

# Old growth and secondary forest site occupancy by nocturnal birds in a neotropical landscape

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## Keywords

secondary forest; old growth; nocturnal birds; occupancy; detection; spatial autocorrelation; Amazon forest.

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## Abstract

High rates of old growth (OG) forest destruction and difficult farming conditions result in increasing cover of secondary forests (SF) in the Amazon. In this setting, it is opportune to ask which animals use newly available SF and which stay restricted to OG. This study presents a comparison of SF and OG site occupancy by nocturnal birds in *terra firme* forests of the Amazon Guianan shield, north of Manaus, Brazil. We tested species-specific occupancy predictions for two owls (*Lophotrix cristata*/*Glaucidium hardyi*), two potoos (*Nyctibius leucopterus*/*Nyctibius griseus*) and two nightjars (*Caprimulgus nigrescens*/*Nyctidromus albigollis*). For each pair, we predicted that one species would have higher occupancy in OG while the other would either be indifferent to forest type or favor SF sites. Data were collected in 30 OG and 24 SF sites with monthly samples from December 2007 to December 2008. Our analytic approach accounts for the possibility of detection failure and for spatial autocorrelation in occupancy, thus leading to strong inferences about changes in occupancy between forest types and between species. Nocturnal bird richness and community composition were indistinguishable between OG and SF sites. Owls were relatively indifferent to forest type. Potoos followed the *a priori* predictions, and one of the nightjars (*C. nigrescens*) favored SF instead of OG as predicted. Only one species, *Nyctib. leucopterus*, clearly favored OG. The landscape context of our SF study sites, surrounded by a vast expanse of continuous OG forest, partially explains the resemblance between SF and OG fauna but leaves unexplained the higher occupancy for SF than OG sites for several study species. The causal explanation of high SF occupancy remains an open question, but the result itself motivates further comparisons for other groups, as well as recognition of the conservation potential of SF.

## Introduction

The value of secondary forest (SF) habitats conditions tropical animal conservation in the Amazon and throughout the world. Large-scale destruction of the Amazon started in the 1960s with the expansion of Brazilian federal highways and subsequent advance of the rural and mining frontier (Hecht & Cockburn, 1989). Since then, more than 600 000 km<sup>2</sup> of primary forest have been lost – the area of France – at yearly rates exceeding 11 000 km<sup>2</sup> year<sup>-1</sup> during the last 20 years (Fearnside, 2005; INPE, 2009). The biological consequences of deforestation have been extensively documented (Myers, 1992; Laurance, 1998; Bierregaard *et al.*, 2001; Wright, 2005; Nepstad *et al.*, 2008; Phillips *et al.*, 2008), potentially entailing an unprecedented wave of species extinctions (Dirzo & Raven, 2003; Sodhi *et al.*, 2004). Deforestation, however, is not as simple as the permanent replacement of old growth (OG) forests by a

new habitat completely inhospitable to the local fauna and flora. When conditions are not propitious for continued use, the cleared areas are abandoned to SF. In the most densely populated areas of rural Amazonia, c. 30% of the original OG is now replaced by SF (Perz & Skole, 2003). At the global level, SF have already replaced at least 15% of tropical OG destroyed in the 1990s (Wright, 2005). The growing availability of SF and the apparent continuity of current trends led Wright & Muller-Landau (2006a) to question the imminence of a tropical mass extinction. In the ensuing debate, there is controversy over the value of SF as a habitat for tropical forest species (Brook *et al.*, 2006; Wright & Muller-Landau, 2006a,b), but agreement about the importance of measuring that value (Laurance *et al.*, 2006; Gardner *et al.*, 2007; Dent & Wright, 2009).

Four recent reviews attempted to generalize comparisons between SF and OG as habitat for forest species. Two are cautiously inconclusive: Bowen *et al.* (2007) and Gardner

*et al.* (2007) reviewed 68 and 37 studies, respectively, emphasizing the methodological limitations and inadequacies of study-site selection that preclude definite statements about the value of SF habitat. The remaining two reviews conditioned their selection of studies on relatively narrow methodological criteria and present conclusions that highlight the potential value of SF. Dunn (2004) reviewed 39 datasets from groups of sites with known ages, concluding that SF may take as little as 20–40 years to recover OG species richness. Bird and ant datasets in Dunn's review, however, suggest that while SF richness may increase relatively quickly, the species composition of these groups takes longer to recover. Finally, Dent & Wright (2009) reviewed studies that not only compared community composition between SF and OG sites but also provided information on similarity between different sites within OG. Upon re-analyzing the data, they found that SF and OG locations resemble each other more than previously appreciated and identified a positive correlation between OG–SF similarity and the similarity between OG sites.

