# THE SPATIAL ECOLOGY OF A DISPERSAL LIMITED MAMMAL ON A

# MOSAIC LANDSCAPE

A Thesis

by

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# ABSTRACT

As human population, food consumption, and the demand for forest products continue to rise, the pressures of land use change on biodiversity are projected to intensify. In tropical regions, countryside habitats and conventional agricultural practices that retain abundant tree cover and a structurally complex canopy may provide habitats and landscape connectivity for many taxa. This research aimed to assess how the spatial distribution of a dispersal-limited mammal, the brown-throated sloth (*Bradypus variegatus),* is shaped by differences in the structure and configuration of countryside habitats in Costa Rica, using a multi-scale framework.

I conducted two studies to better understand the spatial ecology of brown-throated sloths, and identify specific conservation opportunities for the species. First, data on sloth occurrence was collected from line-transect surveys within countryside habitats (*i.e.,* plantations and mixed-use areas). Subsequently, I developed a density surface map to pinpoint hotspot areas of brown-throated sloths. Second, I measured characteristics of the habitat surrounding sloth presence and absence sites at the local scale (tree height, canopy cover, basal area) and at three broader scales (patch area, shape, degree of isolation) using ArcMap 10.2 and FRAGSTATS 4.2. At the local scale, results indicated that sloths were more likely to be present in structurally complex habitats, specifically areas that were heterogeneous in tree height and basal area. Even within a given habitat type, sloths preferred more complex areas over homogenous areas.

At the broader scale, sloths appeared to prefer habitats that encompassed high proportions of secondary forest and those that were nearby large tracts of forest (≥10 ha).

The brown-throated sloths in this study seemed to be able to adapt to the disturbed and fragmented environment by utilizing countryside habitats, specifically riparian forests, tree plantations and mixed-use areas. While there is no substitute for the resources and ecosystem services provided by forests, the management of countryside habitats should also be a priority because of their potential to conserve brown-throated sloths, and other taxa throughout the Neotropics. To locally promote the use of countryside habitats by brown-throated sloths, property owners should retain patches of secondary forest and incorporate more structurally complex vegetation into their lands.

**DEDICATION**


This is dedicated to

all of my three-fingered friends

in Costa Rica and beyond.

# ACKNOWLEDGEMENTS

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# CHAPTER I

## INTRODUCTION

Land use change, often driven by development pressures and a complex array of socio-economic factors, is a key driver of biodiversity loss across all taxa (Offerman et al. 1995, Gardner et al. 2010). Human land use practices commonly result in degraded and fragmented habitats (Foley et al. 2005), reduced connectivity of landscapes (Saunders et al. 1991, Crooks et al. 2011), and declines in species abundance (Newbold et al. 2015). This is of particular concern in the tropics, where human populations are escalating and a considerable proportion of these people depend on forest resources for their livelihoods (Norris et al. 2010). Landscapes that were once predominately forest are being rapidly converted into a mosaic of different land covers under various intensities of human use.

Costa Rica, for example, experienced one of the highest deforestation rates (~30,000 ha/year) in the world in the 1970s and 1980s (De Camino et al. 2000). The staggering rate of deforestation was primarily driven by a booming population, consumption patterns in developed countries, and national land titling policies that rewarded the conversion of forests into agricultural lands and pastures (Rosero-Bixby and Palloni 1998). Despite many legal reforms, such as tax credits and market-based mechanisms that have recently aimed to promote the reforestation of Costa Rica, the consequences of decades of deforestation are still manifested throughout the landscape

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today, where secondary forest fragments are bordered by a mosaic of open pasture and agricultural areas.

As human population, food consumption, and the demand for forest products continue to rise over the next century, the pressures of land use change on biodiversity and the ecosystem services they provide are projected to intensify (Sala et al. 2000, DeFries et al. 2005, Rademaekers et al. 2010). Therefore, a research agenda that integrates human actions as components of Earth's ecosystems is vital for the efficacy of biodiversity conservation efforts in the tropics.

Agricultural development and biodiversity conservation have traditionally been regarded as incompatible, and consequently, the majority of conservation research in the tropics has concentrated on pristine ecosystems (Tscharntke et al. 2005). Historically, conservation scientists have overlooked the potential for human-modified landscapes to sustain biodiversity. Only recently has the focus started to shift from studies of species in natural, pristine habitats to research within human-modified landscapes (Mendenhall et al. 2014). Although the fate of biodiversity is undeniably linked with agricultural development, conservation and agriculture are not necessarily mutually exclusive. In tropical regions, conventional agricultural practices that retain abundant tree cover and a structurally complex canopy may provide suitable habitats, resources, and dispersal pathways for a significant portion of the native biota (Harvey et al. 2006a).

While protected areas are an essential element of any conservation strategy designed to protect biodiversity, particularly obligate forest species, there is an increasing body of evidence that emphasizes the conservation value of countryside

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habitats in developing landscapes (Daily et al. 2001, Mendenhall et al. 2011).

Countryside habitats, such as tree plantations, riparian zones, and remnant clusters of

trees, can increase structural complexity and enhance the connectivity of habitats in

human-modified landscapes (Haslem and Bennett 2008, Brockerhoff et al. 2008).

Similarly, agroforestry systems harbor greater species richness than conventional

systems by enhancing the size and quality of tree cover, reducing edge effects, and

providing stepping stones between habitat patches (Harvey et al. 2006b, Faria et al.

2007). Furthermore, countryside habitats can provide microclimatic refuges, shelter from

predators, and buffers from the effects of agriculture and cattle ranching on neighboring

forests and protected areas (Sekercioglu et al. 2007).

