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RESEARCH ARTICLE

The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter?

Annia Rodríguez-San Pedro · Javier A. Simonetti

Abstract

Context Disentangling the relative effects of forest loss versus fragmentation on species distribution and abundance is crucial for adopting efficient biodiversity conservation actions, which could change with the nature of the landscape matrix.

Objectives We tested the moderating effect of landscape matrix on insectivorous bats response to forest loss and fragmentation.

Methods We conducted acoustic surveys at forest patches surrounded by either an agricultural-dominated matrix or a pine-dominated matrix. We related bat activity to forest amount and the number of forest patches at multiple spatial scales, and compared their effects between landscape matrices.

Results Bat activity was associated with both predictors, however their effects varied with the matrix type. In agricultural landscapes, as the amount of forest increased, the activity of *Histiotus montanus*, *Lasiurus cinereus* and *Tadarida brasiliensis* increased, while activity of *Myotis chiloensis* decreased. Similarly, as fragmentation increased, the activity of *Lasiurus varius* and *M. chiloensis* increased, while activity of *H. montanus* decreased. In production-forest landscapes, only *H. montanus* decreased its activity with increasing forest amount. In contrast, activity of *L. cinereus*, *M. chiloensis* and *T. brasiliensis* increased with increasing fragmentation. Forest amount was a stronger predictor for agricultural landscapes than for production-forest landscapes, suggesting that low contrast matrices can mitigate the effects of forest loss.

Conclusions Fragmented landscapes with native forest patches surrounded by a low contrast matrix may support a higher activity of insectivorous bats. Management efforts in fragmented landscapes should aim to decrease the patch-matrix contrast, which will mitigate the effects of forest loss on bats.

Keywords Habitat fragmentation · Habitat loss · Landscape matrix · Insectivorous bats · Scale-dependent responses

A. Rodríguez-San Pedro (✉) · J. A. Simonetti
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile
e-mail: ar.sanpedro@gmail.com; sanpedro@ug.uchile.cl

Introduction

Landscape change is one of the most important processes causing elevated rates of species extinction and loss of biological diversity (Hooper et al. 2012). This process involves both habitat loss and fragmentation, two highly correlated processes that have different effects on biodiversity (Haila 2002; Fahrig 2003). When the effects of habitat loss and fragmentation are

addressed independently, habitat loss has a greater impact on biodiversity compared to the effects of fragmentation by reducing species richness of many taxa including insects, amphibians, birds, and small mammals (Trzcinski et al. 1999; Nupp and Swihart 2000; Cushman 2006; Ritchie et al. 2009; Cerezo et al. 2010). The effects of fragmentation, meanwhile, are usually much weaker and abundance and species richness can either increase or decrease in fragmented landscapes (Fahrig 2003).

The direction and magnitude of the effects of habitat loss and fragmentation on biodiversity might also be mitigated by the structure of the landscape matrix (Debinski 2006; Kupfer et al. 2006; Prevedello and Vieira 2009). The matrix may compensate for habitat loss providing additional resources for many species or otherwise act as an ecological trap (With 2002; Vergara and Simonetti 2003; Ewers and Didham 2006; Harvey et al. 2006). In addition, matrix structure can influence dispersal of fragment-dwelling biota across the landscape (Ricketts 2001; Baum et al. 2004). Landscapes with structural similarity between matrix and patches of original habitat would allow greater faunal movement, while a contrasting structural matrix would impede movement (Gascon et al. 1999). As a type of forested habitat, plantation forests may make up a higher quality matrix for embedded native forest remnants compared with an agricultural matrix, as they might provide suitable habitats for many forest-dependent species (Lindenmayer and Hobbs 2004; Fischer et al. 2006). In addition, plantations may increase species richness and abundance by improving connectivity between forest remnants (Gascon et al. 1999; Lindenmayer et al. 1999; Ferreras 2001; Renjifo 2001), enhancing survival in human-modified landscapes (Gascon et al. 1999; Kupfer et al. 2006; Rodríguez-San Pedro and Simonetti 2013a). Therefore, the effects of habitat loss and fragmentation in agricultural dominated landscapes might differ from those in production-forest landscapes.

Forests are a key habitat for bats throughout the world. Many species depend on forest attributes such as foliage and cavities of mature trees for roosting, that are reduced in fragmented forest (Lacki et al. 2007). In addition to roosting sites, bats also require suitable sites for foraging with some species forage within forested habitats, in forest gaps or along edges, roads or internal trails in forests (Crome and Richards 1988; Morris et al. 2010; Rodríguez-San Pedro and Simonetti 2013a). In

Chile, most bat species are associated with forested habitats (Galaz and Yáñez 2006). *Lasiurus cinereus* and *Lasiurus varius* roost exclusively in the foliage of trees, while *Histiotus macrotus*, *Histiotus montanus* and *Myotis chiloensis* may utilize forests occasionally for roosting (Galaz and Yáñez 2006). Thus, we would expect a greater bat activity in landscapes with higher forests cover compared to non-forest landscapes. Likewise, landscape configurations with high spatial complementarity between roosting and foraging sites should support a higher bat activity.

Recent work by Ethier and Fahrig (2011) provided the first evidence of a positive effect of forest fragmentation, independent of forest amount, on bat activity, highlighting the importance of both processes when assessing bat response to habitat modifications. However, this study was conducted in fragmented agricultural landscapes, without considering whether their results might be applied in landscapes with low patch-matrix contrast. Rigorously comparing the effects of habitat loss and fragmentation for patches surrounded by a low contrast matrix compared to patches with high contrast matrix will provide important guidance in the context of landscape management for the conservation of biodiversity.

In this paper, we examined how the relative influence of forest amount and fragmentation on bat activity vary among landscapes dominated by agricultural lands (high-contrast system) and forestry plantations-dominated landscapes (low-contrast system). If low contrast matrices mitigate the effects of forest loss and fragmentation on bat activity compared to high contrast matrices then, bat activity would be significantly associated with forest loss and fragmentation in agricultural-dominated landscapes but not in forest-dominated landscapes. To evaluate the relative effects of forest amount and fragmentation on bat activity, we used the same methodology followed by Ethier and Fahrig (2011) in order to make our study comparable.

