

On the meanings of nestedness: back to the basics

Werner Ulrich and Mário Almeida-Neto

W. Ulrich, Dept of Animal Ecology, Nicolaus Copernicus Univ. in Torun, Gagarina 9, PL-87-100 Toruń, Poland. – M. Almeida-Neto (marioeco@gmail.com), Depto de Ecologia, Inst. de Ciências Biológicas, Univ. Federal de Goiás, Goiânia, GO, 74001-970, Brazil.

The ecological concepts of nestedness and β -diversity first appeared more than five decades ago, but there is still controversy over their precise meaning and application. Here, we focus on the concept of nestedness, the ordered loss of species along environmental or ecological gradients. Because there is no species replacement if the distribution of species among a number of sites is perfectly nested, some studies have defined nestedness as the inverse of species turnover. We argue that such a redefinition relies on a misinterpretation of the original concept of nestedness as the inverse of species replacement. Such a narrow interpretation might result in misleading conclusions about the mechanisms regulating species distribution patterns. We argue, in particular, that any quantification of nestedness must be as explicit as possible about the gradient to be analyzed.

Two basic questions in community ecology are 1) whether the variability in species composition along environmental gradients and across spatial scales follows non-random patterns and, subsequently, 2) what mechanisms produce such patterns. To address these issues, ecologists have introduced a multitude of concepts and measurements. The production of many concepts is not a problem in itself, but the resulting lack of clarity (e.g. multiple and partly contradictory definitions for a single concept or term) often causes confusion and fruitless discussion (Peters 1991, Shradler-Frechette and McCoy 1993). β -diversity and nestedness are examples of how apparently simple concepts can be interpreted in so many different ways. Despite several reviews of both concepts (Ulrich and Gotelli 2007, Jurasinski et al. 2009, Ulrich et al. 2009, Tuomisto 2010a, b), their precise meanings still remain contentious. Recently, Baselga (2010a, b, 2012), Podani and Schmera (2011, 2012) and Schmera and Podani (2011) explored the connections between both patterns and tried to develop an integrated framework. Although we acknowledge the valuable insights and contributions of these studies, we feel that they neglected fundamental differences between the concepts.

Whittaker (1960, 1977) termed the level of among-site variation in species composition within a given region ‘ β -diversity’ and proposed a multiplicative relationship between local richness (α -diversity) and regional richness (γ -diversity) of the form $\gamma = \alpha \times \beta$. By definition, if there is no or little variation in species composition among sites, β -diversity has no or only a small relative contribution to overall species richness. Because ‘variation in species composition’ has no precise definition, the term β -diversity has several meanings, ranging from dissimilarity in species

composition between sites to the decomposition of diversity across hierarchical spatial scales (Jurasinski et al. 2009, Tuomisto 2010a). However, regardless of the concept of β -diversity used, there are two basic patterns that cause variation in species composition: 1) differences in species richness and 2) species replacement (i.e. the loss of a species followed by the gain of another). In the absence of species replacement across sites, all variation in species composition is due to differences in species richness. Therefore, in the absence of species replacement any site with n species will be a proper subset of the species at all sites with $n + x$ ($x \geq 1$) species. This subset property is at the heart of the concept of nestedness.

The nestedness concept originated in the context of insular biotas colonized by a source pool of species from the mainland (Hultén 1937, Darlington 1957). According to the ‘immigrant pattern’ proposed by Darlington (1957), better dispersers are expected to colonize the majority of islands, including the more distant ones, whereas poor dispersers would be restricted to less isolated islands. Consequently, there would be a nested pattern of species occurrences on islands and, therefore, an ordered variation in both species richness and species incidence. In meta-communities, the presence of strong nestedness is a clear indication of coupled gradients of site environmental characteristics and species traits (Ulrich et al. 2009); i.e. some ordered variation in species attributes (e.g. abundance, dispersal ability, habitat specialization) responding to some ordered variation in site characteristics (e.g. isolation, habitat heterogeneity). Nested patterns are also common in ecological networks of interacting species (Bascompte et al. 2003, Burns 2007, Vacher et al. 2008, Piazzone et al.

