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RESEARCH ARTICLE

# The relative importance of local versus landscape variables on site occupancy in bats of the Brazilian Cerrado

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**Abstract**

*Context* Species site-occupancy patterns may be influenced by habitat variables at both local and landscape scales. Although local habitat variables influence whether the site is suitable for a given species, the broader landscape context can also influence site occupancy, particularly for species that are sensitive to land-use change.

*Objectives* To examine the relative importance of local versus landscape variables in explaining site occupancy of eight bat species within the Brazilian Cerrado, a Neotropical savanna that is experiencing widespread habitat loss and fragmentation.

*Methods* Bats were surveyed within 16 forest patches over two years. We used a multi-model information-theoretic approach, adjusted for species detection bias, to assess whether landscape variables (percent cover and number of patches of natural vegetation within a 2- and 8-km radius of each forest site) or local site variables (canopy cover, understory height, number of trees, and number of lianas) best explained site occupancy in each species.

*Results* Landscape variables were among the best models ($\Delta AIC_c$ or $\Delta QAIC_c < 2$) for four species (top-ranked model for black myotis), whereas local variables were among the best for five species (top-ranked model for vampire bats). Neither local nor landscape variables explained site occupancy in two frugivorous species.

*Conclusion* Species associated with a particular habitat type will not respond similarly to the amount, distribution or relative suitability of that habitat, or even at the same scale. This reinforces the challenge of species distribution modelling, especially in the context of forecasting species' responses to future land-use or climate-change scenarios.

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## Introduction

Both local and landscape variables can affect a species' probability of occurrence (site occupancy), thereby shaping patterns of diversity and abundance

across a range of scales (Blevins and With 2011; Mortelliti et al. 2012). The relative importance of local versus landscape factors on site occupancy is expected to depend on the scale at which species perceive and respond to environmental heterogeneity, which is a function of their resource needs, body size, and dispersal ability (e.g., With 1994). In the case of bats, a variety of local and landscape factors are known to influence species diversity and abundance within a region (Duchamp and Swihart 2008; Estrada-Villegas et al. 2010; Ethier and Fahrig 2011; Mendenhall et al. 2014; López-González et al. 2014), but few studies have investigated the relative effects of local versus landscape variables on species occurrence (but see Erickson and West 2003; Avila-Cabadilla et al. 2012). As a result, our understanding of the scale at which bat species respond to local versus landscape factors is incomplete at best, or completely inaccurate at worst. This is important because reported species-habitat relationships are being widely used in species distribution modelling in which the simulated response of entire communities is predicted based on the reported response of different species to scenarios of landscape and climatic change (e.g., Peterson et al. 2002; Wiens et al. 2009; Barnagaud et al. 2012). Given that bats provide a variety of important ecosystem services, such as pollination, insect control, and seed dispersal (Quesada et al. 2004; Muscarella and Fleming 2007; Kalka et al. 2008; Fleming et al. 2009; Jacomassa and Pizo 2010), research that takes a multi-scale approach to determine factors that influence species' occurrences, and thus diversity for an area, is vitally important for assessing the impact that current or future land-use changes might have on bat assemblages.

Species' responses to landscape structure are often idiosyncratic, with different bat species exhibiting divergent responses to land use within a given region (Duchamp and Swihart 2008; Avila-Cabadilla et al. 2012; Bellamy et al. 2013; Ducci et al. 2015). Divergent responses to land use may occur because of differences in the flight habits and feeding behaviors of species (Klingbeil and Willig 2010; Avila-Cabadilla et al. 2012; Ducci et al. 2015), although it is unclear whether differences in flight behavior and feeding guild can be used to predict species' responses to landscape structure. In the Neotropics, for example, some frugivorous phyllostomid species are positively related to forest amount while others are not (Gorresen

et al. 2005; Klingbeil and Willig 2010). The same idiosyncratic responses have been observed in aerial insectivores in the Neotropics (Rodríguez-San Pedro and Simonetti 2015). Local variables, such as habitat type and structural complexity, can also be important determinants of bat species abundance (Avila-Cabadilla et al. 2012). Gleaning animalivores may avoid disturbed forests in which the understory or canopy has been removed (Meyer and Kalko 2008; Klingbeil and Willig 2010), whereas some species are abundant in agroforestry areas, such as cocoa and banana plantations, which provide fruits and attract insects and other small vertebrates consumed by these species (Faria et al. 2006; Harvey and Villalobos 2007).

Landscapes worldwide have experienced enormous changes in recent decades due to agricultural conversion (Murphy and Romanuk 2014). Tropical savannas in particular have been among the most threatened (Hoekstra et al. 2004). In this study, we investigate the relative importance of local versus landscape factors on the site occupancy of eight bat species, representing different feeding behaviors, in the Brazilian Cerrado. The Cerrado is the most biologically diverse and threatened tropical savanna in the world (Silva and Bates 2002), and is considered a global biodiversity hotspot (Myers et al. 2000). The exploitation of this biome is ongoing, however, because it is located within a major agricultural frontier in Brazil (Sano et al. 2010). We investigated a number of variables that could potentially affect bat species occurrence in the Brazilian Cerrado at local (site-based) and landscape scales. At the landscape scale, the amount of natural vegetation remaining on the landscape could be an important correlate of species occurrence if it is a good predictor of available habitat for bat species (Gorresen et al. 2005; Duchamp and Swihart 2008; Ripperger et al. 2013; Mendenhall et al. 2014; Arroyo-Rodríguez et al. 2016). Fragmentation—the subdivision of native remnants on the landscape—could also be important since bats can be positively or negatively edge-sensitive (Meyer et al. 2007; Kerth and Melber 2009; Klingbeil and Willig 2010; Ethier and Fahrig 2011; Frey-Ehrenbold et al. 2013; Ducci et al. 2015; Rodríguez-San Pedro and Simonetti 2015). Habitat fragmentation could increase encounters with patch edges and the land-use matrix (Pe'er et al. 2011), which could increase or decrease site occupancy for a specific bat species, depending on whether it is negatively or positively affected by edge. At the local

habitat scale, tree density is related to roost and food availability (Erickson and West 2003; Evelyn and Stiles 2003), and the degree of canopy closure could provide protection against predators, wind, and rain (Fenton et al. 1998). Understory vegetation is expected to be related to the amount or availability of food resources for some bat species (Thies and Kalko 2004; Trevelin et al. 2013), whereas the number of lianas—woody vines—might create obstacles to flight for others (Tabanez and Viana 2000).

Based on the feeding and flight behaviors of each species, we developed a set of a priori predictions as to the relative importance of local versus landscape variables to species occurrence for eight target species (Fig. 1). Hematophagous species like the vampire bat (*Desmodus rotundus*) may benefit from land-use intensification and a decrease in native vegetation at the landscape scale, such as that associated with cattle ranching, given that cattle are a major food source for vampire bats (Medellín et al. 2000; Harvey and Villalobos 2007; García-Morales et al. 2013). Aerial insectivores like the black myotis (*Myotis nigricans*) are expected to respond positively to increased habitat subdivision (i.e., habitat fragmentation), because they forage along habitat edges (Estrada-Villegas et al. 2010; Denzinger and Schnitzler 2013; Chambers et al. 2016). Nectarivores like the Pallas' long-tongued bat (*Glossophaga soricina*) forage widely across the landscape (Aguiar et al. 2014), and are expected to be positively affected by native-vegetation amount. In contrast, understory frugivores like the little yellow-shouldered bat (*Sturnira lilium*) should be dependent on local-scale variables such as understory height (Muscarella and Fleming 2007) and landscape variables such as native-vegetation amount, because they select large-diameter trees for roosting (Evelyn and Stiles 2003). Small canopy frugivorous bats, such as Gervais's fruit-eating bat (*Artibeus cinereus*) and the Incan broad-nosed bat (*Platyrrhinus incarum*), should be affected by local variables, such as canopy density, as well as native-vegetation amount at the landscape scale, because they may travel long distances in search of ripe fruit. Finally, large frugivorous bats, such as the white-lined broad-nosed bat (*Platyrrhinus lineatus*) and the great fruit-eating bat (*Artibeus lituratus*), are not expected to be sensitive to either local or landscape variables, given their high capacity for movement and persistence within human-modified landscapes (Bianconi et al. 2006; Menezes Jr. et al. 2008; Mendes et al. 2009).



