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The tripartite biogeographical index: a new tool for quantifying spatio-temporal differences in distribution patterns

Tom Schils*

Phycology Research Group, Biology Department, Ghent University, Krijgslaan, Ghent, Belgium

ABSTRACT

Aims First, to develop an index that quantifies biogeographical patterns based on the basic descriptors of presence/absence distribution patterns (F, frequency; C, connectivity; G, grouping). Second, to test the proposed biogeographical index on a data set of macrophyte communities in the Arabian Sea using distribution data of macro-algae and seagrasses throughout the Indian Ocean.

Location Arabian Sea (regional macrophyte community data) and the larger Indian Ocean (oceanic distribution data).

Methods The proposed index is derived from the Tulloss tripartite similarity index. The tripartite biogeographical index (TBI $= \sqrt{F \times C \times G}$) is calculated for a specific taxon and incorporates several fundamental parameters of presence/absence data in grid cell (block) patterns. TBI accounts for the relative abundance of a taxon, the average grouping of its occurrences, the average of minimal absence intervals between taxon presences and the largest coherent cluster of taxon occurrences, and also incorporates dispersal aspects. The macrophytes from the case study are among the best documented marine organisms in the Indian Ocean. The regional distribution data from the Arabian Sea result from exhaustive species lists from Masirah Island (Oman) and the Socotra Archipelago (Yemen).

Results TBI values fit a linear scale corresponding to the proportional presence and the distributional spread of taxa within a given geographical area. The three functions that constitute TBI can be evaluated separately or in association with TBI, to give detailed information on the important factors that characterize the biogeographical distribution of a taxon (or larger entities consisting of multiple taxa such as communities). The case study on Arabian macrophytes clarifies the use and explanatory power of the index.

Main conclusions The biogeographical descriptors can be combined into an index which accurately quantifies taxon occurrences and distribution types on a single linear scale from rare/scattered to abundant/grouped. Together with its three functions, the index allows for a non-arbitrary selection of taxa and taxon groupings based on their distribution pattern. The analysis of TBI values for the Arabian macrophyte communities confirms previous biogeographical findings and enables more detailed statistical analyses of the distribution data.

*Correspondence: Tom Schils, University of Guam Marine Laboratory, UOG Station, 96923 Mangilao, Guam, USA.
E-mail: tom@schils.be

INTRODUCTION

Various approaches have been proposed for the analysis of coarse-scale biogeographical patterns based on large species inventories. Dealing with presence/absence data, grid cells are commonly used as input data. Depending on the detail of complete taxon inventories, these grid cells cover various areas defined by geographical limits (e.g. degrees latitude and longitude; O'Hara & Poore, 2000) to *a priori* defined geographical units (Samyn & Tallon, 2005). Generally, these data matrices are analysed using multivariate techniques and traditional similarity indices. Hence the resulting biogeographical patterns are based solely on the common taxa within two or more lists (similarities at the taxon level), and do not take into account similarities in distribution patterns. Upwelling areas of the Arabian Sea, for example, are characterized by species with disjunct distributions that occur in Arabia, South Africa and Western Australia. Different habitats within these upwelling areas can harbour different macrophyte species. Yet the biogeographical affinity of the macrophyte assemblages from these habitats can be analogous, because their composite species display similar distribution patterns within the Indian Ocean. In this study, an alternative index that quantifies the biogeographical spread of a single taxon is presented. In a further step, the biogeographical indices of the taxa that compose a community, a flora or a fauna can be averaged and compared with others.

In our studies on the marine macrophyte communities of the Arabian Sea (Schils & Coppejans, 2003a,b), an index was required that revealed information on the basic descriptors (Table 1) of nominal distribution patterns (presence/absence matrix). The previously defined macro-algal communities (Fig. 1) were correlated with the predominant environmental parameters, particularly those linked with the seasonal upwelling of cold, nutrient-rich water. Biogeographically, these communities differ in the richness of widespread, disjunctly distributed and endemic taxa. The differences in the overall biogeographical signal can be visualized by using the Simpson coefficient (SC; Schils & Coppejans, 2003a). The SC measures the similarity between two lists of taxa as the ratio of common taxa between both lists divided by the number of taxa in the smaller of the two lists. Hence the SC is not sensitive to the relative size of both data sets, which is a necessary requirement if two consistently unequal data sets are compared unidirectionally (e.g. regional macrophyte communities vs. macrophyte inventories on an oceanic scale). Thus the affinity between a regional list of taxa and a biogeographical area increases when the total number of taxa common to both the smaller and larger list increase, and *vice versa*. This method does not calculate similarities based only on the type of distribution pattern, so further numerical analyses (descriptive statistics) or a non-arbitrary selection of taxa based on individual biogeographical patterns are not possible. To enable these further investigations to be performed, the new index must quantify both aspects that characterize the distribution of a taxon (abundance and clustering) into a single linear scale

from rare/scattered to abundant/grouped. Application of the new index is demonstrated using distribution data for macrophytes of the Arabian Sea. Distribution records of macro-algae and seagrasses within the Indian Ocean are among the most complete relative to other major marine groups. One weakness of these data is the low geographical resolution (qualitative species lists at country and island level). This disadvantage is largely countered by the high proportion of the Indian Ocean shoreline that these nations possess and the large number of species that are recorded in the database.

MATERIALS AND METHODS

Distribution patterns

The tripartite biogeographical index (TBI) uses nominal distribution data in block patterns (grid cells). Certain blocks may function only as connectivity (dispersal) blocks where the settlement of a taxon is not possible, for example pelagic areas serving as dispersal routes for tissue fragments, spores, seeds or larvae, but inhospitable for the adult benthic organisms. Connectivity blocks are excluded when counting the total amount of cells that constitute the complete potential distribution range, a value used in calculating TBI. Grid patterns are not necessarily square matrices; areas that are unlikely for the establishment of a taxon and which do not function as connectivity blocks (e.g. dispersal barriers and inhospitable regions) are excluded from the grid.

