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Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system

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ABSTRACT

Habitat fragmentation causes drastic changes in the biota and it is crucial to understand these modifications to mitigate its consequences. While studies on Neotropical bats have mainly targeted phyllostomid bats, impacts of fragmentation on the equally important aerial insectivores remain largely unexplored. We studied species richness, composition, count abundance and feeding activity of aerial insectivorous bats in a system of land-bridge islands in Panama with acoustic sampling. We predicted negative effects of fragmentation on forest species while bats foraging in open space should remain essentially unaffected. Rarefaction analyses indicated higher species richness for islands than mainland sites. For forest species, multivariate analyses suggested compositional differences between sites due to effects of isolation, area and vegetation structure. Contrary to our expectations, count abundance of forest species was similar across site categories. Feeding activity, however, was curtailed on far islands compared to near islands. As expected, bats hunting in open space did not reveal negative responses to fragmentation. Interestingly, they even displayed higher abundance counts on far and small islands. On the species level, two forest bats responded negatively to size reduction or site isolation, respectively, while a forest bat and a bat hunting in open space were more abundant on islands, irrespectively of island isolation or size. Our findings suggest that small forest remnants are of considerable conservation value as many aerial insectivores intensively use them. Hence high conservation priority should be given to retain or re-establish a high degree of forest integrity and low levels of isolation.

1. Introduction

It is now widely accepted that the pervasive biodiversity loss in tropical environments is powered by the conversion of forests into agricultural and grazing landscapes (Laurance and Peres, 2006). This produces a mosaic of isolated remnants, large and small, that harbors a partial selection of the original diversity, where species abundance, richness, and evenness have changed dramatically across taxonomic groups (Laurance et al., 2002; Ewers and Didham, 2006). Following such modifications, ecological interactions such as seed dispersal, pollination and insect predation are transformed, and terminated in the worst case scenario (Restrepo et al., 1999; Laurance et al., 2002).

Changes in assemblage structure in forest fragments are mediated by, among others, the type of matrix surrounding the remnants and by species' perceptions of the matrix (Kupfer et al., 2006). Matrices with low permeability reduce population connectivity among remnants and accentuate the effects of isolation regardless of the real inter-patch distance (Ricketts, 2001). However, tolerance of the matrix and dispersal ability will set the degree of inter-patch movement and therefore determine the species' sensitivity to fragmentation (Ewers and Didham, 2006; Meyer and Kalko, 2008).

Resource availability within fragments and the matrix also shape changes in assemblage structure. For example Gascon et al. (1999) have shown that birds, small mammals and frogs that avoid the matrix tend to decline in fragments while those that can use the matrix often remain stable or even increase in abundance. Finally, the level of contrast in vegetation between fragment and matrix, in addition to remnant size, produces edge effects that modify niche characteristics and ultimately affect animal assemblages (Watson, 2002). As an example, tropical birds and small terrestrial mammals show reduced richness, abundance and probability of

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occurrence in response to forest edges (Beier et al., 2002; Laurance et al., 2002; Lambert et al., 2003).

Bats are well-suited to examine fragmentation effects because they are highly mobile, and ecological diverse with a variety of feeding and roosting habits (Fenton et al., 1992; Gorresen and Willig, 2004; Meyer et al., 2008). While Neotropical bat assemblages are dominated by members of the endemic family Phyllostomidae (New World leaf-nosed bats), the other eight families found in the Americas are also species-rich. Almost half (46%) of the species of the entire bat assemblage known to occur on Barro Colorado Island, Panama, are non-phyllostomid bats (Kalko et al., 2008). Despite their species richness and their important role as control agents of insects (Cleveland et al., 2006) information about aerial insectivores in lowland rainforests is still scarce (Jung et al., 2007).

The ensemble of aerial insectivorous bats consists of species that rely on echolocation as their main sensory input to navigate, orient and forage, thereby capturing insects on the wing. They hunt either inside or above the forest canopy. These sensory capacities, in addition to morphology and foraging habits, allow the separation of aerial insectivorous bats into three functional groups: (1) bats that forage in highly-cluttered space, (2) background-cluttered space and (3) uncluttered space (sensu Schnitzler and Kalko, 2001). Bats hunting for insects in highly-cluttered space forage within vegetation and use special auditory adaptations (i.e., Doppler shift compensation) for prey detection whereas species foraging in background-cluttered space acquire food by capturing insects in aerial pursuits at forest edges, in forest gaps or by trawling insects and/or fish from water surfaces. Bats hunting in uncluttered space are fast flyers and forage on insects above the canopy. Our paucity of knowledge of aerial insectivorous bats likely stems primarily from logistical constraints, as standard mist net protocols are inadequate for a comprehensive assessment of aerial insectivores (O'Farrell and Gannon, 1999; Kalko et al., 2008). Although high forest strata have been intensively surveyed with mist nets (e.g. Kalko and Handley, 2001; Bernard, 2001; Meyer and Kalko, 2008), it is acknowledged that richness and abundance of aerial insectivores was underestimated because these bats avoid mist nets effectively or fly above the canopy where sampling is unfeasible. With advancements made in monitoring aerial insectivores through the use of audio recording devices, we are now able to study this diverse group in more detail (Kalko et al., 2008; MacSwiney et al., 2008) and to complement the few studies on fragmentation effects of aerial insectivorous bats (Law et al., 1999; Estrada et al., 2004).

Using state of the art acoustic monitoring techniques, our objective here was to determine the effects of forest fragmentation, in terms of remnant size and isolation, on species richness and ensemble structure of aerial insectivorous bats within a land-bridge island system of high fragment-matrix contrast in Gatún Lake, Panama. In a previous mist-netting study in the same fragmented landscape, Meyer and Kalko (2008) documented profound differences in phyllostomid species richness, assemblage structure and ensemble composition between islands and mainland forest sites. Consistent with the findings by Meyer and Kalko (2008) and in line with classic island biogeography theory and previously described responses of animals to tropical forest transformation, we hypothesized that aerial insectivorous bats will show changes in species richness, composition, and count abundance at the ensemble and species level. In particular we tested the following predictions:

(1) We expected that bats depending on forested habitats for foraging, i.e. hunting in background-cluttered and highly-cluttered space (hereafter referred to as forest species) to decrease in richness and count abundance on islands in relation to island size and isolation.
(2) In contrast, we predicted that species hunting in open space or over water (hereafter referred to as open space/over water foragers) will not exhibit a strong decline in species richness and count abundance in fragments because of their capability to cover long distances due to their flight behavior.
(3) We also expected rather similar ensemble structures and species richness at sites with similar degrees of isolation, size and vegetation structure.
(4) We anticipated lower richness, count abundance and feeding activity at continuous forest edge sites for forest species because previous studies have shown that biotic and abiotic factors can modify forest structure and available resources at edges (Laurance et al., 2002).

2. Methods

2.1. Study area and sampling sites

Our study was conducted on islands in Lake Gatún and on adjacent mainland peninsulas in the Barro Colorado Nature Monument (BCNM, 9°09′N, 79°51′W, Fig. 1), a 5400 ha biological reserve that is contiguous with Soberanía National Park (22,000 ha). Islands are former hilltops, isolated by the creation of the Panama Canal in 1914. Forests classify as semi-deciduous, lowland tropical moist forest (Holdridge, 1967). Climate is strongly seasonal (total rainfall: 1600 mm) with a rainy season from April or May to December and a marked dry season the rest of the year (Windsor, 1990). The forest on the mainland peninsulas is mature forest (400–600 years) interspersed with small patches of older secondary forest (about 80–100 years) (Leigh, 1999). Most islands are covered with low-stature, secondary forest with high levels of disturbance due to strong and persistent dry-season trade winds, strongly impacting forest structure and dynamics (Leigh et al., 1993; Adler, 2000). There are no light sources (e.g. canal buoys) close to the study sites which might have attracted insects and, subsequently, bats feeding on them. We never saw bats foraging near the buoys nor did we register large swarms of insects around them. Moreover, there were also no large artificial, man-made structures near the study sites. The closest were the lab facilities on Barro Colorado Island or rural areas at a distance of more than 3–5 km from our study sites.

