Trait-related responses to habitat fragmentation in Amazonian bats

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Summary

1. Understanding how interspecific variation in functional traits influences species' capacity to persist in fragments and use patches in fragmented landscapes is fundamental for the creation of effective conservation plans. This study uses phylogenetic comparative methods to investigate which functional traits of bat species are correlated with their vulnerability to fragmentation in a tropical landscape with low fragment–matrix contrast.

2. Bats were captured over two years in eight forest fragments, nine control sites in continuous forest, and in the secondary forest matrix at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil. We tested the hypothesis that there is a significant relationship between species functional traits, environmental gradients (continuous forest and fragment interiors, edges and matrix) and patterns of species distribution using phylogenetic generalized least squares (PGLS) models, as well as a combination of RLQ and fourth-corner analyses.

3. Mobility, body mass, wing morphology, and trophic level were the most important traits linked to fragmentation sensitivity based on the PGLS analysis, while body mass and trophic level emerged as the best predictors in the fourth-corner analysis. These last two traits were correlated with the loss of continuous forest characteristics, such as high-stature trees and forest cover.

4. Many animalivorous bat species rarely persist in small fragments (< 100 ha) and in the secondary forest matrix, reflecting strong effects of trait-mediated environmental filters that selectively benefit the smaller and phytophagous species.

5. *Synthesis and applications.* Functional traits of species and environmental variables jointly predict local variation in patterns of bat occupancy and abundance in fragmented tropical landscapes. To minimize local extinctions, we recommend increasing habitat availability and enhancing structural and functional connectivity at the landscape scale through the creation, restoration and maintenance of corridors and stepping stones. These measures should be coupled with improving matrix quality by promoting secondary forest regeneration and persistence to effectively reduce fragment–matrix contrast.

Key-words: Brazil, Central Amazon, Chiroptera, environmental filters, functional traits, habitat fragmentation, landscape structure, RLQ and fourth-corner analyses, trait–environment relationships, vulnerability

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Introduction

One of the biggest and urgent challenges for conservation biology is to understand species-functional trait associations with ecosystem functions in a context of

human-caused environmental changes. Such knowledge is pivotal for the development of effective management and conservation plans. Biodiversity loss in tropical forests world-wide is expected to increase in the next years if current anthropogenic pressures (e.g. livestock production, large-scale agricultural activities) on these ecosystems continue at present pace (Bradshaw, Sodhi & Brook 2009; Wearn, Reuman & Ewers 2012). Biodiversity loss may lead to loss of functional trait diversity, which potentially affects ecosystem functioning and processes that structure species assemblages (Mayfield *et al.* 2010; Cadotte, Carscadden & Mirotchnick 2011).

Environmental filtering is a fundamental process that may provide critical insights into community assembly (Weiher & Keddy 1995; Mayfield, Boni & Ackerly 2009). Understanding of how functional traits (morphological or physiological characteristics that directly influence individual performance, Violle *et al.* 2007) are filtered by the environment allows identification of species that are functionally similar and provides greater predictive power about community assembly and function compared to traditional approaches that have focused on the taxonomic dimension of biodiversity (Henle *et al.* 2004; Cadotte, Carscadden & Mirotchnick 2011; Mouillot *et al.* 2013). Furthermore, examining how species traits vary across environmental gradients can help to elucidate how land-use changes shape the diversity and composition of assemblages and advance our understanding of the mechanisms underlying species–environment relationships (McGill *et al.* 2006; Mayfield *et al.* 2010). In fragmented landscapes, the quality and permeability of the matrix (as determined by, for instance, vegetation structure, successional stage, spatial extent) and landscape characteristics (e.g. forest cover, fragment connectivity) may act as an environmental filter that determines species' persistence via functional traits (Lees & Peres 2008; Quesnelle, Lindsay & Fahrig 2014). Comparative studies that assess how traits shape species' responses in landscapes that differ in structural contrast between fragments and the intervening matrix are essential for increasing the effectiveness of management and conservation plans (Meyer *et al.* 2008).

Several studies have explored how tropical forest fragmentation affects the presence and abundance of bat species (e.g. Estrada & Coates-Estrada 2001; Klingbeil & Willig 2009; Bobrowiec & Gribel 2010). However, only a few recent studies conducted at a local scale have done so employing functional trait-based approaches (Duchamp & Swihart 2008; Meyer *et al.* 2008; Threlfall *et al.* 2011; Hanspach *et al.* 2012; Cisneros, Fagan & Willig 2015). For tropical ecosystems, the only study investigating relationships between sensitivity to fragmentation and species traits, which accounted for phylogenetic autocorrelation, comes from a fragmented landscape with high fragment–matrix contrast, a land-bridge island system in Panama (Meyer *et al.* 2008). However, species responses in systems with an inhospitable aquatic matrix likely constitute a worst-case scenario (Meyer & Kalko 2008) as they differ

fundamentally from those in many of today's human-modified tropical landscapes, which are characterized by a variety of land cover types that provide resources for many species (Mendenhall *et al.* 2014). From a functional perspective, bats are a good model group to assess how forest fragmentation influences the structure of their ecologically diverse assemblages (Meyer *et al.* 2008; Hanspach *et al.* 2012). Besides their high species richness, bats display wide variation in morphology, foraging behaviour and habitat use (Kunz & Fenton 2003), and they are important seed dispersers, pollinators, prey and regulators of animal populations (Kunz *et al.* 2011). Population reduction or local extinction may significantly impact the services bats provide (Maas, Clough & Tscharntke 2013).