Methods

Study area and site selection

The study was conducted in rural areas of central Chile (Fig. 1). During the last decades, the temperate forest of central Chile has been deforested and fragmented

Fig. 1 Map of south-central Chile showing the location of the 36 surveyed focal patches
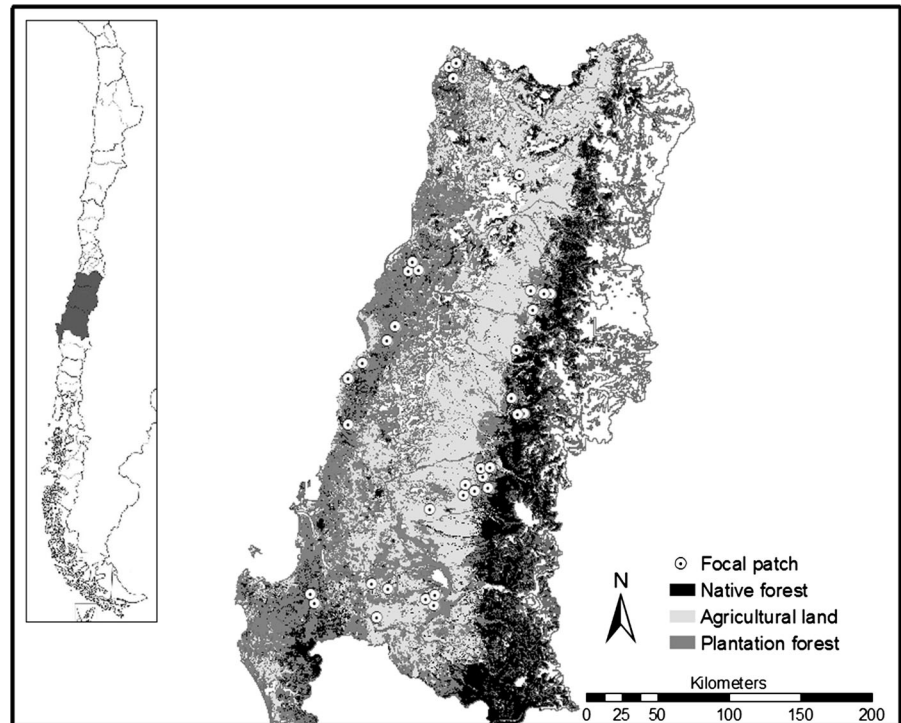
due to agriculture and forestry plantations (Echeverria et al. 2006). Currently, the landscape consists of native forest patches embedded in a matrix of commercial pine (*Pinus radiata*) plantations, pastures and agricultural lands (Echeverria et al. 2006). The estimated cover of native forests decreased from 119,994 ha in 1975 to 39,002 ha in 2000. In 2000, 69 % of the total area of native forest occurred in patches of less than 100 ha and only 3 % had a size greater than 1000 ha.

We selected 36 non-overlapping native forest patches (focal patches) that ranged in size from 4.0 to 25.0 ha, focused on landscapes where the dominant non-forest land cover was either exotic pine plantations (18 focal patches) or agriculture (18 focal patches) (Fig. 1). Landscapes were selected to represent a large variation in forest amount and forest fragmentation and to minimize, as far as possible, the expected correlation between these two variables. To minimize the correlation between forest amount and fragmentation, landscapes were chosen such that the proportion of native forest and the number of forest patches represents a gradient containing not only the common combinations of high forest amount with low fragmentation and low forest amount with high fragmentation, but also the poorly represented combinations of low forest amount

with low fragmentation and high forest amount with high fragmentation (Ethier and Fahrig 2011). Unfortunately, this was not possible in our agricultural-dominated landscapes, where forest amount and fragmentation were highly correlated at some spatial scales (see Supporting Information).

We used ArcGIS 9.3 (ESRI 2006) to calculate the proportion of native forest in the landscape within each buffer distance, as a measure of forest loss, and the number of forest patches as a measure of fragmentation. To account for the possibility that different bat species respond to the landscape at different scales, we measured forest loss and fragmentation using several buffer sizes at radii of 1.0, 1.5, 2.0, 2.5, 3.0, 4.0 and 5.0 km from the center of each focal patch. Unfortunately, little is known about the home range size of Chilean bats. We chose these seven landscapes buffer distances based on distances travelled between roosting and foraging sites by similar small and medium-sized aerial insectivorous bats elsewhere (Elmore et al. 2005; Sparks et al. 2005; Walters et al. 2007; Henderson and Broders 2008; Kniowski and Gehrt 2014). Landscapes buffer distances greater than a 5-km radius were not examined because those areas would overlap substantially,

producing spatial autocorrelation. Moreover, the selected focal scales facilitate comparison with previous research on scale-dependent associations of bats with forest amount and fragmentation (Ethier and Fahrig 2011). Forest amount ranged from 1.1 to 60.2 % in agricultural landscapes and from 6.5 to 66.8 % in forested landscapes, meanwhile the number of forest patches ranged from 3 to 15 in agricultural landscapes and from 4 to 15 in forestry landscapes. The correlation (Pearson's r) between forest amount and fragmentation ranged from 0.16 to 0.81 in agricultural landscapes and from 0.025 to 0.35 in forestry landscapes (see supporting information). All landscape variables were based on land cover data from the Catastro Nacional de Bosque Nativo from Corporación Nacional Forestal, Chile (http://sit.conaf.cl/).

Bat surveys

We conducted bat surveys for each of the 36 focal patches for one night each. At each focal patch, surveys began at dusk and lasted for 4 h to coincide with peak foraging periods of aerial insectivorous bats (Kuenzi and Morrison 2003). Surveys were restricted to the austral summer season (from February to mid-March 2012 and January 2013), the peak season in bat activity in temperate zones. Bats were surveyed using two ultrasound bat-detectors model D240X (Pettersson Elektronik AB, Uppsala, Sweden) per focal patch coupled to a digital recorder MicroTrack II (M-Audio) and operated in time-expanded modes. Time-expanded mode records the full-spectrum echolocation calls with a high-resolution sonogram of each bat vocalization. These full-spectrum echolocation calls were used to classify bat activity to species.