Acoustic surveys were conducted at the same sites used by Meyer and Kalko (2008) in an extensive mist-netting study with the exception of three islands that were not included here due to logistical reasons. Following Meyer and Kalko (2008) we assigned islands to four categories, depending on their shortest distance to the mainland and size: "near" (<*ca.* 500 m) versus "far" (>*ca.* 1500 m), "large" (11.4–50 ha) versus "small" (2.5–5.9 ha) (Table 1, Fig. 1). Continuous forest sites within the BCNM (pensinsulas Bohio, Gigante and Peña Blanca, Fig. 1) were classified as "mainland interior" (>300 m away from shore) and "mainland edge" (next to the shore), respectively. Edge effects in the interior sites are considered to be low at the chosen distance (Laurance et al., 2002; Harper et al., 2005). We adapted our acoustic monitoring scheme to the configuration of the netting plots used by Meyer and Kalko (2008), i.e. one semi-rectangular plot of ca. 0.5 ha per site. Specifically, we used a total of seven recording stations, six stations spaced at equal distances along the perimeter of these plots with their positions matching the ground net locations and one additional station inside each plot corresponding to the location of the canopy net.

2.2. Sound recordings and analysis

Prior to the onset of the surveys, a reference library of echolocation calls from the species known to be present in the BCNM and surroundings was built based on calls compiled over more than

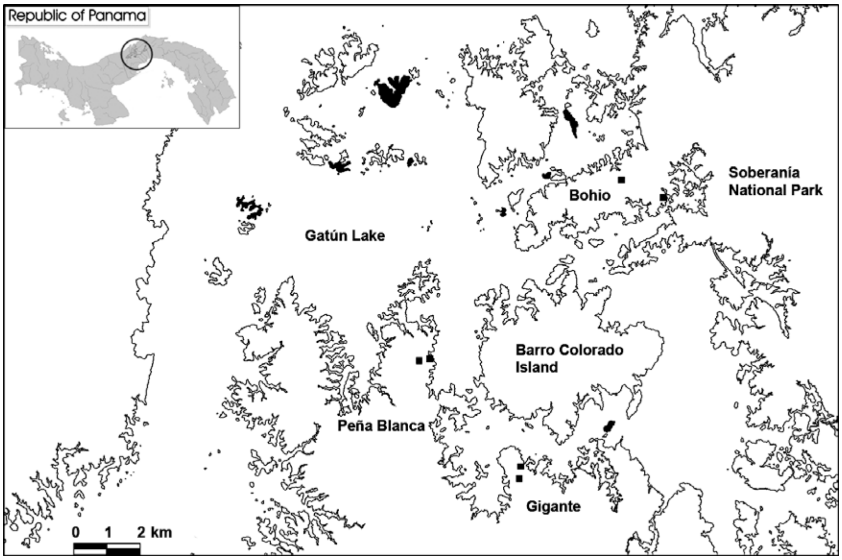


Fig. 1. Map of the study area in central Panama (inset) (modified from a GIS coverage, Kinner and Stallard, US Geological Survey, 2003) showing the locations of sampling sites. Highlighted in black are the eight study islands in Lake Gatún and the six mainland sites (■) in continuous forest on the three peninsulas Bohio, Gigante, and Peña Blanca in the Barro Colorado Nature Monument.

Table 1

Observed (S_{obs}) and estimated species richness (S_{est}) as well as percent inventory completeness for aerial insectivorous bats recorded on islands in Gatún Lake and at mainland sites in the Barro Colorado Nature Monument, Panama. Also provided are the total number of individuals and capture attempts recorded per site.

Site	Site category	S_{obs}	S_{est}	% completeness	Forest species			Open space/over water forages		
					No. of individuals	Capture attempts	Capture attempts/h	No. of individuals	Capture attempts	Capture attempts/h
Islands										
Tres Almendras	Near/small	11	14.3	77.2	112	28	4.0 (1.6)	20	0	0
Cacao	Near/large	13	14.6	89.0	144	37	5.3 (2.1)	40	1	0.1 (0.3)
Mona Grita	Near/small	15	18.3	82.2	136	107	15.3 (9.6)	45	3	0.4 (0.4)
Chicha	Near/small	16	18.4	86.9	126	17	2.4 (2.0)	63	5	0.7 (0.7)
Total		21	22.6	93.1	518	189	6.8 (6.8)	168	9	0.3 (0.5)
León	Far/large	12	15.3	78.7	97	4	0.6 (0.3)	36	0	0
Guava	Far/small	13	16.4	79.4	95	7	1.0 (0.9)	59	5	0.7 (0.3)
Trinidad	Far/large	17	24.4	69.7	150	31	4.4 (4.0)	49	4	0.6 (0.7)
Pato Horqueta	Far/large	16	17.9	89.6	143	12	1.7 (0.7)	87	3	0.4 (0.7)
Total		22	24.2	91.0	485	57	1.9 (2.4)	231	12	0.4 (0.5)
Islands total		23	24.0	92.7	1003	243	4.3 (5.6)	399	21	0.4 (0.5)
Mainland										
Bohío	Interior	15	19.2	78.0	124	16	2.3 (1.6)	14	0	0
Gigante	Interior	14	19.4	72.1	103	41	6.1 (6.6)	16	0	0
Peña Blanca	Interior	17	22.3	76.4	145	34	4.9 (2.2)	24	0	0
Total		19	21.4	88.9	372	91	4.4 (4.0)	54	0	0
Bohío	Edge	14	16.4	85.4	91	26	3.7 (2.4)	52	2	0.3 (0.3)
Gigante	Edge	13	14.2	91.4	124	85	12.1 (11.2)	43	1	0.1 (0.3)
Peña Blanca	Edge	14	16.6	84.3	131	28	4.0 (3.1)	42	1	0.1 (0.3)
Total		18	19.4	92.8	346	143	6.8 (7.1)	137	4	0.2 (0.2)
Mainland total		20	20.6	97.0	718	234	5.6 (5.7)	191	4	0.1 (0.2)
Total		23	24.1	95.6	1721	498		590	25	

15 years by Elisabeth Kalko and colleagues (E. Kalko, unpublished) and a literature review (for details see Table 2). Species names follow the nomenclature of Simmons (2005).

We surveyed all sites three times between March (dry season) and June (early rainy season) of 2006 to account for possible seasonal differences, defining a survey as four walks of one-h duration around each plot. Recording nights started at 18:00, subsequent rounds started on the hour for a total of four rounds until 21:00 to account for possible species-specific differences in activity levels. Activity of aerial insectivores decreases considerably after 22:00 (E. Kalko, pers. obs.; K. Jung, pers. comm.). During each round all recording stations were visited for 5 min and all bats that could be detected were recorded on a real time high-speed recording unit with a sampling rate of 500 kHz and 16 bit resolution (UltraSoundGate 116, Avisoft-RECORDER, Avisoft, Germany; CM16 microphone: flat frequency response 10–180 kHz).