Fig. 1 Conceptual model and expected responses of bat species to environmental variables measured at local versus landscape scales. We expect that the relative importance of local versus landscape covariates on site occupancy will depend on the scale at which species perceive and interact with habitat structure. ©great fruit-eating bat (*Artibeus lituratus*) illustration-Leandro Lopes de Souza. ©vampire bat (*Desmodus rotundus*) photo-Poliana Mendes. ©Incan broad-nosed bat (*Platyrrhinus incarum*) photo-Pedro Henrique Pereira Braga
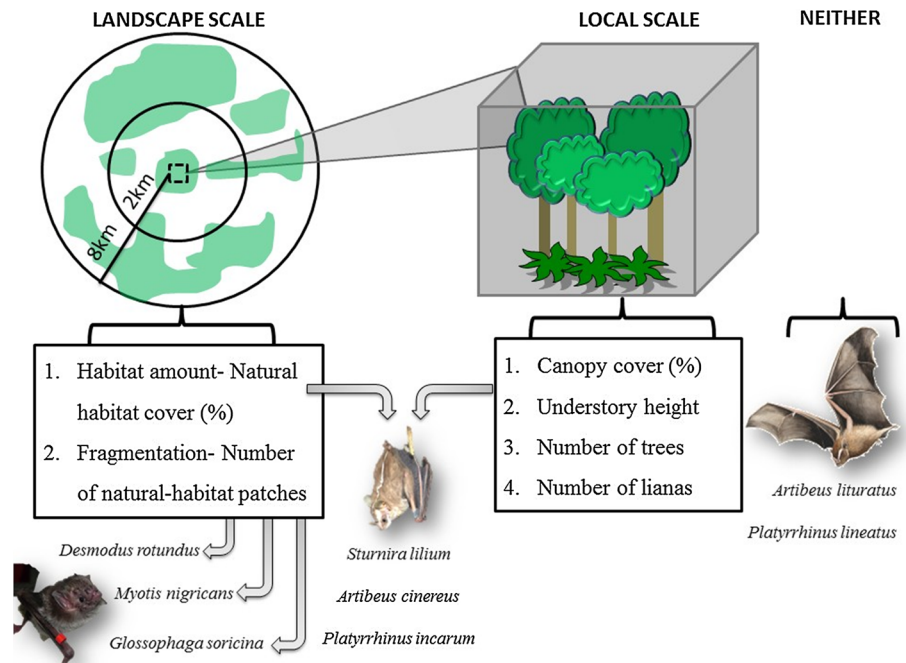
## Methods

### Study area

We surveyed bats year-round within 16 native forest patches in the state of Goiás, which is located in the heart of the Cerrado in central Brazil (Fig. 2), for 2 years from March 2012 to March 2014. This biome has a mosaic of natural vegetation types, including grasslands, dry forests, gallery forests, and wetlands (Sano et al. 2010). We opted to survey native forest patches because these support higher bat species richness relative to other vegetation types in the Cerrado (Monadjem and Reside 2008; Gregorin et al. 2011). Across the study area, we identified forest patches of similar size (90–400 ha) and shape (shape index < 2; shape index = 1 for a square patch) in an effort to minimize patch-based effects on bat abundance. We then defined a 5-km radius around each patch centroid to refine the number of patches to survey to only those patches where the amount and number of patches of natural vegetation were uncorrelated to minimize confounding these two landscape variables in our analysis. We selected this initial "landscape scale" of 5 km based on a previous study of bats in a Paraguayan forest (Gorresen et al. 2005) that showed 5 km to be the best scale for predicting species' responses to landscape structure (including four of the bat species we analyze in this paper). We modified our landscape definition in subsequent analyses, based on landscape scales better suited to the species we studied (see *Local and landscape covariates of species occurrence*).

Landscape data were obtained from the Ministry of Environment of Brazil for the year 2010 (http://siscom.ibama.gov.br/). Owing to logistical and personnel constraints, forest patches were surveyed for bat species presence on different occasions over the course of the study. Within a forest patch, bat surveys were conducted during a single four-night sampling period. In each forest patch, we captured bats using a total of 20 mist nets (10 m × 2.5 m), arranged in four groups of five mist nets along a single transect (∼200 m) that ran from the edge to the center of the patch, with each group of nets situated ∼5 m apart (Fig. 2). Nets were opened at sunset for 6 h, during which time nets were checked every 30 min, and then closed until sunset the following day. All bats were identified to species. The majority of bats were marked

**Fig. 2** Study design. We surveyed bats within 16 landscapes in ▶ the state of Goiás in central Brazil (**a**). Landscapes were chosen to represent a range of variability in the amount and fragmentation (number of patches) of the natural Cerrado habitat (**b**-*large circles*). Each landscape was centered on a focal forest patch, in which we surveyed bats and obtained local-scale measures from three quadrats (10 m × 10 m) oriented along the mist-net transect (**c**). Landscape metrics (amount of natural habitat and number of natural-habitat patches) were obtained at two scales within a 2- and 8-km radius of the focal forest patch (**b**)

with forearm bands, except juveniles and small species (<5 g). Bats were handled and released as soon as possible after capture. This research was authorized by the federal agency Instituto Chico Mendes (license number 36252, 40630, and 34352), which regulates scientific procedures on wild fauna and flora in Brazil. We also followed the guidelines of the American Society of Mammalogists governing the use of wild mammals in research (Sikes and Gannon 2011).

To minimize potential biases in the estimation of species occurrence, we decided at the outset to focus our analyses on species that were captured in 20–80% of forest patches (i.e., species were neither so rare as to make estimates unreliable, nor so common as to make local habitat or landscape effects on species occurrence irrelevant; Kendall and White 2009). Eight of the 33 bat species we captured during our study met this criterion, with a naïve occupancy ($\widehat{\psi}$) that varied from 0.25 to 0.75 among these eight species.

