

Effects of forest fragmentation on nocturnal Asian birds: A case study from Xishuangbanna, China

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ABSTRACT

Owls have the potential to be keystone species for conservation in fragmented landscapes, as the absence of these predators could profoundly change community structure. Yet few studies have examined how whole communities of owls respond to fragmentation, especially in the tropics. When evaluating the effect of factors related to fragmentation, such as fragment area and distance to the edge, on these birds, it is also important in heterogeneous landscapes to ask how 'location factors' such as the topography, vegetation and soil of the fragment predict their persistence. In Xishuangbanna, southwest China, we established 43 transects (200 m×60 m) within 20 forest fragments to sample nocturnal birds, both visually and aurally. We used a multimodel inference approach to identify the factors that influence owl species richness, and generalized linear mixed models to predict the occurrence probabilities of each species. We found that fragmentation factors dominated location factors, with larger fragments having more species, and four of eight species were significantly more likely to occur in large fragments. Given the potential importance of these birds on regulating small mammal and other animal populations, and thus indirectly affecting seed dispersal, we suggest further protection of large fragments and programs to increase their connectivity

to the remaining smaller fragments.

Keywords: Forest fragmentation; Landscape ecology; Nocturnal birds; Owls; Trophic cascades

INTRODUCTION

The majority of the world's species are found in tropical forests, which have been lost rapidly due to anthropogenic activities such as agricultural expansion, logging and urbanization (Haddad et al., 2015). Among tropical regions, Southeast Asia has received particular attention as a priority region for conservation because of high deforestation rates and greater species richness (Sodhi et al., 2010). For example, in parts of Southeast Asia such as Xishuangbanna Prefecture, China, agricultural crops, and specifically rubber plantations, have expanded rapidly during the past thirty years, with a serious loss of forest habitat (Li et al., 2008).

Deforestation produces three interconnected problems for biodiversity: habitat loss, habitat fragmentation and habitat degradation (Fahrig, 2003). A large literature, especially

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extensive for birds, has investigated how 'fragmentation factors' (e.g., fragment size, shape, isolation, and percentage of edge) influence biodiversity, finding mostly negative effects on habitat specialists, insectivores and large frugivores, but positive effects on some generalist species (Bregman et al., 2014; Chang et al., 2013; Matthews et al., 2014). Forest fragmentation is also known to disconnect small populations of organisms from the larger population, leading to a reduction in genetic variation (Hagen et al., 2012). At the same time, in a heterogeneous landscape, 'location factors' (e.g., the topographical position of a fragment and characteristics of its vegetation and soil) could also significantly influence the biodiversity of fragments (Liu & Slik 2014).

Here, as part of an investigation comparing fragmentation and location factors on birds and herpetofauna of Xishuangbanna, we report on the response of a nocturnal bird community to fragmentation. Xishuangbanna is a highly heterogeneous region, with undulating terrains and patchily distributed limestone soils (Tang et al., 2012), and recent studies have suggested that location factors are more important than fragmentation factors in explaining the persistence of trees in fragments (Liu & Slik 2014). We selected nocturnal bird species because of how their presence or absence as predators could affect other species in a fragmented landscape (e.g., Terborgh et al., 2001). Large owls may act as the top predators in some ecosystems, and smaller owls may play a role in the regulation of small rodents, herpetofauna and larger insects (Mikkola, 2014). Although studies on large owls, such as Northern Spotted Owl (*Strix occidentalis*), were important in the development of the fragmentation literature

(e.g., Lande, 1987), less is known about how fragmentation affects small owl species, and species-rich communities of owls, especially in Asia. Also, while there has been considerable work on the effect of fragmentation on birds in the region (e.g., Chang et al., 2013), no study has focused on nocturnal birds or raptors. We hypothesized that owls would show stronger responses to fragmentation factors than to location factors, because they maintain large territories. We hypothesized that some owl species (especially those that are large bodied, or habitat specialists) would be influenced negatively by fragmentation factors, particularly decreasing fragment size.

