Ecological correlates of vulnerability to fragmentation in Neotropical bats

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Summary

1. In the face of widespread human-induced habitat fragmentation, identification of those ecological characteristics that render some species more vulnerable to fragmentation than others is vital for understanding, predicting and mitigating the effects of habitat alteration on biodiversity. We compare hypotheses on the causes of interspecific differences in fragmentation sensitivity using distribution and abundance data collected on 23 species of Neotropical bats.

2. Bats were captured over a 2-year period on 11 land-bridge islands in Gatún Lake, Panama, and on the adjacent mainland. We derived a series of explanatory variables from our capture data and from the literature: (1) natural abundance in continuous forest, (2) body mass, (3) trophic level, (4) dietary specialization, (5) vertical stratification, (6) edge-sensitivity, (7) mobility, (8) wing morphology (aspect ratio and relative wing loading) and (9) ecologically scaled landscape indices (*ESLI*s). After phylogenetic correction, these variables were used separately and in combination to assess their association with two indices of fragmentation sensitivity, species prevalence (proportion of islands occupied) as well as an index of change in abundance.

3. Model selection based on Akaike's information criterion identified edge-sensitivity as the best correlate of vulnerability to fragmentation. Natural abundance and mobility or traits linked to mobility (relative wing loading and *ESLI*) received limited support as predictors. Vulnerability of gleaning animalivorous bats is probably caused by a combination of these traits.

4. *Synthesis and applications.* Our findings emphasize the importance of a local-scale approach in developing predictive models of species fragmentation sensitivity and indicate that risk assessments of Neotropical bats could be based on species tolerance to habitat edges and mobility-related traits. We suggest that, in order to be effective, management efforts should aim to minimize the amount of edge-habitat and reduce the degree of fragment-matrix contrast. Moreover, if high bat diversity is to be preserved in fragmented Neotropical landscapes, conservation measures regarding reserve design should assure spatial proximity to source populations in larger tracts of continuous forest and a low degree of remnant isolation.

Key-words: Chiroptera, ecological traits, habitat fragmentation, land-bridge islands, Panama, sensitivity, vulnerability

Introduction

Human-induced habitat loss and fragmentation continue at an alarming pace and threaten the survival of wildlife species world-wide and particularly in tropical regions (Wade *et al.* 2003). Identifying which species traits are advantageous in the face of habitat alterations, and why, is an important prerequisite for the development of effective conservation strategies to minimize future biodiversity losses (Laurance 1991; Kotiaho *et al.* 2005) and hence has become a pressing need for conservation biologists. Extinction proneness depends on the spatial and temporal scale of the study (Henle *et al.* 2004) and varies widely among taxa (Davies, Margules & Lawrence 2000; Purvis *et al.* 2000; Jones, Purvis & Gittleman 2003). Moreover, empirical evidence suggests differential sensitivities of species to habitat fragmentation (Laurance 1991; Swihart *et al.* 2003b; dos Anjos 2006).

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Even though a wealth of factors has been linked to increased vulnerability to extinction on theoretical grounds, a recent review by Henle *et al.* (2004) suggests that only a limited suite of traits including small population size, high population fluctuations, rarity in the form of low abundance and a high degree of habitat specialization have good empirical support as strong general predictors of species' sensitivity. Other traits that are hypothesized commonly to increase a species' susceptibility to fragmentation are large body size, low mobility, high trophic level and low matrix tolerance (e.g. Laurance 1991; Purvis *et al.* 2000; Tscharntke *et al.* 2002; Ewers & Didham 2006). However, the relative importance of these traits is much less clear, as analyses are often confounded by a high degree of collinearity or synergistic interactions among traits (Davies, Margules & Lawrence 2004; Henle *et al.* 2004).

Bats are well-suited for evaluating sensitivity to habitat fragmentation, as they are mobile animals with the potential to readily move over extensive areas of fragmented landscapes. At the same time, they are ecologically highly diverse, suggesting differential vulnerability contingent upon species-specific ecological traits (Medellín, Equihua & Amin 2000). Because of their diversity and high abundance, bats are important components of tropical faunas where they fulfil crucial roles as pollinators, seed dispersers and arthropod predators (Kalko 1998; Patterson, Willig & Stevens 2003).

Analyses of correlates of extinction risk in bats have been restricted largely to large spatial scales (global, continental) and, to our knowledge, no study has examined in detail differential vulnerability of bats in the context of habitat fragmentation. Jones *et al.* (2003) identified small geographical ranges and low wing aspect ratio as significant global correlates of extinction proneness in bats. Safi & Kerth (2004), focusing on temperate-zone bats, found similarly that wing morphology as a measure of habitat specialization in bats is correlated with extinction risk, whereas dietary specialization was unrelated to extinction vulnerability. While these studies provide important insights into elucidating general endangering traits, they may be too broad in scope to be of practical use for species conservation (Fisher & Owens 2004). Here we present a quantitative assessment of trait-mediated differences in species responses of Neotropical bats to small-scale habitat fragmentation and discuss how determinants of extinction vulnerability compare to those identified by Jones *et al.* (2003) and Safi & Kerth (2004).

We used data on species prevalence and abundance collected in a 2-year study on 23 species of bats in a fragmented landscape of small land-bridge islands in Gatún Lake, Panama. We selected *a priori* nine well-defined and commonly used ecological characteristics and taxon-specific traits to explore their significance as potential predictors of species vulnerability to fragmentation:

1. *Natural abundance.* Based on theory and empirical evidence, species that occur naturally at low abundance should be more susceptible to fragmentation due to an increased risk of stochastic extinction (Davies *et al.* 2000; Henle *et al.* 2004).

2. *Body size.* Larger species are often attributed a higher extinction risk than small-bodied ones as they tend to have smaller populations, slower life histories and larger home ranges because of greater energy requirements (Purvis *et al.* 2000; Tscharntke *et al.* 2002). In line with this reasoning, we hypothesized larger species to be more vulnerable to fragmentation.