2011). Also in this case, coupled gradients of species traits or species abundances have been postulated as the cause of nestedness in species interaction networks (Bascompte and Jordano 2007, Ulrich et al. 2009).

Recently, Baselga et al. (2007) proposed a multiple-site similarity measure based on species overlap that quantifies species replacement (turnover) within a framework of multiplicative diversity partitioning (Baselga 2010a, Tuomisto 2010a, b). Building on Harrison et al. (1992), Baselga et al. (2007) and Baselga (2010a, b) noted that a component of β -diversity due solely to differences in species richness results from nestedness (i.e. ordered species loss or gain). Podani and Schmera (2011, 2012), Schmera and Podani (2011), and Carvalho et al. (2012) developed similar concepts that link nestedness to species replacement. Here, we focus on the basic assumptions behind these concepts and try to clarify the relationship between β -diversity, replacement and nestedness. Specifically, we show that nestedness is more than simply the opposite of replacement or a particular case of β -diversity. Intimately linked to environmental and ecological gradients, nestedness is a concept in its own right that cannot be fully understood solely through a β -diversity framework.

Dissimilarity due to nestedness?

Partitioning β -diversity into its basic components allows for tests of the relative importance of historical and ecological processes along the gradient from alpha to gamma diversity in a given region. In this respect, there is a general consensus that, overall, β -diversity can be partitioned into species replacement and differences in richness (Baselga 2010a, b, 2012, Almeida-Neto et al. 2011, Podani and Schmera 2011, 2012, Schmera and Podani 2011, Carvalho et al. 2012). Two primary points of dispute are 1) how the component of β -diversity related to species replacement is scaled and 2) how the difference in richness component is defined.

Species replacement and nestedness are inversely related. The former is the substitution of one species for another and has been quantified, for instance, as the sum of the number of non-shared occurrences among all pairs of species (Leibold and Mikkelson 2002, Presley et al. 2010).

Thus, replacement is independent of the difference in species richness (Presley et al. 2010, Baselga 2012). Richness differences are also independent of whether a matrix is nested or not because species overlap is not a requisite for a difference in richness between sites (Almeida-Neto et al. 2012). Therefore, we believe that confounding nestedness with richness differences might result in incorrect interpretations of the underlying processes that produce such patterns. Thus, we recommend avoiding the use of the term 'nestedness-resultant dissimilarity' (Baselga 2010b) to refer to the level of β -diversity related to differences in species richness between sites with at least one species in common.

Difference in species richness is a necessary condition for nestedness

According to the formal definition of Patterson and Atmar (1986), nestedness describes a pattern where the species present at species-poor sites form proper subsets of the species in species-richer sites. This definition explicitly implies a gradient in species richness across sites. Nestedness is, therefore, necessarily linked to ordered species loss and therefore to a certain degree of β -diversity. Implicitly, the definition also implies differences in species incidences (Darlington 1957, Ulrich et al. 2009). Thus, the presence-absence matrix of Fig. 1A has perfectly nested columns and highly nested rows having two connected gradients: decreasing species richness and decreasing species incidence. However, the matrix in Fig. 1B with identical numbers of species incidences cannot form a nested subset pattern despite the richness gradient across sites. Indeed, all examples of nestedness in the literature show differences in occurrences across sites and species. This explains why some authors have used visual metaphors such as kitchen bowls, Chinese boxes, Russian dolls or concentric Venn diagrams (Wright and Reeves 1992, Jordano et al. 2006, Bascompte 2009) to represent a perfect nested pattern in which any smaller community contains a proper subset of the species present in any richer one. Based on this logic, Ulrich et al. (2009) identified an additional property of nestedness: the degree of nestedness should be invariant with respect to the placement of species in rows or columns. Therefore, any nestedness

