



Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system

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ABSTRACT

Aim Working within a system of high structural contrast between fragments and the surrounding matrix, we assessed patterns of species loss and changes in species composition of phyllostomid bats on artificial land-bridge islands relative to mainland assemblages, and evaluated the responses of bats to forest edges. We further examined the relative influence of local-scale characteristics (e.g. vegetation structure, island area) versus landscape attributes (e.g. forest cover, patch density) and the importance of spatial scale in determining phyllostomid species richness and composition on islands.

Location Islands in Gatún Lake and adjacent mainland peninsulas in the Barro Colorado Nature Monument, Panama.

Methods Bats were sampled over a 2-year period on 11 islands as well as at forest-edge and interior sites on adjacent mainland, resulting in > 8400 captures.

Results The islands harboured a less diverse and structurally simplified phyllostomid bat fauna. Islands far from the mainland were especially species-poor. This decline in species richness was associated with compositional shifts towards assemblages strongly dominated by frugivores with good dispersal abilities. Members of other ensembles, most importantly gleaning animalivores, were much less common or absent. Although overall species composition was not significantly altered, species richness at continuous forest-edge sites was significantly lower compared with that at interior sites. Distance from the mainland and amount of forest cover in the landscape were the best predictors of species richness and assemblage composition. Responses were scale-dependent. At the local scale, species richness was independent of island area but was correlated positively with distance from the mainland. In contrast, area effects became more important at larger spatial scales, suggesting that many species use multiple fragments.

Main conclusions Our results underline the conservation value of small habitat remnants, which, even when embedded in a hostile matrix, can support a relatively diverse bat fauna, provided that there is a low degree of patch isolation and spatial proximity to larger tracts of continuous forest. Although the results at the assemblage level were inconclusive, we demonstrate that certain bat species and ensembles, particularly gleaning animalivores, exhibit high edge-sensitivity. Our results point to habitat loss rather than changes in landscape configuration as the main process after isolation underlying phyllostomid bat responses, suggesting that conservation efforts should focus on habitat preservation instead of trying to minimize fragmentation *per se* at the expense of habitat amount.

Keywords

Area and isolation, Chiroptera, conservation biogeography, edge effects, forest fragmentation, Gatún Lake, land-bridge islands, landscape structure, Panama, spatial scale.

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INTRODUCTION

Changes in land use have been identified as key drivers of biodiversity loss, particularly in tropical regions, where habitat modification through deforestation, conversion into agricultural lands, pastoralization, and urbanization continues at unprecedented rates (Sala *et al.*, 2000; Laurance *et al.*, 2001; Wade *et al.*, 2003). Hence, the fate of tropical biota will be governed largely by the capacity of species to survive in fragmented landscapes, and by our ability to manage such landscapes to mitigate the effects of habitat loss and isolation (Laurance *et al.*, 2002).

A key finding of recent studies is that species responses to fragmentation are influenced profoundly by the type of the matrix (Gascon *et al.*, 1999; Antongiovanni & Metzger, 2005; Ewers & Didham, 2006), which determines to a large degree an organism's ability to exploit it. At the extreme end of the spectrum are forest-dependent species, which react negatively to small habitat disruptions: Neotropical understorey birds, for example, are reluctant to cross even small road clearings (Laurance *et al.*, 2004). By contrast, many vertebrate species readily traverse matrices composed of secondary growth or mosaics of agricultural vegetation (e.g. Estrada & Coates-Estrada, 2002; Antongiovanni & Metzger, 2005). Thus, the quality and permeability of the matrix, together with the ecological traits of the species, are essential for determining the functional connectivity among forest remnants and ultimately control a species' persistence in patchy and fragmented landscapes. Finally, depending on how similar the matrix is structurally to the original habitat, i.e. the degree of fragment-matrix contrast, edge-related gradients in physical and biotic variables will be more or less pronounced (Laurance *et al.*, 2002). In particular, changes in plant community composition and structure associated with forest edges (Harper *et al.*, 2005) may strongly affect the abundance patterns and composition of animal assemblages, as has been demonstrated for tropical birds (Beier *et al.*, 2002; Watson *et al.*, 2004).

Most fragmentation research has so far concentrated on recently formed systems with low fragment-matrix contrast, and young, high-contrast systems, as exemplified by islands in reservoirs, remain relatively poorly understood (cf. the review by Watson, 2002). However, these systems hold great potential as they allow the study of fragmentation effects separately from potentially confounding matrix effects, for example 'spill-over' of matrix species, which may obscure area and isolation effects (Cosson *et al.*, 1999; Leigh *et al.*, 2002). Population- and assemblage-level responses in low-contrast systems have been examined mainly for plants, birds, and rodents (e.g. Adler & Seamon, 1991; Leigh *et al.*, 1993; Terborgh *et al.*, 1997; Asquith & Mejía-Chang, 2005). For bats, on the other hand, nearly all studies on fragmentation effects save those of Cosson *et al.* (1999) and Pons & Cosson (2002) have been conducted in rather young, low-contrast systems *sensu* Watson (2002) (e.g. Estrada *et al.*, 1993; Sampaio, 2000; Estrada & Coates-Estrada, 2002; Gorresen & Willig, 2004; Faria, 2006).

Bats are an ideal model taxon for evaluating responses to habitat fragmentation as they are ecologically highly diverse

and mobile, with the potential to move over extensive areas of fragmented landscapes. Furthermore, differences in species-specific ecological traits suggest differential vulnerability to habitat disturbance. A previous study in Panama found surprisingly little differences in the structure of bat assemblages between Barro Colorado Island (BCI), a 1600-ha forest isolate in Gatún Lake, and Soberanía National Park (22,000 ha) on the adjacent mainland (von Staden, 2002). This result is in stark contrast to the striking changes in the avifauna (Robinson, 1999). BCI may be large enough and close enough to continuous forest to preserve the full complement of regional bat diversity. Many tropical landscapes, however, are increasingly dominated by much smaller (< 100 ha) fragments, which, nonetheless, may continue to serve important ecological functions (Turner & Corlett, 1996).

We therefore assessed how habitat fragmentation affects bat assemblages on small islands in Gatún Lake. Specifically, we focused on edge effects and on the relative importance of local-scale (e.g. vegetation structure, area, shape, isolation distance) versus landscape (e.g. forest cover, patch density) characteristics in shaping bat responses at various spatial scales, an important but little-explored issue in studies of habitat fragmentation (Graham & Blake, 2001). Although several studies have highlighted the importance of focal scale for detecting ecological relationships (Hill & Hamer, 2004), the majority of studies have typically examined faunal responses to spatial attributes in fragmented landscapes at a single landscape scale (Villard *et al.*, 1999; Numa *et al.*, 2005; Bernard & Fenton, 2007). Recent research by Gorresen & Willig (2004) and Gorresen *et al.* (2005) in fragmented Atlantic forests of Paraguay revealed scale-dependent and species-specific associations between landscape characteristics and both bat abundance and community attributes, and stressed the importance of multi-scale approaches to studies of bat responses to habitat fragmentation.

We focus on phyllostomid bats because (1) they are very species-rich and numerically dominant in Neotropical bat assemblages, (2) they are easily sampled with mist nets (Kalko, 1998), (3) they play pivotal roles as seed dispersers, pollinators, and predators (Kalko, 1998; Patterson *et al.*, 2003), and (4) they are crucial indicator species for the status of Neotropical forests (Fenton *et al.*, 1992; Medellín *et al.*, 2000). We evaluated differences in diversity and structure between mainland and island bat assemblages at the species and ensemble level. Specifically, we asked the following questions.