### Local and landscape covariates of species occurrence

After identifying which bat species occurred with sufficient frequency for analysis, we adopted a more species-centered definition of "landscape" and quantified landscape structure within a radius of 2 and 8 km of each forest patch, so as to bracket the spatial extents of the largest daily flight distances reported for these species (Trevelin et al. 2013; Womack et al. 2013; Aguiar et al. 2014). We quantified the amount (percent cover) and fragmentation (as assayed by the number of patches) of natural vegetation within each landscape at each of these two scales, using the Patch Analyst extension for ArcGIS/ArcMap® version 9.2 (Rempel et al. 2012) on LANDSAT ETM + images obtained during August 2013 (30-m resolution; bands 3, 4 and 5). We performed a supervised classification to

Landscape scale

4km

16km

Local scale

10m

Mist-nets ∿∿
Quadrants ☐
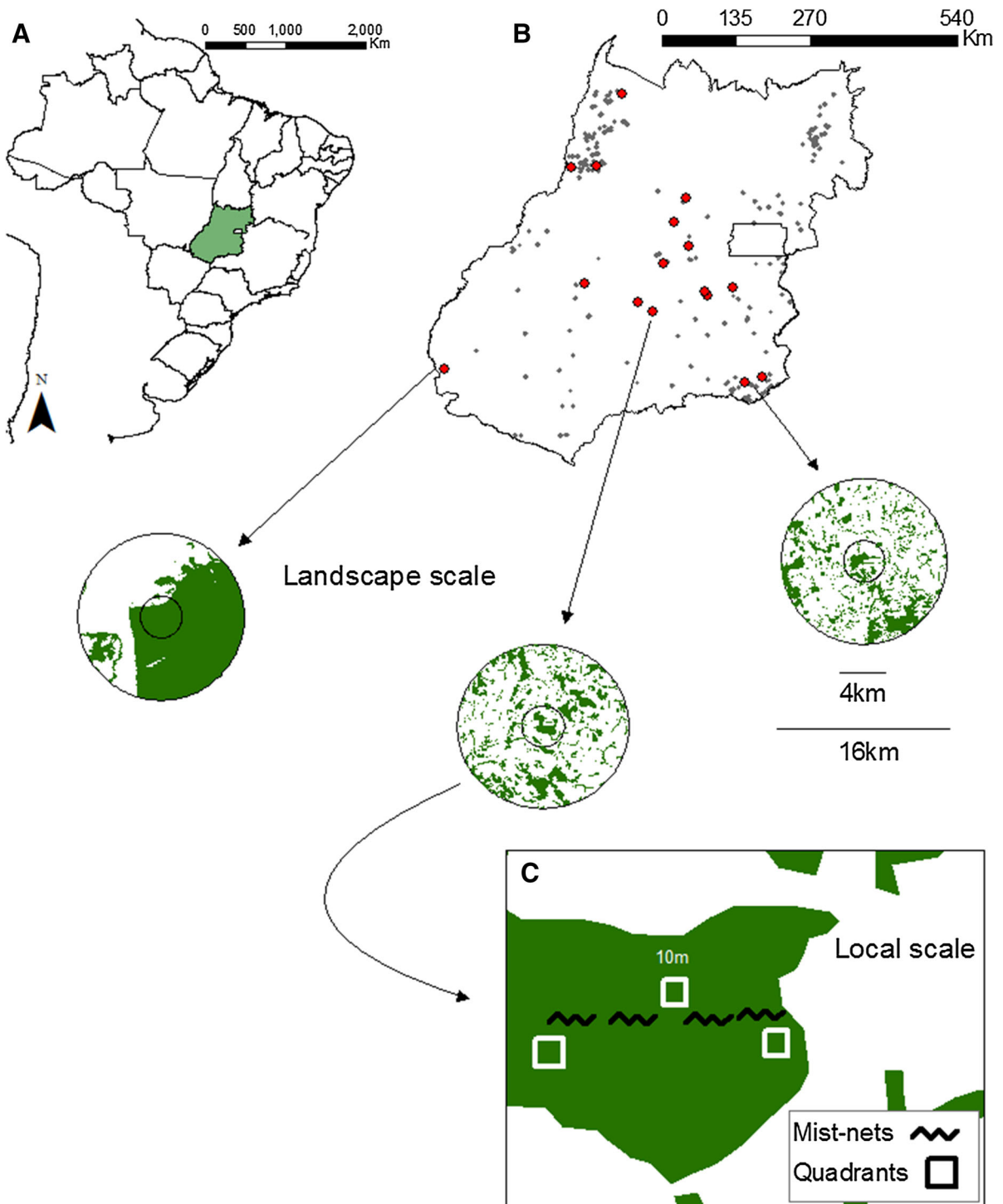
separate savanna (treed grassland) and forests (dry and gallery forests) from all other land covers (i.e., the matrix, which usually comprised pasture and other agricultural land uses). We combined savanna and forest into a simple measure of natural vegetation because the bat species we studied use both types of

vegetation (Bernard and Fenton 2002; Aguirre et al. 2003; Bernard and Fenton 2003; Aguiar and Antonini 2008; Bobrowiec and Gribel 2010; Aguiar et al. 2014). The amount of natural vegetation on the landscape is therefore assumed to correspond to the availability of habitat for these forest-roosting bat species. The number of patches is a measure of landscape configuration, and represents the degree to which natural vegetation is subdivided (i.e., fragmented) on the landscape. Landscapes with a high degree of habitat subdivision have a greater number of small patches and higher edge density, than landscapes with a low degree of habitat subdivision. One consequence of habitat fragmentation is that bats may have a greater likelihood of encountering forest edges or crossing into the matrix, which may be beneficial to some species that forage along edges or within more open habitats, but potentially costly for other species that forage primarily in the forest canopy. Fragmented landscapes may thus support fewer individuals of edge-sensitive or matrix-avoiding species.

At the local site scale, we sampled vegetation within three quadrats (10 m × 10 m) along the mist-net transect in each patch (i.e., at the beginning, middle, and end of the transect). Within each quadrat, we quantified the number of trees (>5-cm trunk diameter), height of understory, canopy density, and number of lianas (woody vines; Supplementary material Appendix 1, Table A1). The number of trees in the quadrat represents an indirect measure of the amount of resources for bats, such as food and shelter. Understory height is potentially important for some bat species, such as the little yellow-shouldered bat, which preferentially uses this part of the forest strata. We assayed understory height as the mean height of the tallest understory tree within each quadrat, by placing a 2-m pole (with 20-cm demarcations) at each corner of the quadrat and then averaging the four height measurements. Canopy density is likely to be an important measure of habitat availability for canopy-foraging species (e.g., the Gervais's fruit-eating bat), as well as a measure of the relative quality of roosting sites, in terms of the protection afforded against predators, wind or rain.

We thus measured canopy density with a convex spherical densiometer at each corner and within the center of the quadrat, and then obtained a mean value for the quadrat. Lastly, the number of lianas may provide an additional measure of the structural complexity of forest stands, in that large hanging vines may present an obstacle to bats during flight. Prior to analysis, we took the average across the three quadrats for each vegetation measure to characterize the local habitat of each forest patch. All local and landscape variables were transformed into $z$-values prior to analysis, so all variables had means equal to zero and standard deviations equal to one. We also calculated the Pearson correlation coefficient for all pairs of local and landscape variables to search for any potential collinearity prior to analysis. The correlation between the two landscape variables (amount versus the number of patches of natural vegetation) was low and non-significant at both landscape scales (2 km: $r = -0.22$, $P = 0.42$; 8 km: $r = -0.30$; $P = 0.25$). As the number of lianas and understory height exhibited a significant correlation ($r = 0.55$, $P < 0.03$), we ended up using only the number of lianas in developing our site-occupancy models, because this variable had fewer missing values than understory height.