We placed the first bat detector at the edge of each focal patch and the second detector 50 m into the focal patch within a partial clearing with the microphone pointing in the same direction as the first one. Calls were displayed and analyzed using BatSound 2.1 (Pettersson Elektronik AB, Uppsala, Sweden). Bat activity was quantified by counting the number of bat passes per night at each point within each local patch and used as a measure of bat relative abundance (Walsh et al. 2004). We defined a "bat pass" as a succession of more than two echolocation pulses emitted by a bat flying by the detector (Law et al. 1999). Since most passes were recorded along forest edges (74.7 and 66.4 % in agricultural and forestry

landscape, respectively), we combined the number of bat passes recorded using both bat detectors (forest edge and interior) to quantify bat activity per site. We used bat activity as a comparative index amongst sites as bat detectors do not allow for individuals to be differentiated and thus an abundance estimate to be determined. Surveys were not conducted on nights with rain or fog to avoid reduced bat activity (Pye 1971; Erickson and West 2002).

For each focal patch, we also measured local habitat variables such as patch size, temperature, wind speed and mean density of trees across six 10×10 m quadrats (Table 1), which has been shown to influence insectivorous bats use of forested areas (Brigham and Grindal 1997; Sleep and Brigham 2003). To control for possible effects of prey availability on bat activity, we used two light traps per site placed at least 50 m from the nearest bat detector to capture nocturnal flying insects simultaneously with the bat surveys. We used the dry weight (biomass) of insects as a measure of prey availability at each site.

Bat species identification

Passes of free-flying bats were classified to species using quadratic discriminant function analysis (DFA). This analysis was used because several variables departed from normal distribution and the within-group variance–covariance matrices were not homogeneous (Quinn and Keough 2002). Classification functions were computed using a library of validated reference calls which consisted of 264 full-spectrum recordings from hand-released bats (*H. montanus*, *L. varius*, *M. chiloensis* and *T. brasiliensis*) at the location of study (Rodríguez-San Pedro and Simonetti 2013b). Variables used in the analysis were call duration, final frequency, slope frequency modulation, peak frequency, minimal and maximal frequency. If there was uncertainty or inconsistency in the classification, that recording was considered unidentifiable and labeled as "unknown".

Statistical analysis

Data were first checked for normality using Shapiro–Wilk test. Only when normality was not achieved even after transformation, non-parametric tests were used. Because our agricultural and forestry landscapes were

Table 1 Results of generalized linear models (GLM) examining the effects of patch local variables (insect biomass, tree density, temperature and wind speed) on bat activity per species

Species	Patch local variables	β	P
Agricultural landscapes			
Histiotus montanus	–	–	–
Lasiurus cinereus	–	–	–
Lasiurus varius	Tree density	0.17	0.005
	Wind speed	−0.18	<0.001
Myotis chiloensis	Wind speed	−0.24	0.048
Tadarida brasiliensis	Tree density	−0.14	0.015
Forestry landscapes			
Histiotus montanus	Temperature	0.23	0.009
	Wind speed	−0.17	0.019
Lasiurus cinereus	Insect biomass	0.21	0.003
	Temperature	0.54	<0.001
Lasiurus varius	–	–	–
Myotis chiloensis	Wind speed	−0.07	0.028
Tadarida brasiliensis	Insect biomass	0.17	0.006

Missing data indicates no significant effects of local variables on bat activity. Degrees of freedom are 1 for all models

distributed in three different regions which differed in terms of their topography (Andes, Intermediate depression and Coastal range), we conducted a preliminary analysis using a non-parametric statistic, Kruskal–Wallis test, to explore for differences in bat activity for each species among regions. No regional difference on bat activity was detected (H from 0.307 to 5.282, $P > 0.05$).

We fitted generalized linear models (GLMs) separately for each matrix type (agricultural and forestry) to assess the relationship between bat activity for each species and the landscape structure (forest amount and the number of forest patches) at each spatial scale. We used a negative binomial with log-link function across all GLM models, since count data for bat activity were not normally distributed and showed evidence of over-dispersion (Quinn and Keough 2002). We built GLM models by first determining local variables (patch size, temperature, wind speed, tree density and insect biomass) that were associated with bat activity for each species. To identify which local variables significantly affected bat activity, we ran separate regressions using the number of bat passes per species at a site (bat activity) as the response variable and included as predictor each local variables. Variables with a significant effect on bat activity ($P < 0.05$) were retained and included in the landscape models (Table 1).

To examine the relative effects of forest amount and fragmentation on bat activity we included in each

landscape model the amount of native forest and the number of forest patches as our landscape predictors of interest as well as any local variable that was significant in previous separate regressions analyses. We estimated the relative effect of forest loss and fragmentation by comparing the partial regression coefficient, as well as the number of species that responded significantly to forest amount and fragmentation. We chose standardized partial regression coefficient because this is a robust method for estimating the relative importance of forest amount and fragmentation, even when both predictors are highly correlated (Smith et al. 2009), which was our case at some spatial scales (see supporting information). The inclusion of correlated predictors in a regression model increases type II errors by raising the standard error of partial coefficients (Neter et al. 1990). However, removing highly correlated predictors can lead to biased coefficient estimates and poor model fit (Smith et al. 2009). We included correlated predictors, forest amount and number of forest patches, because they represent distinct ecological mechanism that potentially influence bat activity and removing one of them would lead to biased estimates of the relative importance for the remaining predictors (Smith et al. 2009). Before analysis, we standardized the scales of all predictors to a mean of zero and a standard deviation of one, so that equal coefficients implied equal effect-strength and to simplify expected variance partitions for each predictor (Quinn and Keough 2002). In all GLMs, we assessed

statistical significance using Wald χ^2 tests. We checked for autocorrelation of the model residuals using the Moran's I.

