BIODIVERSITY RESEARCH

Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets

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ABSTRACT

Aim The concept of nestedness is important in determining the relative contribution to overall system diversity of different habitat patches within a fragmented system. Much of the previous work on nestedness has focused on islands within oceans (islands *sensu stricto*). The largest analysis of habitat island systems to date found significant nestedness to be a near universal feature, but the methods used have since been criticized as inappropriate. Thus, there is a need for an updated, critical examination of the prevalence, underlying drivers and implications of nestedness in multiple habitat island systems.

Location Global.

Methods Here, we collate 97 datasets from published habitat island studies, comprising multiple taxa. We use the NODF metric (nestedness metric based on overlap and decreasing fill) to estimate nestedness and determine significance using the four-step proportional–proportional algorithm to simulate presences/absence matrices. We investigate the role of habitat island area in driving observed nestedness. We use linear modelling to examine the impact of dataset characteristics on the degree of nestedness and assess the conservation biogeographic implications of nestedness in relation to strategic conservation planning.

Results Significant nestedness occurred in only 9% of systems, whilst anti-nestedness (i.e. datasets less nested than expected by chance) occurred in 16% of systems. For the majority of datasets found to be significantly nested, we observed a relationship with fragment area, suggesting that structured extinctions may be important in determining the composition of certain habitat island communities. We found that the degree of nestedness in an archipelago is an important consideration for systematic conservation planning.

Main conclusions Significant nestedness is considerably less common in habitat islands than previously reported. Strategic guidance for conservation planning should proceed on a case by case basis, and previous conservation recommendations based on the assumption of significant nestedness in most fragmented landscapes may need to be re-evaluated.

Keywords

anti-nestedness, conservation biogeography, fragmentation, habitat islands, island biogeography, minimum set problem, nestedness, NODF, null communities, strategic conservation planning.

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Diversity and Distributions

INTRODUCTION

The destruction and fragmentation of natural habitats are generally regarded as the largest drivers of the current terrestrial extinction crisis (Sala *et al.*, 2000; Whittaker & Fernández-Palacios, 2007). The practice of deforestation and land use change generally produces fragments of original habitat (i.e. habitat islands) set in a matrix of modified habitat. To understand and mitigate the impacts of this habitat loss on biodiversity, many researchers have applied methods derived from the field of island biogeography (Diamond, 1975a; Whittaker & Fernández-Palacios, 2007; Ladle & Whittaker, 2011; Wang *et al.*, 2013).

The overall richness of a set of fragments in a disturbed landscape depends not only on the form of the island species–area relationship (ISAR; *sensu* Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2012) but also on the compositional overlap between fragments. Whilst the idea was discussed earlier (e.g. Darlington, 1957), nested structure was first formally defined in the 1980s as the situation in which depauperate island faunas constitute proper subsets of the species in richer islands (Patterson & Atmar, 1986). This definition was based on the idea of ordering a presence/absence matrix of species on islands in relation to island species richness. However, subsequent authors have used other variables (e.g. area) to order the presence/absence matrix (e.g. Kadmon, 1995; Wang *et al.*, 2010, 2013). Hence, nestedness may now be regarded simply as a form of ordered composition of species assemblages involving a significant tendency for packing of the matrix into a series of proper

Table 1 The different factors proposed to contribute towards nestedness or conversely to anti-nestedness in islands and habitat islands

Factors	Explanation/Mechanism	Examples and relevant references
Area	Nestedness is the result of differential area requirements of species. Species with smaller population sizes and larger area requirements have a greater risk of extinction, and thus, a predictable sequence of extinction occurs in relation to island size	Patterson & Atmar (1986), Wright *et al.* (1998) [both for nestedness]
	Anti-nestedness related to area might hypothetically relate to assembly rules mediated through competitive interactions	See below under Assembly rules
Isolation	Nestedness is due to predictable dispersal limitation, such that nestedness occurs due to differential immigration to islands	Kadmon (1995)
	In contrast, diminishing nestedness can result from increased interpatch distances that increase the likelihood of different islands sampling different species pools, and of islands being occupied by different subsets of the regional species pool (or pools) due to differences in, for example, climate and geology	
Habitat nestedness	Habitats exhibit a nested pattern, and there is a strong affinity between species and habitats, generating nestedness	Honnay *et al.* (1999)
Habitat quality	Nestedness is the result of differences in species' tolerance to habitat quality combined with variation in the quality of habitat amongst patches of the same habitat	Triantis & Bhagwat (2011)
Passive sampling	Nestedness structure can simply be the result of a sampling effect: if islands draw species from the regional pool and the pool follows a particular species abundance distribution (e.g. lognormal)	Cutler (1994), Whittaker & Fernández-Palacios (2007)
In situ speciation	Speciation occurring within individual islands will result in single island endemic species and thus will diminish the likelihood of nestedness and increase the likelihood of significant anti-nestedness in a set of islands. This is more likely to occur in oceanic islands than in habitat islands	Whittaker & Fernández-Palacios (2007)*
Different species pools	If different islands within an archipelago draw species from different source pools, the degree of nestedness in the archipelago will be reduced	Whittaker & Fernández-Palacios (2007)*
Human factors	Activities such as hunting may result in an ordered loss of particular species and thus increase nestedness in an archipelago, whereas species introductions may be island specific and thus decrease nestedness	Ladle & Whittaker (2011)*
Disturbance	Differences in disturbance regimes across an archipelago can increase or decrease nestedness	Fleishman & Murphy (1999), Wang *et al.* (2013)
Assembly rules	Diamond (1975b) hypothesized (controversially, as it turned out) that, when focusing on particular guilds, the occurrence of particular assembly rules in an archipelago can result in ordered patterns of community structure; for example, competitive interactions may generate differences in assemblage composition from island to island in a fashion not explicable simply by island area. In this vein, the occurrence of supertramp species (i.e. species that have a higher incidence on species poor islands) will potentially reduce nestedness in an archipelago	Diamond (1975b)

*Represents references that discuss the factor, but not in the context of nestedness or anti-nestedness.