### Modeling detection bias

Species may not be detected in all patches in which they actually occur, so false absences are common in ecological studies. This detection bias can lead to an underestimation of species site occupancy (Mackenzie et al. 2002; Kellner and Swihart 2014). We took certain precautions in our survey methodology to reduce false absences: (1) we avoided surveying bats during the full moon, as this has been shown to reduce bat captures (Mello et al. 2013); (2) our surveys were conducted only during the wet season to avoid any potential seasonal bias on species detections; and, (3) the start time and duration of surveys were standardized to avoid biases in the number of individuals or species captured (e.g., longer surveys should net more bats). Despite these precautions, detection probabilities of species may still vary because of differences between observers ($n = 2$) conducting the surveys (e.g., due to individual variation in setting mist nets), or owing to environmental factors beyond our control but which nevertheless might affect bat activity.

We thus modeled the effect that observer bias and certain environmental variables, such as air temperature, wind or rain, could have on detection probabilities of the eight bat species featured in this analysis (Mello et al. 2008a, b; Barros et al. 2014). We measured air temperature during surveys and noted the

presence of rain or wind. Data for wind velocity and rain were obtained from the Brazilian Meteorology Institute (http://inmet.gov.br) for the meteorological station closest to each study site. Wind velocity was treated as a binary variable: 1 if wind $\geq$ 4 m/s and 0 if wind $\leq$ 4 m/s. Precipitation was likewise treated as a binary variable (presence/absence), with totals >1 mm considered a rain event (i.e., present = 1).

Detection bias was assessed for each species by using a logistic model, which incorporates detection history for each species and covariates (observer bias and environmental variables) that may also be affecting the surveyors' ability to detect (or, in this case, capture) the species (MacKenzie 2005). We used a multi-model information-theoretic approach (described in the next section), in which we explored competing models consisting of each covariate singly (4 models), along with a model that assumed a constant probability of detection (i.e., the null model). Model-selection procedures (described in the next section) were then used to evaluate the best detection model among the candidate set ($\Delta$AIC < 2). If any of the environmental or observer covariates were found to influence a species' detection probability, we then included those covariates in the species occupancy models.

### Species occupancy modeling

The naïve occupancy rate $(\widehat{\psi})$ is the proportion of sites (forest patches) in which the target species was detected. Because of detection bias or insufficient sampling, the naïve occupancy rate tends to underestimate a species' "true" occupancy (incidence), however. We can therefore adjust the naïve occupancy rate to incorporate detection bias (as described in the previous section), while simultaneously exploring how our local and landscape covariates influenced site occupancy. We used single-species, single-season occupancy models (MacKenzie et al. 2002) based on logistic regression and multi-model inference to evaluate a candidate set of nine competing models consisting of: (1) local covariates, either singly or combined (4 models), (2) landscape covariates, singly or combined (3 models), (3) all covariates (global model), or (4) no covariates (the constant or null model, with only an intercept). The same set of models was constructed and analyzed for each scale separately (i.e., at 2 and 8 km).

Model selection was based on the Akaike information criterion corrected for small samples (AIC$_c$; Burnham and Anderson 1998). We first tested whether the data were overdispersed by calculating the overdispersion parameter ($\hat{c}$), which is the observed Pearson chi-square statistic divided by the mean of the chi-square statistic obtained by the bootstrap procedure (10,000 times). When data were overdispersed ($\hat{c} > 1$), we used the Quasi-AIC$_c$ (QAIC$_c$). The overdispersion coefficient ($\hat{c}$) of the global model was >1 for six species (all but the black myotis and Incan broad-nosed bat), and thus we ended up using QAIC$_c$ instead of AIC$_c$ as the basis for model selection in most cases. Our set of top-ranked models consisted of all models with a $\Delta$AIC$_c$ or $\Delta$QAIC$_c$ < 2. In some cases, numerical convergence in the models was not reached, and so parameter estimation was not reliable. In those cases, we changed our optimization method to simulated annealing, which provides a stochastic model for optimization. Both the detection and occupancy model analyses were performed using the package "unmarked" in the statistical computing software R (R Core Team 2015; Fiske and Chandler 2011). The relative importance of variables was assessed by the sum of AIC weights ($w_i$) for all models in which a variable occurred.

### Results

Detection bias was evident for two of the eight species: the Incan broad-nosed bat and Pallas' long-tongued bat (Table 1, Supplementary material Appendix 2, Table A2). Detection (mist-net captures) of Pallas' long-tongued bat was negatively related to wind, whereas detection of the Incan broad-nosed bat was negatively related to air temperature. We therefore used the corresponding covariate to adjust for detection bias in the candidate set of occupancy models for each of these two species. For the other six species, the model with constant detection was the best model, and thus we did not correct for detection bias in the occupancy models for these species. Nevertheless, detection covariates were among the top-ranked models ($\Delta$AIC$_c$ or $\Delta$QAIC$_c$ < 2) for four other species, suggesting that environmental factors may affect detection of these species under certain conditions. For example, both rain and wind had a negative influence on detections of the black myotis. Rainfall

**Table 1** Factors affecting detection of bat species within forest patches in the Brazilian Cerrado

| Model | AIC$_c$ or QAIC$_c$ | $\Delta$AIC$_c$ or $\Delta$QAIC$_c$ | $w_i$ | $k$ | Partial coefficients |
|---|---|---|---|---|---|
| Vampire bat (*Desmodus rotundus*)* | | | | | |
| psi(.),p(.) | 21.5 | 0.0 | 0.44 | 3 | |
| psi(.),p(Obs) | 22.9 | 1.4 | 0.22 | 4 | Obs = −2.54 |
| Black myotis (*Myotis nigricans*) | | | | | |
| psi(.),p(.) | 44.7 | 0.0 | 0.31 | 2 | |
| psi(.),p(Rain) | 45.6 | 1.0 | 0.19 | 3 | Rain = −0.46 |
| psi(.),p(Wind) | 46.6 | 1.9 | 0.12 | 3 | Wind = −8.15 |
| Pallas' long-tongued bat (*Glossophaga soricina*)* | | | | | |
| psi(.),p(Wind) | 53.7 | 0.0 | 0.36 | 4 | Wind = −6.79 |
| psi(.),p(.) | 54.6 | 1.0 | 0.22 | 3 | |
| Little yellow-shouldered bat (*Sturnira lilium*)* | | | | | |
| psi(.),p(.) | 38.9 | 0.0 | 0.44 | 3 | |
| Gervais' fruit-eating bat (*Artibeus cinereus*)* | | | | | |
| psi(.),p(.) | 33.0 | 0.0 | 0.47 | 3 | |
| psi(.),p(Rain) | 34.8 | 1.8 | 0.20 | 4 | Rain = −1.84 |
| Incan broad-nosed bat (*Platyrrhinus incarum*) | | | | | |
| psi(.),p(Temp) | 75.8 | 0.0 | 0.32 | 3 | Temp = −0.67 |
| psi(.),p(.) | 76.9 | 1.1 | 0.19 | 2 | |
| Great fruit-eating bat (*Artibeus lituratus*)* | | | | | |
| psi(.),p(.) | 48.1 | 0.0 | 0.47 | 3 | |
| psi(.),p(Temp) | 50.0 | 1.9 | 0.18 | 4 | Temp = −0.67 |
| White-lined broad-nosed bat (*Platyrrhinus lineatus*)* | | | | | |
| psi(.),p(.) | 36.4 | 0.0 | 0.45 | 3 | |

Only the top-ranked models with $\Delta$AIC$_c$ or $\Delta$QAIC$_c$ < 2 are shown. Models corrected for overdispersion (global model with $\hat{c} > 1$) were evaluated using QAIC$_c$ and are indicated by an asterisk (*). Environmental covariates: temperature (Temp), wind, rain, and observer (Obs)

also had a negative effect on the detection of Gervais' fruit-eating bat, whereas temperature negatively influenced the detection of the great fruit-eating bat. For vampire bats, observer bias may have had some influence on detections, presumably owing to differential success in setting mist nets (Supplementary material Appendix 3, Fig. A3).