We offer a new comparison of OG and SF that quantifies the use of both types of forest by a set of nocturnal bird species while addressing methodological difficulties of previous works. The central goal of the study is to test *a priori* predictions about which species occur most in OG and in SF. For ease of biological interpretation, we group species in single-family pairs with contrasting predictions for each member of the pair. By doing so, we ensure that species share more traits within than across pairs, strengthening the inference based on pair-specific predictions. The biological variable of interest is occupancy – the probability that a given site is occupied by a species. Our analytic and sampling approaches explicitly consider the possibility of detection failure, leading to occupancy estimates that take into account the probability of not finding a species in a place where it actually occurs. These estimates are readily comparable across species and across studies. As occupancy is the outcome of a spatial process of individual movement and establishment in particular sites, we also take into account spatial autocorrelation in occupancy, that is, the possibility that sites that are close to each other resemble each other more than sites that are further apart.

There have been three studies on the importance of SF for birds in our central Amazon study site (Borges & Stouffer, 1999; Antongiovanni & Metzger, 2005; Stouffer *et al.*, 2006), as well as ornithological studies of SF elsewhere in the Amazon (e.g. Barlow *et al.*, 2007; Borges, 2007). All the SF bird studies that we are aware of, however, focus on diurnal birds. This is an undesirable bias because nocturnal birds have a potentially disproportionate ecological importance. Being a relatively small group of organisms that share the behaviors of foraging by night and feeding often at the top of food chains (Cleere, 1999; Cohn-Haft, 1999; Marks, Cannings & Mikkola, 1999), nocturnal birds have the potential to regulate populations of several other animal species. Furthermore, despite the logistic inconveniences of working at night, nocturnal bird vocalizations are few and, with rare exceptions, easy to identify. Given the lack of

information, the ecological relevance and the practicality of the group, we found it sensible to focus our SF–OG comparison on nocturnal birds.

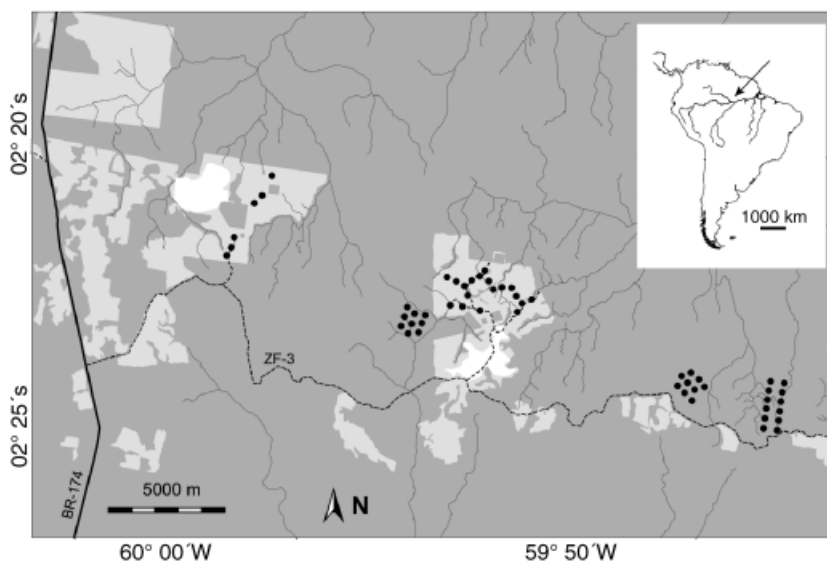
## Methods

### Study area

The data were collected at the Biological Dynamics of Forest Fragments Project area (BDFFP; Bierregaard *et al.*, 2001; Laurance *et al.*, 2002), a network of study sites spanning *c.* 350 km<sup>2</sup> east–west across the highway BR-174, 70 km north of the city of Manaus, Amazonas, Brazil (2°30'S, 60°W; Fig. 1). OG covered the whole area until the construction of the highway, in the early 1970s. In the late 1970s, federal incentives for cattle ranching led to the establishment of three ranches: Dimona, Porto Alegre and Esteio. Clearing for pasture occurred between 1980 and 1984, removing *c.* 15% of the forest cover. As the federal subsidies shrank, in the mid-1980s, cleared areas were gradually abandoned and taken up by SF. Currently, there are *c.* 30 km<sup>2</sup> of SF in the study area, with ages ranging from 25 to 29 years. Different histories of burning before secondary succession resulted in two types of SF – *Vismia*-dominated and *Cecropia*-dominated – that were clearly identifiable in the early 1990s (Mesquita *et al.*, 2001). Three decades after the onset of regeneration, however, the few pioneer species are giving way to a wider variety of trees that are characteristic of more advanced successional stages, blurring the distinction between the two types of SF.