MATERIALS AND METHODS

Study area

The study was conducted within a 10 km radius circle centered on Xishuangbanna Tropical Botanical Garden (XTBG, N21°55', E101°15'), a research institute of the Chinese Academy of Sciences, located in the Menglun township of Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China (Figure 1). Xishuangbanna is bordered by Laos from the south and Myanmar from the southwest and lies within tropical Southeast Asia (Corlett, 2014), with some characteristics of the subtropics (Zhu et al., 2006). The climate is mainly governed by two seasons: dry, from November to April, and wet, from May to October (Cao et al., 2006). The landscape is a mosaic of mostly rubber plantations, with some banana plantations in river catchment areas, and a few large nature reserves with scattered forest patches, varying in sizes and shapes.

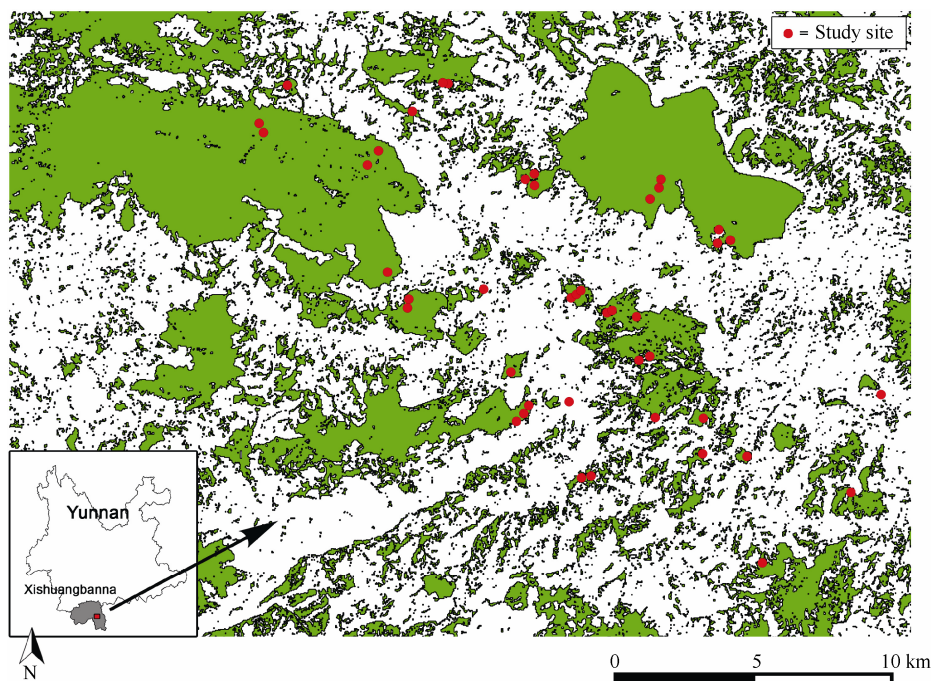


Figure 1 Map showing the study area, natural forest areas (in green) and the 43 sites (red)

The red circle symbol for the sites is not to scale.

Nocturnal bird survey

We selected 43 plots from the 50 vegetation sampling plots, established by the study of Liu & Slik (2014), and established 200 m transects in length inside them. Nocturnal bird surveys were conducted within 30 m on both sides of the transect. We placed the transects on the access paths for the vegetation plots, so that the minimum distance between the starting point of the transect and the forest edge was 25 m for the small fragments ($n=14$ fragments < 100 ha) and 100–200 m for the other transects, and the center of the transect was the center of the vegetation plot. Transects were at least 250 m away from each other. These 43 transects were located in a total of 20 fragments that ranged between 0.45 ha and 1 3837.3 ha in size (including two large nature reserves of mean 5 720.3 ha, and 18 unprotected fragments of mean 307.8 ha \pm 483.4 SD). The midpoint elevation of transects ranged between 541 and 1 477 m a.s.l.. As transects in the same fragment were not independent of each other, we used a mixed model, with fragment as a random factor (see “Data analysis” below).