Table 2

Species abundance counts (mean ± SD) for aerial insectivorous bats recorded at mainland sites in the Barro Colorado Nature Monument and on islands in Gatún Lake, Panama. Results of generalized linear mixed models testing for differences among site categories are given for species with a total of $\geqslant$ 100 passes recorded. Differences among site categories were assessed once with islands sorted by isolation and once with islands grouped by size. For details see text. Main sources for species identification (ID): (a) Kalko et al. (1998); (b) Jung (2009) & unpublished acoustic library by E. Kalko and K. Jung with reference calls (search) of identified bats in different behavioral situations (release calls, free-flying bats in open space and near obstacles); (c) Jung et al. (2007); (d) MacSwiney et al. (2008); (e) Ochoa et al. (2000) and Siemers et al. (2001) (f) O'Farrell and Miller (1997, 1999) and Schnitzler et al. (1994); and (g) Rydell et al. (2002).

Species (Acronym)	Family[a]	ID	Functional group[b]	Mainland		Islands		Difference among categories – isolation		Islands		Difference among categories – size	
				Interior	Edge	Near	Far	*F*	*p*	Small	Large	*F*	*p*
Forest species													
Centronycteris centralis (*Ccen*)	Emb	c	BCS	9.22 (3.56)	8.11 (4.04)	7.17 (7.49)	0.25 (0.62)	6.09	**0.013**	2.75 (3.96)	4.67 (8.06)	2.44	0.125
Cormura brevirostris (*Cbre*)	Emb	c	BCS	1.22 (0.97)	0.67 (0.87)	0.42 (0.90)	1.58 (2.78)	2.08	0.167	0.08 (0.29)	1.92 (2.71)	16.8	**<0.001**
Cyttarops alecto (*Cale*)	Emb	c	BCS	1.11 (1.27)	0.44 (0.88)	0	0.08 (0.29)			0	0.08 (0.29)		
Lasiurus ega (*Lega*)	Ves	b,g	BCS	0	0.11 (0.33)	0.25 (0.62)	0.42 (0.79)			0.25 (0.62)	0.42 (0.79)		
Myotis albescens (*Malb*)	Ves	b	BCS	0.44 (0.73)	0.56 (0.73)	0.33 (0.78)	0.75 (1.42)	0.27	0.842	0.33 (0.78)	0.75 (1.42)	0.27	0.842
Myotis nigricans (*Mnig*)	Ves	e	BCS	2.89 (2.67)	5.67 (3.74)	5.58 (3.23)	5.50 (2.71)	1.07	0.403	6.42 (2.47)	4.67 (3.17)	1.47	0.281
Myotis sonotype 1 (*Mson1*)	Ves	d,g	BCS	0.78 (1.99)	0.44 (1.01)	0.08 (0.29)	0			0.08 (0.29)	0		
Pteronotus gymnonotus (*Pgym*)	Mor	b,d	BCS	0.67 (0.87)	0.11 (0.33)	0	0.25 (0.62)			0.17 (0.58)	0.08 (0.29)		
Pteronotus parnellii (*Ppar*)	Mor	b,d,f,g	HCS	7.56 (4.85)	6.56 (4.28)	4.67 (3.60)	9.17 (3.35)	2.09	0.165	6.17 (4.78)	7.67 (3.34)	0.34	0.794
Pteronotus personatus (*Pper*)	Mor	b,d,f,g	BCS	0.11 (0.33)	0	0.17 (0.39)	0.08 (0.29)			0.25 (0.45)	0		
Saccopteryx bilineata (*Sbil*)	Emb	c,d,f,g	BCS	12.22 (4.60)	11.78 (3.49)	15.83 (3.19)	14.33 (5.23)	1.44	0.288	14.25 (5.14)	15.92 (3.29)	1.50	0.276
Saccopteryx leptura (*Slep*)	Emb	c	BCS	5.11 (2.15)	4.00 (2.18)	8.67 (3.60)	8.00 (3.93)	7.03	**0.008**	8.33 (4.23)	8.33 (3.28)	6.98	**0.008**
Total				3.44 (4.64)	3.20 (4.44)	3.60 (5.58)	3.37 (5.16)	0.40	0.754	3.26 (5.14)	3.71 (5.59)	0.77	0.538
Open space species													
Diclidurus albus (*Dalb*)	Emb	c	US	0	0	0.50 (0.67)	0.08 (0.29)			0.33 (0.49)	0.25 (0.62)		
Eumops sp. (*Eum*)	Mol	b	US	1.00 (1.00)	3.22 (3.49)	1.33 (1.44)	2.25 (2.63)	1.70	0.229	1.17 (1.47)	2.42 (2.54)	2.44	0.125
Molossus rufus (*Mruf*)	Mol	b	US	1.00 (1.22)	3.56 (3.36)	5.17 (3.56)	5.00 (3.28)	4.97	**0.023**	5.83 (3.90)	4.33 (2.64)	5.23	**0.020**
Molossus currentinum (*M.cur*)	Mol	b	US	1.11 (1.27)	2.56 (2.55)	3.08 (2.81)	4.58 (3.34)	1.48	0.279	3.67 (2.96)	4.00 (3.38)	1.31	0.324
Molossus molossus (*Mmol*)	Mol	b	US	0.56 (1.01)	2.56 (2.65)	1.83 (2.21)	2.25 (2.78)	0.81	0.517	2.50 (2.68)	1.58 (2.23)	0.82	0.512
Noctilio albiventris (*Nalb*)	Noc	a	BCS-T	0	0	0.42 (1.00)	0.33 (0.89)			0.42 (1.00)	0.33 (0.89)		
Noctilio leporinus (*Nlep*)	Noc	f	BCS-T	0.89 (1.36)	2.22 (3.63)	0.33 (0.65)	2.33 (4.68)	4.88	**0.024**	0.33 (0.65)	2.33 (4.68)	4.88	**0.024**
Peropteryx kappleri (*Pkap*)	Emb	c	US	0.22 (0.67)	0	0.08 (0.29)	0.17 (0.39)			0.08 (0.29)	0.17 (0.39)		
Peropteryx macrotis (*Pmac*)	Emb	c	US	0.78 (1.39)	0.67 (1.12)	0.83 (1.34)	0.50 (0.90)			0.83 (1.34)	0.50 (0.90)		
Promops centralis (*Pcen*)	Mol	b	US	0.44 (0.88)	0.44 (0.73)	0.08 (0.29)	1.17 (2.62)			0.08 (0.29)	1.17 (2.62)		
Rhynchonycteris naso (*Rnas*)	Emb	c	BCS-T	0	0	0.33 (0.65)	0.58 (0.90)			0.33 (0.65)	0.58 (0.90)		
Total				0.55 (1.00)	1.38 (2.48)	1.27 (2.22)	1.75 (2.91)	5.86	**0.014**	1.42 (2.51)	1.61 (2.69)	4.59	**0.029**

[a] Emb = Emballonuridae, Mol = Molossidae, Mor = Mormoopidae, Noc = Noctilionidae, Ves = Vespertilionidae.

[b] BCS = Background-cluttered space, BCS-T = background-cluttered space trawling insectivore/piscivore, HCS = highly-cluttered space, US = uncluttered space.

Recording parameters were set as follows: 300 kHz sampling rate, 16 bit resolution, 6 s recording time with 5 s pre-trigger time and 1 s post-trigger time, 0.05 s buffer time, and maximal amplification and visualization with a 512 Fast Fourier Transformation (FFT).