We tested our hypothesis about the effects of landscape matrix on the relationship between bat activity and forest amount or fragmentation through an analysis of covariance (ANCOVA) using GLMs with negative binomial and log-link function, because assumptions of normality and homogeneity of variance were not met (Quinn and Keough 2002). We explored if the effect of forest amount or fragmentation on bat activity was similar between matrices comparing the homogeneity of slopes by introducing the interaction term (matrix type × forest amount, and matrix type × number of forest patches) in each GLM model (Quinn and Keough 2002). Significantly different slopes ($P \leq 0.05$) indicate that the relationship between bat activity and forest amount or fragmentation differs between matrix types.

Results

Across the 36 nights and 144 survey hours, we recorded 2134 echolocation passes, 1950 of which (91 %) could be identified and attributed to five of the six species expected to occur in the study area: *H. montanus* (55 passes), *L. varius* (470 passes), *M. chiloensis* (463 passes), *L. cinereus* (145 passes) and *T. brasiliensis* (817 passes). Passes of *L. cinereus* were identified by comparing call parameters with reference calls reported for this species in other regions (O'Farrell et al. 2000). Nine percent of the echolocation passes could not be analyzed due to the low intensity of the recorded calls and were classified as "unknown". These passes, therefore, were not included in the analyses at a species level but were considered for overall activity analysis. The most commonly encountered bat species across all landscapes were *L. varius* and *T. brasiliensis* (present at 35/36 sites) followed by *M. chiloensis* (28/36), *L. cinereus* (21/36) and *H. montanus* (16/36). Bat activity residuals were not significantly spatially autocorrelated for any of the species (Moran's I from −0.045 to 0.009, $P > 0.05$).

In agricultural landscapes, four species responded significantly to forest amount while three species responded significantly to forest fragmentation (Fig. 2). The relationship between forest amount and

bat activity was significantly positive in *H. montanus* at all spatial scales, *L. cinereus* and *T. brasiliensis* at intermediate (1.5–2.5 km) and large scales (4.0–5.0 km) and negative in *M. chiloensis* (at 4.0 km) (Fig. 2). Activity of *L. varius* was not strongly associated with forest amount (Fig. 2). Species responses to forest fragmentation also varied in both direction and magnitude (Fig. 2). The activity of *L. varius* and *M. chiloensis* significantly increased with increasing fragmentation (at intermediate and large scales, respectively), while activity levels significantly decreased for *H. montanus* both at small (1.0–1.5 km) and larger scales (2.5–4.0 km) (Fig. 2). Activity of *L. cinereus* and *T. brasiliensis* were not strongly associated with forest fragmentation (Fig. 2).

In forest-dominated landscapes, only one species (*H. montanus*) responded significantly to forest amount, but in an opposite way to agricultural landscapes, with bat activity decreasing with increasing forest amount at small and intermediate scales (Fig. 3). In contrast, three species (*L. cinereus*, *M. chiloensis* and *T. brasiliensis*) responded significantly to forest fragmentation (Fig. 3), and in all cases, bat activity increased with increasing fragmentation at small and intermediate scales (Fig. 3). Activity of *L. varius* was not significantly associated with either forest amount or fragmentation (Fig. 3).

The analysis of homogeneity of slopes showed a significant interaction between matrix type and both forest amount and the number of forest patches, suggesting that the effects of forest amount and fragmentation on bat activity were different for agricultural and forest-dominated landscapes (Table 2). These effects tended to be stronger for agricultural than for production-forest landscapes (Figs. 2, 3).

Discussion

Bats respond differentially to forest loss, fragmentation and the nature of the intervening matrix. The prediction that forest loss and fragmentation have independent effects on biodiversity has been shown in experimental studies that controlled for their relationship (McGarigal and McComb 1995; Trzcinski et al. 1999; Villard et al. 1999; Ethier and Fahrig 2011). These studies focused attention on the independent effects of forest loss and fragmentation on species, but
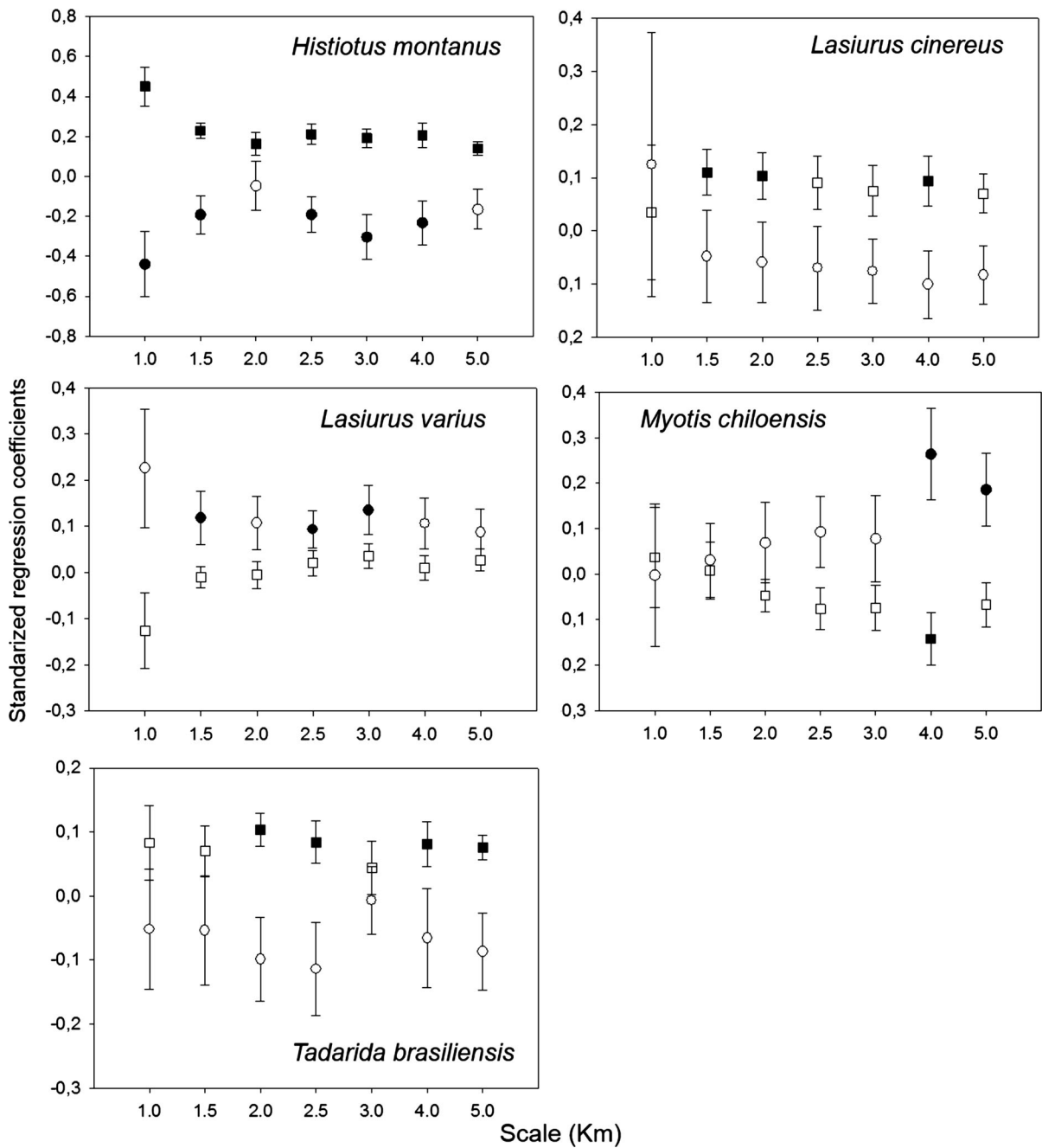
Fig. 2 Scatter plots with *error bars* of standardized regression coefficients from GLM examining the effects of forest amount (*square symbols*) and fragmentation (*circular symbols*) on bat activity in agricultural landscapes at multiple spatial scales. The *black symbols* indicate statistical significant at $P < 0.05$ and *unfilled symbols* indicate no effect. Degrees of freedom are 1 and 15 for *H. montanus* and *L. cinereus*; 1 and 13 for *L. varius*; 1 and 14 for *M. chiloensis* and *T. brasiliensis*