Definition of tripartite biogeographical index

The TBI is derived from the tripartite similarity index (TSI; Tulloss, 1997). The TSI was developed to counter the inconsistencies of the 20 most commonly used similarity indices, inconsistencies that are mainly related to discrepancies of size between two lists of taxa. Three requirements, identified as potentially conflicting for the similarity index, have been translated mathematically into three functions. The parameters used for the calculation of TSI are denoted as follows (Hayek, 1994): a, number of entries common to both lists; b, number of entries in the first list that are not in the second; c, number of entries in the second list that are not in the first. The first function:

$$U = \frac{\log\left(1 + \frac{\min(b,c)+a}{\max(b,c)+a}\right)}{\log 2} \tag{1}$$

is sensitive to size differences between two lists of taxa. The larger the size difference, the lower U and TSI. The second formula:

$$S = \sqrt{\frac{\log 2}{\log\left(2 + \frac{\min(b,c)}{a+1}\right)}} \tag{2}$$

reflects size differences between a subset of common taxa between both lists and the smaller of the two lists. When this difference increases, the value of TSI decreases and *vice versa*.

TBI	Tripartite biogeographical index: a linear scale to quantify distribution patterns based on the frequency, connectivity and grouping of taxon occurrences. TBI = $\sqrt{F \times C \times G}$
F	Frequency: number of areas (#PB) in which a taxon is detected, expressed as a fraction of the total number of areas investigated (#B)
C	Connectivity: measure of connectedness between distribution areas (or populations) of a single taxon within a specific geographical region; C is a function of isolation distance (ABG) and size of distribution areas (PBG)
G	Grouping: spread of distribution areas of a single taxon in relation to the geographical region under study (function of PBC and #PB) and the minimal distance necessary to unite all separate distribution areas (function of ABC and #PB)
B	Block (grid cell) of a distribution grid
#B	Total number of blocks within a specific distribution grid. Connectivity blocks are not part of the potential distribution area for a specific taxon and thus are excluded from the calculation of #B
AB	Absence block: a grid cell where the taxon is not known to occur. Connectivity blocks can count as absence blocks
#AB	Total number of ABs for a specific grid pattern or a specified selection thereof (e.g. ABG or ABC)
PB	Presence block: a grid cell where the taxon occurs
#PB	Total number of PBs for a specific grid pattern or a specified selection thereof (e.g. PBG or PBC)
ABG	Absence block group: a group of ABs that connect two PBGs. Only one set of ABGs is utilized for the calculation of TBI. This set meets the following three requirements: (1) all ABGs together connect all PBGs (2) total number of ABs of the set of ABGs is as low as possible (3) of all potential ABG sets that fulfil the above two requirements, the ultimate set consists of the highest number of ABGs possible (i.e. the average #AB per ABG is the lowest possible).
#ABG	Number of ABs in an ABG
PBG	Presence block group: a group of PBs that form one unity without any absence gaps (continuous distribution area). All PBs belong to a PBG, thus taxa that occur in the studied region (distribution grid) have at least one PBG
#PBG	Number of blocks (grid cells) within a PBG
ABC	Absence block cluster: a selection of ABGs with three requirements – (1) the selection of ABGs must connect all PBGs (2) the selection of ABGs should include the lowest possible number of absence blocks (3) if different selections of ABGs meet both stipulations above, choose a selection with the highest number of ABGs (consequently, the average #ABG within the selection, ABC, is as low as possible)
#ABC	Number of ABs in an ABC
PBC	Presence block cluster: a continuous cluster of PBGs and ABGs. Further requirements of such a cluster are: (1) PBGs are linked by ABGs, when #AB of the ABG is smaller or equal to #PB of each of the PBGs that are connected (2) of all possible clusters of PBGs and ABGs for a specific distribution grid that fulfil the above stipulation, the ultimate PBC contains the highest net number of presence blocks (see #PBC)
#PBC	Net amount of blocks in a PBC, being #AB of the PBC subtracted from #PB of the PBC

The third function:

$$R = \frac{\log\left(1 + \frac{a}{a+b}\right) \cdot \log\left(1 + \frac{a}{a+c}\right)}{(\log 2)^2} \qquad (3)$$