Landscape covariates were included in the top-ranked occupancy models ($\Delta$AIC$_c$ or $\Delta$QAIC$_c$ < 2) of four species: black myotis (at 8 km), little yellow-shouldered bat (at 8 km), Incan broad-nosed bat (at 2 km), and white-lined broad-nosed bat (at 8 km) (Table 2). However, a landscape covariate was ranked the best model only for the black myotis and the little yellow-shouldered bat (both at 8 km). Local covariates were included in the top-ranked occupancy models of five species: vampire bat, black myotis (at 2 km), Pallas' long-tongued bat, Incan broad-nosed bat (at 2 km), and white-lined broad-nosed bat. However, a local covariate was ranked the best model

only for the vampire bat and the white-lined broad-nosed bat. The null model of constant occupancy was among the top-ranked models for six of our eight species, and was ranked as the best (and only) model for the two fruit-eating bats. Only the vampire bat and black myotis did not include the null model among their top-ranked occupancy models.

Canopy cover, a local-scale covariate, best explained occupancy in two species: the vampire bat and the white-lined broad-nosed bat (Table 2). These two species were found in a third of the forest patches we surveyed ($\hat{\psi} = 0.32$), with site occupancy exhibiting a negative association with canopy cover. Although canopy cover was the best model, the null model (constant occupancy) was among the top-ranked models for the white-lined broad-nosed bat, whose site occupancy was also negatively influenced by the broad-scale fragmentation of natural habitat (i.e., the number of patches within an 8-km radius of the focal patch).

**Table 2** Factors explaining site occupancy of bat species within forest patches of the Brazilian Cerrado

| | Models | QAIC$_c$ or AIC$_c$ | ΔQAIC$_c$ or ΔAIC$_c$ | $w_i$ | $k$ | Partial coefficients |
|---|---|---|---|---|---|---|
| Vampire bat (*Desmodus rotundus*) | | | | | | |
| 2 km* | psi(Can),p(.) | 39.6 | 0 | 0.65 | 4 | Can = −2.23 |
| 8 km* | psi(Can),p(.) | 39.6 | 0 | 0.69 | 4 | Can = −1.88 |
| Black myotis (*Myotis nigricans*) | | | | | | |
| 2 km | psi(NP),p(.) | 87.9 | 0 | 0.3 | 2 | NP = −4.06 |
| | psi(.),p(.) | 88.3 | 0.5 | 0.23 | 3 | |
| | psi(Tree),p(.) | 89.8 | 1.9 | 0.11 | 3 | Tree = 1.61 |
| 8 km | psi(NP),p(.) | 38.79 | 0 | 0.72 | 3 | NP = −7.42 |
| Pallas' long-tongued bat (*Glossophaga soricina*) | | | | | | |
| 2 km* | psi(.),p(Wind) | 56.5 | 0 | 0.38 | 4 | |
| | psi(Tree),p(Wind) | 57.2 | 0.7 | 0.27 | 5 | Tree = 8.61 |
| | psi(Lian),p(Wind) | 58.2 | 1.7 | 0.16 | 5 | Lian = 9.47 |
| 8 km* | psi(.),p(Wind) | 59.1 | 0 | 0.36 | 4 | |
| | psi(Lian),p(Wind) | 59.6 | 0.4 | 0.29 | 5 | Lian = 10.00 |
| | psi(Tree),p(Wind) | 60.5 | 1.3 | 0.19 | 5 | Tree = 9.17 |
| Little yellow-shouldered bat (*Sturnira lilium*) | | | | | | |
| 2 km* | psi(.),p(.) | 23.8 | 0 | 0.46 | 3 | |
| 8 km* | psi(Nat8),p(.) | 38.2 | 0 | 0.36 | 4 | Nat8 = 5.91 |
| | psi(.),p(.) | 39.1 | 0.9 | 0.23 | 3 | |
| Incan broad-nosed bat (*Platyrrhinus incarumi*) | | | | | | |
| 2 km | psi(.),p(Temp) | 75.8 | 0 | 0.36 | 3 | |
| | psi(Can),p(Temp) | 76.7 | 0.9 | 0.23 | 4 | Can = −8.71 |
| | psi(Nat2),p(Temp) | 77.7 | 1.9 | 0.14 | 4 | Nat2 = 2.82 |
| 8 km | psi(.),p(Temp) | 75.8 | 0 | 0.42 | 3 | |
| Gervais' fruit-eating bat (*Artibeus cinereus*) | | | | | | |
| 2 km* | psi(.),p(.) | 31 | 0 | 0.5 | 3 | |
| 8 km* | psi(.),p(.) | 24.7 | 0 | 0.49 | 3 | |
| Great fruit-eating bat (*Artibeus lituratus*) | | | | | | |
| 2 km* | psi(.),p(.) | 62.2 | 0 | 0.38 | 3 | |
| 8 km* | psi(.),p(.) | 61.4 | 0 | 0.41 | 3 | |
| White-lined broad-nosed bat (*Platyrrhinus lineatus*) | | | | | | |
| 2 km* | psi(Can),p(.) | 50.9 | 0 | 0.38 | 4 | Can = −1.99 |
| | psi(.),p(.) | 51.5 | 0.5 | 0.29 | 3 | |
| 8 km* | psi(Can),p(.) | 50.9 | 0 | 0.33 | 4 | Can = −1.99 |
| | psi(.),p(.) | 51.5 | 0.5 | 0.25 | 3 | |
| | psi(NP8),p(.) | 52 | 1.1 | 0.19 | 4 | NP8 = −1.21 |

Only the top-ranked models with ΔAIC$_c$ or ΔQAIC$_c$ < 2 are shown. Models corrected for overdispersion (global model with $\hat{c} > 1$) were evaluated using QAIC$_c$ and are indicated by an asterisk (*). Local site covariates: canopy cover (Can), number of trees (Tree) and number of lianas (Lian). Landscape covariates: natural vegetation cover (Nat) and number of patches (NP) measured within either a 2- or 8-km radius of the forest patch

Of all our species, habitat fragmentation (as assayed by the number of natural-habitat patches) appears to have had the greatest effect on site occupancy in the black myotis, especially at the broader landscape scale (i.e., 8 km). The black myotis occurred in a third of the forest patches we surveyed ($\widehat{\psi} = 0.32$), and site occupancy exhibited a strong negative correlation with habitat fragmentation.

Although the number of patches within a 2-km radius of the focal patch was ranked best for explaining site occupancy in this species, the null model and a model including only tree density (a local-scale covariate) were also among the top-ranked models at this scale (Table 2; Fig. 3).

The only other species whose site occupancy was principally influenced by a landscape covariate was the little yellow-shouldered bat, which was detected in a quarter of the forest patches we surveyed ($\widehat{\psi} = 0.25$). The amount of natural habitat cover in the broader landscape (8-km radius) had a positive effect on local site occupancy for this species, although the null model was also among the top-ranked models at this scale (Table 2). Otherwise, no other covariate was associated with the occurrence of this species at either scale. Similarly, no covariate at any scale explained the occurrence of the two fruit-eating bats. The Gervais' fruit-eating bat and the great fruit-eating bat were found in 38 and 63% of the forest patches we surveyed, respectively.