Mammals are widely used as indicators of habitat disturbance and ecosystem

health because of their close relationships with forest cover and habitat complexity

(Fenton et al. 1992, Lopes and Ferrari 2000, Harcourt and Doherty 2005). The

behavioral responses of mammals to spatial elements are often directly related to their

body size, life history traits, and ability to move through the landscape (Gehring and

Swihart 2003). All else being equal, species with poor dispersal ability might be

disproportionately vulnerable to habitat loss and fragmentation (Kotiaho et al. 2005,

Stork et al. 2009, Slatyer et al. 2013). Dispersal ability can play an especially important

role in determining how organisms respond to habitat size, isolation, and permeability,

as well as the quality of the surrounding landscape matrix. For example, the costs of

movement (*i.e.,* predation risk and energetic expenditure) between forest fragments are

likely to be higher for species of low vagility, such as three-toed sloths, than for species

that are able to disperse more easily. These high costs of movement can inhibit

organisms of low vagility from exploiting resources and habitats that would otherwise be

suitable. In addition to the weak dispersal potential of three-toed sloths, their sedentary

lifestyle compounded by their low metabolic rate and reliance on forest cover make them

especially susceptible to land use change (Moss et al. 2012). Therefore, three-toed sloths

can serve as excellent model organisms when studying the responses of species' to

spatial features in a human-modified landscape.

Human-modified habitats should be considered when making conservation and

management decisions for numerous reasons. First, the amount of forest that remains in

agricultural ecosystems is not adequate for protecting biodiversity in the long-term

(Pardini et al. 2009). Moreover, a majority of the forest remaining in these areas exists

on privately owned land and therefore the landowner determines the fate of these

remnant forest fragments. Second, many species present in agricultural areas are unlikely

to view the surrounding environment in a binary manner (*i.e.,* suitable habitat or non-

suitable habitat) (McIntyre and Hobbs 1999). Movement among a mosaic of habitats is a

requirement for many species to obtain resources on a daily or seasonal basis, or during

different stages in their life history (Law and Dickman 1998). This suggests that the

protection of certain habitat types alone (*e.g.,* rainforest) will be insufficient to achieve

conservation goals, and therefore we must move beyond reserves with increasing

emphasis on the study of biodiversity in human-modified landscapes (Chazdon et al.

2009).

Understanding the relative influence of habitat characteristics and spatial features on species distributions is a significant component of mitigating the effects of global land use change on species. Our current knowledge of the potential role of countryside habitats in the conservation of three-toed sloths has stemmed from a limited number of studies focusing on a single scale (Polanco-Ochoa 1998, Castro-Vásquez et al. 2010, Acevedo-Quintero et al. 2011). Scaling issues are fundamental to all ecological investigations, as the scale of an investigation may have profound effects on the patterns detected (Wiens 1989). However, ecologists seeking to investigate the potential value of countryside habitats in sustaining biodiversity often ignore the influence of spatial scale.

Additionally, a majority of the studies of three-toed sloths in countryside habitats occur within a particular geographic region, such as the Caribbean coastal plain of northeast Costa Rica (Vaughan et al. 2007, Ramirez et al. 2011, Peery and Pauli 2014). Moreover, these studies have reported variations in the response of three-toed sloths to agroforestry, living fencerows, and pastures, though none have assessed the use of tree plantations and mixed-use areas by sloths or investigated the effect of landscape context on sloth spatial ecology.

The purpose of this study was to assess how the spatial distribution of a dispersal-limited mammal, the brown-throated sloth (*Bradypus variegatus*), is shaped by differences in habitat structure and spatial patterns of countryside habitats in Costa Rica, using a multi-scale framework. The study occurred along the Caribbean slope of the Monteverde Cloud Forest Reserve, in San Juan de Peñas Blancas, Costa Rica. This region is a landscape mosaic of forests and human-modified habitats. The landscape is

primarily comprised of forests in different successional stages (59.5%), specifically

secondary forests (45.5%), primary forests (11 %), and riparian forests (3%). The next

dominant land uses are cattle pasture and cropland, which respectively cover 19% and

10% of the landscape. Plantations encompass approximately 3.5% of the landscape, the

majority of which are greater than 8 years old and contain both native and non-native

tree species. Mixed-use areas, which contain multiple land use types (*e.g.,* residential,

small-scale agriculture, patches of secondary forest), comprise a smaller portion of the

landscape (~1%), but are generally abutted by pastures and agricultural lands and thus

may be important countryside habitats for biodiversity. Water and urban areas comprise

the remaining 7% of the landscape.

Specifically, in my first study (Chapter II), I used survey and geographic

information systems (GIS) techniques to compare brown-throated sloth densities across

different countryside habitats. I produced a point density surface map to ascertain how

individual sloths are distributed across the landscape and to what degree they utilize

human-modified habitats, with particular focus on tree plantations, riparian forests, and

mixed-use areas. This map can provide guidance in the design of management strategies

aimed to promote the conservation of sloths in the study region.

In my second study (Chapter III), I investigated how local habitat characteristics

and landscape properties of different countryside habitats influence the distribution of

brown-throated sloths. This study was predominantly concentrated on plantations and

mixed-use areas, but riparian forest fragments were also included. These land use types

not only represent countryside habitats that may support brown-throated sloth

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populations, but they are also common in agricultural landscapes throughout Central America (Montagnini et al. 2005, Harvey et al. 2006a), making the results broadly applicable to similar landscapes across the region.

By studying how habitat elements influence the distribution of brown-throated sloths across multiple scales, my goal is to provide an understanding of the effects of land use change and fragmentation on the spatial patterns of species with low dispersal abilities. The analytical approaches I used can be applied to a wide variety of organisms, including other dispersal-limited species, as well as other landscapes experiencing a gradient of anthropogenic pressures. A concrete understanding of multi-scale biodiversity patterns in human-modified landscapes is essential for identifying effective management strategies and setting conservation priorities.

