



Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns

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ABSTRACT

A fundamental goal of ecology is to understand whether ecological communities are structured according to general assembly rules or are essentially dictated by random processes. In the context of fragmentation, understanding assembly patterns and their mechanistic basis also has important implications for conservation. Using distribution data of 20 bat species collected on 11 islands in Gatún Lake, Panama, we tested for non-randomness in presence–absence matrices with respect to nestedness and negative species co-occurrence. We examined the causal basis for the observed patterns and conducted separate analyses for the entire assemblage and for various species submatrices reflecting differences in species' trophic position and mobility. Furthermore, we explored the influence of weighting factors (area, isolation, abundance) on co-occurrence analyses. Unweighted analyses revealed a significant negative co-occurrence pattern for the entire assemblage and for phytophagous bats alone. Weighting analyses by isolation retained a pattern of species segregation for the whole assemblage but nullified the non-random structure for phytophagous bats and suggested negative associations for animalivores and species with low mobility. Area- and abundance-weighted analyses always indicated random structuring. Bat distributions followed a nested subset structure across islands, regardless of whether all species or different submatrices were analysed. Nestedness was in all cases unrelated to island area but weakly correlated with island isolation for incidence matrices of all species, phytophagous bats, and mobile species. Overall, evidence for negative interspecific interactions indicative of competitive effects was weak, corroborating previous studies based on ecomorphological analyses. Our findings indicate that bat assemblages on our study islands are most strongly shaped by isolation effects and species' differential movement and colonization ability. From a conservation viewpoint this suggests that even in systems with high fragment–matrix contrast, a purely area-based approach may be inadequate, and structural and functional connectivity among patches are important to consider in reserve planning.

Keywords

Assembly rules, Chiroptera, habitat fragmentation, land-bridge islands, nestedness, species co-occurrence.

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INTRODUCTION

The question whether communities are shaped predominantly by biotic interactions such as competition or are randomly assembled from species pools has been pondered by ecologists for decades (Weiher & Keddy, 1999). Ever since Diamond (1975) in his seminal paper on assembly of insular communities posited that faunal assemblages are competitively structured,

the identification and explanation of non-random patterns in assemblage composition have been a central theme in community ecology. Moreover, knowledge of patterns and causes of species distribution in insular biotas has been central in providing guidelines to biodiversity conservation, e.g. concerning reserve design (Whittaker, 1998). Diamond's controversial assembly rules model has been the focus of a long-standing and intense debate centred mainly around theoretical and statistical aspects

(Connor & Simberloff, 1979; Strong *et al.*, 1984). In a recent meta-analysis, Gotelli & McCabe (2002) demonstrated for a variety of taxa that assemblages with fewer co-occurring species than expected by chance are common, in line with Diamond's proposition that competitive interactions play a generally important role in structuring many species assemblages. Most recently, tests for species co-occurrence patterns have also been extended to include neutral models (Ulrich, 2004; Bell, 2005; Gotelli & McGill, 2006), which posit ecological equivalence among species and argue for random processes shaping local and regional community structure (Hubbell, 2001). Apart from Diamond's assembly rules a range of other patterns of community non-randomness has been suggested and examined, including Fox's favoured states model (Fox & Brown, 1993), core-satellite organization (Hanski, 1982; Ulrich & Zalewski, 2006), and nested subsets of species (Patterson & Atmar, 1986; Wright *et al.*, 1998).

Nestedness is a pattern frequently reported for faunal assemblages in natural or anthropogenically fragmented systems and has been documented for a broad range of taxa (cf. review by Wright *et al.*, 1998). Assemblages exhibit a nested distributional pattern when the species present at species-poor sites constitute subsets of those from progressively species-rich sites, rather than a random draw of those present in the entire regional species pool (Patterson & Atmar, 1986). The concept of nestedness has been useful in interpreting community structure and function across a range of ecological studies, e.g. in situations where species assemblages are characterized by hierarchical niche relationships among species (Patterson & Brown, 1991) or, more recently, in studies of mutualistic species interactions (e.g. Bascompte *et al.*, 2003). Nested subset theory has also received considerable attention regarding its relevance to biodiversity management and conservation, concerning its potential to identify fragmentation-sensitive species, but particularly as it relates to the SLOSS debate (single large or several small) regarding reserve design where its utility, however, appears to be limited (Boecklen, 1997; Fischer & Lindenmayer, 2005; Martínez-Morales, 2005).

In contrast to Diamond's assembly rules model, nested subset theory does not invoke competition as the structuring mechanism underlying community assembly. Instead, nested patterns in species assemblages are thought to arise as a result of species' differential colonization or extinction, nested habitat structure, passive sampling, as well as distance or area effects (Wright *et al.*, 1998). Nestedness appears to be particularly characteristic of extinction-dominated systems such as habitat fragments or land-bridge islands undergoing faunal relaxation, where species loss has been observed to occur in a predictable order based on species' differential extinction vulnerability (Patterson & Atmar, 1986; Wright *et al.*, 1998).

In this study, we used null model analyses (Gotelli & Graves, 1996) to test for patterns of species co-occurrence and nestedness in presence-absence matrices of phyllostomid bats sampled as part of a comprehensive project investigating fragmentation effects on Neotropical bats within a landscape of small land-bridge islands in Gatún Lake, Panama (Meyer & Kalko, in press). Compared to other taxa, few studies have

assessed bat assemblages with respect to species co-occurrence patterns and nested subset structure, and analyses to date have largely been restricted to bats on oceanic islands (Connor & Simberloff, 1979; Wright *et al.*, 1998; Gotelli & McCabe, 2002; Watling & Donnelly, 2006). Moreover, to our knowledge no study has so far investigated patterns of nestedness and species associations for bats in the context of habitat fragmentation. In view of their high functional significance in Neotropical ecosystems as pollinators, seed dispersers, and arthropod predators (Kalko, 1998; Patterson *et al.*, 2003), it is important to evaluate whether and how fragmentation affects the structure of phyllostomid bat assemblages.