### Study species

We chose pairs of closely related nocturnal species, in which members of each pair differed in the hypothetical pattern of OG and SF occupancy: one pair of owls (Strigidae), one pair of potoos (Nyctibidae) and one pair of nightjars (Caprimulgidae). For each pair, we hypothesize that one of the species has a higher probability of occupying SF sites than the other. Among the owls, both Amazonian pygmy-owl *Glauucidium hardyi* and crested owl *Lophotrix cristata* reportedly favor OG (Marks *et al.*, 1999), but we followed Cohn-Haft, Whittaker & Stouffer (1997) to predict that *L. cristata* should be restricted to OG sites while *G. hardyi* should occur in both environments. The common potoo *Nyctibius griseus* is the most widely distributed bird in its family and also the most versatile in habitat use (Sick, 1997; Cohn-Haft, 1999); the other potoo, white-winged potoo *Nyctibius leucopterus*, is reportedly restricted to the canopy of OG sites (Cohn-Haft, 1993; Cohn-Haft *et al.*, 1997). We predicted that the two potoos would show contrasting occupancy patterns, with *Nyctib. griseus* having higher occupancy in SF than OG and *Nyctib. leucopterus* never occurring in SF. Finally, the nightjar pair consists of common pauraque *Nyctidromus albicollis* and blackish nightjar *Caprimulgus nigrescens*. Several neotropical bird monographs (Wetmore, Pasquier & Olson, 1965; Haverschmidt & Barruel, 1968; Hilty & Brown, 1986; Sick, 1997; Cleere, 1998) indicate that both



**Figure 1** Location of the study area in South America, north of Manaus, Brazil, showing the 54 sampling points (solid circles), in old growth forest (dark gray) and secondary forest (light gray); white represents pasture. The area is bordered on the west by the paved road BR-174 (continuous line) and on the south by the unpaved road ZF-3 (dashed line).

species use open areas; however, while *Nyctid. albicollis* uses a wide variety of disturbed habitats (Cleere, 1999), *C. nigrescens* frequently appears in open areas within OG (Ingels & Ribot, 1983; Roth, 1985). Thus, we found it appropriate to test the local prediction (Cohn-Haft *et al.*, 1997) that *C. nigrescens* should occur more in OG than SF, whereas *Nyctid. albicollis* should show the opposite pattern. Although we focused on three species pairs, the bird list for central Amazon (Cohn-Haft *et al.*, 1997) includes 18 nocturnal species, of which we saw 12. We report the additional species data in two different ways: first, we estimate nocturnal bird richness and differences in composition between OG and SF in our study area; second, we present OG and SF occupancy estimates for four additional owls, for which we had no *a priori* predictions: *Megascops choliba*, *Megascops watsonii*, *Pulsatrix perspicillata* and *Ciccaba* spp. We could not identify calls of the genus *Ciccaba* to the species level; therefore, we refer to the two locally occurring species *Ciccaba huhula* and *Ciccaba virgata* jointly as *Ciccaba* spp.

### Sampling design

Noting the difficulties of estimating and comparing densities of nocturnal birds based on vocalization data (Borges, Henriques & Carvalhaes, 2004), we aimed our design at the estimation of occupancy – the probability that a site is occupied by a species – based on species detection data. Sampling, conducted by M. S., consisted of 12 monthly visits to 54 points between December 2007 and December 2008, requiring 670 km of walking in 64 field nights. Thirty points were placed in OG and the remaining 24 in SF (Fig. 1), their spatial distribution resulting from a tradeoff between the conflicting goals of maximizing independence between points and minimizing walking distance. To reduce the possibility of one individual bird being detected from two adjacent sampling points, we imposed a minimum distance of 400 m between points. Even with independent detection, it is possible that one individual's home range

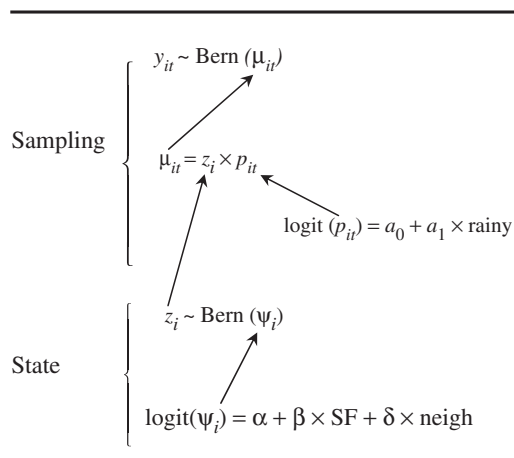
could span the distance between adjacent points compromising spatial independence in occupancy. Because we have no information on home ranges, we rely on the quantification of spatial autocorrelation in occupancy to guard against this possibility.

