



Multi-scale effects of habitat structure and landscape context on a vertebrate with limited dispersal ability (the brown-throated sloth, *Bradypus variegatus*)

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ABSTRACT

As human population, food consumption, and demand for forest products continue to rise over the next century, the pressures of land-use change on biodiversity are projected to intensify. In tropical regions, countryside habitats that retain abundant tree cover and structurally complex canopies may complement protected areas by providing suitable habitats and landscape connectivity for a significant portion of the native biota. Species with low dispersal capabilities are among the most at risk of extinction as a consequence of land-use change. We assessed how the spatial distribution of the brown-throated sloth (*Bradypus variegatus*), a model species for a vertebrate with limited dispersal ability, is shaped by differences in habitat structure and landscape patterns of countryside habitats in north-central Costa Rica using a multi-scale framework. We quantified the influence of local habitat characteristics and landscape context on sloth occurrence using mixed-effects logistic regression models. We recorded 27 sloths within countryside habitats and found that both local and landscape factors significantly influenced their spatial distribution. Locally, sloths favored structurally complex habitats, with greater canopy cover and variation in tree height and basal area. At the landscape scale, sloths demonstrated a preference for habitats with high proportions of forest and nearby large tracts of forest. Although mixed-use areas and tree plantations are not substitutes for protected forests, our results suggest they provide important supplemental habitats for sloths. To promote the conservation and long-term viability of sloth populations in the tropical countryside, we recommend that land managers retain structurally complex vegetation and large patches of native habitat.

Abstract in Spanish is available with online material.

Key words: agroecosystems; Costa Rica; conservation biology; countryside biogeography; habitat use; human-modified landscapes; landscape heterogeneity; spatial ecology.

ANTHROPOGENIC LAND-USE CHANGE IS AMONG THE LEADING DRIVERS OF GLOBAL BIODIVERSITY LOSS, particularly in the tropics (Sala *et al.* 2000, Newbold *et al.* 2015). Given that agricultural development and biodiversity conservation have traditionally been regarded as incompatible, the majority of conservation research in the tropics has concentrated on large, pristine tracts of native habitats (Bruner *et al.* 2001, Lees & Peres 2006, Lovejoy 2006). However, a growing body of research emphasizes the potential of agroecosystems and countryside habitats to alleviate the threats of land-use change on a wide range of species (Daily *et al.* 2001, Manning *et al.* 2006, Harvey *et al.* 2008, Perfecto & Vandermeer 2008). This emerging conservation paradigm focuses on the diversity, abundance, and distribution of species within the agroecological matrix. The tropical countryside (Daily 2001) and high-quality matrix are important for supplementing habitats and resources, facilitating the interpatch migration required for metapopulation survival, and buffering against edge effects (Ricketts 2001, Vandermeer & Perfecto 2007, Fahrig *et al.* 2011). Therefore, an exclusive focus on patches of native habitat may

overlook significant opportunities to conserve biodiversity in tropical human-modified landscapes (Ricketts *et al.* 2001).

Tropical forest biodiversity generally decreases along a broad continuum from mature, old growth forest to secondary forest, agroforestry, plantations, cropland, and pasture (Harvey *et al.* 2006, Gardner *et al.* 2009), mirroring the decline in tree cover and structural complexity (August 1983, Philpott *et al.* 2008). Along this spectrum, species distribution patterns can also be shaped by both landscape and local spatial variation in environmental conditions and resources (Wiens 1976, Tilman & Kareiva 1997). Organisms respond to habitat features at a range of spatial scales (Tscharntke *et al.* 2008, Gardner *et al.* 2009), and both within-patch heterogeneity and landscape attributes can affect species' occurrence (Lindenmayer & Franklin 2002). Despite wide recognition that both local and landscape factors affect the distribution of forest vertebrates (Bowman *et al.* 2001, Panzacchi *et al.* 2010, Gonthier *et al.* 2014), many studies focus on a single or few spatial scales without considering the species' biology (Wheatley & Johnson 2009, Jackson & Fahrig 2015). Selection of inappropriate scales can impact conclusions, with adverse consequences for management or conservation policy (Mitchell *et al.* 2001). Understanding the relative influence of scale-dependent spatial factors on species' distributions is an important

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component of mitigating the effects of habitat fragmentation and land-use change on biodiversity.

Species' behavioral responses to land-use change are influenced by their body size, life history traits, and dispersal abilities (Gehring & Swihart 2003). Dispersal among habitat fragments is vital for long-term metapopulation persistence (Gustafson & Gardner 1996), and landscape properties, such as habitat composition and configuration, can deter, impede, or enhance dispersal and daily movement (MacArthur & Wilson 1967, Michalski & Peres 2005, Anderson *et al.* 2007). Species of low vagility and high reliance on forest cover, such as tree sloths, represent model organisms for investigating the effects of habitat features on the spatial ecology of vertebrates with limited dispersal abilities. As a result of their sedentary lifestyle compounded by their low metabolic rate and dependence on forested habitats, sloths have a weak dispersal potential compared to other mammal species and are likely to be sensitive to the effects of land-use change (Lara-Ruiz *et al.* 2008, Peery & Pauli 2014). Given the high rate of loss and fragmentation of mature forest in the tropics, an improved understanding of the capacity of sloths to use countryside habitats has important implications for evaluating their persistence in human-modified landscapes.