We explored possible mechanisms underlying the observed distribution patterns of bats on islands and examined the use of a series of weighting factors (island area, island isolation, species abundance) on the outcome of co-occurrence analyses. In addition to conducting analyses for the whole species assemblage, we were particularly interested in investigating differences in the outcome of co-occurrence and nestedness analyses for different subsets of species. In the case of analyses testing for negative species associations, this was predicated on the assumption that non-random co-occurrence patterns are less likely to be detected at the assemblage level, i.e. in datasets that include a large number of ecologically disparate species that obviously do not compete for resources. In contrast, at the level of ensembles (Fauth *et al.*, 1996) interactive effects among species can be expected to be stronger, a point that has recently been demonstrated for phyllostomid bats based on ecomorphological analyses (Moreno *et al.*, 2006). We therefore contrasted incidence matrices of phytophagous and animalivorous phyllostomid bats in our analyses. It is conceivable that in the context of habitat fragmentation, alterations in resources (food, roost sites) as a result of fragmentation may disrupt effects of species ecological interactions even at the ensemble level, making the detection of deterministic structure less likely.

Dispersal or mobility is another factor that may shape patterns of species co-occurrence and nestedness (Cutler, 1991; Zalewski & Ulrich, 2006), but so far has rarely been explicitly considered in bat studies (but see Arita, 1997). If species differ in their ability to colonize new patches, then they will be differentially affected by fragmentation, suggesting that differential mobility should influence patterns of species distribution. In addition to conducting separate analyses for phytophagous and animalivorous bats, we therefore divided species based on differences in mobility (high vs. low mobility species). High species mobility can be expected to randomize faunal composition and should hence lead to random co-occurrence patterns. In contrast, we predicted an underdispersed pattern of species co-occurrence, i.e. negative species associations for incidence matrices of less vagile species (cf. Zalewski & Ulrich, 2006).

Like many patterns and processes in ecology, the outcome of nestedness and species co-occurrence analyses may be contingent on spatial scale (Wright *et al.*, 1998; Jenkins, 2006), and this scale dependency has been explicitly addressed in various studies (e.g. Patterson & Brown, 1991; Gotelli & Ellison, 2002; Fischer & Lindenmayer, 2005). Here our analyses focus on the spatial scale of

Table 1 Characteristics of the study islands in Gatún Lake, Panama. Island isolation is given as distance to the nearest mainland. For each island the number of phyllostomid bat species in each of the four species submatrices used in the co-occurrence and nestedness analyses is given.

ID no.	Island	Area (ha)	Isolation (km)	Number of species			
				Phytophagous	Animalivorous	High mobility	Low mobility
1	Guava	2.5	1.93	5	1	3	3
2	Chicha	2.8	0.51	10	0	4	6
3	Tres Almendras	3.4	0.15	12	3	5	10
4	Piña*	4.4	0.02	11	3	5	9
5	Mona Grita	5.9	0.25	9	3	7	5
6	Guanábano	7.2	2.25	4	1	3	2
7	Pato Horqueta	11.4	3.40	10	3	5	8
8	Cacao	12.8	0.16	11	1	5	7
9	Guacha	16.3	1.42	6	1	3	4
10	Trinidad	17.3	2.02	6	1	3	4
11	León	50	1.55	11	2	4	9

*Island no. 8 in Adler & Seamon (1991).

individual islands. Consequently, inferences based on our findings should be viewed as being most relevant at this local scale and may not necessarily apply to the same degree at larger spatial scales.

METHODS

Study area

Lake Gatún is a large artificial reservoir, which was created in 1914 following the damming of the Chagres River as part of the construction of the Panama Canal. Lake formation isolated numerous former hilltops, resulting in a large number of forested islands ranging in size from < 1 ha to the 1560 ha Barro Colorado Island (BCI) (Adler & Seamon, 1991). We surveyed the bat fauna of a total of 11 islands that ranged in size from 2.5 to 50 ha and that were located between 0.02 and 3.4 km from the mainland (Table 1). Islands in the lake are covered with semideciduous lowland tropical moist forest (Holdridge, 1967), which is typically shorter in stature and less diverse in tree species composition than on the adjacent mainland (Leigh *et al.*, 1993). The climate is highly seasonal with a long rainy season punctuated by a severe 4-month dry season (Windsor, 1990).

Bat sampling

On each island, bats were sampled in a standardized manner using at each site six 6-m mist nets set at ground level and one net wall consisting of four stacked 6-m nets, reaching subcanopy or canopy level depending on the height of the forest. Each island was sampled for seven entire nights between October 2003 and October 2005 with a minimum time interval of 30 days between netting nights to reduce possible net-shyness. The bats were marked and standard measurements and demographic data were collected following Handley *et al.* (1991). For a full account of sampling procedures see Meyer & Kalko (in press). Species accumulation curves and species richness estimators indicated a

high level (> 95%) of inventory completeness for all study islands. In total, we obtained 8447 captures of 39 species belonging to five families (Meyer & Kalko, in press).

