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Ecological traits reveal functional nestedness of bird communities in habitat islands: a global survey

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Assessing functional nestedness patterns in habitat islands: an analysis of multiple bird datasets

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Abstract

The widespread destruction and fragmentation of natural habitats around the world creates a strong incentive to understand how species and communities respond to such pressures. The vast majority of research into habitat fragmentation has focused solely on species presence or absence. However, analyses using innovative functional methodologies offer the prospect of providing new insights into the key questions surrounding community structure in fragmented systems. A key topic in fragmentation research is nestedness (i.e. the ordered composition of species assemblages involving a significant tendency for packing of the presence–absence matrix into a series of proper subsets). To date, nestedness analyses have been concerned solely with nestedness of species membership. Here, we capitalize on the publication of a recent nestedness index (traitNODF) in which the branch lengths of functional dendrograms are incorporated into the standard NODF nestedness index. Using bird community data from 18 forest-habitat-island studies, and measurements of eight continuous functional traits from over 1000 bird species, we conduct the first synthetic analysis of nestedness from a functional perspective (i.e. a nestedness analysis which incorporates how similar species are in terms of their ecological traits). We use two null models to test the significance of any observed functional nestedness, and investigate the role of habitat island area in driving functional nestedness. We also determine whether functional nestedness is driven primarily by species composition or by differences in species' traits. We found that the majority (94%) of datasets were functionally nested by island area when a permutation null model was used, although only 11-22% of datasets were significantly functionally nested when a more conservative fixed-fixed null model was used. Species composition was always the most important driver of functional nestedness, but the effect of differences in species traits was occasionally quite large. Our results isolate the importance of island area in driving functional nestedness where it does occur, and the ordered loss of functional traits due to habitat loss. This analysis demonstrates the potential insights that may derive from testing for ordered patterns of functional diversity.

The fragmentation and destruction of natural habitat is the main driver of current biodiversity loss (Sala et al. 2000, Whittaker and Fernández-Palacios 2007). Understanding how species are affected by habitat loss is thus crucial to designing appropriate conservation and management responses (Fischer and Lindenmayer 2007). The majority of habitat loss research, and ecological research more generally, has tended to focus solely on species identities (McGill et al. 2006). However, it is increasingly acknowledged that functional diversity (i.e. the "extent of functional differences among the species in a community", Petchey and Gaston 2002, p.402) is an important component of biodiversity and may provide valuable insight into ecosystem processes (e.g. Petchey and Gaston 2002, 2006, McGill et al. 2006, Naeem et al. 2012). It is also becoming apparent that, alongside species diversity, functional diversity is being eroded due to habitat loss (Flynn et al. 2009, Naeem et al. 2012, Newbold et al. 2013). As a result, it has been argued that researchers should no longer focus solely on species identities and that there is a need for greater integration of functional diversity within traditional ecological subjects (e.g. McGill et al. 2006, Devictor et al. 2010, Safi 2011, Monnet et al. 2014). A focus on functional diversity allows workers to consider the differences between species in terms of their ecological traits, which in turn enable greater understanding of ecosystem functioning (Naeem et al. 2012, Monnet et al. 2014). For instance, maintaining functional diversity of birds in fragmented landscapes is important as birds provide numerous important functional roles, including pollination, the dispersal of seeds between fragments, and the predation of invertebrates and small mammals within fragments (Henle et al. 2004, Tscharntke et al. 2008, Dehling et al. 2014).

Anthropogenic habitat destruction generally produces islands of natural habitat set in a matrix of disturbed landscape. Hence, ecologists have often used theories derived from the field of island biogeography to study such landscapes (Whittaker and Fernández-Palacios

2007). One widely studied insular phenomenon is nestedness, the analysis of which was

formally introduced by Patterson and Atmar (1986). It can be defined as "a form of ordered

composition of species assemblages involving a significant tendency for packing of the

[presence–absence] matrix into a series of proper subsets" (Matthews et al. *in press*; and see

Table 1). Examining the prevalence of nestedness in habitat islands is important from a

conservation perspective as it provides information on the distribution of species in

fragmented landscapes; information which can be used to establish conservation

prescriptions, such as protected area placement (Whittaker and Fernández-Palacios 2007,

Triantis and Bhagwat 2011).

Early studies found significant nestedness to be a near universal finding. For example,

Watling and Donnelly (2006) reported that 94% of the 67 island datasets included in their

synthetic analysis were significantly nested. However, recent studies have questioned the

choice of nestedness indices and null models used in many of these earlier studies, claiming

that the methods suffer from inflated type I errors (e.g. Ulrich and Gotelli 2007). Analyses

using more appropriate null models have found significant nestedness to be evident in only a

minority of island datasets (e.g. Ulrich and Gotelli 2007, 2012, Matthews et al. *in press*).

These methodological issues led to the development of more appropriate indices, such as a

nestedness index based on overlap and decreasing fill (NODF; Almeida-Neto et al. 2008;

Table 1). NODF is based on the twin properties of standardized differences in presence–

absence matrix row and column fills and paired overlap (i.e. the overlap of presences in two

adjacent columns), and is generally considered the most statistically appropriate index

available (Almeida-Neto et al. 2008, Ulrich et al. 2009).

To date, studies of nestedness have focused exclusively on nestedness of species

composition data. This traditional approach overlooks the fact that species which share the

majority of their ecological characteristics will often be functionally redundant in a given

ecosystem (Blackburn et al. 2005, Melo et al. 2014). Recently, Melo et al. (2014) introduced

an adaptation of the standard NODF index, termed treeNODF, in which the branch lengths of

tree structures are incorporated, e.g. functional dendrograms and phylogenies. The variant of

the treeNODF index which incorporates functional diversity was termed traitNODF, and it

can be used to test for nestedness in ecological samples, whilst taking into consideration how

similar species are in terms of their ecological traits ('herein functional nestedness'; see Fig.

1 for an example; and see Table 1 for a glossary of terms).