Table 2 The nestedness metric employed in this study, along with the two null community simulation algorithms used to determine whether the degree of nestedness was significant for a given system

	Abbreviation	Description	References
Metric			
Nestedness metric based on overlap and decreasing fill	NODF	Based on the twin properties of standardized differences in row and column fills and paired overlap (i.e. the overlap of presences in two adjacent columns). Can quantify nestedness for the whole matrix and for rows and columns separately. Increasing NODF equates to increasing nestedness	Almeida-Neto *et al.* (2008)
Simulation algorithm			
Proportional–Proportional (PP)	PP	When a set of null matrices are simulated using the PP algorithm, the column and row totals do not all match the totals of the empirical matrix. Rather, the average totals for the set match the totals of the empirical matrix. The PP algorithm is more ecologically realistic in the context of habitat islands and small patches as stochastic temporal variation in island richness and species incidences (i.e. the biological equivalent of variations in marginal totals) is a frequently observed characteristic of such systems. Both matrix fill and the matrix dimensions are kept constant	Ulrich & Gotelli (2012)
R00	R00	Keeps the number of presences constant, but allows row and columns totals to vary in an equiprobable manner. This algorithm has been criticized for high prevalence of type I errors, and we use it in this study simply to enable comparisons with previous studies of nestedness in habitat islands	Wright *et al.* (1998)

subsets. A variety of mechanisms have been identified as potentially contributing to patterns of nestedness or anti-nestedness differing from random expectation (see Table 1). Anti-nestedness is a term that encompasses several patterns of community structure: high turnover (Leibold & Mikkelson, 2002), perfect checkerboards (Diamond, 1975b), the deviation from nestedness whereby within a set of sites species are only present in a single site (Poulin & Guégan, 2000), or simply to describe a dataset which is significantly less nested than expected by chance (e.g. Gotelli & Ulrich, 2012; Ulrich & Gotelli, 2012, 2013) (Table 1). This latter all-embracing definition is the definition of anti-nestedness used herein.

A number of nestedness metrics have been proposed (Atmar & Patterson, 1993; Wright *et al.*, 1998; Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009), and whilst debate is ongoing, the nestedness metric based on overlap and decreasing fill (NODF) (Almeida-Neto *et al.*, 2008; see Table 2) is generally considered one of the most appropriate nestedness metrics (Almeida-Neto *et al.*, 2008; Ulrich & Almeida-Neto, 2012; Wang *et al.*, 2013). NODF is based on the twin properties of standardized differences in row and column fills and the overlap of presences in two adjacent columns (Table 2). There has also been debate about how to determine the significance of observed departures from random expectations. The usual protocol has been to compare the observed nestedness metric value with a distribution of values generated using a null model, with much debate arising about the choice of algorithms (Wright *et al.*, 1998; Miklós & Podani,

2004; Ulrich & Gotelli, 2007, 2012, 2013; Gotelli & Ulrich, 2012; Strona & Fattorini, 2014). Early studies found significant nestedness to be near universal (e.g. Simberloff & Martin, 1991; Atmar & Patterson, 1993), and it was thus generally assumed that nestedness was a common pattern in oceanic island systems (Wright *et al.*, 1998; Whittaker & Fernández-Palacios, 2007), and by extension, habitat islands. However, the majority of these early studies used null model algorithms based on the concept of random fill (Table 2), an approach which has since been criticized as inappropriate due to an inflation of type I errors (Ulrich & Gotelli, 2007; Gotelli & Ulrich, 2012). Random fill algorithms place no constraints on column and row totals (i.e. site richness and species incidence values), and thus, marginal totals vary between simulated matrices in no systematic manner. More appropriate null algorithms include those which keep row and column totals fixed ('fixed-fixed' algorithms; herein FF; Miklós & Podani, 2004), and an algorithm which varies row and column totals, but for which the average totals for a set of random matrices match the observed row and column totals of the empirical matrix ('proportional-proportional' algorithm; herein PP; Ulrich & Gotelli, 2012). The application of more appropriate algorithms to numerous datasets has led workers to question whether significant nestedness is as common as once assumed (e.g. Ulrich & Gotelli, 2007, 2012, 2013; Almeida-Neto *et al.*, 2008).

The choice between PP and FF depends on the type of data being analysed (Ulrich & Gotelli, 2012). The PP algorithm

characterizes a biological situation in which island richness and species incidences vary between communities and through time (e.g. due to random extinction and colonization), but for which the average marginal totals match the empirical matrix. Random colonization and extinction through time may reasonably be assumed to be a characteristic of habitat island systems, which have more variable dynamics than more isolated continental shelf and oceanic islands (Ladle & Whittaker, 2011). Thus, for this study, we used the PP algorithm. Additionally, many habitat island datasets contain relatively small islands, and the PP model is preferred when the scale of analysis is small (Ulrich & Gotelli, 2012). Finally, metrics that use marginal totals for calculation, such as NODF, do not perform well with FF algorithms, which constrain totals (Ulrich & Gotelli, 2012, 2013).

Previous meta-analyses of insular nestedness (e.g. Wright *et al.*, 1998; Ulrich & Gotelli, 2007, 2013; Almeida-Neto *et al.*, 2008) have relied largely upon Atmar & Patterson's (1995) collection of presences/absence matrices. This collection contains a large number of oceanic and continental shelf island datasets, and not so many non-experimental habitat island systems. The only meta-analysis of nestedness patterns which included a relatively large proportion of habitat island datasets to date, by Watling & Donnelly (2006), found near universal (94%) significant nestedness in the datasets examined, although this study still included some oceanic island datasets. However, these authors used a metric (nestedness temperature) and a random fill algorithm, both of which have since been criticized as being prone to type I errors, that is a tendency to greatly overestimate the degree of nestedness (above). Thus, there is an exigent need to apply more appropriate methods to determine the prevalence of nestedness/anti-nestedness in a larger number of habitat island systems (cf. Sekercioglu & Sodhi, 2007).