This study is conducted within a phylogenetic comparative analysis framework aiming to understand which functional traits of bats are correlated with their vulnerability to fragmentation in a tropical landscape with low fragment–matrix contrast. By employing a modern statistical approach, analysing trait–environment links within a recently developed framework that integrates RLQ and fourth-corner methods (Dray *et al.* 2014), we tested the general hypothesis that there is a significant relationship between species functional traits, environmental gradients (continuous forest and fragment interiors, edges and matrix) and patterns of species distribution. Our specific aims were to (i) assess which functional traits contribute most to species' fragmentation sensitivity, (ii) understand how specific environmental characteristics (local vegetation structure and landscape attributes) set pathways to local loss of functional traits and (iii) identify which bat species are most vulnerable to fragmentation based on the traits identified in (i). We predicted that gleaning animalivorous bats, which are more habitat-specialized, heavier and less mobile, will be more vulnerable to fragmentation and that continuous forest characteristics, such as large, high-stature trees, and forest cover will be key factors for the maintenance of bat functional traits. Our study provides novel insights into the links between species traits and environmental characteristics in determining responses of bats to habitat fragmentation, and the results have wider relevance with regard to management and conservation of bats and other functionally important groups of wildlife in human-modified tropical landscapes.

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

The study was carried out at the Biological Dynamics of Forest Fragments Project (BDFFP) located ca. 80 km north of Manaus (2°25′S, 59°50′W), Central Amazon, Brazil (Fig. 1) (Lovejoy & Bierregaard 1990). The area is characterized by a mosaic of unflooded (*terra firme*) Amazonian rain forest, secondary forest (~8325 ha) and primary forest fragments (~245 ha). Mean annual temperature is 26 °C, and annual rainfall ranges from 1900 to
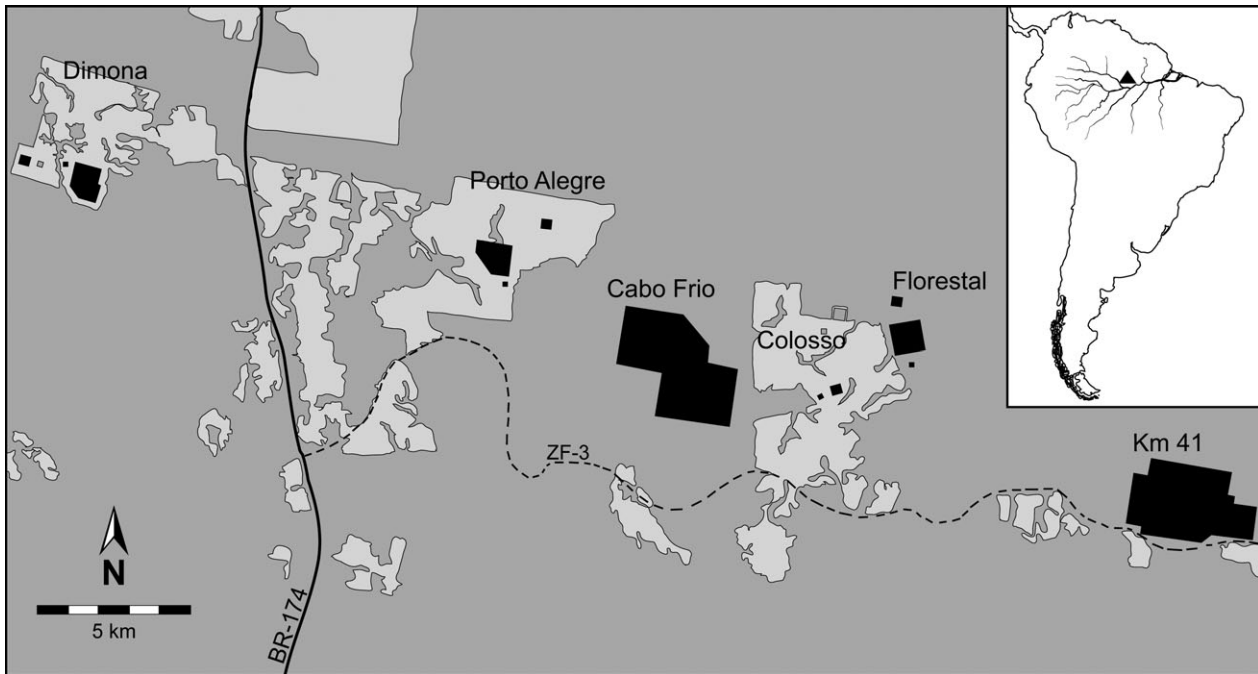
Fig. 1. Map of the study area in the Brazilian Amazon. Black: sampling sites in forest fragments (Dimona, Porto Alegre, Colosso camps) and continuous forest (Cabo Frio, Florestal, Km 41 camps); dark grey: continuous forest; light grey: secondary forest matrix. BR-174: paved highway; ZF-3: unpaved road. The triangle on the map of South America indicates the location of the study area.

3500 mm, with a rainy season from October to May (Laurance *et al.* 2011). The topography is relatively flat (80–160 m elevation), intersected by small streams. The primary forest canopy is 30–37 m tall, with emergent trees up to 55 m (Laurance *et al.* 2011). In the early 1980s, 11 fragments (1, 10 and 100 ha) were isolated from continuous forest by distances of 80–650 m by clearing and burning the surrounding forest. Since then, each fragment was re-isolated on three to four occasions, before this study most recently between 1999 and 2001 (Laurance *et al.* 2011). The matrix is characterized by secondary forests in different successional stages dominated by *Vismia* spp. (areas that were cleared and burned) and *Cecropia* spp. (areas that were cleared without fire) (Mesquita, Delamônica & Laurance 1999).