The treeNODF index is calculated in a similar manner to standard NODF, but instead

of using the sum of species occurrences to estimate the degree of nestedness, the branch

lengths of a tree-like object are used (i.e. species richness/species incidence is replaced with

the branch lengths of a tree-like object). In traitNODF, the tree-like object is a functional

dendrogram constructed using species trait data, whereby the branch lengths of this

dendrogram represent the functional diversity (FD) of the system in question (e.g. Fig. 1).

traitNODF works by first ordering the sites along a particular gradient (e.g. in this example,

island area). All pairwise combinations of sites along this area gradient are then calculated. A

pair of sites is then taken (A & B), whereby it is initially assumed that as A is larger than B,

A is a relatively high FD community and B is a relatively low FD community. The FD of the

two communities is then compared. If the FD of A is found to be lower than the FD of B,

traitNODF takes a value of zero. If the FD of A is greater than the FD of B, the traitNODF

value of these two sites is the proportion of the branches in the dendrogram of B that are also

present in the dendrogram of A (Melo et al. 2014). As Melo et al. state, in the case of using

treeNODF with a phylogenetic tree, if the branch lengths of the phylogenetic tree are

considered proportional to the number of features, then the treeNODF value of these two sites

is the proportion of the features present in the features-poor site that are also present in the

features-rich site. This pairwise comparison of sites is repeated across all sites in the dataset and the resultant traitNODF values are then averaged to give a traitNODF value for all sites.

Melo et al. (2014) illustrated that using traitNODF can be enlightening as standard NODF and traitNODF may show different patterns; that is, a set of isolates may be significantly nested in terms of functional traits but not in terms of species composition (e.g. see Fig. 1) and *vice versa*. A useful feature of treeNODF (and by extension, traitNODF) is that it can be partitioned into two components: 1) S.Fraction – the composition component of the index, i.e. the fraction of treeNODF that would be observed if all species were equally related, and 2) topoNODF – the fraction of the treeNODF value due to the topology of the tree (e.g. the dendrogram). Examining each component separately allows for additional inferences regarding the nestedness of ecological communities (Melo et al. 2014). Furthermore, functional nestedness potentially offers an explanation for taxonomic nestedness in certain instances as it provides a link between species' distributions and the environment.

When testing for nestedness, a sensible approach is to determine an *a priori* hypothesis regarding the particular mechanism(s) likely to be driving any observed nestedness, rather than simply organizing the presence–absence matrix to achieve the maximum possible nestedness value (McAbendroth et al. 2005, Almeida-Neto et al. 2008, Melo et al. 2014). For example, in both true island and habitat island systems island area (i.e. differential area requirements between species) and isolation (i.e. differential dispersal abilities between species) have often been found to be important drivers of both nestedness and functional diversity (e.g. Fig. 1; Patterson and Atmar 1986, McAbendroth et al. 2005, Ulrich et al. 2009, Ding et al. 2013, Whittaker et al. 2014, Matthews et al. *in press*). Thus, in such systems a more fruitful approach to maximally packing the presence–absence matrix is to order sites according to island area (isolation, disturbance intensity, etc., could just as

easily be used) and then compute the nestedness index, keeping these site orders fixed. Using this approach Melo et al. (2014) found that island area was a good determinant of functional nestedness for a Caribbean bat community.

To the best of our knowledge, traitNODF has yet to be used to determine the prevalence of functional nestedness in ecological communities, with the exception of Melo et al.*'s* (2014) single study of Caribbean bat communities. Here, we analyse functional nestedness patterns in 18 bird–forest habitat islands datasets spanning a broad array of ecological contexts. To be clear, in this study we are interested in functional and compositional nestedness between sites. It is possible to calculate overall functional nestedness (i.e. nestedness between sites and species) but it requires site-specific environmental data which were generally lacking from the source papers. We focus on birds because (a) it possible to obtain functional trait data for most species of interest, and (b) birds are known to perform essential ecological functions in forests, including seed dispersal and predation on insect herbivores (Bregman et al. 2014). We use a comprehensive and well-specified database of bird traits (see Tobias et al. 2014), containing eight continuous traits (e.g. bill depth, bill width, tarsus length) to build functional dendrograms for over 1000 bird species in our datasets.

Our study has two primary aims. First, we assess whether habitat islands are more or less functionally nested by island area than expected by chance (based on two null models). Our analyses are based on the idea of ordering presence-absence matrices according to an *a priori* hypothesis (i.e. by island area), and we do not test for maximally packed nestedness values. Based on previous studies which have found: (a) evidence of trait-mediated loss of bird species due to habitat loss (Newbold et al. 2013, Bregman et al. 2014), and (b) significant species–area relationships in fragmented landscapes (Lees and Peres 2008, Matthews et al. 2014), we hypothesize that a large number of our datasets will be

significantly functionally nested by island area. Second, by partitioning treeNODF values into their S.Fraction and topoNODF components we aim to determine whether observed functional nestedness is driven primarily by compositional nestedness or the tree topology. We discuss the implications of our results in the context of ecosystem functioning and conservation biogeography.

Methods

Dataset collection

Habitat island datasets were sourced using several abstracting databases between May 2010 and August 2014, and a variety of keywords, including 'habitat islands', 'species richness', and 'fragments'. Certain datasets were obtained from the authors of the source papers, whilst others were supplemented with additional data from the source paper authors. Following Matthews et al. (2014), suitable datasets were screened based on the following criteria:

1. habitat islands were defined as discrete patches of forest surrounded by contrasting matrix habitat;

2. there were at least six habitat islands;

3. a list of bird species in each habitat island within the dataset was given;

4. it was possible to obtain trait data for nearly all (ideally 100%; for details see below) of species within a dataset

Trait data

For present purposes, a trait was defined as a measurable aspect of an organism that determines the organism's interaction with the environment in some way (Flynn et al. 2009). As we are interested in birds in forested habitat islands, we collected data on traits that are

known to be related to the functional roles of birds in forest fragments (i.e. resource acquisition, locomotion, foraging, dispersal ability, and body size, Miles et al. 1987, Henle et al. 2004, Sutherland et al. 2004, Grant and Grant 2006, Tscharntke et al. 2008, Claramunt et al. 2012). In total, we collected data on eight continuous traits. We focused on continuous traits as these have been argued to produce more accurate representations of species' functional roles in ecosystems (e.g. McGill et al. 2006). The continuous traits measured were bill length (from the nares to the tip, and also a second measure from the first feathering on the culmen to the tip), bill width and depth at nares, tarsus length, Kipp's Distance (distance from the longest primary to the first secondary; Kipp 1959), total wing chord length, and tail length (Sutherland et al. 2004). The majority of trait measurements were obtained from skins in the ornithology collections at the Museum of Natural History, Tring, UK. All measurements followed standardized protocols (Tobias et al. 2014) to homogenize measuring techniques, and all data were both spot-checked for accuracy and later examined for outliers. Any specimen that was the sole representation of its species was measured twice. Whenever possible, for each species at least two adult males and two adult females in good condition were selected for measurement and juveniles, damaged specimens, and potential hybrids were avoided. We then averaged the data from the male and female specimens to create a species average for each morphological trait.