The prevalence of nestedness (and of anti-nestedness) in habitat islands is important from both a fundamental ecological and conservation biogeographic perspective because it potentially informs protected area placement and design in fragmented and degraded landscapes (Cutler, 1994; Fischer & Lindenmayer, 2005a,b; Triantis & Bhagwat, 2011), contributing to the SLOSS ('single large or several small') protected areas debate (see Ovaskainen, 2002), and the minimum set problem (herein, MS). The MS problem is a key component of strategic conservation planning (Watson *et al.*, 2011) and describes the search for a solution to the problem of what is the smallest number of sites/protected areas within a region needed to ensure each species in the region is represented at least once (see Watson *et al.*, 2011). Nestedness is thus linked to the MS solution. For example, if a set of habitat islands in a dataset is perfectly nested according to island area, all the species in the islands can be represented at least once by conserving the largest habitat island. However, as perfect nestedness is extremely uncommon the situation is rarely so simple (Fischer & Lindenmayer, 2005a). The link between nestedness and MS has generally been examined only within individual habitat island datasets (e.g. Fischer &

Lindenmayer, 2005a), and a synthetic analysis of a large number of empirical habitat island datasets is warranted.

There is also a need to improve understanding of the mechanisms driving nestedness where it does occur in habitat island systems (Fischer & Lindenmayer, 2005b; Morrison, 2013) as, from a conservation perspective, the identification of pattern is of limited utility without an understanding of underlying process. Habitat island area has long been known to be one of the most important variables underpinning species composition patterns in fragmented landscapes (Watling & Donnelly, 2006; Whittaker & Fernández-Palacios, 2007), and thus, a rigorous analysis of the role of island area in driving nestedness patterns in habitat islands is needed.

Finally, there is a need to assess whether nestedness patterns in species of conservation interest (i.e. habitat specialists) are masked by the inclusion of generalist species. For example, habitat generalists have been found to depress the slope of the ISAR for birds in forest fragments (Matthews *et al.*, 2014a). This type of deconstruction approach, whereby the total species compliment is split into constituent subsets (e.g. based on habitat specialization), has been advocated as a useful method for conservation oriented research, but has only rarely been applied in nestedness studies (e.g. Blake, 1991; Fischer & Lindenmayer, 2005a).

Here, we undertake a synthetic analysis of 97 habitat island datasets with four aims. First, we quantify the prevalence of nestedness and anti-nestedness in habitat island systems (including several datasets not incorporated in past meta-analyses) using statistically appropriate methods. Second, we investigate the role of island area (Table 1) in observed nestedness patterns. Third, we examine whether habitat specialists and generalists exhibit different nestedness patterns. Finally, we investigate the conservation biogeographic implications of nestedness in our datasets by exploring the linkages between nestedness and the MS problem.

METHODS

Data collection

We searched for relevant habitat island studies and datasets using several abstracting databases between May 2010 and August 2013. Search keywords included combinations of '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.* (2014b), datasets were included based on the following criteria:
1. habitat islands constituted discrete patches of habitat surrounded by contrasting matrix habitat (we also included a small number of datasets consisting of protected areas in which the contrast between the islands and the intervening matrix was not so pronounced);
2. there were at least five habitat islands;

3. the area and species richness of each habitat island were given;

4. data did not overlap with those from any other study already accepted for analysis (data for different taxa within the same study system *were* accepted).

For this study, we considered a few island systems within an aquatic matrix (e.g. rain forest fragment systems created by the construction of a reservoir) as habitat islands, as the range of island areas and dominant assembly processes are more similar to habitat islands than oceanic islands. For each dataset, we recorded a variety of system characteristics: the habitat island type (i.e. forested or non-forested), the taxon studied, the latitude of the centre of the study extent (this was an estimate in certain cases as precise information was not always reported in the source papers), the range of species richness and the habitat island sizes (Table S1 in Appendix S1). A small number of datasets included sites which contained zero species. We removed these sites prior to analysis.

Quantifying nestedness

To quantify nestedness in our datasets, we used the NODF metric as it is widely regarded as the most statistically appropriate (Almeida-Neto *et al.*, 2008; Morrison, 2013; see Table 2). NODF was calculated using the VEGAN R package (Oksanen *et al.*, 2013). The NODF metric allows nestedness to be calculated independently for matrix rows (i.e. nestedness amongst sites) and matrix columns (i.e. nestedness amongst species incidences), as well as combined for the whole matrix (i.e. maximally packed nestedness; herein 'max matrix'). Following Morrison (2013), we calculated all three NODF values and compared the value for rows (sites in our matrices when using VEGAN) with that for columns for each dataset, taking the larger of the two values to indicate that a particular type of nestedness contributed more to the overall nestedness pattern.

Determining the significance of nestedness patterns

To determine whether the observed NODF values were significantly different from values expected for a randomly assembled community, we simulated 1000 binary presence/absence communities in each case, recording the metric values for each simulation. To simulate the null model communities, we used the aforementioned four-step PP algorithm (Ulrich & Gotelli, 2012; see Table 2). To enable a rough comparison between our results and those of Watling & Donnelly (2006), we re-ran our analyses using the R00 algorithm (Table 2). We used R00 simply because Watling & Donnelly used a random fill algorithm, and unless R00 is specifically mentioned, significant relationships reported below were determined using the PP algorithm. The PP communities were simulated using the 'NODF program' (Almeida-Neto & Ulrich, 2010), and we used the one-sided *P* value generated from the NODF program to determine significance (i.e. $P < 0.05$), which is based on the assumption of a normally distributed *Z*-transformed score (discussed below). It should be noted that in contrast to our VEGAN NODF analyses, the NODF program analyses matrices in which species are rows. The R00 communities were simulated using the VEGAN R package, and we used the default *P* value generated by VEGAN.

Does island area underpin observed nestedness in habitat islands?