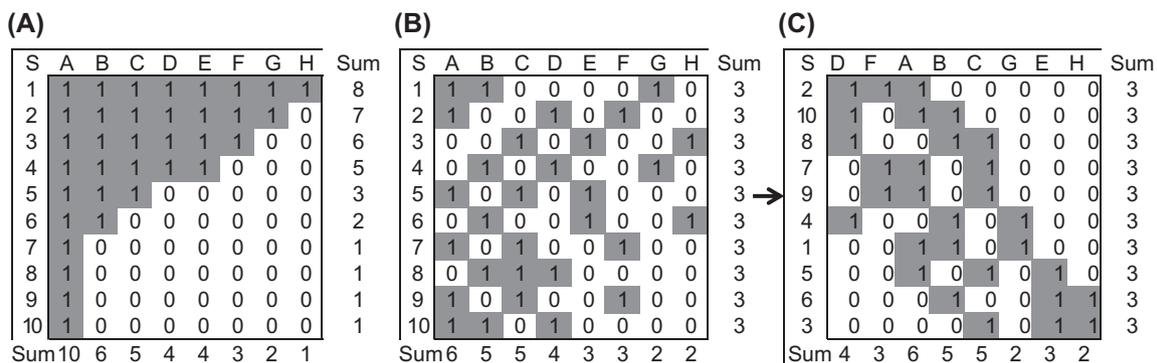


Figure 1. (A) A perfectly nested presence-absence matrix ordered according to row and column totals. (B) A matrix with identical numbers of species incidences cannot be nested because species-poorer sites are not proper subsets of species-richer sites. A reordering of (B) by reciprocal averaging (C) shows that the matrix has a high degree of species turnover. A nestedness metric that focuses on richness differences among sites misses this point and therefore gives an erroneous result.

measure should give identical results for a given presence–absence matrix and its transpose. Ulrich and Gotelli (2007) demonstrated that metrics that do not obey this symmetry property might provide erratic results.

Beginning with Wright and Reeves (1992), researchers have discussed the question of whether ties in species richness among sites (or among incidence totals of species) contribute positively to the overall degree of nestedness (Wright et al. 1998, Almeida-Neto et al. 2008). Both Baselga (2010a) and Carvalho et al. (2012) explicitly acknowledge that a difference in richness is a necessary condition for nestedness, whereas Podani and Schmera (2011, 2012) argued that nestedness is the opposite of species replacement (i.e. the 1-complement of species replacement). Consequently, the presence of a richness difference should not be a condition for nestedness according to Podani and Schmera (2011, 2012). We note that the inclusion or exclusion of tied ranks is metric-dependent. The popular temperature metric that is an averaged distance of a given matrix from its maximally nested counterpart (Atmar and Patterson 1993) and the discrepancy metric that counts steps to transform the matrix into a maximally nested one (Brualdi and Sanderson 1999) implicitly include tied ranks and count them positively towards the matrix-wide degree of nestedness. The PRN index recently proposed by Podani and Schmera (2011, 2012, see below) explicitly includes tied ranks and counts them positively, also. In turn, NODF (Almeida-Neto et al. 2008, see below) penalizes tied ranks by counting them as zero while being normalized by the total number of pairwise row and column combinations. Therefore, a given matrix can achieve the maximum nestedness level that is allowed by the proportion of empty cells, but a high number of tied ranks can cause it to have a lower NODF score than an imperfectly nested matrix without tied ranks.

Including or excluding such ‘tied ranks’ from nestedness calculations might have severe implications for the interpretation of observed community structures. To demonstrate this point, we reanalyzed the well-known biogeographic data set of Atmar and Patterson (1995). All matrices have at least two tied ranks in rows or columns (minimum 25%, average 66% tied ranks). When applied in combination with the standard fixed–fixed null model (Gotelli and Ulrich 2012), PRN (which includes tied ranks) identified significantly more (t -test, $P(H_0) < 0.01$) matrices with a high percentage of tied ranks as being nested. On the other hand, the temperature index (indifferent with respect to

tied ranks) and NODF (which penalizes tied ranks) did not discriminate between matrices with higher or lower proportions of tied ranks. In line with the treatment of tied ranks, the standardized effect sizes of PRN were significantly positively correlated with the proportion of tied ranks in the matrix (Fig. 2A), those of NODF significantly negatively correlated (Fig. 2B), and those of temperature (Fig. 2C) not significantly correlated.