represents the number of taxa common to the two lists in proportion to both the larger and smaller list. R and TSI increase when the proportion of common taxa increases for both lists. The three functions are based on logarithms base 2. In the calculations, log functions are converted to $\log_2$
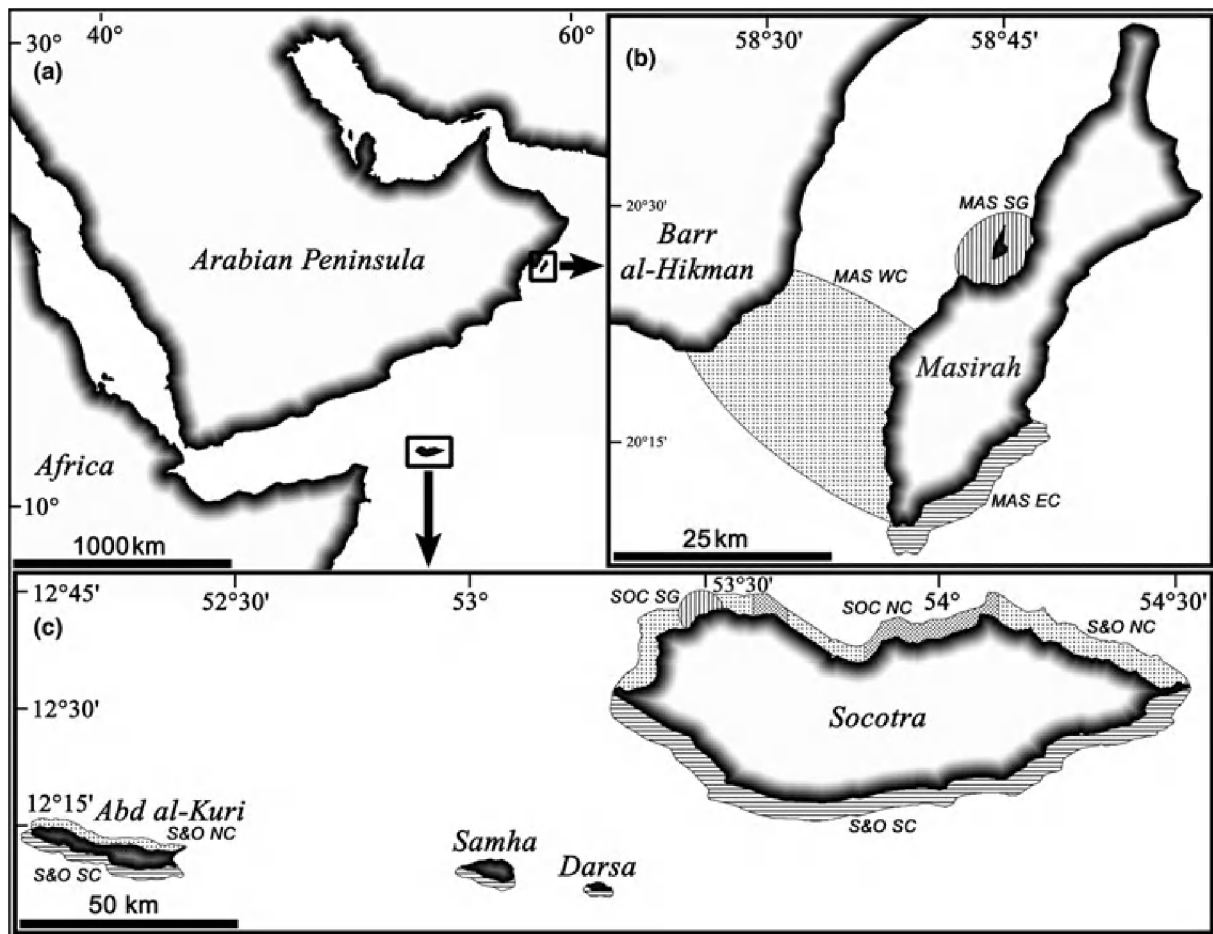
Figure 1 Macroalgal communities of (a) the Arabian Sea; (b) Masirah Island; (c) the Socotra Archipelago. Coasts investigated are characterized by the dominant marine macrophyte communities according to Schils & Coppejans (2003a). Horizontally shaded areas represent the upwelling communities of Masirah's East Coast (MAS EC), and the south coasts of Socotra and the outer islands (S&O SC). The upwelling sheltered shores at Masirah's west coast (MAS WC) and the north coasts of Socotra and the outer islands (S&O NC) are indicated by a sparse dot pattern. Socotra's north coast (SOC NC) is a subentity of the latter community and is depicted by dense dot patterns. Areas with extensive seagrass beds (MAS SG and SOC SG) are vertically shaded. Plate Carrée map projection (equidistant cylindrical map with 0° as standard parallel; Robinson *et al.*, 2000).

functions through a division of log 2. The multiplication of the three functions generates the tripartite similarity index (TSI $= \sqrt{U \times S \times R}$) representing the similarity between two lists of taxa, thereby avoiding anomalies present in other indices. Instead of being a similarity index between two lists of taxa, TBI is a landscape index which quantifies the spread between a number of distribution areas of a single taxon in relation to the entire area investigated. Analogous to the size differences between two lists of taxa or subsets thereof, size differences between distribution parameters also need to be accounted for in TBI. The requirements and the resulting functions for TBI are similar to those of TSI. The similarity parameters of TSI are replaced by landscape parameters (Table 1) relevant to biogeographical distribution patterns, as explained below. The TBI functions are also based on logarithms base 2 and are computed in three steps.

The first function of TSI (Tulloss, 1997), *U*, quantifies the difference in taxon numbers between two lists. In calculating

TBI, a similar function (*F*) is used to quantify the absolute proportion of observed occurrences of a single taxon within a given distribution grid (potential distribution range). Thus the first function, *F*, is a measure for the relative frequency of a taxon:

$$F = \frac{\log\left(1 + \frac{\#PB}{\#B}\right)}{\log 2} \qquad (4)$$

In this function, #PB represents the total number of presence blocks (grid cells where the taxon is observed); and #B represents the total number of blocks where the taxon might occur (potential distribution range of the studied organisms). #B can differ from the total amount of blocks in a distribution and connectivity pattern, when certain blocks are marked as dispersal routes where the taxon cannot settle (connectivity blocks). Hence connectivity blocks are not accounted for in #B. *F* is ≤ 1 and > 0 (a zero value means the taxon does not occur within the area investigated, so is not included in the analysis).

While the function S in TSI quantifies the proportion of common taxa in relation to the smallest list of taxa, the connectivity (C) of TBI represents the number of presences vs. the number of gaps in discontinuous distributions. Thus C measures the distances between the distribution areas for a single taxon. The greater this distance is in relation to the size of the distribution areas, the lower the value of C. As multiple distance paths might be needed to link the distribution areas, the isolation distances are squared and thereafter averaged. A situation in which the total isolation distance between distribution areas is equal, this will favour a greater number of short distances over a smaller number of long distances. As the value of C for a continuous distribution $= 1$, the square root of the average squared distance is multiplied by the total number of grid cells. In order to relate the isolation distance to the size of the distribution, this equation is then divided by the square root of the average squared distribution areas. Thus C is a function of the connectivity (the inverse of distance, defined by absence blocks) between continuous distribution ranges (presence block groups):

$$C = \sqrt{\frac{\log 2}{\log\left(1 + \frac{\left(1 + \sqrt{\frac{\left(\sum_{i=1}^{n}(\#\text{ABG}_i)^2\right)}{n}}\right) \cdot (\#\text{B})}{\sqrt{\frac{\sum_{i=1}^{m}(\#\text{PBG}_i)^2}{m}}}\right)}} \quad (5)$$

In this equation, #PBG represents the maximal size of a presence block group (adjacent presence blocks without absence gaps), that is, the number of blocks composing a continuous distribution range. An absence block group (ABG) is defined as the minimal number of adjoining absence blocks needed to link two or more PBGs, that is, the shortest path between continuous distribution ranges. From all possible ABGs, a selection of ABGs is chosen which connects all PBGs of the distribution grid. A further requirement of the latter selection is that the total number of blocks within this set of ABGs is minimized. In case different sets of ABGs consist of equally low numbers of absence blocks, the ultimate set (termed the absence block cluster, ABC) should consist of absence groups with the lowest average number of blocks per group (the highest number of groups consisting of the lowest total number of absence blocks). #ABC thus represents the total number of absence blocks included in the ultimate set of ABGs. #B accounts for the total number of grid cells (excluding connectivity blocks). C also ranges from values > 0 to a maximum of 1 (being omnipresent in a situation without dividing connectivity barriers).

