Research

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Scale-dependent responses to forest cover displayed by frugivore bats

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Despite vast evidence of species turnover displayed by Neotropical bat communities in response to forest fragmentation, the exact shape of the relationship between fragment area and abundance for individual bat species is still unclear. Bats' ample variation in diet, morphology, and movement behaviour can potentially influence species' perception of the landscape. Thus, studies describing fragment area at a single spatial scale may fail to capture the amount of forest available from the perspective of individual bat species. In the present paper, we study the influence of forest cover on bats inhabiting a fragmented forest in Mexico, focusing on some of the most common frugivore species: *Artibeus jamaicensis*, *Carollia* spp. (*C. brevicauda/C. perspicillata*) and *Sturnira* spp. (*S. lilium/S. ludovici*).

We quantified forest cover at scales ranging from 50 to 2000 m, and measured the influence of forest cover on bat capture success, a surrogate for abundance. The three species displayed positive and significant scale-dependent associations with forest cover. Abundance of *A. jamaicensis* increased with forest cover measured at scales ranging between 500 and 2000 m, while *Carollia* spp. responded more strongly to variation in forest cover measured at scales of 100–500 m. For *Sturnira* spp., abundance was a function of presence of creeks near mist-netting sites, and amount of secondary forest present at a 200 m scale. The observed variation in responses to forest cover can be explained in light of interspecific differences in diet, home range, and body size. Our results illustrate a method for measuring the effect of forest fragmentation on mobile species and suggest that changes in abundance in fragmented landscapes emerge from the interaction between species' traits and landscape structure.

Patchiness is a pervasive pattern in ecology that can be described at a range of spatial scales (Levin 1992, Keitt and Urban 2005). When foraging, individuals must adjust their movement behaviour according to the level of patchiness in resource distribution, and as a result species display adaptations pertaining to dispersal, sensory, and cognitive abilities that dictate their ecological neighbourhood (Addicott et al. 1987, Wiens 1989). Thus species differing in natural history traits are expected to respond to a distinct subset of scales in resource distribution. Vertebrate body mass is a good predictor of home range size (McNab 1963, Swihart et al. 1988, Minns 1995). For bats, the influence of body mass on movement and foraging behaviour has been extensively studied (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Nevertheless, the implications of these relationships for the study of species' response to habitat fragmentation has been little explored. Bat census studies in the Neotropics have revealed important differences in community diversity and composition between fragments and continuous forest (Cosson et al. 1999, Schulze et al. 2000, Estrada and Coates-Estrada 2002, Pineda et al. 2005, Faria 2006, Montiel et al. 2006), but in contrast few studies (Gorresen et al. 2005) have detected a significant effect of fragment area on the abundance of individual bat species. It is possible that, by measuring habitat availability at a single scale, most bat survey studies fail to take into account interspecific differences in ecological neighbourhood.

We focus on species of frugivore bats (family Phyllostomidae) that are common throughout the Neotropics: *Artibeus jamaicensis*, *Carollia brevicauda*, *C. perspicillata*, *Sturnira lilium* and *S. ludovici*. The target species have similar uses of the vertical strata: they are considered gleaning species (Kalko et al. 1996) that fly in the understory and are frequently captured using ground mist-nets (Bonaccorso 1979, Simmons and Voss 1998, Bernard 2001). However, there are important differences in the spatial distribution of their preferred food items. *Artibeus jamaicensis* consumes fruits from late-successional trees such as *Ficus* spp. (Morrison 1978a, Bonaccorso 1979). This preference for a food resource that has a scattered distribution is associated with a larger body mass and home range (Morrison 1978a). On the other hand, species from the genus *Carollia* frequently feed on early-successional plants such as *Piper* spp. (Heithaus and Fleming 1978, Marinho-Filho 1991). *Sturnira* shows a preference for *Solanum* spp. fruits (Marinho-Filho 1991) and is commonly found in early-successional areas near creeks (Emmons and Feer 1997). This variation in resource distribution is likely to influence the scale at which species perceive the landscape, thus scale-sensitive measures of habitat availability are warranted when modeling the causes of variation in bat abundance.

