EFFECTS OF RAINFOREST FRAGMENTATION ON NEOTROPICAL BATS

Land-bridge islands as a model system

DISSERTATION

zur Erlangung des Doktorgrades Dr. rer. nat.
der Fakultät für Naturwissenschaften der Universität Ulm

vorgelegt von

Christoph F. J. Meyer

aus Frankfurt am Main

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COMMUNITY-LEVEL RESPONSES OF BATS TO TROPICAL FOREST FRAGMENTATION: LAND-BRIDGE ISLANDS AS A MODEL SYSTEM

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“The great tragedy of science - the slaying of a beautiful hypothesis by an ugly fact.”

*Thomas H. Huxley, English biologist (1825 - 1895)*
Summary

Impacts of rainforest fragmentation on Neotropical bats

*Land-bridge islands as a model system*

General introduction

The correlated processes of habitat loss and fragmentation are considered the most serious threats to biodiversity and the primary cause for the current extinction crisis (Laurance and Bierregaard 1997; Laurance and Cochrane 2001; Wilcox and Murphy 1985). Worldwide, particularly in tropical countries, deforestation, conversion of native forests into agricultural land, and urbanization, exacerbated by increasing population pressure, continue at alarming rates (Wright 2005), resulting in widespread habitat loss and fragmentation (Wade et al. 2003). Therefore, the fate of the world's tropical biota will hinge on the capacity of species to survive in human-modified and heavily fragmented landscapes, and on our ability to manage such landscapes to help mitigate the negative impacts of habitat loss and fragmentation on many wildlife species. As a consequence, habitat fragmentation has become a central issue in conservation biology (Laurance et al. 2002).

Fragmentation research as a multi-faceted discipline has attracted much interest in recent decades (cf. Debinski and Holt 2000; Ewers and Didham 2006; Fahrig 2003; Laurance and Bierregaard 1997; Turner 1996; Watling and Donnelly 2006). Early research into fragmented landscapes traditionally invoked MacArthur and Wilson’s (1967) equilibrium theory of island biogeography (ETIB) to study distribution patterns. This theory, which describes species richness on islands as a result of a dynamic equilibrium between area-dependent extinction and isolation-dependent colonization, has galvanized studies in ecological biogeography for over three decades (Fox and Fox 2000).

As empirical studies increasingly show that patterns observed in nature often do not conform to the simplified assumptions and generalizations of the ETIB, the applicability of this long-standing paradigm to explain and predict diversity patterns on isolated islands and in terrestrial habitat fragments has been questioned (Brown and Lomolino 2000; Whittaker 2000). This has led to calls to broaden the theory to consider additional parameters, in particular compositional differences, ecological differences among species (e.g. regarding
mobility and dispersal ability), and factors other than area and isolation such as disturbance and species interactions (Brown and Lomolino 2000; Fox and Fox 2000; Lomolino 2000; Whittaker 2000).

Moreover, with respect to forest fragmentation research, the pervasive influence of island biogeography theory has led many earlier studies to focus exclusively on processes occurring within forest remnants without addressing how the effects of changing forest area and isolation are mediated by the surrounding matrix (Kupfer et al. 2006). A growing body of evidence suggests that matrix quality is crucially important in determining species’ responses to fragmentation (Antongiovanni and Metzger 2005; Debinski 2006; Ewers and Didham 2006; Gascon et al. 1999). For instance, the quality and permeability of the matrix, together with ecological traits of the species such as dispersal ability and mobility, determine the functional connectivity among forest remnants. Moreover, the type of matrix can strongly influence within-remnant community dynamics through its influence on colonization and movement patterns of animals and hence species richness and composition within a fragment (Gascon et al. 1999; Laurance et al. 2002). Finally, depending on how similar the matrix is structurally to the original habitat, edge-effects may be more or less pronounced (Laurance et al. 2002), an aspect that the traditional ETIB approach to the study of habitat fragmentation failed to recognize (Ewers and Didham 2006; Murcia 1995).

Differentiating islands from terrestrial fragments and incorporating patch age and patch-matrix contrast, Watson (2002) provided a conceptual framework for assessing diversity patterns in patchy landscapes. Based on his review, most fragmentation research has so far concentrated on recently formed systems with low fragment-matrix contrast while young, high-contrast systems remain relatively poorly understood. These systems, however, hold great potential as they allow the study of fragmentation effects largely uncoupled from potentially confounding matrix effects, e.g., “spill-over” of matrix species, which may obscure area and isolation effects (Cook et al. 2002; Cosson et al. 1999; Leigh et al. 2002). In fact, as recently contended by Debinski (2006), rigorously comparing fragmentation effects between situations where one has patches with a clean (e.g. clearcut) matrix and those with more messy edges of a matrix consisting of irregular regrowth of secondary vegetation can provide important guidance in the management of corridors and reserves. In many tropical regions such as throughout the Brazilian Amazon where development activities and land conversion is accelerating, resulting in extensive clearings for highways, road networks, monocultures of row crops, or cattle pastures (Laurance et al. 2001), situations with
comparatively high-contrast edges and a matrix unsuitable for most forest-dependent species are becoming increasingly common.

Bats (Chiroptera), like many other groups of animals, are at risk from habitat destruction and fragmentation (Racey and Entwistle 2003), especially in tropical lowland forests where they are particularly species-rich. Bats form important components of Neotropical communities as they occupy a large variety of trophic niches and are locally often the most species-rich and abundant mammals (Kalko 1998; Patterson et al. 2003; Voss and Emmons 1996). The ecological importance of bats in tropical ecosystems as pollinators, seed dispersers, and control agents of prey populations is well appreciated. In the Neotropics, especially fruit- and nectar-eating bats of the family Phyllostomidae are considered keystone taxa because of their fundamental roles in maintaining plant diversity and their influence on forest dynamics through promoting secondary succession and forest regeneration (Kalko 1998; Patterson et al. 2003; Wunderle 1997). However, in spite of their widely recognized ecological importance few studies have explored the impact of human-induced habitat fragmentation on the structure and functioning of Neotropical bat assemblages (Estrada et al. 1993; Estrada and Coates-Estrada 2002; Faria 2006; Gorresen and Willig 2004; Sampaio 2000). Moreover, nearly all of those studies were conducted in young low-contrast systems *sensu* Watson (2002) and comparative data from systems with high fragment-matrix contrast are limited to very few studies (Cosson et al. 1999; Pons and Cosson 2002).

Consequently, many effects of habitat fragmentation on the highly diverse tropical bat assemblages remain poorly understood. This is particularly true with respect to the processes and mechanisms underlying the observed patterns, possible scale-dependence in those responses and how they vary depending on the level of fragment-matrix contrast of the study system. For instance, a large gap in our knowledge exists concerning the role sharp habitat boundaries and associated edge-effects play in shaping bat responses to habitat fragmentation. It has been shown that responses of animals to forest edges vary greatly both in terms of direction of response (positive, negative or no effect) as well as among and within taxa (Ewers and Didham 2006; Laurance et al. 2002).

In general, determining the relative influence of local versus landscape attributes on patch use by animals has been considered another important, yet little explored issue in studies of habitat fragmentation (Graham and Blake 2001). Even though several studies have highlighted the importance of spatial scale for detecting ecological relationships (Hill and Hamer 2004), the majority of studies have typically examined faunal responses to spatial
attributes in fragmented landscapes at a single landscape scale (Numa et al. 2005; Villard et al. 1999; Watson et al. 2004). For bats, the degree to which assemblages in fragmented landscapes are affected by local (patch-level) versus landscape characteristics so far has not been examined within a single study. Furthermore, whether bats respond mainly to habitat loss or to the changes in landscape configuration associated with fragmentation as well as possible scale-dependence in those responses remains little explored. Understanding the relative importance of habitat loss versus habitat fragmentation per se as determinants of bat responses to fragmentation has important implications for bat conservation as it sets the focus for management actions. Recent work by Gorresen and Willig (2004) and Gorresen et al. (2005) provided first evidence of scale-dependent and species-specific associations between landscape characteristics and population- and community-level attributes of phyllostomid bats, highlighting the importance of multi-scale approaches to studies of bat responses to habitat fragmentation.

In their quest to identify the causal processes shaping the structure of animal communities and hence provide the knowledge to address and predict effects of disturbance on those systems, ecologists focus on understanding whether communities are randomly assembled or if there are deterministic rules governing how species are assembled into communities. Since Diamond’s (1975) influential assembly rules model, which proposed that faunal assemblages on islands are mainly shaped by competitive interactions, the identification and explanation of non-random patterns in assemblage composition has become a central theme in community ecology (Weiher and Keddy 1999). Moreover, knowledge of patterns and causes of species distribution in insular biotas has been key to providing conservation guidelines, e.g. with respect to the design of nature reserves (Whittaker 1998).

While studies investigating patterns of negative species co-occurrence, i.e. competitive structuring, have traditionally focused on oceanic islands (Gotelli and McCabe 2002; Sfenthourakis et al. 2005), there have also been several recent attempts to apply such analyses within the framework of habitat fragmentation studies, e.g. on birds and beetles (Feeley 2003; Ulrich and Zalewski 2006; Zalewski and Ulrich 2006).

A compositional pattern that has frequently been reported for faunal assemblages on islands and in terrestrial fragmented systems is nestedness, where species present at species-poor sites constitute subsets of those present at more species-rich sites (Patterson and Atmar 1986; Wright et al. 1998). Contrary to Diamond’s assembly rules model, nested subset theory does not invoke competition as the structuring mechanism underlying community assembly. Instead, nested patterns in species assemblages are thought to arise as a result of species’
differential colonization or extinction, nested habitat structure, passive sampling (i.e., large areas sample both common and rare species while small areas sample only common ones), as well as distance or area effects (Wright et al. 1998).

Compared to other taxa, few studies have assessed bat assemblages with respect to species co-occurrence patterns and nested subset structure and analyses to date have largely been restricted to bats on oceanic islands (Gotelli and McCabe 2002; Wright et al. 1998). By contrast, no study has so far investigated patterns of nestedness and species associations for bats in the context of habitat fragmentation and examined possible causal mechanisms. However, such efforts to further our understanding of community assembly patterns and their mechanistic basis in fragmented systems are of great relevance in an applied conservation-oriented context.

In order to mitigate the effects of habitat alteration on biodiversity it is not only necessary to understand the causal processes determining species responses to fragmentation but it also requires predictive models of species fragmentation sensitivity that can help to identify vulnerable species and aid in directing management and conservation efforts. Hitherto, research has established that extinction proneness depends strongly on the spatial and temporal scale of the study (Henle et al. 2004) and varies widely among taxa (Davies et al. 2000; Jones et al. 2003; Owens and Bennett 2000; Purvis et al. 2000). A 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 (Henle et al. 2004). Other traits which are commonly hypothesized to be related to increased fragmentation sensitivity are large body size, low mobility, high trophic level, and low matrix tolerance (Ewers and Didham 2006; e.g., Laurance 1991; Purvis et al. 2000; Tscharntke et al. 2002).

Analyses of correlates of extinction risk in bats have been restricted so far to large spatial scales (global, continental) (Jones et al. 2003; Safi and Kerth 2004) and no study has examined in detail differential vulnerabilities of bats in the context of small-scale habitat fragmentation. While the large-scale 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 and Owens 2004). Quantitative assessments of trait-based differences in bat species responses to small-scale habitat fragmentation are therefore urgently needed.

In addition to such trait-based analyses risk assessments of species in fragmented landscapes should incorporate genetic studies (Lindenmayer and Peakall 2000). Generally, effective management for long-term conservation requires not only a quantitative
understanding of the demographic effects of habitat fragmentation on wildlife species but also necessitates an assessment of its genetic consequences. It is widely recognized that both demographic and genetic factors may affect the vulnerability of species to fragmentation, calling for studies integrating genetic and demographic approaches (Lindenmayer and Peakall 2000; Srikwan and Woodruff 2000). Habitat loss and fragmentation render populations more vulnerable to environmental, genetic, and demographic threats because they reduce their size and confine the remaining subpopulations to isolated patches (Lande 1993). This typically results in loss of genetic diversity and an increase in genetic differentiation among populations due to genetic drift and reduced gene flow (Frankham 1996; Lindenmayer and Peakall 2000). The amount of gene flow in fragmented landscapes is determined, among other things, by the interplay between landscape structure and dispersal or movement ability of species (Keyghobadi et al. 2005).

Neotropical bats differ widely in their movement ability (Albrecht et al. in press; Bernard and Fenton 2003) and may therefore exhibit differential genetic population structuring. However, very few studies on bats have explicitly examined the association between genetic structure and intrinsic ecological attributes such as mobility in bats (see Burland & Worthington Wilmer 2001). The relatively few studies assessing the genetic population structure of tropical bats mainly investigated patterns over large spatial scales (Carstens et al. 2004; Russell et al. 2005; Wilkinson and Fleming 1996) or examined the genetic structure of social groups, especially levels of colony relatedness and differentiation (Dechmann et al. in press; Wilkinson 1985). In contrast, the effects of habitat fragmentation on genetic diversity and population structure in tropical bats have not been assessed on a micro-geographic scale despite the profound impact fragmentation is likely to have on the genetic structure and persistence of bat populations.

**Thesis topics**

The overall objective of this study was to investigate the impact of rainforest fragmentation on Neotropical bats, working within a system of high fragment-matrix contrast, a suite of small land-bridge islands in Gatún Lake, central Panama. Based on extensive field survey data of bats sampled on 11 islands and at 6 mainland control sites obtained over the course of two years (October 2003-October 2005), I explored the following main research topics, summarized in four chapters, each representing a separate publication:
(1) “Community-level responses of bats to tropical forest fragmentation: land-bridge islands as a model system”.

(2) “Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns”.

(3) “Ecological correlates of vulnerability to fragmentation in Neotropical bats”.

(4) “Small-scale fragmentation effects on genetic diversity and population differentiation in three phyllostomid bats with different dispersal abilities”.

Throughout this thesis, I focus on New-World leaf-nosed bats (family Phyllostomidae) because (a) they are highly speciose and numerically dominant in Neotropical bat assemblages, (b) they can be reliably sampled with mist nets (Kalko 1998), (c) they play important roles as seed dispersers, pollinators, and predators (Kalko 1998; Patterson et al. 2003) and (d) they are crucial indicator species for the status of Neotropical forests (Fenton et al. 1992; Medellín et al. 2000).

Summary of chapters

A main aim of this study was to investigate how diversity and assemblage structure of phyllostomid bats are affected by small-scale habitat fragmentation and to determine how bat assemblages respond to forest edges and heterogeneity in vegetation structure (Chapter 1). Due to the hostile nature of the matrix I predicted isolation effects to be stronger than in systems with lower fragment-matrix contrast. Forest-dependent species with low mobility such as most gleaning animalivoruous bats were expected to be less common on isolated islands while I anticipated that they would still be used as temporary foraging grounds by some of the more mobile frugivorous bats. Moreover, I hypothesized that matrix-tolerant species, i.e. those with better movement abilities and not reluctant to cross open water, also exhibit high edge-tolerance. Finally, I predicted that the mostly younger forest on the wind-exposed islands should generally favor species better adapted to habitat disturbance (e.g. some frugivores) and disfavor those that rely more on undisturbed, mature forest (e.g. gleaning animalivores).

Using a combination of ground- and (sub)canopy-level mist netting, I sampled bats over a 2-year period (125 nights of sampling between October 2003 and October 2005) on 11 islands in Gatún Lake as well as at forest edge (n = 3) and interior sites (n = 3) in continuous forest on adjacent mainland peninsulas, resulting in > 8,200 captures belonging to 30 species of phyllostomid bats.
Overall, the islands harbored a less diverse (21 species compared to 30 species on the mainland) and structurally simplified bat fauna where far islands were especially species-poor (15 species). This marked decline in species richness with increasing isolation was associated with compositional shifts towards assemblages strongly dominated by a few frugivores with good movement capabilities: *Artibeus jamaicensis*, *A. lituratus*, and *Uroderma bilobatum*, were by far the most abundant species, accounting for 86.1% of all captures. *Artibeus jamaicensis* and especially *U. bilobatum* showed a pronounced increase in capture rate on islands relative to mainland interior sites. Two understory fruit-eating bats common in mainland forest, *Carollia perspicillata* and *C. castanea*, on the other hand, had overall lower capture rates on islands. Contrasting abundance patterns for these species have been observed in landscapes with low fragment-matrix contrast in Brazil where forest remnants are surrounded by regrowth that provides additional food resources, augmenting the abundance of shrub frugivores like *Carollia* (Faria 2006; Sampaio 2000).

My results thus confirm the notion that matrix quality and a species’ ability to utilize resources in the matrix can profoundly alter the intensity of observed fragmentation effects (Ewers and Didham 2006). Capture rates for the nectarivorous *Glossophaga soricina*, which was infrequently caught at mainland interior sites increased greatly from edge sites over near to far islands, corroborating other studies that this species can adapt well to disturbed and fragmented habitats, probably as a result of its rather generalized habitat requirements and dietary flexibility (Clarke et al. 2005a; Estrada and Coates-Estrada 2002). In contrast, gleaning animalivores were much less common on islands or completely absent, supporting previous studies with respect to the particular sensitivity of this group to forest disturbance, e.g. logging, and fragmentation (Clarke et al. 2005a; Pons and Cosson 2002).

Likely causes for this increased fragmentation sensitivity include various factors possibly acting together, including insufficient resources in fragments, often specialized foraging strategies and, for certain species, specific roosting requirements (e.g. Kalko et al. 2006), as well as limited mobility due to morphological constraints (Clarke et al. 2005b; Estrada and Coates-Estrada 2002). Although overall species composition was not significantly altered, similar trends were already apparent at continuous forest edge sites where species richness was significantly lower compared to interior sites and capture rates for many species, particularly animalivorous bats, declined relative to forest interior plots.

Edge-related effects observed on the level of individual species or guilds may result from species-specific responses to changes in the abundance or distribution of certain resources, an explanation that remains to be tested as pertinent data are largely lacking.
Variation in vegetation structure among sites was found to be important to a certain extent in separating island and mainland assemblages whereas variation in structural heterogeneity among mainland edge and interior sites was low and hence was found to be unrelated to bat species composition.

Another as yet poorly understood facet regarding the effects of forest fragmentation on tropical bat assemblages concerns the processes and mechanisms underlying the observed patterns and possible scale-dependence in those responses. A second focus of Chapter 1 therefore was on determining the causal factors associated with bat community-level attributes in terms of the relative influence of local (patch)-level versus landscape attributes and the importance of habitat loss and landscape configuration in shaping bat community organization. As the detection of ecological relationships is determined, in part, by the focal scale at which characteristics are measured (Gorresen et al. 2005), I expected the importance of factors to vary with spatial scale.

To this end, I explored correlations between bat species richness and assemblage composition, respectively, and a suite of local- and landscape-level characteristics. Restricting inference to a subset of plausible models selected a priori, local-scale variables were modeled separately and in combination with landscape metrics for each of the three spatial scales.

Model selection based on Akaike’s Information Criterion (AIC) revealed distance from the mainland and amount of forest cover in the landscape as the best predictors of phyllostomid richness and species composition. As assumed, responses were found to be scale-dependent, supporting recent findings that responses of bats to landscape characteristics are sensitive to spatial scale (Gorresen et al. 2005). At the smallest spatial scale, species richness was found to be independent of island area but positively correlated with island isolation. The lack of a species-area relationship at this scale may be evidence for a “small island effect”, i.e. the tendency for species-area relationships to be weak or non-significant for groups of small isolates (Lomolino and Weiser 2001). It likely also reflects the hostile nature of water as matrix as a result of which area effects might be partly masked or not be strong enough to become apparent at the patch level.

By contrast, community-level attributes were most strongly associated with forest cover at larger spatial scales suggesting that many species typically make use of multiple fragments. Overall, the modeling results point to habitat loss rather than fragmentation effects per se, i.e. the breaking apart of habitat and associated changes in landscape configuration, being the main process after isolation underlying phyllostomid bat responses on Gatún Lake.
islands. It has been contended that in most studies the effects of fragmentation per se are absent or too weak to be detected or may only become apparent at low levels of habitat amount (Fahrig 2003).

In Chapter 2 I approached the question which processes mainly determine bat assemblage composition on Gatún Lake islands from another perspective, using extensive null model analyses to test for patterns of non-randomness in presence-absence matrices of 20 species of phyllostomid bats. Specifically, I examined whether island bat assemblages are structured with respect to two frequently tested community assembly models: (1) faunal nestedness and (2) negative species co-occurrence reflecting competitive species interactions.

I investigated possible mechanisms underlying the observed patterns and explored the use of a series of weighting factors (island area, island isolation, species abundance) on the outcome of co-occurrence analyses. I performed separate analyses for the whole species set and different species submatrices reflecting differences in species’ trophic position (phytophagous versus animalivorous) and vagility (high versus low mobility).

Unweighted analyses revealed a significant negative co-occurrence pattern for the whole phyllostomid assemblage and when considering phytophagous bats alone. Weighting analyses by island isolation retained a pattern of species segregation for all species but also detected non-randomness in submatrices of animalivorous bats and less mobile species whereas the pattern for phytophagous and highly mobile species was not significant. The use of island area or relative abundance as weighting factors, in contrast, suggested random co-occurrence patterns as the null hypothesis was not rejected for any of the species matrices. Thus, the results indicate that island isolation but not area had to some degree confounded unweighted analyses, a finding in line with a marked species-distance effect and absence of a significant species-area relationship at local scales (Chapter 1). The results further demonstrate that incorporating weighting factors into co-occurrence analyses may improve the detectability of non-random patterns in species presence-absence matrices (Jenkins 2006).

Deviation from randomness was detected in incidence matrices of highly mobile species, which underscores the importance of taking differences in dispersal and movement abilities among species into account in co-occurrence analyses. My findings hence corroborate other studies regarding the importance of dispersal ability as a key trait shaping the structure of insular communities (Azeria 2004; Zalewski and Ulrich 2006). However, standardized effect sizes for incidence matrices which indicated significant deviation from randomness were low compared to those reported for other taxa (Gotelli and McCabe 2002).
Overall, co-occurrence analyses did hence not provide strong evidence for species composition of phyllostomid bats on Gatún Lake islands being highly structured by negative interspecific interactions. This is in agreement with the findings of meta-analyses of various bat assemblages and functional groups throughout the New World which also found little evidence for competitive structuring in most cases (Stevens and Willig 1999; 2000). This may reflect the fact that in studies conducted over large areas high heterogeneity and variability in environmental conditions may prevent competitive interactions from inducing deterministic structure in a ubiquitous way (Moreno et al. 2006; Stevens and Willig 2000). My results suggest that this applies equally well to heterogeneous fragmented landscapes.

Nested subset patterns have been documented for many different island and fragmented systems and a variety of taxa (cf. Wright et al. 1998) and phyllostomid bat assemblages on Gatún Lake islands also exhibited significant nestedness, regardless of whether the entire phyllostomid assemblage or different species submatrices were analyzed. The mechanism underlying faunal nestedness on land-bridge islands in many studies has been shown to be selective extinction driven by area effects (Feeley 2003; Patterson and Atmar 2000). Conversely, isolation-dependent, selective colonization appears to be the likely cause of nestedness in this study. Differential colonization can produce nestedness if highly mobile species are present even on the most isolated islands and less mobile species are restricted to the closer islands. This finding was supported insofar as this pattern seems to be mainly driven by differential movement ability between generally more mobile phytophagous bats and comparatively less vagile animalivorous species.

