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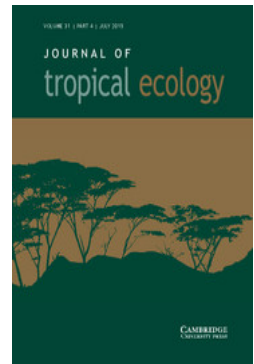
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Plant composition patterns inside an endemic birds' nest fern (*Asplenium goudeyi*) on Lord Howe Island: effects of fern size, fern isolation and plant dispersal abilities

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Abstract: The importance of deterministic and stochastic processes in structuring ecological communities is an enduring debate. Although this debate is nearly a century old, the extent to which communities are structured by species interactions or chance events is a central issue in ecology. We examined the assemblages of plants living inside 119 birds' nest ferns (*Asplenium goudeyi*), which are endemic to Lord Howe Island. Specifically, we investigated whether patterns of species richness and community composition were influenced by fern size, fern isolation and plant dispersal abilities. Fern size and fern isolation significantly predicted plant community richness. At the community level, plant composition patterns did not deviate from randomized expectations. Individual species occurrences increased with increasing community richness, and no species exclusions were observed. Wind-dispersed taxa, which accounted for 29% of all species, were well represented in isolated ferns. Comparatively, poorer dispersers were confined to ferns nearest the forest at the base of the cliffs. We suggest that dispersal plays a key role in structuring plant communities living within birds' nest ferns, and that species interactions are less important. Our study emphasizes the importance of epiphytes with a nest-like growth form as habitat for plants in a harsh environment.

Key Words: Birds' nest fern, community composition, dispersal, isolation, Lord Howe Island

INTRODUCTION

Numerous fundamental ideologies in ecology and evolution have arisen from investigating species distributions on islands. Perhaps the most controversial, is the role of chance in structuring ecological communities. One school of thought maintains that communities are structured in a predictable way, and that niche differentiation or species exclusions play an important role in community assembly dynamics (Chesson 2000, Clements 1916, Dornelas *et al.* 2006, Gause 1934, Hutchinson 1959, Keddy 1992, Silvertown *et al.* 2006, Tilman 1985, Tuomisto *et al.* 2003). However, an opposing argument suggests that communities are structured by chance events, which randomize species compositions (Connor & Simberloff 1979, Gleason 1917, Hubbell *et al.* 1999). While this debate came about nearly

a century ago, the extent to which species compositions are structured by chance is still a major theme in community ecology (Diamond 1975, Grace 1999, Grime 2001, Ricklefs & Lovette 1999, Zobel 1997).

In addition to islands, patterns of community composition have been analysed for forest fragments (Ehrlén & Eriksson 2000, Jacquemyn *et al.* 2001), urban parks (Fernández-Juricic 2000) and freshwater ecosystems (Mouillot 2007). However, in-depth studies on the structure of epiphyte communities are uncommon (Buckley 2011, Johansson 1974, Jüriado *et al.* 2009). Additionally, no studies have analysed the structure of plant communities living within epiphytic plants, which may act as foundation species in some environments. One such environment is on the vertical faces of the southern mountains of Lord Howe Island (hereafter LHI), a volcanic remnant in the South Pacific. Here, many individuals of the endemic birds' nest fern *Asplenium goudeyi* D.L. Jones (Aspleniaceae) persist, and are utilized by plants that may otherwise not survive the harsh cliff environment.

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Birds' nest ferns capture plant material within the upright extensions of their fern fronds. This plant material is broken down into a nutrient-rich soil, which provides a medium for seeds to germinate in (Zhang *et al.* 2010). Patterns in species composition and species richness of plant communities living within birds' nest ferns may be influenced by fern size, age and fern isolation from a major propagule source. For one, plant taxa may establish more frequently in larger ferns as they are able to intercept comparatively more dispersers (Hinsley *et al.* 1995, Ricklefs & Lovette 1999). Additionally, species establishment success may be higher in larger ferns because they are presumably older, contain more microhabitats, and have been exposed to dispersing propagules for a period of time (Paulay 1994, Williams 1964). Furthermore, species immigration rates should theoretically be highest in ferns closest to a major propagule source, which in this case is the forest at the base of the cliffs (MacArthur & Wilson 1967). Another major source of variation in plant community composition may arise from interspecific differences in species dispersal and establishment capabilities (Hubbell 2001, Hurtt & Pacala 1995, Ozinga *et al.* 2004). For example, fleshy-fruited taxa generally have larger seed sizes, and are considered to be poor colonizers compared with wind-dispersed taxa (Howe & Smallwood 1982). However, seed size scales positively with seedling size, and fleshy fruited taxa may be able to utilize resources more efficiently than wind-dispersed taxa once established (Jakobsson & Eriksson 2000). Thus, a colonization-establishment trade-off exists, and may influence plant composition patterns (Smith & Fretwell 1974).