In this paper, we have modeled the relationship between bat capture success (a surrogate for abundance) and forest cover measured at several spatial scales in a tropical rainforest in Mexico. Here, the term 'scale' is equated with focus, the scale at which grains are aggregated (sensu Scheiner et al. 2000), and 'grain' refers to the standardized unit used to count the variable of interest (Scheiner et al. 2000) – in our case, 'grains' are pixels from a satellite image classified as 'forest'. In practice, scale is equated with the radius used to define the area over which forest cover is calculated. Our goal was to employ a scale-sensitive approach to quantify the responses to habitat loss displayed by particular bat taxa.

Methods

Field site

Field work was carried out between June and August 2005 in the region of Los Tuxtlas (Fig. 1) in the municipality of San Andres Tuxtla, Veracruz, Mexico (18°25′N, 95°00′W), a region harbouring the northern limit of lowland Neotropical rainforest. The mean temperature ranges from 24 to 26°C and annual precipitation ranges between 3000 and 4500 mm (Soto and Gama 1997). Bat sampling was performed in privately-owned farms located in the Los Tuxtlas Biosphere Reserve, in an area adjacent to a 3500 ha forest that includes the Biological Field Station Los Tuxtlas of the Univ. of Mexico (UNAM).

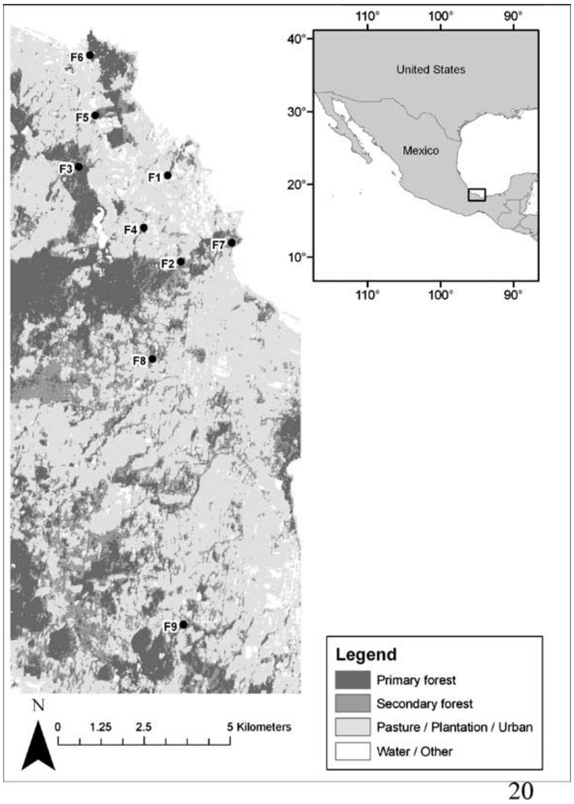

Figure 1. Study site in Los Tuxtlas, Mexico, showing the nine sampling points labeled as F1–F9.

Bat species and mist-netting

The bat species used in the present study are abundant in Los Tuxtlas. Individuals have been captured in continuous forest as well as fragments (Estrada and Coates-Estrada 2002) and represent important seed dispersers in this ecosystem (Galindo-Gonzalez et al. 2000). The mean body size in grams is 46.1 for *A. jamaicensis*, 19.5 for *C. perspicillata*, 18.5 for *C. brevicauda*, 17.6 for *S. lilium*, and 23.2 for *S. ludovici* (Estrada and Coates-Estrada 2002). Due to difficulty identifying individuals, we have pooled data for sister species and will therefore report results for *Carollia* spp. and *Sturnira* spp.

We captured bats in nine sites (F1–F9; Fig. 1) using mist-nets. Each site was sampled for two consecutive nights, starting 15 min after sunset and lasting five h. Two 2 × 12 m mist nets were placed 3–5 m apart and within 25 m of the border of a forest fragment and along a trail. In four fragments, mist-netting was performed within 20 m of a creek. Sampling was interrupted in nights of full moon (due to bat lunar phobia) and during heavy rain. Each individual was identified to species and we determined its sex, age (adult or juvenile), and if female we assessed its reproductive status (pregnant, lactating or non-reproductive). Individuals were also weighed to the nearest 0.5 g. Bat capture success for each site was calculated as the number of captured individuals divided by the number of net-hours, the number of open nets times the number of hours nets were open.