In the context of our analyses it is important to consider whether the observed species distributions represent primarily patterns of occupancy rather than patterns of differential habitat use or foraging behaviour. To assess this, we calculated species turnover between successive sampling years as $T = (J + E) / (S_1 + S_2)$, where J is the number of species recorded in the second but not in the first year, E the number of species found in the first but not in the second year, and S_1 and S_2 the total number of species during both years (Aguirre *et al.*, 2003). Turnover rates can vary between 0 (no turnover) and 1 (complete turnover). Overall species turnover between sampling years was very low (0.08) and mean turnover rates across sites were similarly low (0.16 ± 0.10 SD). Over the temporal scale of our study, we therefore believe that it is reasonable to consider the islands as sufficiently isolated for most species and to regard the presence-absence data used in our analyses as primarily representing species occurrence. It has to be noted, however, that our study sites cannot be considered completely insular for all species as some highly vagile species (mostly *Artibeus jamaicensis*, *A. lituratus*, and *Uroderma bilobatum*) may regularly move among neighbouring islands on a nightly basis (Meyer & Kalko, in press). But even for these highly mobile species, recapture data (Meyer & Kalko, in press) indicate that long-distance cross-water movements are rare. In any case, the water matrix seems to be a movement barrier significant enough that many species apparently do not regularly cross it; otherwise turnover rates should have been much higher.

Data analysis

Species matrices

We excluded all non-phyllotomid species, since they cannot be adequately sampled with mist nets (Kalko, 1998) as well as one

Table 2 Phyllostomid bat species captured on Gatún Lake islands, Panama, and used in nestedness and species co-occurrence analyses. Nomenclature follows Simmons (2005).

ID no.	Species (abbreviation)	Number of islands occupied ($N_{\max} = 11$)	Trophic level*	Mobility
1	<i>Artibeus jamaicensis</i> (Ajam)	11	P	High
2	<i>Artibeus lituratus</i> (Alit)	11	P	High
3	<i>Artibeus phaeotis</i> (Apha)	4	P	Low
4	<i>Artibeus watsoni</i> (Awat)	6	P	Low
5	<i>Carollia castanea</i> (Ccas)	5	P	Low
6	<i>Carollia perspicillata</i> (Cper)	10	P	Low
7	<i>Clitroderma villosum</i> (Cvil)	7	P	High
8	<i>Glossophaga soricina</i> (Gsor)	10	P	Low
9	<i>Lophostoma silvicolu</i> (Lsil)	2	A	Low
10	<i>Micronycteris lirsuta</i> (Mhir)	3	A	Low
11	<i>Micronycteris microtis</i> (Mmic)	9	A	Low
12	<i>Phyllostomus discolor</i> (Pdis)	1	P	High
13	<i>Phyllostomus hastatus</i> (Phas)	2	A	High
14	<i>Platyrrhinus helleri</i> (Phel)	5	P	Low
15	<i>Trinycteris nicefori</i> (Tnic)	1	A	Low
16	<i>Tonatia saurophila</i> (Tsau)	2	A	Low
17	<i>Uroderma bilobatum</i> (Ubil)	11	P	High
18	<i>Vampyrodes caraccioli</i> (Vcar)	4	P	High
19	<i>Vampyressa nymphaea</i> (Vnym)	1	P	Low
20	<i>Vampyressa pusilla</i> (Vpus)	9	P	Low

*P, phytophagous; A, animalivorous (Giannini & Kalko, 2004, 2005).

species, *Centurio senex*, that was present in the study area only during part of the rainy season at low numbers and for which sampling may thus also not have been sufficient. This resulted in a total of 20 phyllostomid species for analysis (Table 2) for which we constructed a species (rows) by site (columns) matrix. We additionally generated presence-absence matrices for four different species subsets as follows: first, we classified bats into phytophagous and animalivorous species based on dietary analyses (Giannini & Kalko, 2004, 2005). Second, we employed principal components analysis (PCA) to divide species according to their mobility (Table 3, Fig. 1). Variables included in the PCA were mean

Table 3 Results of a principal components analysis on four variables related to species mobility, showing the loadings for each variable and the proportion of variance explained by the first two components (PC1 and PC2).

Variable	PC1	PC2
Maximum recapture distance (d_{\max})	-0.48	0.56
Mean recapture distance (d_{mean})	-0.58	0.04
Aspect ratio	-0.37	-0.84
Wing loading	-0.55	0.05
Variance explained (%)	67.0	21.1

and maximum recapture distances as well as two morphological variables, aspect ratio and wing loading (body weight divided by wing area), which are linked to mobility in bats. Species characterized by high wing loading and long and narrow wings (high aspect ratio) are fast and energy-efficient flyers, whereas those with short and broad wings have higher manoeuvrability in cluttered habitats but increased commuting costs over larger distances (Norberg & Rayner, 1987).

Since we obtained reliable mark-recapture data only for a limited set of species during our study period, we calculated movement distances based on a large dataset collected as part of the BCI long-term bat project with > 40,000 capture/recapture data (Kalko *et al.*, 1996; unpublished data), which covered all the species included in our analyses. Although these data mostly constitute movement distances within a rather large patch of unfragmented forest rather than cross-water movements, we believe that they reflect the general movement abilities of the different species reasonably well. Values for aspect ratio and wing loading (Nm^{-2}) were taken from Meyer *et al.* (2008) and von Staden (2002). Based on the ordination diagram two clusters of species characterized by high and low mobility, respectively, could be distinguished (Fig. 1). This categorization (Table 2) was subsequently used for the construction of separate incidence matrices for nestedness and co-occurrence analyses.