The third function of TSI (Tulloss, 1997), R, is a formula based on the relative proportion of common taxa in both lists of taxa. Grouping (G) is also defined by relative proportions. G is high when the spread of taxon occurrences can be confined to an area with a low number of discontinuous gaps (taxon absences). Thus G is based on R where the similarity parameters are replaced by two ratios of landscape parameters: (1) the proportion of the largest presence block cluster to the total grid; and (2) the compactness of clustering. Thus the third function, G, is a measure of the degree of grouping between continuous distribution areas allowing for small absence gaps, which reduce G:

$$G = \frac{\log\left(1 + \frac{\#\text{PBC}}{\#\text{PB}}\right) \cdot \log\left(1 + \frac{\#\text{PB}}{\#\text{PB}+\#\text{ABC}}\right)}{(\log 2)^2} \quad (6)$$

In this equation #PBC is the highest count of presence blocks that can be clustered by connecting them with ABGs: the maximum number of presence blocks in a cluster minus the minimal number of absence blocks in that cluster. A cluster thus consists of a combination of PBGs and ABGs, where each #ABG is smaller or equal to all the connected (flanking) #PBGs. The remaining parameters (#PB and #ABC) for calculating G are described above. G also varies from values > 0 to a maximum of 1.

Analogous to the Tulloss index (Tulloss, 1997), the square root scaling of the multiplication of the three functions results in the tripartite biogeographical index:

$$\text{TBI} = \sqrt{F \times C \times G} \quad (7)$$

Without scaling, TBI values could become disproportionately small in comparison with the values of the three functions. This suggests that more numbers are needed for the decimal accuracy of TBI values in relation to those of the composing functions. Third-order root scaling of the multiplied functions, on the other hand, yields higher TBI values, but the range of values becomes too small.

Case study: macrophyte communities of the Arabian Sea

This example illustrates the use of TBI for the distribution of different taxa in a single spatial distribution index. The biogeographical index was computed for the marine macrophyte communities around Masirah Island (Oman) and the Socotra Archipelago (Yemen), as discussed by Schils & Coppejans (2003a). In order to estimate connectivity and grouping of species distributions within the Indian Ocean, a simplified two-dimensional grid pattern (basically a linear distribution pattern with interrelated dispersal connections) was used in the study.

The distribution data of Indian Ocean algae was taken from PhycoBase (Schils *et al.*, 2004). PhycoBase is primarily based on Silva *et al.* (1996) and supplemented with records from omitted and recent sources: Dickie (1888); Holmes (1903); Cordero (1993); Nizamuddin & Campbell (1995); Shaikh & Shameel (1995); De Clerck & Coppejans (1996); Hayee-Memon & Shameel (1996); Jupp *et al.* (1996); Sohrabi Pour & Rabii (1996); Critchley *et al.* (1997); Kemp (1998); Spalding *et al.* (1998); Wynne (1998); Wynne & Jupp (1998); Aliya & Shameel (1999); De Clerck & Coppejans (1999); OSP (1999);
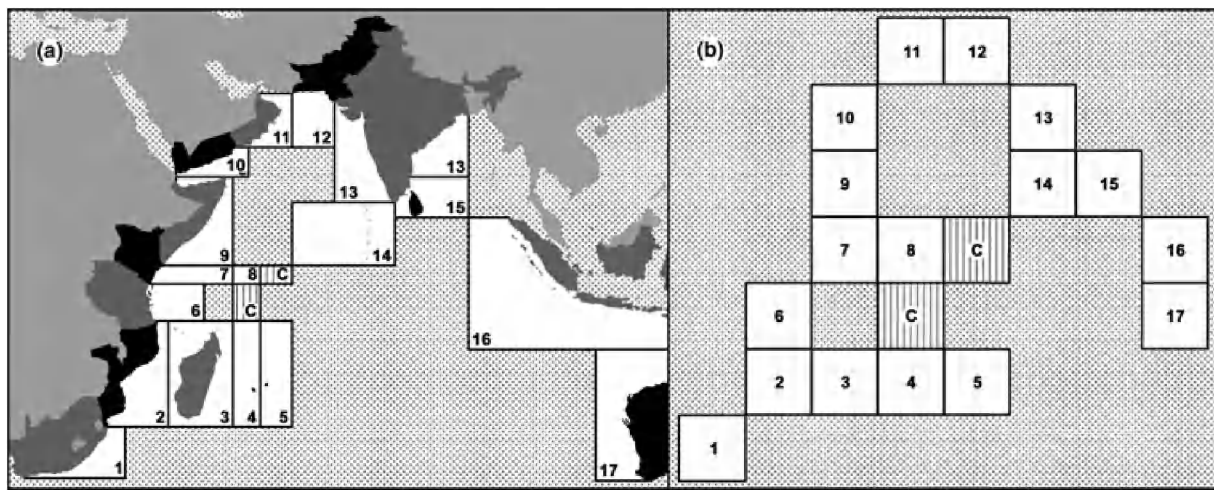
Figure 2 Macroalgal distribution data within the Indian Ocean. (a) Map showing the 17 countries and islands for which detailed species lists are available. (b) Schematic representation of the 17 countries and islands of the Indian Ocean in a grid pattern for the calculation of TBI. Shaded cells marked 'C' indicate connectivity blocks. Numbers correspond to following countries and islands: 1, South Africa (Indian Ocean coast); 2, Mozambique; 3, Madagascar; 4, Réunion; 5, Mauritius; 6, Tanzania; 7, Kenya; 8, Seychelles; 9, Somalia; 10, Yemen; 11, Oman; 12, Pakistan; 13, India; 14, Maldives; 15, Sri Lanka; 16, Indonesia; 17, Western Australia. Countries and islands included correspond to the species distributions listed by Silva et al. (1996).