3. *Edge-sensitivity.* The proportion of habitat edges increases with fragmentation and studies have shown differential responses of species to a range of edge-effects (Harper *et al.* 2005; Ewers & Didham 2006). Long-term persistence in fragmented landscapes requires individuals to cross habitat boundaries regularly and disperse between remnant patches. We therefore predicted edge-avoiding species which depend on the core habitat of forests to exhibit higher fragmentation sensitivity.

4. *Trophic level.* Theory predicts that species at the top of food chains are more extinction-prone than those at lower trophic levels due to more unstable population dynamics (Henle *et al.* 2004). We hence expected animalivorous bats to be affected more negatively by fragmentation than phytophagous species.

5. *Dietary specialization.* Dietary specialists are thought to be more extinction-prone, as they should become more susceptible to an increased variation in the availability of particular food resources as a consequence of fragmentation. Higher diversity of available resources and degree of specialization may lead to an increased importance of this trait for tropical compared to temperate-zone bats (cf. Safi & Kerth 2004).

6. *Vertical stratification.* Bat species which forage mainly in the canopy and depend mainly on patchily distributed resources should also be more mobile and hence be less fragmentation-sensitive than species with limited mobility, such as understory bats, which forage primarily on spatio-temporally predictable but often more locally restricted food resources (Kalko 1998; Bernard 2001; Kalko & Handley 2001). Additionally, we expected generalists that use all forest strata opportunistically to be least fragmentation-sensitive because they are likely to adjust quickly to alterations in forest structure.

7. *Mobility.* We test the prediction that species with high mobility are more likely to persist in fragmented landscapes than less mobile species (Henle *et al.* 2004; Ewers & Didham 2006).

8. *Wing morphology.* In bats, wing morphology has been shown to be an important predictor of many ecological characteristics including foraging habitat, foraging strategy, dispersal ability and home range size (Norberg & Rayner 1987; Arita & Fenton 1997). Bats characterized by high wing loading and long and narrow wings (high aspect ratio) are fast and energy-efficient flyers, while those with shorter and broader wings have higher manoeuverability in cluttered habitats but increased costs for commuting over longer distances (Norberg & Rayner 1987). Wing morphology may hence limit movements in fragmented landscapes and we expected fragmentation sensitivity to be related negatively to wing loading and aspect ratio.

9. *Ecologically scaled landscape indices* (ESLI*s*). Species persistence in fragmented landscapes may also depend upon interactions between ecological and landscape attributes influencing patterns of species occurrence and abundance (Vos *et al.* 2001). *ESLIs* are measures which link explicitly
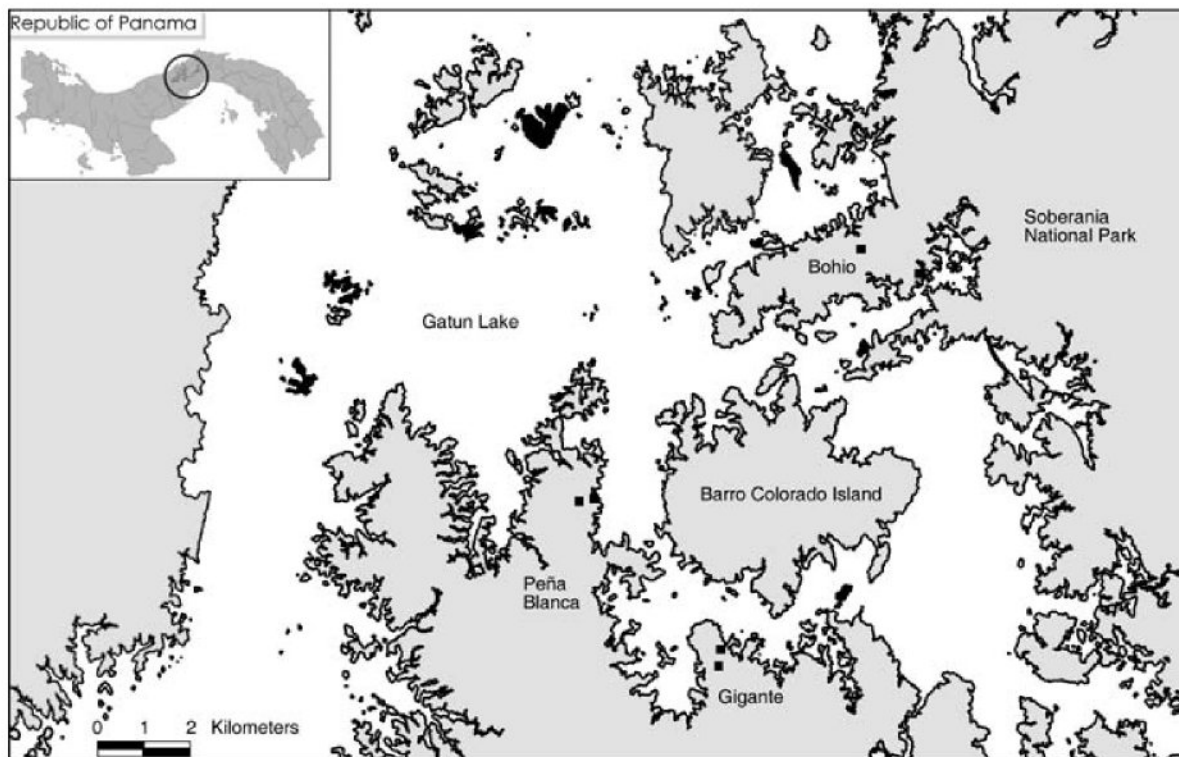
Fig. 1. Map of the study region in the Canal area in central Panama (inset) (modified from GIS coverage, D. Kinner and R. Stallard, US Geological Survey, 2003). Highlighted in black are the locations of the 11 study islands in Gatún Lake and of the six sites (■) in continuous forest on the mainland.

ecologically relevant characteristics of species, such as mobility to landscape structure, and hence provide a more sound alternative to general landscape indices (Vos *et al.* 2001; Swihart & Verboom 2004).