The study included eight forest fragments (three of 1 ha, three of 10 ha, two of 100 ha – Dimona, Porto Alegre and Colosso) and nine control sites in three areas of continuous forest (Cabo Frio, Florestal and Km 41) (Fig. 1). Bats were captured along netting transects established in the interiors and at the edges of all eight fragments, as well as at eight sites located 100 m from one of the borders of each fragment into the adjacent matrix. A similar sampling scheme was employed for continuous forest, using nine sampling sites in the forest interior, three at the edge, and three matrix sites located 100 m from the forest edge. Thus, a total of 39 sites were sampled. Mean distances between interior and edge sites were 245 ± 208 (SD) m for fragments and 1118 ± 488 m for continuous forest.

BAT SAMPLING

Bats were captured using 14 ground-level mist nets (12×2.5 m, 16-mm mesh, ECOTONE, Sopot, Poland) in the continuous forest interiors and fragments, seven at the edges, seven in the matrix and two to three canopy nets (2.5×12 m) in the interiors

of the continuous forest sites and fragments [total capture effort = 20 933 mnh; 1 mist-net-hour (mnh) equals one 12-m net open for 1 h]. Mean height of the top of canopy nets was 18 m. Canopy net data were used merely for assigning species to a particular forest stratum ('vertical stratification' trait, see below), not for obtaining data about abundance or site incidence. Each site was sampled for eight nights over a 2-year period (August 2011 to June 2013). Bias in capture rates due to net shyness (Marques *et al.* 2013) was avoided by spacing visits to the same site three to four weeks apart. Nets were opened from dusk until 6 h after exposure and revised at intervals of 10–30 min. Most adult bats (excluding pregnant females) were individually marked with numbered metal necklaces (frugivorous bats and *Pteronotus parnellii*) or transponders (gleaning animalivorous bats) and released at the capture site. Species identification followed mainly Lim & Engstrom (2001) and Gardner (2007). Taxonomy follows Gardner (2007). We captured 4845 bats representing six families and 59 species. We excluded all non-phyllostomid species, except the mormoopid bat *P. parnellii*, as they cannot be sampled adequately with mist nets (Kalko 1998). Rare species with less than three captures in continuous forest and same-site recaptures were also excluded. This resulted in 26 species for analysis (Fig. 2).

SPECIES TRAITS

We used six functional traits as predictors in modelling species' fragmentation sensitivity: (i) body mass, (ii) trophic level, (iii) dietary specialization, (iv) vertical stratification, (v) mobility and (vi) wing morphology. See Table 1 and Appendix S1 (Supporting information) for a description of these traits, and Meyer *et al.* (2008) for a detailed explanation of the rationale behind selecting these particular trait variables. The same predictor variables were used as in Meyer *et al.* (2008). However, as our focus here was
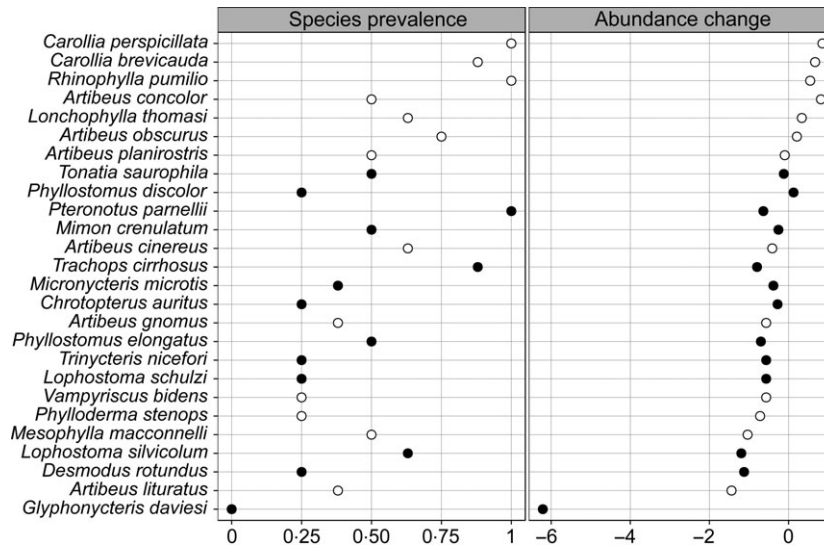
Fig. 2. Responses to forest fragmentation for 26 bat species at the Biological Dynamics of Forest Fragments Project (BDFFP), quantified as species prevalence (fraction of fragment interiors occupied) and through an index of change in abundance (relative species abundance in fragment interiors relative to continuous forest interior sites). Black circles: animalivorous species; white circles: phytophagous species.

on traits that are independent of a particular landscape context, we excluded 'natural abundance in continuous forest', 'edge sensitivity' and 'ecologically scaled landscape indices'.