Analyses

The study site was characterized using a SPOT 3 satellite image taken in 2005 containing 3 spectral bands and 20 m spatial resolution. We performed unsupervised classification using the method ISOCLUSTER from Idrisi (Clark Labs, MA, USA) and the resulting distribution of land cover classes was consistent with aerial photographs of the study area. This classified image was further processed to produce a map with three land cover classes: (1) primary forest, (2) secondary forest, and (3) 'other', including urban areas, crop plantations, pastures, and water (Fig. 1).

Forest cover around all sampling sites was quantified by defining several circles, each one centered where mist nets were located (Fig. 1) and with radii ranging from 50–2000 m (inclusive) at intervals of 50 m. For each radius, we calculated the number of 20 × 20 m pixels classified as 'forest' inside each of those circles. Three forest cover values were produced for each scale: primary forest, secondary forest, and primary + secondary. These quantities represent the amount of potential bat habitat associated with spatial scales ranging from 50 to 2000 m. Besides forest successional stage, one important difference among fragments was the presence of creeks near mist-netting sites. Thus, another predictor variable of bat abundance was 'creek presence', with possible values 0 (absent) and 1 (present).

We used linear regression to model the relationship between capture success and forest cover, performing one regression for each spatial scale and each forest successional type. Values of R^2 and p were computed for each regression, and slope estimates were inspected in order to determine whether bat abundance had a positive or negative relationship with forest cover. The scale for which the largest value of R^2 was found was taken as the scale at which species displayed the strongest response to forest cover (Fig. 2).

The importance of spatial autocorrelation was assessed using Mantel's permutation test (Mantel 1967). Regression residuals were spatially correlated for *A. jamaicensis* (Mantel test, $p < 0.05$), thus for this species we employed a conditional autoregression (CAR, Cressie 1993). CAR is a linear model that partitions the response variable into trend (the spatially-independent component), signal (the spatial component), and noise, taking into account the proximity