- (1) Do species richness and assemblage structure change in a predictable way from mainland forest interior towards sites at the forest edge? We hypothesized that matrix-tolerant species with good dispersal abilities would also be edge-tolerant.
- (2) Which species and ensembles are affected by fragmentation? Owing to the hostile nature of the matrix, we predicted stronger isolation effects than in systems with a lower fragment-matrix contrast.
- (3) Which local attributes and landscape characteristics constitute the best predictors of bat species richness and assemblage composition on islands? Here we expected the importance of factors to vary with spatial scale.

METHODS

Study area

The damming of the Chagres River during the construction of the Panama Canal created an artificial reservoir, Gatún Lake. Lake formation was completed in 1914, isolating numerous hilltops and resulting in the formation of over 200 islands ranging in size from <1 to 1560 ha (Barro Colorado Island; BCI; Adler & Seamon, 1991). Together with five adjacent mainland peninsulas, BCI forms the 5400-ha Barro Colorado Nature Monument (BCNM) and is contiguous with Soberanía National Park, 22,000 ha of forest on the eastern side of the canal (Fig. 1). Forests in the area are classified as lowland tropical moist forest (Holdridge, 1967).

The area experiences a strongly seasonal climate, with a long rainy season punctuated by a 4-month dry season (Windsor, 1990). Strong dry-season winds have a major impact on forest structure and dynamics, particularly on exposed islands, where forest is shorter in stature and less diverse in tree species composition (Leigh *et al.*, 1993).

Site selection

We selected 11 islands that differed in size and isolation as well as six mainland sites (Table 1, Fig. 1). Islands were grouped into two categories based on their shortest distance from the mainland: 'near' islands (< *c.* 500 m) and 'far' islands (> *c.* 1.5 km, Table 1). Mainland sites were located on three peninsulas (Bohío, Gigante, Peña Blanca) within the BCNM. To investigate potential edge effects, one forest edge and one forest interior site at each of these mainland locations was established. Interior sites were situated 312 ± 42 (SE) m from the forest edge; that is, beyond the distance at which commonly observed edge effects are known to be most pervasive (Laurance *et al.*, 2002; Harper *et al.*, 2005). Because of their irregular shape and small size, islands consisted almost exclusively of edge habitat.

Bat sampling

Field work was conducted between October 2003 and October 2005. At each island and mainland site, bats were sampled in a standardized manner with mist nets (6×2.5 m, 70/2 denier, 16-mm mesh size, five shelves) set along the perimeter of plots of *c.* 0.5 ha (typically 100×50 m; one plot per site). Each site was sampled for 7–8 complete nights over the 2-year period, with a minimum time interval of 30 days between netting nights. All sites were sampled with equal effort during all moon phases, and we generally avoided netting immediately before and after a full moon in order to minimize potential bias in capture success as a result of lunar-phobic behaviour (e.g. Morrison, 1978). During each survey night, we used six nets erected at ground level and spaced *c.* 50 m apart. In order also to sample bats flying in higher forest strata, we set up a net wall, typically consisting of four stacked nets, reaching subcanopy (mainland sites) or canopy (islands) level. Canopy height across study sites averaged < 20 m and was often < 15 m on islands (see Table S1 in the Supplementary Material). Species were identified, and standard measurements and demographic data were collected following Handley *et al.* (1991). Nomenclature follows Simmons (2005). Most bats (species > 10 g, excluding juveniles) were marked with individually numbered ball-chain necklaces, or, in the case of larger gleaning animalivores, with passive, subcutaneous transponders (EURO-ID, Weilerswist, Germany). Based on the classification system used by several authors (Stevens & Willig, 2000; Patterson *et al.*, 2003; Giannini & Kalko, 2004, 2005), we assigned bats to one of the following ensembles (Fauth *et al.*, 1996): frugivores, gleaning animalivores, nectarivores, omnivores, and sanguivores.

Environmental characteristics

Local-scale variables

For each of the 17 sites we quantified vegetation characteristics using protocols adapted from various sources (Schemske &

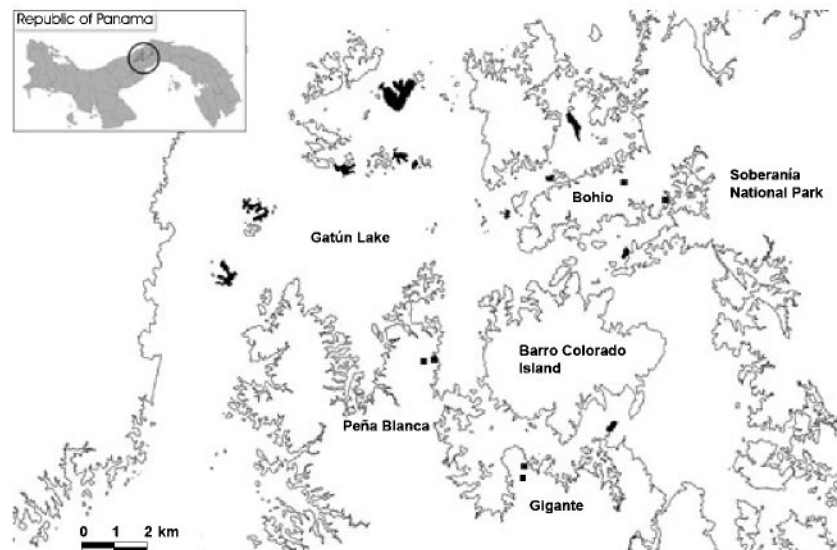


Figure 1 Map of the study area in the Canal zone in central Panama (inset; modified from a GIS coverage, Kinner & Stallard, US Geological Survey, 2003). Highlighted in black are the locations of the 11 study islands in Gatún Lake and of the six mainland sites (■) in continuous forest on the three peninsulas Bohío, Gigante, and Peña Blanca within the Barro Colorado Nature Monument.

Table 1 Overview of site characteristics and capture data for phyllostomid bats mist-netted on islands in Gatún Lake and on mainland peninsulas of the Barro Colorado Nature Monument, Panama. Observed (S_{obs}) and estimated species richness based on the first-order Jackknife (S_{jack}) are presented for each site and for each site category along with percentage inventory completeness (for details see text).

Location	Site category	Island area (ha)	Distance to mainland (km)	No. captures*	Capture effort (mnh)†	Relative abundance (bats/100 mnh)	S_{obs}	S_{jack1} (±SD)	Percentage completeness
Islands									
Cacao	Near	12.8	0.16	371	749	49.52	12	16.3 ± 1.71	73.7
Chicha	Near	2.8	0.51	296	793	37.31	11	12.7 ± 1.11	86.5
Mona Grita	Near	5.9	0.25	304	794	38.28	12	15.6 ± 1.78	77.1
Piña	Near	4.4	0.02	284	809	35.12	14	16.6 ± 1.21	84.5
Tres Almendras	Near	3.4	0.15	417	778	53.59	16	20.3 ± 2.16	78.9
<i>Total</i>	Near			1672	3923	42.62	21	23.9 ± 1.63	87.8
Guacha	Far	16.3	1.42	278	600	46.31	8	8.9 ± 0.86	90.3
Guanábano	Far	7.2	2.25	910	739	123.09	5	5.0 ± 0	100
Guava	Far	2.5	1.93	830	682	121.97	7	8.7 ± 1.11	80.4
León	Far	50	1.54	703	744	94.50	13	14.7 ± 1.11	88.4
Pato Horqueta	Far	11.4	3.4	788	773	101.97	14	18.3 ± 1.71	76.5
Trinidad	Far	17.3	2.02	632	674	93.41	8	8.9 ± 0.86	90.3
<i>Total</i>	Far			4141	4213	98.29	15	16.0 ± 0.98	93.9
<i>Islands total</i>				5813	8136	71.45	21	22.0 ± 0.99	95.5
Mainland									
Bohio	Interior			548	820	66.86	22	25.5 ± 2.65	86.3
Gigante	Interior			245	934	51.56	23	30.0 ± 3.50	76.7
Peña Blanca	Interior			436	902	26.24	23	27.4 ± 1.84	84.0
<i>Total</i>	Interior			1229	2656	46.28	28	31.8 ± 2.26	88.0
Bohio	Edge			544	850	63.98	16	19.5 ± 1.87	82.1
Gigante	Edge			429	832	66.86	18	21.5 ± 1.87	83.7
Peña Blanca	Edge			279	920	51.56	23	30.9 ± 2.45	74.5
<i>Total</i>	Edge			1254	2603	48.18	27	32.8 ± 2.08	82.4
<i>Mainland total</i>				2483	5258	47.22	30	32.9 ± 1.66	91.1

*Without same-night recaptures.