# CHAPTER II

# THE GEOGRAPHIC DISTRIBUTION OF THREE-TOED SLOTHS ON A

# MOSAIC LANDSCAPE IN COSTA RICA

## INTRODUCTION

Brown-throated three-toed sloths (*Bradypus variegatus*) are mid-sized, arboreal mammals associated with Neotropical forests, where they rely on the upper levels of the forest canopy to live, feed, and reproduce (Eisenberg 1989). Because of the poor nutritional quality of their folivorous diets and extremely low metabolic rates, sloths require slow movements and extended periods of inactivity (Montgomery and Sunquist 1975, Nagy and Montgomery 1980, Gilmore et al. 2001). Consequently, sloths have a weak dispersal ability and, combined with their high reliance on forest cover, are likely to be susceptible to forest fragmentation and degradation caused by land use change (Tilman et al. 1997). In eastern Nicaragua, for example, fragmentation of the native forest has adversely affected three-toed sloth populations and, in some cases, caused extinction of local populations (Genoways and Timm 2003).

Brown-throated sloths are common inhabitants of primary and secondary forests from southern Honduras to northern Argentina (Eisenberg 1989). Studies on the home range and resource use of brown-throated sloths in Costa Rica estimated that sloths possess a median home range size of approximately 5.2 ha (Vaughan et al. 2007). Within this relatively restricted home range, a brown-throated sloth typically remains in the

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same tree for 1.5 days before moving to a new tree through the pathways between tree crowns (Montgomery 1983).

Notably, brown-throated sloths are not exclusively dependent on forests to fulfill their resource requirements. Brown-throated sloths have also been observed using countryside habitats, specifically riparian areas, cacao agroforests, and cattle pastures containing living fencerows and remnant trees (Vaughan et al. 2007, Ramirez et al. 2011). Whether brown-throated sloths are able to support a self-sustaining population in these areas remains uncertain. There is a possibility that because of their low vagility, they may need supplementation from source populations in neighboring forest patches to maintain a stable population in countryside habitats (Peery and Pauli 2014).

Because sloths are sedentary and cryptic, making inferences about their habitat associations is often difficult. Few studies on the spatial ecology and habitat use of three-toed sloths have considered multi-scale effects, such as landscape context (*e.g.,* patch area and isolation) and fine-scale aspects of habitat (*e.g.,* tree height and canopy cover). Furthermore, while a handful of ecological studies have focused on the spatial ecology of sloths in human-dominated landscapes (Vaughan et al. 2007, Acevedo-Quintero et al. 2011, Peery and Pauli 2014), no research has examined the extent to which sloths use tree plantations or mixed-use areas. Advancing our understanding about how sloths use countryside habitats and to what degree they use them is important for informing how land use change in the tropics affects species of low vagility.

The principle objective of this study was to investigate the spatial ecology (distribution and habitat selection) of a population of brown-throated sloths in

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countryside habitats in Costa Rica, with specific focus on tree plantations, mixed-use areas, and riparian forests. I predicted that the spatial distribution and relative abundance of brown-throated sloths would differ among habitat types, reflecting differences in their ability to meet the multiple Hutchisonian niche requirements of brown-throated sloths. Specifically, I expected a higher abundance of sloths to be concentrated in mixed-use areas and riparian forests because of the greater structural complexity that is characteristic of the vegetation in those areas compared to the homogenous vegetation structure that is typical of tree plantations.

Lastly, I developed a point density surface map to effectively summarize my findings of sloth presence and the intensity of use of various countryside habitats by brown-throated sloths. This map will allow for efficient identification of high concentration areas of brown-throated sloths and enable managers to prioritize conservation in these habitats. Generating information on the use of countryside habitats by brown-throated sloths will help in the design of scientifically based recommendations and strategies aimed to promote the conservation of sloths and other dispersal-limited vertebrates in human-modified landscapes.

**METHODS**

*Study Area*

This study was carried out in San Juan de Peñas Blancas, Costa Rica (10º23'N, 84º37'W) located about 75 km northwest of the capital city of San José (Figure 1). San Juan de Peñas Blancas is located on the Caribbean slope of the Tilarán Mountains, adjacent to the Bosque Eterno de los Niños and the Monteverde Cloud Forest Reserve.