Because of unpredictable rainy nights and logistic mishaps, not all points were sampled every month: the total number of visits per point ranged between five and 12, with an average of 9.5 visits per point. All visits occurred during crescent and full moon phases (between the eighth and the 18th day of the lunar cycle) in order to maximize nocturnal bird detection (Sick, 1997; Cleere, 1999; Cohn-Haft, 1999). We carried out observations between 19:00 and 23:00 h, always starting after nightfall. For each visit to each point, we registered the time of arrival, moon height above the horizon and a list of all nocturnal bird species heard at the point. Each visit started with a 3-min passive listening period, followed by playback of calls from the six focal species played in a different random sequence for each visit to each point. Even though playback does not constitute an experimental treatment in our study, we sought to follow basic experimental guidelines (McGregor *et al.*, 1992). We used song recordings obtained at or near our study area (Naka *et al.*, 2008), playing each species for *c.* 50 s, followed by a listening period of 15 s before starting playback of the next species. These timings were based on field experience and logistic considerations: the total duration of *c.* 10 min per point made it possible to sample up to 12 points in one night.

### Analysis

We tested predictions about the relative magnitude of occupancy in OG and SF sites using a hierarchical model implemented using an objective Bayesian approach (Link *et al.*, 2002; Royle & Dorazio, 2008). Our model is comparable with MacKenzie *et al.*'s (2002) single-season estimate of occupancy probability with imperfect detection, with the

added feature of spatial autocorrelation in the occupancy probability. As a result of this additional complexity, it was easier to implement the analysis in a Bayesian context than with the maximum likelihood approach used by MacKenzie *et al.* (2002). We used an adaptation of Royle and Dorazio's auto-logistic model (Royle & Dorazio, 2008, panel 9.4), with added covariates in the detection and occupancy probabilities (code in supporting information). The model has two main parts, denoted by the curly brackets in Fig. 2: the top bracket represents the sampling process and the bottom one represents the biological process of occupancy (or state). The index  $i$  designates individual sampling sites while  $t$  represents the sampling occasion. Within the biological part, the latent (unobserved) variable  $z$  represents the true occupancy, such that  $z_i = 1$  indicates an occupied site and  $z_i = 0$  otherwise. The  $z_i$ 's are drawn from a Bernoulli distribution with success probability  $\psi_i$ . Thus,  $\psi_i$  represents the probability of occupancy for site  $i$ , which can take any value between zero and one. The parameter  $\psi_i$  is a logistic function of the environment (OG or SF) and of the occupancy of neighboring sampling sites, described by  $\text{logit}(\psi_i) = \alpha + \beta \times \text{SF}_i + \delta \times \text{neigh}_i$ , where  $\alpha$  is the intercept,  $\beta$  measures the effect of the environment (SF = 1 if site  $i$  is SF, and SF = 0 otherwise) and  $\delta$  is the effect of neighbor occupancy on focal site occupancy (neigh is the proportion of occupied neighboring sampling sites). The neighborhood was defined as those sites within a distance of 900 m from site  $i$ . In the sampling process, we use indices  $i$  and  $t$  because sampling conditions may change between sites and between sampling occasions ( $t$ ).  $\mu_{it}$  is an unconditional detection probability, which becomes zero when  $z_i = 0$



**Figure 2** Diagram of occupancy estimation model specifying a biological state component and a sampling component. The model was implemented on a species-by-species basis.  $\psi_i$ , Occupancy, or probability that point  $i$  is occupied;  $\alpha$ , intercept of the occupancy function;  $\beta$ , effect of secondary forest on occupancy;  $\delta$ , effect of neighbor occupancy on focal site occupancy;  $z_i$ , latent variable indicating the presence or absence of the species in site  $i$ ;  $p_{it}$ , conditional probability of detection in site  $i$  at time  $t$ ;  $a_0$ , intercept of the detection function;  $a_1$ , effect of rainy season on  $p$ ;  $\mu_{it}$ , unconditional probability of detection;  $y_{it}$ , observation of the species in site  $i$  at time  $t$  (data).

(site not occupied) and  $p_{it}$  when  $z_i = 1$ . This  $p_{it}$ , the probability of detection conditioned on occupancy, is a simple logistic function of the season (rainy December–April and dry May–November), specified as  $\text{logit}(p_{it}) = a_0 + a_1 \times \text{rainy}_{it}$ , where  $a_0$  is the intercept and  $a_1$  is the effect of rainy season ( $\text{rainy}_{it} = 1$  if sample  $t$  at site  $i$  was collected during the rainy season; otherwise,  $\text{rainy}_{it} = 0$ ). The data were recorded for each site  $i$  during sampling occasion  $t$  such that  $y_{it} = 1$  when the species is detected and  $y_{it} = 0$  otherwise. The data,  $y_{it}$ , are described in the model as random draws from a Bernoulli distribution with success probability  $p_{it}$ .