In this study, we examined plant communities living within birds' nest ferns on LHI, and determined whether they exhibit any predictable patterns of community composition. First, we tested the hypothesis that plant community richness will be influenced by fern size and fern isolation from forest vegetation. Second, we tested whether patterns of community composition were a reflection of plant dispersal abilities by regressing species allocated to three dispersal modes against isolation from the forest vegetation. Lastly, we used an incidence function approach to test the hypothesis that plant assemblages will show no predictable patterns of community composition or species exclusions.

METHODS

Sampling

The study was conducted on LHI, a subtropical island in the south-west Pacific (31°54′S, 159°08′E; Figure 1). Maximum daily temperatures average from 18°C in

the cooler months (May–September) to 25°C in the warmer months (November–April). Within the study area, precipitation averages 1500 mm per annum. Topography consists of two steep mountains in the south, which are composed of alkaline olivine basalt and hawaiites. The northern end of the island is primarily composed of calcerenite and coral sands (Pickard 1984). Fieldwork was carried out over July 2014 on the western-facing slopes of Mount Lidgbird (Figure 2). Here, we sampled plant communities living inside 119 birds' nest ferns within seven randomly marked 20-m-long transects. Short transects were used for safety purposes. At each fern, we recorded the presence/absence of plant taxa, fern size and fern isolation from the forest vegetation. We used a strict sampling criteria to ensure that plant taxa living within bird's nest ferns did not disperse via vegetative spread. For one, ferns that were not clearly separated from neighbouring ferns by at least 1 m were omitted. Likewise, ferns growing less than 1 m from any other vegetation, such as forest vegetation or vegetation growing directly on the cliff face were also omitted. Vegetation growing below the cliffs was reasonably homogeneous, thus we assumed that each plant community received colonizers from the same species pool. Birds' nest ferns, which typically spend their entire life cycle within trees, were not abundant on forest vegetation growing close to the cliffs. As such, we believe that plants colonizing the cliff-dwelling ferns did not disperse from the forest-dwelling ferns. Woody plant taxa ranged in height from ∼0.5 m (small or juvenile shrubs) to ∼4 m (stunted forest trees). One exception was the kentia palm (*Howea forsteriana*), which on occasion exceeded the height of all other woody taxa. Shrubs and small trees were able to grow directly at the cliff base, while larger trees grew progressively further back. Plants that could not be identified in the field were collected and identified at the LHI museum herbarium.

Statistical analyses

Generalized linear models assessed the relationship between fern size, fern isolation from the forest vegetation and plant community richness. We analysed patterns of community composition using the c-score metric (Stone & Roberts 1990). The c-score is simply the number of 'checkerboard units' between all species pairs in a matrix. A c-score that is significantly larger than randomized expectations is indicative of segregation among taxa (i.e. species co-occur less often than expected by chance). Conversely, a c-score that is significantly less than randomized expectations indicates aggregation among taxa (i.e. species co-occur more often than expected by chance). The observed c-score was compared to 5000
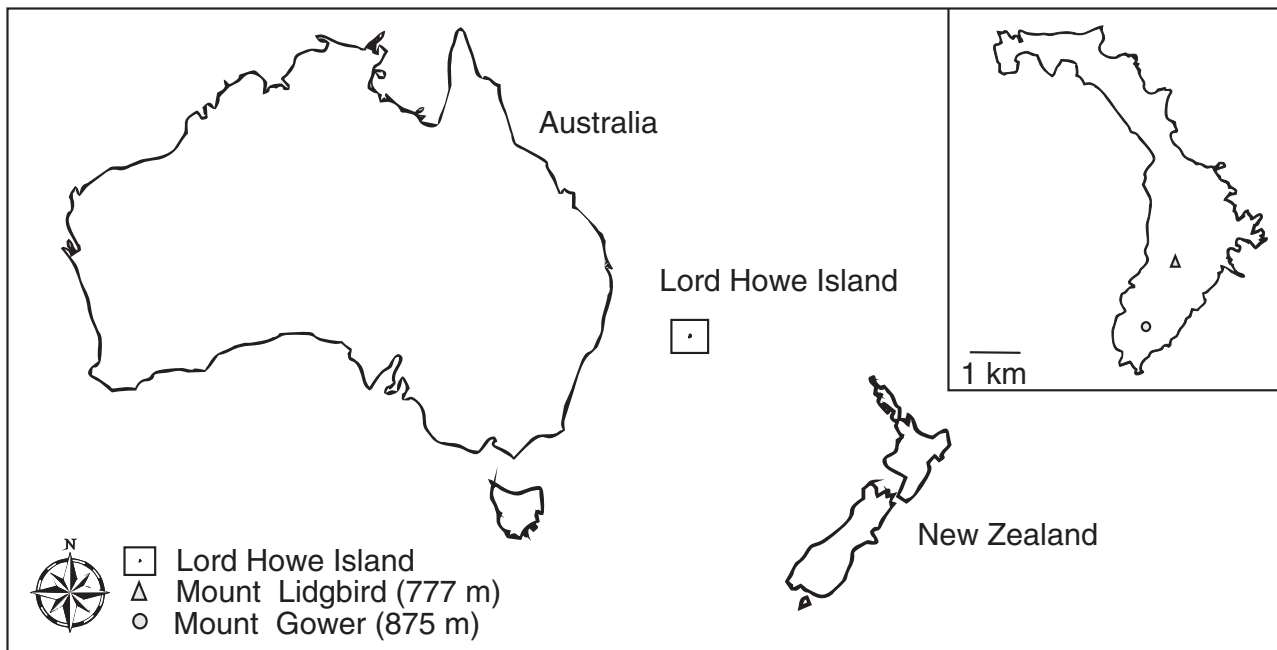
Figure 1. Map of Lord Howe Island and its location in relation to Australia and New Zealand. The mountains on which *Asplenium goudeyi* reside, Mount Lidgbird and Mount Gower, are also shown. Scale is for Lord Howe Island only.