†One mist-net hour (mnh) denotes one 6-m net open for 1 h.

Brokaw, 1981; Schmiegelow *et al.*, 1997; Raman & Sukumar, 2002). Within each netting plot, we assessed density and basal area of trees > 10 cm diameter at breast height (d.b.h.) and the density of poles (stems 2–10 cm d.b.h.). In addition, we recorded or estimated the following parameters within nine 5 × 5 m subplots nested within each netting plot: (1) number of saplings < 2 cm d.b.h., (2) average canopy height using a Leico Disto™ rangefinder (Leico Geosystems, Heerbrugg, Switzerland), (3) canopy closure measured as the mean of four spherical densiometer (Forestry Suppliers, Inc., Jackson, MS, USA) readings taken at the centre of each subplot, (4) vertical foliage structure by noting the presence or absence of foliage at several height intervals (0–1, 1–2, 2–4, 4–8, 8–16, 16–24, 24–32, > 32 m) directly above and in a 0.5-m radius around the centre of each subplot.

Moreover, for each island we measured the following characteristics using ArcView GIS 3.2a (Environmental Systems Research Institute Inc., Redlands, CA, USA) based on a GIS coverage of the study area (D. A. Kinner and R. F. Stallard, US Geological Survey, v1.1, 2003): (1) island area, (2) total edge length, (3) shape index (a measure of complexity of patch shape compared with a standard shape (circle) of the same area (McGarigal & Marks, 1995), and (4) nearest straight-line

distance to the mainland. We considered as mainland any landmass in our study area that was not completely surrounded by water, including Juan Gallegos Island, which is connected to the mainland by a causeway (Fig. 1).

Landscape-level metrics

To investigate whether bat responses to fragmentation were scale-dependent, we delimited the surrounding landscape as a nested set of concentric circles of 0.5-, 1-, and 1.5-km radii centred on each island. Choice of these focal scales was based on considerations to encompass the expected home ranges of different-sized bat species (Gorresen & Willig, 2004) as well as to minimize spatial overlap between neighbouring islands and hence spatial autocorrelation among sampling locations. For each of the three focal scales, we calculated the following landscape-level metrics: (1) mean patch size, (2) patch density, (3) edge density (total length of edge per landscape area), (4) shape index, and (5) forest cover. Because measures such as forest cover do not take isolation of focal patches from other forest fragments into account, we also computed (6) availability of forest cover in the landscape as $I_i = \log_{10} \sum A_j e^{(-D_{ij})}$ (Hanski *et al.*, 1994). Here, I_i is the isolation of the focal patch,

A_j denotes the area of forest cover within the respective radius of fragment j , and D_{ij} is the minimum edge-to-edge distance between focal patch i and fragment j .

Data analysis

Bat inventory completeness

We evaluated inventory completeness with randomized (1000×) sample-based species accumulation curves (Gotelli & Colwell, 2001). In addition, we assessed the number of species expected to occur at each site using a nonparametric species-richness estimator. Based on the estimator choice framework developed by Brose & Martinez (2004), which takes movement heterogeneity of mobile animals such as bats into account, we chose the first-order Jackknife (Jack1). Calculations were made using EstimateS software (Colwell, 2005).

Species diversity, abundance, and assemblage structure

We used EcoSim software (Gotelli & Entsminger, 2006) with 1000 iterations and independent sampling of individuals from the capture pool to compare rarefied species richness and dominance among site categories (mainland interior, mainland edge, near islands, far islands) and between mainland and island assemblages. Dominance was assessed with the Berger-Parker index as the proportional abundance of the most abundant species in a sample (Magurran, 2004). In each case, statistical significance was determined based on the simulated 95% confidence intervals generated by the program (Gotelli & Entsminger, 2006). We generally opted against controlling for elevated experiment-wise error rate in conducting multiple tests on the same independent variables as this approach is controversial (e.g. Moran, 2003).

Kolmogoroff–Smirnov two-sample tests were used to compare rank–abundance curves among bat assemblages. To allow for a comparison of distributions that are not entirely continuous and include ties, P -values were determined through 1000 bootstraps.

We used capture rate [bats per mist net hour (mnh), where one mnh equals one 6-m net open for 1 h] as a standard measure of relative abundance (same-night recaptures excluded), although captures may to some extent also reflect species-specific behaviour and habitat preferences. Differences in nightly capture rates for phyllostomids as a group (log-transformed, captures from ground and high nets combined) among the four site categories and between seasons were assessed with a repeated measures design, with season as within-subjects factor and site category as between-subjects factor. Because of non-orthogonal data, the model was specified as a linear mixed-effects model (fixed effects: site category, season; random effects: site, capture night nested within site) fit by maximum likelihood (Pinheiro & Bates, 2000).

We compared the number of species and captures in ensembles among the four site categories using chi-square tests whereby the number of species and captures at mainland

interior sites was used to generate expected values. Significance was determined through a randomization approach (1000 iterations), where the observed table was compared with a set of randomly generated tables with the same row and column totals (Manly, 1997).

We used the Bray–Curtis coefficient to describe dissimilarity in terms of species composition between pairs of sampling sites (Magurran, 2004). Non-metric multidimensional scaling (NMDS) was then employed to ordinate sites and to evaluate inter-site differences in bat assemblage structure both at the species and at the ensemble level. NMDS is a robust, nonlinear ordination technique regarded as an effective method for analysing ecological community data (McCune & Grace, 2002). Prior to analysis, data were standardized and, as ordination results can be overly sensitive to rare species, only those species with at least five first captures were included in the analysis. Composition differences among the four site categories were assessed with an analysis of similarity (ANOSIM), a nonparametric multivariate permutation procedure broadly analogous to a standard univariate ANOVA, which tests for differences between *a priori*-defined groups of community samples based on a (dis)similarity matrix (Clarke, 1993).

Bat fauna–environment modelling

For each netting plot we calculated tree density and basal area. Average values across replicated subplots were calculated for all other vegetation variables, namely sapling density, canopy height, and percentage canopy closure. Vertical foliage structure was determined as the average number of strata with foliage across the nine subplots sampled in each transect. Following Raman & Sukumar (2002), we used the coefficient of variation of this index as a measure of horizontal heterogeneity in foliage structure. Vegetation structure variables (see Table S1 for summary statistics) were $\log(x + 1)$ -transformed, and NMDS on a matrix of normalized Euclidean distances was used to generate axes representing gradients in forest structure among sites (see Fig. S2 in Supplementary Material) that were subsequently used in modelling.

Landscape metrics can be correlated with habitat area (Villard *et al.*, 1999; Fahrig, 2003). Because it is important to assess separately the influence of habitat loss from the configurational effects of fragmentation (Fahrig, 2003), we statistically controlled for the correlation between forest cover and the various landscape configuration indices by using the residuals of linear regressions as values for the explanatory variables (Villard *et al.*, 1999; Gorresen *et al.*, 2005). Furthermore, because of multicollinearity among both local and landscape variables, pairwise comparisons of predictor variables were made using Spearman rank correlations, and, where pairs of variables were significantly correlated, one of the variables was eliminated. This resulted in a final set of $n = 8$ explanatory variables. Local-scale variables were forest structure (scores of NMDS axes 1 and 2), as well as island size (log-transformed), total edge (significantly correlated with shape index), and distance to the mainland (log-transformed).