Previous research has described the effects of local-scale factors on the habitat use of sloths (Montgomery & Sunquist 1978, Castro-Vásquez *et al.* 2010); however, few studies have considered the influence of habitat characteristics at multiple spatial scales. In this study, we examined how spatial elements and habitat features influence the distribution of the brown-throated sloth (*Bradypus variegatus*) across several spatial scales. Our main objectives were to relate sloth occurrence to (1) local habitat structure within two countryside habitats: tree plantations and mixed-use areas, and (2) landscape composition and configuration at three spatial extents. We expected sloths would be positively associated with countryside habitats that were as follows: (1) high in structural complexity and heterogeneity and (2) contiguous with extensive areas of secondary forest. We predicted that within-patch effects would determine the local distribution of sloths, while composition and configuration of the landscape would determine spatial distribution at broader scales.

METHODS

STUDY AREA.—We conducted the study during May–August 2014, in an area roughly 16 km² within the community of San Juan de Peñas Blancas (10°23' N, 84°37' W) on the Caribbean slope of Cordillera de Tilarán in north-central Costa Rica (Fig. S1). The region is classified as tropical premontane wet forest (Holdridge 1967) with elevations ranging from 275 to 465 m asl. The mean annual temperature is 24°C, and the mean annual precipitation is approximately 4500 mm, with most rainfall occurring from June to December.

The landscape is a mosaic of forest and human-modified habitats. The study area is mainly dominated by primary or selectively logged old growth forest (11%), secondary forests with regenerated native trees aged 15–20 yr (45.5%), and riparian

forests (3%, *i.e.*, linear forest arrangements along streams), while pastures and agriculture are the next most prevalent land uses, covering 19 and 10 percent of the landscape, respectively. Two countryside habitat types, tree plantations and mixed-use areas, also occur within the study region. Mixed-species timber plantations encompass 3.5 percent of the landscape, most of which are relatively well established. Mixed-use areas (*i.e.*, residential areas interspersed with agriculture and small forest patches) comprise a minor portion of the landscape (1%), but often border pasture and cropland and may function as important refuge habitats or corridors for biodiversity. The remaining 7 percent of the study area consists of water, residential, and unpaved roads.

SLOTH SURVEYS.—We determined the use of countryside habitats by sloths using line-transect sampling. The study region was stratified by land-use type, and we selected seven survey sites. Three of the survey sites were located in mixed-use areas, characterized by human settlements with sustainable smallholder agriculture, including both native and non-native crops and livestock, as well as remnant forest fragments. The other four survey sites were located in small-scale tree plantations, ranging from 8- to 12-yr old, and comprised of a mix of native (*e.g.*, *Astronium graveolens* and *Vochysia guatemalensis*) and non-native species (*e.g.*, *Tectona grandis* and *Gmelina arborea*), with cleared understories. Within plantation sites, we established a systematic design of parallel transects to ensure equal coverage and began each survey with a randomized starting location. We established transects at least 15 m from habitat boundaries. Within mixed-use sites, transects were walked along pre-existing trails distributed throughout the entire survey area.

We employed several methods to improve detection probability: (1) long transect lengths guaranteed complete coverage of sites; (2) repeated surveys ensured exhaustive sampling; and (3) high-powered binoculars (Nikon Monarch 7) maximized visibility. We expected individuals would be detected at a constant probability along the sampling effort because species with small area requirements, like three-toed sloths, likely use their entire home range for foraging (de Thoisy *et al.* 2008).

All transects were walked at a rate of 0.5 km/h by the same experienced observer (KDN) during peak activity periods (0800–1600 h; Sunquist & Montgomery 1973, Urbani & Bosque 2007) and visited on four to six separate occasions throughout the study period. Sampling did not occur during heavy rainfall because of reduced detectability rates. When an individual was observed, a photograph was taken using a Canon EOS Rebel T3i DSLR camera with a 200 mm telephoto zoom lens. Sexually mature male brown-throated sloths have a dorsal speculum that is unique in shape, pattern, and intensity, making it possible to recognize specific individuals (Neam & Lacher 2015). Despite the lack of a speculum in females, conclusive identification is still possible through the use of photographs, as well as the time and geographic location of observations. An identification number was assigned to new individuals, and their GPS coordinates were recorded.