Total recording time per survey amounted to 2.33 h for a total of 7 h per site except for Gigante interior (5.83 h). Rainy nights were avoided and recording nights were redone if they were interrupted by long rain. The technique used, "observer on site", has not been as popular as automated recording because it requires more manpower (Law et al., 1999; O'Farrell and Miller, 1999; Frick et al., 2008). However, its virtue lies in the high quality of the obtained recordings because the researcher can follow a bat's flight trajectory (Kalko, 1995; Ford et al., 2005) resulting in enhanced detection and recording possibilities compared to stationary microphones.

Sound sequences were analyzed with AVISOFT SASLAB PRO software, version 4.34 (Raimund Specht, Avisoft, Germany). We first generated spectrograms using a Hamming window with a 256 FFT, a 100% frame and an overlap of 50%. Second, we checked for bat passes on the spectrogram, defining a bat pass as a succession of more than two echolocation pulses emitted by a bat flying on axis with the microphone (Fenton, 2004). Third, we determined how many bat passes were present in each recording. A bat pass was defined as a regular succession of calls. If calls were separated by a gap of three times pulse interval or more they were regarded as two passes. Feeding activity was measured by documenting capture attempts for each species indicated by the presence of a terminal phase or buzz in the echolocation behavior (see definition by Kalko and Schnitzler, 1998). Fourth, a species was assigned to each bat pass taking into consideration a variety of characteristics of search calls measured with the cursor on the screen (pulse duration, pulse interval, general call shape, peak frequency, terminal frequency, harmonic with most energy). Peak frequency refers to the strongest amplitude of the oscillogram, terminal frequency to the lowest frequency of the downward- and shallow-modulated component of broadband signals. Measurements on the screen were generally made on the strongest harmonic and from pulses with the lowest amount of echoes. Recordings with very faint bat passes or recordings where we could not reliably distinguish call shape were excluded from analysis (15.3% from 14,499 recordings).

Species assignation followed our call library and literature survey aforementioned. Recordings with vespertilionid search calls consisting of a downward steep frequency modulated (FM) component followed by a shallow-modulated element with terminal frequencies ranging from 58 kHz to 60 kHz were assigned to *Myotis* sonotype 1 because those calls were considerably higher in frequency than the other two *Myotis* species known from the Barro Colorado Nature Monument with identified call signatures. *Myotis* sonotype 1 might correspond to *Myotis riparius* or *Myotis keasyi* (Rydell et al., 2002), but this identification awaits further confirmation. Recordings with *Myotis*-type search signals and terminal frequencies ranging from 43 to 46 kHz were assigned to *Myotis albescens* (Surlykke and Kalko, 2008) and recordings with similar call types but higher terminal frequencies between 48 and 55 kHz to *Myotis* nigricans (Siemers et al., 2001; Surlykke and Kalko, 2008). We might have missed the very small vespertilionid *Rhogeessa tumida*, which is known to occur in the study area (Meyer and Kalko, 2008), in our recordings as we do not have reference calls. It is likely that this species emits echolocation calls that are rather similar in shape and frequency range to *Myotis* species as has been shown for *Rhogeessa aeneus* (Rydell et al., 2002; MacSwiney et al., 2008). *Rhogeessa tumida* thus might have been erroneously assigned to *M. nigricans* or *M. albescens*. We assume, although we cannot exclude the contrary, that *R. tumida* is rather rare as its capture frequency in mistnets is even lower than of the other two *Myotis* species and as we have so far no confirmed observations of such a tiny bat foraging in the forest.

2.3. Functional groups

We assigned bats to functional groups after Schnitzler and Kalko (2001) (Table 2) expecting that species hunting in the forest versus species that forage in open space or over water will exhibit differential responses to fragmentation. Forest species encompassed bats that either hunt inside the forest close to vegetation or in edge/gap situations. The group of open space/over water foragers included all species that forage for insects in uncluttered space away from vegetation as well as three trawling bats that feed on insects (*Rhynchonycteris naso* and *Noctilio albiventris*) and in case of *Noctilio leporinus* also on fish (Kalko et al., 1998).

2.4. Data analysis

With acoustic monitoring data, comparisons of species richness, evenness, and species composition among different habitats or treatments are generally complicated by the fact that bat passes represent an index of activity rather than a true count of individuals as successive passes can potentially be from the same individual. To deal with this problem of pseudoreplication and to ensure that individual-based analyses can validly be applied, we generated a count of individuals by recording the presence of a particular species in each 5-min sampling point and then pooling across all sampling points per site. We subsequently used these count data (hereafter count abundance) for statistical comparisons of species richness, evenness, relative abundance, and species composition across site categories (see below). We acknowledge that this measure of relative abundance through counts is not equivalent to relative abundances assessed by mistnet captures. However, as neither measure (acoustic monitoring, mistnet sampling) is free from biases, this approach permits comparison of abundance measures with emphasis on relative differences of species among sites. This also applies to the independence of sampling points. Although our approach assumes that sampling points are independent in space and time, i.e. the same individual would not be recorded more than once at more than one sampling point, we believe that the effect this could have on the outcome of our analyses is negligible since we focus on relative differences across sites. Sampling at different times per night and across seasons is essential to account for possible species-specific differences in nightly activity as well as seasonal shifts.

To assess bat inventory completeness, we calculated randomized (1000×) sample-based species accumulation curves for individual sites and per site category, using sampling nights as the basis for the calculations. We then rescaled the curves to number of individuals to allow for direct comparison of species richness (see Gotelli and Colwell, 2001). For our calculation, one individual corresponds to the presence of a species in a 5 min sampling period. We calculated expected species richness, S_{est}, following the estimator choice framework developed by Brose and Martinez (2004). Based on our observed level of sample coverage we selected the Michaelis–Menten richness estimator as the most suitable estimator for our data. The percentage of inventory completeness was calculated as observed species richness (S_{obs})/estimated species richness (S_{est}) × 100. Species accumulation curves and richness estimators were calculated with the program EstimateS 8.0 (Colwell, 2006).

We compared species richness and evenness among site categories (islands: near, far, large, small; mainland: edge, interior) and between all islands and mainland sites using rarefaction techniques (e.g. Magurran, 2004). Predictions were made at a standard number of individuals. Evenness was calculated as Hurlbert's probability of interspecific encounter (PIE; Hurlbert, 1971), i.e. the likelihood that two individuals that are randomly drawn represent two different species. Statistical significance was assessed based on the 95% confidence intervals calculated through 1000 iterations by the program EcoSim (Gotelli and Entsminger, 2001).

We compared rank-abundance curves among site categories using Kolmogoroff–Smirnov two-sample tests with 1000 bootstraps to determine *p*-values, which allows for a comparison of distributions that are not entirely continuous. To assess inter-site differences in species composition we used non-metric multidimensional scaling (NMDS) based on the Bray–Curtis coefficient (e.g. Magurran, 2004). NMDS is commonly regarded as the most robust unconstrained ordination method in community ecology (McCune and Grace, 2002). Two ordinations were constructed, one for forest species and another for open space/over water foragers. For forest bat species, we additionally assessed the importance of forest structure in generating compositional differences among sites using vector fitting, a procedure that determines the direction and strength of the correlation of the independent variables with the ordination scores (McCune and Grace, 2002). Vegetation structure variables included in this analysis were tree density, basal area, number of poles and saplings, canopy height, canopy closure, and an index of horizontal and vertical heterogeneity in foliage structure, respectively. See Meyer and Kalko (2008) for a full description of how these individual vegetation characteristics were quantified for each sampling plot.