In conclusion, I found that bat assemblages on Gatún Lake islands are most strongly shaped by isolation effects and species’ differential movement and colonization ability while there was only weak evidence for negative interspecific interactions congruent with niche-based community assembly.

A further objective of my thesis was to determine which ecological traits of species are associated with high fragmentation sensitivity (Chapter 3). I approached this topic using distribution and abundance data on 23 bat species obtained as part of the 2-year netting study (Chapter 1). Nine well-defined and commonly used ecological characteristics and taxon-specific traits were selected a priori to explore their importance as predictors of species vulnerability to fragmentation: (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 (ESLIs). These explanatory variables were derived either from the capture data or gleaned from the literature and used separately or in combination for model fitting.

Generalized linear model analyses on standardized phylogenetically independent contrasts (Felsenstein 1985) were conducted to assess the relationship between predictor variables and two measures of fragmentation sensitivity, species prevalence, i.e. the proportion of islands occupied by a particular species, and an alternative index describing the change in abundance on islands relative to mainland interior sites. I employed modern information-theoretic model selection methods based on Akaike’s Information Criterion to compare and rank the models. This analytical approach allowed me to take model selection uncertainty into account (Burnham and Anderson 2002), an aspect typically neglected in similar studies.

Overall, edge-sensitivity was identified as the best correlate of vulnerability to fragmentation. Natural abundance in continuous forest and mobility or traits linked to mobility (relative wing loading and ESLI) received limited support as predictors.

My findings indicate that gleaning animalivorous bats are particularly vulnerable to small-scale forest fragmentation so that they may require special attention in conservation and wildlife management programs. The higher vulnerability of this group is probably a consequence of specific trait combinations acting together, such as typically high sensitivity to habitat edges, low natural abundance, and possibly to some extent lower mobility as reflected in wing morphology (comparatively low aspect ratios and wing loadings). My findings emphasize 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 edge-tolerance and mobility-related traits.

While the studies in the first chapters examined how Neotropical bats are affected by fragmentation mainly at the community level, in Chapter 4 I took a focal species approach and explored the effects of small-scale habitat fragmentation by linking genetic with ecological and demographic data.

For this analysis, I selected three species of phyllostomid bats (Uroderma bilobatum, Carollia perspicillata, and Micronycteris microtis), which, based on mark-recapture, radio-tracking, and wing morphological data, differ in their movement abilities and that had been shown to exhibit differential demographic responses to fragmentation (Chapter 1). I assessed genetic diversity and differentiation within and among island and mainland populations,
based on mitochondrial DNA sequence variation. I assumed that comparatively isolating matrix types - like water in the present study system - should translate into particularly low levels of gene flow, leading to genetic erosion in isolated island populations and increased levels of population subdivision. Furthermore, I tested the hypothesis that genetic differentiation within and between mainland and island populations will be a function of geographical distance (isolation by distance) and that such an effect will be lower for the species with high movement ability than for the less mobile species.

Indeed, the results indicated loss of genetic variation on islands, as predicted as a result of fragmentation, in all three species. Genetic diversity and, except in *U. bilobatum*, also allelic richness were lower in island compared to mainland populations. Furthermore, populations of all three species were significantly differentiated based on $F_{ST}$ and exhibited a pattern indicative of isolation by distance. As hypothesized, population subdivision was lowest in the species with the highest movement ability, *U. bilobatum* ($F_{ST} = 0.01$), moderate in the somewhat less mobile *C. perspicillata* ($F_{ST} = 0.06$), and highest in the rather sedentary *M. microtis* ($F_{ST} = 0.18$) where genetic exchange may be limited to infrequent natal dispersal events.

It is remarkable that loss of genetic variation was detectable in all three study species over such a rather small spatial scale (ca. 12 x 12 km) and in spite of the relatively short period of time, ca. 90 years, since the islands had become isolated. This shows that loss of genetic variation can manifest itself even after fairly short periods of time following fragmentation. Consistent with previous findings on other bat species (Burland et al. 1999; Newton et al. 2003), the results suggest that a species’ movement ability can serve as a good predictor of population genetic differentiation and, more generally, indicates that explicitly linking intrinsic attributes to population structure may serve as a useful predictive framework for population genetic analyses. Interestingly, even *U. bilobatum* and *M. microtis*, which both occurred at much higher abundances on the islands than in continuous mainland forest (Chapter 1), showed signs of genetic erosion and significant population genetic differentiation. This highlights the fact that relying exclusively on demographic data when assessing species’ vulnerability to fragmentation may not be sufficient, in line with other authors’ findings (Lindenmayer and Peakall 2000; Srikwan and Woodruff 2000).

**General conclusions**

Overall, this study provides several lines of evidence that Neotropical bats are strongly affected by small-scale habitat fragmentation, at the community-, population-,
individual species-, and genetic level. My study clearly emphasizes the need for paying attention to the effects of spatial scale and the strength of the matrix effect in examining how bats and animals in general respond to fragmentation. Differences with respect to bat community-level attributes between assemblages in unfragmented forest and on Gatún Lake islands were strongly determined by island isolation rather than area or habitat structure at the patch scale whereas area effects were prominent at larger spatial scales encompassing several islands. In agreement with these findings, nestedness- and co-occurrence analyses hinted at isolation-dependent, differential colonization linked to species-specific differences in mobility as the main factor governing species composition on islands. In this context, my study highlights the importance of considering both structural and functional connectivity in determining species’ responses to fragmentation.

Functional connectivity is greatly influenced by the ability and willingness of species to traverse habitat edges or, more generally, by their degree of edge-tolerance, which, in turn, depends in part on the nature of the matrix. Although the results at the community-level were inconclusive, I was able to demonstrate that certain bat species and foraging guilds exhibited high edge-sensitivity. My results further stress that bats respond mainly to habitat loss rather than the changes in landscape configuration associated with fragmentation suggesting that conservation efforts that attempt to minimize fragmentation for a given amount of habitat may often be inadequate and that conservation actions should focus on habitat preservation.

The study islands surrounded by a homogeneous aquatic matrix can be viewed as analogs of anthropogenic landscapes with patches of forest embedded in, e.g., cattle pasture or row crop fields. As such my findings can be regarded to represent a ‘worst-case’-scenario. However, I found that islands close to the mainland still retained surprisingly species-rich bat assemblages. This suggests that, provided a low degree of remnant isolation and spatial proximity to larger tracts of continuous forest (as in this case Soberania National Park with > 22,000 ha), small habitat remnants may act as stepping stones, enhance exchange of individuals and permit local population persistence of phyllostomid bats even when these fragments are embedded in a hostile matrix. This finding has important ramifications for reserve design and conservation planning. First, it underscores the importance of patch connectivity for the maintenance of a species-rich bat fauna in fragmented landscapes. Secondly, it adds to the growing evidence that small habitat remnants can be of substantial conservation value for a variety of animals including mobile groups such as bats. As a complement to preserving larger areas of continuous forest it is thus important to incorporate small habitat patches into conservation and management plans for Neotropical bats.
In my thesis, I presented the first comprehensive study linking ecological traits of bat species with their vulnerability to small-scale habitat fragmentation. My findings suggest that management efforts in fragmented landscapes should aim at minimizing the amount of edge-habitat and reducing the degree of fragment-matrix contrast to mitigate the strength of edge-effects. I conclude that from a conservation perspective, comparative analyses with a narrow geographic focus are the most valuable for developing predictive models of species fragmentation sensitivity crucial for directing research efforts and devising efficient management strategies.

The importance of focusing on local geographic scales is also highlighted by the genetic analyses. Further comparative studies across a range of ecologically different bat species focusing on micro-geographic scales are undoubtedly needed to broaden our knowledge as to the genetic consequences of habitat fragmentation on bat populations. The fact that two species which did not show negative demographic responses already revealed loss of genetic variation as a consequence of fragmentation, underlines the need for jointly considering demographic and genetic data in fragmentation studies. Effective conservation efforts and management strategies can only be successfully implemented by taking such an integrative approach.

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Publications from this thesis and contributions of co-authors

The present thesis is based on the following four papers, which have been accepted for publication (chapter 3) or have been submitted to scientific journals and are currently under review:


Prof. Elisabeth Kalko is co-author on this paper and all other publications resulting from this thesis as she provided valuable comments on the manuscripts and otherwise gave important input through discussions on all aspects of the study.


Jochen Fründ helped with field work, contributed to data analysis and commented on the manuscript. Willy Pineda Lizano provided the data on wing morphology used in the paper.


PD Dr. Gerald Kerth is co-author on this paper as he analyzed the genetic samples and data and contributed to writing.
Zusammenfassung

Effekte von Habitatfragmentierung auf neotropische Fledermäuse

Landbrückeninseln als Modellsystem

Allgemeine Einleitung


Die Schwerpunkte von Fragmentierungs-Studien lagen bisher hauptsächlich auf jungen, rezent isolierten und von einer meist wenig kontrastierenden Habitat-Matrix (z.B. Sekundärvegetation in verschiedenen Sukzessionsstadien) umgebenen Waldfragmenten. Demgegenüber sind Fragmentierungseffekte in Systemen mit hohem Fragment-Matrix-
Zusammenfassung


(1) Effekte von Regenwaldfragmentierung auf tropische Fledermausgemeinschaften: Landbrückeninseln als Modellsystem.


(3) Ökologische Korrelate von Fragmentierungs-Sensitivität bei neotropischen Fledermäusen.
(4) Genetische Effekte kleinräumiger Habitatfragmentierung auf drei Fledermausarten unterschiedlicher Mobilität.

Im Fokus meiner Arbeit standen Neuwelt-Blattnasenfledermäuse (Familie Phyllostomidae), da sie (1) sehr gut über Japannetzfänge inventarisiert werden können, (2) sehr artenreich und in neotropischen Fledermausgemeinschaften numerisch dominant sind, (3) ihnen bedeutende Rollen als Samenausbreiter, Bestäuber und Prädatoren zukommen und sie (4) wichtige Indikatorarten für den Störungsgrad neotropischer Wälder sind.

Zusammenfassung der Kapitel


Abundanzzunahme auf den Inseln im Vergleich zum Festland. Dies galt ebenso für die nektarivore *Glossophaga soricina*. Im Gegensatz dazu zeigten die frugivoren *Piper*-Spezialisten *Carollia perspicillata* und *C. castanea* ein umgekehrtes Muster. Gleanende animalivore Arten, die Nahrung von Oberflächen absammeln, waren auf den Inseln sehr selten oder fehlten ganz. Obwohl die Unterschiede hinsichtlich der Artenzusammensetzung nicht signifikant waren, gab es ähnliche Trends für alle Phyllostomiden in den *forest edge*-Flächen auf dem Festland, die signifikant weniger Arten als *forest interior*-Flächen aufwiesen. Zudem waren sie für viele Arten, vor allem den animalivoren Gleanern, durch niedrigere Fangraten relativ zu den *interior*-Flächen charakterisiert.


Das 4. Kapitel schließlich beschäftigt sich mit den Konsequenzen von kleinräumiger Habitatfragmentierung auf genetischer Ebene am Beispiel von drei Phyllostomiden-Arten (Uroderma bilobatum, Carollia perspicillata, Micronycteris microtis), die sich in ihrer Mobilität und demographischen Antwort auf Fragmentierung unterscheiden. Dabei untersuchte ich die genetische Diversität und Differenzierung innerhalb und zwischen Insel- und Festlandpopulationen und testete die Annahme, daß die genetische Differenzierung innerhalb und zwischen Insel- und Festlandpopulationen einem Muster von Distanzisolation folgt. Aufgrund der Unterschiede in der Mobilität der Arten postulierte ich ferner, daß das
Maß an Populationsdifferenzierung eine Funktion der Mobilität der jeweiligen Art darstellt, wobei die am wenigsten mobile Art am stärksten genetisch differenziert sein sollte. Basierend auf Analysen mitochondrialer DNA war bei allen drei Arten ein Verlust genetischer Variabilität feststellbar. Die Populationen aller drei Arten waren signifikant genetisch differenziert und zeigten ein Muster von Distanzisolation (isolation by distance). In Einklang mit meiner Hypothese wies die Art mit der höchsten Mobilität (U. bilobatum) die geringste Populationsdifferenzierung auf (F<sub>ST</sub> = 0.01). C. perspicillata war als Art mit intermediärer Mobilität geringfügig stärker differenziert (F<sub>ST</sub> = 0.06) im Gegensatz zu Populationen der am wenigsten mobilen Art M. microtis, die am Vergleich zu den beiden anderen Arten am stärksten differenziert waren (F<sub>ST</sub> = 0.18). Besonders hervorzuheben ist, daß genetische Erosion trotz der Kleinräumigkeit der Studie (ca. 12 x 12 km) und des relativ geringen Isolationszeitraums (ca. 90 Jahre) bei allen drei Arten feststellbar war. Meine Ergebnisse zeigen, daß die Mobilität einer Art als guter Prädiktor für genetische Populationsdifferenzierung herangezogen werden kann. Die Tatsache, daß selbst U. bilobatum und M. microtis, die in dieser Studie auf den Inseln durchgehend weitaus höhere Abundanzen erreichten als auf dem Festland, solche ausgeprägten genetischen Effekte zeigten, demonstriert eindrucksvoll die Notwendigkeit der Integration von genetischen und demographischen Studien im Zusammenhang mit der Abschätzung der Fragmentierungssensitivität von Arten.

Schlußfolgerungen und Ausblick

bestimmte Flächengröße zu minimieren, oft inadäquat sind und daher primär Habitat-Präervation im Fokus von Naturschutzbemühungen für neotropische Fledermäuse stehen sollte.


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

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Abstract. - Many effects of habitat fragmentation on diverse assemblages of tropical vertebrates are poorly understood, particularly with respect to the processes underlying the observed patterns, possible scale-dependence in those responses and how they vary depending on the level of fragment-matrix contrast. Working within a system with high fragment-matrix contrast, a set of land-bridge islands in Gatún Lake, Panama, we investigated the relative influence of local-scale (vegetation structure, patch-level metrics such as island area, shape, isolation distance) vs. landscape characteristics (e.g., forest cover, patch density) and the importance of spatial scale in determining species richness and composition of phyllostomid bats on islands. We further assessed patterns of species loss and changes in species composition on islands relative to mainland assemblages and possible edge-related gradients in these attributes between interior and edge sites in continuous forest. Bats were sampled over a 2-year period on 11 islands as well as at forest edge (n = 3) and interior sites (n = 3) on the adjacent mainland, resulting in > 8,400 captures. Overall, the islands harbored a less diverse and structurally simplified bat fauna where far islands were especially species-poor. This decline in species richness was associated with compositional shifts towards assemblages strongly dominated by frugivores with good dispersal abilities while members of other feeding guilds, most importantly gleaning animalivores, were much less common or absent. Although overall species composition was not significantly altered, similar trends were already apparent at continuous forest edge sites where species richness was significantly lower compared to interior sites. Distance from the mainland and amount of forest cover in the landscape were the best predictors of species richness and assemblage composition of bats on our study islands. Responses were scale-dependent. At the local scale, species richness was found to be independent of island area but positively correlated with isolation. This may be evidence for a “small island effect” or reflect the inhospitable nature of the matrix as a result of which area effects might be partly masked at the patch level. By contrast, area effects became more important at larger spatial scales suggesting that many species typically make use of multiple fragments.

Key words: area and isolation, assemblages, bats, conservation, edge-effects, forest fragmentation, Gatún Lake, land-bridge islands, landscape structure, Panama, Phyllostomidae, spatial scale
Introduction

Changes in land use have been identified as key drivers of current and future biodiversity loss, particularly in tropical regions where the extent of habitat modification is projected to be most pronounced (Sala et al. 2000) and where deforestation continues at unprecedented rates (Whitmore 1997, Laurance et al. 2001, Wright 2005) as does conversion into agricultural lands, pastoralization, and urbanization (Sala et al. 2000, Wade et al. 2003). Hence, the fate of the world's tropical biota will be largely governed by the capacity of species to survive in fragmented landscapes, and depend on our ability to manage such landscapes to help mitigate the effects of habitat loss and isolation (Laurance et al. 2002).

One key finding of recent fragmentation studies is that species’ responses to fragmentation are profoundly influenced by the type of the matrix (Gascon et al. 1999, Antongiovanni and Metzger 2005, Ewers and Didham 2006), which will determine to a large degree an animal’s ability to exploit it. At the extreme end of the spectrum are forest-dependent species, which react negatively even to very small habitat disruptions, such as Neotropical understory birds which are reluctant to cross even small road clearings (Develey and Stouffer 2001, Laurance et al. 2004). On the other hand, many species readily cross matrix composed of secondary growth or a mosaic of agricultural vegetation (e.g. Estrada and Coates-Estrada 2002, Antongiovanni and Metzger 2005). Thus, the quality and permeability of the matrix, together with ecological traits of the species such as dispersal ability, are essential in determining the functional connectivity among forest remnants and ultimately control species’ persistence in patchy and fragmented landscapes. Moreover, the type of matrix is a strong determinant of within-remnant community dynamics through its influence on colonization and movement patterns of animals and hence species richness and composition within a fragment (Gascon et al. 1999, Laurance et al. 2002). Finally, depending on how similar the matrix is structurally to the original habitat, edge-related gradients in physical and biotic variables will be more or less pronounced (Murcia 1995, Laurance et al. 2002). In particular, changes in plant community composition and structure associated with forest edges (Harper et al. 2005) may strongly affect abundance patterns and composition of animal assemblages as has been demonstrated for tropical birds (Beier et al. 2002, Watson et al. 2004b).

To date, most fragmentation research has concentrated on recently formed systems with low fragment-matrix contrast while young, high-contrast systems, as exemplified by islands in reservoirs, remain relatively poorly understood (see review by Watson 2002). Yet,
these systems hold great potential as they allow the study of fragmentation effects separately from potentially confounding matrix effects, e.g., “spill-over” of matrix species, which may obscure area and isolation effects (Cosson et al. 1999, Leigh et al. 2002). Population- and community-level responses have been examined in such systems mainly for plants, birds, and rodents (e.g. Adler and Seamon 1991, Leigh et al. 1993, Terborgh et al. 1997, Sieving and Karr 1997, Adler 2000, Lambert et al. 2003, Asquith and Mejía-Chang 2005) and have led to important new insights, particularly regarding the importance of top-down vs. bottom-up regulation of tropical ecosystems (Terborgh et al. 2001). For bats, on the other hand, nearly all of the few published studies on fragmentation effects save those of Cosson et al. (1999) and Pons and Cosson (2002) have been conducted in rather young, low-contrast systems sensu Watson (2002) (e.g. Estrada et al. 1993, Sampaio 2000, Schulze et al. 2000, Pons and Cosson 2002, Estrada and Coates-Estrada 2002, Gorresen and Willig 2004).

Bats are an ideal model taxon for evaluating responses to habitat fragmentation as they are ecologically highly diverse and mobile animals with the potential to move over extensive areas of fragmented landscapes. Furthermore, differences in species-specific ecological traits suggest differential vulnerability to habitat disturbance. A previous study in Panama found surprisingly little differences in the structure of bat assemblages between Barro Colorado Island (BCI), a 1,600 ha forest isolate in Gatún Lake, and Soberanía National Park (22,000 ha) on the adjacent mainland (von Staden 2002) - in stark contrast to the striking changes observed in the avifauna (Robinson 1999). We conclude that BCI is large enough and/or close enough to continuous forest to preserve the full complement of regional bat diversity. Many tropical landscapes, however, are increasingly dominated by much smaller (< 100 ha) fragments, which, nonetheless, may continue to serve important ecological functions (Turner and Corlett 1996). Here, we assess how processes associated with forest fragmentation affect bat assemblages on smaller Gatún Lake islands.

We examined sensitivity of bat assemblages to edge effects, and focused on the relative importance of patch-level (e.g., vegetation structure, area, shape, isolation distance) vs. landscape characteristics (e.g., forest cover, patch density) in shaping bat responses at various spatial scales. Determining the relative influence of local versus landscape attributes on patch use by animals has been considered an important yet little explored issue in studies of habitat fragmentation (Graham and Blake 2001). Moreover, even though several studies have highlighted the importance of focal scale for detecting ecological relationships (Hill and Hamer 2004), the majority of studies have typically examined faunal responses to spatial attributes in fragmented landscapes at a single landscape scale (Villard et al. 1999, Watson et
Recent research by Gorresen and Willig (2004) and Gorresen et al. (2005) in fragmented Atlantic forest of Paraguay revealed scale-dependent and species-specific associations between landscape characteristics and bat abundance as well as community attributes and stresses the importance of multi-scale approaches to studies of bat responses to habitat fragmentation.

We focus in our study on phyllostomid bats because a) they are highly speciose and numerically dominant in Neotropical bat assemblages, b) they are easily sampled with mist nets (Kalko 1998), c) they play pivotal roles as seed dispersers, pollinators, and predators (Kalko 1998, Patterson et al. 2003) and d) they may be crucial indicator species for the status of Neotropical forests (Fenton et al. 1992, Medellín et al. 2000).

We evaluated differences in diversity and structure between mainland and island bat assemblages on the species and functional group level. Specifically, we asked:

(1) Do species richness and assemblage structure change in a predictable way from mainland forest interior towards sites at the forest edge? Here we predict that matrix-tolerant species, i.e. those with better dispersal abilities, are also better adapted to forest edges.

(2) Which species and foraging guilds are affected by fragmentation? Due to the hostile nature of the matrix we predicted stronger isolation effects than in systems with lower fragment-matrix contrast. Forest-dependent species with low mobility such as most gleaning animalivores should be less common on or even be absent from isolated islands while they may still be used as temporary feeding grounds by some of the larger and more mobile frugivores.

(3) What is the contribution of heterogeneity in vegetation structure among sites in relation to the observed patterns of species richness and composition? We hypothesized that the mostly younger forest on the wind-exposed islands should favor species better adapted to habitat disturbance (e.g. some frugivores) and disfavor those that rely more on undisturbed, mature forest (e.g. gleaning animalivores).

(4) Which local attributes (vegetation structure, patch-level metrics) and landscape characteristics constitute the best predictors of bat species richness and assemblage composition on islands? Here we expected the importance of factors to vary with spatial scale.
Material and methods

Study area

Damming of the Chagres River during construction of the Panama Canal created an artificial reservoir, Gatún Lake. Lake formation was completed in 1914, isolating numerous hilltops resulting in over 200 islands ranging in size from < 1 ha to Barro Colorado Island (BCI) with 1,560 ha (Adler and Seamon 1991). Together with five adjacent mainland peninsulas, BCI forms the 5,400 ha Barro Colorado Nature Monument (BCNM) that is contiguous with Soberania National Park, 22,000 ha of forest stretching along the eastern side of the canal (Fig. 1). All study sites are covered with lowland tropical moist forest (Holdridge 1967).