For each dataset found to be significantly nested according to PP, we first calculated the maximum NODF value (row orders were not kept constant). We then ordered the matrices by decreasing area (i.e. largest island as the top row) and calculated NODF after holding the row orders constant. This enabled us to compare the row orders of the matrices ordered by area with the row orders of the max matrix to determine whether the two were significantly correlated using the standard Spearman's correlation test, and thus, whether area may be driving any observed nestedness pattern (cf. Schouten *et al.*, 2007; Wang *et al.*, 2010). In addition to analysing area-ordered nestedness, we originally planned to investigate whether island isolation, habitat nestedness and passive sampling (Table 1) were also driving any observed nestedness in four datasets sourced from our previous work (Matthews *et al.*, 2014a). However, these datasets were not found to be significantly nested according to the PP algorithm, and we were thus unable to proceed with this idea. Nonetheless, in preparation for this work, we developed and coded a model based on Coleman's (1981) passive sampling model in R as it was not available elsewhere. To aid the community, we present the code alongside example passive sampling plots (Fig. S1) in Appendix S2.

Habitat specialization

For a separate study (Matthews *et al.*, 2014a), we took 16 of the 97 datasets pertaining to birds in forest fragments within an agricultural matrix and classified the majority of bird species (over 1000 in total) as forest generalists or specialists using an extensive classification methodology (see Matthews *et al.*, 2014a). In this study, we used that classification to create new matrices of just generalists or specialists for each dataset. In some of these matrices, we had to remove further sites with zero species. We calculated the NODF *Z*-transformed score (hereafter simply *Z*-score) for the generalist and specialist matrices separately for the 16 datasets and compared the *Z*-scores, where $Z = \frac{\text{Obs} - \text{mu}}{\text{SD}}$, and where Obs is the observed nestedness value according to a given metric, mu is the mean nestedness metric value of the PP simulated communities (based on 1000 simulations), and SD is the standard deviation of the 1000 values. The *Z*-score was used in preference to the observed NODF value as the former represents a standardized effect size and can thus be used in comparative analysis (e.g. Ulrich & Gotelli, 2013).

Model selection and dataset characteristics

We fitted generalized linear models (GLMs) with Gaussian variance, using six dataset characteristics as the predictor

variables (number of islands, number of species, minimum island area, taxon studied, habitat island type, latitude). We took the absolute value of latitude. For the response variable, we used the Z-score. The assumptions of linear modelling (i.e. predictor normality, no outliers and minimal multicollinearity) were all tested, and number of species, number of islands and the minimum island area were each log-transformed (natural logarithms were used) prior to analysis. One dataset was removed as an outlier. The model with the lowest Akaike's Information Criterion corrected for sample size (AIC$_c$; Burnham & Anderson, 2002) was considered to be the best model. However, if any model was within Δ AIC$_c$ of < 2 of the best model, we considered that model as having a similar degree of support (Burnham & Anderson, 2002). We determined the weight of evidence for each variable by summing the Akaike weights of all the models in which a variable was included (cf. Brook et al., 2006). We fitted a complete set of models, considering all predictors, using the 'dredge' function in the MuMIn R package (Bartoń, 2012). Our GLMs revealed that the number of species in a dataset was a correlate (potentially a driver) of the Z-score (discussed below). Bivariate plotting indicated a possible boundary effect in the top-right quadrant, and thus, we conducted boundary tests using ECOSIM (Gotelli & Entsminger, 2001).

Minimum set problem

To examine the conservation implications of nestedness in terms of protected area network design (Triantis & Bhagwat,

2011), we developed an algorithm to solve a MS reserve location problem (Watson et al., 2011). That is, for each dataset, we determined the smallest number of habitat islands required in order for all species in the dataset to be represented at least once. For a given dataset, the algorithm worked by first selecting the islands that included singleton species (i.e. species only present on one island in the dataset), storing the island and species identities, and then removing these islands and species. From the remaining islands, the most species-rich island (if there were ties, the first site was taken) was then selected and the unique species names (i.e. species not stored in previous iterations) present on this island were stored. This island was then removed, and the process repeated with the next most species-rich island, and so on until all species in the dataset had been recorded at least once. This algorithm was then applied to each dataset individually. Finally, we adapted the MS algorithm to determine what proportion of a dataset's species was represented in just the largest island. Unless otherwise stated, analyses were conducted in R (R Development Core Team, 2013).