ENVIRONMENTAL VARIABLES

Vegetation characteristics were measured within three plots (5 × 20 m, 100 m²) established 5 m from both sides of the 39 netting transects. In each plot, we quantified seven local-scale vegetation variables that may affect bat distribution and abundance (e.g. Meyer & Kalko 2008; Bobrowiec & Gribel 2010): (i) number of trees ≥10 cm diameter at breast height (d.b.h.), (ii) average d.b.h. of trees ≥10 cm, (iii) vertical stratification in vegetation density (visually classified at 5-m intervals across each plot as the sum of the values obtained by the estimation at seven height intervals [0–1, 1–2, 2–4, 4–8, 8–16, 16–24 and 24–32 m] using six categories varying from no to very dense vegetation), (iv) liana density (visually classified at 5-m intervals in five categories varying from no lianas to very high liana density), (v) number of potential roosts (hollow trees, trees with crevices and large buttress roots), (vi) number of *Vismia* spp. and *Cecropia* spp. trees (these species produce fruits consumed by many frugivorous bat species, e.g. Giannini & Kalko 2004) and (vii) tree height (calculated based on visual estimates of the height of 25 trees ≥10 cm d.b.h. per plot). Values for each sampling site were calculated as the average across replicated plots. We also considered the habitat modification gradient represented by continuous primary forest sites, primary forest fragments of different sizes (1, 10, 100 ha), forest edges and the secondary forest matrix as categorical variable (see 'habitat category' in Table S2). Finally, we included forest cover as a landscape-scale variable, quantified for a circle of 1·5-km radius centred on each of the 39 sampling sites using FRAGSTATS v.4 (McGarigal, Cushman & Ene 2012), based on 2004 LandSat Thematic Mapper images (30 × 30 m resolution). Buffer scale was chosen so as to encompass the home ranges of different-sized bat species while at the same time minimizing spatial overlap between neighbouring sites (Meyer *et al.*

2008). See Table S2 for summary statistics for each of these variables.

DATA ANALYSIS

Trait correlates of fragmentation sensitivity

To ensure comparability with the results of Meyer *et al.* (2008), we used captures in ground nets to derive the same two measures of fragmentation sensitivity as response variables: (i) species prevalence – proportion of fragment interiors in which a particular species was present (arcsine-transformed), (ii) index of change in abundance adapted from Davies, Margules & Lawrence (2000) – the ratio of relative species abundances (RA; bats per mnh) in the interiors of fragments and continuous forest sites: $y = \log_e ((RA_{fragments} + 0.0001)/(RA_{continuous\ forest} + 0.0001))$. A small number (0·0001) was added to the relative abundance of each species because *Glyphonycteris daviesi* was not captured in fragment interiors.

Our candidate set of models included seven single-trait models (body mass, trophic level, dietary specialization, vertical stratification, mobility, aspect ratio and relative wing loading). As fragmentation sensitivity may not be linked only to single traits but rather to combinations of multiple traits (e.g. Verberk, van Noordwijk & Hildrew 2013), we also explored the joint effect of several traits on fragmentation sensitivity by including three additive models in the candidate set of potentially important predictors: (i) dispersal (body mass, mobility and wing morphology), (ii) population size (body mass, trophic level) and (iii) specialization (dietary specialization, vertical stratification). Logarithmic transformations were performed on body mass to normalize values. Continuous predictor variables were standardized to a mean of zero and a standard deviation of one prior to analysis to facilitate comparison of their relative effects.

To avoid problems related to the statistical non-independence of related species, phylogenetic generalized least squares (PGLS) models were used to correct for phylogenetic autocorrelation in

Table 1. List and description of the functional traits used as predictors of bat species vulnerability to forest fragmentation in the Brazilian Amazon

Trait	Scale	Description	Source
1. Body mass	Continuous	Based on the average body mass of each species (excluding pregnant females and juveniles)	Our capture data
2. Trophic level	Categorical	Two broad trophic categories: animalivorous or phytophagous	Literature (Giannini & Kalko 2004; 2005)
3. Dietary specialization	Categorical	Based on the percentage of the contribution of each food item to the total dietary records for each species	Literature (see Table S1 for a complete list of references)
4. Vertical stratification	Categorical	Based on capture rate (bats per mist-net-hour) using the proportion of captures in ground vs. canopy nets	Our capture data
5. Mobility	Categorical	Based on the relationship between mean and maximum recapture distance (see Fig. S3)	Our capture data and Literature (see Table S1 for a complete list of references)
6. Wing morphology	Continuous	Aspect ratio and relative wing loading	Our capture data

See Appendix S1 for more detailed descriptions of some traits.

assessing correlates of variation in bat species sensitivity to fragmentation. Taxonomic relationships between species were based on the phylogeny proposed by Jones *et al.* (2002). Three of the 26 species were not present in the phylogeny and were substituted by their closest congener that was not captured in the study area, as done elsewhere (e.g. Cisneros, Fagan & Willig 2015). PGLS models were fit using the 'pgls' function in the R package *caper* (Orme *et al.* 2013), following the recommendation of Revell (2010) in simultaneously estimating phylogenetic signal (quantified using Pagel's λ, Pagel 1999) and the regression model.

We compared model fit and ranked candidate models using the Akaike information criterion (AIC) corrected for small sample size (AIC$_c$). Delta values ($\Delta_i < 2$) and high values of Akaike weights (w_i) (i.e. closest to 1) identified the models that received the strongest support. We also computed weighted estimates of regression coefficients and unconditional standard errors for the models in the 95% confidence set (Burnham & Anderson 2002) using the R package *MuMIn* (Bartoń 2014).