As individual traits are highly variable (e.g. Trisos et al. 2014), and many of the traits exhibit colinearity, we condensed these trait data into a number of indices. First, following Trisos et al. (2014) we conducted two Principal Components Analyses (PCA): one using the bill shape measurements ('A'; culmen length, width, length from nares, depth), and one using the locomotive measurements ('B'; tarsus length, wing chord, and tail length). The second axes of A (short beak:wide/deep beak) and B (short tarsus:long tail/wing) were then taken as a bill shape index, and a locomotive index, respectively. A further PCA analysis ('C') was

then undertaken using the first axes of A and B as the input; the first axis of C was then taken as a body size index (Trisos et al. 2014). Finally, we created a dispersal index standardizing for bird size, using the hand–wing index (Claramunt et al. 2012). This index was calculated using the formula: $(K/W) * 100$, where K is the Kipp's Distance, and W is the wing chord length (Claramunt et al. 2012). In sum, the traits used in the functional nestedness analyses were the body size index, the locomotive index, the dispersal index, and the beak shape index. All traits were standardized to have a mean of zero and a standard deviation of one (Mouchet et al. 2008) using the scale function in R. These standardized traits were then used to build functional dendrograms (Petchey and Gaston 2002) for each dataset. First, the species-by-trait matrix for a given dataset was converted into a distance matrix using Euclidean distance (Petchey et al. 2004). Second, the distance matrix was subject to a cluster analysis (UPGMA method) to create a dendrogram (Petchey and Gaston 2002, Petchey et al. 2004). The distance matrix was constructed using the 'vegan' package (Oksanen et al. 2013), the cluster analysis was performed in the base stats R package, and the PCA analyses were performed using the 'ade4' R package (Dray and Dufour 2007).

Measuring functional nestedness

The treeNODF index works by assessing the branch lengths in a tree-like object. Thus, each dendrogram (i.e. the dendrogram for each dataset) was converted into a tree object using the 'as.phylo' function in the 'ape' R package (Paradis et al. 2004; and see our Fig. 2). The site–species matrices were ordered according to island area, and the row orders fixed. The traitNODF index (for rows, i.e. sites) was then calculated for each area-ordered dataset using the dataset's sites–species matrix and corresponding dendrogram, and the 'CommEcol' R package (Melo 2012).

In addition to storing the traitNODF value for each dataset, we also stored the partition values: S.Fraction and topoNODF (see Table 1). As S.Fraction is the compositional component of traitNODF it is generally similar to the standard NODF index. However, as standard NODF and S.Fraction are not necessarily identical (A.S. Melo *Personal communication*), we also computed the standard NODF index (again taking the value for rows) for each area-ordered dataset (after removing the species for which we did not have trait data for, below) using the vegan R package.

To determine whether the observed traitNODF, S.Fraction, topoNODF and standard NODF values differed from those expected by chance we first used a permutation test null model approach ('permRows'; Melo et al. 2014). To implement permRows, we used the 'treeNodftest' function in the CommEcol package. This function randomly permuted the rows of the species–sites matrix (i.e. permuted the sites) and calculated the relevant index (e.g. traitNODF, standard NODF) using this permuted matrix. The matrix was then re-permuted and the processes repeated 1000 times, for each dataset. As whole rows are permuted, this null model preserves the number of sites used by each species (i.e. fixed column totals), and the species and functional composition of sites is maintained. Using the permRows test is useful when sites are ordered according to an *a priori* hypothesis and you are interested in determining the mechanisms driving any observed nestedness. We took the *P* value generated by the treeNodftest function which is a one-tailed test, and employed an α level of 0.05. It is important to note that, a "non-significant" result using permRows does not mean that the matrix is not significantly nested, but that the site ordering hypothesis lacks explanatory power for nestedness in the matrix. We also calculated the Z-transformed score for each dataset, where $Z = \dfrac{\text{Obs} - \mu}{\text{sd}}$, and where Obs is the observed nestedness value

according to a given index, μ is the mean nestedness index value of the null model values, and sd is the standard deviation of the 1000 null model iterations.

As the choice of null model has been found to influence results in nestedness studies (Ulrich and Gotelli 2007, 2012), we also ran the more conservative fixed-fixed null model (FF). The FF model creates a randomized presence–absence matrix of the same dimensions as the observed matrix and keeps marginal row and column totals fixed. We ran the FF model to determine the significance of traitNODF values for the area-ordered matrices (i.e. row orders were fixed). We had originally also planned to test the effect of isolation on functional nestedness by running the two null model analysing using isolation-ordered matrices, for a subset of datasets for which isolation data were available. However, as only a few studies were found to have measured isolation and these studies all used different isolation metrics, the results were difficult to interpret. Thus, we decided to focus solely on the role island area.

Sensitivity analyses

The choice of traits to use in functional diversity studies is important and it can be useful to determine how robust the results of analyses are to the removal of individual traits (Blackburn et al. 2005; Petchey and Gaston 2006; Whittaker et al. 2014). To this end we undertook a sensitivity analysis whereby we removed a trait, re-ran the permRows analyses and recorded the results. The removed trait was then re-instated and a different trait removed, and so on until the analyses had been run with each of the traits lacking. Analysis of these results allowed us to determine whether our findings were robust to the removal of a particular trait. In this context, a trait refers to one of the indices (i.e. a combination of multiple traits). Removing an actual individual trait (e.g. tail length) would have the same effect as it would mean an index could not be computed. All analyses were conducted in R (version 3.0.2; R Development Core Team 2013).