Landscape metrics retained in the final analysis were mean patch size (significantly correlated with patch density, shape index and Hanski's I), edge density (significantly correlated with Hanski's I), and forest cover (log-transformed).

We examined correlations between both phyllostomid species richness and assemblage composition, and local- and landscape-level characteristics using generalized linear models (GLMs). For species richness, data were counts, and a Poisson error distribution and log link-function were used. For species composition, as represented by the scores of the first NMDS axis that explained most of the variation among sites, GLMs with a normal error distribution were appropriate, as NMDS scores were normally distributed.

Rather than using stepwise selection procedures, whose use is statistically problematic, we employed an information-theoretic model selection approach to analyse bat fauna–environment relationships (Burnham & Anderson, 2002). We restricted inference to a subset of plausible models selected *a priori* (see Table S2; Burnham & Anderson, 2002), modelling local-scale variables in combination with landscape metrics separately for the three focal scales. For each model we calculated Akaike's information criterion corrected for small sample size (AIC_c) following Burnham & Anderson (2002). Candidate models were then compared and ranked by rescaling the AIC_c values such that the model with the minimum AIC_c has a value of 0; that is, $\Delta_i = AIC_i - AIC_{\min}$. Models for which $\Delta_i \leq 2$ are considered to have substantial support, models with values of 4–7 have considerably less support, and those with $\Delta_i \geq 10$ have essentially no empirical support (Burnham & Anderson, 2002). In addition, we calculated the Akaike weights (w_i) for each candidate model, which provide approximate probabilities that model i is the actual best model in the set of candidate models (Burnham & Anderson, 2002). The relative likelihood of model i vs. model j can be judged by the ratio of the Akaike weights of the best model and the second-ranked model (i.e., w_i/w_j). Model fit was assessed using percentage deviance explained and R^2 . Unless stated otherwise, all analyses were performed using the *R* statistical package (version 2.2.0, R Development Core Team, 2006).

RESULTS

Species richness and dominance

A total of 8447 captures representing five families, 30 genera, and 39 species were obtained during 125 sampling nights (details in the Appendix). Phyllostomid bats made up the majority of captures (98.2%). Species-accumulation curves approximated an asymptotic relationship and indicated a high level of inventory completeness for phyllostomid bats (> 91% for mainland and > 95% for island assemblages; Table 1, Fig. S1).

More species of phyllostomids were recorded for the mainland ($S_{\text{obs}} = 30$) than for the islands ($S_{\text{obs}} = 21$). Similar numbers of species were captured at mainland interior ($S_{\text{obs}} = 28$) and at edge ($S_{\text{obs}} = 27$) sites. Twenty-one species were detected on near islands, but observed species richness was, with 15

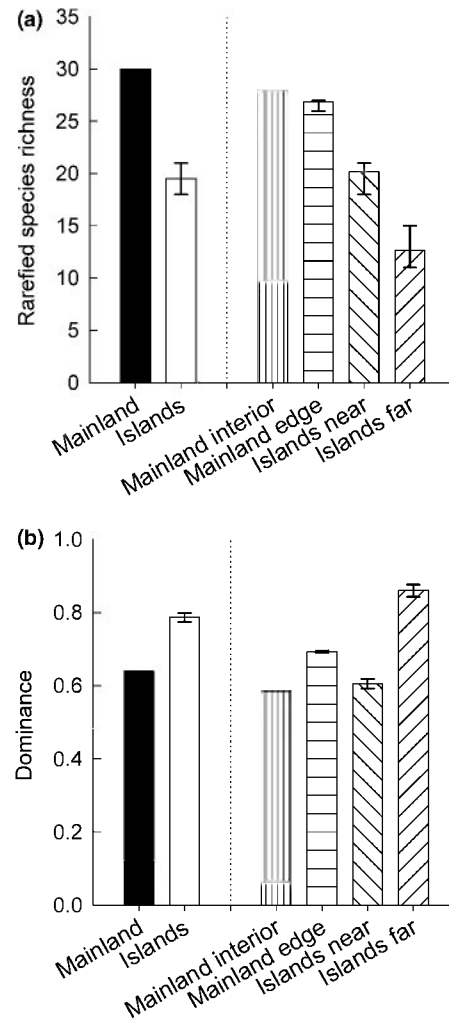


Figure 2 Rarefied species richness (a) and dominance (b).

Comparisons between mainland sites and islands were made at the abundance level of the former ($n = 2485$ individuals), and those among site categories were based on the abundance of mainland interior sites ($n = 1231$ individuals). Error bars represent 95% confidence intervals.

species, much lower on far islands (Table 1). For each site category, the estimate of predicted species richness (S_{Jack1}) was close to the observed species richness (Table 1), corroborating the adequacy of our sampling protocol to detect rare species.

Rarefied phyllostomid species richness differed significantly (as indicated by the 95% confidence intervals) between mainland and island assemblages, as well as among site categories (Fig. 2a). Species richness was highest at mainland interior sites, slightly lower at edge sites, and substantially higher on near compared with far islands. This pattern is consistent with results for observed species richness. Dominance differed significantly among site categories, with island assemblages having higher dominance than mainland assemblages (Fig. 2b). Mainland edge sites had significantly higher dominance than did sites on near islands.

Rank–abundance distributions (Fig. 3) for forest interior and edge sites did not differ significantly ($D = 0.3$, $P = 0.252$);

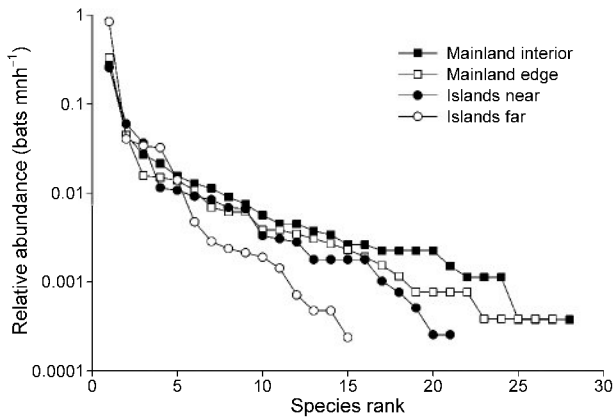


Figure 3 Rank–abundance plots based on captures of phyllostomid bats in continuous forest (mainland interior and edge sites) and on near and far islands in Gatún Lake, Panama.

however, both distributions differed drastically from those for assemblages on far islands ($D \geq 0.65$, $P < 0.001$). There were also significant differences in rank–abundance distributions between mainland interior and near islands ($D = 0.45$, $P = 0.017$), whereas differences were only marginally significant between near islands and edge sites ($D = 0.4$, $P = 0.064$) and between near and far islands ($D = 0.35$, $P = 0.083$).