We conducted visual and playback encounter surveys (VES & PES), which are the most effective sampling methods for nocturnal birds (Kissling et al., 2010). During the first sampling effort (September–October 2014), two observers (SKD and one local assistant) walked on transect for one hour, searching visually and aurally for nocturnal birds. When we conducted the second sampling (July–August 2015), effort was intensified, applying playbacks of territorial calls of all owl species (8) and nightjars (2) known to occur in the study area, according to MacKinnon and Phillipps (2000). We downloaded recordings from Xeno-Canto online bird calls repository (<http://test.xenocanto.org/>). For each species we used three different recordings, selected by their good signal-to-noise ratio, and played them consecutively. We played first calls of small owls and then proceeded to larger owl species, in case the calling of small owls was inhibited in the presence of larger ones, with 2

min intervals between species. All sampling was conducted between 1900h–2400h.

Explanatory and response variables

We collected data on the different transects, with these variables grouped as either ‘fragmentation’, ‘location’ or ‘degradation’ factors. The fragmentation factors were: (1) fragment size in which transects were located, (2) fragment area/perimeter ratio, (3) distance from the edge to the center of transects (shortest projected horizontal distance) and (4) isolation, using the mean proximity index (PROX_MN). PROX_MN measures the degree to which patches are isolated from other patches of the same cover class within a specified search radius (McGarigal et al., 2012; Šímová & Gdulová, 2012; Turner et al., 2001). We used a 2 km search radius because it was large enough for all points to have neighboring patches, and calculated PROX_MN in FRAGSTATS v. 4.0 (McGarigal et al., 2012). The other fragmentation variables were measured using data from Liu & Slik (2014; for further details, please see that article).

The location factors considered were: (1) forest type, where forests were classified into three categories that are nonoverlapping in their tree communities in multivariate analyses (mixed ($n=15$), oak ($n=16$) and limestone ($n=12$, Supplemental Figure 1; note that forest type also is associated with soil type, being either limestone or not), and (2) topology (as three categories; valley ($n=13$), mid-slope ($n=14$) and ridge ($n=16$)). We also considered the degradation factors of: (1) disturbance (transects were considered disturbed if we observed logging and/or ginger planting in them) and (2) whether a transect was in a nature reserve or not. The fragmentation, location and degradation factors collectively were considered as fixed factors in a mixed modeling approach in our data analysis; a summary of the values of these factors for fragments of different sizes is included as Supplemental Table 1. As response variables, we considered species richness and presence-absence of individual species of nocturnal birds.

Table 1 The species detected in the study

Owl species	Body size (cm)	V	A	Slope	SE	P
Asian Barred Owlet (<i>Glaucidium cuculoides</i>)	23.5	30	42	0	N/C ⁺	1.0
Brown Hawk Owl (<i>Ninox scutulata</i>)	30.0	4	4	−0.16	0.16	0.31
Brown Wood Owl (<i>Strix leptogrammica</i>)	47.5	2	18	0.51	0.23	0.031*
Collared Owlet (<i>Glaucidium brodiei</i>)	16.0	3	13	1.06	0.46	0.021*
Collared Scops-owl (<i>Otus lettia</i>)	24.5	2	16	0.13	0.12	0.30
Mountain Scops-owl (<i>Otus spilocephalus</i>)	19.0	0	22	1.20	0.69	0.08
Oriental Bay Owl (<i>Phodilus badius</i>)	26.0	11	5	0.69	0.26	0.008**
Spot-bellied Eagle Owl (<i>Bubo nipalensis</i>)	57.5	0	4	1.84	0.81	0.023*

Each species' body size (head to tail; Mikkola, 2014), sample size (V: number of transects on which the species was visually detected; A: number of transects on which the species was aurally detected and/or responded to playbacks), and regression coefficient ('slope') and associated statistics for a generalized linear mixed model explaining their occurrence (presence/absence) at 43 sites in 20 fragments. Fragment was considered a random factor in the mixed model. A positive slope indicates greater occurrence in larger fragments. ⁺: Calculation not definite because of zero slope. SE: Adjusted standard error; *: $P < 0.05$; **: $P < 0.01$.