As an example of the implications of allowing nestedness between equally rich sites (or between species with the same incidences), consider an archipelago where all things are equal except for isolation from the mainland, forming a perfect gradient. Allowing nestedness between equally rich sites would imply that there is perfect nestedness if all islands have the same species compositions (Fig. 3A). Additionally, this would mean that some nestedness can occur among equally rich sites just because they have at least one species in common. Now, let us consider two other archipelagos with the above-cited perfect isolation gradient. In archipelago B, the assemblages of species on more isolated islands are proper subsets of those on less isolated islands (Fig. 3B). In archipelago C, all islands have the same species richness but with some species turnover (Fig. 3C). Without the ‘inequality condition’, archipelagos A and B would be classified as perfectly nested and archipelago C as highly nested if species overlap is higher than species replacement. Therefore, using a too-broad concept of nestedness that includes tied ranks would not allow us to distinguish between distinct community structures or the possible mechanisms underlying the nested patterns.

Finally, in the context of interaction networks, nestedness is often understood as a special case of asymmetrical interactions between two sets of species (Bascompte et al. 2003), so that the less-connected species are preferentially linked to a core of species with higher numbers of links. Thus, extending the concept of nestedness to tied ranks (i.e. pairs of species with identical numbers of interaction links) would imply that asymmetry is not a necessary characteristic of nested networks. This broad definition of a nested pattern would also have implications for the understanding of the relationship between nestedness and network stability. Recently, Saavedra et al. (2011) argued that in highly competitive networks, the species that contribute the most to network asymmetry (measured by the degree of nestedness) and stability (Bastolla et al. 2009) are most prone to extinction. If network asymmetry was not a necessary constituent of nestedness, then it would no longer

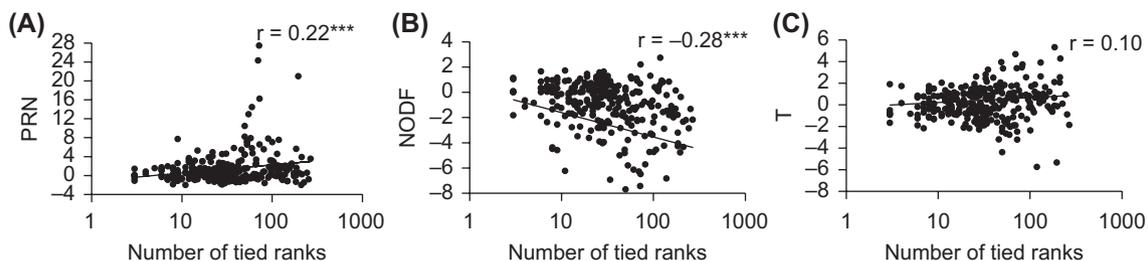


Figure 2. Correlations between the standard effect sizes (assessed from the fixed–fixed null model) of PRN (A), NODF (B), and temperature (C) and the number of tied ranks in 288 biogeographic matrices compiled by Atmar and Patterson (1995). ***: $p < 0.001$.

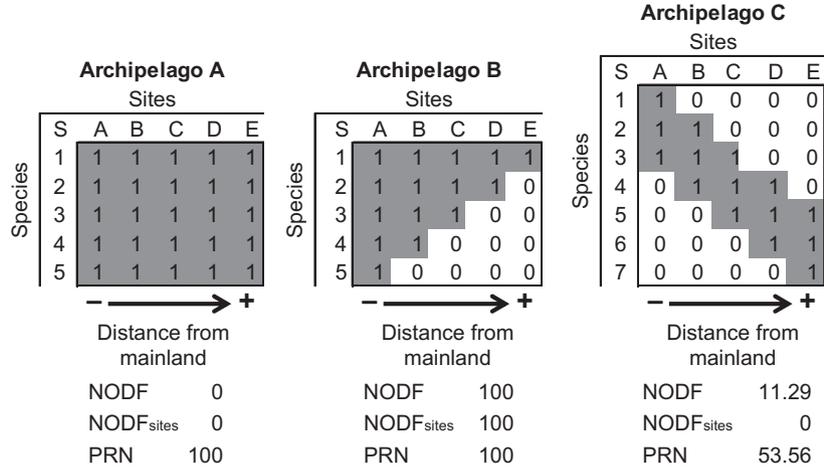


Figure 3. Three model meta-communities showing the qualitative differences between NODEF, which depends on ordering according to some predefined gradient, and the order-free metric PRN.

be possible to link network stability directly to species persistence because the well-established connection between network stability and network asymmetry would have to be redefined.