did not examine how these effects are modulated by the structure of the landscape matrix (Debinski 2006).

Similar to Ethier and Fahrig (2011), we found that the effects of forest amount varied among species. In

addition to forest amount, they found that when there was evidence for an effect of forest fragmentation, independent of forest amount, on bat activity, the effect was positive for most species. These authors
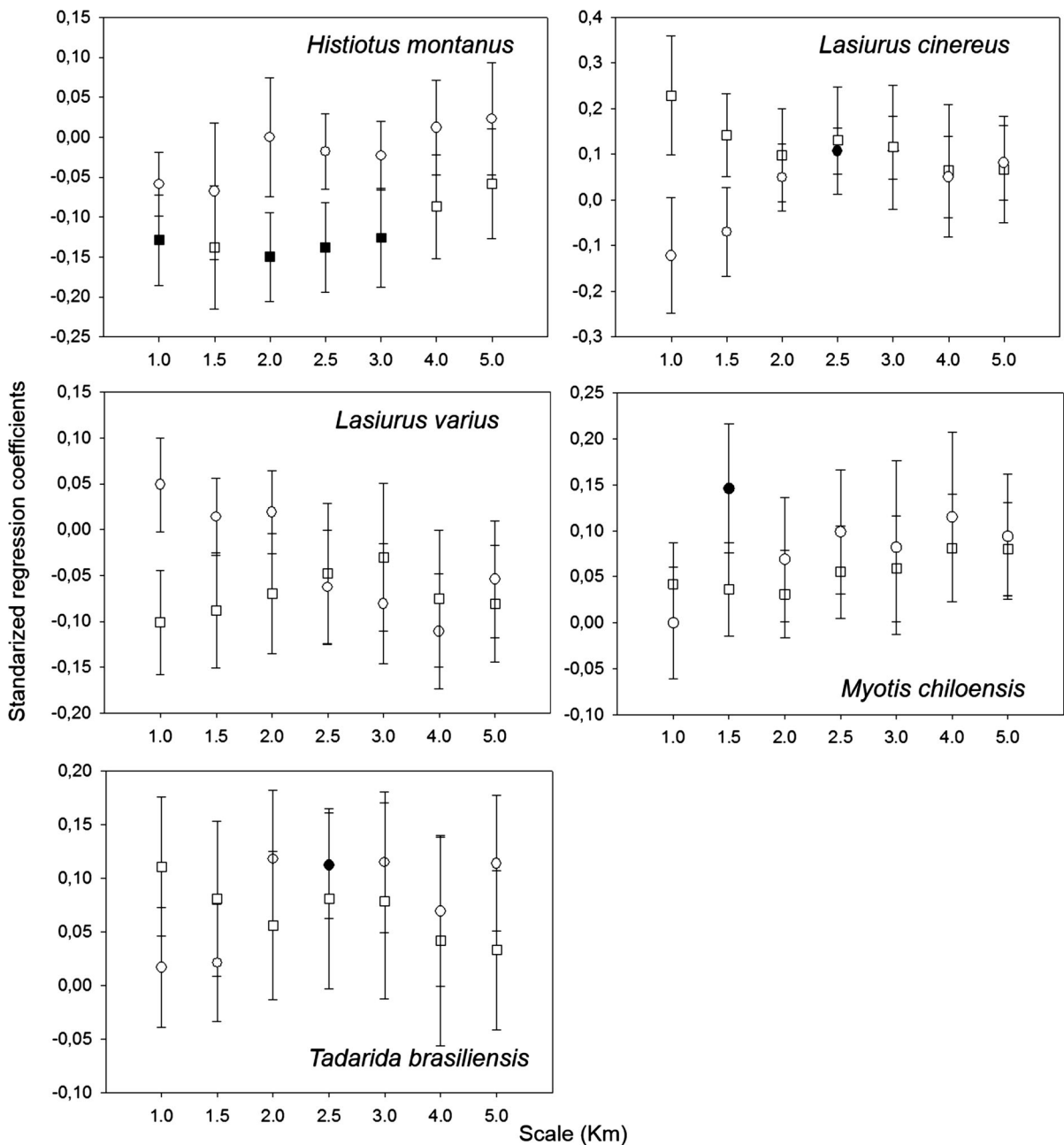
Fig. 3 Scatter plots with *error bars* of standardized regression coefficients from GLM examining the effects of forest amount (*square symbols*) and fragmentation (*circular symbols*) on bat activity in forestry landscapes at multiple spatial scales. The *black symbols* indicate statistical significant at $P < 0.05$ and *unfilled symbols* indicate no effect. Degrees of freedom are 1 and 13 for *H. montanus*, *L. cinereus* and *T. brasiliensis*; 1 and 15 for *L. varius*; 1 and 14 for *M. chiloensis*