Relative abundance

Artibeus jamaicensis, *A. lituratus*, and *Uroderma bilobatum*, all canopy frugivores, were the three most abundant species and accounted for 86.1% of all captures. *Artibeus jamaicensis* and especially *U. bilobatum* showed a higher capture rate on islands than at mainland interior sites (Fig. 4a). Similarly, the capture rate for the nectarivorous *Glossophaga soricina*, which was

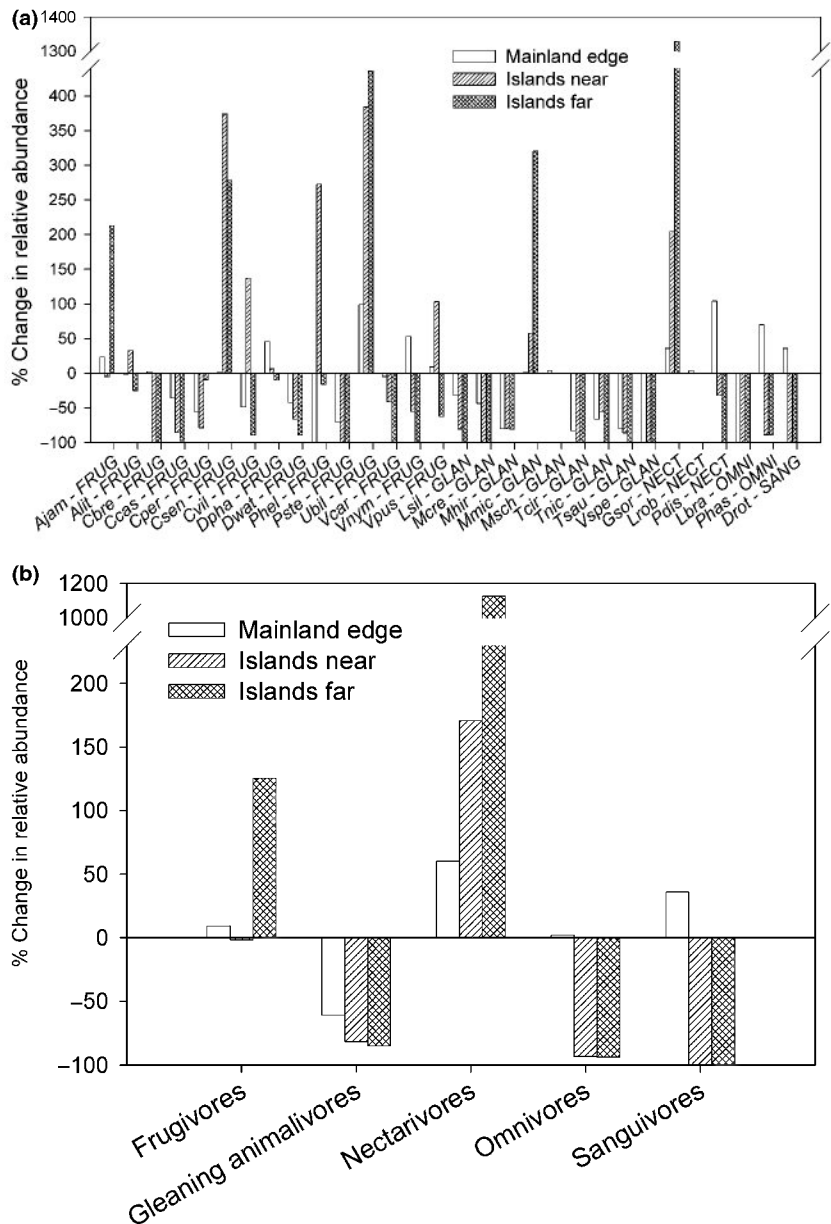


Figure 4 Percentage change in relative abundance of phyllostomid bats relative to mainland interior sites for (a) species and (b) ensembles. See Appendix for species and ensemble abbreviations.

infrequently caught at mainland interior sites, increased towards edge sites and was even higher on near and especially far islands. In contrast, the majority of other species, a few of the smaller frugivores (*Carollia castanea*, *Artibeus watsoni*, *Vampyressa nymphaea*) and most notably gleaning animalivores, substantially decreased in relative abundance from forest interior to forest edge sites to near and far islands or were even absent from the islands altogether (Fig. 4a,b). None of the larger gleaning animalivores that were common on the mainland (i.e. *Lophostoma silvicolium*, *Tonatia saurophila* and *Trachops cirrhosus*) were captured on far islands. *Micronycteris microtis* was the only gleaning animalivore that had higher capture rates on islands than on the mainland. In our study area, most animalivorous gleaners were thus highly sensitive to forest edges, as evidenced by strongly reduced capture rates relative to forest interior sites (Fig. 4a,b).

Linear mixed-effects modelling revealed a significant difference in overall capture rates among site categories ($F = 5.73$, $P = 0.01$). This effect was the result of the highly elevated capture rates, mostly of canopy frugivores, on far islands ($t = 2.84$, $P = 0.014$), which were more than twice as high as those on near islands and at mainland sites (Table 1). There was also a strong seasonal effect ($F = 14.22$, $P < 0.001$), with capture rates increasing from the dry towards the wet season ($t = 3.77$, $P = 0.0003$).

Assemblage structure

In the NMDS ordination (stress = 10.33), three clusters were distinguished, representing a gradient in species composition from mainland sites to near and far islands along dimension 1 (Fig. 5a). Mainland sites clustered together, indicating high similarity in assemblage structure. Near islands and two of the far islands, León and Pato Horqueta, formed a second cluster, clearly separated from the remaining far islands, which grouped to the far right. Assemblage composition differed significantly among site categories (ANOSIM, global $R = 0.698$, $P < 0.001$). Pairwise tests showed no significant compositional differences between mainland edge and interior sites ($R = -0.037$, $P = 0.6$) or between edge sites and near islands ($R = 0.313$, $P = 0.107$), whereas all other comparisons were significant ($R > 0.672$, $P < 0.018$).

Ensemble richness and composition

Regardless of site category, frugivores accounted for the majority of captures (> 90%) and contained the highest species richness, followed by gleaning animalivores (Table 2). Mainland edge and both near and far islands did not differ significantly from mainland interior sites in terms of the number of species per ensemble ($\chi^2 < 2.86$, $P > 0.5$ for all comparisons). In contrast, the number of captures within ensembles differed significantly between mainland interior sites and all other site categories ($\chi^2 > 43.10$, $P < 0.001$). The differences were largely attributable to the pronounced increase in the capture rates of frugivores and nectarivores as well as to

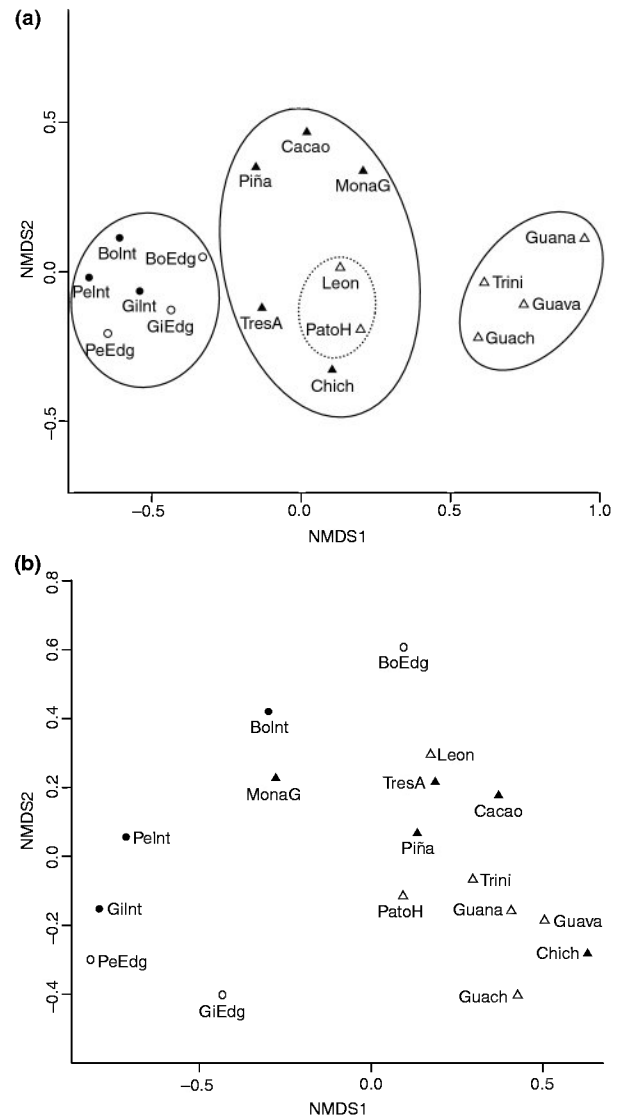


Figure 5 Ordination of study sites along non-metric multidimensional scaling axes for (a) phyllostomid bat species and (b) ensembles. (●) mainland interior sites, (○) mainland edge sites, (▲) near islands, (△) far islands.