RESULTS

Over 1000 published articles were screened, of which 97 were deemed suitable for analysis (Fig. 1, Table S1 in Appendix S1). These 97 datasets comprised 69 vertebrate, 20 invertebrate and eight plant datasets; and 70 forested habitat islands and 27 non-forested habitat islands.
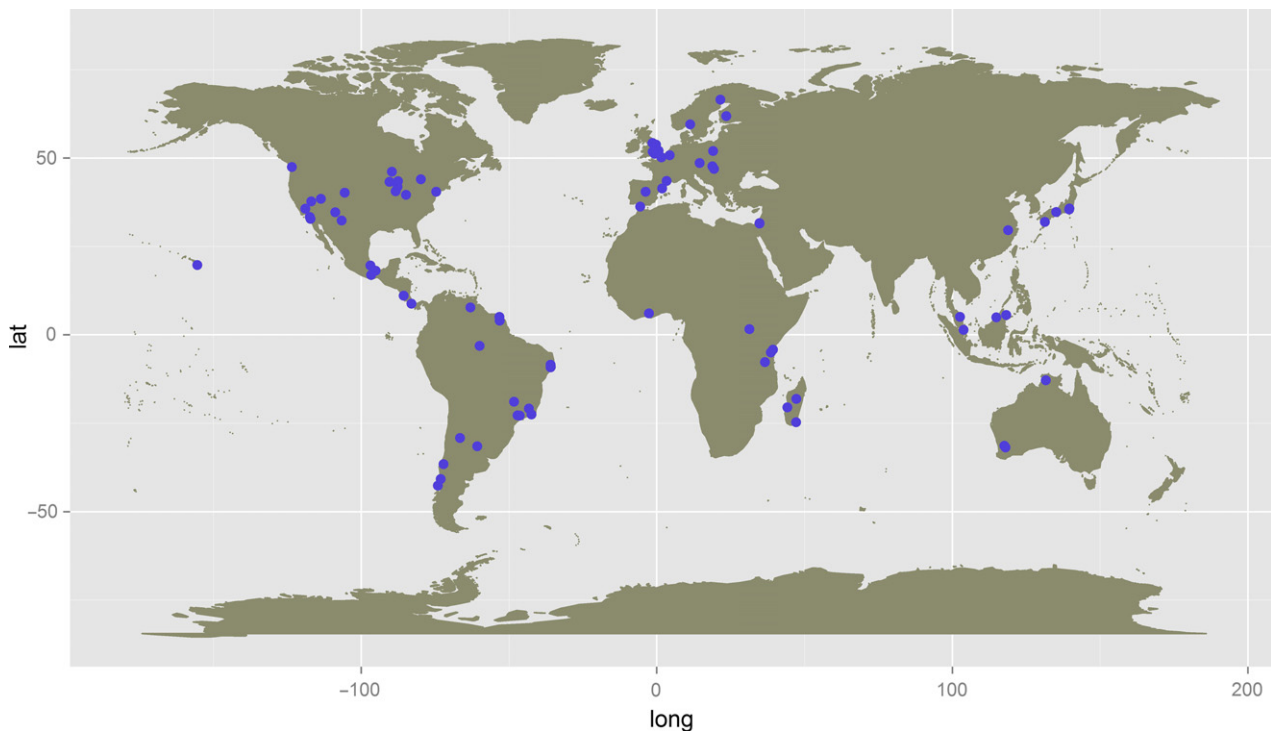

Figure 1 A map of the 97 datasets (blue dots) included in this study. Multiple datasets based in the same location are represented by a single blue dot. Where possible we took the coordinates from the centre of the study extent. However, in a small number of papers, only a general area was listed (e.g. East Central Illinois), and in these instances, we simply used the centre of this area.

Prevalence of nestedness in habitat islands

Considering all 97 habitat island datasets, the NODF values tended towards the nested end of the NODF spectrum, that is the values were generally closer to 100 than 0 (mean value = 64.6; range = 36–88). However, 62 (64%) datasets had negative *Z*-scores (Table S2 in Appendix S3). Based on the PP algorithm, it appears that significant nestedness and anti-nestedness are relatively uncommon in habitat islands. Nine datasets (9%) were found to be significantly nested, and 16 datasets (16%) were significantly antinested (an example of each is provided in Fig. 2); the remaining 72 datasets (74%) had NODF values not significantly different from random. For eight of the nine significantly nested datasets, the NODF value was higher when calculated for matrix rows (i.e. by sites) than for matrix columns (Table S3 in Appendix S3). Considering all datasets, the NODF value was higher when calculated for matrix rows for 83 (86%) datasets (Table S3).

When R00 was used to simulate presence/absence matrices, significant nestedness was almost a universal finding, that is 96 datasets were deemed to be significantly nested (Table S2).

Mechanisms and dataset characteristics

When considering all 97 datasets, the row order of the area-ordered matrix was significantly correlated with that of the max matrix for 53 datasets (55%; Table S4 in Appendix S3). When considering the nine significantly nested datasets, the row order of the area-ordered matrix was significantly correlated with that of the max matrix for eight datasets (89%; mean Spearman's ρ = 0.87; mean Rho for all nine datasets = 0.81; Table 3).

Habitat specialization

Within the analysis of the 16 datasets for which bird species were divided into habitat specialists and generalists,

specialists had a greater *Z*-score for 11 datasets (69%), but specialist *Z*-scores were negative in six cases, indicating anti-nestedness in a number of datasets (Table S5 in Appendix S3). Moreover, the difference between generalist and specialist subset *Z*-scores was marginally significant according to Wilcoxon's rank test (W = 76, P = 0.05).

Model selection results

When NODF was used to calculate the *Z*-score across all datasets, the best model contained only the number of species (Table 4). Number of species had a relatively high weight of evidence value. As an increasing *Z*-score implies increasing nestedness according to NODF, this result indicates that datasets with more species are less nested. However, the best model had an adjusted R^2 value of only 0.19. Whilst a bivariate plot indicated a possible boundary effect in the upper right quadrant, there were no fewer data points in the upper right quadrant than expected by chance according to a boundary test when the sum of squares criterion was used (P = 0.17; see Fig. S2 in Appendix S3), although when the number of points criterion was used the result was marginally significant (P = 0.05). Latitude and island type were included in models within < 2 ΔAIC_c of the best model, but had relatively low weight of evidence values. Taxon was never in the best models and had a low weight of evidence value (Table 4).

Minimum set results

The mean proportion (Prop) of islands required to represent each species at least once (the minimum set: MS) was 40.8% (results for individual datasets are presented in Table S2). Six datasets (6%) required only a single island; for four of these cases, the island in question was the largest island. In contrast, six datasets (6%) needed all islands to represent
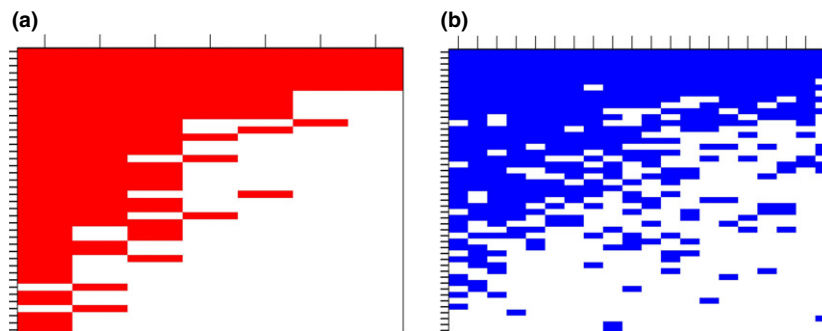