Results

The nature of the datasets

We found 18 datasets that matched criteria 1–4 (see Table S1 in Appendix 1). In order to calculate traitNODF, we removed islands with zero species from the relevant datasets. It was also necessary to remove species from datasets for which we were unable to acquire the trait measurements. This occurred, for example, because the species were endangered and thus specimens were hard to locate. In practice, for 7 of the 18 datasets we had complete coverage of species (i.e. we obtained trait data for 100% of species). For 4 datasets we were missing data on 1 species, 3 datasets had 2 species without trait data, and for 4 datasets we were missing data for between 3 and 8 species (the relevant datasets are highlighted in Table S1). As species with missing data represented a very small proportion of the total number of species within a dataset, we consider it unlikely that these 'missing species' affected our results.

Functional nestedness by island area

When the presence–absence matrices were ordered according to island area the traitNODF values were relatively high, i.e. closer to 100 (maximal nestedness) than 0 (mean traitNODF for area ordered matrices = 71.9). When a permutation test (1000 permutations) was used to test for the significance of the traitNODF values, the observed traitNODF value of the area-ordered matrix was significantly larger than expected by chance in 17 of the 18 datasets, indicating that for these datasets the area-ordered matrix was more functionally nested than the majority of other matrix order permutations (Table 2). The Z-transformed scores for the area-ordered datasets were all positive and were relatively high (mean Z-transformed score = 4.0).

Partitioning the area traitNODF value into its two components (S.Fraction and topoNODF) revealed that, in general, the traitNODF value of a dataset was primarily comprised of the S.Fraction component (i.e. the species composition component), rather than the topoNODF component (i.e. the tree topology component; Table 1). topoNODF accounted for between 4.3% to 35.4% of total traitNODF (mean = 13.0%). In all but one dataset, the permutation test results were consistent between traitNODF, S.Fraction and topoNODF; that is, if the traitNODF value was significant for a dataset, so were the S.Fraction and topoNODF values. For a single dataset (8) the traitNODF and S.Fraction values were significant, whilst the topoNODF value was not (Table 2).

As expected, when the FF model was used, significant functional nestedness was much less prevalent (Table S2 in Appendix S2). Two datasets had a significant traitNODF value and a positive Z-score, whilst four datasets had a significant topoNODF value and a positive Z-score. No dataset had a significant S.Fraction value. A number of the datasets had negative Z-scores, although none of these were significant (Table S2 in Appendix S2).

As the standard NODF index and S.Fraction may not be equivalent we calculated both. The standard NODF values were very similar to the S.Fraction values for each dataset (Pearson's correlation coefficient = 0.93, $P = < 0.001$), and thus for these datasets S.Fraction and standard NODF are roughly interchangeable. Furthermore, the permutation test results for traitNODF always followed the standard NODF permutation test results. That is, for all 18 datasets, both traitNODF and standard NODF produced the same results (Table 2).

Sensitivity analyses

The island area-ordered matrix results were robust to the removal of any single trait/index. In all datasets the significance of the observed traitNODF value did not change in any of the

iterations (i.e. any of the analyses conducted after removing a trait; Table 3). Similarly, the actual traitNODF values varied only slightly between iterations (Table 3).

Discussion

We have undertaken a synthetic analysis of functional nestedness patterns of birds in 18 habitat island datasets. Our results were sensitive to the null model approach used. When a permutation test was used area-driven functional nestedness was found to be relatively common. However, when the more conservative FF model was used, most datasets were not significantly functionally nested. In general, the observed functional nestedness of datasets was more a result of the species composition of islands than the functional differences between species. That being said, topoNODF represented a sizeable proportion of traitNODF for a number of datasets, indicating that the inclusion of functional traits into nestedness analyses can be revealing in certain instances.

The prevalence of functional nestedness in habitat islands

With a single exception (Melo et al. 2014), the study of nestedness in islands has focused exclusively on the nestedness of species composition. The development of treeNODF allows nestedness theory to be applied to other important components of biodiversity, including functional diversity. This is important because examining the different functional roles species undertake in ecological communities is essential if we are to understand how communities are structured (Flynn et al. 2009, Safi 2011). To this end, the search for broad-scale patterns in functional diversity, such as functional nestedness, represents a critical frontier in this field (Petchey and Gaston 2002, Flynn et al. 2009).

It is not possible to directly compare the results of our analyses with previous synthetic analyses of nestedness patterns in habitat islands (e.g. Watling and Donnelly 2006, Matthews et al. *in press*), as we have adopted a different methodological approach. Whereas previous studies have simply organized the presence–absence matrix to achieve the maximum nestedness value, we have ordered the matrix by island area, and our results (e.g. treeNODF and standard NODF values) relate to these matrices.

Using a permutation algorithm we found that when the presence–absence matrices were ordered according to island area, the majority of datasets were functionally nested by area. In almost all cases where the traitNODF value was significantly different from that expected by chance according to permRows, the S.Fraction and topoNODF components were also significant. Thus, based on these results, one could infer that in these datasets small islands do not simply contain species assemblages that are a subset of the larger islands, but the small islands also contain a number of functionally similar species (i.e. species which share a large proportion of their dendrogram branch lengths; see Fig. 1) to the larger islands. However, as to be expected, when FF was used, a much smaller proportion of datasets were significantly functionally nested. Whilst the two null models have generated different results, it is difficult to directly compare the results as permRows and FF represent different approaches to null modelling; that is, using each is to ask a slightly different question regarding significance. Our permRows results indicate that the traitNODF values generated from the area-ordered matrices are larger than most other row-ordered permutations of the matrix. This is why permRows has been argued to represent a useful method when ordering matrices according to an *a priori* hypothesis. In contrast, our FF results indicate that the traitNODF values were generally not significantly different from the values expected after the presences in the area-ordered matrices had been randomized; with the constraint that marginal totals are kept constant. Thus, FF differs in several ways from permRows, and is

known to be a very conservative null model (Ulrich et al. 2009; Strona and Fattorini 2014).
Taking the two sets of results together, a tentative conclusion would be that our area-ordered
matrices are generally not more functionally nested than expected according to a randomly
ordered-matrix, but that island area provides a reasonable explanation for what functional
nestedness is present.