Materials and methods

STUDY AREA

Data on bat species occupancy and abundance were collected between October 2003 and October 2005 on several land-bridge islands in Lake Gatún, Panama (Fig. 1). Formation of this large artificial reservoir was completed in 1914, resulting in more than 200 forested islands ranging in size from < 1 ha to the 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). The BCNM is contiguous with Soberanía National Park, 22 000 ha of forest stretching along the eastern side of the canal (Fig. 1). Forests in the area are classified as lowland tropical moist forest (Holdridge 1967). The study 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, Wright & Herre 1993).

We selected 11 islands that differed in size (2·5–50 ha) and isolation (0·02–3·4 km) as well as six mainland sites on three peninsulas (Bohio, Gigante and Peña Blanca) within the BCNM (Fig. 1). To investigate potential edge-effects, a paired design with one forest edge and one forest interior site at each of these mainland locations was

adopted (mean distance between interior and edge sites 312 ± 42 (SE) m).

BAT SAMPLING

At each island and mainland site, bats were sampled in a standardized manner with mist-nets set along the perimeter of plots of ~0·5 ha (typically 50×100 m). We used six 6-m nets set at ground level and one net wall consisting of four stacked 6-m nets, reaching subcanopy (mainland sites) or canopy level (islands). Canopy height across study sites averaged < 20 m and was often < 15 m on islands. Identification was based on a key for the bats of the lowlands of Panama (Handley *et al.*, unpublished). The nomenclature follows Simmons (2005). Standard measurements and demographic data were collected following Handley *et al.* (1991). Each site was sampled for 7–8 nights (from dusk until dawn) over the 2-year period, with a minimum time interval of 30 days between netting nights. Species accumulation curves indicated that the bat fauna at each site was sampled adequately (C. F. J. Meyer & E. K. V. Kalko, unpublished data). In total, we obtained 8447 captures representing five families and 39 species (C. F. J. Meyer & E. K. V. Kalko, unpublished data). For the purpose of this study we excluded, except for the mormoopid bat *Pteronotus parnellii*, all non-phyllostomid species, as they cannot be sampled adequately with mist-nets (Kalko 1998), as well as species that were captured extremely rarely (< four captures) on the mainland. This resulted in 23 study species for analysis.

DERIVATION OF EXPLANATORY VARIABLES

Values for explanatory variables for each bat species were derived from our capture data and/or collated from the literature.

Natural abundance in continuous forest

Natural abundance was calculated for each species as the mean capture rate (recaptures excluded) per mist-net hour (mnh; 1 mnh = one 6-m net open for 1 h) at mainland interior sites.

Body mass

We used mean adult body mass obtained from our capture data as a measure of body size.

Edge-sensitivity

Following Harper *et al.* (2005), we calculated for each species the magnitude of edge sensitivity (*ES*), i.e. the difference in captures at mainland edge relative to mainland interior sites, as:

$$ES = (N_{edge} - N_{interior})/(N_{edge} + N_{interior}). \qquad \text{eqn 1}$$

We used total captures excluding recaptures, as capture effort was nearly the same for each site. The *ES* index can assume values from −1 (highly edge-sensitive, no captures at edges) to +1 (no captures in forest interior, only at edges).

Trophic level

Species were assigned to one of two broad trophic groups, animalivorous or phytophagous, which best reflects the main trophic structure of phyllostomid assemblages in our study area (Giannini & Kalko 2004, 2005). All animalivorous phyllostomids are gleaning bats that take food from surfaces.

Dietary specialization

Based on the literature (see Table S1 in Supplementary material), we assigned each species to one of three categories of food specialization. The majority of the data consisted of fecal samples, but prey remains from feeding roosts also contributed to the food records. Dietary records were defined as one observation of a particular food item. First, food items were divided broadly into four categories: (a) fruit, (b) nectar or pollen, (c) arthropods and (d) vertebrates. We then calculated the percentage contribution of each food category to total dietary records for each bat species. Species were assigned to the least specialized category if two or more of the food categories contributed > 10% to all food records. The second category consisted of species where one food category contributed > 90% to all food records. Species with an even narrower diet spectrum were separated further based on the relative contribution of particular food items and assigned to the third category. Enhanced consumption of the locally most abundant resource does not necessarily indicate dietary specialization of a species. For example, as there are many more insects than plant species providing food for bats, we considered an animalivorous species as specialized only if one prey order contributed more than three-quarters to the food records. For frugivores, according to our definition, this proportion needed to be from one plant genus. Moreover, because figs constitute the dominant portion of the diet of many frugivorous phyllostomids in the study region (Kalko, Handley & Handley 1996), a species with a mainly fig diet was considered specialized only if figs comprised more than 90% of its dietary records.

Vertical stratification

We derived the vertical niche of each species by calculating the proportion of captures in ground nets vs. high nets. For this, we counted only the two upper nets of the net wall as high nets, reflecting capture heights of *c*. 8–14 m vs. ground nets with < 3 m. Captures were expressed as capture rate per mnh to account for capture effort. Species were assigned to one of three categories of vertical stratification: (U) understorey species, < 33% of all captures in high nets; (N) opportunistic species without preference, 33–66% of all captures in high nets; (C) species with subcanopy/canopy preference, > 66% of all captures in high nets.