Figure 2 Incidence plots for two habitat island datasets: (a) a significantly nested dataset and (b) a significantly antinested dataset. The nested metric employed was NODF (Almeida-Neto *et al.*, 2008) using the maximally packed matrix. The *x*-axis represents the individual habitat islands, and the *y*-axis represents individual species. The coloured bars thus indicate that a given species was sampled in a given site, whilst a blank bar indicates that a species was not found in a site. Significance was determined in each case by comparing the observed NODF statistic with a distribution of values generated by 1000 null communities (using the PP null model). (a) A dataset of frogs in forest fragments, Brazil (number of species = 40; number of islands = 7; NODF value = 80; *Z*-score = 1.74; Zimmerman & Bierregaard, 1986) and (b) a dataset of birds in forest fragments, UK (number of species = 48; number of islands = 20; NODF value = 70; *Z*-score = −2.11; Ford, 1987).

Table 3 The correlation of the row orders of nine habitat island presence/absence matrices ordered according to decreasing area (Area NODF), with the row orders of the maximally packed NODF matrices (Max NODF). Correlation was determined using Spearman's correlation, and the correlation coefficient is presented with the P values. These nine datasets are those that were found to be significantly nested, out of the 97 habitat island datasets examined. The max NODF value and Area NODF value given in the table are the NODF values for matrix rows (i.e. nestedness amongst sites). The significance of the observed NODF value was determined by comparing the observed value with a distribution of values obtained for 1000 simulated null communities, using the PP null model. The correlation results for all 97 datasets are presented in Table S4 in Appendix S4. The dataset numbers correspond to the dataset information in Table S1 in Appendix S2

Dataset	Max NODF	Area NODF	Spearman's ρ	P
4.	91.55	90.03	0.99	< 0.01
25.	84.18	79.71	0.87	< 0.01
30.	85.12	79.23	0.95	< 0.01
41.	73.84	64.81	0.38	0.16
52.	87.81	85.43	0.98	< 0.01
75.	89.68	88.01	0.99	< 0.01
83.	80.60	72.89	0.91	< 0.01
84.	75.26	58.52	0.40	0.04
97.	95.82	82.90	0.89	0.01

every species. As expected, the MS results had strong concordance with the nestedness results. The NODF value was significantly negatively correlated with Prop (-0.45, $P \le 0.001$; Fig. 3a). All datasets which required more than 40% of sites to represent all species ($N = 34$; 35%) had a negative Z-score, indicating anti-nestedness. The mean Prop for significantly antinested datasets was 53.1%, whilst for significantly nested datasets the mean Prop was only 17.7%. The mean proportion of species represented when only the largest patch in a dataset was considered was 63.8% (range = 21.0–100%; Table S2).

A Kruskal–Wallis test indicated that Prop significantly differed between taxa (16.2, $P \le 0.01$), and pairwise Wilcoxon's tests indicated that this difference was driven by vertebrates (Fig. 3b). Vertebrates had a significantly lower Prop than both plants ($W = 456.5$, $P \le 0.01$) and invertebrates ($W = 377.5$, $P \le 0.01$). Prop did not significantly differ between invertebrates and plants ($W = 98.5$, $P = 0.36$).

DISCUSSION

We have undertaken the first synthetic analysis of nestedness patterns in a large number of habitat island datasets using currently recommended statistical methods. Quantifying nestedness in habitat islands is important as it provides information on how species are distributed in patchy landscapes: information that can potentially be used to develop conservation strategies (Triantis & Bhagwat, 2011). Using the four-step PP null model algorithm (Ulrich & Gotelli, 2012), we found that significant nestedness was only apparent in 9% of datasets, whilst 16% of datasets were significantly antinested. Notwithstanding the fact that most datasets were not significantly nested, we have also demonstrated that absolute habitat island area appears to be an important environmental factor correlating with observed nestedness patterns.

Nestedness prevalence and mechanisms

Our finding that nestedness is very much the exception rather than the rule in habitat island datasets contradicts a previous analysis incorporating multiple habitat island datasets (Watling & Donnelly, 2006) but is consistent with recent studies that have incorporated habitat island datasets alongside a larger number of oceanic, continental shelf and simulated island datasets (e.g. Ulrich & Gotelli, 2007, 2013). The core reason for the difference in our findings, which are based on NODF and the PP algorithm, and those of Watling & Donnelly, is their use of the nestedness
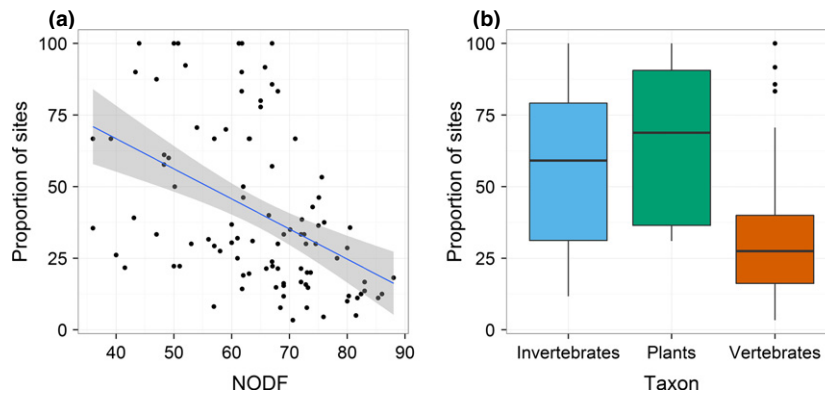
Table 4 Parameter estimates of a set of parsimonious generalized linear models with Gaussian variance, for 96 habitat island datasets. The best model (i.e. lowest AIC$_c$) and all models within approximately ΔAIC$_c$ of < 2 of the best model are given. The predictor variables included the area of the smallest island (Min. area), the number of islands (No. Frag.), the number of species (No. Sp.), the taxon (Taxon), the habitat island type (i.e. forest or non-forest; Hab. type) and latitude of the study area (Lat.). The response variable was the Z-score (calculated using NODF) for each dataset, calculated by simulating 1000 null community matrices using the PP algorithm. The number of model parameters (Par.), the delta AIC$_c$ (ΔAIC$_c$) and the Akaike weights (wAIC$_c$) are also presented. + indicates a significant effect of taxon or habitat type. Following Brook et al. (2006) the weight of evidence of each variable, calculated by summing the Akaike weights of all the models in which a variable was included, is also given. NI (not included) indicates a variable was not included in a model