Figure 2. View of *Asplenium goudeyi* ferns perched on the western-facing slopes of Mount Lidgbird on Lord Howe Island. A large boulder bank and kentia palms (*Howea forsteriana*) are visible in the foreground.

Table 1. Species and family names of plants living inside the epiphytic fern *Asplenium goudeyi*. The number of times each species occurred in a plant community and their mode of dispersal is also shown.

Species	Family	n	Dispersal mode
Ageratina adenophora (Spreng.) King & H.Rob.	Asteraceae	3	Wind
Alyxia ruscifolia R.Br.	Apocynaceae	30	Animal
Callisia fragrans (Lindl.) Woodson	Commelinaceae	40	No adaptations
Coprosma putida C.Moore & F.Muell.	Rubiaceae	7	Animal
Coprosma spp.	Rubiaceae	1	Animal
Cryptocarya triplinervis R.Br.	Lauraceae	1	Animal
Dodonaea viscosa subsp. *burmanniana* (DC.) J.G.West	Sapindaceae	2	No adaptations
Drypetes deplanchei (Brongn. & Gris) Merr.	Putranjivaceae	7	Animal
Ehrharta erecta Lam.	Poaceae	28	Wind
Lagunaria patersonia (Andrews) G.Don	Malvaceae	4	No adaptations
Lilium formosanum Wallace	Liliaceae	10	No adaptations
Melaleuca howeana Cheel	Myrtaceae	4	No adaptations
Microsorum howense Tindale & P.S.Green	Polypodiaceae	26	Wind
Muehlenbeckia complexa (A.Cunn) Meisn.	Polygonaceae	4	Animal
Nephrolepis cordifolia (L.) K. Presl	Lomariopsidaceae	10	Wind
Paspalum spp.	Poaceae	12	Wind
Peperomia urvilleana A.Rich.	Piperaceae	94	Animal
Poa annua L.	Poaceae	21	Wind
Solanum nigrum L.	Solanaceae	5	Animal
Sophora howinsula (W.R.B.Oliv.) P.S.Green	Fabaceae	2	No adaptations
Trifolium spp.	Fabaceae	2	No adaptations

simulation replicates using fixed row and column totals and a swap algorithm (Gotelli 2000). We assessed if patterns in plant composition were related to plant dispersal abilities by regressing species divided into three dispersal modes against distance from the forest vegetation. Grasses, ferns and plants with pappus or wings were considered wind-dispersed; fleshy-fruited taxa were considered animal-dispersed; and plants with no specific adaptations for wind or animal dispersal were considered a separate category (Table 1). Finally, incidence functions were constructed for species that occurred 10 or more times using logistic regression. Incidence functions relate the probability of a species occurring in a plant community, with the overall species richness of combined plant communities (Diamond 1975). All statistical analyses were conducted in R version 3.1.2 (R Development Core Team, Vienna, Austria) with the add-on libraries bipartite version 2.04 (Dormann *et al.* 2009), popbio version 2.4 (Stubben & Milligan 2007) and vegan version 2.0-10 (Dixon 2003).