Figure 1. Map of the study area in the Canal zone in central Panama (inset). Highlighted in black are the locations of the 11 study islands in Gatún Lake and of the six mainland sites (■) in continuous forest on the three peninsulas Bohio, Gigante, and Peña Blanca within the Barro Colorado Monument.

The study area experiences a strongly seasonal climate with an 8-month rainy season and a severe dry season from mid-December to April or May (Windsor 1990). The dry season is characterized by strong trade winds, which have a pronounced drying effect especially on the small exposed islands in Gatún Lake (Leigh et al. 1993). Forest on these islands is
typically shorter in stature and tree species diversity lower compared to more sheltered or larger islands. Storm systems frequently hit the exposed islands and likewise alter forest structure through formation of treefall gaps (Leigh et al. 1993). Vegetation on these islands also varies in age as some islands were forested prior to isolation and hence contain patches of older forest while most are covered with younger, secondary forest that has regenerated following isolation (Adler and Seamon 1991, Leigh et al. 1993, Adler 2000).

**Site selection**

We selected 11 islands that differed in size and levels of isolation and 6 mainland sites (Table 1, Fig. 1). Islands were grouped into two categories depending on their shortest distance from the mainland: “near” islands (< ca. 500 m) and “far” islands (> ca. 1.5 km, Table 1). Mainland sites were located on three peninsulas (Bohio, Gigante, and Peña Blanca) within the BCNM. 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 (Fig. 1). Interior sites were situated 312 ± 42 (SE) m from the forest edge, *i.e.* beyond the distance at which commonly observed edge-effects are known to be most pervasive (Laurance et al. 2002, Harper et al. 2005). Due to their irregular shape and rather small size, islands consisted almost exclusively of edge habitat according to our definition.

**Bat sampling**

Field work was conducted between October 2003 and October 2005 and encompassed two dry and three rainy seasons. At each island and mainland site bats were sampled in a standardized manner with mist nets (6 x 2.5 m, 70/2 denier, 16 mm mesh size, five shelves; Vohwinkel, Avifaunistische Untersuchungen, Velbert, Germany) set within ~ 0.5 ha, typically rectangular (100 x 50 m) transects. We avoided netting 2 days before to 1 day after full moon to minimize potential bias in capture success due to lunar phobic behavior (e.g. Morrison 1978). During each survey night we used six nets erected at ground level and spaced ~ 50 m apart. To also sample bats flying in higher forest strata, we set up a net wall typically consisting of four stacked nets using a rope-and-pulley-system modified after Humphrey et al. (1968). Nets were always deployed for entire nights from shortly before dusk until dawn. Captured bats were removed from the nets, temporarily kept in soft cloth bags and identified using a dichotomous key (Handley et al., unpublished). Standard measurements and demographic data were collected following Handley et al. (1991). Most bats (species > 10 g, excluding juveniles) were marked with individually numbered ball-chain
necklaces or, in case of larger gleaning insectivores/carnivores, with passive, subcutaneous transponders (pit-tags, EURO-ID, Weilerswist, Germany). Bat nomenclature follows Simmons (2005). We assigned bats to one of the following broad feeding guilds (ensembles sensu Fauth et al. (1996)), depending on their main diet: frugivores, gleaning animalivores, nectarivores, omnivores, and sanguivores (Stevens and Willig 2000, Patterson et al. 2003, Giannini and Kalko 2004, 2005).

**Environmental variables**

*Fruit abundance*

To link abundance of frugivorous phyllostomids with resource level we conducted a census of fruit availability focusing on tree species important to bats (Handley et al. 1991, Kalko et al. 1996, Giannini and Kalko 2004): *Ficus* spp., *Calophyllum longifolium*, *Dipteryx panamensis*, *Spondias* spp., *Anacardium excelsum*, and *Cecropia* spp. At each site, individual trees > 10 cm dbh were identified and mapped. For islands up to ~ 3 ha, the census was done for the whole island. For larger islands and all mainland sites, fruit abundance was determined for an equivalent area surrounding the respective netting transect. We conducted the fruit census the day preceding the respective netting session by recording the number of fruiting trees and estimating fruit abundance for each fruiting tree on a relative scale from 0-4 following Chapman et al. (1994) and Stashko & Dinerstein (1988). Number of fruiting trees and the mean rank of fruit abundance multiplied by the number of fruiting trees were used as measures of fruit availability.

*Vegetation structure*

For each of the 17 sites we quantified vegetation characteristics using protocols adapted from various sources (Schemske and Brokaw 1981, Schmiegelow et al. 1997, Raman and Sukumar 2002). For each transect, we assessed density and basal area of trees > 10 cm diameter at breast height (dbh) and the density of poles (stems 2-10 cm dbh). In addition, we recorded or estimated the following parameters within nine 5 x 5 m subplots nested in each transect: (1) number of saplings < 2 cm dbh, (2) average canopy height using a Leico Disto™ rangefinder (Leico Geosystems, Heerbrugg, Switzerland), (3) canopy closure measured as the mean of four spherical densiometer (Forestry Suppliers, Inc., Jackson, MS) readings taken at the center of each subplot, (4) vertical foliage structure by noting the presence or absence of foliage at several height intervals (0-1, 1-2, 2-4, 4-8, 8-16, 16-24, 24-32, > 32 m) directly above and in a 0.5 m radius around the center of each subplot.
Table 1. Overview of site characteristics and capture data obtained for phyllostomid bats mist-netted on islands in Gatún Lake and mainland peninsulas of the Barro Colorado Nature Monument, Panama. Relative abundance is given as bats/100 mist-net hours (mnh). Observed ($S_{obs}$) and estimated species richness based on the first-order Jackknife estimator ($S_{Jack}$) are presented for each of the study sites and for each site category along with percent inventory completeness.

<table>
<thead>
<tr>
<th>Location</th>
<th>Site category</th>
<th>Island area (ha)</th>
<th>Distance to mainland (km)</th>
<th>No. captures(a)</th>
<th>Capture effort (mnh)*</th>
<th>Relative abundance</th>
<th>$S_{obs}$</th>
<th>$S_{Jack}$ (±SD)</th>
<th>% completeness</th>
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<td>0.16</td>
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<td>49.52</td>
<td>12</td>
<td>16.3±1.71</td>
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<td>0.51</td>
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<td>37.31</td>
<td>11</td>
<td>12.7±1.11</td>
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<td>14</td>
<td>16.6±1.21</td>
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<td>773</td>
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<td>71.45</td>
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<tr>
<td>Bohio</td>
<td>Interior</td>
<td></td>
<td></td>
<td>548</td>
<td>820</td>
<td>66.86</td>
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<td>86.3</td>
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<td>Gigante</td>
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<td></td>
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<tr>
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<td></td>
<td></td>
<td>436</td>
<td>902</td>
<td>26.24</td>
<td>23</td>
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</tr>
<tr>
<td><strong>Total Mainland</strong></td>
<td></td>
<td></td>
<td></td>
<td>1229</td>
<td>2656</td>
<td>46.28</td>
<td>28</td>
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<tr>
<td>Bohio</td>
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<td></td>
<td></td>
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<td>16</td>
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<td>Peña Blanca</td>
<td>Edge</td>
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<td>30</td>
<td>32.9±1.66</td>
<td>91.1</td>
<td></td>
</tr>
</tbody>
</table>

\(a\) without same-night recaptures; * one mist-net hour (mnh) equals one six-meter net open for one hour
Patch- and landscape-level metrics

For each study island we measured the following patch-level characteristics using ArcView GIS 3.2a (Environmental Systems Research Institute, Inc., Redlands, California) based on a GIS coverage of the study area (central Panama GIS v1.1, compiled by D. A. Kinner and R. F. Stallard, US Geological Survey): (1) island area, (2) total edge length, (3) shape index (a measure of complexity of patch shape compared to a standard shape (circle) of the same area), and (4) nearest straight-line distance to the mainland. We considered as mainland any landmass in our study area that was not completely surrounded by water, including Juan Gallegos Island which is connected to the mainland by a causeway (Fig. 1). Furthermore, to investigate whether bat responses to fragmentation were scale-dependent, we delimited the surrounding landscape as a nested set of concentric circles of 0.5, 1, and 1.5-km radii centered on each island. Choice of these focal scales was based on considerations to encompass the expected home ranges of different-sized bat species (Gorresen and Willig 2004) as well as to minimize spatial overlap between neighboring islands. For each of the 3 focal scales per island, the following landscape-level metrics were calculated: (1) mean patch size, (2) patch density, (3) edge density (total length of edge per landscape area), (4) shape index, and (5) forest cover. Because measures such as forest cover do not take isolation of focal patches from other forest fragments into account, we also computed (6) availability of forest cover in the landscape as

\[
I_i = \log_{10} \sum A_j * e^{-D_{ij}}
\]

(Hanski et al. 1994). Here, \(I_i\) is the isolation of the focal patch, \(A_j\) denotes the area of forest cover within the respective radius of fragment \(j\), and \(D_{ij}\) is the minimum edge-to-edge distance between focal patch \(i\) and fragment \(j\).

Data analysis

Bat inventory completeness

We evaluated inventory completeness with randomized (1,000 x) sample-based species accumulation curves. Sample-based accumulation curves take spatial heterogeneity among samples into account and are therefore preferable over individual-based curves (Gotelli and Colwell 2001). In addition, we assessed the number of species expected to occur at each site using non-parametric species richness estimators. Based on the estimator choice framework developed by Brose and Martinez (2004), which takes movement heterogeneity of mobile animals such as bats into account, we chose the first-order Jackknife (Jack1) to estimate species richness. This estimator has also been shown to perform best in recent
simulation studies (Brose et al. 2003, O'Hara 2005, Sampaio et al. submitted). Species accumulation curves and richness estimators were computed using EstimateS software (Colwell 2005).

**Species diversity, abundance, and bat assemblage structure**

We used the ‘Species Diversity’ module of the program EcoSim (Gotelli and Entsminger 2001) with 1,000 iterations and independent sampling of individuals from the capture pool to compare rarefied species richness, evenness and dominance among site categories (mainland interior, mainland edge, near islands, far islands) and between mainland and island assemblages. Evenness was calculated as Hurlbert’s probability of interspecific encounter (PIE), i.e. the probability that two randomly sampled individuals from an assemblage represent two different species (Hurlbert 1971). Dominance was assessed with the Berger-Parker index as the proportional abundance of the most abundant species in a sample (Magurran 2004). In each case statistical significance was determined based on the simulated 95% confidence intervals generated by the program (Gotelli and Entsminger 2001).

Kolmogoroff-Smirnov two-sample tests were used to compare rank-abundance curves among bat assemblages. To allow for a comparison of distributions which are not entirely continuous and include ties, P-values were determined through Monte Carlo simulations (1,000 bootstraps). Capture rate (bats per mist net hour (mnh), where one mnh equals one 6-m net open for one hour) was used as standard measure of relative abundance. Same-night recaptures were excluded from analyses. Differences in nightly capture rates (log-transformed, captures from ground and high nets combined) among the four site categories and between seasons were assessed with a nested ANCOVA (individual sites nested within site categories), with fruit abundance and number of fruiting trees as covariates. Post hoc comparisons were made using Tukey’s HSD test.

We compared the number of species and captures in guilds among the four site categories with r x c contingency tables whereby the number of species and captures at mainland interior sites was used to generate expected values. Significance was determined through a randomization approach (1,000 iterations) where the observed table was compared to a set of randomly generated r x c tables with the same row and column totals (Manly 1997).

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

Vegetation structure

For each transect we calculated tree density and basal area. Average values across replicated subplots were calculated for all other vegetation variables, i.e. sapling density, canopy height, and percent canopy closure. Vertical foliage structure was determined as average number of strata with foliage across the nine subplots sampled in each transect. Following Raman & Sukumar (2002) we used the coefficient of variation of this index as a measure of horizontal heterogeneity in foliage structure.

Vegetation structure variables were log(x+1) transformed and NMDS on a matrix of normalized Euclidean distances was used to generate axes representing gradients in forest structure among sites. The importance of individual forest structure variables in generating differences among sites was assessed 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). Vector fitting was also used to examine the relationship between forest structure variables and the arrangement of bat assemblages in ordination space.

Bat fauna – environment modeling

We examined correlations between bat species richness and assemblage composition, respectively, and local- and landscape-level characteristics using generalized linear models (GLMs). For species richness, data were counts and a Poisson error distribution and log link function was used. For species composition, as represented by the scores of the first NMDS axis that explained most of the variation among sites, GLMs with a normal error distribution were appropriate.
Landscape metrics can be correlated with habitat area (Villard et al. 1999, Fahrig 2003). Since it is important to separately assess the influence of habitat loss and the configurational effects of fragmentation (Fahrig 2003), we statistically controlled for the correlation between forest cover and the various landscape configuration indices by using the residuals of linear regressions as values for the explanatory variables (Villard et al. 1999, Gorresen et al. 2005). Furthermore, because of multicollinearity among both local and landscape variables, pairwise comparisons of predictor variables were made using Spearman rank correlations and, where pairs of variables were significantly correlated, one of the variables was eliminated. This resulted in a final set of $N = 8$ explanatory variables. Local-scale variables were forest structure (NMDS axes 1 and 2), as well as island size (log-transformed), total edge (significantly correlated with shape index), and distance to the mainland (log-transformed). Landscape metrics retained in the final analysis were mean patch size (significantly correlated with patch density, shape index and Hanski’s $I$), edge density (significantly correlated with Hanski’s $I$), and forest cover (log-transformed).

In preference to frequently applied stepwise selection procedures whose use is statistically problematic (Quinn and Keough 2004) we employed an information-theoretic model selection approach to analyze bat fauna-environment relationships (Burnham and Anderson 2002). Rather than testing all potential models, we restricted inference to a subset of plausible models selected a priori (see Appendix F; Burnham and Anderson 2002, Johnson and Omland 2004), modeling local-scale variables in combination with landscape metrics separately for the three focal scales. For each model we calculated the second-order version of Akaike’s Information Criterion corrected for small sample size ($\text{AIC}_c$) following Burnham and Anderson (2002). Candidate models were then compared and ranked by rescaling the $\text{AIC}_c$ values such that the model with the minimum $\text{AIC}_c$ has a value of 0, i.e. $\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}}$. Models for which $\Delta_i \leq 2$ are considered to have substantial support, values of 4-7 have considerably less support and those with $\Delta_i \geq 10$ have essentially no empirical support (Burnham and Anderson 2002). In addition, we calculated the Akaike weights ($w_i$) for each candidate model which provide approximate probabilities that model $i$ is the actual best model in the set of candidate models (Burnham and Anderson 2002). The relative likelihood of model $i$ versus model $j$ can be judged by the ratio of the Akaike weights of the best model and the second ranked model (i.e., $w_i / w_j$). Model fit was assessed using the relevant statistics (percent deviance explained and $R^2$, respectively).
Unless stated otherwise all data analyses were performed using the R statistical package (version 2.2.0, R Development Core Team 2006).

Results

Forest structure

There was pronounced overall variation in vegetation attributes among sites (Appendix A). A two-dimensional ordination (Fig. 5a, stress = 4.92) showed that this was largely due to variation among islands while mainland sites clustered together indicating high structural similarity. Vector fitting revealed significant correlations between ordination scores and tree density, basal area, and canopy height as well as number of poles and saplings ($P \leq 0.001$, Appendix A). Mainland sites were characterized by high basal area and canopy height as were two islands that contained more mature, high-stature forest, Pato Horqueta and Tres Almendras. In contrast, variation in forest structure among the remaining islands was mainly related to tree and understory density (Fig. 5a). Differences in forest structure variables among site categories were significant for tree density (one-way ANOVA, $F = 5.27$, $P = 0.013$) and marginally significant for canopy height ($F = 3.39$, $P = 0.051$) and canopy cover ($F = 3.34$, $P = 0.053$, Appendix A).

Bat species richness, evenness, and dominance

A total of 8,447 captures representing 5 families, 30 genera, and 39 species were obtained during 125 sampling nights (Appendix B). Phyllostomid bats made up the majority of all captures (98.2%). Species-accumulation curves approximated an asymptote and indicated a high level of inventory completeness for phyllostomids (> 91% for mainland and > 95% for island assemblages; Table 1, Appendix C).

Overall, more species of phyllostomids were recorded for the mainland ($S_{\text{obs}} = 30$) than for the islands ($S_{\text{obs}} = 21$). A similar number of species was captured at mainland interior ($S_{\text{obs}} = 28$) and at edge sites ($S_{\text{obs}} = 27$). Twenty one species were detected on near islands while observed species richness dropped to 15 species on far islands (Table 1). For all site categories, estimates of predicted species richness ($S_{\text{Jack1}}$) were close to observed species richness (Table 1), corroborating the adequacy of our sampling protocol.

Rarefied species richness differed significantly (as indicated by the 95% confidence intervals) between mainland and island assemblages as well as among site categories (Fig. 2a). Species richness was highest at mainland interior sites, slightly lower at edge sites, and
substantially declined from near to far islands. This pattern is consistent with our results on observed species richness. Both evenness and dominance differed significantly among site categories with island assemblages being characterized by lower evenness and higher dominance compared to mainland assemblages (Fig. 2b,c). Interestingly, mainland edge sites had significantly lower evenness and higher dominance than assemblages on near islands.

Figure 2. Rarefied species richness, evenness, and dominance. Comparisons between mainland sites and islands were made at the abundance level of the former, those among site categories are based on the abundance of mainland interior sites.

Rank-abundance distributions (Fig. 3) for forest interior and edge sites did not differ significantly from one another ($D = 0.3, P = 0.252$), however, both differed drastically from the curve for bat assemblages on far islands ($D \geq 0.65, P = 2.2E-16$). Rank-abundance curves for near islands differed significantly from curves for mainland interior sites ($D = 0.45, P = 0.017$) and marginally significantly from those for edge sites ($D = 0.4, P = 0.064$).
Distribution of species’ abundances between assemblages on near and far islands were also marginally significantly different ($D = 0.35, P = 0.083$).

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

**Relative abundance**

*Artibeus jamaicensis, A. lituratus,* and *Uroderma bilobatum,* all frugivores, were the three most abundant species and accounted for 86.1% of all captures. *Artibeus jamaicensis* and especially *U. bilobatum* showed a pronounced increase in capture rates on islands relative to mainland interior sites (Fig. 4a). Similarly, capture rates for the nectarivorous *Glossophaga soricina,* which was infrequently caught at mainland interior sites increased greatly from edge sites over near to far islands. The majority of other species, in contrast, most notably almost all of the gleaning animalivores, either substantially decreased in relative abundance from forest interior over forest edge sites to near and far islands or were absent from the islands altogether (Fig. 4a,b). None of the larger gleaning animalivores that were rather common on the mainland, namely *Lophostoma silvicolum, Tonatia saurophila* and *Trachops cirrhosus,* were captured on far islands. The small *Micronycteris microtis* was the only exception with higher capture rates on islands than on the mainland. Many gleaners are
Figure 4a. Percent change in relative abundance relative to mainland interior sites. See Appendix B for species abbreviations.
sensitive to forest edges as evidenced by highly reduced capture rates relative to forest interior sites (Fig. 4a,b).

Nested ANCOVA revealed significant differences in capture rates among site categories, seasons, and individual sites after controlling for variation in fruit abundance (multiple $R^2 = 0.66$, $F_{34,74} = 4.26$, $P < 0.001$; Table 2). Capture rates for far islands (98.3 bats/100 mnh) were more than twice as high and differed significantly (Tukey HSD test, $P < 0.001$) from near islands (42.6 bats/100 mnh) and both mainland edge (48.2 bats/100 mnh) and interior sites (46.3 bats/100 mnh), which were characterized by overall very similar relative abundances (Table 1). There was a strong seasonal effect with more bats being caught in the wet than in the dry season, and a significant interaction between site and season reflected in a pronounced increase in capture rates on islands towards the wet season.
Table 2. Results of a nested ANCOVA model examining seasonal and site-related variation in bat abundance with number of fruiting trees and fruit abundance as covariates. The latter was not retained in the minimal adequate model after model simplification.

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<td>2.70</td>
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</tr>
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</table>

**Assemblage structure**

Examination of the stress values of an ordination of study sites by NMDS showed that a two-dimensional solution was sufficient to achieve low stress (final stress = 10.33). Three distinct clusters could be distinguished representing a gradient in species composition from mainland sites to near and far islands along dimension 1 (Fig. 5b). Overall, mainland sites clustered together, indicating high similarity in assemblage structure. Near islands and two of the far islands, León and Pato Horqueta, formed a second cluster, clearly separated from the remaining far islands which grouped to the far right. Vector fitting identified three variables describing variation in forest structure to be significantly (basal area: $r^2 = 0.38$, $P = 0.031$; canopy height: $r^2 = 0.42$, $P = 0.028$) or marginally significantly (number of poles: $r^2 = 0.31$, $P = 0.067$) correlated with inter-site variation in species composition, mainly along the second NMDS axis (Fig. 5b, Appendix D). The observed variation in bat assemblage composition along NMDS axis 2 hence largely reflects a gradient in vegetation structure among sites from low-stature forest dominated by high densities of small trees to older and more mature forest with higher mean basal area and a higher canopy. Assemblage composition differed significantly among site categories (ANOSIM, global $R = 0.698$, $P < 0.001$). Pairwise tests showed no significant compositional differences between mainland edge and interior sites ($R = -0.037$, $P = 0.6$) as well as between edge sites and near islands ($R = 0.313$, $P = 0.107$), whereas all other comparisons were significant ($R > 0.672$, $P < 0.018$).

The ordination plot of species scores (Fig. 5c) showed one cluster encompassing species characteristic of continuous forest that were either completely absent or substantially less abundant on islands (Fig. 4a). Those were, except for *M. microtis*, all of the insectivorous gleaners, a few of the smaller frugivores (*Carollia castanea*, *Artibeus watsoni*, *Vampyressa*
nymphaea) and the omnivorous Phyllostomus hastatus. Glossophaga soricina, A. jamaicensis, U. bilobatum, and M. microtis, all species with much higher capture rates in remnants than in continuous forest, formed a second group while the remaining fraction of species showed no tight clustering.

Figure 5. Ordination of (a) vegetation structure, (b) study sites, (c) species, and (d) feeding guilds along non-metric multidimensional scaling axes. Forest structure variables significantly correlated with ordinations are plotted as vectors. (●) mainland interior sites, (○) mainland edge sites, (▲) near islands, (Δ) far islands. See Appendix B for species abbreviations.
**Guild richness and composition**

Frugivores accounted for the majority of captures (> 90%) and comprised the most speciose guild throughout all site categories, followed by gleaning animalivores (Appendix E). Mainland edge and both near and far islands did not differ significantly from mainland interior sites in terms of number of species per guild ($\chi^2 < 2.86, P > 0.5$ for all comparisons). In contrast, the number of bat captures within guilds differed significantly between mainland interior sites and all other site categories ($\chi^2 > 43.10, P < 0.001$). The differences were largely attributable to the pronounced increase in the capture rates of frugivores and nectarivores as well as the decrease in capture rates of gleaning animalivores at these sites relative to interior plots in continuous forest (Fig. 4b).