This region is classified as tropical premontane wet forest (Holdridge 1967) with elevational gradient of 275 – 465 meters above sea level. The mean annual temperature of this region is 23˚ C and the mean annual precipitation is approximately 4500 mm. Mean monthly precipitation varies from 154 mm in February to 540 mm in November.
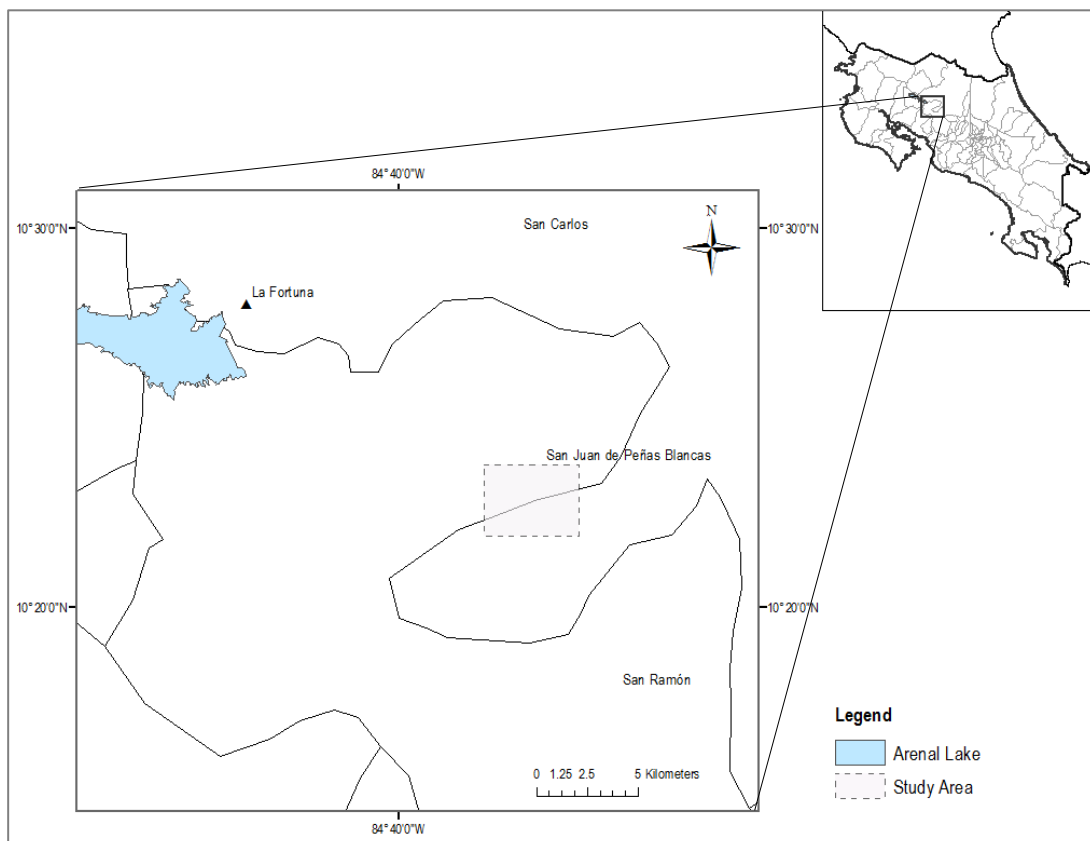


**Figure 1.** The location of the study region in north-central Costa Rica. The study was conducted in the town of San Juan de Peñas Blancas, denoted by the dashed box (10º23'N, 84º37'W).

The study area was approximately 4 km$^2$ (1,600 ha) and composed of a mosaic of forests and human-modified habitats. The landscape is primarily comprised of forests in different successional stages (59.5%), specifically secondary forests (45.5%), primary forests (11 %), and riparian forests (3%). The next dominant land uses are pastures and small-scale monocultures which cover 19% and 10% of the landscape, respectively. Tree plantations encompass approximately 3.5% of the landscape. Most plantations in the study region are relatively established ($\geq$ 8 years old), possess a cleared understory, and consist of native and non-native tree species such as ronrón (*Astronium graveolens*), teak (*Tectona grandis*), American mahogany (*Swietenia humilis*), and gmelina (*Gmelina arborea*). Mixed-use areas, which contain multiple land uses (residential, small-scale agriculture, patches of secondary forest), comprise a smaller portion of the landscape (~1%), but are usually adjacent to pastures and agricultural lands and thus, may be important countryside habitats for biodiversity. Urban areas, bare ground, and water cover the remaining 7% of the landscape.

*Data Collection*

<u>*Sloth Surveys*</u>

I conducted sloth surveys during May-August 2014. The study region was stratified according to land use type and seven survey sites were selected from two countryside habitats of interest (Figure 2). I selected sites that were well distributed across the study area and consisted of a range of different patch sizes. Four sites were located in tree plantations (4.9 – 15.8 ha) and three sites were located in mixed-use areas (2.9 – 9 ha). Survey sites and their respective sizes are shown in Table 1.
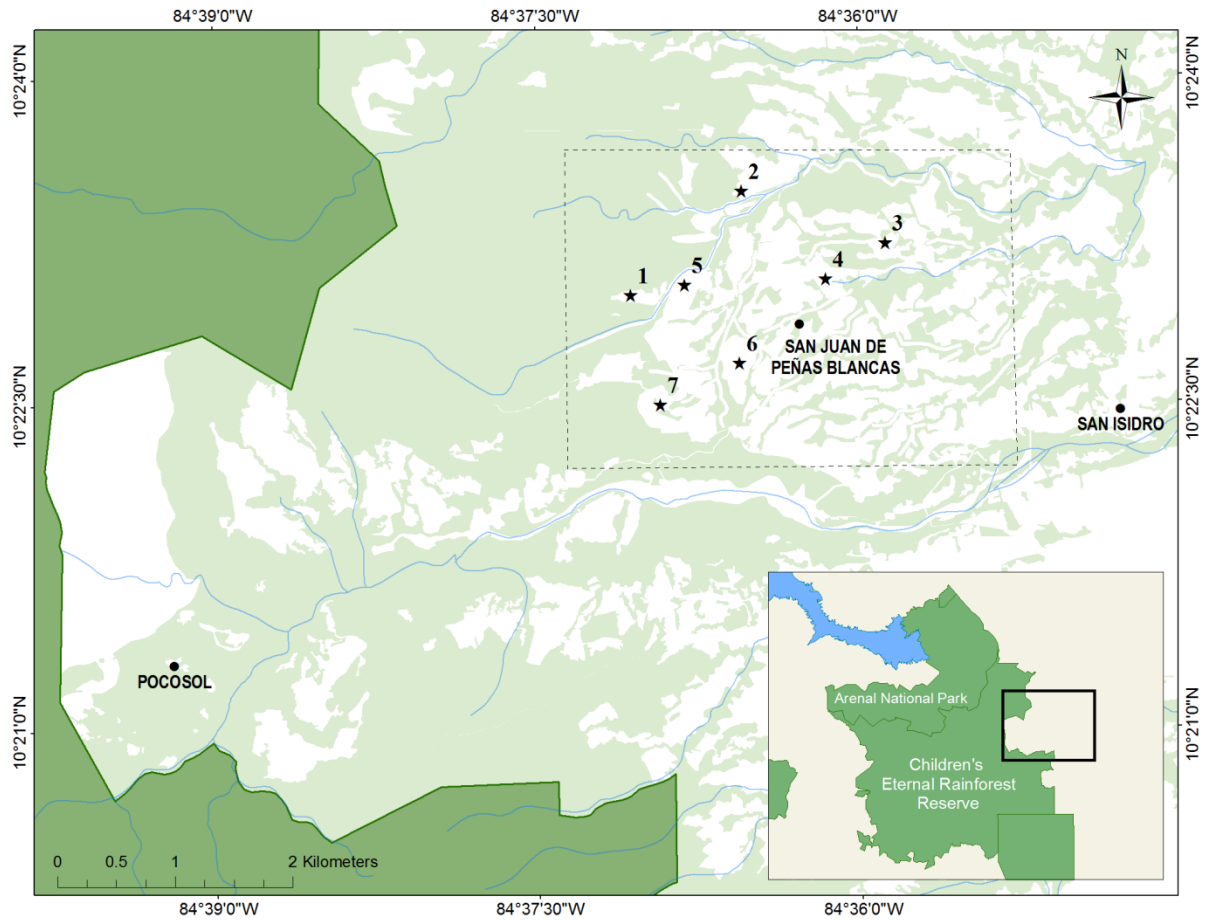
**Figure 2.** The locations of survey sites (numbered 1 – 7) where transects were conducted during May – August 2014 in San Juan de Peñas Blancas, Costa Rica. The dotted box in the northwest portion of the map delineates the study region.