Shameel (1999); Sohrabipour & Rabii (1999); Wynne (1999a,b); Coppejans et al. (2000); Huisman (2000); Shameel et al. (2000); Wynne (2000); Bandeira et al. (2001); Wynne (2001a,b); Wynne & Leliaert (2001); Coppejans et al. (2002); De Clerck et al. (2002); Huisman & Schils (2002); Schils & Coppejans (2002); Shameel (2002); Wynne (2002a,b); Wynne & de Jong (2002); Carvalho & Bandeira (2003); De Clerck (2003); Green & Short (2003); Richards & Wynne (2003); Schils et al. (2003a,b); Schils & Coppejans (2003a,b); Wynne (2003a,b, 2003c); Coppejans et al. (2004); De Clerck et al. (2004); Huisman et al. (2004); Leliaert (2004); Schils et al. (2004); Wynne & Freshwater (2004); Wynne (2004); Guiry & Nic Dhonncha (2005); Wynne (2005). The above references encompass practically all macrophyte species records for the Indian Ocean that have been published to date. The large majority of these publications are written by experienced algal taxonomists and are to some extent validated by Silva et al. (1996).

Since distribution data of macro-algae within the Indian Ocean have the highest resolution (information and detail) at country level, grids are equated with the countries and islands for which detailed species lists exist (Fig. 2). Although unequal in size, these country blocks represent coherent aggregates of coordinate grids and reflect oceanographic conditions at a coarse scale. As this example examines biogeographical affinities at a coarse scale (coastal areas within the Indian Ocean), the use of these broadly defined grids suffices. Furthermore, most macrophytes have high dispersal capacities, making the assumption of connectivity between these large grid cells plausible. It was not feasible to account for current patterns, many varying seasonally in intensity and direction. An analysis of this data set using the TBI should (1) confirm the previous results; and (ideally) (2) reveal more detailed

information about the distribution patterns within the different species assemblages.

In a first step, TBI was calculated for 189 taxa. These 189 macrophytes represent the marine flora of the sampled sites of the Socotra Archipelago and Masirah Island (Schils & Coppejans, 2003a). However, enigmatic algae (e.g. small epiphytes and crustose algae) were excluded from this data set, and Indian Ocean records of related taxa that might have been misidentified were lumped. For clarification, the distribution pattern of two species, the calculation parameters, the computed functions and the TBI are presented in Fig. 3.

Thereafter, the linear scale of TBI was compared with two descriptors (proportional presence and distributional spread) that characterize different types of distribution pattern. The moving averages of the latter two parameters have been correlated with TBI. Moving averages (interval = 10) were chosen because: (1) the graphic representation is clearer as several species contained the same TBI values; and (2) this method evens out the inverse relationship between extremes of the descriptors that compose TBI (proportional presence and distributional spread). In these correlations the proportional presence is defined as #PB/#B. The distributional spread has been calculated using two independent methods and the results have been compared. Analogous to the calculation of TBI, one way of representing the distributional spread was counting the minimal number of absence blocks that link all presence clusters. The second approach consisted of measuring the minimal total distance (km) that links the continuous distribution ranges (plate carrée map projection: equidistant cylindrical map with 0° as standard parallel; Robinson et al., 2000). These correlations also resulted in a TBI scale that could be related to different types of distribution pattern. Subsequently, the average TBI values and the proportional
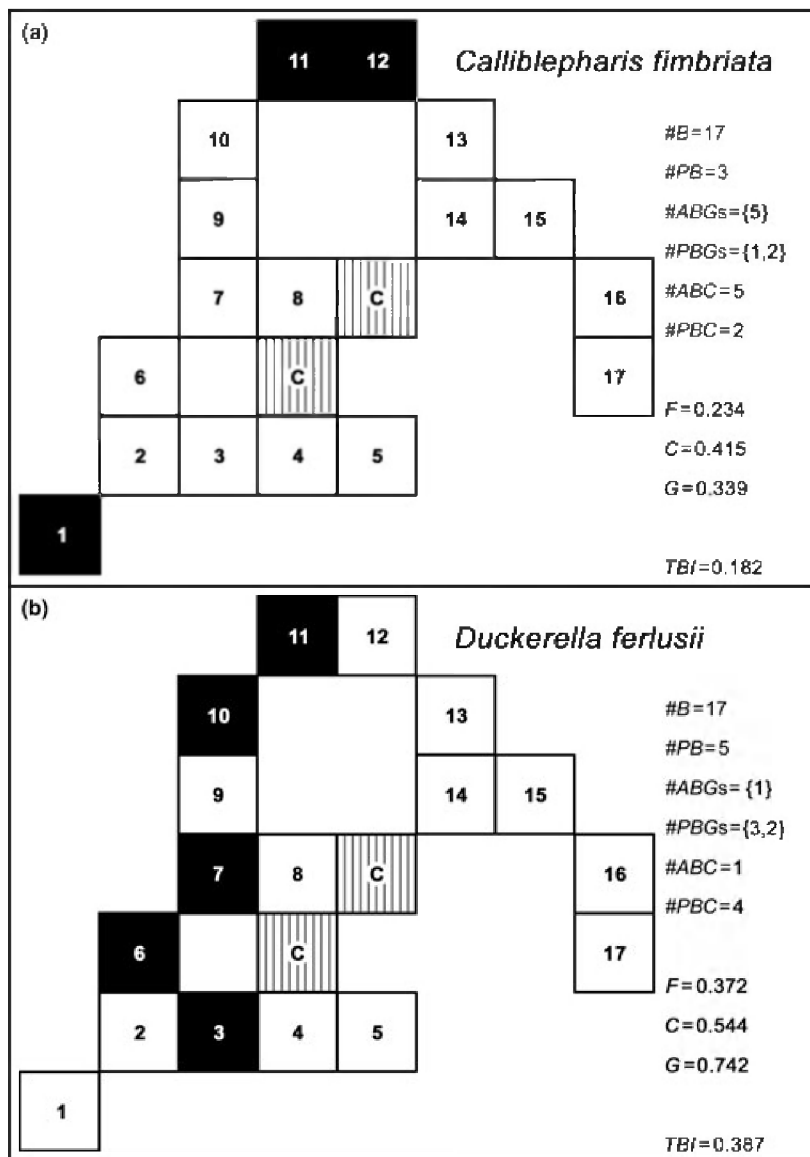
Figure 3 Distribution pattern of two macroalgae with indication of the different parameters (#B, #BP, #ABG, #ABG, #PBG, #PBC), the computed functions (F, C, G), and the tripartite biogeographical index (TBI). Black blocks indicate species presence, absence blocks are empty. Country numbers and connectivity blocks are represented as in Fig. 2. (a) *Calliblepharis fimbriata* (Greville) Kützing; (b) *Duckerella ferlusii* (Hariot) Wynne.
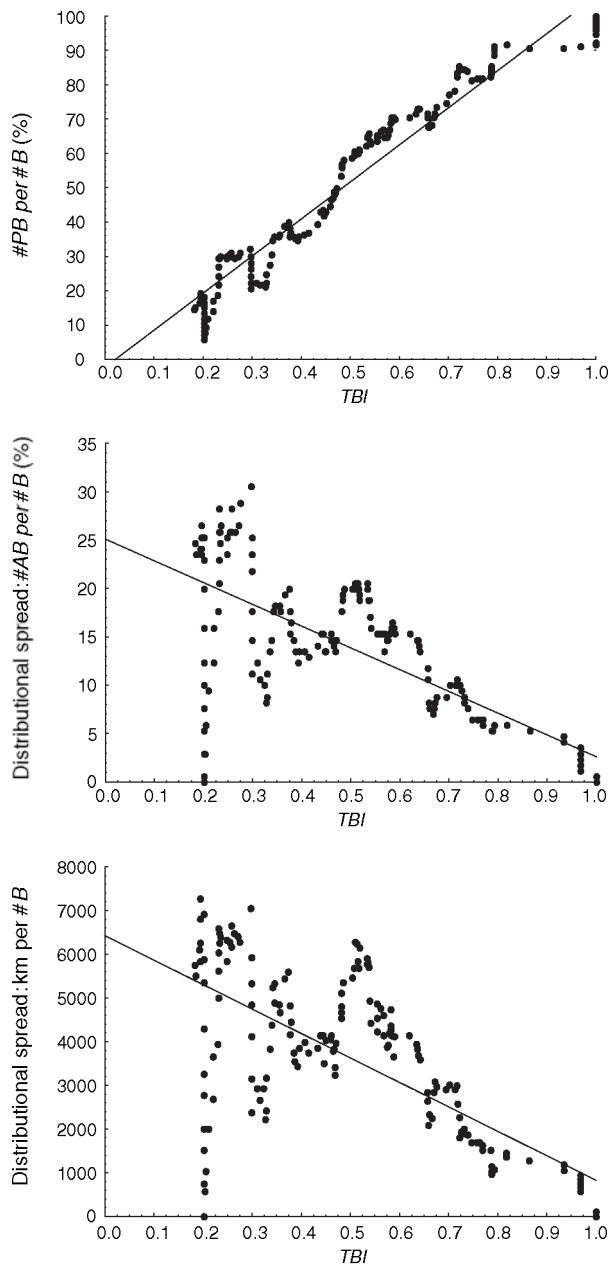
distribution of taxa in four categories (TBI $\leq$ 0.25; $0.25 \leq$ TBI ≤ 0.50; $0.50 \leq$ TBI ≤ 0.75; $0.75 \leq$ TBI) of the different communities were compared with their general biogeographical affinity within the Indian Ocean, as computed by Schils & Coppejans (2003a). Assumptions on the proportion of endemic and disjunctly distributed species for two similar communities were analysed by: (1) selecting the taxa with a TBI ≤ 0.25 for each community (endemic and disjunctly distributed taxa); and (2) analysing the functions of the species selected.