Count data were collapsed into a binary response variable. A presence (1) indicates the occurrence of a unique individual, while

an absence (0) refers to a 100-m² area where, after extensive surveys, no sloths were observed. To qualify, an absence had to be within 126 m (*i.e.*, radius of *B. variegatus* median home range; Ramirez *et al.* 2011, Pauli & Peery 2012) of any presence site to ensure that it would be: (1) potentially occupied by a sloth, since we knew one occurred in the vicinity and (2) of the same habitat type as the occupied site. Since mixed-use areas and plantations can vary in their level of disturbance and recovery, nesting the absence site within the same patch would avoid confounding these variables in our vegetation measurements. Additionally, since brown-throated sloths are considered resource specialists (Mendoza *et al.* 2015), we aimed to exclude the potential influence of preferred tree occurrence by including at least one preferred tree species, such as *Cecropia* or *Ficus* spp., in each absence site. All absence sites were registered for subsequent selection and inclusion in the landscape or local-scale analyses as appropriate.

HABITAT CLASSIFICATION.—To verify whether structural complexity differed across vegetation types in the study area, we randomly established twenty-seven 100-m² plots in three habitat types: ten mixed-use, 11 plantation, and six secondary forest plots. In each plot, we recorded: (1) diameter at breast height (DBH, cm) of trees with DBH ≥ 10 cm; (2) mean tree height (HEIGHT, m) of trees with DBH ≥ 10 cm using a clinometer and laser rangefinder; (3) number of trees with DBH ≥ 10 cm (DENSITY); and (4) percent canopy cover (COVER, %) using a spherical densiometer following methods from Lemmon (1956). A measure of total basal area (AREA, cm²) was derived from the DBH of all trees in each sample. The standard deviations of basal area (SDAREA) and height (SDHEIGHT) were calculated for each plot to capture a measure of dispersion of the variables AREA and HEIGHT, respectively.

LOCAL-SCALE HABITAT.—The structural complexity of presence and absence sites was evaluated to determine how local-scale habitat characteristics influence the probability of sloth occurrence. Vegetation plots were centered on presence and absence sites and conducted using the same variables and methods described above. Candidate predictor variables were selected based on their ability to predict sloth occurrence at the local level in similar studies (Castro-Vásquez *et al.* 2010, Acevedo-Quintero *et al.* 2011, Falconi *et al.* 2015).

LANDSCAPE-SCALE HABITAT.—To characterize landscape heterogeneity, we performed a manual habitat classification by digitizing high-resolution (0.5 m) imagery captured on March 20, 2012 (Bing Maps, Microsoft Corporation), using ArcGIS 10.2 (ESRI 2014). Eleven land-use types were classified as follows: (1) old growth forest; (2) secondary forest; (3) riparian forest; (4) croplands; (5) pastures; (6) water bodies; (7) tree plantations; (8) mixed-use areas; (9) urban areas; (10) bare ground; and (11) unpaved roads. Rivers were delineated using contour lines from topographic maps (Costa Rica Instituto Geográfico Nacional) and buffered 15 m to define riparian forests according to the Costa Rican Forestry Law of 2006 (no. 7575).

We investigated the influence of landscape structure on sloth occurrence at three spatial scales: 0.5, 2, and 5 ha. For each presence and absence site, metrics describing landscape composition and configuration were measured at the three scales (*i.e.*, concentric circles) using the program FRAGSTATS (McGarigal *et al.* 2012). We selected the smallest spatial extent (0.5 ha) to represent the maximum daily movement of *B. variegatus* (Sunquist & Montgomery 1973), while the largest extent (5 ha) corresponds with the median home range size of *B. variegatus* (Ramirez *et al.* 2011). An intermediate scale of 2 ha, representing a sloth's core area, was used to determine whether sloths respond to landscape characteristics at a scale between their daily movement and home range.

We used a suite of patch, class, and landscape metrics most biologically relevant to sloths and our hypotheses. Sixteen metrics were selected for analysis, representing five categories: (1) area/edge; (2) shape; (3) contrast; (4) aggregation; and (5) diversity (Table S1; McGarigal & Marks 1995). In addition, habitat isolation was quantified by three measurements: Euclidean distance from the center of each presence and absence site to the nearest patch of secondary forest (≥ 10 ha), riparian forest, and road, using ArcGIS 10.2 (ESRI 2014). Ten hectares was selected as the minimum forest patch size because it corresponds to twice the median home range size of *B. variegatus*, which we consider sufficient for fulfilling an individual's resource and habitat requirements.

DATA ANALYSIS.—Variables were first log or logit transformed to achieve normality and reduce heteroscedasticity. Differences in structural complexity among secondary forest, plantation, and mixed-use areas were analyzed using a one-way ANOVA, followed by Tukey's *post-hoc* comparisons.