Site occupancy by the Pallas' long-tongued bat and Incan broad-nosed bat was essentially constant (i.e., the best model included only the relevant detection covariate). These species were found in a majority of the forest patches we surveyed, with a naïve occupancy ($\widehat{\psi}$) of 63 and 75%, respectively. Still, there was some support for the effect of local-scale factors on site occupancy, which appeared in the top-ranked models of both species (i.e., $\Delta QAIC_c$ or $\Delta AIC_c < 2$). For the pallas' long-tongued bat, the number of trees and lianas were both positively correlated with site occupancy, regardless of scale. In contrast, canopy cover was negatively correlated with the occurrence of the Incan broad-nosed bat, but only among the candidate model sets evaluated at the 2-km scale. At this scale, a landscape covariate, the amount of natural habitat within a 2-km radius of the forest patch, appears to have positively influenced the occurrence of the Incan broad-nosed bat, although this association was not evident at a broader landscape scale (i.e., at 8 km).

## Discussion

Our study underscores the difficulty in attempting to predict the expected responses of species to local habitat or landscape structure based on limited information a priori. Although local and landscape-scale variables were important to varying degrees for predicting site occupancy in the forest-roosting bat species in our study, their specific responses varied in ways that were not well-predicted by our original framework (Fig. 1), which was based on available information regarding the ecology of these species such as diet, movement distances, and body mass. Our predictions as to which covariates were likely to influence site occupancy were correct for one species (great fruit-eating bat), partially correct for four species (black myotis, Incan broad-nosed bat, white-lined broad-nosed bat, and little yellow-shouldered bat), and incorrect for three species (vampire bat, Pallas' long-tongued bat, and Gervais' fruit-eating bat) (Table 3).

Given that we were partially or wholly incorrect in our expectations for seven of our eight focal species, we offer some possible explanations as to why our predictions might have fallen short. Although we had hypothesized that landscape-scale factors would be most important in predicting the occurrence of the black myotis, this relationship turned out to be in the opposite direction predicted. Initially, we had expected that the incidence of black myotis would increase in more fragmented landscapes (Chambers et al. 2016), given that it is an aerial insectivore that forages along forest edges (Kalko et al. 2008; Denzinger and Schnitzler 2013), and fragmentation increases the amount of edge habitat in the landscape.

Contrary to our expectations, however, the incidence of this species was negatively related to the degree of fragmentation, as assayed by the number of natural-habitat patches within the landscape. This unexpected response to fragmentation may have to do with the different landscape context and the types of forest edges in our study area relative to these other studies. Previous research citing a positive relationship between aerial insectivores such as the black myotis and fragmentation were conducted in predominantly forested landscapes, such as in the Amazon Basin and in temperate forests (Ethier and Fahrig 2011; Rodríguez-San Pedro and Simonetti 2015; Chambers et al. 2016). In contrast, the Cerrado biome is a heterogeneous mosaic of open habitats and forests (Sano et al. 2010), and thus includes many different forest-edge types. The black myotis may thus respond differently to different forest-edge types, perhaps even avoiding the use of edges adjacent to agricultural

**Fig. 3** Importance of each covariate for assessing site occupancy of eight forest-roosting bat species in the Brazilian Cerrado. Local predictors are: canopy cover (Can), number of trees (Tree), number of Lianas (Lian). Landscape predictors are natural vegetation cover (Nat) and the number of natural-habitat patches (NP). The weight of the null model is also shown. Positive and negative signs above bars represent positive or negative relationships with occupancy for those covariates in the set of top-ranked models ($\Delta AIC_c$ or $\Delta QAIC_c < 2$). Species codes: 1-vampire bat, 2-black myotis, 3-Pallas' long-tongued bat, 4-little yellow-shouldered bat, 5-Gervais' fruit-eating bat, 6-Incan broad-nosed bat, 7-great fruit-eating bat, and 8-white-lined broad-nosed bat
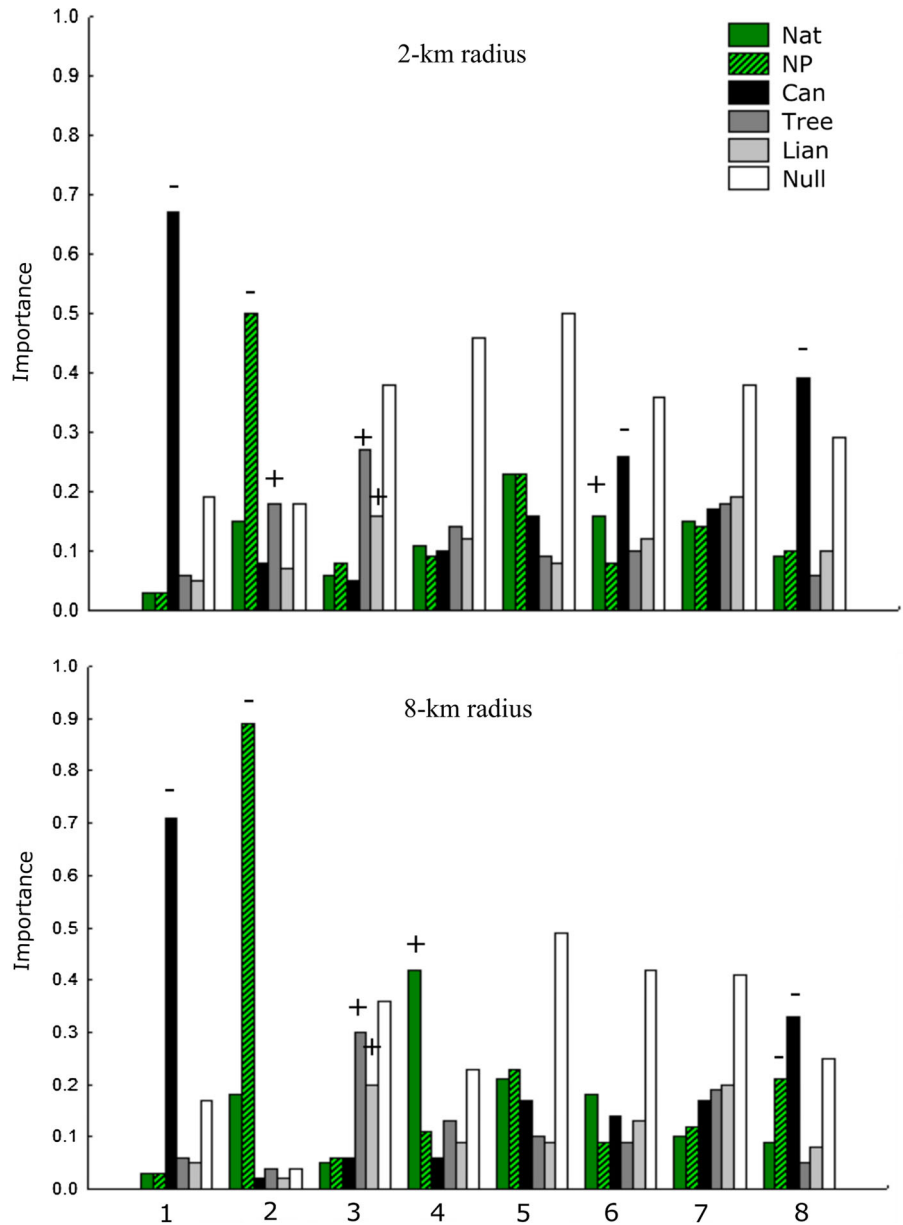


areas. Given the prevalence of agriculture in the Cerrado, an avoidance of forest-agricultural edges might well translate into the sort of negative response between the black myotis and fragmentation that we observed, but the edge response of this species needs to be evaluated by future research.