Nested or partly nested?

The popular NODF metric is a simultaneous measure of species overlap from species-poor to species-rich sites and co-occurrence from limited to widely distributed species. Denoting a_{kl} as the number of joint occurrences at sites k and l , b_{kl} as the number of species specific to site k , and c_{kl} as the number of species specific to site l , the NODFs across sites ($NODF_{species}$) and across species ($NODF_{sites}$) are calculated as

$$NODF_{species} = \frac{200}{m(m-1)} \sum_{k < l} \frac{a_{kl}}{a_{kl} + \min(b_{kl}, c_{kl})} | S_k \neq S_l \quad (1)$$

$$NODF_{sites} = \frac{200}{n(n-1)} \sum_{k < l} \frac{a_{kl}}{a_{kl} + \min(b_{kl}, c_{kl})} | S_k \neq S_l \quad (2)$$

where m is the number of rows, n the number of sites, and S_k and S_l are the total numbers of occurrences at rows (sites) k and l , respectively (Almeida-Neto et al. 2011, Podani and Schmera 2011). NODF is then the weighted average of $NODF_{species}$ and $NODF_{sites}$.

Almeida-Neto et al. (2008) introduced the terms nestedness among rows ($NODF_{species}$) and nestedness among columns ($NODF_{sites}$), allowing the calculation of the extent to which columns and rows contribute to whole-matrix nestedness. Unfortunately, they were not clear about whether rows and columns can be independently nested. Decomposing nestedness into its among-row and among-column components does not imply that nestedness is caused by disconnected gradients/factors in the characteristics of sites and species. Nestedness is a concept that applies to whole matrices, and $NODF_{sites}$ and $NODF_{species}$ are only terms in the calculation. Thus, to avoid confusion, $NODF_{sites}$ and $NODF_{species}$ might better be termed nestedness components.

Formally, $NODF_{sites}$ is similar to the well-known Simpson coefficient of similarity averaged over all pairs of sites (Simpson 1943):

$$Simpson = \frac{2}{n(n-1)} \sum_{k < l} \frac{a_{kl}}{a_{kl} + \min(b_{kl}, c_{kl})} \quad (3)$$

where $Simpson$ is calculated across all pairs of sites and $NODF_{sites}$ only across those sites with different numbers of species (Almeida-Neto et al. 2012). Thus, $NODF_{sites}$ equals the averaged pairwise Simpson coefficient for sites with unequal species richness. This formal similarity, in combination with the terminological imprecision, has recently caused some misinterpretation about the concept of nestedness. Podani and Schmera (2011) tried to link species turnover (β -diversity) as measured by $Simpson$ and similar overlap metrics with nested subset patterns. They correctly address $NODF_{sites}$ but throughout the mentioned publications refer to nestedness and to NODEF. This is highly misleading because $NODF_{sites}$ alone is only a term within the calculation of NODEF. Therefore, it should not be used as a stand-alone metric of the degree nestedness of a community because a nested pattern is necessarily connected to differences in species incidences across sites and across species. $NODF_{sites}$ alone does not meet this prerequisite. Incidence identity across rows is only possible if sites that are poorer in species are not proper subsets of species-richer sites. The matrix of Fig. 1B is, in fact, scattered and has a high degree of species turnover. NODF correctly identifies this pattern ($NODF = 13.47$; $p > 0.5$ when compared to the equiprobable-equiprobable null model expectation). To be comparable with standard nestedness metrics, $Simpson$ would have to be calculated across sites and across species. However, this extension would break the connection between $Simpson$ and β -diversity.

Order-free metrics of nestedness?