The influence of habitat structure and landscape context on sloth occurrence was tested at several spatial scales using mixed-effects logistic regression with site included as a random intercept. All presence and absence data were included in the analyses at the local scale. However, to reduce the effects of spatial autocorrelation at broader scales, we identified absence sites occurring within 500 m of each other and randomly selected one to retain for the landscape-scale analyses. Model selection was performed via backward stepwise procedure, until the removal of non-significant parameters significantly reduced the fit of the model to the data. To overcome issues of multicollinearity, we conducted principal components analyses (PCA) using correlation matrices of the predictor variables at each spatial scale. We retained principal components (PCs) as new predictor variables based on the Kaiser-Guttman criterion and visual inspection of scree plots. PCA was conducted using the package 'vegan' (Oksanen *et al.* 2013) in RStudio version 0.99.473 (RStudio Team 2015). For variables that loaded heavily on significant PCs, we performed t-tests between presence and absence sites to explore which variables may be driving sloth occurrence.

RESULTS

USE OF COUNTRYSIDE HABITATS.—A total of 27 brown-throated sloths were detected using countryside habitats during

May–August 2014. The total sampling effort was 18.7 km in mixed-use areas and 26.5 km in plantations; however, the effort per unit area was relatively consistent across sites (Table 1). Sloths were more abundant in mixed-use areas ($N = 22$) than in plantations ($N = 5$).

Multiple individuals were recorded in the same set of trees over the course of the study. These observations were collapsed into a single presence, reducing the number of individuals in mixed-use areas by five. Local-scale habitat data were unavailable

for four presence sites (three mixed-use and one plantation) and were excluded from the analyses. One tree plantation observation was considered to be an outlier based on abnormal fine-scale habitat characteristics and was removed from local-scale analyses only. This resulted in 17 presence sites (14 mixed-use and three plantation) for local-scale analyses and 18 presence sites (14 mixed-use and four plantation) for landscape-scale analyses.

Repeated sampling efforts verified the absence of sloths at a total of 15 sites (three in mixed-use areas and 12 in plantations). However, following the elimination of absence sites outlined in the methods, only seven of these sites (three mixed-use and four plantation) were included in the landscape-scale analyses (Fig. 1).

TABLE 1. Characteristics of survey sites and sampling effort for three-toed sloth surveys in San Juan de Peñas Blancas, Costa Rica during May–August 2014.

Habitat type	Site	Total			Mean effort/area (km/ha)
		Area (ha)	sampling effort (km)	Effort/area (km/ha)	
Mixed-use	1	2.9	3.9	1.3	1.1
	2	4.5	4.0	0.9	
	3	9.0	10.8	1.2	
Tree plantation	4	4.9	4.5	0.9	0.8
	5	5.6	4.9	0.9	
	6	11.6	8.1	0.7	
	7	15.7	9.0	0.6	

HABITAT CLASSIFICATION.—Five variables were significantly different among secondary forest, mixed-use, and plantations, indicating a gradient of structural complexity across habitat type (Table 2). Secondary forest was the most complex habitat, with significantly greater total basal area, canopy cover, variation in tree height and basal area, and larger trees than plantations and mixed-use areas. While mixed-use areas had significantly more variation in tree height and basal area than plantations, they did not differ regarding the other four habitat variables.

LOCAL SCALE.—The first three PCs accounted for 82.9 percent of the total variation of the local-scale habitat variables and were