Differences in species composition among site categories were assessed with a permutational multivariate analysis of variance (e.g. McArdle and Anderson, 2001) based on Bray–Curtis dissimilarity matrices and 1000 permutations using the 'adonis' function as implemented in the 'vegan' package (Oksanen et al., 2008) in R (R Development Core Team, 2009). This is a robust technique that allows partitioning of distance matrices among sources of variation and uses *F*-tests based on sequential sums of squares from permutations of the raw data to assess statistical significance. This analysis was performed once contrasting mainland interior and edge sites with islands grouped by isolation (near, far) and once with islands sorted by size (small, large).

To test for differences in relative abundance and relative feeding activity among site categories we employed (generalized) linear mixed-effects models ((G) LMMs; Zuur et al., 2009), modeling site category as a fixed effect and site as well as recording night nested within site as random effects. Abundance count data, generated as previously described, were modeled as a Poisson GLMM using function glmmPQL in the 'MASS' package (Venables and Ripley, 2002). For the comparison of relative feeding activity we applied Gaussian LMMs on log($x + 1$)-transformed data, using capture attempts per hour as a measure of relative feeding activity. LMMs were fitted using the 'nlme' package in R (Pinheiro et al., 2008). Significant responses in models were further evaluated by conducting multiple comparison tests using Tukey contrasts as implemented in the 'multcomp' package in R (Hothorn et al., 2008). In all cases, we constructed separate models for forest species and open space/over water foragers. In addition, we tested for differences in abundance counts among site categories for individual species. However, due to the overall low number of recordings obtained for several species we limited this analysis to those species for which at least a total of 100 bat passes were recorded. In all cases we fitted two separate models, specifying site category as either including islands sorted by isolation or grouped by island area. Because the use of adjustments of significance levels for multiple tests conducted on the same independent variable is controversial, particularly in the context of exploratory analyses (e.g. Moran, 2003), we generally chose to present exact *p*-values for all analyses.

3. Results

We recorded a total of 12,287 bat passes from 23 species, 22 of which could be identified to species level. Of those, 12 were classified as forest species and 11 were bats foraging in open space or over water. Emballonuridae was the family represented by the most species (nine species), followed by Molossidae (four species and one genus), Vespertilionidae (four species), Mormoopidae (three species), and Noctilionidae (two species). Inventory completeness was estimated at around 90% for each site category and exceeded 95% for all sites combined (Table 1). Species accumulation curves showed that new species were accumulated at a fast rate and provided further evidence that our acoustic survey protocol was highly effective at sampling aerial insectivorous bats (Supplementary Fig. 1).

A similar number of abundance counts were recorded on near (686 or 29.7%) and far islands (716 or 30.9%). Continuous forest sites likewise were characterized by similar, albeit lower levels of relative abundance than islands (mainland edge sites: 483 or 20.9%, interior sites: 426 or 18.4%). Feeding activity was highest on near islands (198, 39.8%) and at mainland edge sites (143, 28.7%), while the number of capture attempts was considerably lower at mainland interior sites (91, 18.2%) and far islands (66, 13.3%) (Table 1).

3.1. Species richness and evenness

Overall, observed species richness was higher on islands (23 species) than on the mainland (20 species), while a similar number of species was recorded on near and far islands, and at mainland interior and edge sites, respectively (Table 1). Rarefaction analyses that compared species richness at a standardized number of count abundances also revealed significantly higher species richness for islands than mainland sites (Fig. 2a). Moreover, mainland edge sites had significantly lower rarefied species richness than forest interior sites or islands grouped by isolation or large islands

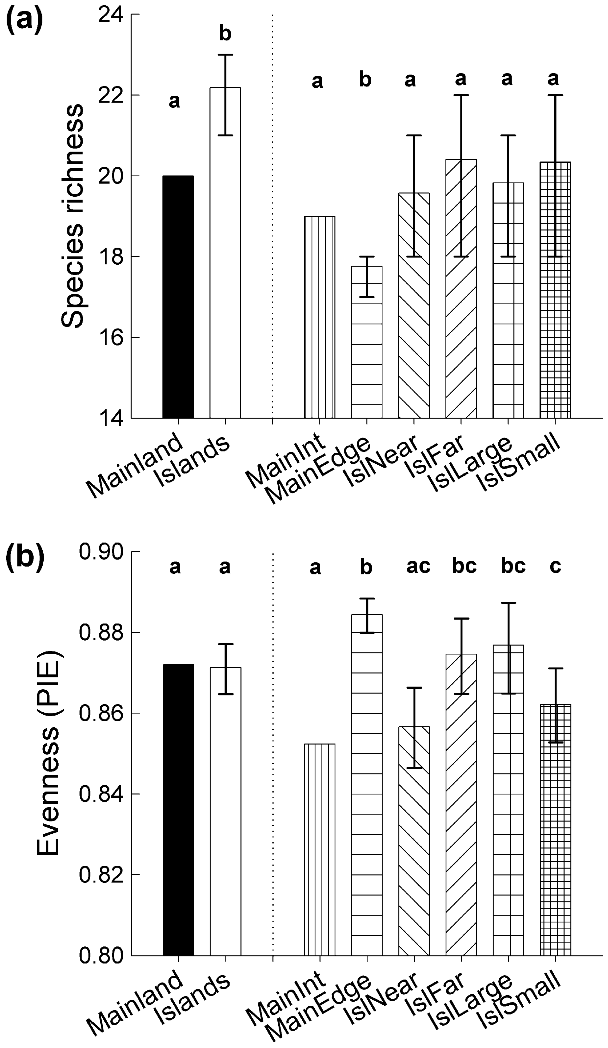
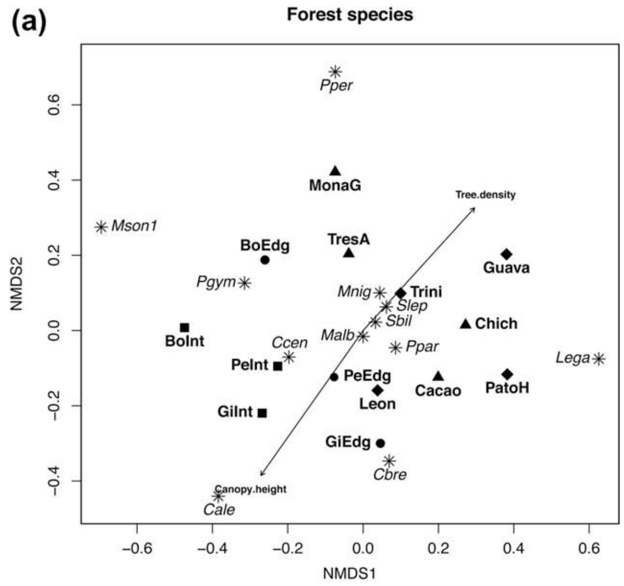


Fig. 2. Rarefied species richness (a) and evenness (b) for aerial insectivorous bats recorded on Lake Gatún islands and in continuous forest sites. Comparisons were made between mainland sites and islands as well as between site categories. Different alphabetic designations indicate significant differences between site categories as based on the simulated 95% confidence intervals (error bars). See text for details.

(Fig. 2a). On the other hand, rarefaction indicated lower evenness for islands than mainland sites. This was largely due to the high evenness of mainland edge compared to interior sites and most island categories (Fig. 2b).