RESULTS

Generalized linear models showed a significant effect of fern size and fern isolation from the forest vegetation on plant community richness (GLM: $F_1 = 20.57$; $P < 0.001$ and $F_1 = 6.13$; $P = 0.03$ respectively; Figure 3). Patterns of community composition were not significantly different from randomized expectations as depicted by the c-score metric (CS = 2.73; ZS = 1.27; P = 0.11). Additionally, non-significant deviations from randomized expectations were found between dispersal modes; animal-dispersed taxa (CS = 0.28; ZS = −0.34; P = 0.42), wind-dispersed taxa (CS = 1.03; ZS = 0.90; P = 0.18), and taxa with no specific dispersal adaptations (CS = 0.51; ZS = −0.53; P = 0.29). The percentage of animal-dispersed taxa and taxa with no specific dispersal adaptations significantly decreased with increasing isolation from the forest vegetation (GLM: $F_1 = 27.7$; $P < 0.001$ and $F_1 = 7.37$; $P = 0.01$ respectively). Conversely, the percentage of wind-dispersed taxa in plant communities significantly increased with increasing isolation from the forest vegetation (GLM: $F_1 = 53.8$; $P < 0.001$; Figure 4). In all cases, the probability of an individual occupying plant communities significantly increased with fern community richness (Table 2). Incidence functions, which were constructed using logistic regression, found no evidence for species exclusions (Figure 5).

DISCUSSION

Our results suggest that plant communities living within the bird's nest fern *Asplenium goudeyi* are structured by dispersal. Plant taxa with better dispersal capabilities were well represented in isolated ferns. Comparatively,
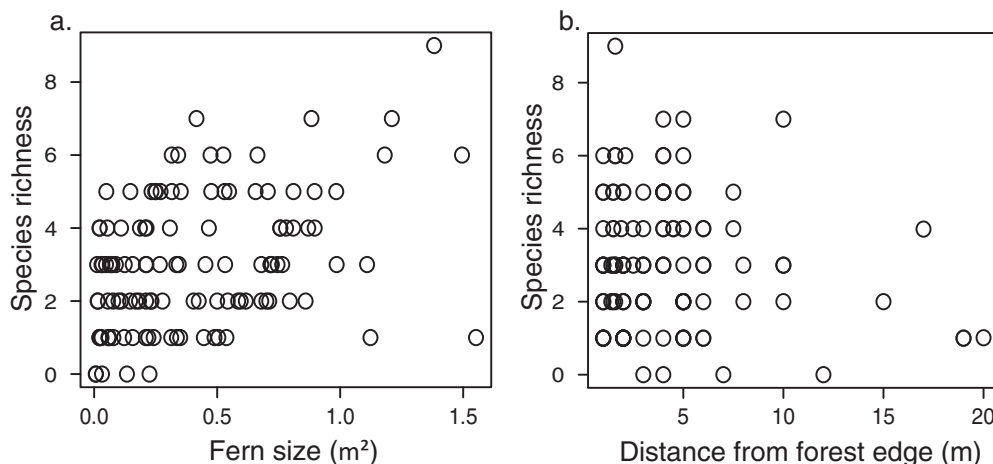
Figure 3. The effect of fern size (a) and fern isolation (b) on species richness of plant communities living inside the epiphytic fern *Asplenium goudeyi* on Lord Howe Island.

Table 2. Results of the logistic regression model used to create incidence functions of species that occurred in 10 or more plant communities. The coefficient represents the log odds of a species occurring in a plant community for every increase in species richness. Standard error (SE), confidence intervals (CI) at the 95%, and significance (P) are also shown.

Species	Coefficient $\pm$ SE	95% CI	P
Alyxia ruscifolia	0.70 $\pm$ 0.15	0.42, 1.02	<0.001
Callisia fragrans	0.67 $\pm$ 0.14	0.41, 0.97	<0.001
Ehrharta erecta	0.62 $\pm$ 0.15	0.35, 0.93	<0.001
Lilium formosanum	0.77 $\pm$ 0.21	0.40, 1.25	<0.001
Microsorum howense	0.55 $\pm$ 0.13	0.31, 0.82	<0.001
Nephrolepis cordifolia	0.87 $\pm$ 0.57	0.72, 0.96	0.001
Paspalum spp.	0.88 $\pm$ 0.21	0.51, 1.34	<0.001
Peperomia urvilleana	0.49 $\pm$ 0.17	0.19, 0.84	0.002
Poa annua	0.43 $\pm$ 0.14	0.17, 0.71	0.001

poorer dispersers were lacking. Furthermore, patterns in community composition did not deviate from randomized expectations, which suggests that species interactions are less important in structuring plant communities. At the species level, individual species occurrences increased with plant community richness. This is consistent with the significant effect of fern size on plant community richness.