Mobility

We derived species mobility from mark–recapture data of the BCI long-term bat project (Kalko *et al.* 1996; unpublished data), consisting of nearly 50 000 captures and recaptures from BCI and adjacent peninsulas. We calculated the distance between marking and recapture site, excluding juveniles from the calculations as they may exhibit different movement patterns than adults. One species, *A. jamaicensis*, had several hundred recaptures in the database, so 50 recaptures were selected randomly, which was sufficient as variance in distances stabilized after 50 records. For the other species, all recaptures were included. To assess the degree of mobility (i.e. activity range), mean (excluding zeros) and maximum recapture distance were calculated and plotted. We then grouped the species into three categories of mobility (low, intermediate, high; see Supplementary material, Table S1 and Figure S1).

Wing morphology

We used data on aspect ratio and relative wing loading (mass-corrected index of wing loading; Norberg 1998) collected by one of us (W. P. L.) in Costa Rica and Panama. Values were determined from photographs (Olympus μ-II camera) taken of the extended left wing of each bat and analysed with the program analySIS 3·1 (Soft Imaging System Corp., Lakewood, CO, USA). Following Norberg & Rayner (1987), the head was excluded from calculations of wing area.

ESLIs

We calculated two *ESLIs*, average carrying capacity and patch connectivity, as proposed by Vos *et al.* (2001). First, average carrying capacity of patch *i* in a landscape of *n* patches is defined as:

$$ESLI_{\bar{K}} = \sum_{i=1}^{n} \frac{A_i}{IAR_i} \Big/ n, \qquad \text{eqn 2}$$

where A_i is the area of patch *i* and IAR_i is the individual area requirement of one reproductive unit (e.g. home range) of a particular species in patch *i*. In the same landscape, this index is higher for species with small individual area requirements than for species with greater area requirements. Secondly, Vos *et al.* (2001) combined a measure of patch isolation with individual species mobility in an index of average patch connectivity:

$$ESLI_{\bar{C}} = \sum_{i=1}^{n} A_i e^{-\alpha d_{ij}} \Big/ n, \qquad \text{eqn 3}$$

where d_{ij} is the distance between patches i and j, and α is a species-specific dispersal parameter. Species with good dispersal abilities, i.e. small α, therefore exhibit larger connectivity values than relatively poor dispersers. For $ESLI_C$, the dispersal parameter was calculated based on maximum dispersal distances derived from mark–recapture data of the BCI long-term bat project (see above). To obtain values that yield close to zero contributions at distances beyond the maximum dispersal distance, α was calculated as $\alpha = -\ln(0 \cdot 001)/d_{max}$ (Vos *et al.* 2001; Swihart *et al.* 2003a). $ESLI_C$ was quantified for landscapes delimited as circular buffer zones with a radius of $1 \cdot 5$ km surrounding each study island. The focal scale encompassed the expected home ranges of different-sized bat species and minimized spatial overlap between neighbouring islands. For the calculation of $ESLI_R$, individual area requirements were taken either directly from published accounts on maximum home range sizes or were predicted by regressing maximum recapture distances against published data on maximum home range sizes ($F_{1,7} = 8 \cdot 74$, $P = 0 \cdot 021$, $r^2 = 0 \cdot 56$).

Model set explored

Our *a priori* set of candidate models consisted of a total of 13 models. We did not consider interaction effects because of limited sample size but, in addition to the nine above-mentioned predictor variables, we included four additive models, each of which explored the joint contribution of several factors:
1. Dispersal model: mobility, body mass, relative wing loading, aspect ratio and edge-sensitivity.
2. Population size model: natural abundance, body mass and trophic position.
3. Specialization model: dietary specialization, vertical stratification and edge-sensitivity.
4. *ESLIs*: $ESLI_C$ and $ESLI_R$.

DATA ANALYSIS

It is important to correct for the statistical non-independence of taxa in such a multi-species study, and we therefore performed all analyses on phylogenetically independent contrasts (Felsenstein 1985), generated with the PDAP package implemented in Mesquite (Midford, Garland & Maddison 2005). Taxonomic relationships between species were inferred based on the phylogeny provided by Baker *et al.* (2003). Branches were set to equal length (Garland, Harvey & Ives 1992). We also conducted species-level analyses on data not corrected for phylogeny, and for comparison provide those results in the supplementary Table S2.

We conducted separate analyses to compare two measures of fragmentation sensitivity. First, we used the proportion of islands on which a particular species was present (arcsine-transformed). As an alternative measure of fragmentation sensitivity we calculated an index of change in abundance adapted from Davies *et al.* (2000) as the ratio of relative species abundances (RA) on islands and at mainland interior sites:

$$y = \log_e(RA_{islands} + 0 \cdot 0001/RA_{mainland\ interior} + 0 \cdot 0001). \qquad \text{eqn 4}$$

A small number ($0 \cdot 0001$) was added to the relative abundance of each species, as several species had zero captures on islands. We used generalized linear models (GLMs) on standardized independent contrasts to examine correlates of variation in bat species sensitivity to fragmentation. As both response variables followed a normal probability distribution (Shapiro–Wilk test, $P > 0 \cdot 6$) after phylogentic correction, they were modelled using GLMs with a Gaussian error structure and identity link function, forcing the regression through the origin (Garland *et al.* 1992). For each response variable, goodness-of-fit was examined based on the global model as percentage of deviance explained (Crawley 2005).

Prior to analyses, logarithmic transformations were performed on body mass, natural abundance and *ESLIs*. In preference to traditionally applied stepwise selection procedures whose use is statistically problematic (Quinn & Keough 2004; Whittingham *et al.* 2006), model selection was performed using an information-theoretic approach based on Akaike's information criterion (AIC), a measure which considers both model fit and complexity (Burnham & Anderson 2002). For each model, we calculated the AIC, corrected for small-sample size (AIC$_c$), following Burnham & Anderson (2002). Alternative models were ranked by rescaling the AIC$_c$ values such that the model with the minimum AIC$_c$ had a value of 0, i.e. $\Delta_i = AIC_i - AIC_{min}$. Models for which $\Delta_i \leq 2$ are considered to have substantial support, values of 4–7 have considerably less support, while those with $\Delta_i \geq 10$ essentially have no empirical support and can be ignored (Burnham & Anderson 2002).