Table 2 Species richness (S), number of bat captures (N), and percentage relative abundance (%) of bat ensembles in continuous forest and on islands in Gatún Lake, Panama.

	Mainland			Islands								
	Interior	Edge		Near		Far						
Ensemble	S	N	%	S	N	%	S	N	%	S	N	%
Frugivores	15	1113	91	14	1192	95	13	1617	97	11	3981	96
Gleaning animalivores	8	96	8	8	37	3	5	26	2	2	23	1
Nectarivores	2	7	1	3	11	1	2	28	2	1	136	3
Omnivores	2	10	1	1	10	1	1	1	0	1	1	0
Sanguivores	1	3	0	1	4	0	0	0	0	0	0	0

the decrease in capture rates of gleaning animalivores at these sites relative to interior plots in continuous forest (Fig. 4b).

In a two-dimensional NMDS plot of sites in ensemble space (Fig. 5b; stress = 6.18), mainland sites were more dispersed along both axes than based on species composition. Islands grouped loosely together. However, there was some overlap between near and far islands, as the largest of the far island group, León, was closer in ordination space to near islands, and one of the near islands, Chicha, had an ensemble composition typical of far island assemblages (Fig. 5b).

ANOSIM revealed significant differences in ensemble composition among site categories (global $R = 0.45$, $P = 0.002$). Pairwise comparisons indicated significant compositional differences between mainland interior sites and both near ($R = 0.64$, $P = 0.036$) and far ($R = 0.98$, $P = 0.012$) islands as well as between mainland edge and far islands ($R = 0.63$, $P = 0.012$).

Bat fauna–environment modelling

Different variables were important at different spatial scales in determining both species richness and species composition of bats on Gatún Lake islands. Area effects were more important and distance effects were less pronounced at larger spatial scales. For species richness, distance from the mainland received the strongest support for a model set that included local-scale characteristics (i.e. vegetation structure and patch-level metrics) and landscape metrics of the smallest (0.5 km) focal scale (Table 3; see Table S2 for complete modelling results). Edge density likewise had considerable support ($\Delta_i = 1.85$), suggest-

ing that phyllostomid assemblages react to habitat boundaries to some degree; however, this model was about 2.5 times less likely based on Akaike weights and also had a much lower regression coefficient (Table 3). For model sets incorporating 1-km and 1.5-km landscape metrics besides local-scale variables, the best-ranking model was amount of forest cover in the landscape. It was also the most likely according to Akaike weights, which had values of 0.661 and 0.710, respectively, whereas the model ranked second, distance to the mainland, had weights of $w_i = 0.252$ and 0.210, respectively.

For species composition, amount of forest cover was the single best model selected, receiving overriding support ($w_i > 0.98$) at the two larger spatial scales examined. In contrast, at the 0.5-km scale, distance from the mainland was again the best predictor of species composition on islands ($w_i = 0.518$). However, there were two other plausible models in this set, one single-process model containing edge density that was only 1.6 times less likely ($w_i = 0.316$), and one model examining additive effects among landscape characteristics that also received some degree of support ($w_i = 0.102$) but was about five times less likely than the top-ranked model.

DISCUSSION

Assemblage patterns

Our analyses revealed strong contrasts in phyllostomid bat assemblages between continuous forest and islands in terms of rank–abundance distributions and assemblage-level attributes, with isolation as the main factor underlying bat responses.

Table 3 Best-approximating generalized linear model sets ($w_i > 0.1$) for assessing the association between, respectively, bat species richness and assemblage composition on islands in Gatún Lake, and local-scale characteristics and landscape-level metrics for three focal scales. For each model, the number of estimable parameters (K), log-likelihood ($\log(L)$), sample-size adjusted Akaike information criterion (AIC_c), Akaike differences (Δ_i), Akaike weights (w_i) as well as parameter estimates (β) and their standard errors are presented. Model fit for the most highly parameterized model in each set is given as deviance explained or R^2 . See Table S2 for complete modelling results.

Model description	K	$\log(L)$	AIC_c	Δ_i	w_i	β_0	SE	β_1	SE	β_2	SE	β_3	SE
Species richness													
0.5-km landscape (% dev. = 0.73)													
Distance to mainland	2	-24.67	54.83	0	0.569	3.182	0.368	-0.150	0.059				
Edge density	2	-25.59	56.68	1.85	0.226	2.245	0.099	-0.014	0.007				
1-km landscape (% dev. = 0.81)													
Forest cover	2	-23.70	52.90	0	0.661	0.514	0.650	0.451	0.162				
Distance to mainland	2	-24.67	54.83	1.93	0.252	3.182	0.368	-0.150	0.059				
1.5-km landscape (% dev. = 0.88)													
Forest cover	2	-23.46	52.42	0	0.710	0.871	0.516	0.300	0.106				
Distance to mainland	2	-24.67	54.83	2.41	0.212	3.182	0.368	-0.150	0.059				
Species composition													
0.5-km landscape ($R^2 = 0.81$)													
Distance to mainland	3	0.13	9.17	0	0.518	-0.790	0.345	0.170	0.052				
Edge density	3	-0.37	10.16	0.99	0.316	0.298	0.083	0.017	0.006				
Edge density + mean patch size + forest cover	5	4.79	12.42	3.24	0.102	0.773	0.340	0.024	0.005	0.032	0.012	-0.170	0.119
1-km landscape ($R^2 = 0.84$)													
Forest cover	3	4.46	0.51	0	0.982	2.239	0.334	-0.511	0.088				
1.5-km landscape ($R^2 = 0.86$)													
Forest cover	3	5.08	-0.74	0	0.989	1.781	0.243	-0.329	0.053				

In addition, several species and ensembles showed a negative response even towards edge habitats in continuous forest (see below). Mainland sites were characterized by higher species richness and lower dominance, whereas islands harboured a less diverse and structurally simplified bat fauna, with remote islands being especially species-poor. This pattern is consistent with previous studies on bats in disturbed or fragmented systems (Estrada *et al.*, 1993; Cosson *et al.*, 1999; Medellín *et al.*, 2000; Sampaio, 2000).

Compared with studies conducted in systems with a low fragment–matrix contrast, the observed magnitude of responses was, as hypothesized, often greater, probably as a result of the particular nature of the matrix. Gleaning animalivores, as in other studies (Fenton *et al.*, 1992; Sampaio, 2000; Pons & Cosson, 2002; Clarke *et al.*, 2005), were the most adversely affected ensemble, with markedly reduced abundance or complete absence on the islands. Causes for this fragmentation sensitivity may include insufficient resources in fragments, i.e. food and roosts (e.g. Kalko *et al.*, 2006), specialized foraging strategies, high sensitivity towards habitat edges, and limited mobility (Estrada & Coates-Estrada, 2002; Clarke *et al.*, 2005; Meyer *et al.*, 2008). The latter may be one of the main reasons why none of the larger gleaning animalivores was found on far, isolated islands, as these species are adapted to slow manoeuvrable flight inside dense vegetation: this makes prolonged and regular commuting flights across unsuitable matrix habitat energetically costly. Limited dispersal capacity has also been considered a key factor in determining the sensitivity of tropical insectivorous birds to fragmentation (Sekercioglu *et al.*, 2002), and constituted a major predictor of avian distribution patterns on Gatún Lake islands (Moore, 2005). *Micronycteris microtis* was the only gleaning animalivore not negatively affected by isolation or habitat area. On the contrary, it was much more frequently caught on islands than in continuous forest (Fig. 4a). *Micronycteris microtis* has very small area requirements (core foraging areas c. 0.5 ha; Albrecht *et al.*, 2007). This and the presence of colonies on some of the islands suggest that these bats may be able to persist in small, isolated habitat remnants for quite a long time once they have colonized them, which probably occurs mainly during natal dispersal.