suggested that the mechanism driving a positive response of bats to fragmentation might be a higher complementation between (or access to) foraging and roosting habitats in more fragmented landscapes or a

positive response to forest edges. Bats use forest edges for commuting and foraging (Grindal and Brigham 1999; Morris et al. 2010; Rodríguez-San Pedro and Simonetti 2013a) and the high number of bat passes

Table 2 Summary statistics of the analysis of covariance (ANCOVA) to examine the effects of landscape matrix on the relationship between bat activity and forest amount or fragmentation (covariates) at each spatial scale

Radius (km)	Main effects	*Histiotus montanus*		*Lasiurus cinereus*		*Lasiurus varius*		*Myotis chiloensis*		*Tadarida brasiliensis*	
		Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P
1.0	Matrix	4.06	0.044	1.28	0.259	1.14	0.285	6.58	0.010	0.15	0.704
	Matrix × forest amount	14.57	**<0.001**	1.46	0.227	0.18	0.669	0.05	0.829	0.06	0.800
	Matrix × number of forest patches	2.96	0.085	2.86	0.091	2.19	0.139	0.09	0.764	0.41	0.524
1.5	Matrix	3.43	0.064	2.41	0.120	1.47	0.226	5.25	0.022	0.59	0.444
	Matrix × forest amount	6.93	**0.008**	0.23	0.630	2.24	0.134	0.23	0.629	0.59	0.441
	Matrix × number of forest patches	0.72	0.397	0.19	0.667	3.41	0.065	1.45	0.228	0.25	0.614
2.0	Matrix	3.05	0.080	2.12	0.145	1.29	0.256	6.47	0.011	0.64	0.425
	Matrix × forest amount	6.24	**0.012**	0.36	0.551	1.62	0.203	1.63	0.202	1.28	0.257
	Matrix × number of forest patches	0.15	0.701	0.22	0.636	2.33	0.127	0.00	0.974	1.72	0.189
2.5	Matrix	4.06	0.044	1.66	0.197	1.20	0.273	6.59	0.010	0.31	0.580
	Matrix × forest amount	6.19	**0.013**	0.74	0.391	2.02	0.155	2.55	0.110	0.09	0.765
	Matrix × number of forest patches	2.22	0.137	3.34	0.068	5.18	**0.023**	0.23	0.632	11.82	**0.001**
3.0	Matrix	4.89	0.027	1.67	0.196	1.37	0.242	7.35	0.007	0.08	0.774
	Matrix × forest amount	3.94	**0.047**	1.06	0.302	1.02	0.313	2.77	0.096	0.58	0.445
	Matrix × number of forest patches	4.71	**0.030**	4.82	**0.028**	7.62	**0.006**	0.53	0.467	7.89	**0.005**
4.0	Matrix	4.04	0.044	2.42	0.120	1.17	0.280	7.08	0.008	0.31	0.576
	Matrix × forest amount	3.12	0.078	0.91	0.340	3.14	0.076	5.14	**0.023**	0.23	0.631
	Matrix × number of forest patches	2.61	0.106	2.61	0.107	13.25	**<0.001**	0.00	0.968	4.99	**0.025**
5.0	Matrix	3.44	0.063	2.30	0.129	1.03	0.310	7.17	0.007	0.35	0.553
	Matrix × forest amount	1.18	0.277	1.49	0.222	6.07	**0.014**	3.82	0.051	0.72	0.397
	Matrix × number of forest patches	1.48	0.224	1.19	0.274	5.21	**0.022**	0.08	0.778	4.28	**0.039**

Significant results in bold

recorded along forest edges in our study (74.7 and 66.4 % in agricultural and forestry landscape, respectively) seems to support this hypothesis. However, an analysis of the relationship between bat activity and forest edge density confirmed these assumptions only for *L. varius* in agricultural landscapes, where we found a significant positive effect of forest edge, but not for the other four species. Therefore, we suggest that our results of fragmentation effects on bat activity are consistence with both the landscape complementation and the positive edge response hypotheses. Future research should focus on the mechanism behind individual bats species' responses to fragmentation.

As forest amount increased, the activity of *M. chiloensis* decreased in agricultural landscapes, a surprising result for an assumed forest-dependent bat species. *M. chiloensis* can either forage inside the forest, close to vegetation, or in edge and gaps created by natural or anthropogenic disturbance in central Chile (Galaz and Yáñez 2006; Rodríguez-San Pedro and Simonetti 2013a). Individuals of this species are able to use artificial structures, such as farmhouses, for roosting in rural landscapes where a considerable amount of forest has been removed (Galaz and Yáñez 2006). It is therefore possible that the availability of forest edges and open areas for foraging and

anthropogenic structures for roosting may be driving the observed negative relationship of *M. chiloensis* with forest amount in agricultural landscapes. Surprisingly, the activity of *L. varius* was unaffected by forest amount, even though this species has been associated with forested habitats (Galaz and Yáñez 2006; Rodríguez-San Pedro and Simonetti 2013a), suggesting that even species exhibiting a definitive association with a particular habitat type at the patch level have a great deal of variation in activity among landscapes that could not be explained by forest amount alone. It is not surprising that activity of *T. brasiliensis* and *L. cinereus* were not affected by fragmentation. This is probably because high wing loading and high wing aspect ratio, features characteristic of species foraging in open space (Norberg and Rayner 1987), confer high speeds that make visiting isolated patches energetically cheap. On the other hand, some forest bat species, such as *H. montanus*, are adapted to slower and more maneuverable flights because of their lower wing loading and lower aspect ratio. Thus, this and similar species may not be able to afford prolonged commuting flights over an inhospitable matrix like an agricultural landscape to isolated forest patches because such flights would be energetically costly for them (Norberg and Rayner 1987).