Partitioning the observed traitNODF values into their constituent components
(S.Fraction and topoNODF; see Table 1) indicated that the S.Fraction component (i.e. the
compositional component of traitNODF) always comprised a greater proportion of
traitNODF than the topoNODF component. In Melo et al.'s (2014) analysis of Caribbean bat
communities, topoNODF also made up a smaller proportion of traitNODF (~29%) than
S.Fraction. Nonetheless, in our study topoNODF was occasionally quite large (e.g. 35% for
dataset 17; Table 2), and with one exception was always significant when traitNODF was
significant, when permRows was used. As the number of datasets involved in the present
study is relatively small, further tests for functional nestedness in habitat islands will be
necessary to determine the generality of our findings.

That topoNODF often comprised a low fraction of traitNODF could potentially be a
result of us not selecting the most appropriate traits. The choice of traits to use in functional
diversity studies can be critical (Petchey and Gaston 2006, Mouchet et al. 2008), and given
the complex nature of ecological communities it is relatively easy to (a) overlook important
traits, and/or (b) incorporate uninformative traits (Cadotte et al. 2013). Our sensitivity
analyses and use of composite trait indices makes the second of these possibilities unlikely,
but the first possibility is harder to rule out. However, we have obtained continuous trait data
relating to eight different measurements that are known to characterize the functional roles of
bird species (Henle et al. 2004, Sutherland et al. 2004, Tobias et al. 2014, Trisos et al. 2014),
and thus we are confident that the key traits have been incorporated and quantified.

Driver of functional nestedness

Rather than simply ordering the presence–absence matrices to obtain the maximum possible traitNODF value, we have based our analyses on an *a priori* hypothesis: that island area will underpin observed functional nestedness patterns. Area has been postulated to drive nestedness due to area-dependent extinctions, and species are known to have varying minimum area requirements, such that large patches contain species with small and large minimum area requirements, whilst smaller patches only contain species with small area requirements (Patterson and Atmar 1986, Matthews et al. *in press*). For example, the area of ponds was found to drive nestedness patterns of macroinvertebrates in the UK (McAbendroth et al. 2005). From a functional perspective, forest specialist species possess traits (e.g. large body size, low dispersal ability) which demand larger area requirements relative to taxonomically similar generalist species (Henle et al. 2004, Matthews et al. 2014). The island area results provide more evidence for the importance of habitat island area in maintaining species diversity in fragmented landscapes (discussed below; Whittaker and Fernández-Palacios 2007, Matthews et al. 2014).

Implications for conservation and ecosystem functioning

Until recently, the majority of conservation theory has been based on analyses of taxonomic diversity. However, a number of studies have shown that taxonomic diversity does not necessarily have high congruence with other facets of diversity, including functional diversity (e.g. Monnet et al. 2014). One major issue with purely compositional approaches is that they do not allow inferences to be made regarding the effects of species loss on ecosystem

functioning (Ding et al. 2013) – an important issue given that the loss of species with particular traits can impact the delivery of particular ecosystem functions, depending on the level of functional redundancy (Newbold et al. 2013). Studies that have examined the effects of anthropogenic environmental change on functional diversity have found that functional diversity often declines in human dominated landscapes at a greater rate than species richness (Flynn et al. 2009, Ding et al. 2013, Boyer and Jetz 2014). For example, up to 80% of the original functional diversity of bird communities has been lost from certain oceanic islands due to pre-historical and historical extinctions (Boyer and Jetz 2014). Several authors have argued, on the basis of such findings, that functional diversity should be more explicitly considered in biodiversity conservation, for instance in the location of protected areas (e.g. Naeem et al. 2012, Devictor et al. 2014). In this regard, functional nestedness represents a potentially useful index for conservation planners looking to account for broad scale patterns of functional diversity.

There are linkages between the concept of functional nestedness and Diamond's (1975) assembly rules (reviewed in Whittaker and Fernández-Palacios 2007). Diamond (1975) argued that the distribution of bird species across islands in the Bismark Archipelago followed a set of rules mediated by interspecific competition; new species could only enter an island/community in accord with these assembly rules. In relation to functional nestedness, if we observe functional nestedness by island area, it suggests that there is a particular sequence in which different types of species are added to a system as it increases in size. However, whilst Diamond's assembly rules were largely based on interspecific competition, functional nestedness may occur for a number of reasons, such as area-dependent loss of trait space (discussed above). To take a simple hypothetical example, if a set of fragments are functionally nested in terms of feeding guild, such that the loss of guilds occurs in an ordered manner according to island area, one might envisage insectivores being the most area-

sensitive species (e.g. Şekercioḡlu et al. 2002, found insectivore species to be particularly sensitive to forest loss in Costa Rica), with frugivores being less area-sensitive (Bregman et al. 2014). In this example insectivores would be absent from the smallest islands and only occur in the largest islands. Thus, the valuable functional role of pest control and insect herbivory would be lost from smaller fragments. This ordered loss of guilds by area would also provide an explanation for the observation that this system was taxonomically nested. However, whilst our results do indicate at least a small degree of functional nestedness by area, as topoNODF often represented a low fraction of traitNODF, there must be an additional explanation for the observed taxonomic nestedness. Analysis of phylogenetic relationships between species in the datasets may prove enlightening in this regard (Melo et al. 2014).