Co-occurrence patterns

Co-occurrence indices. We calculated two metrics of co-occurrence, the checkerboard score (*C*-score) introduced by Stone & Roberts (1990) and the variance ratio (*V*-ratio) popularized by Schluter (1984). The number of checkerboards and the number of species combinations, two other commonly employed co-occurrence measures, have been shown to be prone to type II errors and may not reveal significant patterns in noisy datasets. Conversely, the *C*-score and the *V*-ratio are based on the average co-occurrence and covariance, respectively, of all species pairs and are therefore relatively insensitive to noise in the data (Gotelli, 2000). The *C*-score in particular has been demonstrated to be superior to the other indices with respect to type I and II error rates. For a detailed account of the statistical properties and performance of these indices, see Gotelli (2000). The *C*-score measures the extent to which species are segregated across sites but does not require perfect checkerboard distributions (Gotelli, 2000). For any two species, the number of 'checkerboard units' (*CU*) is defined as $CU = (R_i - S)(R_j - S)$, where R_i and R_j are the number of occurrences (= row totals) for species *i* and *j*, respectively, and *S* denotes the number of co-occurrences. The *C*-score is the average number of checkerboard units over all possible pairs of species in the matrix.

The *V*-ratio measures the variability in the number of species per site and represents the ratio between the variance in species richness per site (= variance of column sums), and the sum of the variances of species occurrence over sites (= sum of row variances) (Schluter, 1984; Gotelli, 2000). The ratio equals 1 if the average covariance between species pairs is 0. In the case of positive or negative covariance between species pairs, the *V*-ratio is smaller or greater than 1, respectively (Gotelli, 2000). In an assemblage structured by negative species interactions, the *C*-score should be

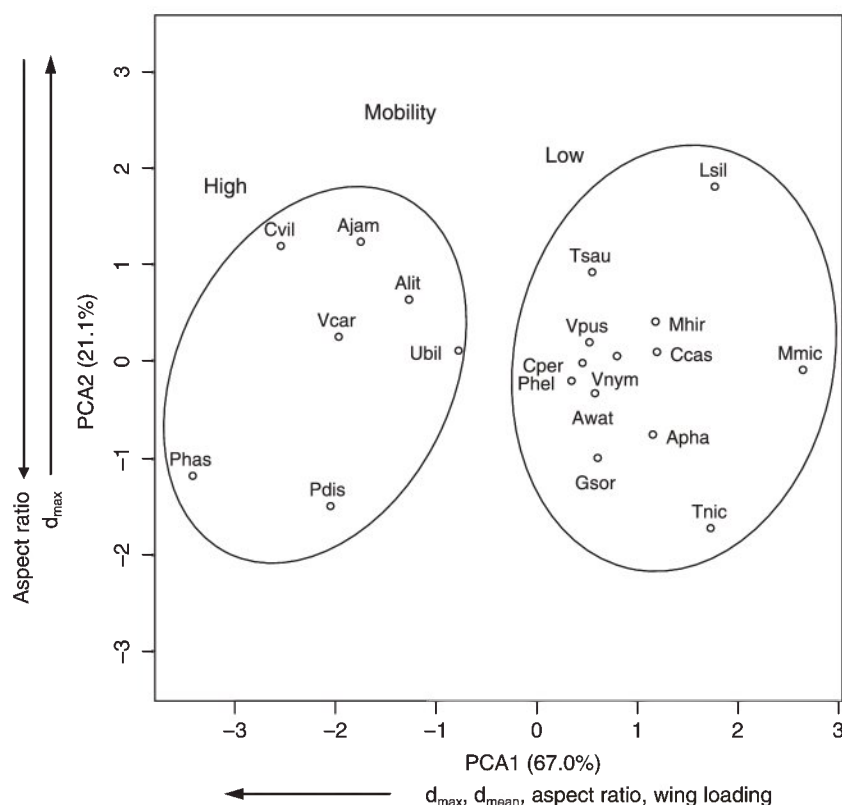


Figure 1 Ordination of 20 phyllostomid bat species in the principal components space of a set of variables related to species mobility. For full species names see Table 2; d_{mean} and d_{max} = mean and maximum recapture distance, respectively.

significantly larger than expected by chance, while the opposite should be true for the *V*-ratio (Gotelli, 2000; Gotelli & McCabe, 2002).

Null models and randomization algorithms. We calculated the above indices and compared them to those of 5000 randomly assembled communities using the software EcoSim 7.72 (Gotelli & Entsminger, 2006). The outcome of species co-occurrence analyses is sensitive to the selection of appropriate null models and choice of the randomization algorithm. We used the sequential-swap algorithm to generate random null matrices (Gotelli, 2000; Gotelli & Entsminger, 2001). Although use of the swap algorithm has been subject to criticism (Sanderson *et al.*, 1998; Manly & Sanderson, 2002), re-evaluation (Gotelli & Entsminger, 2003) confirmed its overall good statistical properties and performance. We compared three alternative null models, differing in the way row and column totals are treated:

1 Fixed-fixed (FF). With this algorithm, both the row and the column totals of the original matrix are fixed, thus preserving differences in occurrence frequencies among species (row sums) and differences in species richness among sites (column sums). Gotelli (2000) advocated these constraints particularly for island datasets. As the *V*-ratio is exclusively determined by the row and column totals of the matrix, it cannot be derived for this null model (Gotelli, 2000).