Starting with Wright and Reeves (1992), several authors have tried to define nestedness measures that are independent of

the ordering of rows and columns (Hausdorf and Hennig 2007, Podani and Schmera 2011). Podani and Schmera (2011, 2012) particularly advocate the use of order-invariant measures in the case of bipartite ecological networks and proposed the PRN metric, defined as (cf. Appendix 1 for a proof):

$$\begin{aligned} PRN &= \frac{200}{n(n-1)} \sum_{k<l} \frac{a_{kl} + |b_{kl} - c_{kl}|}{a_{kl} + b_{kl} + c_{kl}} |a_{kl} > 0 \\ &= 100 - \frac{200}{mn(n-1)} \sum_{k<l} \min(b_{kl}, c_{kl}) |a_{kl} > 0 \end{aligned} \quad (4)$$

The left side of Eq. 4 is equivalent to the normalized sum of the proportions of joint species (overlap) and richness differences across sites. After rearrangement (right part of Eq. 4), it becomes clear that the PRN can also be understood as the complement of the normalized sum of the minimum number of unique species at two sites. The numerator in the left part of Eq. 4 implies that PRN increases with species overlap or with richness difference if $a_{kl} > 0$, $b_{kl} > 0$ and $c_{kl} > 0$. Thus, one component can compensate for the other to increase the degree of nestedness between two sites. If the poorer site is a proper subset of the richer site, then the increase in nestedness equals b_{kl} and the richness difference does not contribute to nestedness according to the approach of Podani and Schmera (2011). An undesirable consequence of this compensation is that PRN does not quantify the degree of the subset property. Because PRN is generally the 1-complement of species replacement, it equates nestedness (the joint contribution of richness difference and species overlap) with the pairwise sum of species among sites (see Baselga 2012 for further considerations on this issue).

In fact, the use of PRN and other order-free measures implicitly redefines the concept of nestedness. It no longer addresses predefined ecological gradients but merely species overlap. Furthermore, it reduces the complex pattern of nested subsets to a pattern across sites and ignores differences in species incidences so that nestedness appears to be simply the opposite of species replacement or a particular case of β -diversity. Following Koleff et al. (2003) and Tuomisto (2010a), Podani and Schmera (2011) explicitly present in their Fig. 1 the nestedness component N of a community as the difference between total species richness (γ -diversity) and species replacement across sites, which in turn is the difference between β -diversity and richness difference (δ) $N = \gamma - (\beta - \delta)$. We note that this whole approach is only valid under an additive partitioning of diversity with β -diversity being measured in units of species (Tuomisto 2010a).

In our view, any redefinition of nestedness is unnecessary and introduces more confusion than clarity. Ulrich et al. (2009) reviewed possible causes of nested subset patterns in ecology. With respect to biogeography, they highlighted the importance of colonization trajectories (Patterson 1990), selective extinction (Patterson and Atmar 2000), nested habitats (Wright and Reeves 1992), selective environmental tolerances along stress gradients (Blake 1991),

and gradients in habitat quality (Simberloff and Martin 1991). Regarding bipartite networks, asymmetric interaction strength and complementarity, both leading to gradients in species specialization, have been reported (Bascompte et al. 2003, Rezende et al. 2007). All of these causes involve ecological gradients across sites and differences in richness (incidences) across species. Order-free measures would be unable to represent these gradients, and the primary goal of nestedness analysis, the identification of ecological gradients, would be out of reach.

Apart from ecological drivers of nestedness, passive sampling (Andr en 1994) and neutrality (Ulrich and Zalewski 2007) might cause nested subset patterns. Passive sampling involves the random occupancy (according to a mass effect) of sites in proportion to abundance differences at the community level and differences in habitat capacity (often area). Such a process induces strong nested patterns. Ecological drift works similarly, but the introduction of stochastic variability in dispersal ability might cause very different degrees of nestedness (Ulrich and Zalewski 2007). Both statistical drivers do not require other gradients, and order-free metrics might have applications here.

Another critical but neglected issue is the ordering of species according to their incidences (Podani pers. comm.). Previous nestedness analyses that sorted sites according to some predefined gradient implicitly assumed the incidence ordering as a standard convention. However, if we include ecological gradients across sites, then we might simultaneously consider respective gradients for species, too. Such gradients might involve the distribution of community abundance, differences in dispersal ability, or, as an artifact, unequal detection probabilities. Because nestedness necessarily results from coupled gradients of both species characteristics and site attributes, future nestedness analyses should consider both sides of nestedness whenever possible. For example, the gradient in site suitability might influence the gradient in dispersion and abundance differences. In these cases, combined effects might influence the degree of nestedness and should be considered in the interpretation and in statistical testing. Reciprocal dependencies of row and column gradients might particularly apply to mutualistic networks where gradients in interaction strength directly affect the incidence distributions of both groups of species.

