 94, 517–538.

Sunil, J.K., 2012. The spider fauna of Maldive islands in Indian Ocean (Araneae). Munis Entomol. Zool. 7, 424–431.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A., Wiegand, T., 2013. Identification of 100 fundamental ecological questions. J. Ecol. 101, 58–67.

Szabo, J.K., Mundkur, T., 2017. Conserving wetlands for migratory waterbirds in South Asia, in: Prusty, B.A.K. (Ed.), Wetland Science: Perspectives From South Asia. Springer, pp. 1–587.

Szabo, K., 2012. Terrestrial hermit crabs (Anomura: Coenobitidae) as taphonomic agents in circum-tropical coastal sites. J. Archaelogical Sci. 39, 931–941.

Taiti, S., 2014. The terrestrial Isopoda (Crustacea, Oniscidea) of the Maldives. Trop. Zool. 27, 9–33.

Takemoto, K., Kajihara, K., 2016. Human impacts and climate change influence nestedness and modularity in food-web and mutualistic networks. PLoS One 11, e0157929.

Taylor, E.W., 1988. A functional analysis of the shift from gill- to lung-breathing during the evolution of land crabs (Crustacea, Decapoda). Biol. J. Linn. Soc. 34, 229–247.

Tekin, E., Diamant, E.S., Cruz-Loya, M., Enriquez, V., Singh, N., Savage, V.M., Yeh, P.J., 2020. Using a newly introduced framework to measure ecological stressor interactions. Ecol. Lett. 23, 1391–1403.

Telford, S.R., Dangerfield, J.M., 1993. Mating tactics in the tropical millipede Alloporus uncinatus (Diplopoda: Spirostreptidae). Behaviour 124, 45–56.

Thaman, R.R., 2008. Atolls - the “biodiversity cool spots” vs “hot spots”: a critical new focus for research and conservation. Micronesica 40, 33–61.

Thaman, R.R., Puia, T., Tongabaea, W., Namona, A., Fong, T., 2010. Marine biodiversity and ethnobiodiversity of Bellona (Mungiki) Island, Solomon Islands. Singap. J. Trop. Geogr. 31, 70–84.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80, 1455–1474.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E. Vanden, Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466, 1098–1101.

Tracy, C.R., Brussard, P.F., 1994. Preserving biodiversity: species in landscapes. Ecol. Appl. 4, 205–207.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T. V, Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89, 944–951.

Underwood, A.J., 1990. Experiments in ecology and management: their logics, functions and interpretations. Aust. J. Ecol. 15, 365–389.

Urban, M.C., Strauss, S.Y., Pelletier, F., Palkovacs, E.P., Leibold, M.A., Hendry, A.P., de Meester, L., Carlson, S.M., Angert, A.L., Giery, S.T., 2020. Evolutionary origins for ecological patterns in space. Proc. Natl. Acad. Sci. U. S. A. 117, 17482–17490.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. Funct. Ecol. 29, 299–307.

Vance, R.R., 1972a. The role of shell adequacy in behavioral interactions involving hermit crabs. Ecology 53, 1075–1083.

Vance, R.R., 1972b. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53, 1062–1074.

Vannini, M., 1976. Researches on the coast of Somalia. The shore and the dune of Sar Uanle 7. Field observations on the periodical transdunal migrations of the hermit crab *Coenobita rugosus* Milne Edwards. Monit. Zool. Ital. 7, 145–185.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 1–11.

Wardle, D.A., Zackrisson, O., 2005. Effects of species and functional group loss on island ecosystem properties. Nature 435, 806–810.

Welch, R., 1982. Spatial resolution requirements for urban studies. Int. J. Remote Sens. 3, 139–146.

Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. J. Biogeogr. 28, 453–470.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H. V, Damschen, E.I., Jonathan Davies, T., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13, 1310–24.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. Biol. Rev. 88, 15–30.

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# XII. Statutory Declarations

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

*Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).*

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*Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.*

(§ 9 Satz 2 Nr. 4 PromO BayNAT)

*Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.*

(§ 9 Satz 2 Nr. 7 PromO BayNAT)

*Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.*

(§ 9 Satz 2 Nr. 8 PromO BayNAT)

*Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.*

…………………………………………………………………………………………

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