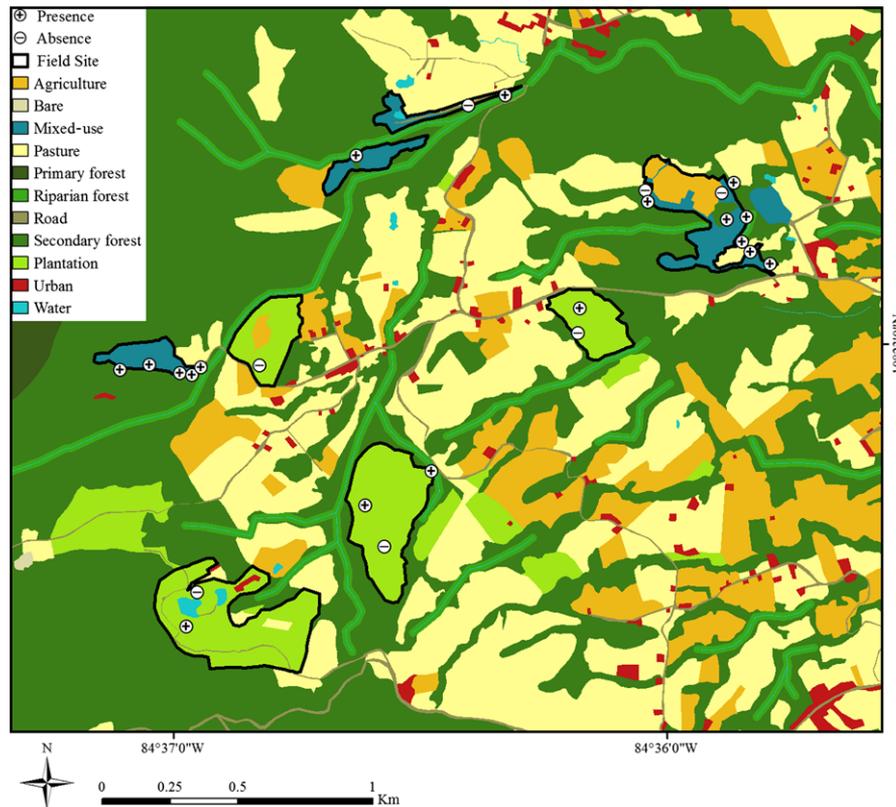


FIGURE 1. Map showing distribution of land-use types and three-toed sloth (*Bradypus variegatus*) presence ($N = 18$; plus signs) and absence ($N = 7$; minus signs) sites used in landscape-scale analyses. Survey sites, outlined in bold, are located in north-central Costa Rica.

TABLE 2. Summary of ANOVAs of local habitat features across secondary forests (N = 6), mixed-use areas (N = 10), and plantations (N = 11) in San Juan de Peñas Blancas, Costa Rica, May–August 2014. Group means were tested with Tukey's range tests. Superscript letters indicate significant differences at $\alpha = 0.05$ among habitat types. Significant values of $P < 0.05$ are in bold.

Variable (unit)	Land-use type			ANOVA	
	Forest	Mixed-use	Plantation	F	P
DENSITY	6.7 ^a	6.1 ^a	7.0 ^a	0.73	0.493
COVER (%)	85.4 ^a	71.3 ^b	68.3 ^b	6.33	0.006
AREA (cm ²)	9995.6 ^a	3756.3 ^b	3474.8 ^b	10.12	<0.001
SDAREA	1993.9 ^a	618.4 ^b	288.4 ^c	21.20	<0.001
HEIGHT (m)	26.1 ^a	16.8 ^b	16.8 ^b	4.94	0.016
SDHEIGHT	14.5 ^a	6.3 ^b	3.8 ^c	36.53	<0.001

retained for regression analysis. The first component (PC1: 44.9% variation) was interpreted as a proxy for structural complexity, the second component (PC2: 23.2%) as tree density, and the third component (PC3: 14.8%) as successional stage. Sites positively associated with PC1 were more structurally complex, with greater AREA, SDAREA, SDHEIGHT, and COVER, while those positively correlated with PC2 contained a higher DENSITY, and a positive correlation with PC3 indicated shorter HEIGHT, on average.

The probability of sloth occurrence was positively correlated with PC1 (habitat complexity), PC2 (tree density), PC3 (successional stage), as well as the interaction between PC1 and PC3 (Table 3). Of the predictor variables that loaded heavily on PC1, only SDAREA ($t = -4.22$, $P < 0.001$), SDHEIGHT ($t = -2.49$, $P = 0.02$), and COVER ($t = -2.14$, $P = 0.04$) were statistically different between presence and absence sites. Although PC2 and PC3 were also significant in the best-fit model, DENSITY ($t = 0.23$, $P = 0.82$) and HEIGHT ($t = 0.21$, $P = 0.83$) were not significantly different across presence and absence sites.

Thus, at the local scale, sloths tended to occur in more structurally complex microhabitats, specifically those that were more heterogeneous in tree height (Fig. 2A), more variable in basal area (Fig. 2B), and with greater canopy cover (Fig. 2C). These relationships were similar regardless of habitat type (Fig. 2D–F).

TABLE 3. Summary of the mixed-effects logistic regression model for predicting sloth occurrence as a function of local-scale habitat characteristics. Significant values of $P < 0.05$ are in bold.

Predictor variable	Parameter estimate (β)	Standard error	P
Intercept	-10.35	3.88	0.008
PC1	129.50	15.97	<0.001
PC2	-56.13	14.45	<0.001
PC3	149.49	15.87	<0.001
PC1:PC3	508.38	39.76	<0.001

LANDSCAPE SCALE.—At the 5-ha scale, the first five PCs explained 89.5 percent of the variance in the original data. At the 2-ha scale, the first three PCs explained 83 percent of the variance. At the 0.5-ha scale, the first two PCs explained 81.6 percent of the variance.

The regional distribution and habitat use of sloths were significantly affected by the composition and configuration of the surrounding landscape; however, the strengths of the associations differed as a function of scale. While landscape variables were unable to predict the probability of occurrence at the 0.5-ha and 2-ha extents, sloths demonstrated significant responses to landscape characteristics at the broadest spatial scale. At the 5-ha scale, sloth occurrence was inversely correlated with PC4 (Table 4), with percentage of secondary forest (−), distance to secondary forest (≥ 10 ha) (+), distance to riparian forest (+), edge contrast index (+), contagion (+), and Simpson's evenness index (+) strongly associated with this axis.