To compare models we further computed Akaike weights, which are normalized model likelihoods, such that the values for all R models sum to 1. Akaike weights are approximate probabilities that model i is the actual best model in the set and in this sense provide an estimate of model selection uncertainty (Burnham & Anderson 2002). Akaike weights are additive and can be summed to provide a confidence set of models, with a particular probability that the best approximating model is contained within the confidence set (Burnham & Anderson 2002). To incorporate further model selection uncertainty into inference, we generated 10 000 bootstrap samples from the original data set and applied the model selection procedure independently to each resample by recording the proportion of times each candidate model returned the lowest AIC$_c$ (Burnham & Anderson 2002). These model selection frequencies (π_i) provide a measure of relative support for alternative models that is robust to the effects of sampling error in the original data.

Finally, we computed weighted estimates of regression coefficients for the predictor variables in a confidence set as

$$\hat{\bar{\theta}}_j = \sum_{i=1}^{R} w_i \hat{\theta}_{j,i}^+, \qquad \text{eqn 5}$$

where w_i is the Akaike weight of model i, and $\hat{\theta}_{j,i}^+$ is the estimator of the regression coefficient if predictor j is included in model i, or is zero otherwise. We report these parameter estimates along with unconditional standard errors, which incorporate a variance component due to model selection uncertainty and hence reflect more accurately the precision of a given model coefficient (Burnham & Anderson 2002). Analyses were performed using the R statistical package (R Development Core Team 2006).

Results

The 23 bat species included in the analyses exhibited considerable variation in sensitivity to fragmentation (Table 1). There was no obvious single best model supported by the data

Table 1. Responses to forest fragmentation recorded for 23 species of Neotropical bats in a fragmented landscape of islands in Gatún Lake, Panama. Fragmentation effects were estimated as species prevalence, i.e. the fraction of islands occupied, and using an index of change in abundance describing the decline/increase in species abundance relative to mainland interior sites

Species	Fraction of islands occupied	Change in abundance
Artibeus jamaicensis	1·00	0·692
A. lituratus	1·00	−0·001
A. phaeotis	0·36	0·081
A. watsoni	0·55	−1·684
Carollia castanea	0·45	−2·321
C. perspicillata	0·91	−0·659
Chiroderma villosum	0·64	0·154
Glossophaga soricina	0·91	2·144
Lampronycteris brachyotis	0·00	−2·776
Lophostoma silvicolum	0·18	−2·462
Micronycteris hirsuta	0·36	−1·529
M. microtis	0·82	1·022
Mimon crenulatum	0·00	−3·552
Phylloderma stenops	0·00	−3·309
P. hastatus	0·18	−1·920
Platyrrhinus helleri	0·45	0·779
Pteronotus parnellii	0·91	−1·096
Tonatia saurophila	0·18	−2·506
Trachops cirrhosus	0·00	−3·833
Uroderma bilobatum	1·00	1·578
Vampyressa nymphaea	0·09	−1·209
V. pusilla	0·82	0·159
Vampyrodes caraccioli	0·36	−1·318

(i.e. $w_{max} \leq 0.9$). For species prevalence, comparison of Δ_i values indicated the model incorporating edge-sensitivity to be the best approximating model in the candidate set, although an Akaike weight of 0·45 suggests considerable model selection uncertainty (Table 2, Fig. 2a). Natural abundance was ranked second, but based on Akaike weights was more than three times less likely than the best ranking model. Bootstrap selection frequencies generally indicated substantial uncertainty in model rankings as well. Of the 10 000 bootstrap samples generated, edge-sensitivity was selected as the best model in 34·9% of all cases ($\pi_i = 0.349$) while natural abundance was ranked first only half as often ($\pi_i = 0.175$). There was limited evidence for an effect of mobility and relative wing loading, while the subsequent five models had similar Δ_i values but generally received equivocal support based on model weights and selection frequencies (Table 2, Fig. 2a). Overall, the first nine models formed a ~94% confidence set. Parameter estimates for the best-supported models in the confidence set ($w_i > 0.1$, Table 3) indicate positive relationships between bat species prevalence and edge-sensitivity (the sign of the coefficient is positive because high edge-sensitivity is expressed as negative values) and natural abundance. However, the strength of the coefficient associated with natural abundance was much lower in magnitude than the one for edge-sensitivity (Table 3), placing relatively more importance on the latter variable in predicting patterns of bat species prevalence on our study islands.

Table 2. Results of Akaike information criterion (AIC)-based model selection assessing the association between two measures of fragmentation sensitivity and a set of candidate GLMs. For each model, the log-likelihood (Log-L), number of estimable parameters (K), sample-size adjusted AIC), Akaike differences (Δ_i), Akaike weights (w_i) and bootstrap selection frequencies (π_i) are presented. Model fit as evaluated based on the global model is given for each response variable as percentage deviance explained (% dev). Confidence sets as explained in the text are shown in italics