Strikingly higher capture rates on islands relative to mainland interior sites substantiate previous findings that the nectarivorous *G. soricina* is able to acclimate well to disturbed and fragmented habitats, as has been documented in other studies, although quantitatively not to this extent (Estrada & Coates-Estrada, 2002; Clarke *et al.*, 2005; Willig *et al.*, 2007).

Similarly, frugivores were much more abundant on the islands than on the mainland. This was almost entirely as a result of a pronounced increase in the capture rates of the canopy frugivores *A. jamaicensis* and *U. bilobatum*, both of which were particularly common on far islands (Fig. 4a). This corroborates several other studies that have demonstrated an increase in the abundance of a few canopy or understory frugivores following fragmentation or disturbance (Medellín *et al.*, 2000; Sampaio, 2000; Clarke *et al.*, 2005; Willig *et al.*, 2007). It contrasts, however, with the findings of Cosson *et al.*

(1999), who reported an overall reduction in phyllostomid abundance after fragmentation on land-bridge islands in French Guiana and no noticeable increase of any particular species.

Empirical evidence is mounting that short- to medium-term time lags in species responses are ubiquitous (Ewers & Didham, 2006). Bat assemblages on Gatún Lake islands, which are > 90 years old, have probably reached a fairly stable species richness and composition, a notion that is supported by the fact that there is very little turnover in species composition between successive sampling years (Meyer & Kalko, 2008). Given that Cosson *et al.* (1999) examined short-term responses of bats immediately following fragmentation, in their study the time frame may not have been long enough for fragmentation effects to be fully exhibited. In spite of the low temporal species turnover, our mark-recapture data (Table S3) suggest that some highly vagile species (mostly *A. jamaicensis*, *A. lituratus*, and *U. bilobatum*) may regularly move among neighbouring islands on a nightly basis. However, even for *A. jamaicensis*, the species with the largest number of extra-site recaptures (38.1%) and by far the most mobile, our recapture data indicate that long-distance cross-water movements are rather infrequent, as inter-habitat movements occurred mostly within the same site category (Table S3). Generally, the water matrix seems to be a movement barrier significant enough that many species apparently do not regularly cross it.

Limited mobility is probably the main factor responsible for the low capture rates of many of the smaller frugivores such as *A. watsoni*, *V. nymphaea*, and *V. pusilla* on far islands. Two understory bats common in mainland forest, *Carollia perspicillata* and *C. castanea*, which specialize to different degrees on fruits of *Piper* spp. (Thies & Kalko, 2004), also had overall lower capture rates on islands. The fact that *Piper* is rather uncommon on most islands (C. Meyer, unpublished data) may hence be a direct consequence of limited seed dispersal events because of the bats' reluctance to regularly traverse the hostile matrix. Contrasting abundance patterns for understory frugivores have been observed in fragmented landscapes in Brazil where forest remnants are surrounded by regrowth (*Piper*, *Vismia*) that provides additional food resources, augmenting the abundance of species such as *Carollia* (Sampaio, 2000; Faria, 2006). Our results thus confirm the idea that matrix quality and a species' ability to utilize resources in the matrix can alter the intensity of observed fragmentation effects (Ewers & Didham, 2006).

Responses to forest edges

Although our data show marked differences in bat species richness and assemblage structure between islands and the mainland, they provide only limited evidence for a distinct edge–interior gradient in these attributes in continuous forest. Species richness was significantly higher for mainland interior compared to edge sites, in line with findings by Faria (2006), who reported a decrease in phyllostomid species richness at edges relative to the interior of mature stands of Atlantic rain forest in Brazil. However, in our study, rank–abundance

distributions between edge and interior sites were indistinguishable, and no significant differences were found for species composition. Gradual edge-related changes in species composition might generally be hard to detect owing to the fact that they are a composite of individual species responses, which can be extremely varied (Ewers & Didham, 2006).

An edge effect was discernible for certain species and ensembles in our study. Species that exhibited high matrix tolerance were also edge-tolerant, consistent with our prediction, whereas species that were absent or less common on islands typically also had lower capture rates at edge sites. In fact, a modelling analysis examining ecological correlates of fragmentation sensitivity suggested edge sensitivity as the species trait most strongly associated with bat species occurrence and abundance on the study islands, whereas there was no strong relationship with other traits such as body mass or dietary specialization (Meyer *et al.*, 2008). Some gleaning animalivores, most notably *T. saurophila*, *T. cirrhosus*, *M. hirsuta*, and *L. silvicolum*, were edge-sensitive, as indicated by an often pronounced decrease in capture rates relative to that at forest interior sites (Fig. 4). In contrast, the canopy frugivores *U. bilobatum* and *A. jamaicensis*, as well as the nectarivore *G. soricina*, can be classified as edge-preferring based on their higher capture rates at edge sites (Fig. 4).

Our findings are largely congruent with those from studies on tropical birds that have reported lower species richness at edges and a more or less pronounced shift in ensemble composition whereby frugivores and nectarivores were typically more abundant and many gleaning insectivores were less common at forest edges (Restrepo & Gomez, 1998; Dale *et al.*, 2000; Laurance *et al.*, 2004; but see Watson *et al.*, 2004). For birds, changes in habitat structure and concurrent alterations in microclimatic conditions at forest edges have been shown to be linked to edge sensitivity (Watson *et al.*, 2004). In the present study, however, mainland interior and edge sites were similar with respect to the forest structural variables measured (Table S1, Fig. S2). The observed effects on the level of individual species or ensembles may therefore be a corollary of species-specific responses to changes in the abundance or distribution of certain resources rather than to structural features of the habitat, a notion which, however, remains to be tested.

Importance of local vs. landscape characteristics and scale dependence

Our results corroborate the findings of Gorresen & Willig (2004) and Gorresen *et al.* (2005) that the responses of bats to characteristics of fragmented landscapes are sensitive to spatial scale. Species richness and structure of phyllostomid assemblages on the study islands were most strongly determined by distance from the mainland, which was the prominent factor at the smallest spatial scale, and by the amount of forest cover in the surrounding landscape, which was the best predictor at larger spatial scales.

Our finding of a lack of a species–area relationship and overall dominant distance effect in governing species richness

at the island level may be explained by at least two, probably interacting, effects. First, our results support the existence of a small-island effect; that is, the tendency for species–area relationships to be weak or nonsignificant for groups of small isolates (Lomolino & Weiser, 2001; Turner & Tjørve, 2005). Small-island effects may become apparent at a range of island sizes where resource levels are insufficient to maintain populations of most species and where habitat characteristics, episodic disturbances, and isolation are much more likely to determine how many and which species are able to maintain populations (Lomolino, 2000; Lomolino & Weiser, 2001). In our study system, the range of island sizes (2.5–50 ha) was rather small compared with levels of isolation, thus supporting the idea of a small-island effect. In addition, the fact that isolation was much more important than island area in determining bat species richness at the patch level may be related to the type of matrix in this study. Owing to the inhospitableness of water, that is, its ability to act as a fine-pored selective filter, which only a subset of the more mobile canopy frugivores appear to regularly pass, area effects might be obfuscated at local scales.