Of the six predictor variables highly correlated with PC4, only the proportion of secondary forest ($t = 2.82$, $P = 0.016$) and Euclidean distance to secondary forest ($t = -2.68$, $P = 0.019$) differed significantly between presence and absence sites (Fig. 3). Sloths therefore exhibited strong differential use of habitats comprising a greater proportion of secondary forest (Fig. 3A), as well as those significantly closer to large forest tracts (Fig. 3B). These relationships were similar across both habitat types (Fig. 3C–D).

DISCUSSION

Brown-throated sloths were observed using countryside habitats in the study region, albeit to varying degrees, and did not appear to be entirely dependent upon forest fragments. As expected for an arboreal mammal of low vagility, structural elements associated with canopy connectivity and vegetation complexity were favored by sloths. At a fine spatial scale, sloths selected habitats of greater structural complexity, regardless of habitat type. For example, within plantations, sloths were more abundant in microhabitats with closed canopies and trees with variable height and basal area, while areas of uniform structure and less canopy cover were generally avoided. The daily movement and dispersal of sloths require vertical and horizontal travel to evade predators and prevent injuries, and uninterrupted connectivity of the canopy allows for enhanced access to scattered food resources (Cassano *et al.* 2011). Positive correlations between canopy cover and three-toed sloth presence have been similarly documented (Falconi *et al.* 2015), although associations with low canopy cover have been observed during the dry season in Colombia (Castro-Vásquez *et al.* 2010, Acevedo-Quintero *et al.* 2011). This discrepancy could be due to seasonal variation in leaf phenology or differences in methodology for quantifying canopy cover. While floristic composition was not fully accounted for in our study, it influences the habitat selection of three-toed sloths and should be incorporated into future models (Vaughan *et al.* 2007, Mendoza *et al.* 2015).

The significant association of sloth occurrence and PC2 (*i.e.*, tree density) found in this study is consistent with previous