Response variable	Model description	Log(L)	K	AIC$_c$	Δ_i	w_i	π_I
Species prevalence	*Edge-sensitivity (ES)*	−4·01	2	12·65	0·00	0·449	0·349
(% dev. = 44·9)	*Natural abundance (NA)*	−5·19	2	15·01	2·36	0·138	0·175
	Mobility (M)	−6·07	2	16·77	4·12	0·057	0·045
	Relative wing loading (RWL)	−6·08	2	16·78	4·13	0·057	0·018
	Trophic level (TL)	−6·24	2	17·11	4·45	0·048	0·019
	Vertical stratification (VS)	−6·26	2	17·14	4·49	0·048	0·008
	Dietary specialization (DS)	−6·26	2	17·14	4·49	0·048	0·014
	Aspect ratio (AS)	−6·31	2	17·24	4·59	0·045	0·011
	Body mass (BM)	−6·31	2	17·25	4·59	0·045	0·020
	Specialization (DS + VS + ES)	−3·96	4	18·27	5·61	0·027	0·007
	$ESLI_C + ESLI_K$	−5·73	3	18·79	6·13	0·021	0·036
	Population size (NA + BM + TL)	−4·98	4	20·31	7·66	0·010	0·058
	Dispersal (M + RWL + AR + BM + ES)	−1·62	6	20·85	8·19	0·007	0·240
Change in abundance	*Edge-sensitivity (ES)*	−30·78	2	66·19	0·00	0·489	0·377
(% dev. = 45·5)	*$ESLI_C + ESLI_K$*	−31·08	3	69·49	3·31	0·094	0·156
	Natural abundance (NA)	−32·69	2	70·00	3·82	0·073	0·056
	Trophic level (TL)	−32·86	2	70·35	4·16	0·061	0·053
	Body mass (BM)	−33·05	2	70·74	4·55	0·050	0·073
	Dietary specialization (DS)	−33·28	2	71·19	5·01	0·040	0·024
	Aspect ratio (AS)	−33·33	2	71·30	5·11	0·038	0·010
	Vertical stratification (VS)	−33·34	2	71·31	5·12	0·038	0·011
	Relative wing loading (RWL)	−33·34	2	71·31	5·13	0·038	0·015
	Mobility (M)	−33·36	2	71·35	5·17	0·037	0·010
	Specialization (DS + VS + ES)	−30·65	4	71·65	5·46	0·032	0·035
	Population size (NA + BM + TL)	−32·10	4	74·54	8·36	0·007	0·035
	Dispersal (M + RWL + AR + BM + ES)	−29·29	6	76·18	10·00	0·003	0·146

Table 3. Parameter estimates ($\hat{\theta}$) and unconditional standard errors (SE) for each variable in the confidence set

| Response variable	Variable	Coefficient	Unconditional SE
Species prevalence	Edge-sensitivity	0·221	0·153
	Natural abundance	0·019	0·020
	Mobility	0·005	0·008
	Relative wing loading	−0·002	0·003
	Trophic level	−0·007	0·019
	Vertical stratification	−0·002	0·007
	Dietary specialization	−0·003	0·009
	Aspect ratio	0·002	0·016
	Body mass	0·001	0·007
Change in abundance	Edge-sensitivity	0·848	0·549
	ESLIs		
	($ESLI_C$)	−0·134	0·137
	($ESLI_R$)	−0·048	0·057
	Natural abundance	−0·026	0·033
	Trophic level	−0·072	0·099
	Body mass	−0·020	0·032
	Dietary specialization	0·010	0·026
	Aspect ratio	0·010	0·044
	Vertical stratification	−0·004	0·018
	Relative wing loading	0·001	0·006
	Mobility	0·000	0·015
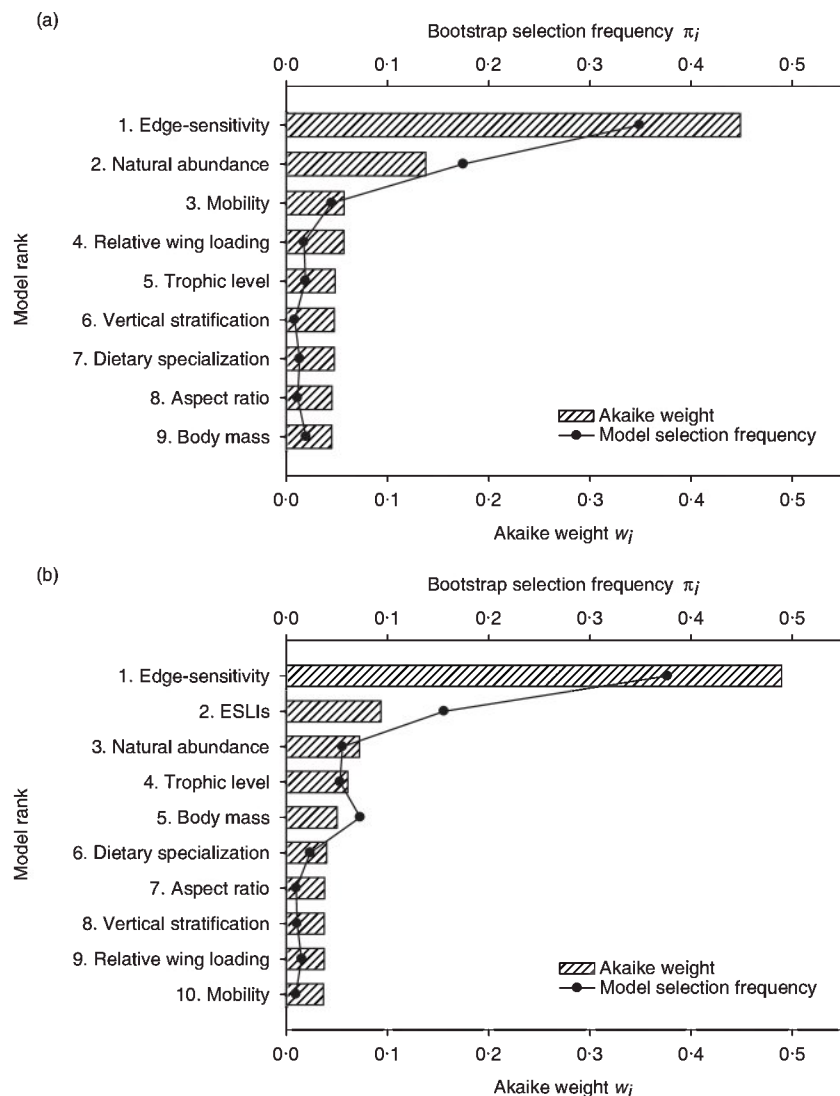
Fig. 2. Akaike weights and bootstrap selection frequencies indicating the relative support and selection uncertainty for each model included in the confidence set for (a) species prevalence and (b) the index of abundance change.