3.2. Species composition

For both species groups, a two-dimensional NMDS ordination adequately displayed compositional variation among sites with little distortion and high goodness of fit between fitted values and ordination distances (forest species: stress = 16.8, linear fit $R^2 = 0.81$; open space/over water foragers: stress = 18.3, $R^2 = 0.79$). In the ordination of forest species (Fig. 3a), NMDS axis 1 separated mainland sites from islands, the latter being quite heterogeneous in terms of species composition as ordination distances between sites were in some cases large, indicating considerable differences in species composition. Species composition for forest species differed significantly among site categories both when islands were grouped by isolation (permutational MANOVA, $F = 2.00$, $p = 0.025$) and when sorted by size ($F = 1.91$, $p = 0.037$). Vector fitting of vegetation structure variables onto the forest species NMDS ordination revealed significant correlations with canopy height ($r^2 = 0.54$, $p = 0.017$) and tree density ($r^2 = 0.47$, $p = 0.032$; Fig. 3a). In contrast to the forest species ordination, for open space bats variability in species composition among sites was higher along both NMDS axes and there was no distinct grouping as islands and mainland sites were intermingled throughout the ordination diagram (Fig. 3b). There were no significant compositional differences among site categories, neither with islands grouped by isolation nor when sorted by size (permutational MANOVA, isolation: $F = 0.87$, $p = 0.623$; area: $F = 0.92$, $p = 0.570$).



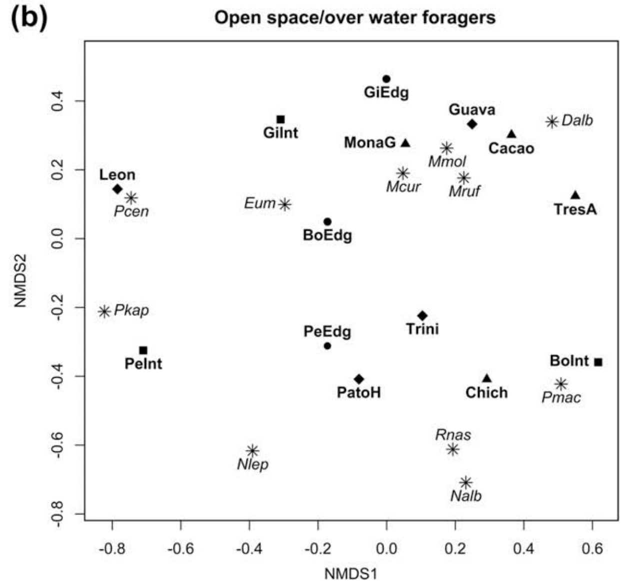


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity for the ensemble of aerial insectivorous bats on eight Gatún Lake islands and at six continuous forest sites in the Barro Colorado Nature Monument, Panama. (a) forest species, (b) open space/over water foragers. In (a) fitted vectors indicate the direction and strength of forest structural variables significantly correlated with the bat NMDS. (■) mainland interior sites, (●) mainland edge sites, (▲) near islands, (♦) far islands. See Table 2 for species abbreviations.

3.3. Patterns of abundance counts

Distributions of species abundance counts were indistinguishable from one another across site categories, regardless of the species group analyzed and the level of island isolation or size (forest species: $0.09 \leqslant D \leqslant 0.36$, $p > 0.387$; open space bats: $0.27 \leqslant D \leqslant 0.55$, $p > 0.062$).

At the guild level, forest species did not respond to habitat fragmentation in terms of abundance counts whereas open space/over water foragers showed significant differences among site categories, with higher abundance counts on islands and at continuous forest edges compared to mainland interior sites (Table 2, Fig. 4). Feeding activity of forest species was significantly lower on far islands than on either near island or at mainland edge sites (LMM, isolation: $\chi^2 = 9.25$, $p = 0.026$, area: $\chi^2 = 1.96$, $p = 0.580$). Open space bats, however, exhibited similar levels of feeding activity across site categories (isolation: $\chi^2 = 3.03$, $p = 0.386$, area: $\chi^2 = 3.87$, $p = 0.275$; Fig. 4).

At the species-level, *Saccopteryx bilineata* was the most abundant species at all sites, followed by *Pteronotus parnellii*, *Saccopteryx leptura* and *Centronycteris centralis*, the last with less than half of the abundance counts for *S. bilineata*. These three species accounted for 60.5% of all bat passes. Five out of 12 species with at least a total of 100 bat passes recorded, three forest species, *C. centralis*, *C. brevirostris*, and *S. leptura* as well as two open space bats, *Molossus rufus* and *N. leporinus* revealed a statistically significant response to fragmentation in species-level analyses (Table 2, Fig. 5). *C. centralis* evinced a strong negative response to isolation as abundance levels on far islands were considerably reduced relative to both near islands and mainland sites. In contrast, *Cormura brevirostris* responded negatively to forest area, being less active on small than on large islands or at mainland sites. *S. leptura* and *M. rufus* both showed higher abundance counts on islands compared to mainland sites, regardless of whether comparisons were based on islands sorted by isolation or size (Fig. 5). *S. bilineata* likewise displayed higher abundance counts on islands than in continuous forest, although the difference was not significant (Table 2). Interestingly, *N. leporinus* showed highest abundance counts at mainland edge sites and far, large islands (Fig. 5). The other two trawling species, *N. albiventris* and *R. naso* were not recorded on the mainland, and *Diclidurus albus* was also only recorded on islands (Table 2).

4. Discussion

We documented a rich and abundant insectivorous bat ensemble with acoustic monitoring in a system of land-bridge islands.

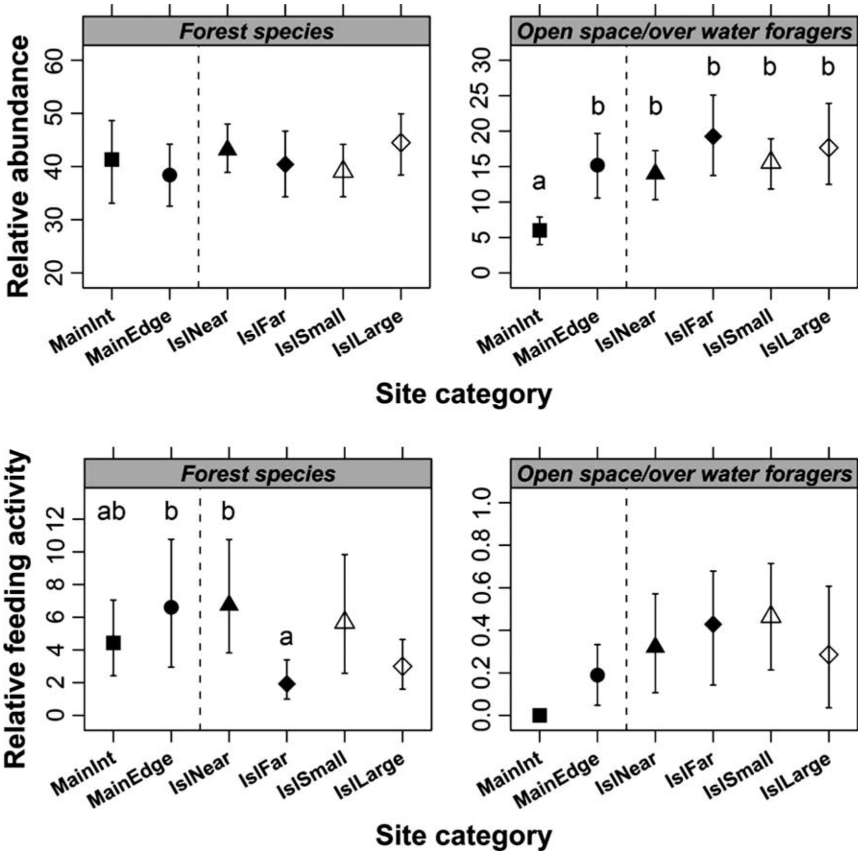


Fig. 4. Comparison of overall species abundance counts and relative feeding activity, respectively, between site categories for forest bat species and open space/over water foragers. Data are presented as mean ± bootstrapped 95% confidence interval. Different alphabetic designations indicate significant differences ($p < 0.05$) between site categories in post hoc tests following (generalized) linear mixed model analyses (see Table 2).