**Table 1.** Area (ha) and habitat type of the seven sites that were surveyed for brown-throated sloths in San Juan de Peñas Blancas, Costa Rica during May – August 2014.

| Site | Area (ha) | Habitat Type |
|------|-----------|--------------|
| 1 | 2.87 | Mixed-Use |
| 2 | 4.53 | Mixed-Use |
| 3 | 9.02 | Mixed-Use |
| 4 | 4.87 | Tree plantation |
| 5 | 5.63 | Tree plantation |
| 6 | 11.63 | Tree plantation |
| 7 | 15.73 | Tree plantation |

Line transects are a practical and effective method for obtaining qualitative data on the distribution of sedentary organisms, which can then be compared across different sites (Anderson et al. 1979). Therefore, this study used line transects to collect information on the distribution and relative abundances of brown-throated sloths in different countryside habitats. Within plantation sites, transects were established using a systematic design of parallel transects to ensure equal coverage of the site and a random first start to provide an element of randomization. Transects were established at least 15 m from the surrounding habitats to reduce edge effects. In mixed-use areas, transects were walked along pre-existing trails distributed throughout the entire sampling area. Riparian areas were also sampled, but harsh terrain and safety concerns prohibited the inclusion of transects in such sites. Therefore, any observations of brown-throated sloths in riparian areas were preformed from dirt roads, *ad libitum*.

Multiple methods were used to improve detection probability: 1) extensive transect length guaranteed adequate coverage of each site 2) repeated surveys ensured exhaustive sampling, and 3) high powered binoculars assisted in locating sloths in the

canopy. Since species with small area requirements, like the brown-throated sloth, are more liable to regularly use their entire home range for foraging, it is expected that they will be observed at a constant probability along the sampling effort (de Thoisy et al. 2008).

All transects were walked at a speed of approximately 0.5 km/h during peak sloth activity periods (0800 – 1600 h). To avoid a potential bias in the ability to detect sloths, all transects were walked by the same experienced observer (KDN). Depending on the length of the each transect between four and six transects were surveyed each day. At the start of each transect, the ambient temperature (˚C) and estimated percent cloud cover were recorded. Surveys were not carried out during periods of heavy rainfall because of the extremely low detectability rates during these conditions. To overcome the problem of variable sizes of sampling sites, sampling effort was relatively proportional to the total area of each site. The total survey effort by habitat type was 18.7 km (6.23 ± 3.9 km) in mixed-use areas and 26.1 km (6.63 ± 2.26 km) in tree plantations. The survey effort by individual site is shown in Table 2.

**Table 2.** The number of line transects, cumulative transect length (m), and total survey effort (km) for the seven sites in which brown-throated sloth surveys were conducted during May – August 2014.

| Site | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|------|---|---|---|---|---|---|---|
| Habitat type | | Mixed-use | | | Tree plantation | | |
| No. of transects | 3 | 3 | 6 | 4 | 4 | 4 | 5 |
| Cumulative length (m) | 775 | 1000 | 1200 | 900 | 975 | 1350 | 1500 |
| Total effort (km) | 3.9 | 4.0 | 10.8 | 4.5 | 4.9 | 8.1 | 9.0 |

When a sloth was encountered on a transect, a unique identifier was assigned and a GPS reading was taken at the base of the tree in which the sloth was located, using a Garmin eTrex 20 device. If the base of the tree was not easily accessible, the distance from the observer to the tree was measured to the nearest meter using a laser rangefinder and a compass bearing was recorded to the nearest degree. This information was used along with a GIS to determine the precise geographic location of the sloth. Tree height and the height of the sloth above ground were calculated using a clinometer, and the tree was identified to genus or species when possible.

Individual brown-throated sloths were identified based on natural markings on their fur. Male brown-throated sloths have a speculum, an orange patch of fur on their back. Each male has a different speculum that differs slightly in color, brightness, size, and shape, making it possible to recognize a particular individual (Figure 3). Individual female brown-throated sloths may also be identified by distinct coloration patterns of their pelage, but their lack of a speculum makes it slightly more challenging. Although the same sloths were often observed in the same area on multiple occasions, I only used information on sloth presence for this study.