Trait–environment relationships

The relationships between species traits and environmental variables were tested by RLQ and fourth-corner analyses (Dolédec *et al.* 1996; Dray *et al.* 2014) as implemented in the R package *ade4* (Dray & Dufour 2007). These are two complementary multivariate analyses linking data from three tables: R (environmental variables per site), L (species relative abundances per site) and Q (functional traits per species). RLQ analysis maximizes the covariance between sites and species based on environmental variables and traits (Dray *et al.* 2014). The L species table was analysed by correspondence analysis (CA), and the R environmental and Q traits tables by Hill-Smith principal components analysis (PCA), which allows for mixed continuous and categorical variables (Hill & Smith 1976), using the CA site scores of the species ordination as row weights for the R table and species scores of the sites ordination as row weights for the Q table. This allows the link between the tables R and Q with the L table. We compared the variance explained (%) by the first two RLQ axes. Significance was assessed based on 49 999 permutations (Dray *et al.* 2014).

We followed the new approach recommended by Dray *et al.* (2014) in applying the fourth-corner tests to the output of the RLQ analysis, which allows quantifying and statistically testing the relationships between environmental variables and species traits. The result is a correlation matrix between environmental variables (R table) and traits (Q table) with species composition (L table). We used a combination of model 2 – which links the matrices L and Q and tests the null hypothesis that the distribution of species with fixed (i.e. site-independent) traits is not influenced by environmental conditions, with model 4 – which links the matrices L and R and tests the null hypothesis that the species composition of sites with fixed environmental conditions is not influenced by the species traits (Dray *et al.* 2014). According to Dray *et al.* (2014), this new approach combining these two permutation models has correct type I error rates. Significance of the relationship between species traits and environmental variables was assessed based on 49 999 permutations. Due to multiple tests on environmental variables, the *P* values were corrected by the false discovery rate method (FDR; Benjamini & Hochberg 1995; Dray *et al.* 2014). All analyses were performed using R v.3.0.1 (R-Development Core Team 2013).

Results

TRAIT CORRELATES OF FRAGMENTATION SENSITIVITY

Species exhibited considerable variation in sensitivity to fragmentation, and responses as assessed by species prevalence and abundance change measures were largely congruent (Pearson correlation, $r = 0.52$, $P = 0.006$; Fig. 2). Species that occupied more than half of the fragments (species prevalence ≥ 0.5) included primarily phytophagous bats while most animalivorous species were captured in less than half of the fragments (species prevalence ≤ 0.5; Fig. 2). Similarly, a decline in species abundance in fragments compared to control sites (abundance change) was more common and stronger in animalivorous than in phytophagous bats (Fig. 2).

There was substantial model selection uncertainty for both response variables. For species prevalence, mobility was the top-ranked model and received the strongest support ($w_i = 0.225$), however, body mass, relative wing

loading, aspect ratio, trophic level and vertical stratification were equally plausible predictors ($\Delta AIC_c < 2$, $w_i = 0.130$–0.153; Table 2). Model-averaged parameter estimates indicated positive associations between species prevalence and aspect ratio and negative relationships with mobility, body mass and relative wing loading (Table 3). For the abundance change index, trophic level and relative wing loading were nearly equally supported as best models in the candidate set ($w_i = 0.3$). Body mass

was also a plausible ($\Delta AIC_c < 2$), but somewhat less supported predictor ($w_i = 0.148$; Table 2). Parameter estimates indicated greater abundance changes in phytophagous bats than animalivores while relative wing loading and body mass were, respectively, positively and negatively associated with abundance change (Table 3). Phylogenetic signal in PGLS models was pervasive, especially for species prevalence, as indicated by large (>0.5) values of Pagel's λ in most cases (Table S3).

Table 2. Best-supported models from the 95% confidence set of candidate phylogenetic generalized least squares (PGLS) models for the two measures of fragmentation sensitivity

Response variable	Model description	AIC_c	Δ_i	w_i
Species prevalence	Mobility (M)	21.4	0.00	0.225
	Body mass (BM)	22.2	0.77	0.153
	Relative wing loading (RWL)	22.3	0.92	0.142
	Aspect ratio (AR)	22.4	0.95	0.139
	Trophic level (TL)	22.4	0.98	0.138
	Vertical stratification (VS)	22.5	1.10	0.130
	Dietary specialization (DS)	23.7	2.24	0.073
Change in abundance	Trophic level (TL)	86.8	0.00	0.315
	Relative wing loading (RWL)	86.8	0.06	0.306
	Body mass (BM)	88.3	1.52	0.148
	Population size (BM + TL)	89.2	2.45	0.093
	Vertical stratification (VS)	89.5	2.70	0.082
	Aspect ratio (AR)	90.2	3.46	0.056

Sample-size adjusted AIC (AIC_c), Akaike differences (Δ_i) and Akaike weights (w_i) are given. Full model selection results are provided in Table S3.

Table 3. Model-averaged parameter estimates (θ) and unconditional standard errors (SE) for each variable in the 95% confidence set

Response variable	Functional trait	θ	SE
Species prevalence	Intercept	1.123	0.235
	Mobility: linear	−0.141	0.110
	Mobility: quadratic	−0.136	0.084
	Body mass	−0.037	0.082
	Relative wing loading	−0.020	0.075
	Aspect ratio	0.013	0.072
	Trophic level: phytophagous	−0.020	0.222
	Vertical stratification: no preference	0.248	0.164
	Vertical stratification: understorey	0.115	0.154
	Dietary specialization: linear	0.186	0.231
	Dietary specialization: quadratic	0.088	0.144
Change in abundance	Intercept	−0.657	0.552
	Trophic level: phytophagous	0.912	0.480
	Relative wing loading	0.459	0.237
	Body mass	−0.326	0.340
	Vertical stratification: no preference	0.389	0.594
	Vertical stratification: understorey	−0.720	0.558
	Aspect ratio	−0.097	0.250

TRAIT–ENVIRONMENT RELATIONSHIPS

The first axis of the RLQ analysis accounted for 80.3% of the total co-inertia (i.e. link between the traits and environmental variables) and the second axis for 8.9% (Table 4). This represented 72.9% of the correlation expressed for the first axis in the CA of species composition (table L), and 87.7% and 84.9% of the total variance expressed for the first axis in the Hill-Smith PCA of the environmental variables (table R) and functional traits (table Q), respectively (Table 4), indicating variability in species trait values across the environmental gradient.