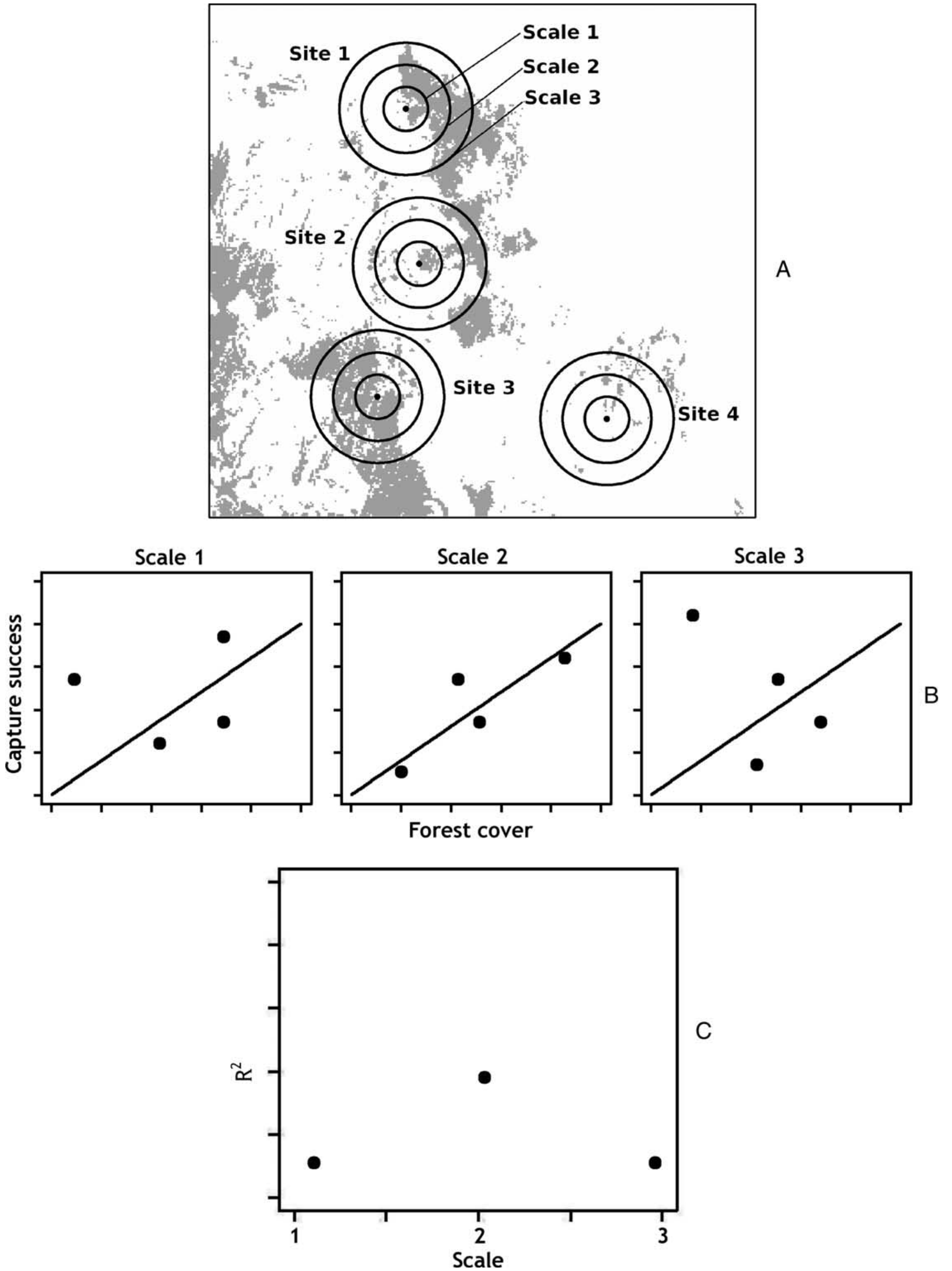

Figure 2. Schematic illustration of the general approach used to measure scale-dependent associations with forest cover. (A) for each site, forest cover is measured at increasingly larger scales. (B) one linear regression is performed for each scale, relating bat capture success and forest cover. The regression fit (R^2 or log likelihood) is computed. (C) plots of scale X regression fit may show a peak representing the scale at which the species display the strongest response to forest cover.

between sampling points. In this case, we report the log likelihood as the estimate of model fit, and p-values associated with the slope of the trend term. In all regressions, we used a significance level of 0.05. The language R (R Development Core Team) was employed to quantify forest cover and to perform all statistics.

Results

Captures totaled 135 for *Carollia* spp., 71 for *Artibeus jamaicensis*, and 143 for *Sturnira* spp. The number of net hours per site ranged from 13 to 19 (mean = 16.25). A positive and significant relationship between forest cover and capture success was found for all three groups, however species responded differently to forest successional stages and scale of measurement of forest cover. Adding the variable 'creek presence' did not have a substantial impact on the fit of the models for *Carollia* spp. or *Artibeus jamaicensis*, thus this variable was only used to model abundance of *Sturnira* spp.

In the regression for *Artibeus jamaicensis*, we removed one point consisting of a site (F1) where the netting was performed adjacent to a day roost. *A. jamaicensis* responded to large-scale variation in forest cover and was differentially influenced by forest successional stage. The strongest correlation between bat capture success and forest cover was observed when primary forest was measured at a 1500 m scale, secondary forest was measured at a 1000 m scale, and primary + secondary forest was measured at a 1500 m scale (Fig. 3a). In the regression using primary + secondary forest as the independent variable (Fig. 3a) we show only the points associated with CAR models that successfully eliminated the spatial autocorrelation in the data.

Contrasting with *A. jamanceisis*, *Sturnira* spp. and *Carollia* spp. responded to small-scale variation in forest cover. We obtained one significant model for *Sturnira* spp. relating abundance to the presence of a creek near mist-netting sites, and amount of secondary forest measured at a 200 m scale ($R^2 = 0.64$; $p = 0.044$; Fig. 3b). For *Carollia* spp., the strongest relationship between abundance and forest cover was obtained when successional stages were aggregated (primary + secondary forest) and forest cover was measure at scales ranging between 100 and 500 m (Fig. 3c).

Discussion

We have studied responses to forest cover displayed by three common bat genera in a tropical fragmented landscape in Los Tuxtlas, Mexico. In agreement with studies performed in a subtropical forest (Gorresen et al. 2005), bats displayed scale-dependent responses to forest cover. Abundance of *Carollia* spp. and *Sturnira* spp. was a function of small-scale variation in forest cover (Fig. 3b–c), while abundance measured for *A. jamaicensis* was largely a function of large-scale variation in forest cover (Fig. 3a). *Sturnira* spp. responded to a very narrow range of spatial scales (Fig. 3b). For this species, local conditions were as important as the distribution of forested areas in predicting abundance patterns: significant models were obtained only after taking into account the presence of creeks near mist-netting sites.