In conclusion, if we focus on ecological processes caused by species interactions and environmental variables, we should accept that differences in species richness (and/or species incidence) are a necessary condition for nestedness. Then, the degree of nestedness will depend on what explanatory variable (often species richness) is used to sort species and/or sites in the matrix. The degree of nestedness depends, therefore, on the ordering of rows and columns. Thus, any analysis that aims at identifying the ecological drivers that cause nested subsets should use a metric that focuses on the gradient property among rows and among columns.

Acknowledgements – We are grateful to Andr es Baselga and Janos Podani for their valuable comments and suggestions. WU was supported by a grant from the Polish National Science Center (N 304 372839).

References

- Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – *Oikos* 117: 1227–1239.
- Almeida-Neto, M. et al. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. – *Environ. Model. Softw.* 26: 173–178.
- Almeida-Neto, M. et al. 2012. Rethinking the relationship between nestedness and beta diversity – a comment on Baselga (2010). – *Global Ecol. Biogeogr.* 21: 772–777.
- Andrén, A. 1994. Can one use nested subset pattern to reject the random sample hypothesis? Examples from boreal bird communities. – *Oikos* 70: 489–494.
- Atmar, W. and Patterson, B. D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. – *Oecologia* 96: 373–382.
- Atmar, W. and Patterson, B. D. 1995. The nestedness temperature calculator: a Visual Basic program, including 294 presence-absence matrices. – AICS Research, Univ. Park, NM and Field Museum, Chicago, <<http://aics-research.com/nestedness/tempcalc.html>>.
- Bascompte, J. 2009. Disentangling the web of life. – *Science* 325: 416–419.
- Bascompte, J. and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 38: 567–593.
- Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – *Proc. Natl Acad. Sci. USA* 100: 9383–9387.
- Baselga, A. 2010a. Multiplicative partition of true diversity yields independent alpha and beta components, additive partition does not. – *Ecology* 91: 1974–1981.
- Baselga, A. 2010b. Partitioning the turnover and nestedness components of beta diversity. – *Global Ecol. Biogeogr.* 19: 134–143.
- Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness and nestedness. – *Global Ecol. Biogeogr.* in press.
- Baselga, A. et al. 2007. A multiple-site similarity measure independent of richness. – *Biol. Lett.* 3: 642–645.
- Bastolla, U. et al. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. – *Nature* 458: 1018–1021.
- Blake, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. – *Conserv. Biol.* 5: 58–66.
- Brualdi, R. A. and Sanderson, J. G. 1999. Nested species subsets, gaps, and discrepancy. – *Oecologia* 119: 256–264.
- Burns, K. C. 2007. Network properties of an epiphyte metacommunity. – *J. Ecol.* 95: 1142–1151.
- Carvalho, J. C. et al. 2011. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. – *Global Ecol. Biogeogr.* 21: 760–771.
- Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. – Wiley.
- Gotelli, N. J. and Ulrich, W. 2012. Statistical challenges in null model analysis. – *Oikos* 121: 171–180.
- Harrison, S. et al. 1992. Beta-diversity on geographic gradients in Britain. – *J. Anim. Ecol.* 61: 151–158.
- Hausdorf, B. and Hennig, C. 2007. Null model tests of clustering of species, negative co-occurrence patterns and nestedness in meta-communities. – *Oikos* 116: 818–828.
- Hultén, E. 1937. Outline of the history of Arctic and Boreal biota during the Quaternary period. – Thule, Stockholm.
- Jordano, P. et al. 2006. The ecological consequences of complex topology and nested structure in pollination webs. – In: Waser, N. M. and Ollerton, J. (eds), *Plant-pollinator interactions: from specialization to generalization*. Chicago Univ. Press, pp. 173–199.