Model Rank	Hab. type	Min. area	No. Frag.	No. Sp.	Taxon	Lat.	ΔAIC$_c$	wAIC$_c$	Par.
1	NI	NI	NI	−0.62	NI	NI	0	0.20	1
2	NI	NI	0.17	−0.63	NI	NI	1.27	0.11	2
3	+	NI	NI	−0.61	NI	NI	1.46	0.10	2
4	NI	NI	NI	−0.63	NI	< −0.01	1.85	0.08	2
Weight of evidence	0.33	0.25	0.37	1.00	0.09	0.32			

Figure 3 The relationship between (a) the smallest proportion of sites required to represent all species in a dataset (i.e. the solution to the minimum set problem), and the NODF value (maximally packed matrix), and (b) the variation in this proportion across taxa, for 97 habitat island datasets. To determine the solution to the minimum set problem, we first ran an algorithm to determine the smallest number of habitat islands required to include all the species in a dataset. This number was then represented as a proportion of the total number of sites in the dataset. In (a), the blue line represents the fit of a standard linear model, and the grey shading represents the 95% confidence interval around this line. The box plots display the median (thick black line), the first and third quartiles (thin black box). The whiskers extend from the hinge to the highest value that is within 1.5 multiplied by the interquartile range of the hinge. Outliers are indicated by black circles.

temperature calculator which used a random fill algorithm that has since been shown to be extremely prone to type I errors (see also Ulrich & Gotelli,, 2007; Gotelli & Ulrich, 2012). This is clearly shown by the near universal significant nestedness indicated when we ran the R00 algorithm, for purely comparative purposes, on our 97 datasets (see Results and Table S2). Additionally, Watling & Donnelly used the nestedness temperature index: although re-running our analyses using nestedness temperature generates very similar results. Given that we found significant nestedness in only 9% of our datasets using the preferred PP algorithm, it follows that conservation managers should not assume significant nestedness *a priori* in fragmented systems.

The importance of island area in driving observed nestedness

Understanding the mechanisms and variables underpinning nested structure is arguably more important than simply quantifying nestedness, but these have been much less well studied, especially in habitat islands, as the relevant information cannot simply be gleaned from the observed nestedness values (Morrison, 2013). Whether considering either the significantly nested datasets, or all datasets, area seems to be an important environmental factor correlating with the observed extent of nestedness in our datasets. This is conventionally taken as evidence for selective extinction being an important underlying mechanism (Table 1; see also Schouten *et al.*, 2007). This finding implies that extinction is a fairly deterministic process in these datasets, with the species possessing large area requirements being lost first, although this effect is far from being overwhelming. In regard to datasets that had a positive *Z*-score but for which the area-ordered matrix was not correlated with the

max matrix, it is likely that there are other important variables, such as disturbance and habitat heterogeneity, for which we lacked data (Fleishman & Murphy, 1999; Wang *et al.*, 2013; Table 1).

The potential significance of habitat island area was further indicated by the finding that the observed row-ordered NODF value was generally larger than the column-ordered value. This signifies that nestedness between sites is more important to the overall nestedness pattern than nestedness amongst species (Morrison, 2013). That being said, another potential explanation for larger row-ordered NODF values compared to column-ordered values relates to the fact that datasets generally contain a small number of singleton species (i.e. species present in only one site). By definition, there is no nestedness amongst singleton species. In contrast, very few datasets contain sites with only a single species. Thus, this finding may be due to the differences in the level of ties between species incidences (i.e. column totals) and the level of ties between species richness values (i.e. row totals).

Explanations for anti-nestedness (i.e. datasets less nested than expected by chance) require further exploration, reflecting that this phenomenon can reflect diverse patterns and causes (see Table 1; Ulrich & Gotelli, 2013). We did not examine the effect of area on significantly antinested datasets as a separate group (although the results are presented in our analysis of an area effect in all datasets; Table S4); for this very reason, that is, because of the nebulous nature of anti-nestedness, we were unsure what such an analysis would achieve. Furthermore, multiple mechanisms, many of which require considerable data to examine (Table 1), may well be acting in tandem, with the effect of diluting any nestedness patterns (Ulrich & Gotelli, 2013). This dilution may partly explain the high number of

datasets with non-significant NODF values. Additional possibilities underpinning the non-significant results are (1) the varying responses of different types of species, namely generalists and specialists, to landscape composition and (2) the small number of islands in many datasets. On the whole, generalists were found to be less nested than specialists (discussed below), and thus, datasets with a high proportion of generalist species may tend towards anti-nestedness. Other ecological types of species, especially transient species and those species that benefit from fragmentation (Blake, 1991; Fischer & Lindenmayer, 2005a), may also contribute towards anti-nestedness patterns.

The relationship between the Z-score and the number of species

The number of species was included in all GLMs with an $\Delta AIC_c < 2$, and the variable had a high weight of evidence value. However, further analysis revealed that the R^2 values of these models were low (roughly 0.20), and a boundary test revealed that there were not fewer data points in the upper right quadrant than expected by chance. Furthermore, in previous studies based on extensive simulations, the Z-score derived using both a different type of proportional null model and fixed-fixed null model has been found to be independent of matrix size (Almeida-Neto et al., 2008; Strona & Fattorini, 2014). It thus appears unlikely that the Z-scores calculated in the present study are particularly biased in regard to the number of matrix columns.

Are habitat specialists more nested than generalists?