Researchers have used standard compositional nestedness indices for over twenty years to argue for specific conservation prescriptions, and in efforts to address the SLOSS debate (i.e. is a single large reserve more or less effective than several small reserves; see Whittaker and Fernández-Palacios 2007, Matthews et al. *in press*). However, finding that an archipelago is or is not nested in species composition does not necessarily predict functional nestedness (Melo et al. 2014). traitNODF does provide this information, and significant functional nestedness, as we have found in some of our datasets, indicates that the loss of traits from islands of decreasing area is proceeding in an ordered manner. That is, species with unique traits are being lost in a systematic fashion – not perfectly, but to a significant degree (see also Flynn et al. 2009). This is important because the order of species loss from a community can have substantial impacts on ecosystem functioning in that community (Petchey and Gaston 2002). Nonetheless, as has been argued in the context of taxonomic nestedness, it is problematic to generate conservation guidance when a system is significantly functionally nested, but not perfectly functionally nested (Fischer and Lindenmayer 2005).

Perfect functional nestedness in an area-ordered matrix would imply that by conserving the largest island in an archipelago, the total spectrum of species' traits would be conserved. As we never found perfect functional nestedness in our datasets, we do not recommend such an approach (i.e. conserving the largest island only) to be used for habitat island systems. However, our results do indicate that there is at least a small degree of ordered loss of bird traits in some of our datasets: smaller islands contain a number of functionally similar species to the species on larger islands. At the very least, this needs to be considered in future studies that attempt to estimate functional diversity loss resulting from habitat fragmentation.

Concluding remarks

Nestedness in island systems has been studied intensively over the last two decades, but these studies have been focused on species richness and composition and have ignored the importance of species traits in driving ordered patterns of biodiversity. Global environmental change continues to have a detrimental effect on all facets of diversity, including functional diversity (Flynn et al. 2009, Devictor et al. 2010). Further work is clearly needed to test for and evaluate the causes of ordered patterns of functional diversity (Naeem et al. 2012). Functional nestedness analysis presents one such way to meet this challenge. We found that "significant" functional nestedness was relatively common when presence–absence matrices were ordered according to island area and a permutation null model approach was used, but was much less prevalent when the FF null model was used. Whilst acknowledging that our results depend in part on the null model used, our findings are consistent with (but don't test explicitly) previous work that has found species traits to provide valuable information in modelling species at risk of extinction due to habitat loss (e.g. Şekercioḡlu et al. 2002, Bregman et al. 2014). As such, we demonstrate that traitNODF can reveal interesting functional patterns that are masked when one focuses purely on species composition. Future

studies should expand our analyses to test for functional nestedness using different taxa, and

different types of study system (e.g. oceanic islands and food web networks).

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TABLES

Table 1. A glossary of terms used in this study.

Term (with abbreviation)	Description
A nestedness index based on overlap and decreasing fill (NODF)	NODF is a nestedness index based on the twin properties of standardized differences in presence–absence matrix row and column fills and paired overlap (i.e. the overlap of presences in two adjacent columns).
Fixed-fixed null model (FF)	A null model which creates a randomized presence–absence matrix that preserves row and column totals.
Functional nestedness	Used in this study to refer to the type of nestedness measured by traitNODF (below).
Nestedness (taxonomic)	A form of ordered composition of species assemblages involving a significant tendency for packing of the matrix into a series of proper subsets. In classic richness-ordered nestedness, the species composition of species-poor assemblages is a nested subset of the species composition of species-rich assemblages.
Permutation test null model (permRows)	A method for determining whether an observed index value is significantly different than expected by chance, whereby the rows of the species–site matrix are randomly re-ordered. The relevant index is calculated using this re-ordered matrix, and the process repeated *n* times to produce a distribution of null model values. permRows works best when then the original presence–absence matrix is organised according to an *a priori* hypothesis.
S.Fraction	The fraction of treeNODF that would be observed if all species were equally related.
topoNODF	The fraction of the treeNODF value due to the topology of the tree, i.e. the functional differences between species.
traitNODF	The variant of the treeNODF index which measures the nestedness of communities, taking into account how species are related in terms of their traits. The relationship between species in terms of their traits is determined by the construction of a dendrogram from the trait data.
treeNODF	An extension of the NODF index "in which the resemblance of descriptors, represented by a tree-like object, is taken into account. This can be carried out simply by replacing the incidence index (e.g. species richness of sites, frequency of occurrence of species) by the total branch length of descriptor variables" (Melo et al. 2014, p. 564). treeNODF can be generalised for use with any tree-like object, such as a phylogenetic tree, or a functional dendrogram constructed using species traits. treeNODF can be partitioned into two values: S.Fraction and topoNODF (see above).
Z-transformed score (Z)	A method for standardising observed index values, using the formula: $(Obs - \mu)/sd$. Where Obs is the observed nestedness value according to a given index, μ is the mean nestedness index value of the *n* null model permutations and sd is the standard deviation of the *n* values.

Table 2. traitNODF and standard NODF values (by rows) for the area ordered matrices of 18 bird-habitat island datasets. Prior to calculation of the nestedness indices, for each dataset the presence–absence matrix was ordered according to habitat island area, and the row (site) orders fixed. traitNODF (Trait) values were partitioned into their two components: S.Fraction (S.Frac.) and topoNODF(Topo). The standard NODF (Standard) index (by rows) was also calculated for each area-ordered matrix. For each of the four measures (traitNODF, S.Fraction, topoNODF, and standard NODF) significance was determine using a permutation test (1000 permutations), and a P value generated from the resultant index values. From these permutations, a Z-transformed score was also generated for traitNODF (Z). The proportion of traitNODF represented by topoNODF (Topo Prop.) is also presented. The dataset numbers correspond to those in Table S1 in Appendix 1 (see Table S1 for full dataset information).