In a two-dimensional NMDS plot of sites in functional group space (Fig. 5d; stress = 6.18), mainland sites exhibited greater variation along both axes than based on species composition. Islands overall grouped loosely together. However, there was some overlap between near and far islands as the largest of the far island group, León, was closer in ordination space to near islands and one of the near islands, Chicha, had a guild composition typical of far island assemblages (Fig. 5d). ANOSIM revealed significant differences in guild composition among site categories (global $R = 0.45, P = 0.002$). Pairwise comparisons indicated significant compositional differences between mainland interior assemblages and both near ($R = 0.64, P = 0.036$) and far islands ($R = 0.98, P = 0.012$) as well as between mainland edge and far islands ($R = 0.63, P = 0.012$).

**Bat fauna-environment modeling**

Generalized linear modeling revealed that different variables were important at different spatial scales in determining both species richness and species composition of bats on Gatún Lake islands. Overall, we found area effects to become more important and distance effects less pronounced at larger spatial scales. For species richness, comparison of $\Delta_i$ values indicated that distance from the mainland received the strongest support for a model set that included local-scale variables (i.e., vegetation structure and patch-level metrics) and landscape metrics of the smallest (0.5 km) focal scale (Table 3, see Appendix F for a complete table of modeling results). Edge density likewise had considerable support ($\Delta_i = 1.85$), suggesting that phyllostomid assemblages react to habitat boundaries to some degree, however, this model was about 2.5 times less likely based on Akaike weights and also had a much lower regression coefficient (Table 3). For model sets incorporating 1-km and 1.5-km
Table 3. Best approximating generalized linear model sets ($w_i > 0.1$) for assessing the association between, respectively, bat species richness and assemblage composition on Gatún Lake islands, and local-scale characteristics and landscape-level metrics for three different focal scales. For each model, the number of estimable parameters ($K$), log-likelihood ($\log(L)$), sample-size adjusted Akaike Information Criterion ($AIC_c$), Akaike differences ($\Delta_i$), Akaike weights ($w_i$) as well as parameter estimates ($\beta$) and their standard errors are presented. Model fit for the most highly parameterized model in each set is given as deviance explained or $R^2$, respectively. See Appendix F for complete modeling results.

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landscape metrics besides local-scale variables, the best ranking model was amount of forest cover in the landscape. It was also the most likely with Akaike weights of 0.661 and 0.710, respectively, compared to the model ranked second in terms of $\Delta_i$, distance to the mainland ($w_i = 0.252$ and 0.210, respectively). For species composition, amount of forest cover was the single best model selected receiving overriding support ($w_i > 0.98$) at the two larger spatial scales examined. In contrast, at the 0.5-km scale, distance from the mainland was again the best predictor of species composition on islands ($w_i = 0.518$). However, there were two other plausible models in this set, one single-process model containing edge density that was only 1.6 times less likely ($w_i = 0.316$) and one model examining additive effects among landscape characteristics that also received some degree of support ($w_i = 0.102$) but was about 5 times less likely than the top ranked model.

**Discussion**

*General aspects*

Our analyses revealed strong contrasts in bat assemblages between continuous forest and islands in terms of species abundance patterns and community-level attributes and identified isolation as the main factor underlying phyllostomid bat responses. Sites in continuous forest were characterized by higher species richness and evenness while islands harbored a less diverse and structurally simplified bat fauna, a pattern consistent with previous studies in other disturbed or fragmented systems (Cosson et al. 1999, Sampaio 2000, Medellin et al. 2000). Isolated islands far away from the mainland were especially species-poor and this decline in species richness was associated with a marked shift in species composition. The influence of isolating distance on species richness has earlier been demonstrated by Estrada et al. (1993) for forest remnants in agricultural habitats, *i.e.* systems with low fragment-matrix contrast. Similarly, we found that near islands still retained surprisingly species-rich assemblages. This suggests that, provided a low degree of remnant isolation and spatial proximity to larger tracts of continuous forest, small habitat remnants may act as stepping stones, enhance exchange of individuals and permit local population persistence of phyllostomid bats even when these fragments are embedded in a hostile matrix (Albrecht et al. in press).
Assemblage patterns

Compared to studies conducted in systems with low fragment-matrix contrast our study revealed some interesting differences despite broadly similar patterns with respect to bat community-level attributes. Responses, as hypothesized, were often stronger probably due to the particular nature of the matrix. Gleaning animalivores were the most adversely affected supporting other studies (Fenton et al. 1992, Sampaio 2000, Schulze et al. 2000, Pons and Cosson 2002, Clarke et al. 2005). The majority of species were markedly reduced in abundance or absent altogether from the islands and several species showed a negative response even toward edge habitats in continuous forest (see below). Causes for this fragmentation sensitivity may include a variety of factors likely acting in concert, including insufficient resources in fragments, often specialized foraging strategies and, for certain species, specific roosting requirements (e.g. Kalko et al. 2006), as well as limited mobility due to morphological constraints (Estrada and Coates-Estrada 2002, Clarke et al. 2005). The latter may be the primary reason why none of the larger gleaning animalivores was caught on far, isolated islands as these species are adapted for slow maneuverable flight inside dense vegetation. This makes prolonged commuting flights over an unsuitable matrix habitat energetically costly. Limited dispersal capacity has also been considered a key factor determining the sensitivity of insectivorous birds to fragmentation (Sekercioglu et al. 2002).

*Micronycteris microtis*, a small 5-7 g bat, was the only gleaning animalivore not negatively affected. On the contrary, it was much more frequently caught on islands than in continuous forest (Fig. 4a). Radiotracking indicates that *M. microtis* has very small area requirements, probably due to its very effective foraging strategy (Albrecht et al. in press). This and the presence of colonies of *M. microtis* on some of the islands suggests that these bats may be able to persist in small, isolated habitat remnants for quite a long time.

In contrast to gleaning animalivores we found frugivores to be much more abundant on the islands than on the mainland. This was almost entirely due to a pronounced increase in the capture rates of *A. jamaicensis* and *U. bilobatum* both of which were particularly common on far islands (Fig 4a). This corroborates several other studies that have demonstrated an increase in the abundance of a few frugivorous species following fragmentation or disturbance (Sampaio 2000, Medellin et al. 2000, Clarke et al. 2005) but contrasts with the findings of Cosson et al. (1999) who studied phyllostomid bat assemblages on land-bridge islands in French Guiana. They reported an overall large reduction in bat abundance after fragmentation and no noticeable increase in the abundance of any particular species. As Cosson et al. (1999) examined short-term responses of bats immediately following
fragmentation the time frame may not have been long enough for fragmentation effects to be fully exhibited. Empirical evidence is mounting that short- to medium-term time lags in species responses are ubiquitous (Ewers and Didham 2006). Although no comparative data are available for bats, community-relaxation has been estimated to occur over time scales of several decades for other long-lived taxa such as birds (Ferraz et al. 2003). While bat assemblages on Gatún Lake islands, which are > 90 years old, have likely reached an equilibrium species richness and composition, bat assemblages on the islands studied by Cosson et al. (1999) are probably still undergoing relaxation, which might explain, at least in part, the contrasting responses observed in terms of species abundances.

Schulze et al. (2000) also reported lower capture rates of large frugivorous phyllostomids in forest fragments near Tikal, Guatemala, and attributed this to reduced abundance of mature forest tree species and hence fruit availability. Our data, in contrast, suggest that the study islands constitute profitable resource patches at least for the more mobile frugivorous bats. Figs (*Ficus* spp.), which form the core diet of many frugivorous phyllostomids (Giannini and Kalko 2004), occur on the islands at high densities (C. Meyer, unpublished data). On numerous occasions a single fruiting fig tree was responsible for attracting hundreds of bats, predominantly *A. jamaicensis*, to a particular island. This is reflected in the fact that presence or absence of fruiting trees rather than the index of fruit abundance was found to be a significant covariate associated with nightly capture rates.

In frugivorous phyllostomids long-range detection of fruiting fig trees is likely mediated by olfaction whereby the bats are attracted by the distinct odor plume associated with the synchronous production of large fruit crops (e.g. Kalko et al. 1996). One could speculate that fruiting trees that occur in small, distinct habitat patches may be easier to detect than those in larger expanses of continuous forest, which could explain why the bats made such extensive use of the islands. A high proportion of extra-site recaptures in *A. jamaicensis* (C. Meyer, unpublished data) points to frequent movements across the fragmented landscape and suggests that these bats regularly include multiple fragments in their foraging range, as has been suggested by other authors (Estrada et al. 1993, Schulze et al. 2000).

Limited mobility probably is the main factor responsible for the low capture rates of many of the smaller frugivorous bats such as *Chiroderma villosum*, *A. watsoni*, *V. nymphaea* and *V. pusilla* on far islands. Two understory fruit-eating bats common in mainland forest, *Carollia perspicillata* and *C. castanea*, which specialize to different degrees on fruits of *Piper* spp. (Thies and Kalko 2004), also had overall lower capture rates on islands. However, the smaller *C. castanea* was much more affected by habitat isolation as it was never caught
on any of the far islands except the largest one, León, while *C. perspicillata* was caught occasionally even on the most isolated islands. This difference in mobility is supported by our recapture data and radiotracking studies (e.g. Bernard and Fenton 2003). The fact that *Piper* is rather uncommon on most islands (C. Meyer, unpublished data) may hence be a direct consequence of limited seed dispersal events because of the bats’ reluctance to traverse the hostile matrix although constraints regarding abiotic conditions may also contribute to this pattern. Contrasting abundance patterns have been observed in fragmented landscapes in the Amazon lowland where forest remnants are surrounded by regrowth that provides additional food resources, augmenting the abundance of shrub frugivores like *Carollia* (Sampaio 2000). Our results thus confirm the idea that matrix quality and a species’ ability to utilize resources in the matrix can alter the intensity of observed fragmentation effects (Ewers and Didham 2006).

Strikingly higher capture rates on islands relative to mainland interior sites substantiate previous findings that the nectarivorous *G. soricina* is able to adapt well to disturbed and fragmented habitats as has already been documented for other sites, although quantitatively not to this extent (Estrada and Coates-Estrada 2002, Clarke et al. 2005). The notion that disturbed, secondary forest on the islands may sustain overall higher levels of flower production compared to mainland forest seems an unlikely explanation for the observed abundance pattern given that most *G. soricina* were caught during the rainy season when flower production is low. However, like most frugivores, nectarivorous phyllostomids have rather generalized habitat requirements and are dietary generalists, often with the ability to adapt to seasonal changes in the availability of their main food types (Patterson et al. 2003). This flexibility is probably a preadaptation that enables them to survive well in human-modified landscapes (Estrada and Coates-Estrada 2002, Clarke et al. 2005).

Our results hint at limited dispersal being a major cause underlying the decline of many bat species on our distant study islands. It has been proposed that habitat fragmentation may lead to local selection pressures that simultaneously favor both ends of the spectrum of dispersal ability (Ewers and Didham 2006) as has for instance been demonstrated for butterfly species (Thomas 2000). Our findings agree with this insofar as highly mobile species like *A. jamaicensis* or *U. bilobatum* on the one end, and species with very small home ranges such as *M. microtis*, on the other end were not negatively affected by fragmentation. In the case of the latter species this may simply reflect that fact that due to its foraging strategy it is able to acquire sufficient resources even within small fragments and hence doesn’t have to move. In contrast, we found species with intermediate mobility like many
larger gleaning animalivores whose resource requirements cannot be met on a particular island or some of the smaller frugivores, which feed on patchily distributed resources to be more likely to decline in abundance, especially on isolated islands. These species may be more prone to dispersal-related mortality, e.g. due to increased predation risk in open areas.

**Response to forest edges**

Responses of animals to forest edges vary greatly both in terms of direction of response (positive, negative or no effect) as well as among and within taxa (Laurance et al. 2002, Ewers and Didham 2006). While our data show marked changes in bat species richness and assemblage structure between islands and the mainland, our results provide only limited evidence for a distinct edge-interior-gradient in continuous forest with respect to bat assemblage attributes. Standardized species richness was significantly higher for mainland interior compared to edge sites, however, rank-abundance distributions were indistinguishable and no significant differences were found for species composition. Similarly, Campi & MacNally (2001), studying responses of bird assemblages to forest-agricultural land edges in large forest blocks in southeastern Australia, found abrupt changes in species richness and assemblage composition from open country to forest but only little evidence of an avifaunal gradient from interior to edge habitats. Changes in species composition might generally be hard to detect due to the fact that they are a composite of individual species responses, which can be extremely varied (Ewers and Didham 2006).

Certain bat species and foraging guilds indeed appeared to respond to forest edges. Species that exhibited high matrix tolerance also were edge-tolerant, consistent with our predictions, whereas species that were absent or less common on islands typically also had lower capture rates at edge sites. Some gleaning animalivores, most notably *T. saurophila*, *T. cirrhosus*, *M. hirsuta* and *L. silvicolum* seem to be edge-sensitive as indicated by an often pronounced decrease in capture rates relative to forest interior sites (Fig. 4). *Lampronycteris brachyotis* was exclusively caught at interior sites, however, too few captures were obtained for this to be conclusive evidence of edge-avoidance. On the other hand, of the species for which data were sufficient, the frugivores *U. bilobatum* and *A. jamaicensis* as well as the nectarivorous *G. soricina* can be classified as edge-preferring based on their higher capture rates at edge sites (Fig. 4).

While comparative studies on bats are lacking, our findings are largely congruent with results from studies on tropical birds which have also reported lower species richness at edges and a more or less pronounced shift in guild composition with frugivores and nectarivores
typically being more abundant and many gleaning insectivores being less common at forest edges (Restrepo and Gomez 1998, Dale et al. 2000, Laurance et al. 2004, but see Watson et al. 2004b). In birds, changes in habitat structure and concurrent alterations in microclimatic conditions at forest edges have been shown to be linked to edge-sensitivity (Watson et al. 2004b). In the present study, however, mainland interior and edge sites were characterized by similar forest structure and variation in structural heterogeneity among those sites was found to have little influence on bats, at least at the assemblage level. The observed effects on the level of individual species or guilds may therefore be a corollary of species-specific responses to changes in the abundance or distribution of certain resources rather than structural features of the habitat. For gleaning insectivores, changes in the densities of their preferred arthropod prey, e.g. katydids, with distance from the forest edge could underlie the particular edge-sensitivity exhibited by this group.

Edge effects have been shown to change over various temporal scales (Restrepo and Gomez 1998, Laurance et al. 2002). Further insight into how bats are affected by habitat edges may therefore be gained by addressing the influence of edge dynamics in future studies.

Bat fauna – environment associations: Importance of local vs. landscape characteristics and scale dependence

Our results corroborate the findings of Gorresen & Willig (2004) and Gorresen et al. (2005) that responses of bats to characteristics of fragmented landscapes are sensitive to scale. Species richness and structure of phyllostomid assemblages on the study islands were most strongly determined by distance from the mainland and the amount of forest cover in the surrounding landscape, with the former being the prominent factor at the smallest spatial scale examined and the latter becoming more important toward larger spatial scales. Fahrig (2003) argued that negative edge effects could translate into a negative effect of fragmentation per se at the landscape scale because it increases the amount of edge in the landscape. Our modeling results agree with this notion to some degree on the smallest spatial scale as edge density, although being less likely than the most likely factor, distance from the mainland, still received considerable support. Our finding of a lack of a clear species-area relationship and overall dominant distance effect in governing species richness on islands at local scales may be explained by at least two, likely interacting effects. First, our results support the existence of a “small island effect”, i.e. the tendency for species-area relationships to be weak or non-significant for groups of small isolates (Whittaker 2000,
Lomolino 2000, Lomolino and Weiser 2001, Turner and Tjørve 2005). Small island effects may become apparent at a range of island sizes where resource levels are insufficient to maintain populations of most species and where habitat characteristics, episodic disturbances, and isolation are much more likely to determine how many and which species are able to maintain populations (Lomolino 2000, Lomolino and Weiser 2001). In our study system, the range of island sizes compared to levels of isolation was rather small (the largest island sampled being 50 ha and most islands being < 20 ha), hence supporting the idea of a small island effect in our particular case. Secondly, the fact that isolation distance was found to be much more important than island area in determining bat species richness at the patch-level may also be directly related to the type of matrix in this study. Due to the inherent inhospitableness of water, i.e. its property to act as a fine-pored selective filter, which only a subset of the more mobile forest-dependent bat species appear to be able to pass, area effects might be partly masked and not be strong enough to manifest themselves at local scales. Interestingly, our findings contrast with those for birds in the same study system for which species richness has been found to be positively correlated with island area (R. Moore, pers. comm.). Bat species richness was positively associated with area, i.e. the amount of forest cover in the surrounding landscape, at larger spatial scales. Many species appear to have minimum area requirements, which, however, for the majority of tropical bat species, have not been estimated quantitatively or remain poorly known. Nonetheless, larger areas can generally be expected to meet the minimum area requirements of more species, resulting in increases in species richness with area (Lomolino 2000, Turner and Tjørve 2005).

Although local vegetation structure has been documented to be a potentially strong determinant of species diversity and composition in many study systems and for a variety of different taxa including bats (Schmiegelow et al. 1997, Raman and Sukumar 2002, Erickson and West 2003, but see Graham and Blake 2001), we found no evidence for bats on our study islands to respond to structural heterogeneity with respect to community-level attributes, probably because overall variation in vegetation structure among islands was low. However, variation in forest structure was important to a certain degree in separating mainland from island bat assemblages. Islands that contained relatively mature forest (Tres Almendras, Pato Horqueta, León) were more species-rich and resembled more closely mainland assemblages in terms of species composition than islands with younger forest (Fig. 5b).

Overall, our modeling results point to habitat loss rather than fragmentation effects per se, i.e. the breaking apart of habitat and associated changes in landscape configuration (Fahrig 2003) such as increased edge density, being the main process after isolation...
underlying phyllostomid bat responses on Gatún Lake islands. This concurs with the findings from a recent review by Fahrig (2003) who argued that in most studies the effects of fragmentation per se are absent or too weak to be detected or may only become apparent at low levels of habitat amount suggesting that conservation efforts that attempt to minimize fragmentation for a given amount of habitat may often be inadequate.

**Implications for conservation**

The forested islands surrounded by a homogeneous aquatic matrix can be viewed as analogs of anthropogenic landscapes with patches of forest embedded in heavily grazed pasture without trees or bushes, *i.e.* can be construed to represent a ‘worst-case’-scenario. The fact that even small islands embedded in such a hostile matrix can support a relatively diverse bat fauna, provided a low degree of patch isolation and spatial proximity to larger blocks of continuous forest, has important ramifications for reserve design and conservation planning. Our findings add to the growing evidence that small habitat remnants are of substantial conservation value for a variety of animals including mobile groups such as bats (Turner and Corlett 1996, Gorresen and Willig 2004). Furthermore, our study emphasizes the importance of considering both structural and functional connectivity in determining responses to fragmentation (see, e.g., Uezu et al. 2005). Long-term metapopulation persistence in fragmented landscapes requires individuals to cross habitat boundaries and disperse between remnant patches. Those phyllostomid bats that exhibit high mobility and are not reluctant to move through deforested areas around fragments can link small populations that would otherwise be isolated and prone to local extinction, enhance the “rescue-effect” (Brown and Kodrick-Brown 1977), therefore improve the survival chances of many forest-dependent bats in fragmented neotropical landscapes and assure the continued functioning of ecosystem services provided by these animals.

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Literature cited


Lomolino, M. V. 2000. Ecology's most general, yet protean pattern: the species-area


### Appendices for Ecological Archives

**Appendix A:** Summary of the vegetation characteristics of the study islands in Gatún Lake and adjacent mainland sites. Given are summary statistics (mean ± SE) for all sites as well as separately for each site category. Significant differences ($P < 0.05$, ANOVA, Tukey’s HSD) among site categories are denoted as superscripts. Also given are the results of vector fitting of individual forest structure variables on NMDS ordination axes ($P$-values based on 1,000 permutations).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean (SE)</th>
<th>Min</th>
<th>Max</th>
<th>Mainland</th>
<th>Islands</th>
<th>$F$</th>
<th>$P$</th>
<th>Vector fitting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree density/ha</td>
<td>441.9 (33.5)</td>
<td>271.1</td>
<td>676.6</td>
<td>343.3 (50.3)$^a$</td>
<td>365.6 (31.0)$^a$</td>
<td>591.6 (45.2)$^b$</td>
<td>404.5 (50.2)$^b$</td>
<td>5.27</td>
</tr>
<tr>
<td>Basal area (m²/ha)</td>
<td>31.7 (3.0)</td>
<td>15.2</td>
<td>56.7</td>
<td>30.0 (4.8)</td>
<td>37.0 (4.0)</td>
<td>32.4 (6.4)</td>
<td>29.3 (6.3)</td>
<td>0.25</td>
</tr>
<tr>
<td>No. of poles/ha</td>
<td>1124.7 (96.0)</td>
<td>608.0</td>
<td>1867.3</td>
<td>876.8 (93.2)</td>
<td>825.2 (42.4)</td>
<td>1315.2 (162.8)</td>
<td>1239.6 (199.8)</td>
<td>1.73</td>
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<tr>
<td>No. of saplings/subplot</td>
<td>17.0 (1.5)</td>
<td>5.4</td>
<td>24.7</td>
<td>19.9 (0.9)</td>
<td>19.5 (1.9)</td>
<td>15.1 (3.9)</td>
<td>15.8 (2.8)</td>
<td>0.54</td>
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<tr>
<td>Canopy height (m)</td>
<td>19.8 (0.9)</td>
<td>13.9</td>
<td>25.1</td>
<td>23.6 (0.6)</td>
<td>22.1 (1.6)</td>
<td>16.9 (1.4)</td>
<td>19.1 (1.6)</td>
<td>3.39</td>
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<tr>
<td>Canopy cover (%)</td>
<td>95.5 (0.3)</td>
<td>93.1</td>
<td>97.6</td>
<td>94.2 (0.7)</td>
<td>95.3 (0.7)</td>
<td>95.2 (0.5)</td>
<td>96.4 (0.3)</td>
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<tr>
<td>Vertical heterogeneity</td>
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<td>2.8</td>
<td>5.2</td>
<td>4.3 (0.8)</td>
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<td>4.0 (0.3)</td>
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<td>0.3 (0.0)</td>
<td>0.3 (0.0)</td>
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Appendix B: List of bat species recorded and number of captures obtained in this study. Also presented are captures of non-phyllostomid bats, which were not included in the analyses. Taxonomy follows Simmons (2005).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Abbreviation</th>
<th>Guild*</th>
<th>Mainland</th>
<th>Islands</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>Edge</td>
<td>Near</td>
</tr>
<tr>
<td>Phyllostomidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Carollinae</td>
<td></td>
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<tr>
<td><em>Carollia brevicauda</em></td>
<td>Cbre</td>
<td>FRUG</td>
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<td>1</td>
<td>0</td>
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<tr>
<td><em>Carollia castanea</em></td>
<td>Ccas</td>
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<td>57</td>
<td>36</td>
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<tr>
<td><em>Carollia perspicillata</em></td>
<td>Cper</td>
<td>FRUG</td>
<td>41</td>
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<td>13</td>
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<td>Desmodontinae</td>
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<td></td>
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<tr>
<td><em>Desmodus rotundus</em></td>
<td>Drot</td>
<td>SANG</td>
<td>3</td>
<td>4</td>
<td>0</td>
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<tr>
<td>Glossophaginae</td>
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<td></td>
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<tr>
<td><em>Glossophaga soricina</em></td>
<td>Gsor</td>
<td>NECT</td>
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<tr>
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<td></td>
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<tr>
<td><em>Lampronycteris brachyotis</em></td>
<td>Lbra</td>
<td>OMNI</td>
<td>4</td>
<td>0</td>
<td>0</td>
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<tr>
<td><em>Lophostoma silvicolum</em></td>
<td>Lsil</td>
<td>GLAN</td>
<td>24</td>
<td>16</td>
<td>7</td>
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<tr>
<td><em>Mimon crenulatum</em></td>
<td>Mcre</td>
<td>GLAN</td>
<td>9</td>
<td>5</td>
<td>0</td>
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<tr>
<td><em>Micronycteris hirsuta</em></td>
<td>Mhir</td>
<td>GLAN</td>
<td>10</td>
<td>2</td>
<td>3</td>
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<tr>
<td><em>Micronycteris microtis</em></td>
<td>Mmic</td>
<td>GLAN</td>
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<td>3</td>
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<td><em>Micronycteris schmidtorum</em></td>
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<td>0</td>
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<tr>
<td><em>Phylloderma stenops</em></td>
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<td>FRUG</td>
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<tr>
<td><em>Phyllostomus discolor</em></td>
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<td>NECT</td>
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<tr>
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<td>OMNI</td>
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<tr>
<td><em>Trachops cirrhosus</em></td>
<td>Tcir</td>
<td>GLAN</td>
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<tr>
<td><em>Triniteris nicefori</em></td>
<td>Tnie</td>
<td>GLAN</td>
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<td>1</td>
<td>2</td>
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<tr>
<td><em>Tonatia saurophila</em></td>
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<tr>
<td><em>Vampyrum spectrum</em></td>
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<td>0</td>
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<td>Stenodermatinae</td>
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<tr>
<td><em>Artibeus jamaicensis</em></td>
<td>Ajam</td>
<td>FRUG</td>
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<td>869</td>
<td>1010</td>
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<td><em>Artibeus lituratus</em></td>
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<td><em>Artibeus phaeotis</em></td>
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<td><em>Centurio senex</em></td>
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<td><em>Chiroderma villosum</em></td>
<td>Cvil</td>
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<td><em>Lonchophylla robusta</em></td>
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## Appendix B: continued