Data analysis

Statistical analyses were conducted in R v.3.1.3 (R Development Core Team, Geneva, Switzerland, 2015). We first checked for spatial autocorrelation in species richness by examining Moran's I values constructed from model residuals, using the 'ape' package (Paradis et al., 2004). We did not find significant spatial autocorrelation in our data ($P > 0.1$). We also estimated species richness per transect, using the 'vegan' package (Oksanen et al., 2015); however, we found estimated species richness (e.g., Chao I estimator) to be highly correlated with the original species richness, and we used the original species richness in subsequent analyses. The species accumulation curve at the landscape scale reached an asymptote, demonstrating that all the species in the study area were sampled (Supplemental Figure 2). We ran random effect mixed models with Poisson error structure, using the 'lme4'

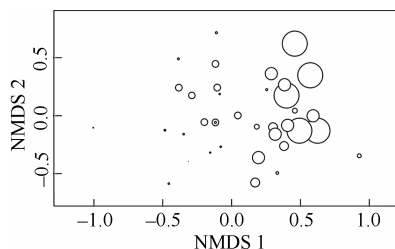


Figure 2 A non-metric multi-dimensional scaling of nocturnal bird assemblages

Fragment size, represented by the diameter of the circles, is related to community composition.

package (Bates et al., 2014), to determine the effects of forest fragmentation on nocturnal bird species richness; forest fragment identity was included in the model as a random factor. We employed a multimodel inference approach (Burnham & Anderson, 2002) to determine the most important variables that explain the observed variation in species richness, using the 'MuMIn' package (Barton & Barton 2015). MuMIn grades the models according to their Akaike Information Criterion (AIC) with a correction for small sample sizes (AICc); we obtained the subset of models with $\Delta AICc$ of less than 4.

We then ran a multivariate generalized linear model with negative-binomial error structure to determine the effects of fragmentation on nocturnal bird community composition in study area, using the 'mvabund' package (Wang et al., 2012). Note that this program does not allow the use of random factors; however, the other analyses in our study showed the influence of the random variable of fragment to be very small (explaining less than one percent of the variation). We assessed the significance of explanatory variables using 999 permutations of a Monte-Carlo test. We used non-metric multidimensional scaling to visualize differences in bird composition, using the 'vegan' package. We also determined the effects of fragment size on the occurrence probability (presence-absence) of each species using generalized linear mixed models with binomial errors and forest fragment as a random factor.

As it is possible that visual detections could be influenced by canopy density, which itself could vary due to the fragmentation, location or degradation factors, we re-analyzed the data using only aural detections, and found qualitatively similar results (Supplemental Table 2).

Table 2 Results of the model averaging approach on how owl species richness was influenced by 'fragmentation' and 'degradation' factors ('location' factors were eliminated in the model averaging process)

	Factor	Estimate	SE	CI 2.5%	CI 97.5%	Imp	<i>n</i>
Fragmentation factors	Fragment size	0.168	0.049	0.070	0.266	1.00	9
	Distance to edge	0.055	0.079	-0.104	0.215	0.22	3
	Isolation (PROX_MN)	0.028	0.110	-0.195	0.249	0.14	2
Degradation factors	Nature reserve inclusion	0.229	0.232	-0.239	0.698	0.31	4
	Disturbance	-0.122	0.184	-0.495	0.249	0.22	3

Estimate: model-averaged coefficients; CI: confidence intervals (2.5% and 97.5%, respectively); SE: adjusted standard error; Imp: relative importance of the factor; *n*: number of models with $\Delta AICc < 4$ that included the factor; there were 9 such models in total. The adjusted R^2 value for the full model (all factors fragmentation, location and degradation factors included) was 0.40.