**Figure 3.** The speculum of a male brown-throated sloth is unique for each individual. Speculums may differ in brightness, size, and shape and can be used for identification purposes.

*Density Surface Mapping*

Simply plotting sloth localities on a map does not provide sufficient information about where sloths are more or less concentrated. Surface modeling, however, involves the translation of discrete point data into a continuous surface that represents the geographic distribution of the data (Berry et al. 2005). Density surfaces are generated in a GIS as a grid of cells (*i.e.,* raster layers) where each cell is assigned a density value based on the number of points within a specified area around the cell center (*i.e.,* the neighborhood). The density analysis is primarily based on the size of the grid cells (*i.e.,*

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grain size) and the area of the neighborhood around the cell centers. In general, a smaller grain size and a larger neighborhood will result in a smoother density surface.

A point density surface map was created to summarize the brown-throated sloth presence data and identify high-density clusters of sloths using the point density function in the Spatial Analyst extension of ArcGIS 10.2. For this study, I determined that a neighborhood of 5 ha would be suitable for representing patterns at the scale of the brown-throated sloths' home range. A grain size of 10 x 10 m was selected, taking into consideration the minimum distance between sloth presence points and the resolution of the original data. For each cell in the raster, the total number of sloth presence points that fell within the 5 ha neighborhood was divided by the total area of the neighborhood. The subsequent output was a smoothed surface map representing relative sloth density in the study region.

**RESULTS**

*Distribution and Habitat Use by* B. variegatus

A total of 38 sloths were detected in countryside habitats throughout the study area during May – August 2014 (Figure 4). A higher number of sloths were observed within mixed-use areas (n=22) than in plantations (n=5). Sloths were also detected in riparian forest (n=5) and secondary forest fragments (n=6) from along dirt roads between survey sites.

Of the 38 sloths detected, 58% were males (n=22), 34% were females (n=13), and 8% were juvenile or infant sloths (n=3). On four separate occasions, two or more adult sloths, usually one male and one female, were observed together in the same tree.

Many of the sloths were resighted on multiple occasions (*i.e.,* identified by patterns in their pelage and other distinguishing markings).
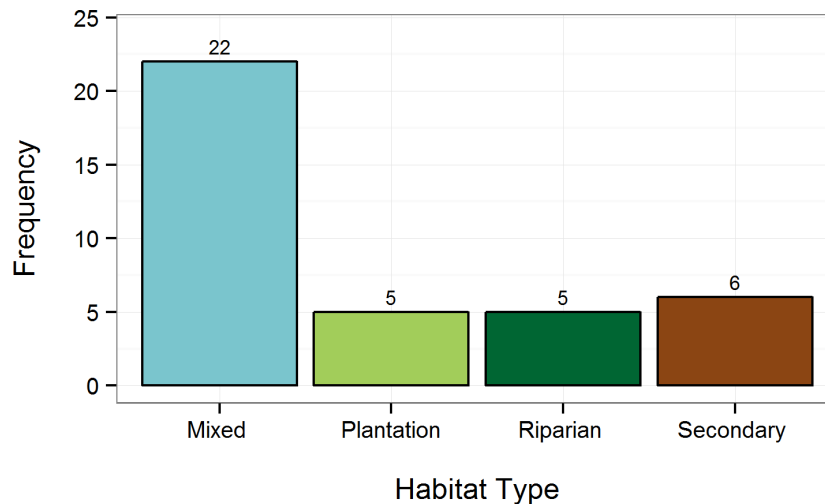


**Figure 4.** Histogram of brown-throated sloths in four different habitat types in San Juan de Peñas Blancas, Costa Rica during May – August 2014. Numbers above histograms indicate the number of individuals observed.

*Density Surface Mapping*

Density surface mapping generated a continuous surface representation of the geographic distribution of brown-throated sloths in the study region (Figure 5). Two high-density areas were identified, denoted by regions in red and orange. These areas contained between 0.8 and 1.6 sloths per hectare. Several other areas with a moderate density of sloths were identified, marked by the regions in yellow. The green and blue regions characterize areas that contained a lower density of sloths ranging from 0.2 to 0.6 sloths per hectare. Because the point density method calculates sloth density based

solely on occurrence points, assumptions were not made about densities at locations where no observations were made or where surveys were not conducted (Alessa et al. 2008). These areas are represented as No Data in the density surface map (Figure 5).
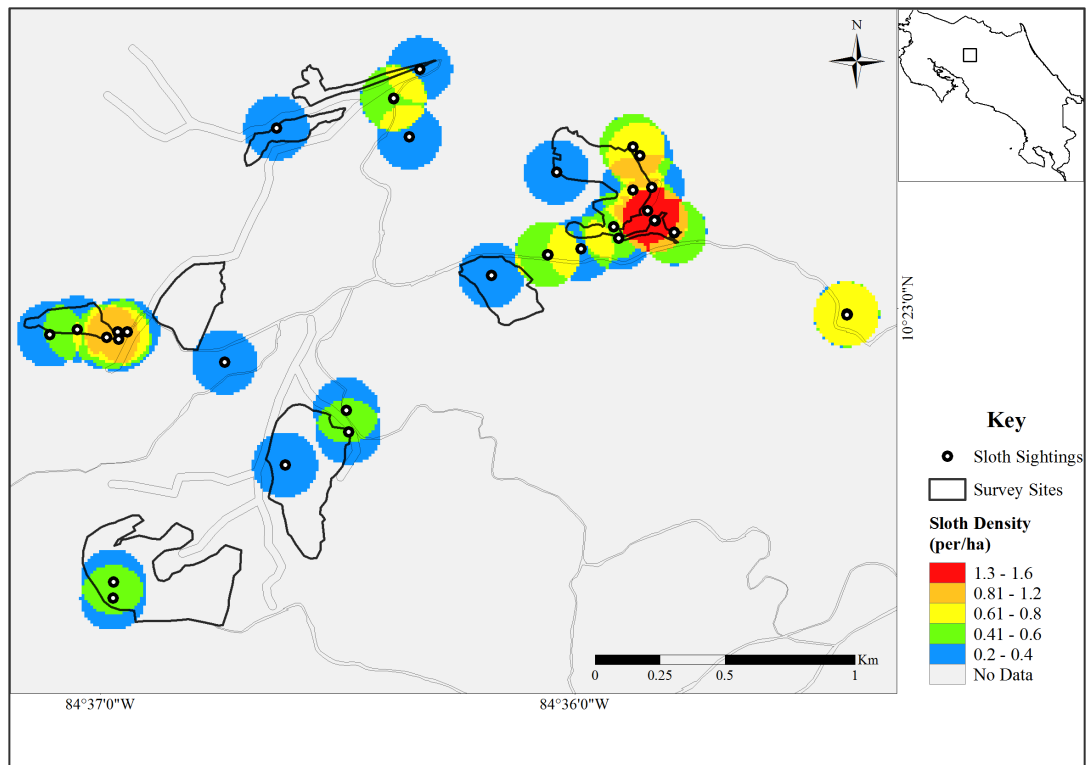