The effects of fragmentation were evident both at the ensemble and at the species level. Composition of forest bats was negatively affected by island isolation and size in contrast to abundance counts that remained unaltered. This contrasts with an increase of abundance counts of bats foraging in open space or over water with increasing island size or isolation. Individual species responses were also varied. Some species were more active on islands, regardless of isolation or size, than in continuous forest, while others were equally active at all sites. One forest species, *C. centralis*, was negatively affected by isolation whereas another forest species, *C. brevirostris*, was negatively affected by size. On the other hand, *S. leptura*, also a forest species, and two open space bats, *M. rufus* and *N. leporinus*, showed a positive response with higher abundance counts for the islands than for the mainland forest.

To our knowledge our study is the first to examine the effects of forest fragmentation on Neotropical aerial insectivorous bats in detail at the functional group and species level. Our findings are based on a rigorously standardized sampling protocol and support the view that responses to forest fragmentation in bats are linked to patch size, isolation and vegetation structure that act in concert in shaping bat assemblages (Estrada and Coates-Estrada, 2002; Estrada et al., 2004; Faria, 2006; Medina et al., 2007; Meyer and Kalko, 2008).

Contrary to our predictions a decrease in forest area did not have a strong negative impact on species richness of aerial insectivorous forest species, results that differ from another study of aerial insectivorous bats in a near-shore archipelago in México (Frick et al., 2008). This disparity most likely rises from the different nature and history of the fragmented systems; Gatún is a recent artificial land-bridge island system whereas the one in México is a natural archipelago. The lack of a clear species-area relationship in our system probably stems from the presence of the small island effect; a phenomenon that may become apparent in islets with the size range of our sites and where vegetation that is subjected to episodic disturbances is not able to support the level of resources that would be predicted by their size (Lomolino and Weiser, 2001). This may be the case for the Gatún islands because different levels of exposure to the strong trade-winds leads to marked differences in vegetation structure (Leigh et al., 1993). Nonetheless, these results need to be interpreted with caution because our comparison across site categories involves only four replicates per category. Furthermore, three of four large islands are also far islands and three of four small islands are in the 'near' category, making it difficult to disentangle the effects of area and isolation on species richness.

Forest size and isolation discernibly altered composition of aerial insectivorous forest bat species, a result that is in line with studies on phyllostomid bats in the Neotropics (Cosson et al., 1999; Faria, 2006; Meyer and Kalko, 2008) but that contrasts with findings on Paleotropical insectivorous bats by Struebig et al. (2008) who found that patch area, but not isolation, influenced species composition. Differences between studies may be associated with variations in matrix type and fragmentation history. Matrix type, in particular, determines the level of contrast between fragments and matrix (Watson, 2002). For example, agricultural matrices are usually more porous than water matrices because they still contain some vegetation, so animal movement is less hampered when fragments and matrix have similar vegetation structures regardless of the distance between patches (Kupfer et al., 2006).

In low contrast matrices, many species are still able to exploit the fragmented mosaic as it has been found for frugivorous bats, birds, and other taxa (e.g. Gascon et al., 1999; Faria, 2006). Moreover, low contrast matrices reduce the effect of isolation because species might perceive the matrix as habitat. High contrast systems, as exemplified by the islets in Gatún Lake, can be regarded as less porous as they do not contain vegetation. Hence, forest species and forest specialists in particular might perceive it as an unsuitable environment.

Despite the overall high richness and relative abundance levels of forest species on isolated islands, the effects of forest size and isolation in our study system are apparently strong enough to alter species composition of the forest ensemble. The low number of capture attempts on far islands seems to further corroborate this negative effect, at least for isolation. Although forest species visit isolated sites, explaining the high species richness, feeding opportunities on those islets appear to be reduced. In contrast, among-site variation in species composition for bats foraging in open space or over water did not differ among site categories and was not affected by either island size or isolation, suggesting that this ensemble is not affected by fragmentation in the Lake Gatún area.

Differential responses to fragmentation at the compositional level have also been associated with species-specific traits such as mobility or foraging strategies for a variety of taxa (Henle et al., 2004; Ewers and Didham, 2006). For phyllostomid bats that have been studied in the same system, edge-sensitivity and mobility-related traits such as wing morphology have been identified as those traits that best explained species sensitivity to fragmentation (Meyer et al., 2008), an approach that needs to be pursued in the future.

On the one hand, we found, as predicted, that species foraging in open space were not affected by fragmentation. This is probably because high wing loading and high wing aspect ratio, attributes characteristic of species foraging in open space such as members of the genus *Molossus* (Norberg and Rayner, 1987), confer high flight speeds that make visiting isolated sites energetically cheap. On the other hand, forest species such as *C. centralis*, that are adapted for slower and more maneuverable flight because of their lower wing loading and lower aspect ratio, probably cannot afford prolonged commuting flights over an inhospitable matrix to isolated sites because they are energetically very costly. Other traits such as body size, alone or in conjunction with other traits, might also explain contrasting responses to fragmentation. Perhaps larger species, such as *M. rufus* or *N. leporinus*, might reach small and isolated sites if it is valid to assume that foraging ranges might be scaled to body size. In case of *N. leporinus*, the proximity of water