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<th>Taxon</th>
<th>Abbreviation</th>
<th>Guild&lt;sup&gt;a&lt;/sup&gt;</th>
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<th>Islands</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>Edge</td>
<td>Near</td>
</tr>
<tr>
<td><em>Platyrrhinus helleri</em></td>
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<td><em>Uroderma bilobatum</em></td>
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<td><em>Vampyrorudes caraccioli</em></td>
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<td>FRUG</td>
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<td><em>Vampyressa mympheae</em></td>
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<td>Vpus</td>
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Emballonuridae

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<th>Mainland</th>
<th>Islands</th>
<th>Total</th>
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<tbody>
<tr>
<td></td>
<td></td>
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<td>Interior</td>
<td>Edge</td>
<td>Near</td>
</tr>
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<td><em>Centronycteris maximiliani</em></td>
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<tr>
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<td>0</td>
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<tr>
<td><em>Diclidurus albus</em></td>
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<td>AEIN</td>
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<td>0</td>
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<tr>
<td><em>Saccopteryx bilineata</em></td>
<td>Sbil</td>
<td>AEIN</td>
<td>3</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td><em>Saccopteryx leptura</em></td>
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<td>AEIN</td>
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<td>5</td>
<td>3</td>
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Mormoopidae

<table>
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<th>Abbreviation</th>
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<th>Mainland</th>
<th>Islands</th>
<th>Total</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>Edge</td>
<td>Near</td>
</tr>
<tr>
<td><em>Pteronotus parnellii</em></td>
<td>Ppar</td>
<td>AEIN</td>
<td>24</td>
<td>8</td>
<td>5</td>
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Noctilionidae

<table>
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<th>Abbreviation</th>
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<th>Mainland</th>
<th>Islands</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>Edge</td>
<td>Near</td>
</tr>
<tr>
<td><em>Noctilio leporinus</em></td>
<td>Nlep</td>
<td>TRIN</td>
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</table>

Vespertilionidae

<table>
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<th>Abbreviation</th>
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<th>Mainland</th>
<th>Islands</th>
<th>Total</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Interior</td>
<td>Edge</td>
<td>Near</td>
</tr>
<tr>
<td><em>Lasiurus ega</em></td>
<td>Lega</td>
<td>AEIN</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Rhogeessa tumida</em></td>
<td>Rtum</td>
<td>AEIN</td>
<td>3</td>
<td>0</td>
<td>2</td>
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</tbody>
</table>

<sup>a</sup>AEIN = aerial insectivore, FRUG = frugivore, GLAN = gleaning animalivore, NECT = nectarivore, OMNI = omnivore, SANG = sanguivore, TRIN = trawling insectivore/piscivore
Appendix C: Species-accumulation curves for bats captured on islands in Gatún Lake and at mainland sites. The sample order was randomized 1,000 times to smooth curves. Also indicated is the estimated mean number of species (± SD) based on the Jackknife 1 estimator.
Appendix D: Results of vector fitting of forest structure variables on non-metric multidimensional scaling axes of the ordination of bat assemblages ($P$-values are based on 1,000 permutations). NMDS1 and 2 are the direction-cosines of the vectors.

<table>
<thead>
<tr>
<th>Variable</th>
<th>NMDS1</th>
<th>NMDS2</th>
<th>$r^2$</th>
<th>$P$</th>
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<tbody>
<tr>
<td>Tree density</td>
<td>0.235</td>
<td>0.972</td>
<td>0.11</td>
<td>0.432</td>
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<tr>
<td>Basal area</td>
<td>-0.260</td>
<td>-0.966</td>
<td>0.38</td>
<td>0.031</td>
</tr>
<tr>
<td>No. of poles</td>
<td>0.380</td>
<td>0.925</td>
<td>0.31</td>
<td>0.067</td>
</tr>
<tr>
<td>No. of saplings</td>
<td>-0.376</td>
<td>0.927</td>
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<td>0.340</td>
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<tr>
<td>Canopy height</td>
<td>-0.701</td>
<td>-0.713</td>
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<td>Canopy closure</td>
<td>0.974</td>
<td>0.224</td>
<td>0.23</td>
<td>0.150</td>
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<tr>
<td>Vertical heterogeneity</td>
<td>-0.980</td>
<td>-0.198</td>
<td>0.03</td>
<td>0.820</td>
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<td>Horizontal heterogeneity</td>
<td>-0.047</td>
<td>0.999</td>
<td>0.10</td>
<td>0.487</td>
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Appendix E: Guild species richness ($S$), number of bat captures ($N$) and percent relative abundance (corrected for sampling effort) of bat guilds in continuous forest and on islands in Gatún Lake, Panama.

<table>
<thead>
<tr>
<th>Guild#</th>
<th>Mainland</th>
<th>Islands</th>
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<td>Interior</td>
<td>Edge</td>
</tr>
<tr>
<td></td>
<td>$S$</td>
<td>$N$</td>
</tr>
<tr>
<td>FRUG</td>
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<td>1113</td>
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<tr>
<td>GLAN</td>
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<td>96</td>
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<tr>
<td>NECT</td>
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<td>7</td>
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<td>OMNI</td>
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<td>10</td>
</tr>
<tr>
<td>SANG</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>

*FRUG = frugivore, GLAN = gleaning animalivore, NECT = nectarivore, OMNI = omnivore, SANG = sanguivore*
Appendix F: Generalized linear model selection results for examining the association between, respectively bat species richness and assemblage composition on Gatún Lake islands, and local-scale characteristics and landscape-level metrics for three different focal scales. For each candidate model, the number of estimable parameters ($K$), log-likelihood (Log-$L$), sample-size adjusted Akaike Information Criterion ($AIC_c$), Akaike differences ($\Delta_i$), and Akaike weights ($w_i$) are presented.

<table>
<thead>
<tr>
<th>Model description</th>
<th>$K$</th>
<th>Log($L$)</th>
<th>$AIC_c$</th>
<th>$\Delta_i$</th>
<th>$w_i$</th>
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<tbody>
<tr>
<td><strong>Species richness</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><strong>0.5 km-landscape</strong></td>
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<tr>
<td>Distance to mainland</td>
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<td>0.569</td>
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<td>56.68</td>
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<td>0.226</td>
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<tr>
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<td>58.80</td>
<td>3.97</td>
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<td>Mean patch size</td>
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<td>60.37</td>
<td>5.54</td>
<td>0.036</td>
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<td>Forest cover</td>
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<td>60.47</td>
<td>5.64</td>
<td>0.034</td>
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<td>Island area</td>
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<td>60.61</td>
<td>5.78</td>
<td>0.032</td>
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<td>-23.86</td>
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<tr>
<td>Forest structure</td>
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<td>64.25</td>
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<td>Patch-level metrics+Forest structure</td>
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<td>-23.08</td>
<td>79.16</td>
<td>24.33</td>
<td>0.000</td>
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<td>Patch-level metrics+landscape-level metrics</td>
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<td>98.98</td>
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<td>0.000</td>
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<td><strong>1 km-landscape</strong></td>
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The study islands in Gatún Lake:

- View from Barro Colorado Island towards the Las Brujas archipelago (top left)
- Part of the Tres Almendras island group with Juan Gallegos in the back (top right)
- View of Isla Guanabano during the dry season (above)
- Secondary forest on Isla Guanabano (right)
A motor boat was used to reach the study sites and to transport field equipment (top left). Bats were captured using a high net wall to sample bats flying in higher forest strata (top right and middle left) in combination with several mist nets set in the forest understory (middle right), a method that proved very effective (bottom left). Captured bats were transported to the field camp and kept in cloth bags until further processing (bottom right).
Potpourri of bat species caught during the study. Top left to bottom right:
- *Artibeus jamaicensis* (2x)
- *Artibeus lituratus*
- *Trinectes nicotii*
- *Dermanura phaeotis*
- *Diclidurus albus*
- *Mimon crenulatum*
- *Dermanura watsoni*
- *Lasiurus ega*
- *Micronycteris microtis*
- *Vampyrodes caraccioli*
Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns

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Abstract. - A fundamental goal of ecology is to understand whether ecological communities are structured according to general assembly rules or whether community organization is essentially dictated by random processes. In the context of habitat fragmentation, understanding community assembly patterns and their mechanistic basis also has important implications for conservation. Using distribution data of 20 phyllostomid bat species collected on a set of 11 land-bridge islands in Gatún Lake, Panama, we employed null model analysis to test for patterns of non-randomness in presence-absence matrices with respect to two assembly rule models: nestedness and negative species co-occurrence. We examined the causal basis for the observed patterns and conducted separate analyses for the entire assemblage and for various species submatrices reflecting differences in species’ trophic position (phytophagous vs. animalivorous) and mobility (high vs. low). Furthermore, we explored the influence of weighting factors (island area, isolation, abundance) on co-occurrence analyses by comparing different alternative randomization algorithms. Unweighted analyses revealed a significant negative co-occurrence pattern for the entire assemblage and for phytophagous bats alone. Weighting analyses by island isolation retained a pattern of species segregation for the whole assemblage but nullified the non-random structure for phytophagous bats and suggested negative species associations for animalivores and species with low mobility. Area- and abundance-weighted analyses always suggested random structuring. Phyllostomid bat distributions followed a nested subset structure across islands, regardless of whether all species or different submatrices were analyzed. Rank correlations between matrix reorganization vectors and extrinsic factors showed that nestedness was in all cases unrelated to island area but weakly correlated with island isolation for incidence matrices of all species, phytophagous bats, and mobile species. Overall, our findings indicate that bat assemblages on our study islands are most strongly shaped by isolation effects and species’ differential movement and colonization ability. On the other hand, evidence for negative interspecific interactions indicative of competitive effects was weak, corroborating previous studies based on ecomorphological analyses.

Key-words: assembly rules, bats, Chiroptera, community organization, habitat fragmentation, land-bridge islands, nested subsets, null models, Panama, species co-occurrence
Introduction

The question whether communities are shaped predominantly by biotic interactions such as competition or are randomly assembled from species pools has been pondered by ecologists for decades (Weiher and Keddy 1999). Ever since Diamond (1975) in his seminal paper on assembly of insular communities posited that faunal assemblages are competitively structured, the identification and explanation of non-random patterns in assemblage composition has been a central theme in community ecology. Moreover, knowledge of patterns and causes of species distribution in insular biotas has been central in providing guidelines to biodiversity conservation, e.g. concerning reserve design (Whittaker 1998). Diamond’s controversial assembly rules model has been the focus of a long-standing and intense debate centered mainly around theoretical and statistical aspects (cf. Gotelli and McCabe 2002). In a recent meta-analysis, Gotelli and McCabe (2002) demonstrated for a variety of taxa that species co-occurrence is usually less than expected by chance hence lending support to Diamond’s proposition that competitive interactions play a generally important role in structuring many species assemblages. Most recently, tests for patterns in biogeography and species co-occurrence have also been extended to include neutral models (Ulrich 2004; Gotelli and McGill 2006), which posit ecological equivalence among species and argue for random processes shaping local and regional community structure (Hubbell 2001). Apart from Diamond’s assembly rules a range of other patterns of community non-randomness has been suggested and examined, including Fox’s favored states model (Fox and Brown 1993), core-satellite organization (Hanski 1982; Ulrich and Zalewski 2006), and species nestedness (Patterson and Atmar 1986; Wright et al. 1998).

Nestedness is a pattern frequently reported for faunal assemblages in natural or anthropogenically fragmented systems and has been documented for a broad range of taxa (cf. review by Wright et al. 1998). Assemblages exhibit a nested distributional pattern when the species present at species-poor sites constitute subsets of those from progressively species-rich sites, rather than a random draw of those present in the entire regional species pool (Patterson and Atmar 1986). Nested subset theory has received considerable attention regarding its relevance to biodiversity management and conservation, concerning its potential to identify fragmentation-sensitive species, but particularly as it relates to the SLOSS-debate (single large or several small) regarding reserve design where its utility, however, appears to be limited (Patterson 1987; Boecklen 1997; Fischer and Lindenmayer 2005; Martinez-Morales 2005).
Chapter 2  

Nestedness and co-occurrence patterns

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

In this study, we used null model analyses (Gotelli and Graves 1996) to test for patterns of species co-occurrence and nestedness in presence-absence matrices of phyllostomid bats sampled as part of a comprehensive project investigating fragmentation effects on Neotropical bats within a landscape of small land-bridge islands in Gatún Lake, Panama (Meyer and Kalko submitted). Compared to other taxa, few studies have assessed bat assemblages with respect to species co-occurrence patterns and nested subset structure and analyses to date have largely been restricted to bats on oceanic islands (Wright et al. 1998; Gotelli and McCabe 2002; Watling and Donnelly 2006). By contrast, to our knowledge no study has so far investigated patterns of nestedness and species associations for bats in the context of habitat fragmentation. In view of their high functional significance in Neotropical ecosystems as pollinators, seed dispersers, and arthropod predators (Kalko 1998; Patterson et al. 2003) it is important to evaluate whether fragmentation still allows conclusions to be drawn concerning predictable structuring of phyllostomid bat assemblages in fragmented habitats.

We explored possible mechanisms underlying the observed distribution patterns of bats on islands and examined the use of a series of weighting factors (island area, island isolation, species abundance) on the outcome of co-occurrence analyses. In addition to conducting analyses for the whole species assemblage, we were particularly interested in investigating differences in the outcome of co-occurrence and nestedness analyses for different subsets of species. In the case of analyses testing for negative species associations this was predicated on the assumption that non-random co-occurrence patterns are less likely to be detected at the assemblage-level, i.e. in data sets that include a large number of ecologically disparate species that obviously do not compete for resources. In contrast, at the level of functional groups (ensembles sensu Fauth et al. 1996) interactive effects among species can be expected to be stronger, a point that has recently been demonstrated for
phyllostomid bats based on ecomorphological analyses (Moreno et al. 2006). We therefore contrasted incidence matrices of phytophagous and animalivorous phyllostomid bats in our analyses.

It is conceivable that in the context of habitat fragmentation, alterations in the resource base (food, roost sites) as a result of fragmentation may disrupt effects of species ecological interactions even at the functional group level, making the detection of deterministic structure less likely. Dispersal or mobility is another factor that may play an important role in shaping patterns of species co-occurrence and nestedness, a fact that has recently been brought attention to by Zalewski & Ulrich (2006), but so far has not been explicitly considered in bat studies. Even within a trophic level, if species differ in their ability to colonize new patches, then they will be differentially affected by fragmentation, suggesting that differential mobility should influence patterns of species distribution.

In addition to conducting separate analyses for phytophagous and animalivorous bats, we therefore divided species based on differences in mobility (high versus low mobility species). High species mobility can be expected to randomize faunal composition and should hence lead to random co-occurrence patterns. In contrast, we predicted an underdispersed pattern of species co-occurrence, i.e. negative species associations for incidence matrices of less vagile species (cf. Zalewski and Ulrich 2006).

Material and methods

Study area

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

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<tr>
<td>11</td>
<td>Leon</td>
<td>50</td>
<td>1.55</td>
<td>11</td>
<td>2</td>
<td>4</td>
<td>9</td>
</tr>
</tbody>
</table>

* island #8 in Adler & Seamon (1991)

Bat sampling

On each island, bats were sampled in a standardized manner using at each site six 6-m mist nets set at ground level and one net wall consisting of four stacked 6-m nets, reaching subcanopy or canopy level depending on the height of the forest. Each island was sampled for 7 entire nights between October 2003 and October 2005 with a minimum time interval of 30 days between netting nights to reduce possible net-shyness of the bats. Standard measurements and demographic data were collected following Handley et al. (1991). For a full account of sampling procedures see Meyer & Kalko (submitted). Species accumulation curves and species richness estimators indicated a high level (> 95%) of inventory completeness for all study islands (Meyer and Kalko submitted). In total, we obtained 8,447 captures of 39 species belonging to 5 families (Meyer and Kalko submitted).

Data analysis

Species matrices

For the purpose of this study we excluded all non-phyllostomid species, since they cannot be adequately sampled with mist nets (Kalko 1998) as well as one species, Centurio
Table 2. Phyllostomid bat species captured on Gatún Lake islands, Panama, and used in nestedness and species co-occurrence analyses. Nomenclature follows Simmons (2005).

<table>
<thead>
<tr>
<th>ID#</th>
<th>Species (acronym)</th>
<th>Number of islands occupied ($N_{\text{max}} = 11$)</th>
<th>Trophic level$^a$</th>
<th>Mobility</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Artibeus jamaicensis</em> (Ajam)</td>
<td>11</td>
<td>P</td>
<td>High</td>
</tr>
<tr>
<td>2</td>
<td><em>Artibeus lituratus</em> (Alit)</td>
<td>11</td>
<td>P</td>
<td>High</td>
</tr>
<tr>
<td>3</td>
<td><em>Artibeus phaeotis</em> (Apha)</td>
<td>4</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>4</td>
<td><em>Artibeus watsoni</em> (Awat)</td>
<td>6</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>5</td>
<td><em>Carollia castanea</em> (Cc)</td>
<td>5</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>6</td>
<td><em>Carollia perspicillata</em> (Cper)</td>
<td>10</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>7</td>
<td><em>Chiroderma villosum</em> (Cvil)</td>
<td>7</td>
<td>P</td>
<td>High</td>
</tr>
<tr>
<td>8</td>
<td><em>Glossophaga soricina</em> (Gsor)</td>
<td>10</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>9</td>
<td><em>Lophostoma silvicolum</em> (Lsil)</td>
<td>2</td>
<td>A</td>
<td>Low</td>
</tr>
<tr>
<td>10</td>
<td><em>Micronycteris hirsuta</em> (Mhir)</td>
<td>3</td>
<td>A</td>
<td>Low</td>
</tr>
<tr>
<td>11</td>
<td><em>Micronycteris microtis</em> (Mmic)</td>
<td>9</td>
<td>A</td>
<td>Low</td>
</tr>
<tr>
<td>12</td>
<td><em>Phyllostomus discolor</em> (Pdis)</td>
<td>1</td>
<td>P</td>
<td>High</td>
</tr>
<tr>
<td>13</td>
<td><em>Phyllostomus hastatus</em> (Phas)</td>
<td>2</td>
<td>A</td>
<td>High</td>
</tr>
<tr>
<td>14</td>
<td><em>Platyrrhinus helleri</em> (Phel)</td>
<td>5</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>15</td>
<td><em>Trinycteris nicefori</em> (Tnic)</td>
<td>1</td>
<td>A</td>
<td>Low</td>
</tr>
<tr>
<td>16</td>
<td><em>Tonatia saurophila</em> (Tsau)</td>
<td>2</td>
<td>A</td>
<td>Low</td>
</tr>
<tr>
<td>17</td>
<td><em>Uroderma bilobatum</em> (Ubil)</td>
<td>11</td>
<td>P</td>
<td>High</td>
</tr>
<tr>
<td>18</td>
<td><em>Vampyrodes caraccioli</em> (Vcar)</td>
<td>4</td>
<td>P</td>
<td>High</td>
</tr>
<tr>
<td>19</td>
<td><em>Vampyressa nymphaea</em> (Vnym)</td>
<td>1</td>
<td>P</td>
<td>Low</td>
</tr>
<tr>
<td>20</td>
<td><em>Vampyressa pusilla</em> (Vpus)</td>
<td>9</td>
<td>P</td>
<td>Low</td>
</tr>
</tbody>
</table>

$^a$P: phytophagous; A: animalivorous (Giannini and Kalko 2004; 2005)

...senex, that occurred only seasonally in the study area. This resulted in a total of 20 phyllostomomid species for analysis (Table 2) for which we constructed a species (rows) by site (columns) matrix. We additionally generated presence-absence matrices for four different species subsets as follows: first, we classified bats into phytophagous and animalivorous species based on dietary analyses (Giannini & Kalko (2004; 2005). Second, we employed principal components analysis (PCA) to divide species according to their mobility (Table 3, Fig. 1). Variables included in the PCA were mean and maximum recapture distances as well as two morphological variables, aspect ratio and wing loading, which are linked to mobility in bats (Norberg and Rayner 1987).
Table 3. Results of a principal components analysis on four variables related to species mobility, showing the loadings for each variable and the proportion of variance explained by the first two components (PC1 and PC2).

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum recapture distance (d_{max})</td>
<td>-0.48</td>
<td>0.56</td>
</tr>
<tr>
<td>Mean recapture distance (d_{mean})</td>
<td>-0.58</td>
<td>0.04</td>
</tr>
<tr>
<td>Aspect ratio</td>
<td>-0.37</td>
<td>-0.84</td>
</tr>
<tr>
<td>Wing loading</td>
<td>-0.55</td>
<td>0.05</td>
</tr>
<tr>
<td>Variance explained (%)</td>
<td>67.0</td>
<td>21.1</td>
</tr>
</tbody>
</table>

Fig. 1. Ordination of 20 phyllostomid bat species in the principal components space of a set of variables related to species mobility. For full species names see Table 2.
Recapture distances were calculated based on a large data set collected as part of the BCI long-term bat project with > 40,000 capture/recapture data (Kalko et al. 1996; unpublished data). Values for aspect ratio and wing loading (Nm²) were taken from Meyer et al. (accepted) and von Staden (2002). Based on the ordination diagram two clusters of species characterized by high and low mobility, respectively, could be distinguished (Fig. 1). This categorization (Table 2) was subsequently used for the construction of separate incidence matrices for nestedness and co-occurrence analyses.