2 Fixed-weighted (FW). Results of co-occurrence analyses can be strongly affected by the use of weighting factors, although this approach so far has only infrequently been applied (but see Gotelli & Ellison, 2002; Jenkins, 2006). Column weighting adjusts

the probability of a species occurring at a particular site during randomization using factors thought to contribute to intersite differences in community composition. Here, we explored the influence of two weighting factors, island area and island isolation (distance from the mainland), on the outcome of null model analyses.

3 Weighted-fixed (WF). Co-occurrence scores may be affected by sampling artefacts due to differences in species abundances or detection probabilities (MacKenzie *et al.*, 2004; Peres-Neto, 2004; Ulrich & Zalewski, 2006). We explored the possible influence of such sampling errors by using a null model with fixed column totals but weighting the row totals by setting the occurrence frequency of each species proportional to its total relative abundance across all sites.

To allow for meaningful comparisons of our results with those from other studies, we calculated a standardized effect size (SES) as $([\text{observed score} - \text{mean simulated score}] / \text{standard deviation of simulated scores})$, which indicates the number of standard deviations that the observed index is above or below the mean index of simulated matrices (Gotelli & McCabe, 2002; Gotelli & Entsminger, 2006).

Quantification of nestedness

A variety of different methods are available for calculating the nestedness of presence-absence matrices (reviewed by Wright *et al.*, 1998). Of these, Atmar & Patterson's Nestedness Temperature Calculator (NTC; Atmar & Patterson, 1995) is the most widely used in biogeographical studies and analyses of habitat fragmentation.

Table 4 Summary of species co-occurrence analyses of phyllostomid bats with observed and simulated co-occurrence metrics, standardized effect sizes [SES], and associated tail probabilities (in parentheses) for each of the different species presence-absence matrices and null model algorithms. For details see text. Significant and marginally significant results are highlighted in bold. na, not applicable, as the *V*-ratio cannot be tested with the fixed-fixed null model.

Index	Species matrix	Score				
		obs	sim _{FF}	sim _{FW-area}	sim _{FW-isolation}	sim _{WF}
C-score [SES]	All species	1.368	1.245 (0.026) [2.28]	1.417 (0.554) [−0.16]	0.915 (0.033) [1.93]	1.513 (0.634) [−0.38]
	Phytophagous	0.890	0.764 (0.041) [2.14]	1.311 (0.878) [−1.15]	0.710 (0.256) [0.64]	1.366 (0.869) [−1.13]
	Animalivorous	2.267	2.399 (0.679) [−0.49]	1.693 (0.222) [0.83]	1.493 (0.076) [1.59]	3.686 (0.902) [−1.23]
	High mobility	0.143	0.143 (1.000) [0.00]	0.613 (0.923) [−1.29]	0.453 (0.876) [−1.04]	0.456 (0.818) [−0.82]
	Low mobility	1.821	1.733 (0.188) [0.88]	1.863 (0.535) [−0.09]	1.166 (0.048) [1.79]	2.288 (0.761) [−0.74]
V-ratio [SES]	All species	4.053	na	3.746 (0.661) [0.37]	5.021 (0.083) [−1.42]	4.128 (0.432) [−0.27]
	Phytophagous	3.819	na	2.808 (0.946) [1.55]	4.005 (0.406) [−0.32]	3.624 (0.814) [0.82]
	Animalivorous	1.264	na	1.785 (0.253) [−0.91]	1.811 (0.151) [−1.21]	1.201 (0.753) [0.45]
	High mobility	2.119	na	1.529 (0.956) [1.40]	1.694 (0.927) [1.15]	1.954 (0.839) [0.82]
	Low mobility	3.157	na	3.022 (0.609) [0.19]	4.066 (0.070) [−1.55]	3.054 (0.712) [0.46]

The matrix temperature *T* calculated by the NTC is a measure of unexpected species presences and absences or system ‘disorder’ where 0° corresponds to a perfectly nested matrix and 100° indicates a random species distribution pattern. However, recent research cautions against use of the NTC as it has been demonstrated to have a number of important shortcomings relating to the definition of the isocline of perfect order, the way of matrix reorganization, the robustness of the packing algorithm, and choice of an appropriate null model (Fischer & Lindenmayer, 2002; Rodríguez-Gironés & Santamaría, 2006; Ulrich & Gotelli, 2007).

Here we used the binary matrix nestedness temperature calculator (BINMATNEST) recently developed by Rodríguez-Gironés & Santamaría (2006), which is the latest in a growing line of algorithms to quantify nestedness which overcome these difficulties. BINMATNEST implements an isocline of perfect order that is unambiguously defined, is based on robust genetic algorithms to determine the reordering of rows and columns that leads to minimum matrix temperature, and provides a set of three alternative null models to assess the statistical significance of matrix temperature (Rodríguez-Gironés & Santamaría, 2006). Following the authors’ recommendations, we used the null model 3 in evaluating statistical significance as it has been shown to be associated with the smallest type I error. Reported *P*-values are based on 5000 random matrices. To evaluate the causal role of colonization and extinction in shaping community structure, we used a Spearman rank correlation between the matrix

reorganization vectors, i.e. island rank order in the maximally packed matrix, and island isolation and area, respectively (Patterson & Atmar, 2000; Rodríguez-Gironés & Santamaría, 2006).