The model structure reflects our best intuition about the sampling process and the natural history of the species. We explored alternative models without spatial autocorrelation in preliminary analyses using a maximum likelihood approach in program PRESENCE (Hines, 2004). Model comparison based on the Akaike information criterion (Burnham & Anderson, 2004) revealed no evidence of association between detection and either clock time or moon height, hence the simple detection model. We also considered the possibility of different detection probabilities in primary and SF but found no support for such a distinction. Season was considered a relevant factor of detection mostly because muddy trails and frequent rainfall make it relatively difficult to detect birds in the rainy season. One potential source of heterogeneity not explicitly included in the model is that transient, non-territorial individuals might be detected while occupying a site for only part of the study period – possibly violating the assumption of closure in occupancy between sampling occasions. This is a common concern in occupancy studies, which, in our case, is addressed by interpreting occupancy results in terms of proportion of the habitat used by a species rather than the proportion covered by territorial birds of that species (MacKenzie *et al.*, 2006).

The parameters describing the occupancy state ( $\alpha$ ,  $\beta$  and  $\delta$ ) had normally distributed priors with mean zero and variance 20; priors for the detection function parameters ( $a_0$  and  $a_1$ ) were described as uniform on the interval  $(-10, 10)$ . Despite the different specification, which was computationally convenient, all priors are non-informative. We estimate the posterior distribution of model parameters using a Markov chain Monte Carlo with 20 000 iterations and a burn-in phase of 5000 steps (Link *et al.*, 2002). The model was fit individually for each species using a combination of freely available software packages R (R Development Core Team, 2008) and WinBUGS (Spiegelhalter, Thomas & Best, 1999) via the R package R2WinBUGS (Sturtz, Ligges & Gelman, 2005).

To compare the richness and composition of nocturnal bird communities in OG and SF sites, we grouped sites within an environment and treated each set of two consecutive monthly visits as a sample. Recognizing that species are detected imperfectly and with varying detection probabilities, we used information from the multiple samples of each environment to infer the number of species that may be present in that environment but not detected. To this end,

we used jackknife estimates (Burnham & Overton, 1979) of species richness obtained with the freely available program COMDYN (Hines *et al.*, 1999). COMDYN is particularly useful for comparisons between two sets of samples as it provides an estimate of how many species from one set are also present in the other. We used parameter  $\gamma$  to estimate the proportion of OG species that also appear in SF sites.

## Results

We registered 12 species of nocturnal birds (Table 1): eight were detected in both environments, two exclusively in OG and two exclusively in SF. The jackknife estimate of species richness (and its SE) was  $12 \pm 1.81$  for OG and  $11 \pm 1.28$  for SF. The estimated proportion ( $\gamma$ ) of OG species that also occur in SF is  $0.88 \pm 0.13$ .

All focal species, except *L. cristata* and *C. nigrescens*, fulfilled the predictions (Fig. 3, Table 1). Both owls had higher occupancy in OG than in SF even though the estimates did not differ significantly between environments for either species. *Lophotrix cristata*, predictably restricted to OG, also occupied SF sites. Potoo occupancies matched the predictions: *Nyctib. griseus* had higher occupancy in SF than OG, the opposite of *Nyctib. leucopterus*, which was never seen in SF and has a near-zero occupancy estimate there. Both nightjars have higher occupancy in SF than OG, as predicted for *Nyctid. albicollis* but not for *C. nigrescens*. The 95% confidence bounds of the OG and SF occupancy estimates for *C. nigrescens* overlapped slightly, but the estimate of  $\beta$ —which measures the effect of SF on occupancy—is significantly greater than zero (Fig. 4). Overall, four out of the six focal species (*L. cristata*, *Nyctib. griseus*, *Nyctid.*

*albicollis* and *C. nigrescens*) have positive  $\beta$  estimates, with particularly strong effects for *Nyctib. griseus* and the two nightjars. Both *G. hardyi* and *Nyctib. leucopterus* show a negative point estimate of  $\beta$ , but the effect is only significantly different from zero in the potoo. We found no evidence that occupancy of neighboring points affects occupancy of a target point, as indicated by the estimates of  $\delta$ , with 95% confidence bounds that always include zero.