RESULTS

On calculation of the TBI values and composing functions for each of the 189 species, the relation between TBI and the proportional presence ($r = 0.98$; $s_r = 0.02$; $P < 0.001$) and the distributional spread ($r = -0.73$; $s_r = 0.05$; $P < 0.001$) were analysed (Fig. 4a–c). Both relationships were linear and certain

TBI values were classified as outliers, allowing an interpretation of the TBI scale. Species with TBI values ranging from 0.10 to 0.20 are characterized by a low number of presence blocks, and high values of distributional spread (measured in absence blocks, Fig. 4b, as well as kilometres, Fig. 4c: $r = -0.70$; $s_r = 0.05$; $P < 0.001$). The latter distribution patterns can be described as rare and disjunctly distributed. Species with a TBI value of 0.20 have exceptionally low values for the proportional presence (one block) and the distributional spread (zero blocks or zero km). These are local endemic species, known from only one grid cell within the Indian Ocean. From 0.20 to 0.25 the proportional presence and distributional spread increase, being species with an occasional and disjunct or a scattered occurrence within the Indian Ocean. The general pattern from 0.25 to 0.50 is an increase in the proportional presence, while the distributional spread decreases. At a TBI of 0.50, species occur frequently within the Indian Ocean (98% of species with a TBI ≥ 0.500 occur in at

Figure 4 Linear relationships between TBI and distribution characteristics. (a) TBI vs. moving average (interval = 10) of the proportional presence (#PB/#B). (b) TBI vs. moving average (interval = 10) of the distributional spread (minimal number of absence blocks linking all species occurrences). (c) TBI vs. moving average (interval = 10) of the distributional spread (minimum distance linking all species occurrences).

Table 2 TBI values and general distribution patterns for macro-algae within the Indian Ocean

TBI	Distribution pattern
± 0.15	Rare, disjunctly distributed
± 0.20	Local endemics
± 0.25	Occasional, disjunct or scattered distribution
	Regional endemics and onwards: increasing presence and decreasing distributional spread
± 0.50	Frequent, scattered
± 0.65	Frequent, grouped
± 0.75	Abundant
1	Omnipresent

synthesizes the linear scale of TBI values and the corresponding distribution pattern.