RESULTS

Co-occurrence patterns

Results of analyses depended considerably on the type of null model algorithm employed (Table 4). For the *FF*-model, the observed *C*-score for the incidence matrix of the entire assemblage and for the submatrix of phytophagous bats was significantly higher than expected by chance, suggesting a negative pattern of species co-occurrence. Conversely, for the submatrices of animalivorous bats and species of both high and low mobility, the *C*-score did not deviate from null model expectations, indicating random species co-occurrence. Using island isolation as a column constraint in the analysis (*FW-isolation*) produced partly contrasting results. This model detected significant non-randomness in species co-occurrence again for all species but also for the subsets of animalivorous bats and less mobile species, whereas the pattern for phytophagous and highly mobile species was not significant (Table 4). The use of island area as weighting factor (*FW-area*), on the other hand, suggested random co-occurrence patterns as the null hypothesis was never rejected for any of the species matrices. This was similarly true for the abundance-weighted (*WF*) model (Table 4).

Table 5 Results of nestedness analyses conducted on the species by site matrix for all phyllostomid bats and for different subsets of phyllostomid species caught on 11 islands in Gatún Lake, Panama. Given are observed matrix temperatures (T_{obs}), expected nestedness temperatures (T_{exp}), as well as Monte Carlo-derived probabilities that the matrix was randomly generated. Also indicated are the results of Spearman rank correlations of island rank order in the maximally nested matrix with the rank order of island area and isolation.

Species matrix	T_{obs}	T_{exp} (SD)	P	Rank correlation with island			
				Area		Isolation	
				r_s	P	r_s	P
All	14.80	37.40 (5.36)	< 0.0001	0.109	0.745	0.618	0.046
Phytophagous	10.47	28.71 (6.45)	0.001	-0.073	0.839	0.582	0.063
Animalivorous	9.16	21.48 (8.63)	0.062	0.100	0.765	0.473	0.141
High mobility	0.83	19.63 (7.38)	< 0.0001	0.100	0.765	0.536	0.091
Low mobility	14.04	33.78 (6.38)	0.0004	-0.064	0.860	0.509	0.110

The V -ratio detected marginally significant deviations from null expectations only for the FW -model weighted by island isolation and when either all species or bats characterized by low mobility were considered. In the remainder of the cases, the V -ratio did not differ significantly from random expectations (Table 4).

Nestedness

Phyllostomid bat assemblages on Gatún Lake islands were highly significantly nested when all species were considered ($P < 0.0001$, Table 5, Fig. 2). The bat distribution across islands remained more significantly nested ($P \leq 0.001$) than expected by chance using incidence matrices of phytophagous species alone

or based on the data sets comprising species of both mobility classes. For gleaning animalivores, the difference between observed and expected nestedness temperature was marginally significant ($P = 0.062$) (Table 5). Spearman rank correlations between row order in the maximally nested matrix with causal factors suggested that island isolation was an important determinant of nestedness in phyllostomid bat distributions for incidence matrices of the whole phyllostomid assemblage ($r_s = 0.62$, $P = 0.046$), phytophagous bats ($r_s = 0.58$, $P = 0.063$), and mobile species ($r_s = 0.54$, $P = 0.091$) but not for animalivorous ($r_s = 0.47$, $P = 0.141$) or less vagile species ($r_s = 0.51$, $P = 0.110$). In contrast, the nested order of islands was unrelated to the rank order of island areas for all five species matrices (Table 5), indicating that island area is not causally linked to nested structure in our study system.

DISCUSSION

Co-occurrence patterns

Overall, co-occurrence analyses did not provide strong evidence that species composition of phyllostomid bats on Gatún Lake islands is highly structured by negative interspecific interactions. Corroborating recent findings by Jenkins (2006), the outcome of analyses was sensitive to weighting factors, adding further support to the notion that, whenever possible, co-occurrence analyses should incorporate weights for important factors likely to contribute to the observed patterns, such as in our case, island isolation. Moreover, as expected, different results emerged depending on whether the whole assemblage or particular species subsets were considered. Unweighted analyses based on the C -score showed a negative pattern of co-occurrence indicating mutually exclusive species distributions for the entire assemblage as well as for phytophagous species, whereas a random pattern was suggested for all other species matrices examined. Area- and abundance-weighted analyses always indicated random assemblage structure for both co-occurrence indices and irrespective of the species matrix analysed. Weighting analyses by island isolation, however, retained a non-random pattern for the whole species set but rendered the result non-significant for phytophagous bats.

Species	ID	Sites										
		3	4	5	7	11	8	2	10	9	1	6
1	1	1	1	1	1	1	1	1	1	1	1	1
17	1	1	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1	1	1
8	1	1	0	1	1	1	1	1	1	1	1	1
6	1	1	1	1	1	1	1	1	1	1	1	0
11	1	1	1	1	1	0	0	1	1	1	1	1
20	1	1	1	1	1	1	1	1	1	1	0	0
7	1	1	1	1	1	1	1	1	0	0	0	0
4	1	1	0	1	1	1	1	1	0	0	0	0
18	1	1	1	0	0	1	0	0	0	0	0	0
5	0	1	1	0	1	1	1	1	0	0	0	0
14	1	1	0	1	1	1	1	0	0	0	0	0
3	1	0	0	1	1	0	1	1	0	0	0	0
16	1	1	0	0	0	0	0	0	0	0	0	0
10	1	0	0	1	1	0	0	0	0	0	0	0
9	0	0	1	0	0	1	0	0	0	0	0	0
13	0	0	1	1	0	0	0	0	0	0	0	0
12	0	0	1	0	0	0	0	0	0	0	0	0
15	0	1	0	0	0	0	0	0	0	0	0	0
19	1	0	0	0	0	0	0	0	0	0	0	0

Figure 2 Maximally nested presence-absence matrix of phyllostomid bat distributions on Gatún Lake islands, Panama. For island and species ID numbers refer to Tables 1 and 2, respectively.