Bat activity in our study was associated with forest amount and fragmentation, however their effects varied between agricultural and forestry dominated landscapes. In accordance with other studies, forest amount was a significant predictor of activity of most species in agricultural landscapes (McGarigal and McComb 1995; Villard et al. 1999; Klingbeil and Willig 2009; Ethier and Fahrig 2011), but not in those dominated by forest plantations where only one species responded significantly to forest amount. Forest plantations might represent a "soft" matrix for the biota inhabiting native forest patches, as exemplified by the willingness of some taxa to move through tree plantations particularly when it has a well-developed understory (Estades et al. 2012; Simonetti et al. 2013). For example, in landscapes where native forests have been replaced by exotic forestry plantations, bats are able to use such lands for commuting, foraging and roosting (Borkin and Parsons 2010a, b, 2011). The exotic pine plantations, might provide habitat for some species of forest-dwelling bats such as *H. montanus*, *L. cinereus*, *L. varius* and *M. chiloesnis* in central Chile (Rodríguez-San Pedro and Simonetti 2013a), and thus could compensate for habitat loss.

Like bats in temperate forests of Canada and tropical forests of Peru and subtropical Atlantic forest of Paraguay (Gorresen and Willig 2004; Klingbeil and Willig 2009; Ethier and Fahrig 2011), bat species in Chile displayed scale-dependent responses to forest amount and fragmentation. In agricultural landscapes, bat activity for most species was strongly determined by both forest amount and fragmentation at large spatial scales. Although limited information is available on the movements and home range size of Chilean bat species, these scales are larger than the average maximum distance traveled by similar small and medium-sized aerial insectivorous bats during foraging activity elsewhere (Elmore et al. 2005; Sparks et al. 2005; Walters et al. 2007; Henderson and Broders 2008; Kniowski and Gehrt 2014). The fact that bat activity was associated with forest amount and fragmentation at scales larger than the home range of individual bats suggests that local bat activity reflects a number of factors operating at different scales probably depending on species-specific behavioral or life-history characteristics.

In contrast to agricultural landscapes, bat activity was associated significantly with forest amount and/or fragmentation at the smallest spatial scales in forested landscapes suggesting that the type of matrix could affect not only the direction and magnitude of forest amount and fragmentation on bat activity, but also the spatial scale at which their effects operate on species. Landscapes dominated by an agricultural matrix, with smaller and more distant suitable habitat patches, are likely associated with bats needing long commuting flights. Whereas bats associated with forested landscapes have shorter home ranges and, consequently, may respond to shorter scales in a modified landscape (Chaverri et al. 2007; Saïd et al. 2009; Kniowski and Gehrt 2014). For example, the Indiana bat (*Myotis sodalis*) home ranges within a highly agricultural landscape are larger compared to other studies in forested and rural–urban landscapes (Kniowski and Gehrt 2014). Our results suggest that multiple-scale assessment are necessary to adequately quantify the effects of forest amount and fragmentation on mobile species that inhabit complex landscapes where habitat patches are difficult to define and thus, may be critical to the success of management and conservation strategies in human modified landscapes.

This study reinforces that of Ethier and Fahrig (2011), adding the role of matrix complexity to the analysis of the independent role of habitat loss and fragmentation and providing evidence that low contrast matrices can mitigate the effects of forest loss. Our results indicate that fragmented landscapes with many embedded native forest patches surrounded by a low contrast matrix such as pine plantation (albeit species depauperate) may support a higher activity of insectivorous bats than fragmented landscapes with an agricultural matrix. The fact that landscapes with small forest patches embedded in such production-forests can mitigate the effects of forest loss, enhances the capacity of many taxa, including bats, to persist in landscapes modified by humans. Forestry plantations are an important component of these landscapes. We recommend that effective conservation efforts and management strategies in anthropogenically altered landscapes should aim to reduce the degree of patch-matrix contrast in order to mitigate the impact of forest loss and improve biodiversity conservation.

References

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85(10):2671–2676

Borkin KM, Parsons S (2010a) Plantation forests are used by the lesser short-tailed bat, *Mystacina tuberculata rhyacobia*. N Z J Zool 37(1):13–17

Borkin KM, Parsons S (2010b) The importance of exotic plantation forest for the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). N Z J Zool 37(1):35–51

Borkin KM, Parsons S (2011) Home range and habitat selection by a threatened bat in exotic plantation forest. For Ecol Manag 262(5):845–852

Brigham R, Grindal S (1997) The influence of structural clutter on activity patterns of insectivorous bats. Can J Zool 75(1):131–136

Cerezo A, Perelman S, Robbins CS (2010) Landscape-level impact of tropical forest loss and fragmentation on bird

occurrence in eastern Guatemala. Ecol Model 221(3):512–526

Chaverri G, Quirós OE, Kunz TH (2007) Ecological correlates of range size in the tent-making bat *Artibeus watsoni*. J Mammal 88(2):477–486

Crome FHJ, Richards GC (1988) Bats and gaps: microchiropteran community structure in a queensland rain forest. Ecology 69:1960–1969

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol Conserv 128(2):231–240

Debinski DM (2006) Forest fragmentation and matrix effects: the matrix does matter. J Biogeogr 33(10):1791–1792

Echeverria C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton A (2006) Rapid deforestation and fragmentation of Chilean temperate forests. Biol Conserv 130(4):481–494