For focal species, dry-season detection probabilities ( $p_d$ ) range from 0.07 with *C. nigrescens* to 0.59 with *Nyctid. albicollis* (Table 1). Estimates of  $a_1$  for *L. cristata*, *Nyctib. griseus* and *Nyctid. albicollis* are significantly negative, evidence that  $p$  is higher during the dry than during the rainy season. There is no evidence of higher detection during the rainy season than during the dry season for any species.

Three of the four additional owls (Table 1, Fig. 4) show higher point estimates of occupancy for SF than for OG, but only the genus *Ciccaba* has a  $\beta$  estimate significantly greater than zero. These four species, which were sampled without playback, generally had lower estimates of  $p$  (ranging from 0.04 to 0.21) without any evidence of change in detection between seasons. As in the focal species,  $\delta$  estimates of the four additional owls were not distinguishable from zero.

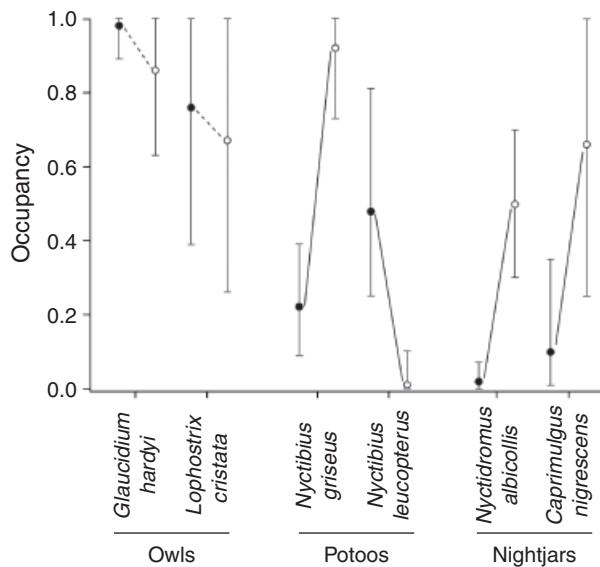
## Discussion

Less than 30 years after the onset of secondary growth, the number of nocturnal bird species in OG and SF sites is indistinguishable. Only one species, *Nyctib. leucopterus*, seems to be convincingly absent from the SF habitat. The broader result that SF is not necessarily species-poor when compared with OG agrees with ornithological studies from

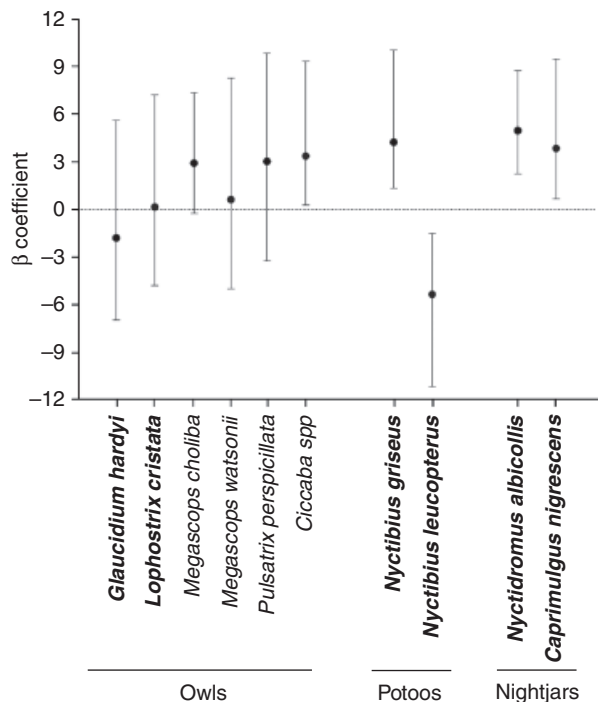
**Table 1** Scientific names and parameter estimates for the nocturnal species observed in this study