By contrast, we found that less vagile bats, and based on the *C*-score also animalivorous species, tended to occur together less often than expected by chance, whereas our results suggest random structuring for species with high mobility. This finding is consistent with our initial hypothesis that high species mobility should lead to random assemblage composition while incidence matrices of less mobile species should be more likely to exhibit non-random structure. This is because colonization rates compared to local persistence should be higher in mobile species, whereas those with limited mobility should be more affected by local extinction processes (Zalewski & Ulrich, 2006). Our results generally support Zalewski & Ulrich's (2006) call for taking species' differential dispersal abilities into account when analysing patterns of community assembly. Moreover, our results indicate that island isolation but not area had to some degree confounded unweighted analyses, a finding in line with a marked species–distance effect and absence of a significant species–area relationship at local scales (Meyer & Kalko, in press).

A meta-analysis by Gotelli & McCabe (2002) of nearly one hundred species presence–absence matrices of a diverse array of invertebrate and vertebrate taxa revealed that assemblages of plants, ants, birds, bats, and non-volant mammals exhibited non-random patterns of species co-occurrence consistent with Diamond's (1975) assembly rules model stressing the importance of competitive interactions. Non-random matrices are characterized by having SES for the *C*-score $> |2.0|$ (Gotelli & McCabe, 2002). These authors reported strong deviations from randomness as based on average SES values for birds (3.65) and non-volant mammals (3.10). Particularly strong effects of species segregation were also indicated for three presence–absence matrices of bats (average SES > 4.0). In the present study, incidence matrices that showed significant or marginally significant deviation from randomness had absolute SES values between 1.42 and 2.28 (Table 4), i.e. values closer to those found for herps and most invertebrate assemblages (average SES < 1.5) (Gotelli & McCabe, 2002). Spatial scale of the study may have a strong effect on *C*-scores and SES obtained in co-occurrence analyses (Jenkins, 2006). As Gotelli & McCabe's (2002) analysis for bats was exclusively based on presence–absence matrices of bats on oceanic islands, the discrepancy between studies likely indicates different structuring mechanisms prevailing on old oceanic islands vs. recently isolated land-bridge islands. More specifically, it possibly reflects fundamental differences between these systems regarding geographical scale, size, age, habitat diversity, and resource abundance and echoes the importance of evolutionary processes and historical events in shaping patterns of species distribution on oceanic islands (Drake *et al.*, 2002).

Ulrich (2004) and Bell (2005) recently evaluated whether patterns of species co-occurrence could be accounted for by invoking a neutral community model in which species are regarded as being ecologically equivalent and local assemblage structure is determined by random colonization, migration, and extinction (Hubbell, 2001). Interestingly, they found that non-random patterns of species segregation may indeed be generated just as well by neutral ecological drift models as by

traditional null models. By analogy with genetic drift, zero-sum ecological drift models imply that relative abundances of species that are ecologically equivalent should change only owing to chance events (Hubbell, 2001). However, in Ulrich's (2004) analysis SES values generated by the neutral model for the *C*-score were comparatively low (*c.* 0.5). Therefore, it has been argued that the strong negative co-occurrence patterns found by Gotelli & McCabe (2002) for some taxa cannot be accounted for solely on the basis of a neutral model (Gotelli & McGill, 2006). This may also be because neutral theory is mainly concerned with resident organisms and neutral models may therefore have limited applicability for mobile animals (Chave, 2004). Moreover, because many of the important parameters in neutral models can rarely be measured directly, this greatly limits their utility as a null hypothesis for testing empirical patterns (Gotelli & McGill, 2006). Finally, in a more applied context, it has been contended that neutral theory cannot adequately address the question of how fragmentation will differentially alter the composition of species and their interactions with other species in the community (Chase, 2005). This is because the neutral theory explicitly disregards differences in species traits even though species are known to be differentially affected by fragmentation based on their traits (Henle *et al.*, 2004). Mobility in our case apparently plays an important role in determining assemblage structure, which would be generally congruent with a neutral model. However, whether the non-random patterns observed to some degree in our analyses reflect competitive interactions or are attributable mainly to stochastic processes, remains an open question.

Competitive interactions could result in ecomorphological size divergence via character displacement. Alternatively, competition may not be sufficiently strong to effect the local extinction of species but may reduce the abundance of those species that experience more competitive pressure, a phenomenon known as density compensation (Patterson *et al.*, 2003). Meta-analyses that evaluated the degree to which each of five ensembles (aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, and nectarivores) from 15 bat assemblages throughout the New World show signs of competitive species interactions, have provided little support for pervasive and consistent deterministic structuring across most locations based on these two independent lines of evidence, although non-randomness was detected in a few cases (Stevens & Willig, 1999, 2000). This may reflect the fact that, in studies conducted over large areas, high heterogeneity and variability in environmental conditions may prevent competitive interactions from inducing deterministic structure in a ubiquitous fashion (Stevens & Willig, 2000; Moreno *et al.*, 2006).

Our results suggest that this probably applies equally well to heterogeneous fragmented landscapes. Nevertheless, certain evidence for effects of ecological interactions on bat community assembly mechanisms comes from a recent study by Moreno *et al.* (2006). Also following an ecomorphological approach and focusing on the local habitat scale, they detected significant non-random patterns at the ensemble level for frugivorous phyllostomid bats, indicating that when environmental conditions are sufficiently homogeneous, interspecific interactions may to some degree structure local bat assemblages.