Elmore L, Miller D, Vilella F (2005) Foraging area size and habitat use by red bats (*Lasiurus borealis*) in an intensively managed pine landscape in Mississippi. Am Midl Nat 153(2):405–417

Erickson JL, West SD (2002) The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropt 4(1):17–24

Estades CF, Grez AA, Simonetti JA (2012) Biodiversity in Monterrey pine plantations. In: Simonetti JA, Grez AA, Estades CF (eds) Biodiversity conservation in agroforestry landscapes: challenges and opportunities. Editorial Universitaria, Santiago, pp 77–98

Ethier K, Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. Landscape Ecol 26(6):865–876

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81(1):117–142

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Ferreras P (2001) Landscape structure and asymmetrical interpatch connectivity in a metapopulation of the endangered Iberian lynx. Biol Conserv 100(1):125–136

Fischer J, Lindenmayer DB, Manning AD (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front Ecol Environ 4(2):80–86

Galaz J, Yáñez J (2006) Los Murciélagos de Chile: Guía para su reconocimiento. Ediciones del Centro de Ecología Aplicada, Santiago

Gascon C, Lovejoy TE, Bierregaards RO Jr, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species richness in tropical forest remnants. Biol Conserv 91(2):223–229

Gorresen PM, Willig MR (2004) Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. J Mammal 85(4):688–697

Grindal S, Brigham R (1999) Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. Ecoscience 6:25–34

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecol Appl 12(2):321–334

Harvey CA, Medina A, Sánchez DM, Vílchez S, Hernández B, Saenz JC, Maes JM, Casanoves F, Sinclair FL (2006)

Patterns of animal diversity in different forms of tree cover in agricultural landscapes. Ecol Appl 16(5):1986–1999

Henderson L, Broders H (2008) Movements and resource selection of the northern long-eared myotis (*Myotis septentrionalis*) in a forest-agriculture landscape. J Mammal 89(4):952–963

Hooper DU, Adair EC, Cardinale BJ, Byrnes JE, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486(7401):105–108

Klingbeil BT, Willig MR (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. J Appl Ecol 46(1):203–213

Kniowski AB, Gehrt SD (2014) Home range and habitat selection of the Indiana bat in an agricultural landscape. J Wildl Manag 78(3):503–512

Kuenzi AJ, Morrison ML (2003) Temporal patterns of bat activity in Southern Arizona. J Wildl Manag 67:52–64

Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Glob Ecol Biogeogr 15(1):8–20

Lacki M, Hayes J, Kurta A (eds) (2007) Bats in forests: conservation and management. JHU Press, Baltimore

Law BS, Anderson J, Chidel M (1999) Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. Biol Conserv 88(3):333–345

Lindenmayer DB, Hobbs RJ (2004) Fauna conservation in Australian plantation forests—a review. Biol Conserv 119(2):151–168

Lindenmayer D, Cunningham R, Pope M (1999) A large-scale "experiment" to examine the effects of landscape context and habitat fragmentation on mammals. Biol Conserv 88(3):387–403

McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol Monogr 65(3):235–260

Morris AD, Miller DA, Kalcounis-Rueppell MC (2010) Use of forest edges by bats in a managed pine forest landscape. J Wildl Manag 74(1):26–34

Neter J, Wasserman W, Kutner M (1990) Applied linear statistical models, 3rd edn. Irwin, Chicago

Norberg U, Rayner J (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philos Trans R Soc Lond B Biol Sci 316:335–427

Nupp TE, Swihart RK (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. J Mammal 81(2):512–526

O'Farrell MJO, Corben CHC, Gannon WLG (2000) Geographic variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*). Acta Chiropt 2(2):185–196

Prevedello JA, Vieira MV (2009) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19(5):1205–1223

Pye JD (1971) Bats and fog. Nature 229:572–574

Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Renjifo LM (2001) Effect of natural and anthropogenic landscape matrices on the abundance of subandean bird species. Ecol Appl 11(1):14–31

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158(1):87–99

Ritchie LE, Betts MG, Forbes G, Vernes K (2009) Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. For Ecol Manag 257(9):1920–1929

Rodríguez-San Pedro A, Simonetti JA (2013a) Foraging activity by bats in a fragmented landscape dominated by exotic pine plantations in central Chile. Acta Chiropt 15(2):393–398

Rodríguez-San Pedro A, Simonetti JA (2013b) Acoustic identification of four species of bats (Order Chiroptera) in central Chile. Bioacoustics 22(2):165–172

Saïd S, Gaillard JM, Widmer O, Débias F, Bourgoin G, Delorme D, Roux C (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118(9):1299–1306

Simonetti JA, Grez AA, Estades CF (2013) Providing habitat for native mammals through understory enhancement in forestry plantations. Conserv Biol 27(5):1117–1121

Sleep D, Brigham R (2003) An experimental test of clutter tolerance in bats. J Mammal 84(1):216–224

Smith AC, Koper N, Francis CM, Fahrig L (2009) Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. Landscape Ecol 24(10):1271–1285

Sparks DW, Ritzi CM, Duchamp JE, Whitaker JO (2005) Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. J Mammal 86(4):713–718

Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol Appl 9(2):586–593

Vergara P, Simonetti J (2003) Forest fragmentation and rhynocriptid nest predation in central Chile. Acta Oecol 24(5):285–288

Villard M-A, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv Biol 13(4):774–783

Walsh A, Barclay R, McCracken G (2004) Designing bat activity surveys for inventory and monitoring studies at local and regional scales. In: Brighamm R, Kalko E, Jones G, Parsons S, Limpens HJGA (eds) Bat echolocation research: tools, techniques and analysis. Bat Conservation International, Austin, pp 157–165

Walters BL, Ritzi CM, Sparks DW, Whitaker JO Jr (2007) Foraging behavior of eastern red bats (*Lasiurus borealis*) at an urban-rural interface. Am Midl Nat 157(2):365–373

With KA (2002) The landscape ecology of invasive spread. Conserv Biol 16(5):1192–1203