Family and species	$\psi_{OG}$	$\psi_{SF}$	$p_d$	$\beta$	$\delta$	$a_1$
Strigidae						
<b><i>Glaucidium hardyi</i></b>	<b>0.98 [0.89–1.00]</b>	<b>0.86 [0.63–1.00]</b>	<b>0.23 [0.18–0.29]</b>	<b>–1.80 [–7.0 to 5.6]</b>	<b>3.82 [–5.5 to 12.9]</b>	<b>0.07 [–0.3 to 0.5]</b>
<b><i>Lophotrix cristata</i></b>	<b>0.76 [0.39–1.00]</b>	<b>0.67 [0.26–1.00]</b>	<b>0.11 [0.06–0.20]</b>	<b>0.15 [–4.8 to 7.2]</b>	<b>6.40 [–4.9 to 16.0]</b>	<b>–0.94 [–1.9 to –0.1]</b>
<i>Megascops choliba</i>	0.02 [0.00–0.10]	0.18 [0.03–0.55]	0.21 [0.04–0.47]	2.93 [–0.3 to 7.3]	5.73 [–2.3 to 13.3]	–1.01 [–3.1 to 0.9]
<i>Megascops watsonii</i>	0.84 [0.44–1.00]	0.81 [0.34–1.00]	0.08 [0.04–0.14]	0.59 [–5.0 to 8.2]	1.44 [–7.3 to 9.8]	–0.08 [–0.8 to 0.7]
<i>Pulsatrix perspicillata</i>	0.63 [0.10–1.00]	0.88 [0.37–1.00]	0.04 [0.01–0.10]	2.99 [–3.3 to 9.8]	–0.75 [–10.0 to 8.6]	–0.70 [–2.3 to 0.7]
<i>Ciccaba</i> spp.	0.20 [0.03–0.71]	0.71 [0.27–1.00]	0.07 [0.02–0.16]	3.39 [0.3–9.3]	0.39 [–8.4 to 9.4]	0.07 [–1.1 to 1.2]
Nyctibiidae						
<b><i>Nyctibius griseus</i></b>	<b>0.22 [0.09–0.39]</b>	<b>0.92 [0.73–1.00]</b>	<b>0.36 [0.27–0.44]</b>	<b>4.27 [1.3–10.0]</b>	<b>2.18 [–5.9 to 10.1]</b>	<b>–1.52 [–2.2 to –0.9]</b>
<b><i>Nyctibius leucopterus</i></b>	<b>0.48 [0.25–0.81]</b>	<b>0.01 [0.00–0.10]</b>	<b>0.14 [0.06–0.25]</b>	<b>–5.33 [–11.1 to –1.5]</b>	<b>3.03 [–4.8 to 10.8]</b>	<b>0.12 [–0.9 to 1.1]</b>
<i>Nyctibius grandis</i>	–	–	–	–	–	–
<i>Nyctibius bracteatus</i>	–	–	–	–	–	–
Caprimulgidae						
<b><i>Nyctidromus albicollis</i></b>	<b>0.02 [0.00–0.07]</b>	<b>0.50 [0.30–0.70]</b>	<b>0.59 [0.46–0.70]</b>	<b>4.98 [2.2–8.7]</b>	<b>–0.02 [–6.1 to 6.2]</b>	<b>–1.37 [–2.1 to –0.6]</b>
<b><i>Caprimulgus nigrescens</i></b>	<b>0.10 [0.01–0.35]</b>	<b>0.66 [0.25–1.00]</b>	<b>0.07 [0.02–0.17]</b>	<b>3.82 [0.7–9.5]</b>	<b>0.94 [–8.3 to 9.8]</b>	<b>0.32 [–0.8 to 1.5]</b>

Focal species pairs appear in bold font. The first three parameters are old growth (OG) forest occupancy ( $\psi_{OG}$ ), secondary forest (SF) occupancy ( $\psi_{SF}$ ), and dry-season probability of detection ( $p_d$ ). The remaining columns show coefficients from the occupancy and detection models:  $\beta$  measures the effect of the binary covariate SF on occupancy, and  $\delta$  measures the effect of the proportion of occupied neighbouring points on the occupancy of the focal point. The coefficient  $a_1$  measures the effect of the binary covariate 'rainy season' on the probability of detection,  $p$ . The values in square brackets indicate 95% confidence bounds, from the posterior distribution of each parameter. Potoos *Nyctib. grandis* and *Nyctib. bracteatus* were only detected twice each, having no sufficient data for parameter estimation.



**Figure 3** Estimates of the mean occupancy probability of focal species for old growth forest (OG) (filled circles) and secondary forest (SF) (open circles) sites, with error bars showing 95% confidence bounds on the posterior distribution. Species, with scientific names abbreviated from Table 1, are paired in the order: owls, potoos and nightjars. The diagonal lines, connecting estimates from the same species, are continuous when the  $\beta$  coefficient of change in occupancy from OG to SF is significantly different from zero and dotted otherwise.



**Figure 4** Estimates of the  $\beta$  coefficient of change in occupancy from old growth forest to secondary forest, for the six focal species (bold font) plus four additional owls (regular font). When 95% confidence bounds do not overlap the dotted line, we consider that the species' occupancy differs significantly between habitats. Positive  $\beta$  values indicate higher occupancies in SF and negative  $\beta$  values indicate higher occupancy in OG.

other neotropical sites. For example, Borges (2007) documented a fast recovery in the number of bird species in SF growing on small abandoned agricultural fields in Jaú National Park, Amazonas, Brazil; Blake & Loiselle (2001) detected more species in SF than in OG forests of La Selva Biological Station, Costa Rica. The idea that SF provides habitat to a large number of species is also corroborated by at least two recent reviews about SF fauna (Dunn, 2004; Dent & Wright, 2009). Bird mobility and the proximity of a vast source of colonizers (our study area is surrounded by thousands of square kilometers of OG) certainly help to explain why the number of species is similar between habitats. What is not easily explained is why several species have higher occupancy probabilities in SF than in OG sites. Below, we interpret the occupancy results for each family.