- Jurasinski, G. et al. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. – *Oecologia* 159: 15–26.
- Koleff, P. et al. 2003. Measuring beta diversity for presence-absence data. – *J. Anim. Ecol.* 72: 367–382.
- Leibold, M. A. and Mikkelsen, G. M. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. – *Oikos* 97: 237–250.
- Patterson, B. D. 1990. On the temporal development of nested subset patterns of species composition. – *Oikos* 59: 330–342.
- Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. – *Biol. J. Linn. Soc.* 28: 65–82.
- Patterson, B. D. and Atmar, W. 2000. Analyzing species composition in fragments. – *Bonner Zool. Monogr.* 46.
- Peters, R. H. 1991. A critique for ecology. – Cambridge Univ. Press.
- Piazzon, M. et al. 2011. Are nested networks more robust to disturbance? A test using epiphyte-tree, commensalistic networks. – *PLoS One* 6: e19637.
- Podani, J. and Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. – *Oikos* 120: 1625–1638.
- Podani, J. and Schmera, D. 2012. A comparative evaluation of pairwise nestedness measures. – *Ecography* in press.
- Presley, S. J. et al. 2010. A comprehensive framework for the evaluation of metacommunity structure. – *Oikos* 119: 908–917.
- Rezende, E. et al. 2007. Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. – *Oikos* 116: 1919–1929.
- Saavedra, S. et al. 2011. Strong contributors to network persistence are the most vulnerable to extinction. – *Nature* 478: 233–235.
- Schmera, D. and Podani, J. 2011. Comments on separating components of beta diversity. – *Comm. Ecol.* 12: 153–160.
- Shrader-Frechette, K. S. and McCoy, E. D. 1993. *Method in ecology: strategies for conservation*. – Cambridge Univ. Press.
- Simberloff, D. and Martin, J. L. 1991. Nestedness of insular avifaunas – simple summary statistics masking complex species patterns. – *Ornis Fenn.* 68: 178–192.
- Simpson, G. G. 1943. Mammals and the nature of continents. – *Am. J. Sci.* 241: 1–31.
- Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. – *Ecography* 33: 2–22.
- Tuomisto, H. 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta-diversity and related phenomena. – *Ecography* 33: 23–45.
- Ulrich, W. and Gotelli, N. J. 2007. Null model analysis of species nestedness patterns. – *Ecology* 88: 1824–1831.
- Ulrich, W. and Zalewski, M. 2007. Are ground beetles neutral? – *Basic Appl. Ecol.* 8: 411–420.
- Ulrich, W. et al. 2009. A consumer's guide to nestedness analysis. – *Oikos* 118: 3–17.
- Vacher, C. et al. 2008. Architecture of an antagonistic tree/fungus network: the asymmetric influence of past evolutionary history. – *PLoS One* 3: e1740.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – *Ecol. Monogr.* 30: 279–338.
- Whittaker, R. H. 1977. Evolution of species diversity in land communities. – *Evol. Biol.* 10: 1–67.
- Wright, D. H. and Reeves, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. – *Oecologia* 92: 416–428.
- Wright, D. H. et al. 1998. A comparative analysis of nested subset patterns of species composition. – *Oecologia* 113: 1–20.

Appendix 1

Proof of Eq 4. We use the equalities $m - |b - c| = a + 2\min(b, c)$ (Podani and Schmera 2011a) and $m = a + b + c$ for any pair of sites. Because the total number of site combinations is $n(n-1)/2$, we get

$$\begin{aligned} PRN &= \frac{200}{n(n-1)} \sum_{k < l} \frac{a_{kl} + |b_{kl} - c_{kl}|}{a_{kl} + b_{kl} + c_{kl}} = \frac{200}{n(n-1)} \sum_{k < l} \frac{m - 2\min(b_{kl}, c_{kl})}{m} \\ &= \frac{200}{n(n-1)} \left(\sum_{k < l} 1 - \left(\frac{2\min(b_{kl}, c_{kl})}{m} \right) \right) \\ &= 100 - \frac{400}{n(n-1)} \sum_{k < l} \left(\frac{\min(b_{kl}, c_{kl})}{m} \right) \\ &= 100 - \frac{400}{mn(n-1)} \sum_{k < l} \min(b_{kl}, c_{kl}) \end{aligned}$$