A comparison of both independent measures for distributional spread reveals that their linear relationship with respect to TBI is similar. Measuring distance gaps between continuous distribution ranges by counting absence blocks fits the linear trend best ($R^2 = 0.54$; Fig. 4b). The method based on geographical distances (km) shows a slightly larger spread ($R^2 = 0.49$; Fig. 4c). Ungrouped distribution ranges are more pronounced in the latter approach, as absence distances are relatively larger. When the degree of distributional spread relative to the total distribution range is correlated to TBI (Fig. 5a,b), the geographical distance and the absence block count show a similar fit to the exponential trend ($r = -0.76$, $P < 0.001$). Furthermore, both graphs (Fig. 5a,b) show that the most pronounced deviations from the general trend are to be found at lower TBI values (< 0.25), being mainly species with disjunct or scattered distribution patterns. Nevertheless, both measurements of distributional spread are highly correlated ($r = 0.99$, $s_r = 0.01$; $P < 0.001$); have similar responses to TBI; and reveal the same results. These findings justify the use of the simplified grid.

Next, the average TBI of the composing species was calculated for each community, which correlates well ($r = 0.99$; $s_r = 0.08$; $P < 0.001$) with the SC of these communities as reported by Schils & Coppejans (2003a); Table 3). Table 3 lists the communities according to their average TBI values, and shows the proportional species representation (percentage) in each of the four designated TBI categories. The communities with a similar species composition (TSI values in Schils & Coppejans, 2003a), such as MAS EC and S&O SC, also show similar TBI values (see Fig. 1 for definitions). The latter two communities are characterized by a high proportion of species ($\geq$ 50%) with a TBI < 0.5. These upwelling communities contain a high proportion of species with an endemic, disjunct and scattered distribution. The TBI values of the upwelling protected macrophyte communities of SOC NC and MAS WC still contain a mixture of species that belong to TBI categories 1–2 (30.1 and 33.3%, respectively) and 3–4 (remaining percentage), but with a marked dominance of widespread species.

least 50% of the total distribution range) and display a scattered distribution pattern. Species with higher TBI values are typified by being more widespread and having a more continuous distribution within the Indian Ocean. Of the included species with a TBI of $\geq$ 0.75, 95% occurs in at least 85% of the total distribution range. Species with a TBI value of 1 occur in all 17 countries or islands investigated. Table 2

Figure 5 Exponential relationships between TBI and distribution characteristics (a) TBI vs. moving average (interval = 10) of the ratio: distributional spread (minimal number of absence blocks linking all species occurrences)/proportional presence (#PB). (b) TBI vs. moving average (interval = 10) of the ratio: distributional spread (minimum distance linking all species occurrences)/proportional presence (#PB).

Table 4 Average TBI and average functions for both upwelling communities of the Arabian Sea, based solely on species within TBI category 1 (TBI ≤ 0.25)

Community*	Average			
	TBI	F	C	G
MAS EC	0.195	0.218	0.451	0.517
S&O SC	0.198	0.257	0.452	0.426

*For definitions see Fig. 1.

Higher proportions of widespread tropical species (> 75% in TBI categories 3–4) characterize the upwelling sheltered communities of SOC SG, S&O NC and MAS SG.

Subsequently, attention is paid to the category TBI ≤ 0.250 (Table 2) which contains the most particular species, differentiating between the communities. Both upwelling communities (MAS EC and S&O SC) are characterized by the highest proportion of endemic and disjunctly distributed species (TBI ≤ 0.250). The function values that constitute the TBI of the two communities are listed in Table 4. The average connectivity (C) does not differ between both upwelling communities. The average frequency (F) and especially the average grouping (G), on the other hand, differ. MAS EC shows the lowest average F, where S&O SC shows the lowest average G. This leads to the suspicion that the former marine macrophyte community comprises more endemic species, whereas the latter consists of a higher proportion of species with a scattered distribution and a slightly higher number of disjunctly distributed species (equal average C). In order to verify this deduction, the distribution patterns of the species belonging to TBI category 1 (≤ 0.250) from both upwelling communities were analysed and classified into three groups of distribution pattern

Community*	SC (%)	Average TBI	TBI ≤ 0.25 (%)	0.25 > TBI TBI ≤ 0.50 (%)	0.50 > TBI TBI ≤ 0.75 (%)	0.75 > TBI TBI ≤ 1 (%)
MAS EC	33.5	0.496	23.6	27.8	31.9	16.7
				51.4		48.6
S&O SC	33.6	0.515	23.4	28.2	26.6	21.8
				51.6		48.4
SOC NC	40.2	0.611	13.7	16.4	39.7	30.1
				30.1		69.9
MAS WC	42.6	0.611	15.7	17.6	33.3	33.3
				33.3		66.7
SOC SG	44.8	0.660	0.0	16.7	66.7	16.7
				16.7		83.3
S&O NC	46.5	0.667	9.8	13.7	35.3	41.2
				23.5		76.5
MAS SG	47.8	0.675	4.3	19.1	36.2	40.4
				23.4		76.6

*For definitions see Fig. 1.

Table 3 Biogeographical affinity within the Indian Ocean (Simpson coefficient, SC; Schils & Coppejans, 2003a); average TBI; and proportion of species within the four TBI categories for each of the marine macrophyte communities from the Arabian Sea

Table 5 TBI, functions and synopsis of distribution patterns for species from upwelling communities with a TBI ≤ 0.25