The effect of fern size on plant community richness follows one of the most general rules in ecology; the species-area relationship. Like other debris-capturing epiphytes birds' nest ferns increase their catchment area with age (Karasawa & Hijii 2006, Reich *et al.* 2003). Larger ferns are able to intercept comparatively more dispersing propagules simply by chance. In addition, a greater amount of organic debris may be intercepted, which eventually decomposes into a nutrient-rich humus (Zhang *et al.* 2010). Similarly, the

effect of fern isolation on plant community richness is consistent with another well-documented pattern in ecology (Kadmon & Pulliam 1993, Laan & Verboom 1990, MacArthur & Wilson 1967, Van Dorp & Opdam 1987). Isolation effects may arise from interspecific differences in species colonizing or establishment capabilities, propagule limitations and establishment limitations.

Dispersal limitations, produced by interspecific differences in plant dispersal abilities, may explain why not all ferns were occupied by the same species (Ehrlén & Eriksson 2000). Fleshy-fruited taxa generally have larger seeds, and isolation from a major propagule source can limit species dispersal (Dettki *et al.* 2000, Sillett & Goslin 1999). Moreover, selection pressures on insular taxa have further reduced dispersibility by selecting for larger seed sizes (Kavanagh & Burns 2014). Exotic species, which make up 67% of all wind-dispersed plants, do not have the same selection pressures acting on reduced dispersibility as insular taxa. Furthermore, wind-dispersed taxa tend to have smaller seeds, which come in greater quantities. As such, wind-dispersed taxa make efficient colonizers (Nathan 2006), and were well represented in isolated ferns. Dispersal limitations may be lessened by the presence of neighbouring ferns. Neighbouring ferns may act as agents of dispersal, not only increasing the rate of colonization, but also reducing extinctions in plant communities that have experienced disturbances (Ruchty *et al.* 2001). Species with the ability to spread vegetatively, such as *N. cordifolia*, *M. howense* and *C. fragrans*, were assumed to be dispersed by wind to *A. goudeyi* ferns. However, without long-term observation of plant communities, we cannot definitively say that dispersal via vegetative spread did not occur. Nevertheless, ferns growing less than 1 m from
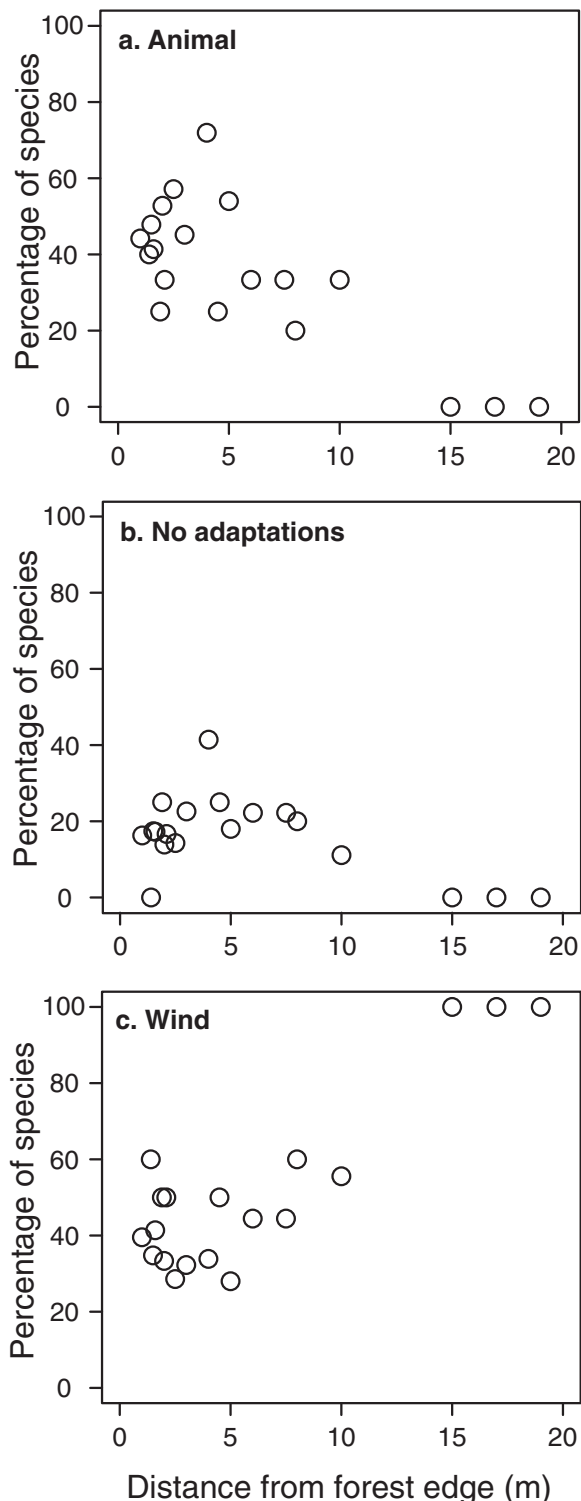
Figure 4. Percentage of species from three dispersal modes; animal-dispersed (a), no specific dispersal adaptations (b) and wind-dispersed (c), plotted against *Asplenium goudeyi* isolation from forest vegetation on Lord Howe Island.

neighbouring vegetation were omitted in an attempt to exclude dispersal via vegetative spread. As observed in previous studies, vegetation may grow directly on cliff faces in areas where soil has accumulated (Yuan *et al.* 2006). Thus, the uncommon occurrences of vegetation growing directly on the cliff face rather than within birds' nest ferns may be an additional source of colonizers. While these occurrences were mainly grasses, incidences of *M. howeana*, *A. adenophora* and *S. nigrum* were also noted.