Nestedness

According to our analysis, assemblages of phyllostomid bats on Gatún Lake islands exhibit a highly nested structure such that species that occur on depauperate islands are also found on larger, more species-rich islands. While nested subset patterns seem to be common in ecological systems, comparative assessments indicate that nestedness is particularly prevalent in systems that are mainly shaped by extinction processes mediated through area effects (Patterson & Atmar, 1986; Wright *et al.*, 1998; Patterson & Atmar, 2000; Feeley, 2003; Watling & Donnelly, 2006). Land-bridge islands or habitat fragments are typically uniformly colonized patches where species loss occurs in most cases selectively and in a predictable order based on species' differential extinction vulnerability, e.g. due to differences in area requirements, resulting in a nested subset structure. Such a mechanism of area-related extinction during faunal relaxation has for instance been reported for resident bird assemblages on islands in Lake Guri, an artificial reservoir in Venezuela (Feeley, 2003), where islands were isolated only 20 years ago.

By contrast, we found that island nested rank order was significantly or marginally significantly correlated with the rank order of island isolation but not island area for the entire assemblage as well as for phytophagous and highly mobile species. This mainly reflects, and is in agreement with the finding of a strong effect of island isolation on species richness and lack of a significant species–area relationship at the local scale (Meyer & Kalko, *in press*). Thus, isolation-dependent, selective colonization, enhanced by the rescue effect (Brown & Kodric-Brown, 1977) by lowering local extinction rates of mobile species (Wright *et al.*, 1998), appears to be the likely cause of nestedness and dominant process structuring phyllostomid bat assemblages on our study islands. The reason for this may also be that bat assemblages on Gatún Lake islands, which are > 90 years old, have likely reached a quite stable species richness and composition, which is suggested by the very low turnover rates observed across sampling years. Conversely, avian assemblages on the much more recently isolated Lake Guri islands are probably still undergoing relaxation, whereby local extinction continues to be the dominant structuring process (Feeley, 2003). This may explain, at least in part, the contrasting patterns observed with respect to the causal factors underlying nestedness in both systems.

Differential colonization can produce nested subset patterns if highly mobile species are present even on the most isolated islands and less vagile species occupy only the closer islands. Our findings support this notion insofar as this pattern seems to be mainly driven by differential mobility between generally more mobile phytophagous bats and comparatively less vagile animalivorous species. This suggests that factors related to species' fragmentation sensitivity can be important in determining patterns of faunal nestedness and assemblage composition in fragmented landscapes.

Even though we found nestedness to be unrelated to area on the scale of individual islands, i.e. at the spatial scale at which sampling was performed, area-dependent local extinction may well be the dominant structuring process shaping assemblages at the landscape scale. At this larger spatial scale the amount of

forest cover was the chief determinant of species richness and composition (Meyer & Kalko, *in press*). This suggests that our findings regarding the underlying causes of nestedness in our study system may be scale-dependent, as has been found in other studies that have explicitly addressed the scale-dependency of nestedness patterns (e.g. Fischer & Lindenmayer, 2005).

Martínez-Morales (2005) advocated the use of nestedness analyses as a potentially valuable tool for conservation to identify species sensitive to fragmentation. He found that certain groups of tropical cloud forest birds exhibited a nested structure significantly correlated with fragment area. This contrasts with our findings as phytophagous bats, which showed a nested arrangement correlated with island isolation, can generally be considered relatively fragmentation-tolerant compared to animalivores (Meyer *et al.*, 2008) and suggests that such an approach may not be generally applicable and needs to be explored further in future studies. Also, responses to fragmentation are often species-specific, with some species being negatively affected and others benefiting from fragmentation. Therefore, because of their focus on a unidirectional change in species composition, nestedness analyses may not be an ideal tool to identify fragmentation-sensitive species (Fischer & Lindenmayer, 2005).

Nested habitat distributions may also produce nested subsets if many species are habitat specialists, however, this is unlikely to contribute to the observed pattern of nestedness in our case as habitat heterogeneity is relatively low across the study islands (Meyer & Kalko, *in press*). Recently, Higgins *et al.* (2006) showed that stochastic processes, such as the random placement of individuals according to different species-abundance and island-size distributions, can by itself result in nested subset structure. Their study demonstrated that in interactive systems in which the species-abundance distribution of each island is determined largely by colonization dynamics rather than *in situ* dynamics, individual-based processes become important in generating non-random patterns of species composition such as nestedness. For bats, our study islands can clearly be regarded as such an interactive system suggesting that random processes may, at least in part, account for the strong degree of nestedness detected in our analyses.

Conclusions

In summary, there was limited evidence for negative species associations congruent with niche-based community assembly invoking competitive interspecific interactions. In line with previous findings our results suggest that deterministic structuring may be hard to detect in situations with high heterogeneity in environmental conditions such as in fragmented landscapes. Patterns of nestedness and species co-occurrence indicate that assemblage composition of phyllostomid bats on Gatún Lake islands is in large part determined by isolation-dependent, differential colonization reflecting species-specific differences in mobility. In an applied context, our results imply that community-level nestedness indices, when applied at a spatial scale that better matches patch-utilization than birth–death processes, may be inadequate as conservation planning tools (see also Fischer &

Lindenmayer, 2005). Even if assemblages exhibit significant nestedness, particularly in fragmented landscapes with a high patch to matrix contrast, conservation strategies should entail measures to incorporate the importance of structural and functional connectivity among remnant patches into reserve planning.

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