RESULTS

We recorded 8 species of owls with 211 individual observations, which include both visual and aural encounters within 30 m of the transects (see Table 1 for species). No nightjar species was recorded during the systematic data collection, but Large-tailed Nightjar (*Caprimulgus macrurus*) was observed in two large fragments actively foraging on insects. Four species of owls, Collared Owlet (*Glaucidium brodiei*), Mountain Scops-owl (*Otus spilocephalus*),

Oriental Bay-owl (*Phodilus badius*) and Spot-bellied Eagleowl (*Bubo nipalensis*) were never recorded within forest fragments smaller than 100 ha.

The model-averaged estimates from mixed models indicate that only fragmentation and degradation factors influenced owl species richness; location factors did not appear in any of the models with $\Delta AICc$ of less than 4 (Table 2). The factor in the most models was fragment size (9 of 9 models), with transects in larger fragments having more species; this was the only factor for which the 95% confidence interval did not include zero (see Table 2). Reserve status (protected reserves had more

species), disturbance (less disturbed sites had more species), distance to the edge (greater distances had more species), and isolation (less isolated transects had more species) were included in four, three, three and two models, respectively. The multivariate generalized linear model demonstrated that fragmentation was a significant influence on composition ($P=0.02$), with transects in fragments of the same size

clustering together in multivariate space (Figure 2).

The occurrence probability of four owl species increased at transects in larger fragments, with the other four species not having any significant effect (see Table 1, Figure 3). The largest owl recorded was Spot-bellied Eagle-owl (*B. nipalensis*), which was the most sensitive owl species to fragment size, only found in fragments above 3 200 ha.