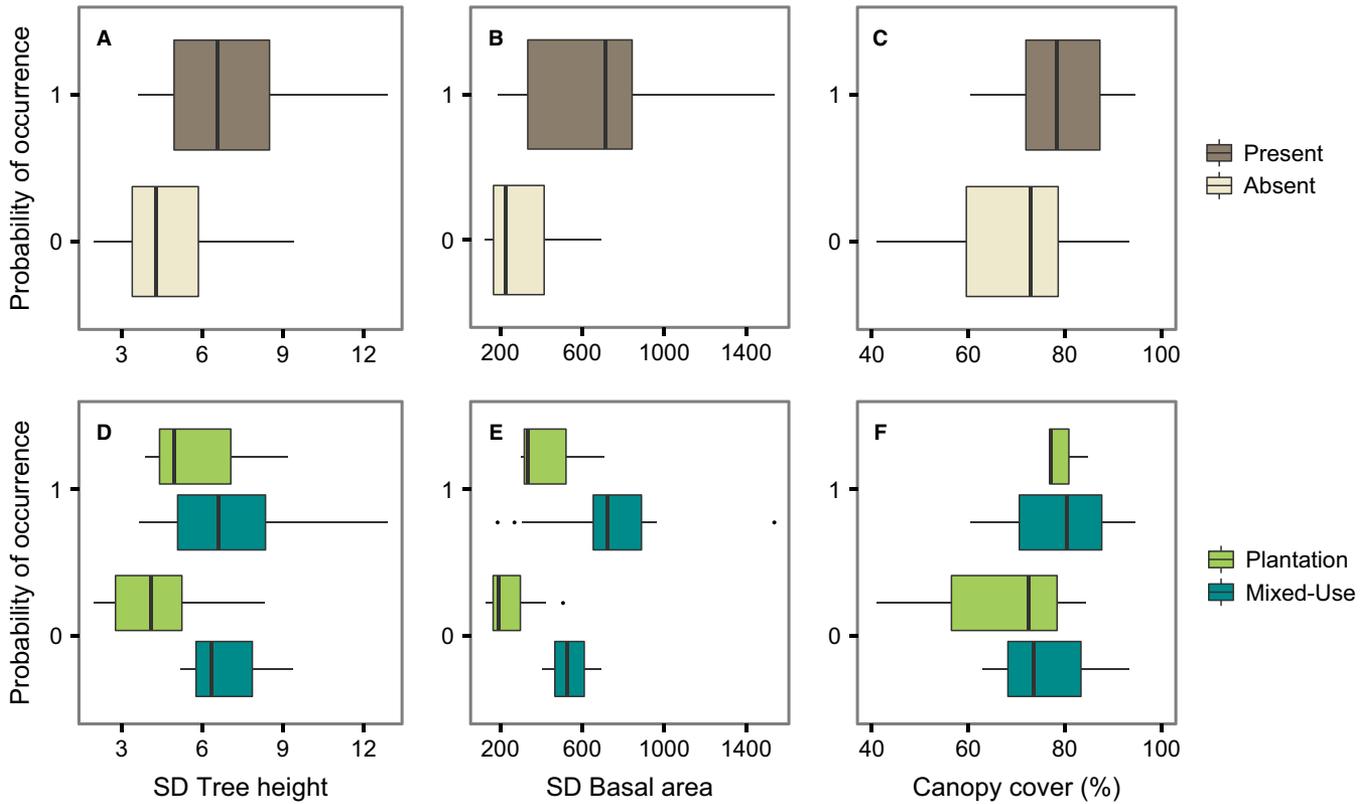


FIGURE 2. Box plot summaries with columns representing standard deviation (SD) of tree height, SD of tree basal area, and percent canopy cover by sloth occurrence (presence in brown, absence in beige) across all sites (A–C), and separated by land-use type (D–F; plantations in light green, mixed-use in teal). Vertical bars indicate medians, horizontal lines indicate minimum and maximum values, and points indicate outliers.

TABLE 4. Summary of the mixed-effects logistic regression model for predicting sloth occurrence as a function of landscape-scale habitat characteristics. Significant values of $P < 0.05$ are in bold.

Predictor variable	Parameter estimate (β)	Standard error	P
Intercept	2.88	1.42	0.042
PC1	-1.24	1.17	0.289
PC2	7.50	4.36	0.086
PC3	-2.94	3.42	0.389
PC4	-11.21	5.40	0.038
PC2:PC4	-28.02	16.10	0.082

research on the habitat selection of three-toed sloths (Falconi *et al.* 2015). Sites with low tree density may signify open areas or areas with a few, old growth trees, neither of which is preferred sloth habitat, whereas sites with greater tree density might reflect high rates of secondary growth and increased connectivity, thereby promoting sloth occurrence. The significant relationship found between sloth occurrence and PC3 (*i.e.*, stand height) in the local-scale analysis suggests that sloths tend to favor tree stands that are slightly shorter on average. This may reflect a tendency for sloths to prefer habitats with high exposition to

sunlight and light levels of disturbance (*e.g.*, where pioneer species colonize treefall gaps) or could be a consequence of lower detection rates in taller trees. While other studies have shown that *Bradypus* sloths prefer taller trees (Castro-Vásquez *et al.* 2010, Acevedo-Quintero *et al.* 2011), these findings are based on comparisons of individual trees rather than average stand height, which make direct comparison difficult. We also found that the incidence of sloths increased in a nonlinear fashion with the combined effects of structural complexity and stand age. When the vegetation structure is less complex, there is a stronger effect of stand age on sloth occurrence. This suggests sloths have a tendency to prefer shorter stands when overall structural complexity is low, perhaps when there is improved canopy connectivity because of a denser sub-canopy resulting from fewer large emergent trees.

Both local and landscape habitat characteristics influenced the occurrence of brown-throated sloths in our study area. At the landscape level, sloth occurrence was associated with landscape composition and configuration only at the 5-ha scale, favoring habitats higher in secondary forest cover and closer to tracts of secondary forest (≥ 10 ha). These findings are consistent with other studies on arboreal vertebrates, which have shown that the amount of available habitat (Michalski & Peres 2005, Faria & Baumgarten 2007) and distance to forest (Anderson *et al.* 2007, Bali *et al.* 2007) is important in predicting species distributions.