Co-occurrence patterns

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

The V-ratio measures the variability in the number of species per site and represents the ratio between the variance in species richness per site (= variance of column sums), and the sum of the variances of species occurrence over sites (= sum of row variances) (Schluter 1984; Gotelli 2000). The ratio equals 1 if the average covariance between species pairs is 0. In the case of positive or negative covariance between species pairs, the V-ratio is smaller or greater than 1, respectively (Gotelli 2000). In an assemblage structured by negative species interactions, the C-score should be significantly larger than expected by chance, while the opposite should be true for the V-ratio (Gotelli 2000; Gotelli and McCabe 2002).

Null models and randomization algorithms. - We calculated the above indices and compared them to those of 5,000 randomly assembled communities using the software
EcoSim 7.72 (Gotelli and Entsminger 2006). The outcome of species co-occurrence analyses is sensitive to the selection of appropriate null models and choice of the randomization algorithm. We used the sequential swap algorithm to generate random null matrices (Gotelli 2000; Gotelli and Entsminger 2001). Although use of the swap algorithm has been subject to criticism (Sanderson et al. 1998; Manly and Sanderson 2002), re-evaluation (Gotelli and Entsminger 2003) confirmed its overall good statistical properties and performance. We compared three alternative null models, differing in the way row and column totals are treated:

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

2) **Fixed-weighted (FW)**. Results of co-occurrence analyses can be strongly affected by the use of weighting factors, although this approach so far has only infrequently been applied (but see Gotelli and Ellison 2002; Jenkins 2006). Column weighting adjusts the probability of a species occurring at a particular site during randomization using factors thought to contribute to inter-site differences in community composition. Here, we explored the influence of two weighting factors, island area and island isolation (distance from the mainland), on the outcome of null model analyses.

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

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

A variety of different methods are available for calculating the nestedness of presence-absence matrices (reviewed by Wright et al. 1998). Of these, Atmar & Patterson’s Nestedness Temperature Calculator (NTC; Atmar and Patterson 1995) is currently the most popular and widely used in biogeographical studies and analyses of habitat fragmentation. The matrix temperature $T$ calculated by the NTC is a measure of unexpected species presences and absences or system “disorder” where $0^\circ$ corresponds to a perfectly nested matrix and $100^\circ$ indicates a random species distribution pattern. However, recent research cautions against use of the NTC as it has been demonstrated to have a number of important shortcomings relating to the definition of the isocline of perfect order, the way of matrix reorganization, the robustness of the packing algorithm, and choice of an appropriate null model (Fischer and Lindenmayer 2002; Rodríguez-Gironés and Santamaría 2006).

Here we used the binary matrix nestedness temperature calculator (BINMATNEST) recently developed by Rodríguez-Gironés & Santamaría (2006), which overcomes these difficulties. BINMATNEST implements an isocline of perfect order that is unambiguously defined, is based on robust genetic algorithms to determine the reordering of rows and columns that leads to minimum matrix temperature, and provides a set of three alternative null models to assess the statistical significance of matrix temperature (Rodríguez-Gironés and Santamaría 2006). Following the authors’ recommendations we used null model 3 in evaluating statistical significance as it has been shown to be associated with the smallest Type I error. Reported $P$-values are based on 5,000 random matrices. To evaluate the causal role of colonization and extinction in shaping community structure we used a Spearman rank correlation between the matrix reorganization vectors, i.e. island rank order in the maximally packed matrix, and island isolation and area, respectively (Patterson and Atmar 2000; Rodríguez-Gironés and Santamaría 2006).

Results

Co-occurrence patterns

Results of analyses depended considerably on the type of null model algorithm employed (Table 4). For the $FF$-model, the observed $C$-score for the incidence matrix of the entire assemblage and for the submatrix of phytophagous bats was significantly higher than expected by chance, suggesting a negative pattern of species co-occurrence. Conversely, for the submatrices of animalivorous bats and species of both high and low mobility, the $C$-score
Table 4. Summary of species co-occurrence analyses of phylllostomid bats with observed and simulated co-occurrence metrics, standardized effect sizes [SES], and associated tail probabilities (in parentheses) for each of the different species presence-absence matrices and null model algorithms. For details see text. Significant and marginally significant results are highlighted in bold. n.a.: the $V$-ratio cannot be tested with the fixed-fixed null model.

<table>
<thead>
<tr>
<th>Index</th>
<th>Species matrix</th>
<th>Score</th>
<th>sim_{FF}</th>
<th>sim_{FW-area}</th>
<th>sim_{FW-isolation}</th>
<th>sim_{WF}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>obs</td>
<td>sim_{FF}</td>
<td>sim_{FW-area}</td>
<td>sim_{FW-isolation}</td>
<td>sim_{WF}</td>
</tr>
<tr>
<td>C-score</td>
<td>All species</td>
<td>1.368</td>
<td>1.245 (0.026)</td>
<td>1.417 (0.554)</td>
<td>0.915 (0.033)</td>
<td>1.513 (0.634)</td>
</tr>
<tr>
<td>[SES]</td>
<td>Phytophagous</td>
<td>0.890</td>
<td>0.764 (0.041)</td>
<td>1.311 (0.878)</td>
<td>0.710 (0.256)</td>
<td>1.366 (0.869)</td>
</tr>
<tr>
<td></td>
<td>Animalivorous</td>
<td>2.267</td>
<td>2.399 (0.679)</td>
<td>1.693 (0.222)</td>
<td>1.493 (0.076)</td>
<td>3.686 (0.902)</td>
</tr>
<tr>
<td></td>
<td>High mobility</td>
<td>0.143</td>
<td>0.143 (1.000)</td>
<td>0.613 (0.923)</td>
<td>0.453 (0.876)</td>
<td>0.456 (0.818)</td>
</tr>
<tr>
<td></td>
<td>Low mobility</td>
<td>1.821</td>
<td>1.733 (0.188)</td>
<td>1.863 (0.535)</td>
<td>1.166 (0.048)</td>
<td>2.288 (0.761)</td>
</tr>
<tr>
<td>$V$-ratio</td>
<td>All species</td>
<td>4.053</td>
<td>n.a.</td>
<td>3.746 (0.661)</td>
<td>5.021 (0.083)</td>
<td>4.128 (0.432)</td>
</tr>
<tr>
<td>[SES]</td>
<td>Phytophagous</td>
<td>3.819</td>
<td>n.a.</td>
<td>2.808 (0.946)</td>
<td>4.005 (0.406)</td>
<td>3.624 (0.814)</td>
</tr>
<tr>
<td></td>
<td>Animalivorous</td>
<td>1.264</td>
<td>n.a.</td>
<td>1.785 (0.253)</td>
<td>1.811 (0.151)</td>
<td>1.201 (0.753)</td>
</tr>
<tr>
<td></td>
<td>High mobility</td>
<td>2.119</td>
<td>n.a.</td>
<td>1.529 (0.956)</td>
<td>1.694 (0.927)</td>
<td>1.954 (0.839)</td>
</tr>
<tr>
<td></td>
<td>Low mobility</td>
<td>3.157</td>
<td>n.a.</td>
<td>3.022 (0.609)</td>
<td>4.066 (0.070)</td>
<td>3.054 (0.712)</td>
</tr>
</tbody>
</table>

The use of island area as weighting factor ($FW$-area), on the other hand, suggested random co-occurrence patterns as the null hypothesis was never rejected for any of the species matrices. This was similarly true for the abundance-weighted ($WF$) model (Table 4).
The $V$-ratio detected marginally significant deviations from null expectations only for the $FW$-model weighted by island isolation and when either all species or bats characterized by low mobility were considered. In the remainder of the cases the $V$-ratio did not differ significantly from random expectations (Table 4).

**Nestedness**

Phyllostomid bat assemblages on Gatún Lake islands were highly significantly nested when all species were considered ($P < 0.0001$, Table 5, Fig. 2). The bat distribution across islands remained more significantly nested ($P \leq 0.001$) than expected by chance using incidence matrices of phytophagous species alone or based on the data sets comprising species of both mobility classes. For gleaning animalivores, the difference between observed and expected nestedness temperature was marginally significant ($P = 0.062$) (Table 5). Spearman rank correlations between row order in the maximally nested matrix with causal factors suggested that island isolation was an important determinant of nestedness in phyllostomid bat distributions for incidence matrices of the whole phyllostomid assemblage ($r_s = 0.62$, $P = 0.046$), phytophagous bats ($r_s = 0.58$, $P = 0.063$), and mobile species ($r_s = 0.54$, $P = 0.091$) but not for animalivorous ($r_s = 0.47$, $P = 0.141$) or less vagile species ($r_s = 0.51$, $P = 0.110$). In contrast, the nested order of islands was unrelated to the rank order of island areas for all five species matrices (Table 5), indicating that island area is not causally linked to nested structure in our study system.

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

<table>
<thead>
<tr>
<th>Species matrix</th>
<th>$T_{obs}$</th>
<th>$T_{exp}$ (SD)</th>
<th>$P$</th>
<th>Rank correlation with island area</th>
<th>Rank correlation with island isolation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$r_s$</td>
<td>$P$</td>
</tr>
<tr>
<td>All</td>
<td>14.80</td>
<td>37.40 (5.36)</td>
<td>$&lt; 0.0001$</td>
<td>0.109</td>
<td>0.745</td>
</tr>
<tr>
<td>Phytophagous</td>
<td>10.47</td>
<td>28.71 (6.45)</td>
<td>0.001</td>
<td>-0.073</td>
<td>0.839</td>
</tr>
<tr>
<td>Animalivorous</td>
<td>9.16</td>
<td>21.48 (8.63)</td>
<td>0.062</td>
<td>0.100</td>
<td>0.765</td>
</tr>
<tr>
<td>High mobility</td>
<td>0.83</td>
<td>19.63 (7.38)</td>
<td>$&lt; 0.0001$</td>
<td>0.100</td>
<td>0.765</td>
</tr>
<tr>
<td>Low mobility</td>
<td>14.04</td>
<td>33.78 (6.38)</td>
<td>0.0004</td>
<td>-0.064</td>
<td>0.860</td>
</tr>
</tbody>
</table>
Fig. 2. Maximally nested presence-absence matrix of phyllostomid bat distributions on Gatún Lake islands, Panama. Island and species ID numbers refer to Tables 1 and 2, respectively.

**Discussion**

**Co-occurrence patterns**

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

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

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

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

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

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

**Nestedness**

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

By contrast, we found that island nested rank order was significantly or marginally significantly correlated with the rank order of island isolation but not island area for the entire
assemblage as well as for phytophagous and highly mobile species. This mainly reflects, and is in agreement with the finding of a strong effect of island isolation on species richness and lack of a significant species-area relationship at the local scale (Meyer and Kalko submitted). Thus, isolation-dependent, selective colonization appears to be the likely cause of nestedness and dominant process structuring phyllostomid bat assemblages on our study islands. The reason for this may also be that bat assemblages on Gatún Lake islands, which are > 90 years old, have likely reached an equilibrium species richness and composition, whereas avian assemblages on Lake Guri islands are probably still undergoing relaxation, whereby local extinction continues to be the dominant structuring process (Feeley 2003). This may explain, at least in part, the contrasting patterns observed with respect to the causal factors underlying nestedness in both systems.

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

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

Conclusions

In summary, our analyses of patterns of nestedness and species co-occurrence indicate that assemblage composition of phyllostomid bats on Gatún Lake islands is in large part determined by isolation-dependent, differential colonization reflecting differences in species mobility. Evidence for negative species associations congruent with niche-based community assembly invoking competitive interspecific interactions was limited. In line with previous findings our results suggest that deterministic structuring may be hard to detect in situations with high heterogeneity in environmental conditions such as in fragmented landscapes.

Acknowledgements

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Literature cited

Park, NM and The Field Museum, Chicago, IL.


Chapter 2


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 addressed this topic using distribution and abundance data collected on 23 species of Neotropical bats to compare hypotheses on the causes of interspecific differences in fragmentation sensitivity.

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 (ESLIs). 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 at minimizing the amount of edge-habitat and reducing the degree of fragment-matrix contrast. Moreover, if a maximum of 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, habitat fragmentation, ecological traits, 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 worldwide 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 (Purvis et al. 2000; Davies, Margules & Lawrence 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).

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 commonly hypothesized 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 (Henle et al. 2004; Davies, Margules & Lawrence 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 (Medellin, Equihua & Amin 2000). Because of their diversity and high abundance bats are important components of tropical faunas where they fulfill 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 largely restricted 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 geographic ranges and low wing aspect ratio as significant global correlates...
Chapter 3  

Correlates of fragmentation sensitivity in Neotropical bats

of extinction proneness in bats. Safi & Kerth (2004), focusing on temperate-zone bats, likewise found 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 two-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 regularly cross habitat boundaries 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 more negatively affected 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 mostly depend on patchily distributed resources should also be more mobile and hence be less fragmentation sensitive than species with limited mobility like understory bats, which primarily forage on spatio-temporally predictable, but often more locally restricted food resources (Kalko 1998; Bernard 2001; Kalko & Handley 2001). Additionally, we expected generalists that opportunistically use all forest strata to be least fragmentation sensitive because they are likely to quickly adjust 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 maneuverability 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 negatively related to wing loading and aspect ratio.

(9) Ecologically scaled landscape indices (ESLIs). - Species persistence in fragmented landscapes may not only depend on biological characteristics of the target species but ecological attributes can be expected to interact with landscape attributes thus influencing patterns of species occurrence and abundance in patchy landscapes (Vos et al. 2001). ESLIs are measures which explicitly link 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).

Material 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 5,400 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-months 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 6 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, for details see Meyer & Kalko submitted).
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 x 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 to 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 were asymptotic and indicated that the bat fauna at each site was adequately sampled (Meyer & Kalko submitted). In total, we obtained 8447 captures representing 5 families and 39 species (Meyer & Kalko submitted). For the purpose of this study we excluded, except for the mormoopid bat *Pteronotus parnellii*, all non-phyllostomid species, since they cannot be adequately sampled with mist nets (Kalko 1998) as well as species that were captured extremely rarely (< 4 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 mistnet hour (mnh; one mnh = one 6-m net open for one hour) 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 $ES = (N_{\text{edge}} - N_{\text{interior}}) / (N_{\text{edge}} + N_{\text{interior}})$ (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 broadly divided into four categories: (a) fruit, (b) nectar or pollen, (c) arthropods, and (d) vertebrates. We then calculated the percent 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 is not necessarily indicating dietary specialization of a species. For example, since there are many more insects than plant species providing food for bats, we considered an animalivorous species only as specialized if one prey order contributed more than three quarters to the food records. For frugivores, this proportion needed to be from one plant genus according to our definition. 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 mainly a fig diet was considered specialized only if figs comprised more than 90 percent of its dietary records.

Vertical stratification. - We derived the vertical niche of each species by calculating the proportion of captures in ground nets versus high nets. For this, we counted only the two upper nets of the net wall as „high nets“, reflecting capture heights of ca. 8 - 14 m versus 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) understory 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 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 (WPL) in Costa Rica and Panama. Values were determined from photographs (Olympus μ-II camera) taken of the extended left wing of each bat and analyzed with the program analySIS 3.1 (Soft Imaging System Corp.). Following Norberg & Rayner (1987) the head was excluded from calculations of wing area.

**Ecologically scaled landscape indices (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:

\[
ESLI_K = \frac{\sum_{i=1}^{n} A_i IAR_i}{n}
\]

(eqn 2),

where *A*<sub>*i*</sub> is the area of patch *i* and *IAR*<sub>*i*</sub> are the individual area requirements 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:

\[
ESLI_\alpha = \frac{\sum_{i=1}^{n} A_i e^{-\alpha d_{ij}}}{n}
\]

(eqn 3),

where *d*<sub>*ij*</sub> 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_\alpha*, 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, $\alpha$ was calculated as $\alpha = - \ln(0.001)/d_{\text{max}}$ (Vos et al. 2001; Swihart et al. 2003a). \( ESLI_\alpha \) was quantified for landscapes delimited as circular buffer zones with a radius of 1.5 km surrounding each study island. The focal scale encompassed the expected home ranges of different-sized bat species and minimized spatial overlap between neighboring islands. For the calculation of \( ESLI_\alpha \), 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 ($F_{1,7} = 8.74, P = 0.021, r^2 = 0.56$).

**Model set explored.** - Our \textit{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 9 abovementioned predictor variables, included 4 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: \( ESLI_\alpha \) and \( KESLI \)

**Data analysis**

It is important to correct for the statistical non-independence of taxa in such a multispecies 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:

$$ y = \log_e \left( RA_{\text{islands}} + 0.0001 / RA_{\text{mainland interior}} + 0.0001 \right) \quad \text{(eqn 4)} $$
A small number (0.0001) 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, \( P > 0.6 \)) after phylogenetic correction they were modeled 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 percent 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 and 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 further incorporate 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 (\( \pi_i \)) 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
\[ \hat{\theta}_j = \sum_{i=1}^{\mathcal{R}} w_i \hat{\theta}_{j,i} \quad \text{(eqn 5)}, \]

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 better reflect 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 (i.e. \( w_{\text{max}} \leq 0.9 \)). For species prevalence, comparison of \( \Delta_i \) 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). 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 \( \Delta_i \) values but generally received equivocal support based on model weights and selection frequencies (Table 2). Overall, the first nine models formed a \( \sim 94\% \) confidence set. Parameter estimates for the best-supported models in the confidence set \((w_i > 0.1, \text{Table 3})\) 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 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Fraction of islands occupied</th>
<th>Change in abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Artibeus jamaicensis</em></td>
<td>1.00</td>
<td>0.692</td>
</tr>
<tr>
<td><em>Artibeus lituratus</em></td>
<td>1.00</td>
<td>-0.001</td>
</tr>
<tr>
<td><em>Artibeus phaeotis</em></td>
<td>0.36</td>
<td>0.081</td>
</tr>
<tr>
<td><em>Artibeus watsoni</em></td>
<td>0.55</td>
<td>-1.684</td>
</tr>
<tr>
<td><em>Carollia castanea</em></td>
<td>0.45</td>
<td>-2.321</td>
</tr>
<tr>
<td><em>Carollia perspicillata</em></td>
<td>0.91</td>
<td>-0.659</td>
</tr>
<tr>
<td><em>Chiroderma villosum</em></td>
<td>0.64</td>
<td>0.154</td>
</tr>
<tr>
<td><em>Glossophaga soricina</em></td>
<td>0.91</td>
<td>2.144</td>
</tr>
<tr>
<td><em>Lamproonycteris brachyotis</em></td>
<td>0.00</td>
<td>-2.776</td>
</tr>
<tr>
<td><em>Lophostoma silvicolum</em></td>
<td>0.18</td>
<td>-2.462</td>
</tr>
<tr>
<td><em>Micronycteris hirsuta</em></td>
<td>0.36</td>
<td>-1.529</td>
</tr>
<tr>
<td><em>Micronycteris microtis</em></td>
<td>0.82</td>
<td>1.022</td>
</tr>
<tr>
<td><em>Mimon crenulatum</em></td>
<td>0.00</td>
<td>-3.552</td>
</tr>
<tr>
<td><em>Phylloderma stenops</em></td>
<td>0.00</td>
<td>-3.309</td>
</tr>
<tr>
<td><em>Phyllostomus hastatus</em></td>
<td>0.18</td>
<td>-1.920</td>
</tr>
<tr>
<td><em>Platyrhinus hilleri</em></td>
<td>0.45</td>
<td>0.779</td>
</tr>
<tr>
<td><em>Pteronotus parnellii</em></td>
<td>0.91</td>
<td>-1.096</td>
</tr>
<tr>
<td><em>Tonatia saurophila</em></td>
<td>0.18</td>
<td>-2.506</td>
</tr>
<tr>
<td><em>Trachops cirrhosus</em></td>
<td>0.00</td>
<td>-3.833</td>
</tr>
<tr>
<td><em>Uroderma bilobatum</em></td>
<td>1.00</td>
<td>1.578</td>
</tr>
<tr>
<td><em>Vampyressa nymphaea</em></td>
<td>0.09</td>
<td>-1.209</td>
</tr>
<tr>
<td><em>Vampyressa pusilla</em></td>
<td>0.82</td>
<td>0.159</td>
</tr>
<tr>
<td><em>Vampyrodes caraccioli</em></td>
<td>0.36</td>
<td>-1.318</td>
</tr>
</tbody>
</table>
Table 2. Results of 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 Akaike Information Criterion \((AIC_c)\), Akaike differences \((\Delta_i)\), Akaike weights \((w_i)\), and bootstrap selection frequencies \((\pi_i)\) are presented. Model fit as evaluated based on the global model is given for each response variable as percent deviance explained \((% \text{ dev.})\). Confidence sets as explained in the text are highlighted in italics.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model description</th>
<th>Log(L)</th>
<th>K</th>
<th>(AIC_c)</th>
<th>(\Delta_i)</th>
<th>(w_i)</th>
<th>(\pi_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species prevalence</td>
<td><strong>Edge-sensitivity (ES)</strong></td>
<td>-4.01</td>
<td>2</td>
<td>12.65</td>
<td>0.00</td>
<td>0.449</td>
<td>0.349</td>
</tr>
<tr>
<td>(%) dev. = 44.9</td>
<td>Natural abundance (NA)</td>
<td>-5.19</td>
<td>2</td>
<td>15.01</td>
<td>2.36</td>
<td>0.138</td>
<td>0.175</td>
</tr>
<tr>
<td>Mobility (M)</td>
<td>-6.07</td>
<td>2</td>
<td>16.77</td>
<td>4.12</td>
<td>0.057</td>
<td>0.045</td>
<td></td>
</tr>
<tr>
<td>Relative wing loading (RWL)</td>
<td>-6.08</td>
<td>2</td>
<td>16.78</td>
<td>4.13</td>
<td>0.057</td>
<td>0.018</td>
<td></td>
</tr>
<tr>
<td>Trophic level (TL)</td>
<td>-6.24</td>
<td>2</td>
<td>17.11</td>
<td>4.45</td>
<td>0.048</td>
<td>0.019</td>
<td></td>
</tr>
<tr>
<td>Vertical stratification (VS)</td>
<td>-6.26</td>
<td>2</td>
<td>17.14</td>
<td>4.49</td>
<td>0.048</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td>Dietary specialization (DS)</td>
<td>-6.26</td>
<td>2</td>
<td>17.14</td>
<td>4.49</td>
<td>0.048</td>
<td>0.014</td>
<td></td>
</tr>
<tr>
<td>Aspect ratio (AS)</td>
<td>-6.31</td>
<td>2</td>
<td>17.24</td>
<td>4.59</td>
<td>0.045</td>
<td>0.011</td>
<td></td>
</tr>
<tr>
<td>Body mass (BM)</td>
<td>-6.31</td>
<td>2</td>
<td>17.25</td>
<td>4.59</td>
<td>0.045</td>
<td>0.020</td>
<td></td>
</tr>
<tr>
<td>Specialization (DS+VS+ES)</td>
<td>-3.96</td>
<td>4</td>
<td>18.27</td>
<td>5.61</td>
<td>0.027</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td>ESLI_C + ESIK</td>
<td>-5.73</td>
<td>3</td>
<td>18.79</td>
<td>6.13</td>
<td>0.021</td>
<td>0.036</td>
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</tr>
<tr>
<td>Population size (NA+BM+TL)</td>
<td>-4.98</td>
<td>4</td>
<td>20.31</td>
<td>7.66</td>
<td>0.010</td>
<td>0.058</td>
<td></td>
</tr>
<tr>
<td>Dispersal (M+RWL+AR+BM+ES)</td>
<td>-1.62</td>
<td>6</td>
<td>20.85</td>
<td>8.19</td>
<td>0.007</td>
<td>0.240</td>
<td></td>
</tr>
<tr>
<td>Change in abundance</td>
<td><strong>Edge-sensitivity (ES)</strong></td>
<td>-30.78</td>
<td>2</td>
<td>66.19</td>
<td>0.00</td>
<td>0.489</td>
<td>0.377</td>
</tr>
<tr>
<td>(%) dev. = 45.5</td>
<td>ESLI_C + ESIK</td>
<td>-31.08</td>
<td>3</td>
<td>69.49</td>
<td>3.31</td>
<td>0.094</td>
<td>0.156</td>
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<tr>
<td>Natural abundance (NA)</td>
<td>-32.69</td>
<td>2</td>
<td>70.00</td>
<td>3.82</td>
<td>0.073</td>
<td>0.056</td>
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</tr>
<tr>
<td>Trophic level (TL)</td>
<td>-32.86</td>
<td>2</td>
<td>70.35</td>
<td>4.16</td>
<td>0.061</td>
<td>0.053</td>
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</tr>
<tr>
<td>Body mass (BM)</td>
<td>-33.05</td>
<td>2</td>
<td>70.74</td>
<td>4.55</td>
<td>0.050</td>
<td>0.073</td>
<td></td>
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<tr>
<td>Dietary specialization (DS)</td>
<td>-33.28</td>
<td>2</td>
<td>71.19</td>
<td>5.01</td>
<td>0.040</td>
<td>0.024</td>
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<tr>
<td>Aspect ratio (AS)</td>
<td>-33.33</td>
<td>2</td>
<td>71.30</td>
<td>5.11</td>
<td>0.038</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>Vertical stratification (VS)</td>
<td>-33.34</td>
<td>2</td>
<td>71.31</td>
<td>5.12</td>
<td>0.038</td>
<td>0.011</td>
<td></td>
</tr>
<tr>
<td>Relative wing loading (RWL)</td>
<td>-33.34</td>
<td>2</td>
<td>71.31</td>
<td>5.13</td>
<td>0.038</td>
<td>0.015</td>
<td></td>
</tr>
<tr>
<td>Mobility (M)</td>
<td>-33.36</td>
<td>2</td>
<td>71.35</td>
<td>5.17</td>
<td>0.037</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>Specialization (DS+VS+ES)</td>
<td>-30.65</td>
<td>4</td>
<td>71.65</td>
<td>5.46</td>
<td>0.032</td>
<td>0.035</td>
<td></td>
</tr>
<tr>
<td>Population size (NA+BM+TL)</td>
<td>-32.10</td>
<td>4</td>
<td>74.54</td>
<td>8.36</td>
<td>0.007</td>
<td>0.035</td>
<td></td>
</tr>
<tr>
<td>Dispersal (M+RWL+AR+BM+ES)</td>
<td>-29.29</td>
<td>6</td>
<td>76.18</td>
<td>10.00</td>
<td>0.003</td>
<td>0.146</td>
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</tr>
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Table 3. Parameter estimates ($\hat{\theta}$) and unconditional standard errors (SE) for each variable in the confidence set.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Variable</th>
<th>Coefficient</th>
<th>Unconditional SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species prevalence</td>
<td>Edge-sensitivity</td>
<td>0.221</td>
<td>0.153</td>
</tr>
<tr>
<td></td>
<td>Natural abundance</td>
<td>0.019</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td>Mobility</td>
<td>0.005</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>Relative wing loading</td>
<td>-0.002</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Trophic level</td>
<td>-0.007</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td>Vertical stratification</td>
<td>-0.002</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>Dietary specialization</td>
<td>-0.003</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Aspect ratio</td>
<td>0.002</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>Body mass</td>
<td>0.001</td>
<td>0.007</td>
</tr>
<tr>
<td>Change in abundance</td>
<td>Edge-sensitivity</td>
<td>0.848</td>
<td>0.549</td>
</tr>
<tr>
<td></td>
<td>ESLIs ($ESLI_{\tau}$)</td>
<td>-0.134</td>
<td>0.137</td>
</tr>
<tr>
<td></td>
<td>ESLIs ($ESLI_{\tau}$)</td>
<td>-0.048</td>
<td>0.057</td>
</tr>
<tr>
<td></td>
<td>Natural abundance</td>
<td>-0.026</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>Trophic level</td>
<td>-0.072</td>
<td>0.099</td>
</tr>
<tr>
<td></td>
<td>Body mass</td>
<td>-0.020</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>Dietary specialization</td>
<td>0.010</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>Aspect ratio</td>
<td>0.010</td>
<td>0.044</td>
</tr>
<tr>
<td></td>
<td>Vertical stratification</td>
<td>-0.004</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>Relative wing loading</td>
<td>0.001</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Mobility</td>
<td>0.000</td>
<td>0.015</td>
</tr>
</tbody>
</table>