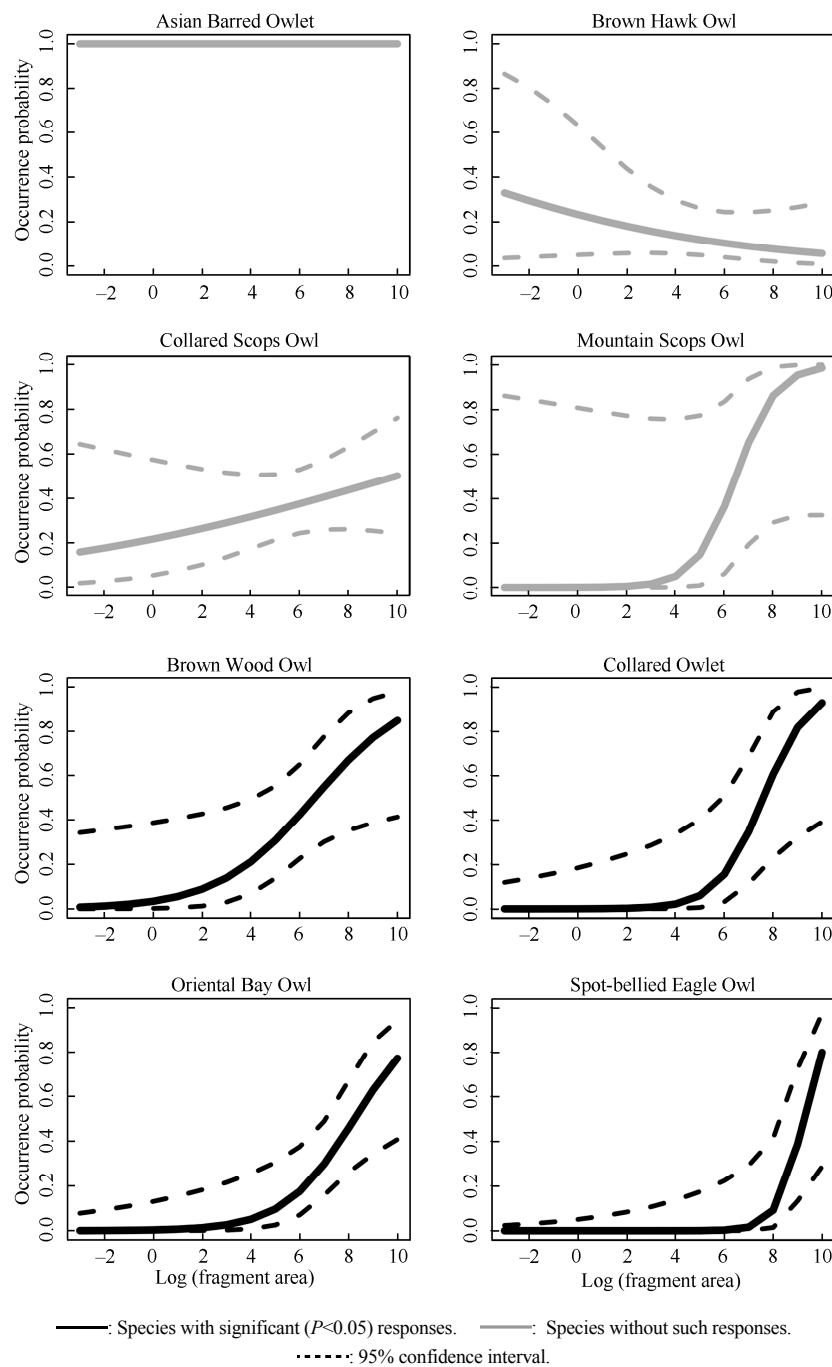


Figure 3 Occurrence probability of each owl species with increasing forest fragment size (log transformed)

DISCUSSION

As expected, our results showed that the fragmentation factors had a dominant effect on owl species richness in this area. The occurrence probability analysis showed that for eight species of owls, four species had a significant positive relationship with increasing fragment size. Small fragments thus appear inhospitable to most of the owl species recorded in this landscape. Several characteristics of small fragments could be driving this effect. Small fragments may not be big enough to support larger territories and prey volumes that the large species require (Mikkola, 2014), and/or small fragments may lack large old trees with hollows to serve as nests (Kavanagh & Bamkin, 1995). Dense canopies (which were poorly developed in the small forest fragments) are also a crucial microhabitat requirement for owls to avoid sunlight/heat, during their retreat/day roost (Hayward & Garton, 1984). It should be noted that both our visits to forest fragments were in the wet season, and owl habitat selection might differ in the dry season. A further limitation of the study is that we do not have data on characteristics of the vegetation, such as the presence of nesting trees or canopy density, that could be used to see exactly how microhabitat differences between transects influence the results.

Some owl species were widely distributed within the study area, with high tolerance to habitat disturbance. For example, Asian Barred Owlet (*G. cuculoides*), was abundant at all sites, and Brown Hawk Owl (*N. scutulata*), known to prefer open landscapes (Olsen et al., 2016), non-significantly declined with increasing fragment size. Kavanagh & Bamkin (1995) and Weaving et al. (2011) also showed that some owl species are tolerant to logging and other anthropogenic disturbances in semi-urban environments. We can conclude that in a nocturnal avian community within any given area, there are some generalist species that have the flexibility to adapt to a changing environment, as well as specialized species that have a higher risk of vanishing locally (Loyn et al., 2001). In this study, we found that fragment size affected not only large-bodied owl species but also smaller owls, including the smallest species in the community, Collared Owlet (*G. brodiei*). This species has relatively large eyes relative to its body length, and may avoid forest edges and the more well-lit parts of the forest, as shown recently in the study of Martínez-Ortega et al., (2014) for large-eyed owl species.

Nocturnal bird communities play an important role in regulating the populations of rodents, herpetofauna and large insects in forests. Most of the recorded small-bodied owl species in this study preyed on large insects; they are opportunistic hunters by nature (Mikkola, 2014). All the recorded large owl species (Spot-bellied Eagle Owl, Brown Wood Owl and Oriental Bay Owl) feed mostly on rodents, small reptiles and amphibians (Mikkola, 2014). Thus the local extinction of these nocturnal avian predators may cause a cascading effect on the food webs of the small fragments. In particular, the lack of these large owl species may trigger an increase in rodent populations. Indeed, some studies have

shown high densities of rats in small fragments (Gibson et al., 2013). A high density of rats, in turn, may directly influence seed germination, as rodents are known to be seed predators as well as dispersers (Heithaus, 1981; Loayza et al., 2014).