For the index of change in abundance as response variable, edge-sensitivity was again the model best supported by the data (Table 2, Fig. 2b). However, with Akaike weights of 0·49 and bootstrap selection frequencies of 37·7%, model selection uncertainty was again rather high. The second-ranked model focusing on the additive effects of the two ecologically scaled landscape indices (*ESLIs*) was more than five times less likely ($w_i = 0.094$) and bootstrap support was also lower ($\pi_i = 0.156$) than for edge-sensitivity. Taken together, the first 10 models formed a ~96% confidence set (Table 2, Fig. 2b). As with species prevalence, the regression coefficient indicated a positive association between change in abundance and edge-sensitivity and a negative relationship with *ESLIs*, and the strength of the coefficient implied that this effect was due largely to $ESLI_C$ (Table 3).

Discussion

PREDICTORS OF FRAGMENTATION SENSITIVITY

For the set of 23 Neotropical bat species studied within a fragmented landscape of land-bridge islands in Panama, high vulnerability to fragmentation was associated most strongly with high edge-sensitivity. Low natural abundance in continuous forest was also associated positively with vulnerability to fragmentation and there was limited evidence for an effect of movement ability (models mobility and relative wing loading) on species prevalence. Our results also suggest a negative relationship between the change in abundance and the index of patch connectivity ($ESLI_C$). All other ecological traits examined were far inferior predictors of fragmentation sensitivity. Highly parameterized models generally received very little support.

The fact that edge-sensitivity, natural abundance and variables related to species mobility were the top-ranked models common to the confidence sets of both measures of fragmentation sensitivity points to overall largely similar determinants of species presence/absence and change in abundance in our study system. Compared to species prevalence, the index of abundance change constitutes an indirect measure of fragmentation sensitivity which, however, also reflects extinction risk as a species' decline in fragments relative to control sites generally equates with increased vulnerability (Davies *et al.* 2000). Species prevalence is a widely used measure of species sensitivity (Swihart *et al.* 2003b; Swihart & Verboom 2004; Viveiros de Castro & Fernandez 2004) and is regarded as a generally useful predictor of metapopulation viability (Vos *et al.* 2001). However, one principal problem with this measure may arise because of differences in species abundance. Less abundant or rare species are most likely to be absent from an island due to sampling effects (Wright 1991). Consequently, fragmentation sensitivity of these species could, partly, be an artefact or may also be artificially amplified if a species does not occur at each site in continuous forest, either because of natural rarity or as a result of clumped distribution (spatial heterogeneity). This problem could only be addressed properly in a pre- vs. post-fragmentation comparison.

As historical data on species occurrences were lacking in our study we compared data from islands with unfragmented controls (e.g. Davies *et al.* 2000). We explored this issue further with a null model. Assuming a Poisson distribution for species abundance at each site, we derived the probability for zero abundance at a particular site *i* from the mainland interior capture data. This was used as the probability of 'absence from site *i*' in a binomial model of species prevalences, from which we derived the expected prevalence values for each species. These were significantly greater than the observed values, except for five species. However, expected prevalence values were also correlated significantly with natural abundance ($P < 0.001$, logistic regression). This, and the fact that natural abundance received weaker support as a determinant of species change in abundance, questions the overall importance of this trait in our case and the suitability of species prevalence as an index of fragmentation sensitivity in general.

We found no strong association between body mass as well as trophic level and vulnerability to fragmentation in the comparative analyses. Trophic level was, however, an important predictor in species-level analyses on data not corrected for phylogeny (see Supplementary material, Table S2). In general, effects of body size on fragmentation sensitivity are arguable based on current empirical evidence, which probably reflects the fact that body size is merely a surrogate for other traits known to influence vulnerability (Davies *et al.* 2000; Henle *et al.* 2004). Body size tends to be correlated positively with trophic level and species at higher trophic levels are often characterized by lower abundance and increased population fluctuations (Henle *et al.* 2004). However, the relationship of body size and trophic position with these demographic parameters is not always straightforward. Scale-dependent effects and interactions among traits may be responsible ultimately for the observed fuzzy association between trophic position and body mass in relation to extinction proneness (Henle *et al.* 2004).

Contrary to expectations, neither foraging stratum as a measure of habitat specialization nor dietary specialization were good predictors of bat vulnerability to fragmentation. While tropical bird communities exhibit a high degree of vertical stratification (e.g. Walther 2002) and terrestrial birds have been shown to be especially susceptible to fragmentation (Stratford & Stouffer 1999; Laurance *et al.* 2002; but see dos Anjos 2006), studies on bats point to a more flexible use of forest strata within and among species and an overall less clear pattern of vertical habitat partitioning (Bernard 2001; Kalko & Handley 2001). If habitat specialization is indeed an important trait considering fragmentation sensitivity in bats, vertical stratification at least does not reflect this. Regarding dietary specialization there is contention over its relationship with extinction risk, with conflicting results among studies (e.g. Laurance 1991; Swihart *et al.* 2003b; Safi & Kerth 2004). Our results corroborate the findings of Safi & Kerth (2004), who found no evidence in temperate-zone bats for the hypothesis that narrow dietary niche breadth is related to elevated extinction risk. They argued that the lack of association could be due to an insufficient resolution of fecal analyses, an

explanation equally plausible in our case. Furthermore, dietary specialization in bats may vary between different localities due to differences in the locally most abundant food resources (E. K. V. Kalko, unpublished results) and tends to be generally less pronounced than in other taxa such as butterflies (Kotiaho *et al.* 2005).