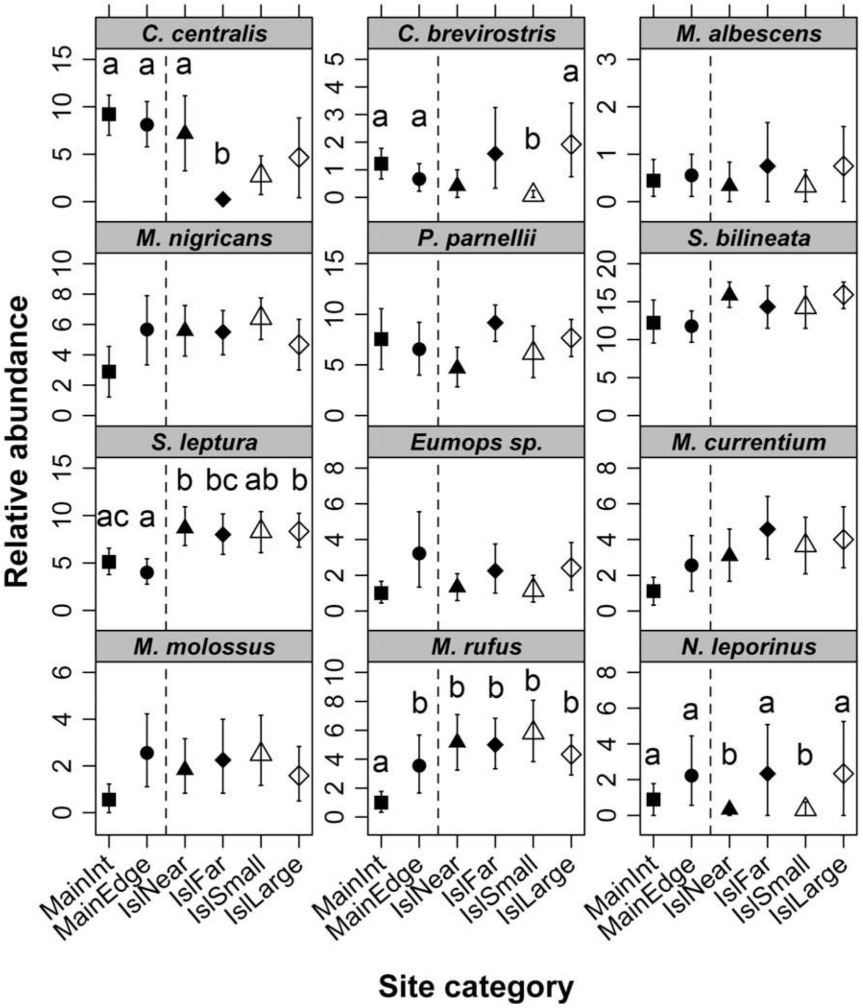


Fig. 5. Comparison of abundance counts (mean ± bootstrapped 95% confidence interval) between site categories for 12 species of aerial insectivorous bats for which at least 100 bat passes were recorded. The first seven panels (left to right) correspond to forest species; the remaining ones comprise open space bats/over water foragers. Different alphabetic designations indicate significant differences ($p < 0.05$) between site categories in post hoc tests following generalized linear mixed model analyses (see Table 2).

might also play an important role as this species feeds to a large extent, even though not exclusively, on small fish and freshwater shrimp (see Schnitzler et al., 1994).

Isolation can also play a role in shaping forest species composition through its effect on microclimatic variables at the boundaries of remnants, often leading to drastic changes in vegetation structure at forest edges (Harper et al., 2005). Such changes may alter assemblage structure of species and their interactions within the system (e.g. Fagan et al., 1999). The Gatún island system is characterized by a gradient of disturbance-related changes where an increase in island isolation is associated with an increase in the number of tree fall gaps produced by tradewinds. This, in turn, modifies forest structure as evidenced by a decrease in canopy height and higher density of tree regrowth with increasing island isolation (Leigh et al., 1993; Adler, 2000). These forest structural changes may influence aerial insectivorous bats either directly through an increase in clutter which may affect flight maneuverability or indirectly by altering insect abundance or distribution (Didham et al., 1996). Future research that jointly explores the relative importance of species-specific traits of forest bat species and forest structural variables across a range of isolation distances may lead to a better understanding of the proximate and ultimate causes underlying bat responses to fragmentation at the species and ensemble level.

Our sampling design provides only limited opportunity for detailed analysis of edge effects because we did not sample a thorough cross section of the boundaries as it has been done elsewhere (Sampaio, 2000; Laurance et al., 2002). Nonetheless, whereas both functional groups had similar abundance counts in interior and edge sites in continuous forest, we found that species richness, evenness and composition of forest species were noticeably altered at forest edges. A decrease in species richness at forest edges is supported by studies on phyllostomid bats and other taxa (Laurance et al., 2002; Faria, 2006; Meyer and Kalko, 2008). In contrast to our initial expectations, evenness was higher at continuous forest edges than at interior sites. It is likely that bats foraging in open space, over water or near edges (e.g. *M. currentinum* and *N. leporinus*) had a higher detection probability than others.

Overall, bat abundance counts were surprisingly high on islands in both species groups, but there were differences at the species level. The low feeding activity of forest species on far and large islands combined with the island size-isolation distribution of our study sites, suggest that a reduction in relative feeding activity goes hand in hand with increased isolation of the forest fragment. Although larger islands should provide more resources than smaller ones (Ewers and Didham, 2006; Kupfer et al., 2006), they may provision forest bats with adequate roosting sites but perhaps may not fulfill their feeding needs. Strong fluctuations in food availability as they are likely to occur on the islands seem a plausible explanation for the observed differences in feeding activity. Here, frequent tree fall gaps in the Gatún area might produce plant regrowth and increased production of biomass through leaf flush that enhances the proliferation of herbivorous insects (Basset et al., 2001). This in turn might provide enough food resources to sustain local populations or make small and isolated islands sufficiently attractive for bats to include them as regular foraging grounds. We observed several times emerging swarms of termites and ants during the study time that attracted many forest bats of several species in a single night (S.E.V., pers. obs.). To conclude, the islands seem to offer attractive resources, at least for brief periods. Likewise, the high feeding activity of bats foraging in open space or over water on isolated islands may also indicate enhanced availability of insects at these sites. However, this rather positive effect that we observed may be system-specific and may not necessarily be applicable to other fragmented landscapes differing in matrix type and patterns of food availability.

Bat abundance counts at the species level are also related to species-specific requirements and traits. For example, reduction of forest area often leads to loss of appropriate roost sites; however, some species might tolerate forest reduction if roosting needs in small fragments are still fulfilled (Ewers and Didham, 2006). In our case, several common and rare species of both forest species (e.g. *S. bilineata*) and open space bats (e.g. *D. albus*) were found roosting on small islands and also frequently used them as foraging grounds. The small home ranges that have been reported for some forest species such as *S. bilineata* in Costa Rica (95% kernel foraging areas averaging about 15 ha, mean 50% kernel core foraging areas of about 2 ha; Hoffmann et al., 2007) indicate that islands as small as the ones we sampled are likely to meet the roosting and foraging requirements of a range of forest species. More detailed knowledge of the roosting ecology, size of home ranges and mobility across habitats of other Neotropical aerial insectivorous bats, particularly in fragmented landscapes, could provide valuable information to better understand species-specific traits, requirements and their relation to forest fragmentation.

4.1. Conservation implications and methodological insights

Our study highlights the fact that studying habitat disturbance at various organizational levels (functional groups or species) can provide a better understanding of how bats are impacted by habitat fragmentation (compare also Struebig et al., 2008). The high levels of richness and abundance counts of aerial insectivorous bats in small forest patches found in our study suggest that small-sized forest remnants are of conservation value not only for phyllostomid bats as has been previously demonstrated (Gorresen and Willig, 2004; Faria, 2006; Meyer and Kalko, 2008) but that they can also contribute substantially to the preservation of a rich aerial insectivorous bat fauna in Neotropical fragmented landscapes. However, a relatively high degree of forest integrity and structural connectivity appears to be important to support forest-dependent aerial insectivores and to ensure the sustained functioning of ecosystem services provided by these bats in terms of controlling insect populations (Cleveland et al., 2006). Nonetheless, the conservation of small and isolated remnants should be tightly linked with the preservation of larger tracts of forest to ensure the long-term persistence of an intact bat assemblage at the landscape level. Even though our study system is an example of extreme matrix contrast, which may most closely resemble extensively grazed pasture landscapes or landscapes subjected to intensive mechanized agriculture, our results suggest that more research should be devoted to how small and isolated remnants may sustain ecosystem services in inhospitable matrices, as they will become more and more common with the advancement of the agricultural frontier.

The inability to properly sample aerial insectivorous bats is perhaps the main reason why this important species group was rarely considered in community studies and impact assessments of forest fragmentation (Kalko et al., 2008). However, as this and other studies increasingly demonstrate (see for example, Jung and Kalko, in press; MacSwiney et al., 2008), acoustic sampling with modern, state-of-the-art technology has become an effective means by which the effects of habitat transformation on Neotropical aerial insectivorous bats can be reliably assessed.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.11.009.

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