The negative relationship between canopy cover, a local-scale variable, and the incidence of vampire bats also was not expected. We had initially expected that the probability of occurrence in vampire bats would be predominantly related to a landscape-scale factor, in

this case exhibiting a negative relationship with the amount of natural vegetation in the landscape (i.e., a positive relationship with increased agricultural land use), given their affinity for feeding on cattle blood (Greenhall et al. 1983). We posit that landscape disturbance from cattle grazing may be having an indirect effect on the occurrence of vampire bats. Cattle seek shade in forest stands, where they can damage trees (Adams 1975), thereby decreasing canopy cover. Thus, the apparent importance and negative association between vampire bats and forest

**Table 3** Comparison of the predicted and observed relationships as to how local and landscape factors influence the occurrence of bat species in the Brazilian Cerrado

| Species | Feeding habits | Max. dispersal[a] | Prediction[b,c] | Best models 2 km[b,c] | Best models 8 km[b,c] | Prediction corroborated? |
|---|---|---|---|---|---|---|
| Vampire bat | Hematophagous | 5.5 km | Landscape (−Nat) | **Local (−Can)** | **Local (−Can)** | **No** |
| Black myotis | Insectivore | 13 km | Landscape (+ NP) | Landscape<br>Constant<br>Local (+Tree) | **Landscape (−NP)** | **Partially** |
| Pallas' long-tongued bat | Nectarivore | 6 km | Landscape (+Nat) | Constant | Constant | No |
| Little yellow-shouldered bat | Frugivore | 5 km | Landscape (+Nat) and Local (+Lian) | Local (+Tree, Lian) | Local (+Tree, Lian) | Partially |
| Incan broad-nosed bat | Frugivore | Not found | Landscape (+Nat) and Local (+Can) | Constant<br>Local (−Can)<br>Landscape (+Nat) | Landscape (+Nat)<br>Constant | Partially |
| Gervais' fruit-eating bat | Frugivore | 2 km | Landscape (+Nat) and Local (+Can) | Constant | Constant | No |
| Great fruit-eating bat | Frugivore | 70 km | Constant | Constant | Constant | Yes |
| White-lined broad-nosed bat | Frugivore | 9 km | Constant | Local (−Can)<br>Constant | Local (−Can)<br>Constant<br>Landscape (−NP) | Partially |

Feeding habits and maximum dispersal are included as biological traits that we used to predict a bat species' response to covariates. The top-ranked models ($\Delta AIC_c$ or $\Delta QAIC_c < 2$) are sorted by rank (i.e., by increasing $AIC_c$ or $QAIC_c$). Models highlighted in bold were found to be better than the null (constant) model and are therefore considered "significant"

[a] Sources: Wilson and La Val (1974), Lourenço and Esbérard (2011)

[b] Local covariates: canopy cover (Can), number of trees (Tree), and number of lianas (Lian). Landscape covariates: natural vegetation cover (Nat) and number of patches (NP) within either a 2- or 8-km radius of the forest patch

[c] Number of lianas was found to be positively correlated with understory height, and thus understory height was not included in the model analysis of species occupancy

canopy cover at a local scale might still reflect their association with the broader-scale land use (cattle grazing), but we are unable to evaluate this possibility with our data.

We had predicted that neither local nor landscape variables would influence the occupancy patterns of two species, the great fruit-eating bat and the white-lined broad-nosed bat. Both are large frugivores that have been encountered in a range of environments, from intact forest to urban areas (Menezes Jr. et al. 2008; Trevelin et al. 2013). Our initial expectations were met in the case of the great fruit-eating bat, but our prediction regarding the white-lined broad-nosed bat was only partially correct. Although the null model was among the top-ranked occupancy models for this species (suggesting that neither local nor landscape variables were important), a local-scale covariate (canopy cover) was ranked as the best model, and a landscape variable (number of patches at the 8-km scale) was also among the top-ranked models for this species, which suggests that these variables may be having some influence on site occupancy. The negative relationship with canopy cover could be explained by the need for some obstacle-free space to fly by large fruit-eating species (Stockwell 2001), while the negative relationship with number of patches could be related to an unexpected sensitivity to habitat fragmentation for this species.

Conversely, we had expected that both local- and landscape-scale covariates (canopy cover and the amount of native vegetation) would positively influence the occurrence of the two small, canopy-frugivores, Gervais' fruit-eating bat and Incan broad-nosed bat. Instead, we found that while no covariate was inherently better than the constant (null) model, a local- and landscape-scale covariate were among the top-ranked models for the Incan broad-nosed bat at least. In this case, however, the species exhibited a negative relationship with canopy cover (contrary to our expectations), but a positive relationship with native-vegetation amount at the 2-km scale (consistent with expectations). The negative relationship with canopy cover observed in this species could again be related to a need for obstacle-free flying space in large and medium-sized frugivores (Stockwell 2001), and the positive relationship with native-vegetation amount was expected because small canopy frugivores must forage across the landscape in search of ripe fruits (Ramos Pereira 2010), and so require a certain

amount of native vegetation at the landscape scale to provide a sufficient availability of fruiting trees.

We had expected that the occupancy patterns of the little yellow-shouldered bat, an understory frugivore, would be positively influenced by the broader landscape context (amount of natural habitat) as well as by a local-scale factor (understory height, which was later found to exhibit a positive correlation with the number of lianas). Our prediction for the little yellow-shouldered bat was only partially corroborated: site occupancy was best explained by a landscape factor (amount of natural habitat at 8 km), but not by any of the local-scale covariates, and the null model was among the top-ranked occupancy models for this species. The positive relationship with native-vegetation amount was expected given this species roosts in tree cavities and is known to have a large home range, use a variety of night roosts, and select large-diameter trees for roosting (Evelyn and Stiles 2003; Mello et al. 2008b).

Finally, we had predicted that the Pallas long-tongued bat, a nectar-eating species, would be positively influenced by native-vegetation amount at the landscape scale, but found that no model was inherently better than the null model for this species. This species forages over a broad spatial extent (Aguiar et al. 2014) and has a high natural abundance (Zortéa and Alho 2008), which might explain the lack of a strong response to either local-scale or landscape-scale variables. Still, two local-scale covariates (a positive relationship with tree density and the number of lianas) were among the top-ranked models at both landscape scales for the Pallas' long-tongued bat. Nectar-eating bats have high flight maneuverability, and are capable of sustaining hovering flight, so having obstacle-free flight space is perhaps less of an issue than it is for other bat species (Norberg and Rayner 1987). Pallas' long-tongued bats might even benefit from an increase in resources provided by trees and lianas, such as roosts or bat-pollinated flowers (Machado and Vogel 2004). A larger sampling of forest patches may thus have revealed a stronger relationship between site occupancy and local-scale covariates in this species.