We found strong evidence that bat species which exhibit low edge-tolerance are predisposed to decline in forest fragments. Fragmentation causes serious habitat changes, especially close to forest edges, with some effects reaching several hundred metres into the forest (Laurance *et al.* 2002; Harper *et al.* 2005). Species may avoid edges because of structural habitat changes or because they often constitute significant movement barriers. Also, habitat edges can alter species interactions and thereby modify ecological processes such as competition and predation (Ewers & Didham 2006). For instance, species could be edge-sensitive due to vulnerability of their prey or the decline of particular food resources near edges. Contrary to the findings of some studies on tropical birds (e.g. Watson, Whittaker & Dawson 2004), changes in forest structure do not seem to underlie the edge-avoidance observed in some bat species of our study (C. F. J. Meyer & E. K. V. Kalko, unpublished data). Instead, changes in the densities of some preferred arthropod prey, e.g. katydids, with distance from the forest edge could reinforce the edge-sensitivity exhibited by many of the gleaning insectivorous bats. Our results confirm previous findings that gleaning animalivorous bats are particularly prone to habitat disturbance and fragmentation effects (Fenton *et al.* 1992; Medellín *et al.* 2000; Clarke, Pio & Racey 2005) and suggest that this is probably a corollary of specific trait combinations acting in concert such as high edge-sensitivity, low natural abundance and limited mobility.

It is likely that edge-sensitive species are often habitat specialists and are thus vulnerable to fragmentation (Tscharntke *et al.* 2002; Ewers & Didham 2006). Habitat specialization has also been linked indirectly to extinction proneness in bats (Jones *et al.* 2003; Safi & Kerth 2004) through its relationship with wing morphology. The magnitude of an edge-effect can be greatly moderated by the degree of contrast between fragments and the matrix, with the strongest effects in landscapes with high-contrast edges (Laurance *et al.* 2002; Ewers & Didham 2006). This may explain why edge-sensitivity was such a strong predictor of fragmentation sensitivity in our case. The notion that edge-sensitivity is not a static trait but may vary depending on the degree of fragment-matrix contrast is supported by studies of bats in other fragmented Neotropical landscapes, where the matrix is terrestrial habitat (Estrada & Coates-Estrada 2002; Bernard & Fenton 2003).

In line with theoretical predictions and corroborating other studies, e.g. on birds in Mexican cloud forest fragments (Watson 2003), our findings suggest a strong effect of movement ability on fragmentation sensitivity. The categorical variable mobility and relative wing loading as another measure of species vagility were among the top-ranked models for species prevalence, although unimportant as predictors of change in abundance. Jones *et al.* (2003) identified aspect

ratio as an important correlate of extinction risk in bats at the global scale, while Safi & Kerth (2004), in concordance with our results, found size-independent measures of wing morphology (wing tip shape) to influence extinction risk in temperate-zone bats.

A probable explanation for the overall lower predictive power of wing morphological variables in our case is that the larger data sets of those studies encompassed species foraging in cluttered habitats and species hunting in open space, while we focused on forest-dependent bats. Therefore the range of variation in wing loadings and aspect ratios in our species set was comparatively low, and wing morphology may have been a generally more important predictor if open-space aerial insectivorous bats had been included in the analysis.

ESLIs have been found to be useful predictors of patch occupancy in fragmented landscapes (Vos *et al.* 2001); however, the predictive capabilities of the two *ESLIs* for species prevalence were low in this study. This could in part result from rather large variation in the precision of these measures among species, particularly $ESLI_{\bar{R}}$, as home range sizes for many species had to be predicted from regression. None the less, we found evidence for a negative relationship between change in abundance and the index of patch connectivity ($ESLI_{\hat{C}}$), which links species' mobility to landscape structure, substantiating the notion that movement ability is an important trait shaping species susceptibility to fragmentation. The fact that current formulations of *ESLIs* do not discriminate among different matrix types suggests that further refinements incorporating differential matrix permeabilities may improve their usefulness as predictors of species fragmentation sensitivity (Swihart & Verboom 2004).

Conclusions

Our study provides evidence that edge-sensitivity is a key trait influencing the vulnerability of Neotropical bats to local-scale fragmentation. Hence, conservation efforts for the preservation of bat species that are affected negatively by habitat boundaries should be targeted at minimizing the amount of edge-habitat and reducing the degree of fragment-matrix contrast. This could, for instance, be achieved by actively promoting regrowth vegetation along forest edges, which would mitigate the strength of edge-effects and decrease the effective isolation of habitat remnants. The finding that fragmentation sensitivity was to some extent related to movement ability implies that risk assessments of Neotropical bat species could be based, in part, on mobility-related traits. In this regard, the utility of measures of functional connectivity such as $ESLI_{\hat{C}}$, which may serve as important planning tools for land-use managers, should be explored further.

Gleaning animalivorous bats, which are edge-sensitive, occur at low natural abundances and have limited mobility, may be able to persist in heavily fragmented landscapes only if the degree of remnant isolation and patch-matrix contrast is low and if there is spatial proximity to larger tracts of continuous forest – aspects that should be taken into consideration in management plans and in reserve design.

Further studies focusing on local-scale fragmentation sensitivity in bats from a wider range of geographical localities and including systems with different fragment-matrix contrast are necessary to determine whether traits identified by us as important prove useful as general predictors of local species decline in bats. From a conservation perspective, comparative analyses with such a narrow geographical focus will probably be the most valuable for developing predictive models of species fragmentation sensitivity which can aid in directing research efforts and devising efficient management strategies.

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Supplementary material

The following supplementary material is available for this article.

Table S1. Explanatory variables used in modelling fragmentation sensitivity.

Table S2. Model selection results based on analyses without phylogenetic correction.

Fig. S1. Plot used to group species into three mobility categories.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01389.x.
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