**Figure 5.** Point density surface map of brown-throated sloths (n = 38) throughout San Juan de Peñas Blancas, Costa Rica during May – August 2014. Survey sites are outlined in bold. Points represent localities where a sloth was present. Areas in red correspond with a higher density of sloths, while areas in blue correspond with a lower density of sloths.

## DISCUSSION

The brown-throated sloths that occupy this human-modified landscape appear to be able to adapt to the disturbed and fragmented environment by utilizing countryside

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habitats, specifically riparian forests, tree plantations and mixed-use areas. This may be a consequence of the high abundance of pioneer species that is typical of these early-mid successional habitats. A higher abundance of brown-throated sloths were observed in mixed-use areas than in plantations. These results support my hypothesis that brown-throated sloths are more likely to be present in mixed-use areas, probably because of the greater structural complexity of the vegetation in these areas than in tree plantations.

Previous studies have found three-toed sloths to favor habitats based on their floristic composition (Urbani and Bosque 2007, Falconi et al. 2015), where many pioneer tree species, specifically *Cecropia*, are highly preferred and an essential component of sloths' diets (Vaughan et al. 2007). The brown-throated sloths in this study were consistently observed in *Cecropia* trees in mixed-use areas. Interestingly, even though *Cecropia* were sparse in tree plantations, it appeared that sloths sought out the few *Cecropia* trees that existed, remained in them for several days before departing, and returned to the same tree frequently. This suggests that while sloths do not appear to be regularly using plantation trees for feeding, they may potentially be using them to aid in dispersal to preferred trees. Plantations could possibly serve as more valuable habitats to brown-throated sloths if they comprised a greater abundance of preferred foraging trees, such as *Cecropia* and *Ficus* species.

The point density surface method identified areas of major concentrations of brown-throated sloths within a limited geographical area. There were two high-density areas of sloths, both of which occurred in mixed-use areas about 2 km apart. These locations with the highest concentration of sloths represent hotspots, which can be used

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in the development of sustainable land management plans that aim to conserve sloths, and other biodiversity, without compromising rural livelihoods. Each landscape, however, has a distinct suite of human activities and land uses, which may or may not be compatible with sustaining biologically productive and resilient ecosystems (Alessa et al. 2008). In addition, because of the lack of landscape context in point density surface maps, the generation of hotspots from point densities may create inaccurate portrayal of sloth habitat use *(i.e.,* hotspots overlapping with pastures or bodies of water). Therefore, while the identification of sloth hotspots aids in pinpointing areas that warrant attention from land managers, it does not reveal any information about neighboring land uses, degree of fragmentation, or local habitat structure that may be linked with the observed sloth hotspot areas. Nevertheless, the density surface map produced in this study provides valuable information on the geographic distribution of brown-throated sloths in the study region, facilitates visual detection of patterns in the data, and may be used in further analyses, such as quantifying changes in brown-throated sloth distribution over time by comparing maps from different seasons.

I believe that because of the cryptic and sedentary nature of brown-throated sloths, this study is a conservative estimate of the relative use of countryside habitats by sloths. A greater number of sloths are likely using tree plantations and mixed-use areas during periods that were unable to be included in my surveys (*e.g.,* at night, during breeding periods, or throughout the dry season), so the potential for these countryside habitats to support a high abundance of sloths appears promising.

An opportunity for further study may be to sample in the dry season to investigate the temporal variation in countryside habitat use by brown-throated sloths. Seasonal differences in activity and behavior have previously been shown for the maned three-toed sloth (*Bradypus torquatus*); less resting and more feeding sessions were observed during the colder dry season than during the hotter wet season (Chiarello 1998). If activity levels of brown-throated sloths are similarly correlated with ambient temperatures, there may also be differences in their use of habitats across seasons. It would also be interesting to conduct surveys during breeding periods (*i.e.,* variable, but generally before the wet season) when sexually mature males may be actively searching throughout their home ranges to locate mates. Additionally, future studies may compare sloth habitat use in the countryside to that of secondary forests to examine how often sloths use human-modified habitats in proportion to their native habitats.

It still remains unclear, however, whether brown-throated sloths are able to support a self-sustaining population in these areas. It is possible that because of their limited spatial flexibility, they might require immigration from surrounding forest patches to sustain a stable population (Peery and Pauli 2014). This is a similar concern among other taxa, including birds and insects (Hughes et al. 2002, Horner-Devine et al. 2003). Detailed population studies are needed to assess the potential for countryside habitats to support populations that are sustainable.