## Importance of detection bias for bat-species distribution modelling

Given that a majority of studies find evidence of detection bias (i.e., probability of detection <1;

Kellner and Swihart 2014), this should obviously be considered in the development and testing of species distribution models. For example, seasonality, sampling method, and moon phase have all been shown to be important factors determining bat detections (Esbérard 2007; Meyer et al. 2011; Mello et al. 2013), which is why we attempted to control for these issues in our surveys. Nevertheless, it is not possible to control for every environmental factor that could influence species detections, especially given that bats have species-specific detection probabilities (Meyer et al. 2011; this study). In particular, species may exhibit different sensitivities to ambient temperatures: some species are better at regulating their body temperature than others, such that some bats can suffer hypothermia when subjected to lower-than-normal temperatures (McNab 1969). For example, small stenodermatines, such as the Incan broad-nosed bat, have been found to decrease their body temperature in response to low temperatures (McNab 1969). Conversely, bats may avoid flight activity during periods of high temperatures to avoid overheating; in fact, this may explain the prevalence of nocturnal flight activity in most species of bats (Voigt and Lewanzik 2011). Avoidance of hyperthermia may thus offer a plausible explanation for the negative relationship between temperature and detection of the Incan broad-nosed bat that we observed in this study. Besides temperature, wind speed may also be an important determinant of bat-species detections. Wind can alter bat flight behavior in ways that influence species detection (Sapir et al. 2014), although a recent study did not find any relationship between wind speed and the flight activity of Neotropical insectivorous bats (Barros et al. 2014). Nevertheless, the feeding behavior of the Pallas' long-tongued bat, which is a nectarivore that forages by hovering at flowers, has been shown to be affected by strong wind (Lemke 1984), which is consistent with the negative relationship we found between wind and detection of this species.

In view of the influence that environmental factors such as temperature and wind speed can have on bat detections, we recommend that future studies test and correct for detection bias, if needed, in the development or application of species distribution models involving bat species. We note that environmental detection covariates were contained in the set of top-ranked occupancy models for six of eight species,

representing a wide range of foraging ecologies and flight habits, although detection bias was significant for only two of these species (Incan broad-nosed bat and Pallas' long-tongued bat). In those two species, however, environmental correlates (temperature and wind, respectively) were the only factors to influence detection, and ultimately, apparent site occupancy. For species that are sensitive to environmental or weather-related factors, which may include a wide range of small endothermic as well as ectothermic animals, these sorts of detection covariates may be as important as other habitat or landscape factors for modeling species distributions.

## Conclusion

In this study, we sought to clarify whether local, site-based habitat variables or landscape-scale variables were generally most important in explaining the occurrence of eight different bat species within forest fragments across an agricultural disturbance gradient in the Brazilian Cerrado. The results were mixed. A local-scale covariate—canopy cover—was ranked the best model for two species (vampire bat and white-lined broad-nosed bat), whereas a landscape covariate was the best model for two other species (black myotis and the little yellow-shouldered bat). For each type of covariate, the null model (constant detection) was amongst the top-ranked model set for two of these species (white-lined broad-nosed bat and little yellow-shouldered bat), however. Neither type of covariate was important to the occurrence of the two fruit-eating bat species in our study, whereas an environmental detection covariate (wind or temperature, respectively) represented the best model for the Incan broad-nosed bat and the Pallas' long-tongued bat.

From a community assemblage perspective, both local and landscape variables may be important for predicting site occupancy in some forest-roosting bats, although the strength and direction of those relationships vary among species. For a given covariate, we observed both positive and negative relationships with species occurrence, which highlights the idiosyncratic pattern of response across species. Because of these idiosyncratic responses among species, however, it would be difficult to implement a single, comprehensive management plan that addresses the specific habitat needs of each and every species. Instead, a

focus on landscape-scale management may provide more comprehensive guidance to land managers. Such a top-down approach to management emphasizes the amount and configuration of habitat on the landscape, which is often related to the degree and pattern of human land-use (e.g., the agricultural transformation of landscapes reduces the cover of natural vegetation), and fits well within current approaches for spatial conservation prioritization (Moilanen et al. 2008; Grantham et al. 2009).

Furthermore, landscape variables are more readily spatialized over a broader range of spatial scales than local-scale vegetation measures, owing to the availability of satellite imagery and landscape metrics. Measuring landscape variables at more than one scale can also help ensure that the potential importance of landscape factors on species occurrence will not be missed, especially given that our analysis revealed that some species exhibited a relationship with landscape factors at only one of the two "landscape scales" we assessed in this study (i.e., at either 2 or 8 km). As a caveat, however, the amount of native vegetation on the landscape is not always a good proxy for the amount of suitable habitat for a given species, especially for habitat specialists in landscapes that have experienced a significant degree of habitat loss and fragmentation (Almeida-Gomes et al. 2015). Although the natural vegetation of the Cerrado is being altered at both local and landscape scales, the wholesale agricultural transformation of this region represents the greater threat to most species at this time, and thus demands a landscape-scale approach to land management and species conservation.

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**Supplementary Material**

**Table A1.** Covariates used in modeling detection bias and site occupancy for forest-roosting bats in the Brazilian Cerrado. Occupancy covariates include both local and landscape variables.

| Covariates | Variable | Variable Type | Description |
|---|---|---|---|
| **Detection** | | | |
| Constant | . | None | Detection assumed to be constant |
| Temperature | Temp | Continuous | Mean temperature measured during bat survey ($^{o}$C) |
| Observer | Obs | Categorical | Observer that performed the survey (n = 2) |
| Wind | Wind | Categorical | Presence of wind during the survey (> 4m/s) |
| Rain | Rain | Categorical | Presence of rain during the survey (>1 mm) |
| **Occupancy** | | | |
| Natural vegetation amount (2-km radius) | Nat2 | Continuous | Proportion of natural vegetation within a 2-km radius of the survey site |
| Number of patches (2-km radius) | NP2 | Continuous | Number of patches within a 2-km of radius of the survey site |
| Natural vegetation amount (8-km radius) | Nat8 | Continuous | Amount of natural vegetation within a 8-km radius of the mist-net location |
| Number of patches (8-km radius) | NP8 | Continuous | Number of patches within a 8-km radius of the mist-net location |
| Understory | Under | Continuous | Understory height measured at 12 locations in the vicinity of the mist-net location |

| | | | |
|---|---|---|---|
| Canopy cover | Can | Continuous | Canopy density measured with a densitometer at 15 locations in 15 locations in the vicinity of the mist-net location |
| Number of trees | Tree | Continuous | Number of trees counted in 3 quadrats (10 x10 m) at each mist-net location |
| Lianas | Lian | Continuous | Number of lianas counted in 3 quadrats (10 x10 m) at each mist-net location |

**Table A2.** Multi-model selection of factors affecting detection bias and site occupancy for forest-roosting bats in the Brazilian Cerrado. Landscape variables included two different landscape sizes, representing either a 2-km or 8-km radius around the focal forest patch.  When global models had overdispersion coefficients $\hat{c} > 1$, all the competing models were  corrected by this overdispersion factor, and $QAIC_C$ was used to evaluate model fit instead of  $AIC_C$.

# See Excel spreadsheet file (Mendes_etal_2017_Supplementary Material 2.xls)

**Figure A3.** Expected site occupancy of forest-roosting bats in the Brazilian Cerrado, as a function of either the amount (proportion) or fragmentation (number of patches) of natural vegetation for those species in which these landscape variables were in the top-ranked model set ($\Delta AIC_c$ or $\Delta QAIC_c < 2$). Dashed lines represent the 95% confidence interval around these estimates.