Continuous forest and 100 ha fragment interiors formed distinct groups relative to smaller fragments in the PCA ordination and along RLQ axis 1 of environmental variables (Figs 3 and S1). Most species (20, 77%) were positioned close to continuous forest and 100 ha fragment interiors in the PCA ordination (Fig. S1a,b), indicating that species richness increases with habitat integrity. Animalivorous bats that exhibit either low or high dietary specialization or mobility were associated with continuous forest, 100 ha fragment interiors, forest cover and tree height. In contrast, phytophagous bats with larger relative wing loading and intermediate mobility were associated with smaller fragments, edge and matrix habitats, abundance of *Vismia* and *Cecropia* trees and liana density. No

Table 4. Results of RLQ analysis using environmental variables and species traits. (a) Eigenvalues (and % of total co-inertia) for the first two axes. Ordinations of tables R (principal components analysis – PCA), L (correspondence analysis – CA) and Q (PCA). (b) Summary of RLQ analysis: eigenvalues and percentage of total co-inertia accounted for by the first two RLQ axes, covariance and correlation (and % variance) with the correspondence analysis of the L matrix and projected variance (and % variance) with the R and Q matrices

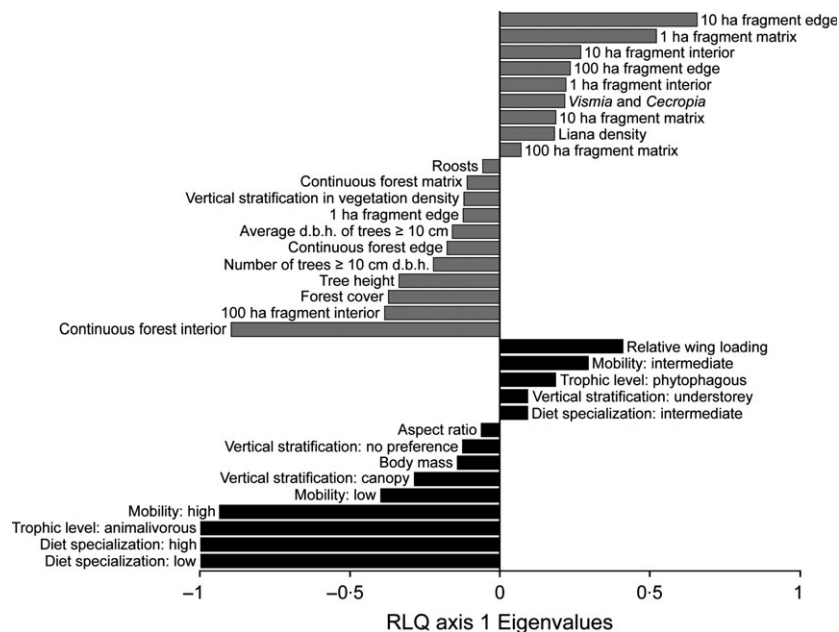|	Axis 1 (%)	Axis 2 (%)
(a)		
R table PCA (Hill-Smith)	3.72 (19.55)	2.19 (11.51)
L table CA	0.15 (25.54)	0.08 (13.52)
Q table PCA (Hill-Smith)	2.79 (27.93)	2.04 (20.44)
(b)		
RLQ axis eigenvalues	0.64 (80.30)	0.07 (8.95)
Covariance	0.80	0.27
Correlation: L	0.29 (72.93)	0.17 (60.41)
Projected variance: R	3.26 (87.70)	5.00 (84.62)
Projected variance: Q	2.37 (84.98)	3.74 (77.33)

Fig. 3. Plot of RLQ analysis relating bat species traits (black bars) and environmental variables (grey bars) along RLQ axis 1.

other traits were strongly correlated with the environmental variables (Figs 3 and S1).

The global test of the fourth-corner analysis found a highly significant relationship between species distribution and environmental variables (model 2, $P < 0.001$). In contrast, the association between species composition and functional traits was not significant (model 4, $P = 0.2$), as was the combined test of models 2 and 4 ($P = 0.2$). These results indicate that species composition is mostly dependent on the environmental conditions of the sites and not influenced by species' functional attributes.

Forest generalists and phytophagous species were positively correlated with fragmented or regenerating forest habitats according to the fourth-corner analysis (Fig. 4). In contrast, animalivores and heavier species had a negative association with increasing habitat alteration (Fig. 4). Some traits revealed a strong association with the environmental gradient. Body mass and trophic level were significantly correlated with the first two RLQ axes for environmental variables (AxR1/AxR2; Fig. 4a). We further found a significant association of continuous forest interior, high-stature trees and forest cover with the first RLQ axis for trait variables (AxQ1/AxQ2; Fig. 4b).