No.	Trait (NODF)	Trait (P)	Trait (Z)	Topo (NODF)	Topo (P)	S.Frac. (NODF)	S.Frac. (P)	Standard (NODF)	Standard (P)	Topo Prop.
1	95.38	<0.01	4.25	4.08	<0.01	91.29	<0.01	90.03	<0.01	4.28
2	61.89	<0.01	4.65	8.03	<0.01	53.87	<0.01	53.89	<0.01	12.97
3	77.33	0.03	2.14	9.65	0.04	67.68	0.02	62.86	0.03	12.48
4	74.53	<0.01	7.48	16.25	<0.01	58.29	<0.01	58.28	<0.01	21.80
5	75.12	<0.01	3.40	8.85	<0.01	66.27	<0.01	66.58	<0.01	11.78
6	69.35	<0.01	3.44	5.54	<0.01	63.82	<0.01	60.98	<0.01	7.99
7	68.04	<0.01	3.44	4.20	0.02	63.83	<0.01	62.17	<0.01	6.17
8	88.04	<0.01	3.69	5.86	0.05	82.18	<0.01	81.90	<0.01	6.66
9	52.63	0.24	0.75	6.32	0.43	46.32	0.21	55.32	0.06	12.01
10	69.87	0.01	2.12	8.35	0.03	61.52	0.01	65.49	0.01	11.95
11	70.89	<0.01	5.43	12.29	<0.01	58.59	<0.01	61.00	<0.01	17.34
12	71.99	<0.01	6.36	11.27	<0.01	60.71	<0.01	61.68	<0.01	15.65
13	64.69	<0.01	4.92	9.40	<0.01	55.29	<0.01	54.26	<0.01	14.53
14	70.34	<0.01	5.33	7.60	<0.01	62.74	<0.01	64.25	<0.01	10.80
15	63.90	<0.01	2.96	5.70	<0.01	58.20	<0.01	55.35	<0.01	8.92
16	78.42	<0.01	5.72	6.65	<0.01	71.78	<0.01	72.75	<0.01	8.48
17	69.43	<0.01	3.73	24.57	<0.01	44.86	<0.01	42.72	<0.01	35.39
18	73.21	<0.01	2.85	10.8	<0.01	62.41	<0.01	50.79	0.03	14.75

Table 3. TraitNODF area results from the sensitivity analysis. For the sensitivity analysis we first calculated traitNODF for each dataset using all four trait indices. Prior to computation of treeNODF the presence–absence matrix was re-ordered according to island area (i.e. the tables presents the treeNODF values from the area-ordered matrices). We then removed a trait index, and re-ran the analyses. This trait index was then re-instated and the next trait index removed, and so on. Trait 1 = dispersal index, trait 2 = beak shape index, trait 3 = locomotive index, trait 4 = body size index. The dataset numbers correspond to those in Table S1 in Appendix 1. For each analysis the traitNODF value (tN) and associated P value are given for each dataset. The P value was generated using a permutation null model approach with 1000 simulations.

| No.	All		Trait Removed							
			Trait 1		Trait 2		Trait 3		Trait 4	
	tN	P	tN	P	tN	P	tN	P	tN	P
1	95.4	<0.01	96.2	<0.01	95.9	<0.01	93.7	<0.01	94.6	<0.01
2	61.9	<0.01	63.7	<0.01	63.0	<0.01	61.3	<0.01	62.9	<0.01
3	77.3	0.03	78.9	0.02	77.8	0.03	78.9	0.02	78.3	0.02
4	74.5	<0.01	76.5	<0.01	75.0	<0.01	77.8	<0.01	74.8	<0.01
5	75.1	<0.01	71.1	<0.01	79.2	<0.01	71.7	<0.01	72.8	<0.01
6	69.4	<0.01	70.7	<0.01	68.9	<0.01	70.5	<0.01	69.1	<0.01
7	68.0	<0.01	68.7	<0.01	68.8	<0.01	71.2	<0.01	71.2	<0.01
8	88.0	<0.01	87.7	<0.01	86.6	<0.01	90.1	<0.01	88.2	<0.01
9	52.6	0.24	61.4	0.11	62.0	0.11	52.9	0.21	53.8	0.24
10	69.9	0.01	71.0	0.02	77.3	0.01	67.9	0.04	71.2	0.01
11	70.9	<0.01	68.0	<0.01	70.4	<0.01	73.2	<0.01	69.0	<0.01
12	72.0	<0.01	73.6	<0.01	71.6	<0.01	72.6	<0.01	74.3	<0.01
13	64.7	<0.01	67.4	<0.01	65.1	<0.01	66.9	<0.01	63.7	<0.01
14	70.3	<0.01	71.4	<0.01	74.2	<0.01	70.7	<0.01	71.6	<0.01
15	63.9	<0.01	65.2	<0.01	68.1	<0.01	64.3	<0.01	60.0	0.01
16	78.4	<0.01	79.4	<0.01	77.9	<0.01	79.5	<0.01	79.3	<0.01
17	69.4	<0.01	71.6	<0.01	71.6	<0.01	68.4	<0.01	72.7	<0.01
18	73.2	<0.01	67.3	0.01	78.7	<0.01	72.9	<0.01	70.1	<0.01