Several studies have found and argued that, as habitat specialists are generally more affected than generalists by habitat loss, specialists should exhibit a more nested structure (e.g. Blake, 1991; Fischer & Lindenmayer, 2005a; Schouten et al., 2007; Sekercioglu & Sodhi, 2007). For example, Blake (1991) observed that in Illinois woodlots forest core bird species were more nested than edge bird species. Our results are consistent with this assertion, although not entirely conclusively. Whilst specialists were more nested than generalists in 69% of cases, the specialists' subsets had a negative Z-score in 38% of datasets, indicating a tendency towards anti-nestedness. Based on these findings, further analyses of subsets of species may prove enlightening. Deconstructing species into subsets prior to data analysis has revealed interesting patterns of conservation relevance in ISARs (Matthews et al., 2014a), and there is a need for a more comprehensive analysis of the impacts of, for example, generalist, migrant and transient species on nestedness patterns, particularly in fragmented landscapes.

Conservation implications

The mechanisms and environmental factors responsible for non-random assembly/disassembly patterns of (some) habitat island biotas remain poorly understood. According to our data, island area is an important environmental factor. This finding in isolation suggests that protecting few large habitat islands in a given region should be effective in conserving the majority of species in a region. However, when using the PP algorithm significant nestedness was uncommon, the area-ordered matrix was not always significantly correlated with the max matrix (e.g. Table 3), and moreover, we never observed perfect nestedness according to any metric (see also Fischer & Lindenmayer, 2005a). This point is further evidenced by the fact that our minimum set (MS) analyses showed that generally a high proportion of sites (mean = 40.8%) was required to represent all species in a dataset at least once. Intuitively, one would expect the MS problem to be linked in some way with nestedness (Fischer & Lindenmayer, 2005a; Triantis & Bhagwat, 2011), and this is indeed the case in our habitat island datasets.

The goal of seeking representation of all elements (species, ecosystems, etc.) is a fundamental principle in strategic conservation planning (Watson et al., 2011), and the link between nestedness and the MS solution has been argued elsewhere, particularly in the context of the SLOSS debate (e.g. Whittaker & Fernández-Palacios, 2007). However, to our knowledge, it has not been empirically tested using a large number of habitat island datasets. In the context of SLOSS, the 'single large' argument is based on the premise that a single large reserve is more effective than several small reserves of equivalent total area (Ovaskainen, 2002). Under a scenario of perfect, or at least high, nestedness-by-area, the largest island should include all of the species in the landscape. It is rarely so simple in practice. For example, in a study of forest birds in a fragmented landscape in Australia, Fischer & Lindenmayer (2005a) reported a pattern of habitat islands being significantly nested by island area. However, the islands were not perfectly nested and over a quarter of the study area was necessary to represent 80% of species classified as forest sensitive (Fischer & Lindenmayer, 2005a). In our analyses, the largest island contained all species in only four datasets, whilst on average the largest patch contained only 63.8% of the species in a dataset. These findings highlight that, in almost all instances, multiple islands of differing size are required to represent all species. In sum, we are unable to recommend a one-size-fits-all guideline for protected area design based on empirical patterns of nestedness.

The low number of plant ($n = 8$) and invertebrate ($n = 20$) datasets relative to vertebrate datasets ($n = 69$) makes it problematic to discern a simple explanation for the difference in Prop (i.e. the mean proportion of islands required to represent each species at least once) between taxa (Fig. 3b), and further research is needed as this observation may have important conservation implications. It is important to note that our MS analyses are necessarily a simplification of the ecological reality as we only have static 'snap shots' of species composition. Whilst representation is a key

component of strategic conservation planning, persistence is also important; the presence of a species in a site does not necessarily mean the species will survive at the site in the long run (Whittaker & Fernández-Palacios, 2007). Furthermore, our analyses assume that the habitat islands included in a dataset are the only islands in the landscape available for conservation: an unlikely situation in most cases. However, despite these simplifications, the analyses provide a useful first approximation of the issues involved in assuming a specific protected area plan *a priori* (see also Fischer & Lindenmayer, 2005a).

Most nestedness meta-analyses have incorporated large numbers of oceanic and continental shelf island datasets. As habitat islands differ from such 'true' islands in many ways (Whittaker & Fernández-Palacios, 2007), it is important to look for general patterns within habitat island datasets when attempting to formulate conservation guidance. Using NODF and the PP algorithm, we found that only 9% of datasets were significantly nested. Hence, previous conservation recommendations based on the assumption of significant nestedness in most fragmented landscapes may need to be re-evaluated. Thus, we conclude that strategic guidance for conservation planning in fragmented landscapes should proceed on a case by case basis, rather than presuming any degree of nested structure *a priori*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Dataset information.

Appendix S2 Passive sampling R code.

Appendix S3 Supplementary results.

Table S1 Datasets characteristics for the 97 habitat island datasets used in the analyses, including the taxon, range of island area and range of island richness.

Table S2 The NODF values for the maximally packed matrix, null community simulation results, and the results of our minimum set problem analyses, for 97 habitat island datasets.

Table S3 Values for the nestedness metric based on overlap and decreasing fill (NODF), for 97 habitat island datasets.

Table S4 The correlation of the row orders of 97 habitat island presence/absence matrices ordered according to decreasing island area, with the row orders of the maximally packed NODF matrices.

Table S5 The NODF *Z*-scores (of the maximally packed matrix) calculated separately for habitat generalist and habitat specialist bird species subsets, for 16 forest fragment datasets.

Figure S1 Diagnostic plots of Coleman *et al.*'s (1982) random placement model.

Figure S2 The relationship between the number of species in a dataset (log transformed) and the NODF *Z*-score for the maximally packed matrix, for 97 habitat island datasets.

BIOSKETCH

Tom Matthews is a doctoral student at the University of Oxford. He is interested in the study of macroecological patterns in habitat islands and the application of island theory to fragmented landscapes. His recent work has focused on species abundance distributions in fragmented landscapes and the use of piecewise regression to detect thresholds in the species–area relationship.

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