The regime shift from animal-dispersed plant taxa to wind-dispersed taxa as isolation from the forest vegetation increased may be a result of propagule limitations, here defined as the failure of seeds to reach suitable fern establishment sites (Tilman 1994). For one, birds' nest ferns may contain insufficient resources to mature plant taxa, particularly trees and shrubs (Stephenson 1981). Moreover, exposure to the elements and lack of food may discourage pollinators and dispersers from leaving the protection of the forest. Propagule limitations may be lessened for plant communities growing closest to the forest vegetation simply because there is access to a greater variety of colonizers, pollinators and dispersers. Additionally, propagule limitations may be lessened for annual plants, particularly smaller-seeded species, which have a colonization advantage simply because they mature before perennials.

Non-significant patterns of between-fern variation in community composition were observed, which suggests that species interactions play a lesser role in structuring plant communities. However, individual species occurrences increased with plant community richness, which may result from resident plants facilitating the establishment of later-colonizing species. The importance of facilitation by resident species in low resource or harsh environments is frequently observed (Bertness & Hacker 1994, McAuliffe 1984, Valente *et al.* 2014). Similar observations on the coexistence of ecologically distinct species in cliff habitats have been made on escarpments throughout the British Isles (Cooper 1997, Hepburn 1943, Jarvis 1974). Dominant species may be suppressed in cliff habitats due to frequent disturbances. For one, rock falls and high winds may dislodge species from plant communities or restrict species from attempted establishment. Additionally, disturbances may create new microsites that cater for less dominant species (Cooper 1997).

This study highlights the importance of birds' nest ferns in providing suitable establishment sites for plants that may otherwise not persist in a cliff environment. Interspecific differences in species dispersal abilities explains the regime shift from animal-dispersed taxa in non-isolated communities to wind-dispersed taxa in isolated communities. Additionally, the lack of species exclusions suggests that species interactions
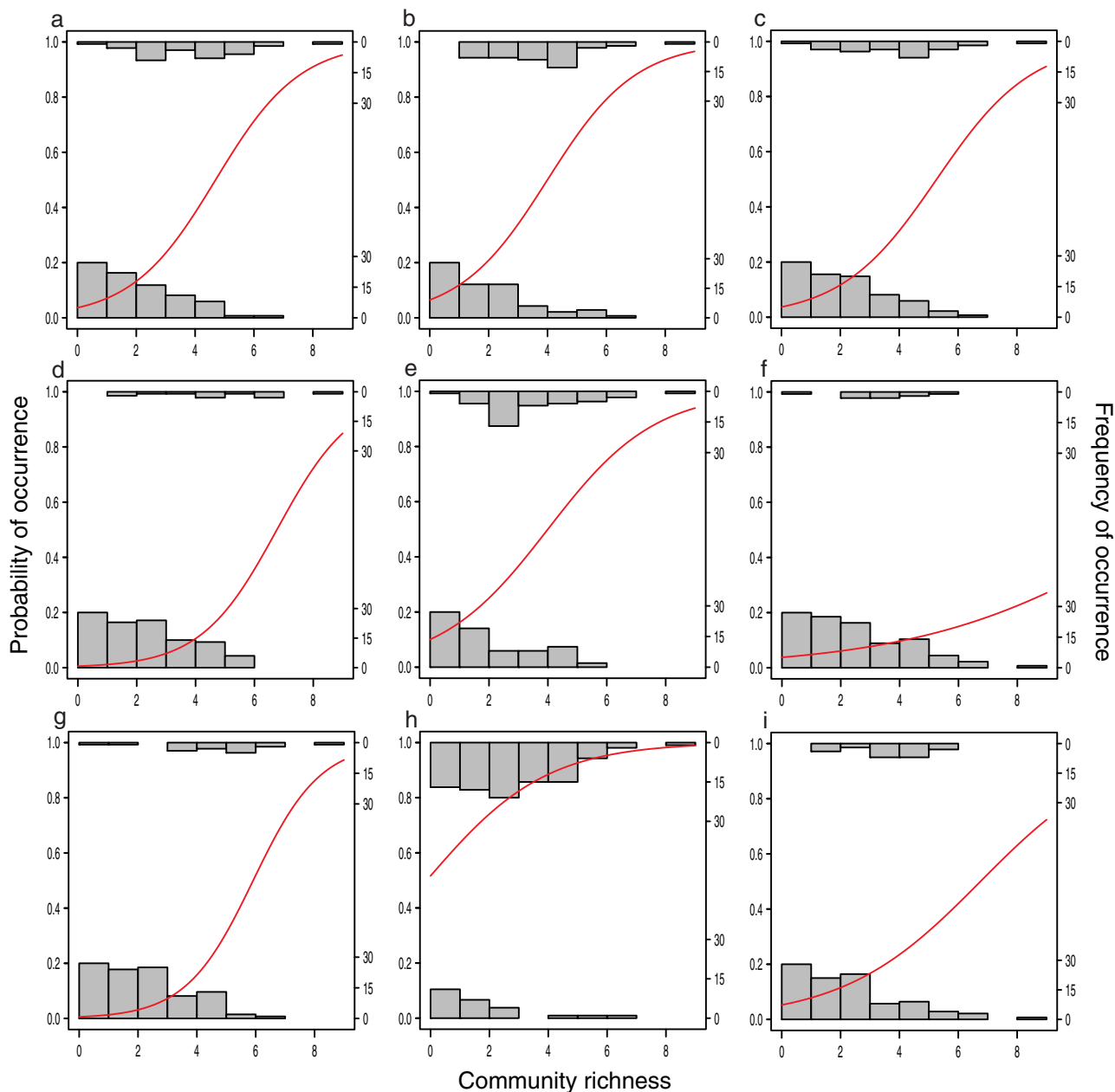
Figure 5. Incidence functions of species that occurred 10 or more times in *Asplenium goudeyi* ferns on Lord Howe Island. Incidence functions relate the probability of a species occurring in a plant community, with plant community richness. The red line represents the probability that a species will be present or absent at a particular measurement of community richness. The frequency at which each species was either present or absent at each measurement of species richness is depicted as a frequency histogram. The above frequency histogram is the number of times each species was present in a community, and the below histogram is the number of times each species was absent. Species used in this analyses were *Alyxia ruscifolia* (a), *Callisia fragrans* (b), *Ehrharta erecta* (c), *Lilium formosanum* (d), *Microsorum howense* (e), *Nephrolepis cordifolia* (f), *Paspalum* spp. (g), *Peperomia urvilleana* (h) and *Poa annua* (i).