FIGURES
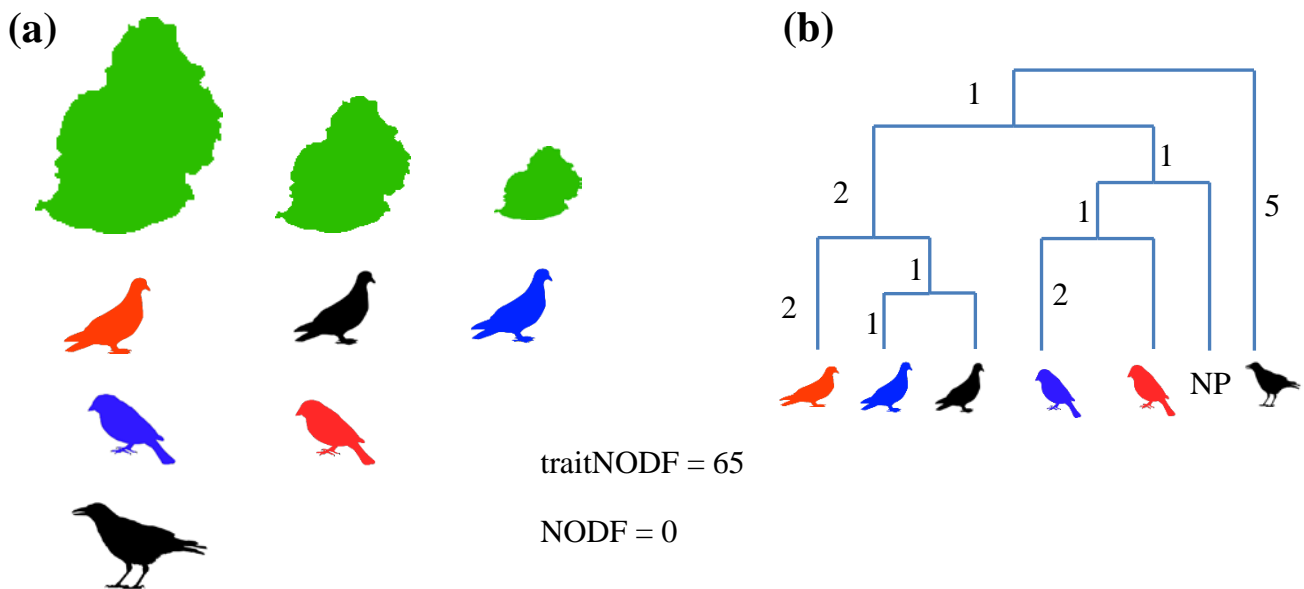
Figure 1. A hypothetical example illustrating the concept of functional nestedness, and in particular the situation where a set of islands can be functionally nested but not taxonomically nested. In (a), a number of different bird species are distributed across a set of islands of varying size (green shapes), such that the largest island has the most species. There are six different species of birds in the archipelago, each represented by a different colored symbol. The different colored versions of the same bird symbol indicate species which have only recently diverged, and are thus functionally similar. The exact relationship between these species in terms of their traits is given in the tree-object in (b). The numbers in (b) represent the branch lengths. It can be seen that the functionally similar species (i.e. the different colored versions of the same symbols) share most of their branch lengths, but not all. Using A and B it is then possible to calculate both traitNODF and the standard NODF index values, which are 65 and 0 respectively. Standard NODF is zero because this index only focuses on species incidences (i.e. not the functional similarity of species), and none of the species occur on more than one island (A). NP = a species not present in this archipelago. The bird outlines were provided by Susan Spear, courtesy of the Cornell Lab of Ornithology.
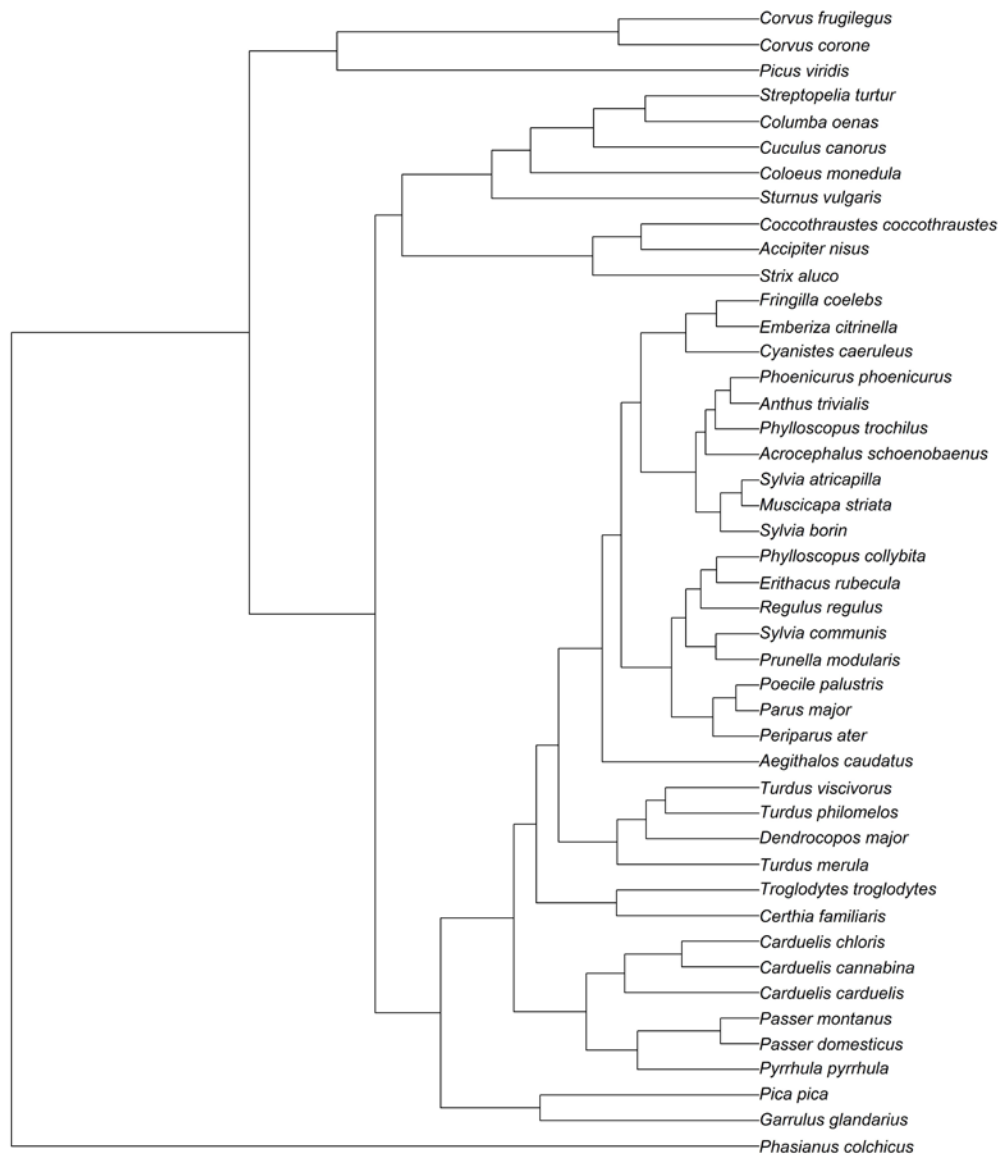
Figure 2. An exemplar dendrogram converted into a tree object, to be used with traitNODF. The data are from McCollin (1993; see Table S1 in Appendix 1). The dendrogram was constructed by first transforming the species–trait data into a distance matrix (Euclidean distance), and then using the UPGMA clustering algorithm. The resulting dendrogram was then converted into a tree object (see 'Methods').