For the index of change in abundance as response variable, edge-sensitivity was again the model best supported by the data (Table 2). 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 5 times less likely ($w_i = 0.094$) and bootstrap support was also lower ($\pi_i = 0.156$) than for edge-sensitivity. Together the first ten models formed a ~ 96% confidence set (Table 2). As with species prevalence, the regression coefficient indicated a positive association between change in abundance and edge-sensitivity and a negative relationship with $ESLIs$, whereby the strength of the coefficient implied that this effect was largely due to $ESLI_{\tau}$ (Table 3).
Discussion

Analytical issues

Most studies that have investigated correlates of extinction proneness (Purvis et al. 2000; Jones et al. 2003) or sensitivity to fragmentation have typically used a conventional stepwise modeling approach (e.g. Laurance 1991; Davies et al. 2004; Viveiros de Castro & Fernandez 2004). However, stepwise regression has several limitations, among them an inherent bias in parameter estimation, overfitting, inconsistencies among model selection algorithms, and an inappropriate reliance on a single best minimum adequate model while ignoring model selection uncertainty (Quinn & Keough 2004; Whittingham et al. 2006). We therefore addressed these problems by using an information-theoretic model selection approach instead, which allowed us to quantify model selection uncertainty (Burnham & Anderson 2002). The importance of taking such an analytical approach is well illustrated by our findings as we did not find unambiguous support for a single best model for either response variable and Akaike weights and bootstrap selection frequencies indicated considerable model selection uncertainty.

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 most strongly associated with high edge-sensitivity. Low natural abundance in continuous forest also received some support 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 response variable change in abundance and the index of patch connectivity ($CESLI_C$). All other ecological traits examined were much 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 artifact 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 from the mainland interior capture data the probability for zero abundance at a particular site $i$. 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 significantly correlated 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 Table S2). In general, effects of body size on fragmentation sensitivity are arguable based on current empirical evidence, which likely reflects the fact that it is merely a surrogate for other traits known to influence vulnerability (Davies et al. 2000; Henle et al. 2004). Body size tends to be positively correlated 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 ultimately be responsible 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 (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 meters 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 (Meyer & Kalko submitted). 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 likely 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 indirectly linked 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 likely 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 $ESLI_F$, as home range sizes for many species had to be predicted from regression. Nonetheless, we found evidence for a
negative relationship between change in abundance and the index of patch connectivity ($ESLI_T$), 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 negatively affected 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 in part be based on mobility-related traits. In this regard, the utility of measures of functional connectivity like $ESLI_T$ 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 only be able to persist in heavily fragmented landscapes 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 geographic 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 geographic focus will likely be the most valuable for developing predictive models of species fragmentation sensitivity which can aid in directing research efforts and devising efficient management strategies.
Acknowledgements

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in southern Brazil. *Biotropica*, **38**, 229-234.


Correlates of fragmentation sensitivity in Neotropical bats

Chapter 3

Oaxaca, Mexico. Biological Conservation, 111, 283-303.


Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com:

Table S1 Explanatory variables used in modeling fragmentation sensitivity.

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

Figure S1 Plot used to group species into three mobility categories.
Chapter 3  

Correlates of fragmentation sensitivity in Neotropical bats

<table>
<thead>
<tr>
<th>Species</th>
<th>BM</th>
<th>NA</th>
<th>ES</th>
<th>MO</th>
<th>TL</th>
<th>DS</th>
<th>VS</th>
<th>AR</th>
<th>RWL</th>
<th>ESLI_C</th>
<th>ESLI_K</th>
</tr>
</thead>
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<td>3</td>
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<td>2</td>
<td>N</td>
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<td>20.28</td>
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<td>P</td>
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<td>U</td>
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<td>22.70</td>
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<tr>
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<td>25.73</td>
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<td>C</td>
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<td>23.71</td>
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</table>

1 Categories: 1 = low, 2 = intermediate, 3 = high; no recapture data were available for *Micronycteris microtis*, the species was assigned to the low mobility category based on radiotracking data (Albrecht, Meyer & Kalko in press).
2 P: phytophagous, A: animalivorous (Giannini & Kalko 2004; 2005)
4 U = understory preference, N = no preference, C = canopy preference
References to Table S1


### Table S2. Model selection results of species-level analyses conducted on data not corrected for the effects of phylogeny. For each model, the log-likelihood (Log-\(L\)), number of estimable parameters (\(K\)), sample-size adjusted Akaike Information Criterion (\(AIC_c\)), Akaike differences (\(\Delta_i\)), Akaike weights (\(w_i\)), and bootstrap selection frequencies (\(\pi_i\)) are presented. Species prevalence was modeled using generalized linear models (GLMs) with a logit link function, for the index of change in abundance GLMs with a Gaussian error distribution were used. For species prevalence, the quasi-likelihood modification \(QAIC_c\), rather than \(AIC_c\), was used to account for overdispersion in the data. Model fit as evaluated based on the global model is given for each response variable as percent deviance explained (% dev.).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model description</th>
<th>Log(L)</th>
<th>(K)</th>
<th>(\Delta_i)</th>
<th>(w_i)</th>
<th>(\pi_i)</th>
</tr>
</thead>
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<tr>
<td>Species prevalence (% dev. = 64.3)</td>
<td>Natural abundance (NA)</td>
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<td>0.000</td>
<td>0.298</td>
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<td>0.964</td>
<td>0.184</td>
<td>0.104</td>
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<td>1.048</td>
<td>0.176</td>
<td>0.127</td>
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<td>0.140</td>
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<td>4.360</td>
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<td>ESLI_c + ESLI_k</td>
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<td>6.768</td>
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<td>0.034</td>
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<tr>
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<td>7.938</td>
<td>0.006</td>
<td>0.054</td>
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<td>8.033</td>
<td>0.005</td>
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<td>Abundance change (% dev. = 66.5)</td>
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<td>97.93</td>
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<td>0.006</td>
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Figure S1 Plot used to assign species to categories of low, intermediate, and high mobility. For the two data points on the left labeled “few recapture data“ radiotracking data indicated large home ranges. Besides, if there are few recapture data, smaller maximum distances can be expected.
Small-scale fragmentation effects on genetic diversity and population differentiation in three phyllostomid bats with different dispersal abilities

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submitted to Molecular Ecology

Abstract. - Habitat fragmentation is one of the greatest threats to biodiversity. Despite their importance for conservation, the genetic consequences of small-scale habitat fragmentation for bat populations are largely unknown. In this study, we linked genetic with ecological and demographic data to assess the effects of habitat fragmentation on three species of phyllostomid bats (Uroderma bilobatum, Carollia perspicillata, and Micronycteris microtis) that differ in their movement abilities and demographic response to fragmentation. We hypothesized that the effect of habitat fragmentation on levels of genetic population differentiation and diversity will be a function of the species’ mobility. We sequenced mtDNA from 281 bats living on 11 small islands in Gatún Lake, Panama, isolated from the mainland since ca. 90 years, and in adjacent, continuous forest on the mainland. Genetic erosion as a result of fragmentation was detectable in all three species: gene diversity and, except in U. bilobatum, also allelic richness were lower in island compared to mainland populations. Populations of all three species showed significant genetic differentiation (FST) and exhibited a pattern indicative of isolation by distance. Consistent with our prediction, population subdivision was lowest in the highly mobile U. bilobatum (FST = 0.01), moderate in the somewhat less vagile C. perspicillata (FST = 0.06) and highest in the rather sedentary M. microtis (FST = 0.18). Our results provide evidence for loss of genetic variation and increased population structuring in response to anthropogenic small-scale habitat fragmentation in Neotropical bat species. Moreover, our data demonstrate that genetic erosion can manifest itself well before any detectable onset of demographic decline.

Key words: Chiroptera, dispersal ability, fragmentation, isolation by distance, landbridge islands, population genetic structure
Introduction

The correlated processes of habitat loss and fragmentation constitute the greatest threat to biodiversity worldwide. In tropical regions habitat loss due to deforestation is particularly severe and conversion of native forests into human-modified landscapes continues unabated (Whitmore 1997; Wright 2005), resulting in widespread habitat fragmentation (Wade et al. 2003). Loss of suitable habitat and fragmentation make populations more vulnerable to environmental, genetic, and demographic threats because they reduce their size and confine the remaining subpopulations to isolated patches (Lande 1993). This results in a loss of genetic diversity and an increase in genetic differentiation among populations due to genetic drift and reduced gene flow (Lande & Barrowclough 1987; Frankham 1996; Dudash & Fenster 2000; Lindenmayer & Peakall 2000).

Like many other groups of animals, bats (Chiroptera) are at risk from habitat destruction and fragmentation (Racey & Entwistle 2003), especially in tropical lowland forests where they are particularly species-rich. Tropical bats are among the ecologically most diverse mammals present in local communities, filling pivotal roles as pollinators, seed dispersers, and predators (Kalko 1998; Patterson et al. 2003). Recent molecular studies have provided a wealth of new insights with respect to population structuring in migratory versus non-migratory species, social organization, and effects of geographical barriers on gene flow (reviewed in Burland & Worthington Wilmer 2001). At macro-geographical scales it has been shown that, with few exceptions (e.g. Miller-Butterworth et al. 2003), migratory bat species typically exhibit low levels of genetic differentiation, indicating high levels of gene flow among populations (Wilkinson & Fleming 1996; McCracken & Gassel 1997; Petit & Mayer 1999; Russell et al. 2005). In contrast, for non-migratory species the majority of studies have demonstrated considerable genetic population structuring (Worthington Wilmer et al. 1994; Burland et al. 1999; Rossiter et al. 2000; Maharadatunkamsi et al. 2000; Kerth et al. 2000). Pronounced population divergence and isolation by distance in non-migratory bat species may be the result of a variety of factors, including limited dispersal ability (Burland et al. 1999), social factors (Kerth et al. 2002), barriers to gene flow (Castella et al. 2000; Carstens et al. 2004), and historical events (Ditchfield 2000; Burland & Worthington Wilmer 2001).

Dispersal is a fundamental life-history trait affecting gene flow, and dispersal ability has been demonstrated to be negatively correlated with genetic population structure across a range of taxonomic groups (Waser & Strobeck 1998). At the genetic level, one could assume that bats may be relatively unaffected by local-scale habitat fragmentation because their
ability to fly may allow them to move relatively easily between habitat patches, both on a nightly basis while foraging and during natal dispersal. A recent study on the temperate Bechstein’s bat (Kerth & Petit 2005), however, showed that forest fragmentation can have a considerable effect on the genetic population structure of bats as it creates a sex-specific barrier to gene flow, impeding colonization of empty patches by females.

The relatively few studies assessing the genetic population structure of tropical bats mainly investigated patterns over large spatial scales (Wilkinson & Fleming 1996; Ditchfield 2000; Carstens et al. 2004; Russell et al. 2005) or examined the genetic structure of social groups, in particular levels of colony relatedness and differentiation (McCracken & Bradbury 1977; Wilkinson 1985; Dechmann et al. in press). We are not aware of any study assessing the effects of forest fragmentation on the genetic variation and population structure in tropical bats on a micro-geographic scale despite the profound impact habitat fragmentation is likely to have on the genetic structure and persistence of populations and the importance of forests for bats.

Mark-recapture data and radio-tracking studies indicate that Neotropical bat species differ widely in their mobility (Bernard & Fenton 2003; Albrecht et al. in press; Meyer et al. accepted) and, as a consequence, may exhibit different levels of genetic population structuring, as has recently been demonstrated for two species of nectar-feeding bats (Newton et al. 2003). Comparative analyses revealed that wing-morphology and hence movement capabilities are correlated with extinction risk in bats at a global scale (Jones et al. 2003; Safi & Kerth 2004). Broad-winged, non-migratory bat species are, on average, more endangered than narrow-winged species, probably because the latter can more easily reach isolated habitat patches (Safi & Kerth 2004), but this explanation awaits further testing and may not necessarily be of the same importance at a small-scale (Meyer et al. accepted).

It is widely recognized that both demographic and genetic factors may affect the vulnerability of species to fragmentation, calling for an integration of genetic and demographic approaches (Gaines et al. 1997; Lindenmayer & Peakall 2000; Srikwan & Woodruff 2000; Tallmon et al. 2002). Moreover, very few studies have explicitly examined the association between genetic structure and intrinsic ecological attributes such as mobility in bats (see Burland & Worthington Wilmer 2001).

In this study, we linked demographic with genetic data to explore the consequences of small-scale habitat fragmentation for three syntopic species of phyllostomid bats that differ in their movement abilities. The three species (Uroderma bilobatum, Carollia perspicillata, and Micronycteris microtis) were sampled as part of a comprehensive project investigating
Genetic effects of rainforest fragmentation on bats

Chapter 4

The genetic effects of rainforest fragmentation on Neotropical bats within a landscape consisting of small forested islands in Gatún Lake, an artificial reservoir in central Panama (Meyer et al. accepted; Meyer & Kalko submitted). The islands in Gatún Lake offer unique advantages for a study of the influence of fragmentation on the genetic population structure of bats. First, the exact date of their origin and their history in terms of land use are known. Second, the matrix around the islands (water) differs drastically from the forest habitat on the islands, enhancing the effective isolation of the habitat patches (Ricketts 2001). Comparatively resistant matrix types, such as water, are likely to result in particularly low levels of gene flow, leading to genetic erosion in isolated populations and increased levels of population subdivision. This scenario is reinforced by the fact that some bat species are known to be reluctant to fly over open bodies of water (Castella et al. 2000; Albrecht et al. in press).

We assessed the genetic diversity and differentiation within and among island and mainland populations of the three phyllostomid bats, using mitochondrial DNA. Our aim was to infer levels of population connectedness in a landscape that had been fragmented ca. 90 years ago as a result of human activities. Specifically, we tested the hypothesis that genetic differentiation within and between mainland and island populations is a function of geographical distance (isolation by distance) and that such an effect will be lower for the species with high vagility than for less mobile species. We also tested whether the size of an island and its distance to the nearest mainland affect genetic diversity of bat populations living on these islands.

The integrative approach taken in this study, linking demographic data with genetics, is particularly useful for the a priori determination of those species most vulnerable to fragmentation and hence for providing valuable background information pertinent to the development of management plans for bat conservation.

Material and methods

Study area

In 1914, the impoundment of the Chagres River in central Panama as part of the construction of the Panama Canal led to the creation of a large artificial reservoir, Gatún Lake. Lake formation isolated numerous former hilltops, resulting in over 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 5,400 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 Panama Canal corridor are classified as semi-deciduous, lowland tropical moist forest (Holdridge 1967). The study area experiences a strongly seasonal climate with a long rainy season punctuated by a severe dry season typically lasting from mid-December to April or May (Windsor 1990). Strong and persistent dry-season trade winds have a major impact on forest structure and dynamics particularly on exposed islands where forest is less diverse in tree species composition, typically shorter in stature and large trees are often scarce (Leigh et al. 1993).

![Map of the study area in the Panama Canal area in central Panama (inset). The locations of the 11 study islands in Gatún Lake and of the six mainland sites in continuous forest on the three peninsulas Bohio, Gigante, and Peña Blanca within the Barro Colorado Nature Monument (BCNM) are highlighted in black (■).](image)

**Fig. 1** Map of the study area in the Panama Canal area in central Panama (inset). The locations of the 11 study islands in Gatún Lake and of the six mainland sites in continuous forest on the three peninsulas Bohio, Gigante, and Peña Blanca within the Barro Colorado Nature Monument (BCNM) are highlighted in black (■).

**Study species**

Choice of the three focal species was mainly based on their abundance on the study islands in order to obtain appropriate sample sizes and on availability of quantitative data with regard to movement abilities. Based on these criteria, we selected *Uroderma bilobatum*, *Carollia perspicillata*, and *Micronycteris microtis* for our analysis. All three species are forest-dwelling bats adapted to forage in cluttered situations but otherwise differ from one
another in a range of ecological attributes including mobility, wing morphology, foraging strategy, body size, sensitivity to forest edges, as well as in their demographic response to fragmentation.

*Uroderma bilobatum* and *C. perspicillata* are comparable in size (17 and 18 g, respectively) and frugivores (Giannini & Kalko 2004), one eating mainly fruits of *Ficus* sp. (*U. bilobatum*) and the other mostly *Piper* sp. (*C. perspicillata*). *Micronycteris microtis* is a small (6 g) animalivorous bat, which gleans insects and small vertebrates from the vegetation (Kalka & Kalko 2006; Kalko, unpublished data). In a previous study (Meyer *et al.* accepted), *Uroderma bilobatum* and *M. microtis* differed from *C. perspicillata* in their demographic response to fragmentation. They were either uncommon (*U. bilobatum*) or rare (*M. microtis*) on the mainland but increased substantially in abundance on the islands, whereas *C. perspicillata* was a common understory bat regularly captured in mainland forest but that declined in abundance on the islands, pointing to rather high fragmentation sensitivity.