Frugivore bats do not present a single spatial scale of movement. Fine-scale movements include daily commuting from a day roost to a feeding area and movement between feeding areas and night roosts (Emmons and Feer 1997). Bats also perform large-scale movements, including exploratory flights and roost changes (Heithaus and Fleming 1978, Bernard and Fenton 2003). Due to the small temporal scale of our study, it is reasonable to expect our results to reflect differences in fine-scale movements that occur daily rather than occasional exploratory flights and roost changes. Past ratio telemetry studies have revealed significant differences in bat commuting distances. In Los Tuxtlas, female *A. jamaicensis* have been observed to fly an average of 8 km between day roosts and feeding areas (Morrison 1978b), whereas radio tracking studies in Costa Rica estimate an avegage distance of 0.81 km between day roosts and feeding areas for *C. perspicillata* (Heithaus and Fleming 1978).

When quantifying forest cover, we produced separate estimates for primary and secondary forest. In general, abundance of *Carollia* spp. increased with estimates of forest cover that aggregated both successional stages (Fig. 3c). One possible interpretation of this result is that the combination of primary and secondary forests forms a more continuous habitat than either classes alone (Fig. 1), and habitat connectivity is more important than successional stage for this species. Abundance of *Sturnira* spp. increased only with amount of secondary forest (Fig. 3b), which reflects its preference for shrubs that grow in early-successional habitats.

Abundance of *A. jamaicensis* increased significantly with both primary and secondary forest (Fig. 3a), confirming this species' status as a habitat generalist (Bonaccorso 1979). In addition, our results were driven by the interaction between spatial scale and successional stage: bat abundance was positively correlated with secondary forest measured at a 1000 m scale, and primary forest measured at a 1500 m scale. This may reflect the use of different resources by *A. jamaicensis.* Previous work in Los Tuxtlas reports consumption of fruits that typically grow in early-successional habitat (Galindo-Gonzales et al. 2000). Areas of secondary forest can also function as links between feeding areas in mature forest. Although obstacle course experiments have suggested that *A. jamaicensis* is less efficient in negotiating obstacles in highly cluttered habitats (Stockwell 2001), many disturbed areas such as Los Tuxtlas contain trails that can be used as flyways by *A. jamaicensis.*

Changes in bat communities due to forest fragmentation have been widely documented in the Neotropics (Cosson et al. 1999, Schulze et al. 2000, Estrada and Coates-Estrada 2002, Pineda et al. 2005, Faria 2006, Montiel et al. 2006). But researchers employing single-scaled measures of fragment area have been unable to detect a significant effect of habitat loss on bat abundance (Faria 2006). Using a scale-dependent measure of forest cover has enabled us to predict a large amount of variation in bat abundance (>70% for *Carollia* spp. and >60% for *Sturnira* spp.; Fig. 3b–c). These results support the assertion that grid-based indices are well suited to study mobile species – particularly central-place foragers – that inhabit complex landscapes where