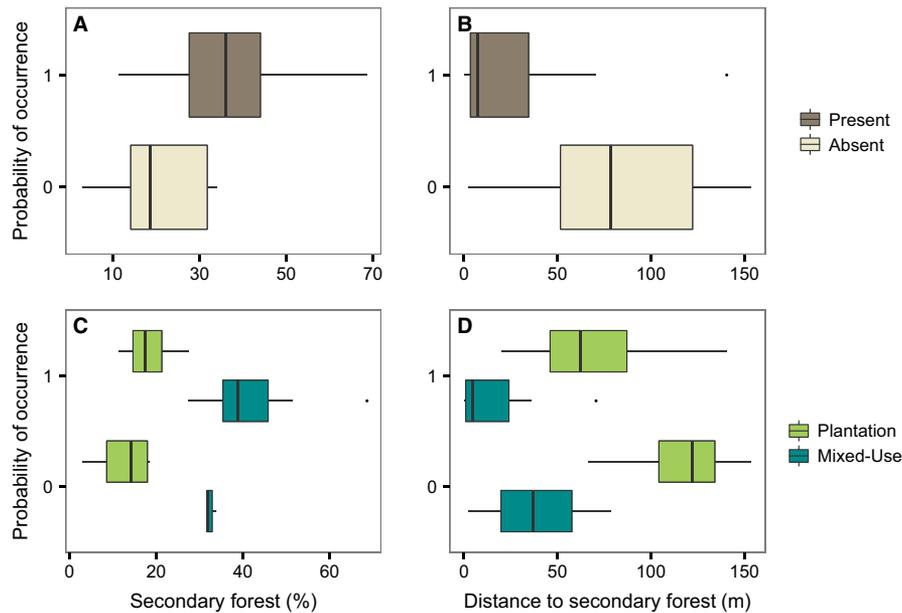


FIGURE 3. Box plot summaries of proportion of secondary forest and distance to secondary forest (≥ 10 ha) in columns by sloth occurrence (rows) across all sites (A, B), and separated by land-use type (C, D). Colors are the same as in Figure 2. Vertical bars indicate medians, horizontal lines indicate minimum and maximum values, and points indicate outliers.

Isolation from nearby forest patches shifts species' distribution patterns, preventing dispersal or forcing individuals to traverse unsuitable areas in search of favorable habitat fragments. Susceptibility to increasing isolation is especially high for sedentary species, like *B. variegatus*, and therefore habitat patches must be close enough to minimize their effective isolation (Ricketts 2001, Ewers & Didham 2006).

Five hectares corresponds to the median home range size for *B. variegatus*, which could explain the significant response of sloths to landscape attributes at this spatial scale. At the 0.5- and 2-ha scales, sloth occurrence was not associated with landscape features, but rather was likely more influenced by fine-scale habitat characteristics. Our results indicate that models predicting species distribution based solely on local habitat attributes or broader landscape structure may be inadequate for brown-throated sloths. While other factors may influence sloth occurrence, such as historical biogeography, physiology, population density, presence of predators, and random processes, understanding the influence of environmental variables on local distribution is a critical step in characterizing the habitat use of sloths.

Our study complements previous research in highlighting the importance of considering multiple spatial scales when evaluating species-specific responses to fragmentation (Mazerolle & Villard 1999, Krawchuk & Taylor 2003, Panzacchi *et al.* 2010) and their use of human-modified habitats (Haslem & Bennett 2008). While countryside habitats are not a substitute for protected areas, our findings suggest that they may provide an opportunity for increasing the population viability of sloths in a region that is experiencing continual land-use change. By understanding how habitat features at multiple scales influence

organisms of low vagility, conservation strategies in multi-functional landscapes can be designed to promote increased connectivity for a range of species.

CONSERVATION IMPLICATIONS.—The habitat requirements and preferences of sloths depend on structural complexity, which is directly affected by specific land-management practices. Our study emphasizes the importance for landowners to manage biodiversity and natural capital on their own land. To promote the movement of sloths and decrease effects of isolation, land managers should increase structural complexity by retaining habitat with high canopy cover and heterogeneity in basal area and height. Active management by plantation managers, including increased rotation lengths and partial cutting, is necessary to maintain structural complexity, improve connectivity, and mitigate the decline of key structural attributes (Lindenmayer & Franklin 2002).

While the potential for countryside habitats to enhance the conservation of sloths is promising, it is important to consider that species occurrence does not indicate the ability to maintain stable populations (Peery & Pauli 2014). The presence of large tracts of old growth forest in our study area may function as source patches promoting the existence of brown-throated sloths in countryside habitats, while more agriculturally dominated regions may lack such areas (*e.g.*, Limón Province; Vaughan *et al.* 2007). As land-use change intensifies in the future, sloths will likely face increasing pressures related to habitat connectivity, particularly because of their relatively low gap-crossing ability (Montgomery & Sunkist 1978, Dale *et al.* 1994). Moreover, plantations are intended for eventual harvest, so the long-term contribution

of plantations as potential habitat may depend on designed harvest rotations and patch geometry (Goldstein *et al.* 2003). The extent and ecological quality of countryside habitats will ultimately determine whether tropical vertebrates can persist in these areas without depending on contiguous, extensive forests (Sekercioglu *et al.* 2007).

What is clear is that opportunities to increase yields with fewer detrimental effects on biodiversity, as well as those to increase forest protection with fewer detrimental effects on peoples' livelihoods, need to be identified and established (Norris *et al.* 2010). Provided that multi-functional landscapes retain forest fragments and areas of high structural complexity in an appropriate configuration, it is likely that many species can coexist with small-scale agricultural development (Harvey *et al.* 2006, Mendenhall *et al.* 2011). The sole emphasis on large areas of native vegetation for biodiversity conservation represents an outdated conceptual model of landscape modification (Fischer & Lindenmayer 2007). Although plantations and mixed-use areas are not surrogates for reserves, these countryside habitats should be perceived as complementary to large patches of native vegetation in maintaining biological diversity.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n8tt5> (Neam & Lacher 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Map of the study area located in north-central Costa Rica.

TABLE S1. FRAGSTATS metrics used to quantify landscape composition and configuration of three-toed sloth presence and absence sites in north-central Costa Rica.

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