Discussion

Trait-based approaches have proven extremely useful for making recommendations concerning conservation plans (e.g. Cadotte, Carscadden & Mirotchnick 2011; Mouillot *et al.* 2013; Quesnelle, Lindsay & Fahrig 2014). Our results show that functional traits and environmental variables jointly predict variation in bat occupancy and abundance patterns in a fragmented landscape at a local scale. Occupancy patterns and changes in abundance indicated

that species with similar traits responded in similar ways to fragmentation, negatively affecting the heaviest species and animalivorous bats. The fourth-corner permutation models assessing the trait–environment link suggested that the distribution of species with fixed traits was influenced by environmental characteristics, that is there have been pervasive effects of vegetation structure of the fragments and secondary forests on the bat assemblages in the study area, with loss of functional traits in response to deforestation and fragmentation. On the other hand, species composition of sites with given environmental characteristics was not influenced by species traits. The outcome of the fourth-corner analysis thus is in line with the results of the PGLS analysis based on which several traits were plausible predictors of fragmentation sensitivity, yet overall received fairly low support. Mobility, body mass, wing morphology and trophic level were the best variables selected based on the PGLS analysis, while body mass and trophic level were the best predictors of vulnerability to habitat fragmentation in the fourth-corner analysis. These last two traits were correlated with the loss of continuous forest characteristics, such as high-stature trees and forest cover.

The relative importance of certain traits as predictors of species sensitivity to fragmentation may depend on the overall extent of deforestation and the particular compositional and structural characteristics of the landscape. Reanalysis of the data from Meyer *et al.*'s (2008) study in a Panamanian land-bridge island system using the same set of bat functional traits as predictors and the same method of analysis (PGLS) as employed herein indicated relative wing loading and body mass as best-ranked models (Table S4). Relative wing loading, body mass and trophic level are also among the highest-ranked traits

(a)

AxR1	AxR2	
0·968	0·019	Body mass
0·968	0·968	Aspect ratio
0·588	0·968	Relative wing loading
0·000	0·968	Trophic level: animalivorous
0·000	0·968	Trophic level: phytophagous
0·968	0·968	Diet specialization: low
0·726	0·979	Diet specialization: intermediate
0·654	0·968	Diet specialization: high
0·968	0·588	Mobility: low
0·174	0·588	Mobility: intermediate
0·726	0·968	Mobility: high
0·968	0·968	Vertical stratification: understorey
0·968	0·968	Vertical stratification: no preference
0·968	0·968	Vertical stratification: canopy

(b)

AxQ1	AxQ2	
0·788	0·789	Continuous forest edge
0·885	0·739	1 ha fragment edge
0·222	0·875	10 ha fragment edge
0·730	0·330	100 ha fragment edge
0·019	0·837	Continuous forest interior
0·739	0·871	1 ha fragment interior
0·511	0·504	10 ha fragment interior
0·612	0·791	100 ha fragment interior
0·871	0·866	Continuous forest matrix
0·143	0·789	1 ha fragment matrix
0·714	0·103	10 ha fragment matrix
0·871	0·595	100 ha fragment matrix
0·074	0·789	Number of trees ≥ 10 cm d.b.h.
0·187	0·875	Average d.b.h. of trees ≥ 10 cm
0·714	0·122	Vertical stratification in vegetation density
0·412	0·421	Liana density
0·791	0·730	Roosts
0·074	0·791	*Vismia* and *Cecropia*
0·019	0·946	Tree height
0·019	0·946	Forest cover

Fig. 4. Combination of fourth-corner and RLQ results. (a) Fourth-corner tests between the first two RLQ axes for environmental variables (AxR1/AxR2) and traits. (b) Fourth-corner tests between the first two RLQ axes for functional traits (AxQ1/AxQ2) and environmental variables. Significant ($P < 0.05$) positive associations are represented by dark grey cells; significant negative associations by light grey cells. Black lines separate different variables; grey lines separate different modalities for categorical variables. Variables with no significant associations are shown in white. P values are given in each cell.

based on AIC_c in both studies, indicating that these are traits whose importance as predictors of bat species vulnerability to fragmentation may be independent of matrix permeability. Habitat fragmentation and disturbance is expected to mostly affect larger, habitat-specialist species with lower relative wing loading and those of higher trophic levels (like secondary consumers) (Meyer *et al.* 2008). To reduce local extinction risk of these species, we recommend to increase habitat availability at the landscape scale.

As expected, our results confirm previous findings that animalivorous phyllostomids are most vulnerable to habitat disturbance and fragmentation, while phytophagous bats are more tolerant of edge and matrix habitats. This pattern has widely been documented in neotropical bat

studies (e.g. Estrada & Coates-Estrada 2001; Meyer *et al.* 2008; Klingbeil & Willig 2009; Bobrowiec & Gribel 2010). Many animalivorous bats rarely persist in small fragments (<100 ha) and in the secondary forest matrix due to strong environmental filtering based on their functional traits. This may explain the strong association of animalivorous bats with continuous forest and 100 ha fragment interiors in the RLQ analysis. The relationship between the vulnerability of some animalivorous species and body mass in our study is in accordance with Henle *et al.* (2004), who postulate that species at higher trophic levels tend to be larger, and larger species tend to be more vulnerable to fragmentation. At the BDFFP, the abundant production of fruits of successional plants in the secondary forest matrix, mainly *Vismia* spp. and *Cecropia* spp. (Bobrowiec & Gribel 2010), facilitates interpatch movements and fragment use by frugivorous bats, which are often good dispersers. This indicates that functionally similar species are not excluded from the fragments and secondary vegetation as a result of competition, but filtered according to functional traits that allow them to use disturbed areas. In addition to maintaining existing primary forest patches in the landscape, management efforts in fragmented tropical landscapes thus should focus on the natural regeneration or active restoration of degraded matrix habitats to increase seed dispersal by frugivorous bats and accelerate functional recovery.