Community*	Species	TBI	*F*	*C*	*G*	Distribution type†
MAS EC	*Amansia seagriefii*	195	234	426	379	D
MAS EC	*Balliella repens*	184	305	427	262	D
MAS EC	*Calliblepharis fimbriata*	182	234	415	339	D
MAS EC	*Chauviniella jadinii*	116	160	394	212	D
MAS EC	*Chondria dangeardii*	233	305	469	381	S
MAS EC	*Chrysymenia grandis*	201	82	490	1000	E
MAS EC	*Cladophora catenata*	195	234	426	379	D
MAS EC	*Codium ovale*	220	372	459	284	S
MAS EC	*Dictyopteris macrocarpa*	230	305	456	381	D
MAS EC	*Padina elegans*	195	234	426	379	D
MAS EC	*Platoma heteromorphum*	201	82	490	1000	E
MAS EC	*Plocamium fimbriatum*	201	82	490	1000	E
MAS EC	*Plocamium microcladioides*	201	82	490	1000	E
MAS EC	*Predaea weldii*	112	234	398	134	D
MAS EC	*Pterocladiella caerulescens*	248	372	484	340	S
MAS EC	*Reticulocaulis mucosissimus*	201	82	490	1000	E
S&O SC	*Amphisbetema indica*	232	372	469	309	S
S&O SC	*Asteromenia peltata*	210	372	452	262	S
S&O SC	*Avrainvillea lacerata*	232	436	472	261	S
S&O SC	*Balliella repens*	184	305	427	262	D
S&O SC	*Chauviniella coriifolia*	195	234	426	379	D
S&O SC	*Chondria dangeardii*	233	305	469	381	S
S&O SC	*Chondrophycus columellaris*	248	372	484	340	S
S&O SC	*Chrysymenia kaernbachii*	195	234	426	379	D
S&O SC	*Cryptonemia kallymenioides*	116	160	394	212	D
S&O SC	*Dasya flagellifera*	155	160	435	342	E
S&O SC	*Dictyopteris macrocarpa*	230	305	456	381	D
S&O SC	*Dictyota grossedentata*	205	305	444	310	S
S&O SC	*Dudresnaya capricornica*	193	305	432	284	D
S&O SC	*Erythrocolon podagricum*	116	160	394	212	D
S&O SC	*Gibsmithia larkumii*	201	82	490	1000	E
S&O SC	*Griffithsia globulifera*	172	305	464	210	S
S&O SC	*Halophila decipiens*	231	436	469	261	S
S&O SC	*Padina australis*	159	234	446	243	S
S&O SC	*Padina elegans*	195	234	426	379	D
S&O SC	*Pterocladiella caerulescens*	248	372	484	340	S
S&O SC	*Reticulocaulis obpyriformis*	201	82	490	1000	E
S&O SC	*Sargassum decurrens*	195	234	426	379	D
S&O SC	*Sympodothamnion leptophyllum*	201	82	490	1000	E
S&O SC	*Zellera tawallina*	125	160	403	243	D

*For definitions see Fig. 1.
†E, endemic; D, disjunct; S, scattered.

(Table 5): (1) endemic; (2) disjunct; (3) spread or scattered distribution. The distribution types within this TBI category were defined numerically as follows. Disjunct distributions: small clusters of presence blocks [#PB ≤ 4] separated by at least three absence blocks [max(#ABG) ≥ 3]. Endemic distributions: small clusters of presence blocks [#PB ≤ 4] in a restricted area separated by maximally two blocks [max(#ABG) ≤ 2]. Spread or scattered distributions: the remaining distribution types. The proportional analysis of the distribution patterns complies with the results obtained from the average functions: MAS EC is characterized by a

Table 6 Proportion of species with an endemic (%E), disjunct (%D) and scattered (%S) distribution of species from both upwelling communities with a TBI ≤ 0.25

Community*	%E	%D	%S
MAS EC	31.3	50.0	18.8
S&O SC	16.7	41.7	41.7

*For definitions see Fig. 1.

higher proportion of endemic species, while S&O SC contains a higher amount of species with a scattered distribution (Table 6).

DISCUSSION

TBI and its underlying functions prove to be useful in comparing and quantifying spatial (e.g. biogeographical spread) distribution patterns. The index is particularly helpful for selecting organisms with similar distribution types, this being a shortcoming of previous biogeographical analyses. The approach presented does not compute similarities in taxon composition between two or more communities, but calculates the similarity in distribution patterns. It is noteworthy that the biogeographical analyses of distribution patterns presented here are quite robust for data based on morphological–anatomical identifications. The problem of cryptic diversity, usually demonstrated in molecular population or phylogenetic studies, is relatively minor since related and structurally similar taxa have similar ecological requirements and physiological traits, resulting in a high environmental biogeographical affinity (Verbruggen *et al.*, 2005). Furthermore, undetected cryptic diversity in studies using traditional similarity indices erroneously strengthens biogeographical affinities between localities. Their influence is, however, minor in the approach described here, as taxa with specific distribution patterns (e.g. widespread taxa) can be filtered out using the three functions.

TBI and its underlying functions also serve as a filter to focus on specific distribution patterns within large data sets, for example in relation to the statement of Jetz & Rahbek (2002), p. 1548: 'Geographic patterns in species richness are mainly based on wide-ranging species because their larger number of distribution records has a disproportionate contribution to the species richness counts.' TBI and its functions might be more suitable as quick and informative exploratory tools for tracking changes in populations on a temporal scale (e.g. habitat fragmentation). On a population level, the values of connectivity (C) and grouping (G) are most relevant if the size of the grid cells can be related to the dispersal capacities of the organisms. Nevertheless, even if intrinsic dispersal capacities are a lot smaller than the grid cells, TBI can show changes in population demography and the potential connectivity of populations by external factors. The comparison of TBI values between taxa or taxon groupings (e.g. communities) is relevant only if the total grid and its cells are of a similar size and structure. TBI values that correspond to specific distribution patterns (e.g. the scale from scarce and dispersed to abundant and grouped distributions, as in the case study described here) cannot be generalized, because the values depend on the relative size of a grid cell in comparison with the maximum of the potentially occupied area.

Future developments of TBI might focus on the weighting of grid cells. Blocks that are more (or less) likely to serve as dispersal blocks can be weighted accordingly. This is especially useful for connectivity blocks in applications where streams, rivers, birds, etc. serve as favourable vectors along specific pathways within the distribution area (Fagan, 2002). Presence blocks, on the other hand, might also be weighted depending on the abundance, population size or biomass of the organisms investigated. Other improvements might focus on standard-ization of the index based on comparisons with randomized distribution patterns for the specific grid. Application of the index can also be expanded to combine statistical analyses of quantitative data and TBI, related to nestedness analyses, or coupled with taxonomic diversity measurements.

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BIOSKETCH

Tom Schils is a researcher with the Fund for Scientific Research at Ghent University, Belgium. His research interests include the ecology, biogeography and taxonomy of marine macrophytes, with current focus on the flora of the Arabian Seas.

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Contents

Front cover: *Nizamuddinia zanardinii* (Schiffner) P.C. Silva, a monotypic brown alga endemic to the Arabian Sea. This keystone species forms extensive macroalgal stands and has been used as a flagship to characterize the upwelling areas of the north-western Indian Ocean (see p. 560 in this Issue). Photo: Tom Schils.