The species in each focal pair can be described as indifferent (owls), contrasting (potoos) and concurrent (nightjars) in their responses to SF habitat. This is itself in contrast to our prediction that all pairs would show opposite or near-opposite responses between species. For the owls, there is no evidence that either species favors one type of habitat over the other. This was expected for *G. hardyi* but not for *L. cristata*, which showed no evidence of greater occupancy in either habitat, even though we supposed it was restricted to OG. The unexpected tolerance of SF extends to the extra owl species that were sampled without playback. Two of them clearly favor SF, one is indifferent and one (*P. perspicillata*) appears to have higher occupancy in SF than OG sites. This pattern will be most intriguing if the animals are breeding in SF because most owls, including *P. perspicillata* and many *Glaucidium* species (Marks *et al.*, 1999), nest in tree holes that are presumably easier to find in OG. Conversely, many owls feed largely on small mammals (Sick, 1997; Marks *et al.*, 1999) and small mammal abundance is believed to be higher in local isolated forest patches than nearby undisturbed OG (Malcolm, 1997). If the high abundance in the patches can be attributed to high abundance in SF, one might speculate that a greater availability of food is leading to high owl occupancy in SF sites.

The occupancy patterns of the potoos, *Nyctib. leucopterus* and *Nyctib. griseus*, matched our predictions, and it is noteworthy that the pair from the least species-rich family revealed the most divergent results. *Nyctibius griseus* is a habitat generalist, known to occur in primary and SF in both *terra firme* and seasonally flooded areas; thus, it is not surprising that it occupies more SF than OG sites. On the other hand, *Nyctib. leucopterus* does indeed appear to be a habitat specialist, from the canopy of primary *terra firme* forest (Cohn-Haft, 1999); it was the only species in our sample that clearly avoided SF. We have no information about the nesting of *Nyctib. leucopterus*, but *Nyctib. griseus* is known to nest on shallow depressions on the top of broken tree stumps (Muir & Butler, 1925; Tate, 1994). It is not yet clear whether nest site availability plays a limiting role in potoo SF or OG occupancy.

Both species of nightjars had higher occupancy in SF than in OG sites. This was contrary to expectation only for *C. nigrescens*; yet, the underlying mechanism may be the

same for both species. Nightjars forage by sallying into open air after flying insects. Thus, both species probably require open areas as a microhabitat. Although *C. nigrescens* is found within extensive primary forest, it is known to nest on bare rock surfaces in openings within OG (Ingels & Ribot, 1983; Cleere, 1998). There are no rocks in our study sites, but there is a higher density of roads (and adjacent bare ground) in SF than in OG areas. It is also noteworthy that the only OG sites where we detected *C. nigrescens* were in an area with several new large tree falls due to wind damage that occurred 3 months before the beginning of the observations.

Some species (e.g. *C. nigrescens*, Table 1) had remarkably low detection probabilities while others were relatively easy to detect (*Nyctid. albicollis*). The variability in detection across species emphasizes the importance of explicitly accounting for the detection process in quantitative comparisons of occupancy. The formal treatment of detection failure strengthens our confidence in the parameter estimates: five of the 10 species analyzed have higher occupancy in SF than OG sites. This result must be interpreted in the specific context of our study area: a relatively small area of advanced SF embedded in a vast expanse of OG. If we were merely observing that some OG species also occupy SF sites, we might imply that birds from the OG are occasionally appearing in SF. The result, however, is of a higher proportion of occupied sites in SF than in OG, which suggests the possibility of habitat preference. Would the same pattern arise in a landscape dominated by SF? Are these species breeding successfully in SF? Such questions require estimates of occupancy from an SF-dominated landscape and a more detailed understanding of the natural history of nocturnal birds in our study area. Depending on their natural history, SF-favoring species may be completing all stages of their life cycle in SF, surviving and reproducing successfully without using resources from OG. Alternatively, SF sites may be frequently occupied (even more so than OG sites), but a population of SF individuals will not be able to survive without some form of resource or demographic input from the OG (Pulliam, 1988). Regardless of the mechanism behind each species' occupancy pattern, it is clear that SF provides habitat for most of the nocturnal birds in the study area. SF are not lost habitat and should be legally treated as appropriate targets of conservation effort.

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### Appendix S1. WinBUGS model specification.

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