Given the positive effect of fragment size on owl community in our study, we strongly recommend that conservation efforts preserve large fragments in this area and work towards connecting smaller fragments with larger ones. Large-bodied owls have been used with success as 'umbrella species' for conservation in northern temperate countries (Lamberson et al., 1994; Loyn et al., 2001), and perhaps more diverse tropical assemblages of owls can be used both as bio-indicators of environmental health, and as educational tools for increasing support for conservation.

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SUPPLEMENTARY MATERIALS

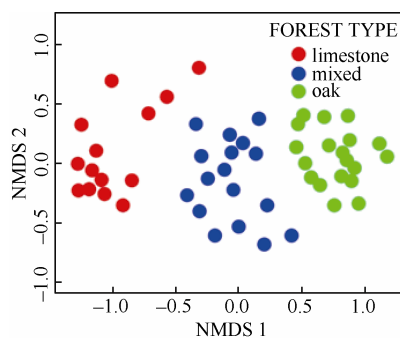
Supplementary Table 1 Characteristics of the transects as to the fragmentation, location and degradation factors considered in the analysis

	Transects in small forest fragments (<i>n</i> =14)	Transects in other forest fragments (<i>n</i> =18)	Transects in nature reserves (<i>n</i> =11)
Fragmentation factors			
Mean fragment area (ha)	31.30	753.64	5720.25
Mean area/ perimeter ratio	0.0363	0.0140	0.0123
Mean distance to the edge (m)	70.3	147.5	315.3
Mean isolation index (PROX_MN 2km)	62.64	242.07	267.52
Location factors			
Forest types (M: mixed, O: Oak, L: Limestone)	M=43%, O=43%, L=14%	M=11%, O=39%, L=50%	M=73%, O=14%, L=09%
Topography (V: valley, MS: Mid-slope, R: ridge-top)	V=21%, MS=43%, R=36%	V=22%, MS=28%, R=50%	V=55%, MS=27%, R=18%
Degradation factors			
Disturbed proportion	57%	50%	36%

Supplemental Table 2 Model averaging results (when only data from aural detections were used)

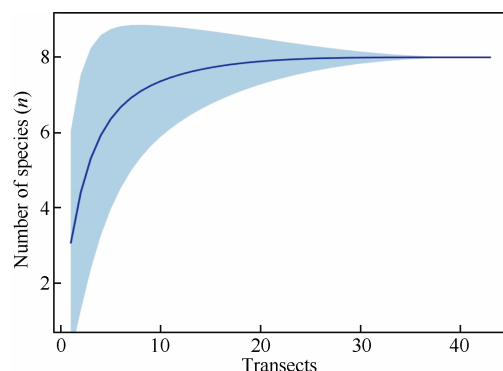
	Factor	Estimate	CI 2.5%	CI 97.5%	SE	Imp	<i>n</i>
Fragmentation factors	Fragment size	0.167	0.072	0.261	0.048	1.00	5
	Distance to edge	0.024	-0.137	0.186	0.083	0.13	1
	Isolation (PROX_MN)	0.021	-0.204	0.246	0.115	0.12	1
Degradation factors	Nature reserve inclusion	0.211	-0.260	0.683	0.240	0.18	1
	Disturbance	-0.129	-0.501	0.242	0.189	0.16	1

This Table is similar to Table 2 in the text, except it uses a subset of the data. See Table 2 for explanation of abbreviations. The adjusted R^2 value for the full model was 0.39.



Supplemental Figure 1 Forest type of the study site, with three relatively discrete categories: limestone forests, mixed forests and oak forests

Here tree species composition data is used to show that these forest types do not overlap each other. The NMDS shows the tree diversity at the vegetation plots that were in the same locations as our transects.



Supplemental Figure 2 Species accumulation curve for nocturnal birds, detected at 43 transects located in 20 fragments

The shaded area depicts 95% confidence intervals. The lack of increase of the accumulation curve after 20 transects suggests that all the species in the area during the study period were detected.