Several lines of evidence suggest that the three species differ profoundly in their movement ability and can be arranged along a continuum from high (*U. bilobatum*), through intermediate (*C. perspicillata*) to low mobility (*M. microtis*). Persistence in fragmented landscapes requires individuals to cross habitat boundaries and move between patches. Mark-recapture data indicate that both *U. bilobatum* and *C. perspicillata* regularly fly over open water whereby *U. bilobatum* clearly is the more mobile of the two species with mean recapture distances being about twice as large (Table 1). In contrast to *U. bilobatum*, *C. perspicillata* appears to be reluctant to cross water (Meyer *et al.* accepted), providing further evidence for greater mobility in *U. bilobatum*. For *M. microtis* no recapture data were available but radio-tracking data suggest that this species has very small area requirements (mean home ranges 4 ha, core areas 0.5 ha; Table 1) and is generally very reluctant to traverse open areas. A regular exchange of individuals between habitat patches is probably very rare (Albrecht *et al.* in press). Limited foraging ranges and low vagility in this species are further supported by eco-morphological evidence. Compared to the other two species *M. microtis* has much lower aspect ratio wings and wing loadings (Table 1). Bats characterized by high wing loading and aspect ratio wings are typically fast and efficient flyers while those with short, broad wings have higher maneuverability in cluttered habitats but increased costs for long-distance flights (Norberg & Rayner 1987).
Table 1 Data on movement capabilities of the three study species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Recaptures&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Home range size&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Wing morphology&lt;sup&gt;c&lt;/sup&gt;</th>
<th>ESLI&lt;sub&gt;c&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Marked</td>
<td>Recaptured</td>
<td>Same-site</td>
<td>Extra-site</td>
</tr>
<tr>
<td>U. bilobatum</td>
<td>2134</td>
<td>54</td>
<td>17</td>
<td>37</td>
</tr>
<tr>
<td>C. perspicillata</td>
<td>1654</td>
<td>52</td>
<td>22</td>
<td>30</td>
</tr>
<tr>
<td>M. microtis</td>
<td>4.0</td>
<td>2.0 (8)</td>
<td>5.73 ± 0.26 (5)</td>
<td>6.45 ± 1.40</td>
</tr>
</tbody>
</table>

<sup>a</sup> this study; Kalko et al. 1996; Kalko, unpublished data

<sup>b</sup> Minimum Convex Polygon (MCP in ha), van de Sand 2004; Albrecht et al. in press

<sup>c</sup> Meyer et al. accepted
Landscape connectivity, which ultimately defines relative levels of gene flow among habitat patches, results from the interaction between the spatial structure of the landscape and individual movement behavior (Keyghobadi et al. 2005). Vos et al. (2001) combined a measure of patch isolation with individual species mobility in an ecologically scaled landscape index (ESLI) of average patch connectivity, ESLIc. In the same landscape, species with good movement abilities generally exhibit larger connectivity values than relatively poor dispersers. ESLIc values previously calculated for the three study species (Meyer et al. accepted, Table 1) further confirm the pattern of differential movement abilities presented above.

Sampling procedure

Genetic samples of the three focal species were obtained from the same sites (Fig. 1) used for the demographic study (Meyer & Kalko submitted), 11 islands differing in size (2.5-50 ha) and degree of geographic isolation from the nearest mainland (0.02-3.4 km) as well as six mainland sites located on three peninsulas within the BCNM (Bohio, Gigante, and Peña Blanca). Since M. microtis was very rare on the mainland, we sampled this species also on Barro Colorado Island (BCI). Because of its rather large size (15.6 km²) we expected BCI to resemble the situation of mainland populations. For our analysis, we assumed that mainland populations were representative of pre-fragmentation populations and provide the source pool for the island populations. Bats were captured with mist nets (U. bilobatum, C. perspicillata) or, in the case of M. microtis, were additionally caught with hand nets inside diurnal roosts. Upon capture, individuals were identified, weighed, sexed, and marked prior to release (for details see Meyer & Kalko, submitted). Wing tissue samples were collected using 5 mm diameter biopsy punches (Stiefel Laboratories Inc., USA) following Worthington Wilmer & Barratt (1996). Biopsies were stored in 96% ethanol until DNA extraction. Tissue samples were obtained from a total of 281 bats; the number of individuals sampled per species and the sampling locations are given in Table 2.

DNA extraction, amplification, and sequencing

We extracted DNA from wing tissue samples using a salt-chloroform method (Müllenbach et al. 1989). Double stranded mitochondrial DNA from the control region (d-loop) was amplified from total cellular DNA using the polymerase chain reaction with one primer pair (primer E: CCT GAA GTA G GA ACC AGA TG, Wilkinson & Chapman 1991; and primer P*: CCC CAC CAT CAA CAC CCA AAG CTG A, Wilkinson et al. 1997). To
obtain sequences of about 340 bp in length, 20-50 ng of mtDNA was amplified using 1x Amplimix buffer (Microsynth; including 1.5 mM MgCl2, and 0.2 mM dNTP mix), 0.5 units taq polymerase (Pharmacia), and 0.24 μM of each primer. All ingredients are given in final concentrations. Total reaction volume was 15.0 μL. A PTC-200 thermocycler (MJ Research) was programmed to perform 31 cycles of 94°C/30 s, 55°C/45 s, 72°C/60 s after an initial 94°C/4 min step and followed by 72°C/20 min. We tested 5 μL of the PCR-product on a 1.4% agarose gel (1 h: 4.5V/cm) stained with ethidium bromide. PCR products were purified using the ExoSAP-IT USB Corporation purification kit (37°C/15 min and 80°C/20 min). As a previous study on another phyllostomid bat species had confirmed the reliability of sequencing this part of the d-loop (Dechmann et al. in press), we sequenced all samples in only one direction (P*) using the ABI prism Big Dye Terminator cycle sequencing ready reaction kit (Applied Biosystems). We ran the resulting PCR products on an ABI Prism 3730 48 capillary sequencer. Data were exported with Sequencing Analysis 3.4 (Applied Biosystems) and sequences were aligned and edited with Sequencher 4.1 (Gene Codes Corp).

**Data analysis**

We counted the number of sequence types (sequences differing by their number and/or pattern of variable sites) per sampled site to quantify the genetic diversity of local bat populations. Based on the sequence type frequencies, we estimated allelic richness and gene diversities, using FSTAT 2.9.3 (Goudet et al. 1996). We then compared allelic richness and gene diversities for each species between islands and mainland sites, using Mann-Whitney U-tests, to investigate whether island populations had lower genetic diversity than mainland populations. Subsequently, we analyzed whether patch size and isolation had an influence on the genetic diversity of the bat populations by correlating local gene diversities and allelic richness of island populations with island sizes and distances from the mainland.

The population structure analyses were based on Weir and Cockerham’s (1984) estimate of $F_{ST}$ and included all populations (mainland and islands) with more than one individual per site. We used a log-likelihood G-test to test for population differentiation, not assuming random mating. To evaluate whether sex-specific dispersal rates existed, we used a two-sided $F_{ST}$-test in all populations in which we caught more than one individual per sex. To test for isolation by distance and the effect of fragmentation, we performed partial Mantel-tests. We compared matrices of pairwise $F_{ST}$-values of populations with more than one individual to matrices coding for the geographical distances and the fragmentation between the different sampling sites (islands were coded as fragments, mainland as continuous habitat,
compare Kerth & Petit 2005). All calculations were performed using FSTAT 2.9.3 (Goudet et al. 1996). Significance levels were estimated through 10,000 permutations. We give the $P$-value for each test and, whenever available, the proportion of variance explained by the model.

To depict genetic distances between sequences we calculated mean pairwise differences and designed minimum spanning trees for each of our three study species, using Arlequin 2.0 (Schneider et al. 2000). Deletion and transition weights were set to 1 and the epsilon value was $10^{-7}$. We allowed for 5% of missing data and set the number of bootstrap replicates to 10,000.

**Results**

*Uroderma bilobatum*

Among the 151 bats sequenced for 337 bp we detected 35 variable sites, resulting in a total of 43 sequence types (Fig. 2a). The mean number of pairwise distances between sequence types was with $4.5 \pm 2.3$ (range: 1-11) lower than in the other two species. On average, each type was present at 2.5 locations. Sequence types were not equally distributed among the sampled sites. The same sequence type was found in a maximum of 11 sites and 24 of the 43 types were found only in a single site. Gene diversity (GD) but not allelic richness (AR) was significantly lower in the 10 island populations than in the five mainland populations (U-test, GD: $U = 3.5$, $P < 0.01$; AR: $U = 20.5$, $P = 0.58$; Table 2). Neither the size of an island nor its distance from the mainland had a significant effect on the observed genetic diversity found in the 10 island populations (Spearman rank correlation, island size: GD: $r_s = 0.06$, $P = 0.88$; AR: $r_s = -0.06$, $P = 0.88$; island isolation: GD: $r_s = -0.35$, $P = 0.32$; AR: $r_s = -0.45$, $P = 0.19$; Table 2). The total population ($N = 15$ sites) showed a low $F_{ST}$-value (0.01) but was significantly differentiated (G-test, $P < 0.05$). We also observed a significant effect of isolation by distance, fragmentation, however, had no significant additional effect (partial Mantel-test; distance: $r_m = 0.25$, $P < 0.01$; fragmentation: $r_m = 0.12$, $P = 0.22$). Males ($N = 73$) and females ($N = 63$) showed similar $F_{ST}$-values (0.02 and 0.00; two-sided $F_{ST}$-test: $N = 10$ populations, $P = 0.30$) and the populations of neither of the sexes were significantly differentiated (males: $P = 0.09$; females: $P = 0.65$). Our data suggest that *U. bilobatum* is a good disperser and that movement patterns are not sex-biased. Distance between sites, however, affects population structure already over the rather small spatial scale of our study.
**Carollia perspicillata**

We detected 51 variable sites among the 81 bats sequenced for 337 bp, resulting in a total of 41 sequence types (Fig. 2b). The mean number of pairwise distances between sequence types (11.1 ± 5.4, range: 1-26) was higher than in *U. bilobatum*. The different sequence types were rather equally distributed among the sampled sites. On average, each type was present in 1.6 locations. The same sequence type was found in a maximum of 4 sites and 26 of the 41 sequence types were found only in a single site. Both, gene diversity (GD) and allelic richness (AR) were significantly lower in the six island populations than in the six mainland populations (U-test, GD: $U = 4.5$, $P < 0.03$; AR: $U = 5.5$, $P < 0.05$; Table 2). The size of an island but not its distance from the mainland had a significant effect on the observed gene diversity in the six island populations while no significant effect on allelic richness was observed (island size: GD: $r_s = -0.81$, $P = 0.05$; AR: $r_s = 0.71$, $P = 0.11$; island isolation: GD: $r_s = -0.31$, $P = 0.54$; AR: $r_s = -0.55$, $P = 0.26$; Table 2). The total population ($N = 12$ sites) showed a moderate $F_{ST}$-value (0.06) and was significantly differentiated (G-test, $P < 0.02$). We also observed a highly significant effect of isolation by distance and fragmentation (partial Mantel-test; distance: $r_m = 0.45$, $P < 0.0001$; fragmentation: $r_m = 0.31$, $P < 0.0001$). Males ($N = 36$) and females ($N = 35$) differed somewhat in their $F_{ST}$-values (0.05 versus 0.10) but this difference was not significant (two-sided $F_{ST}$-test: $N = 9$ populations, $P = 0.40$). For both sexes the population was significantly differentiated (males: $P < 0.05$; females: $P < 0.005$). Our data suggest that *C. perspicillata* is a species with moderate to poor mobility, movement patterns are not influenced by gender, and both, distance and fragmentation, affect population structure.

**Micronycteris microtis**

Forty-eight variable sites were detected among the 344 bp sequenced in 49 bats, resulting in a total of 25 sequence types (Fig. 2c). The mean number of pairwise distances between sequence types was with 10.1 ± 4.8 (range: 1-16) larger than in *U. bilobatum* but similar to the one observed for *C. perspicillata*. The different sequence types were equally distributed among the sampled sites. On average, each type was present in only 1.2 locations and the same sequence type was found in a maximum of 2 sites. Nineteen of the 25 sequence types were found only in a single site. Both, gene diversity (GD) and allelic richness (AR) were lower in the 5 island populations than in the two mainland populations (including BCI; Table 2) but sample sizes were too low for testing.
**Table 2** Genetic data of the three study species of phyllostomid bats sampled on 11 small islands, one large island (BCI) and at six mainland sites. Sample size (n bats), local gene diversity (GD), and local allelic richness (AR) are given. For islands, size and distance to the mainland is presented (see text for further details).

<table>
<thead>
<tr>
<th>Site</th>
<th>Island</th>
<th>distance from mainland (m)</th>
<th>U. bilobatum</th>
<th>C. perspicillata</th>
<th>M. microtis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Islands</td>
<td>size (ha)</td>
<td>n bats</td>
<td>GD</td>
<td>AR</td>
</tr>
<tr>
<td>Cacao</td>
<td></td>
<td>12.8</td>
<td>12</td>
<td>0.88</td>
<td>3.13</td>
</tr>
<tr>
<td>Chicha</td>
<td></td>
<td>2.8</td>
<td>10</td>
<td>0.93</td>
<td>3.34</td>
</tr>
<tr>
<td>Guacha</td>
<td></td>
<td>7.2</td>
<td>0</td>
<td>0</td>
<td>0.87</td>
</tr>
<tr>
<td>Guanabano</td>
<td></td>
<td>16.3</td>
<td>10</td>
<td>0.93</td>
<td>3.35</td>
</tr>
<tr>
<td>Guava</td>
<td></td>
<td>2.5</td>
<td>17</td>
<td>0.88</td>
<td>3.24</td>
</tr>
<tr>
<td>Leon</td>
<td></td>
<td>50</td>
<td>16</td>
<td>0.97</td>
<td>3.63</td>
</tr>
<tr>
<td>Mona Grita</td>
<td></td>
<td>5.9</td>
<td>10</td>
<td>0.96</td>
<td>3.46</td>
</tr>
<tr>
<td>Pato Horqueta</td>
<td></td>
<td>11.4</td>
<td>14</td>
<td>0.88</td>
<td>3.21</td>
</tr>
<tr>
<td>Piña</td>
<td>a</td>
<td>4.4</td>
<td>13</td>
<td>0.92</td>
<td>3.38</td>
</tr>
<tr>
<td>Tres Almendras</td>
<td></td>
<td>3.4</td>
<td>11</td>
<td>0.93</td>
<td>3.36</td>
</tr>
<tr>
<td>Trinidad</td>
<td></td>
<td>17.3</td>
<td>4</td>
<td>0.50</td>
<td>1.79</td>
</tr>
<tr>
<td>BCI</td>
<td></td>
<td>1560</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**Mainland**

<table>
<thead>
<tr>
<th>Site</th>
<th>n bats</th>
<th>GD</th>
<th>AR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bohio Edge</td>
<td>8</td>
<td>0.96</td>
<td>3.43</td>
</tr>
<tr>
<td>Bohio Interior</td>
<td>5</td>
<td>1.00</td>
<td>3.14</td>
</tr>
<tr>
<td>Gigante Edge</td>
<td>16</td>
<td>0.95</td>
<td>3.54</td>
</tr>
<tr>
<td>Gigante Interior</td>
<td>1</td>
<td>1.00</td>
<td>3.14</td>
</tr>
<tr>
<td>Peña Blanca Edge</td>
<td>3</td>
<td>1.00</td>
<td>2.80</td>
</tr>
<tr>
<td>Peña Blanca Interior</td>
<td>2</td>
<td>1.00</td>
<td>2.00</td>
</tr>
</tbody>
</table>

*a island #8 in Adler & Seamon (1991)*
Fig. 2 Minimum spanning tree for the three phyllostomid bat species (*Uroderma bilobatum* Fig. 2a, *Carollia perspicillata* Fig. 2b, and *Micronycteris microtis* Fig. 2c). The numbers in the circles depict different haplotypes. The distances are indicated by the number of black dots representing missing haplotypes. The radius of the circles depicts the absolute frequencies of the haplotypes in the study populations.
Neither the size of an island nor its distance from the mainland had a significant effect on the gene diversity and allelic richness in the 5 island populations (island size: GD: $r_s = -0.10$, $P = 0.87$; AR: $r_s = -0.30$, $P = 0.62$; island isolation: GD: $r_s = 0.00$, $P = 1.00$; AR: $r_s = -0.30$, $P = 0.62$). The overall population ($N = 7$ sites) showed a high $F_{ST}$-value (0.18) and was highly significantly differentiated (G-test, $P \leq 0.0001$). The effect of isolation by distance was almost significant (Mantel-test: $r_m = 0.41$, $P = 0.06$). We could not test for fragmentation because *M. microtis* could only be caught at very few mainland sites. Males ($N = 17$) and females ($N = 13$) had similar $F_{ST}$-values (0.23 versus 0.15; two-sided $F_{ST}$-test: $N = 3$ populations, $P = 0.76$). Moreover, for both sexes the population was significantly differentiated (males: $P < 0.001$; females: $P < 0.03$). Overall our data suggest that, of the three study species, *M. microtis* is the least vagile species, with strongly differentiated populations.

**Discussion**

Our study elucidated the degree of genetic erosion and population subdivision in three species of Neotropical bats following anthropogenic local-scale habitat fragmentation. Few, if any, other studies appear to have investigated genetic patterns in tropical bats at a similarly small spatial scale (*ca.* 12 x 12 km). All three species showed loss of genetic diversity on islands, as predicted as a consequence of forest fragmentation. In the less mobile species, *C. perspicillata* and *M. microtis*, both gene diversity and allelic richness declined as a result of fragmentation. Even *U. bilobatum*, assumed to be a good disperser not reluctant to cross open water, was characterized by reduced gene diversity, albeit not allelic richness, on islands compared to continuous forest. This finding is particularly interesting and rather unexpected as *U. bilobatum* was much more abundant on the islands than in mainland forest. Likewise, *M. microtis* was captured more frequently on the islands than in continuous forest (Meyer *et al.* accepted). Thus, it is remarkable that loss of genetic variation was detectable in these two species in spite of their positive demographic response to fragmentation. Srikwan & Woodruff (2000), studying genetic erosion in small mammal populations on land-bridge islands in Thailand, similarly reported genetic erosion for a species which was favored by fragmentation and showed no signs of demographic decline. Our findings highlight the importance of jointly considering genetic and demographic data to unravel species’ responses to fragmentation and add to the growing number of studies, which advocate such an approach (Lindenmayer & Peakall 2000; Srikwan & Woodruff 2000; Tallmon *et al.* 2002).
The loss of genetic variation observed in our case probably occurred mainly due to genetic drift and due to an increase in population subdivision. The formation of genetic differentiation is regarded as an important, though sometimes neglected, early indicator of fragmentation effects, often likely to precede detectable loss of genetic diversity (Lindenmayer & Peakall 2000). Our data show significant levels of genetic subdivision in a landscape that has only been fragmented less than 100 years ago, pointing towards strong bottleneck effects.

Populations of the canopy frugivore *U. bilobatum* were overall only weakly differentiated ($F_{ST} = 0.01$) while genetic subdivision was moderately higher in the understory frugivore *C. perspicillata* ($F_{ST} = 0.06$). These relatively low levels of genetic differentiation suggest that there is, at least occasionally, exchange of individuals of *U. bilobatum* and, to a lesser extent, *C. perspicillata*, between islands. This interpretation of ongoing dispersal is further supported by the significant pattern of isolation by distance observed in these two species but only an additional effect of fragmentation in *C. perspicillata*. While significant population differentiation and genetic isolation by distance has been documented for several tropical bat species at larger geographic scales (Maharatatunkamsi *et al.* 2000; Newton *et al.* 2003), to our knowledge, only two studies on the temperate zone bats, *Plecotus auritus* (Burland *et al.* 1999) and *Myotis bechsteinii* (Kerth & Petit 2005), have described isolation by distance and significant population differentiation at a micro-geographical scale.

In contrast to our two frugivorous study species, we detected marked genetic differentiation across populations of *M. microtis* ($F_{ST} = 0.18$) pointing to very limited contemporary gene flow among island populations. This notion is in accordance with telemetry data indicating site faithfulness during foraging behavior and very low area requirements in this species (van de Sand 2004; Albrecht *et al.* in press). The lack of a significant effect of isolation by distance in *M. microtis* may be explained by the fact that, irrespective of the degree of isolation, inter-island movements are very rare and may be limited to situations when individuals disperse from their natal patch. For comparison, populations of *Myotis bechsteinii* that lived in a fragmented landscape in Germany showed a stronger effect of forest fragmentation than of isolation by distance (Kerth & Petit 2005). Finally, the absence of a significant effect of isolation by distance could also be a consequence of the rather small number of samples obtained for *M. microtis* due to its very low abundance at mainland sites.

We are not aware of any study on tropical bats at a similar spatial scale which would allow for comparisons with the results of our study. For most animal groups such as birds
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(Bates 2002; Brown et al. 2004) and small non-volant mammals (Gaines et al. 1997), studies of habitat fragmentation have mainly focused on geographic areas much larger than the scale of our study, typically reporting significant levels of population subdivision. However, some recent studies on small mammals (Lindenmayer & Peakall 2000; Mossman & Waser 2001), including temperate zone bats (Kerth & Petit 2005), discovered significant inter-population differentiation at a scale comparable to our study.

Although populations of all three species exhibited significant mtDNA sequence divergence, estimates of genetic differentiation based on $F_{ST}$ were consistent with our prediction and matched the relative movement ability of the respective species estimated on the basis of mark-recapture, radio-tracking, and wing morphological data (Table 1). The idea that population structure in bats may be associated with species’ intrinsic characteristics such as mobility, reflected in wing morphology, was first shown for the non-migratory long-eared bat, *Plecotus auritus* (Burland et al. 1999; Entwistle et al. 2000). Since then it also been demonstrated for the migratory species *Leptonycteris curasoae* (Newton et al. 2003) and *Miniopterus schreibersii* (Miller-Butterworth et al. 2003). Our results corroborate these findings for non-migratory Neotropical bats and suggest that, as advocated earlier by Burland & Worthington Wilmer (2001), explicitly linking intrinsic attributes to population structure may generally serve as a useful predictive framework for population genetic analyses. Its further application to studies of local-scale habitat fragmentation may provide particularly fruitful avenues for future research.

The explanation of differential movement abilities for the observed levels of genetic differentiation could be confounded by variation in the degree of female philopatry among our focal species. Male-biased dispersal is considered typical for mammals (Greenwood 1980) including many bats (e.g. Kerth et al. 2000; 2002; but see Miller-Butterworth et al. 2003; Dechmann et al. in press). Our genetic data however suggest that dispersal is at least not strongly sex-biased in either of our study species. This finding is supported by capture-mark-recapture data (Meyer et al. accepted) but it is in contrast to the strong female philopatry observed in many temperate bat species (e.g. Burland et al. 1999; Castella et al. 2000; Kerth et al. 2000; Rossiter et al. 2000).

**Conclusions**

Our analyses revealed several interesting findings. First, loss of genetic variation can manifest itself even after fairly short periods of time following fragmentation. Second, in accordance with previous findings, our results suggest that a bat species’ mobility, which is
typically linked to wing morphology, can serve as a good predictor of population genetic
differentiation. Third, even species, which in terms of their demographic response were
seemingly unaffected by fragmentation, showed signs of genetic erosion and population
divergence. Notwithstanding the insights that demographic studies alone may reveal about
species’ responses to habitat fragmentation, this underscores the fact that effective
monitoring of population trends in conjunction with detailed genetic analyses are crucial if
conservation efforts and management strategies are to be successful. Further comparative
studies across a range of bat species focusing on local geographic scales are undoubtedly
needed to broaden our knowledge as to the genetic consequences of habitat fragmentation on
bat populations and are a prerequisite for the formulation of fruitful broad-scale conservation
strategies for bats.

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