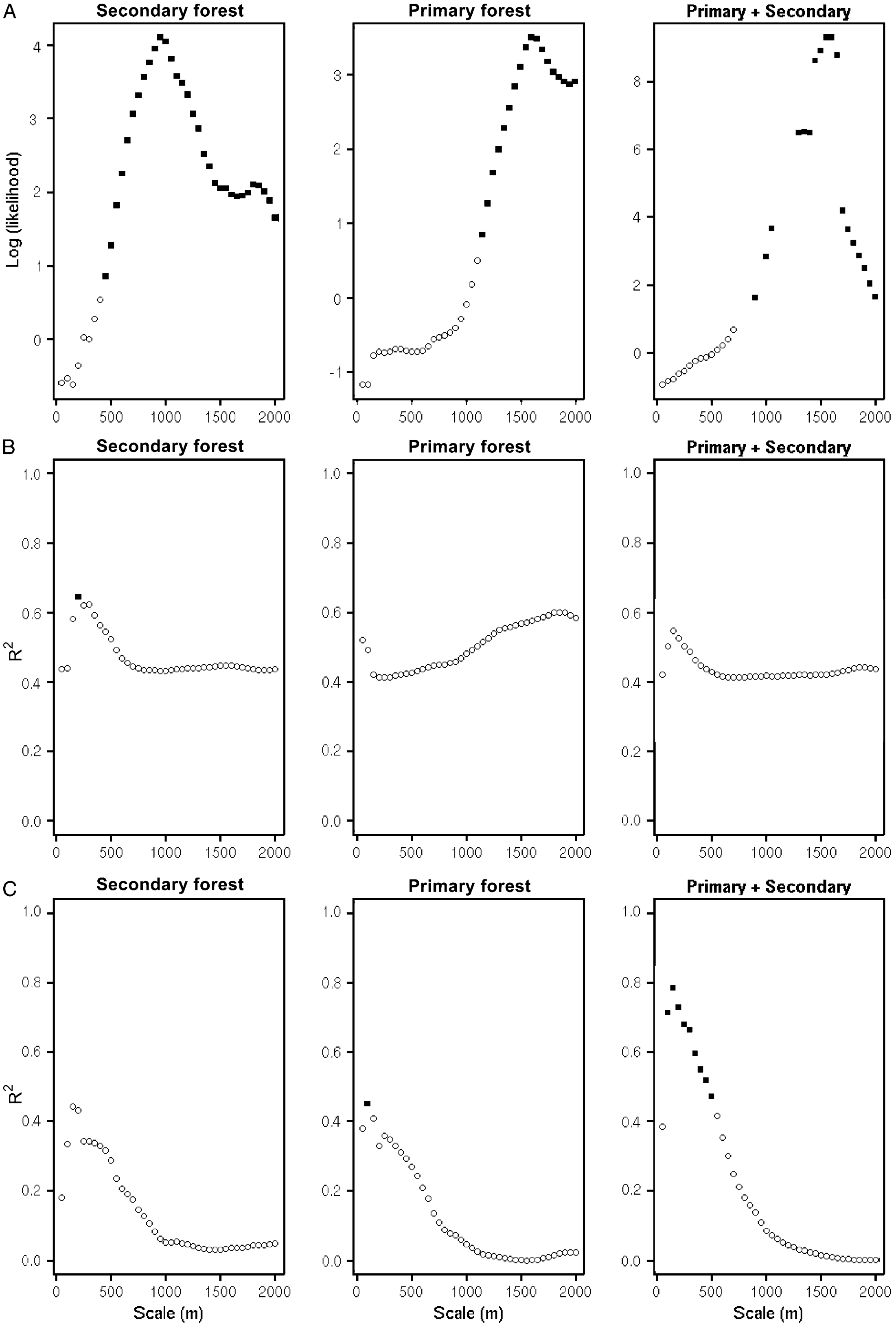

Figure 3. Graphs representing the fit of regression models relating forest cover and bat abundance. The x-axis contains the scales at which forest cover was measured, ranging from 50 to 2000 m at intervals of 50 m. The y-axis contains the R^2 value or log likelihood value for the linear model relating bat abundance and forest cover. Closed squares indicate significant models ($p < 0.05$) and open circles indicate non-significant models ($p > 0.05$). (A) *Artibeus jamaicensis*, (B) *Sturnira* spp., (C) *Carollia* spp.

habitat patches are difficult to define (Kremen et al. 2004, Winfree et al. 2005). From a practical perspective, the approach exemplified here facilitates among-site comparisons, because the task of delineating fragments brings some subjectivity to analyses. We deliberately employed a simple measure of habitat availability which might not be appropriated for less common, specialist bat species. One possible modification of the metric used here is to weight each habitat pixel by its estimated quality (Betts et al. 2006) or by the relative cost to reach it given a movement model (Verbeylen et al. 2003, Drielsma et al. 2007).

Our results illustrate a simple approach for quantifying the effects of habitat fragmentation on mobile species. From a conservation perspective, the species' differential responses to landscape structure observed here may represent one of the mechanisms underlying community turnover in fragmented landscapes, a pattern that has been demonstrated for vertebrates and invertebrates in the Amazon (Laurance et al. 2002). Studies with larger number of species and feeding guilds should elucidate whether body mass, diet, and other traits that correlate with movement behavior are in general correlated with bats' responses to landscape structure.

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