are less important in structuring plant communities. Disturbances and facilitation by other plants may prevent competitive species from becoming dominant. We conclude that plant communities growing inside bird's nest ferns show no predictable patterns of community composition, and are strongly influenced by species dispersal abilities.

LITERATURE CITED

BERTNESS, M. D. & HACKER, S. D. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144:363–372.

BUCKLEY, H. L. 2011. Isolation affects tree-scale epiphytic lichen community structure on New Zealand mountain beech trees. *Journal of Vegetation Science* 22:1062–1071.

CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.

CLEMENTS, F. E. 1916. *Plant succession: an analysis of the development of vegetation.* Carnegie Institution of Washington, Washington, DC. 512 pp.

CONNOR, E. F. & SIMBERLOFF, D. 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132–1140.

COOPER, A. 1997. Plant species coexistence in cliff habitats. *Journal of Biogeography* 24:483–494.

DETTKI, H., KLINTBERG, P. & ESSEEN, P. A. 2000. Are epiphytic lichens in young forests limited by local dispersal? *Ecoscience* 7:317–325.

DIAMOND, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129–146.

DIXON, P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* 14:927–930.

DORMANN, C. F., FRÜND, J., BLÜTHGEN, N. & GRUBER, B. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecology Journal* 2:7–24.

DORNELAS, M., CONNOLLY, S. R. & HUGHES, T. P. 2006. Coral reef diversity refutes the neutral theory of biodiversity. *Nature* 440:80–82.

EHRLÉN, J. & ERIKSSON, O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81:1667–1674.

FERNÁNDEZ-JURICIC, E. 2000. Bird community composition patterns in urban parks of Madrid: the role of age, size and isolation. *Ecological Research* 15:373–383.

GAUSE, G. F. 1934. *The struggle for existence*. Williams & Wilkins, Baltimore. 163 pp.

GLEASON, H. A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* 44:463–481.

GOTELLI, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.

GRACE, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 2:1–28.

GRIME, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties.* (Second edition). Wiley, Chichester. 456 pp.

HEPBURN, I. 1943. A study of the vegetation of sea-cliffs in North Cornwall. *Journal of Ecology* 31:30–39.

HINSLEY, S., BELLAMY, P., NEWTON, I. & SPARKS, T. 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. *Journal of Avian Biology* 26:94–104.

HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.

HUBBELL, S. P. 2001. *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, New Jersey. 392 pp.

HUBBELL, S. P., FOSTER, R. B., O'BRIEN, S. T., HARMS, K., CONDIT, R., WECHSLER, B., WRIGHT, S. J. & DE LAO, S. L. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557.

HURTT, G. C. & PACALA, S. W. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93:145–159.

JACQUEMYN, H., BUTAYE, J. & HERMY, M. 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography* 28:801–812.

JAKOBSSON, A. & ERIKSSON, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88:494–502.

JARVIS, S. 1974. Soil factors affecting the distribution of plant communities on the cliffs of Craig Breidden, Montgomeryshire. *Journal of Ecology* 62:721–733.

JOHANSSON, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecica* 59:1–136.

JÜRIADO, I., LIIRA, J., PAAL, J. & SUIJA, A. 2009. Tree and stand level variables influencing diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests. *Biodiversity and Conservation* 18:105–125.

KADMON, R. & PULLIAM, H. R. 1993. Island biogeography: effect of geographical isolation on species composition. *Ecology* 74:978–981.

KARASAWA, S. & HIJII, N. 2006. Effects of distribution and structural traits of bird's nest ferns (*Asplenium nidus*) on oribatid (Acari: Oribatida) communities in a subtropical Japanese forest. *Journal of Tropical Ecology* 22:213–222.

KAVANAGH, P. H. & BURNS, K. C. 2014. The repeated evolution of large seeds on islands. *Proceedings of the Royal Society B: Biological Sciences* 281:20140675.

KEDDY, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3:157–164.

LAAN, R. & VERBOOM, B. 1990. Effects of pool size and isolation on amphibian communities. *Biological Conservation* 54:251–262.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography.* Princeton University Press, Princeton. 224 pp.

MCAULIFFE, J. R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* 64:319–321.

MOUILLOT, D. 2007. Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *Journal of Applied Ecology* 44:760–767.

NATHAN, R. 2006. Long-distance dispersal of plants. *Science* 313:786–788.

OZINGA, W. A., BEKKER, R. M., SCHAMINEE, J. H. & VAN GROENENDAEL, J. M. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92:767–777.

PAULAY, G. 1994. Biodiversity on oceanic islands: its origin and extinction. *American Zoologist* 34:134–144.

PICKARD, J. 1984. Exotic plants on Lord Howe Island: distribution in space and time, 1853–1981. *Journal of Biogeography* 11:181–208.

REICH, A., EWEL, J. J., NADKARNI, N. M., DAWSON, T. & EVANS, R. D. 2003. Nitrogen isotope ratios shift with plant size in tropical bromeliads. *Oecologia* 137:587–590.

RICKLEFS, R. E. & LOVETTE, I. J. 1999. The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68:1142–1160.

RUCHTY, A., ROSSO, A. L. & MCCUNE, B. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. *The Bryologist* 104:274–281.

SILLETT, S. C. & GOSLIN, M. N. 1999. Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest. *Canadian Journal of Forest Research* 29:1204–1215.

SILVERTOWN, J., MCCONWAY, K., GOWING, D., DODD, M., FAY, M. F., JOSEPH, J. A. & DOLPHIN, K. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B: Biological Sciences* 273:39–44.

SMITH, C. C. & FRETWELL, S. D. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.

STEPHENSON, A. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253–279.

STONE, L. & ROBERTS, A. 1990. The checkerboard score and species distributions. *Oecologia* 85:74–79.

STUBBEN, C. & MILLIGAN, B. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:1–23.

TILMAN, D. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* 108:827–852.

TILMAN, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.

TUOMISTO, H., RUOKOLAINEN, K. & YLI-HALLA, M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299:241–244.

VALENTE, L. M., ETIENNE, R. S. & PHILLIMORE, A. B. 2014. The effects of island ontogeny on species diversity and phylogeny. *Proceedings of the Royal Society B: Biological Sciences* 281:20133227.

VAN DORP, D. & OPDAM, P. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* 1:59–73.

WILLIAMS, C. B. 1964. *Patterns in the balance of nature and related problems of quantitative ecology*. Academic Press, New York. 324 pp.

YUAN, J. G., FANG, W., FAN, L., CHEN, Y., WANG, D. Q. & YANG, Z. Y. 2006. Soil formation and vegetation establishment on the cliff face of abandoned quarries in the early stages of natural colonization. *Restoration Ecology* 14:349–356.

ZHANG, L., NURVIANTO, S. & HARRISON, R. 2010. Factors affecting the distribution and abundance of *Asplenium nidus* L. in a tropical lowland rain forest in Peninsular Malaysia. *Biotropica* 42:464–469.

ZOBEL, M. 1997. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution* 12:266–269.