Our findings contrast with those for birds in the same study system, for which species richness was positively correlated with island area (Moore, 2005). In our case, an area effect was apparent only at the landscape scale, where we observed a positive relationship between phyllostomid species richness and the amount of forest cover. Although the minimum area requirements are not fully known for the majority of tropical bat species, larger areas should meet the minimum area requirements of more species, resulting in increases in species richness with area (Lomolino, 2000; Turner & Tjørve, 2005).

Local vegetation structure is a potentially strong determinant of species diversity and composition in many study systems and for a variety of taxa, including bats (Schmiegelow *et al.*, 1997; Raman & Sukumar, 2002; Erickson & West, 2003; but see Graham & Blake, 2001). However, we found no strong evidence for bats on our study islands to respond to structural heterogeneity with respect to species richness and assemblage composition. A limited effect of forest age, however, is suggested by the fact that two far islands that contained relatively mature forest (Pato Horqueta, León) resembled more closely assemblages on near islands in terms of species richness and composition (Table 1, Fig. 5a).

Implications for conservation

Forested islands surrounded by a homogeneous aquatic matrix can be viewed as analogues of anthropogenic landscapes with patches of forest embedded in heavily grazed pasture without trees or bushes; that is, they can be construed to represent a worst-case scenario. The fact that even small islands embedded in such a hostile matrix can support a relatively diverse bat fauna, provided that there is a low degree of patch isolation and spatial proximity to larger blocks of continuous forest, has important ramifications for reserve design and conservation planning. Our findings add to the growing evidence that small

habitat remnants can be of substantial conservation value for a variety of animals, including mobile groups such as bats (Turner & Corlett, 1996; Gorresen & Willig, 2004; Faria, 2006). Furthermore, our study emphasizes the importance of considering both structural and functional connectivity in determining responses to fragmentation (e.g. Uezu *et al.*, 2005; Henry *et al.*, 2007). Long-term metapopulation persistence in fragmented landscapes requires individuals to cross habitat boundaries and disperse among remnant patches. Those phyllostomid bats that exhibit high mobility and are not reluctant to move through deforested areas around fragments can link small populations that would otherwise be isolated and prone to local extinction (i.e. enhance the rescue effect *sensu* Brown & Kodric-Brown, 1977), therefore improving the survival chances of many forest-dependent bats in fragmented landscapes and assuring the maintenance of the ecosystem services provided by these animals.

Our modelling results generally point to habitat loss rather than fragmentation *per se* as the main process after isolation underlying phyllostomid bat responses on islands in Gatún Lake. This concurs with a recent review by Fahrig (2003), who argued that in most studies the effects of fragmentation *per se* are absent or too weak to be detected or may only become apparent at low levels of habitat amount, suggesting that conservation efforts that attempt to minimize fragmentation for a given amount of habitat may often be inadequate.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Summary of vegetation characteristics of the study sites.

Table S2 Complete modelling results assessing the association between bat species richness and assemblage composition on

islands in Gatún Lake, and local-scale characteristics and landscape-level metrics.

Table S3 Mark–recapture data and inter-habitat movements.

Figure S1 Species-accumulation curves for phyllostomid bats sampled in this study.

Figure S2 Non-metric multidimensional scaling plot of the study sites based on vegetation characteristics.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/10.1111/j.1365-2699.2008.01916.x> (This link will take you to the article abstract.)

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BIOSKETCHES

Christoph F. J. Meyer conducted this work as part of his PhD at the University of Ulm. He has research interests in bat ecology, particularly relating to biodiversity research, community and landscape ecology, and conservation.

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APPENDIX

List of bat species and number of captures. Captures of non-phyllostomid bats were not included in the analyses. Taxonomy follows Simmons (2005).

Taxon	Acronym	Ensemble	Mainland		Islands		Total
			Interior	Edge	Near	Far	
Phyllostomidae							
<i>Carollia brevicauda</i>	Cbre	FRUG	1	1	0	0	2
<i>Carollia castanea</i>	Ccas	FRUG	57	36	12	2	107
<i>Carollia perspicillata</i>	Cper	FRUG	41	18	13	59	131
<i>Desmodus rotundus</i>	Drot	SANG	3	4	0	0	7
<i>Glossophaga soricina</i>	Gsor	NECT	6	8	27	136	177
<i>Lamproncycteris brachyotis</i>	Lbra	OMNI	4	0	0	0	4
<i>Lophostoma silvicolum</i>	Lsil	GLAN	24	16	7	0	47
<i>Mimon crenulatum</i>	Mcre	GLAN	9	5	0	0	14
<i>Micronycteris hirsuta</i>	Mhir	GLAN	10	2	3	3	18
<i>Micronycteris microtis</i>	Mmic	GLAN	3	3	7	20	33
<i>Micronycteris schmidtorum</i>	Msch	GLAN	0	1	0	0	1
<i>Phyloderma stenops</i>	Pste	FRUG	7	2	0	0	9
<i>Phyllostomus discolor</i>	Pdis	NECT	1	2	1	0	4
<i>Phyllostomus hastatus</i>	Phas	OMNI	6	10	1	1	18
<i>Trachops cirrhosus</i>	Tcir	GLAN	12	2	0	0	14
<i>Trinycteris nicefori</i>	Tnic	GLAN	3	1	2	0	6
<i>Tonatia saurophila</i>	Tsau	GLAN	34	7	7	0	48
<i>Vampyrum spectrum</i>	Vspe	GLAN	1	0	0	0	1
<i>Artibeus jamaicensis</i>	Ajam	FRUG	718	869	1010	3560	6157
<i>Artibeus lituratus</i>	Alit	FRUG	120	116	235	143	614
<i>Artibeus phaeotis</i>	Dpha	FRUG	7	10	11	10	38
<i>Artibeus watsoni</i>	Dwat	FRUG	72	41	36	12	161
<i>Centurio senex</i>	Csen	FRUG	1	1	7	6	15
<i>Chiroderma villosum</i>	Cvil	FRUG	12	6	42	2	62
<i>Lonchophylla robusta</i>	Lrob	NECT	0	1	0	0	1
<i>Platyrrhinus helleri</i>	Phel	FRUG	6	0	33	8	47
<i>Uroderma bilobatum</i>	Ubil	FRUG	20	39	143	170	372
<i>Vampyrodes caraccioli</i>	Vcar	FRUG	30	28	26	0	84
<i>Vampyressa nymphaea</i>	Vnym	FRUG	6	9	4	0	19
<i>Vampyressa pusilla</i>	Vpus	FRUG	15	16	45	9	85

APPENDIX

(Continued)

Taxon	Acronym	Ensemble	Mainland		Islands		Total
			Interior	Edge	Near	Far	
Emballonuridae							
<i>Centronycteris centralis</i>	Ccen	AEIN	0	1	2	0	3
<i>Cormura brevirostris</i>	Cbrev	AEIN	0	0	3	0	3
<i>Diclidurus albus</i>	Dalb	AEIN	0	0	0	1	1
<i>Saccopteryx bilineata</i>	Sbil	AEIN	3	10	4	8	25
<i>Saccopteryx leptura</i>	Slep	AEIN	1	5	3	1	10
Mormoopidae							
<i>Pteronotus parnellii</i>	Ppar	AEIN	24	8	5	18	55
Noctilionidae							
<i>Noctilio leporinus</i>	Nlep	TRIN	0	0	0	2	2
Vespertilionidae							
<i>Lasiurus ega</i>	Lega	AEIN	1	0	0	0	1
<i>Rhogeessa tumida</i>	Rtum	AEIN	3	0	2	0	5

AEIN, aerial insectivore; FRUG, frugivore; GLAN, gleaning animalivore; NECT, nectarivore; OMNI, omnivore; SANG, sanguivore; TRIN, trawling insectivore/piscivore.