Differential fragmentation sensitivity in neotropical bats has been shown to be related to some extent to species' movement ability. At the BDFFP, small distances between fragments and continuous forest and high fragment connectivity as a result of matrix regeneration (10–20 years) enhance species movement, particularly of those tolerant to disturbed areas. According to the RLQ analysis, bats with intermediate mobility were less vulnerable to fragmentation than bats with either low or high mobility. However, this was not supported by the PGLS analysis based on the index of abundance change and the fourth-corner analysis. In this context, it is important to note that for mobility there was low precision with which this trait could be quantified due to lack of data or low sample sizes for many species. Mobility, as quantified here, is sensitive to sample size since the maximum recapture distance is bound to increase with a greater number of recaptures.

The relatively high predictive power of wing morphology in explaining fragmentation sensitivity for forest-dependent bats is a result of differences in aspect ratio and relative wing loading between animalivorous and phytophagous species (Meyer *et al.* 2008; Marinello & Bernard 2014). Wing morphology also was a good predictor of extinction risk in bats as assessed based on IUCN threat criteria, both at a global scale (Jones, Purvis & Gittleman 2003) and for temperate zone insectivorous bats (Safi & Kerth 2004). Low aspect ratio and relative wing loading in neotropical bats are strongly associated with an animalivorous diet, and these characteristics predict

slower flight speed and good manoeuvrability, ideal for spatially complex environments as continuous forest interiors (Marinello & Bernard 2014). On other hand, higher aspect ratio and relative wing loading of frugivorous bats indicate higher flexibility in the use of space and ability to move between fragments.

Vertical foraging niche as a measure of habitat specialization had low support as predictor of bat vulnerability to fragmentation. Vertical stratum is a highly flexible trait (Meyer *et al.* 2008; García-García, Santos-Moreno & Kraker-Castañeda 2014). Many bat species are in fact difficult to assign to a particular stratum, given that capture height may not reflect foraging height (Rex *et al.* 2011). For phytophagous bats, flowers and fruits in neotropical rain forests are usually available at all vertical strata from ground level to the canopy (Schaefer, Schmidt & Wesenberg 2002). Fruits of pioneer plants can be found in lower strata at fragment edges and in the upper strata of secondary forests (>10 years), fragment interiors and in continuous forest (Voigt 2010). In line with Safi & Kerth (2004), we found no strong association between species vulnerability and dietary specialization. In general, this trait appears to be a better predictor for open-space aerial insectivorous bats in the temperate zone (e.g. Boyles & Storm 2007; Duchamp & Swihart 2008). The suite of traits important for predicting vulnerability may therefore depend on functional group and geographic locality.

CONCLUSIONS

The low fragment–matrix contrast and heterogeneity of secondary vegetation (i.e. quality and type of the matrix) enables many bat species at the BDFFP to use small fragments (≤10 ha). Those species with greater ability to use the matrix (i.e. most small frugivores) are also the ones that predominate in small fragments (≤10 ha). The importance of functional traits such as body mass, trophic level and mobility-related measures as predictors of fragmentation sensitivity indicates that forest integrity and functional connectivity among remnant patches, as conveyed here by the secondary vegetation at an advanced successional stage, are the main factors determining persistence of bat species in fragments. This finding provides an applied tool for landscape management through protected areas design.

As a practical suggestion for minimizing local extinctions of bat species and functional trait loss in fragmented landscapes, we recommend investing in the creation, restoration and maintenance of natural corridors and stepping stones. Moreover, management of the matrix by improving its quality is crucial, since the matrix functions as a buffer zone to edge effects, increasing the effective area of fragments (Mesquita, Delamônica & Laurance 1999; Bobrowiec & Gribel 2010), and effectively bolsters the persistence of functional diversity of bat assemblages. This, in turn, may be pivotal for sustaining overall ecosystem functionality. Restoration plans in fragmented landscapes must incorporate environmental information on the landscape scale to assure the re-establishment of key ecological services provided by bat populations. Our results indicate that gleaning animalivorous bats are mainly associated with large areas of continuous forest, underscoring the irreplaceability of old-growth forests and the need for megareserves (Laurance 2005; Gibson *et al.* 2011) for safeguarding this functionally important bat ensemble in particular, and Amazonian biodiversity in general.

Data accessibility

Data on bat species occupancy and abundance change, as well as functional trait data: uploaded as online supporting information (Table S1). Environmental descriptors of the study sites: uploaded as online supporting information (Table S2).

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Supporting Information

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

Appendix S1. Descriptions of some functional traits used as predictors of fragmentation sensitivity.

Fig. S1. Results of the first two axes of the RLQ analysis.

Fig. S2. Plots used to predict mean and maximum dispersal distances for nine bat species.

Fig. S3. Plot used to group species into three mobility categories.

Table S1. Explanatory variables used in modelling fragmentation sensitivity.

Table S2. Summary of vegetation variables used in the study.

Table S3. Model selection results for PGLS analyses examining correlates of bat fragmentation sensitivity at the BDFFP.

Table S4. Model selection results for PGLS analyses examining correlates of bat fragmentation sensitivity for Panamanian land-bridge islands.

Table S5. Model-averaged coefficients and unconditional standard errors for Panamanian land-bridge islands.