*Conservation Implications*

A key management challenge in human-modified landscapes is to maintain a balance between agricultural production and biodiversity conservation. There is no

substitute for the habitats, resources, and ecosystem services provided by forests, and therefore the preservation of large tracts of intact forest must take precedence in conservation planning. However, the management of countryside habitats should also be a priority because of their potential to maintain and restore biodiversity throughout the Neotropics (Lees and Peres 2006, Haslem and Bennett 2008). In integrated landscapes formerly dominated by forest, countryside habitats can complement conservation reserves and protected areas (Daily et al. 2001, Mendenhall et al. 2011).

Hotspot maps provide graphical tools for land managers and local actors that facilitate the visualization of focal areas for conservation efforts. It is important to note that the methods, as well as the resulting map, are subject to several limitations and managers should be mindful of these. Specifically, there are two parameters that influence the density analysis: area of the neighborhood and grain size. In this study, a value of 5 ha (*i.e.,* the median home range of the brown-throated sloth) was used as the neighborhood size, and 10 x 10 m was the grain size. Different neighborhood and grain sizes will likely have an effect on the scale of the density surface output, and therefore land managers should take these parameters into consideration when interpreting hotspot maps, such as the one produced in this study.

Nonetheless, the identification of hotspots may stimulate further research in these areas to determine which factors are driving the spatial patterns of brown-throated sloth populations. Future research should seek to understand how habitat characteristics influence the occurrence of brown-throated sloths in human-modified landscapes so that conservation efforts can be effectively prioritized.

**CHAPTER III**

**THE INFLUENCE OF HABITAT FEATURES ON THE DISTRIBUTION OF**

**THREE-TOED SLOTHS ACROSS MULTIPLE SPATIAL SCALES**

**INTRODUCTION**

Anthropogenic land use change is among the leading drivers of global

biodiversity loss, particularly in the tropics (Sala et al. 2000, Hilton-Taylor 2000,

Newbold et al. 2015). While a tremendous amount of research has traditionally, and

appropriately, focused on large, pristine tracts of forest (Lees and Peres 2006), there is a

growing body of research that suggests the conservation potential of countryside habitats

in alleviating the threats of expanding and intensifying agricultural development on

biological diversity (Daily et al. 2003, Manning et al. 2006). As part of a new emerging

paradigm for conservation, countryside biogeography is the study of diversity,

abundance, and distribution of species in rural areas, farmland and minimally human-

altered habitats (Daily 2001, Mendenhall et al. 2014). Countryside habitats may be

important for supplementing species' habitats or resources, promoting dispersal between

isolated patches, and dampening the edge effects (Daily et al. 2001, Ewers and Didham

2006). It is important to understand the relative effects of land use change, habitat

fragmentation, and matrix quality on biodiversity, as well as assess the potential for

countryside habitats to support a variety of taxa.

The behavioral responses of species to land use change and fragmentation are

often influenced by their body size, life history traits, and dispersal abilities (Gehring

and Swihart 2003). For example, an organism's ability to disperse or cross gaps can greatly affect how it responds to patch area and isolation, permeability of the habitat, and matrix quality. Variations in landscape properties, such as the amount and spatial configuration of forest cover, can deter, impede or enhance the dispersal and movement of organisms (MacArthur and Wilson 1967, Fitzgibbon 1997, Smith et al. 2011). Dispersal among habitat fragments is vital for long-term metapopulation persistence (Gustafson & Gardner 1996) and is becoming increasingly important as human populations continue to develop and fragment landscapes.

The relative effects of land use change and habitat fragmentation on biodiversity is often scale-dependent (Bowman et al. 2001, Panzacchi et al. 2010). There is a strong scientific basis that spatial variation in environmental conditions or resources dictates species distribution patterns (Wiens 1976, Tilman and Kareiva 1997). Generally, organisms are sensitive to habitat features and resources at a range of scales (Kotliar and Wiens 1990) and may be influenced by both local and regional characteristics of a landscape (Gorresen et al. 2005). For instance, an organism may respond to the presence of a resource at a fine scale, and simultaneously respond to features at broader scales (*e.g.,* amount of forest cover in the surrounding landscape). Furthermore, most species experience their surroundings at spatial scales beyond the plot level during their lifetime (Tscharntke et al. 2008, Gardner et al. 2009). Understanding the relative influence of scale-dependent spatial factors on species distributions is a significant component of mitigating and managing the effects of fragmentation and land use change on biodiversity. Nevertheless, ecological studies often ignore the influence of spatial scale.

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Regardless of taxon-specific differences in behavioral response patterns, forest biodiversity usually decreases along a broad continuum from mature, primary forest to secondary forest, agroforestry, plantations, cropland and pasture (Harvey et al. 2006a, Gardner et al. 2009), generally mirroring the decline in tree cover and structural complexity (August 1983, Philpott et al. 2008). While it is widely recognized that habitats characterized by high structural heterogeneity and complexity (*i.e*., many vegetation strata, dense foliage) have greater capacities to sustain biodiversity, the influence of landscape context is frequently neglected in study designs (Watling and Donnelly 2006).

Both local habitat structure and landscape context are known to affect the distribution of forest vertebrates (Bowman et al. 2001, Faria et al. 2007). The combination of local habitat effects (habitat quality), landscape context (composition and configuration) and species functional traits (*e.g.,* body size and dispersal ability) can produce an array of species distribution patterns. Understanding how all of these characteristics influence the spatial patterns of populations is especially important in human-modified landscapes, where anthropogenic activities alter the size and shape of patches and affect the connectivity of habitats.

In recent years, there have been calls for studies to assess how dispersal-limited species use human-dominated ecosystems (Mendenhall et al. 2011). Previous research on dispersal-limited species, such as sloths, have described local scale environmental variables that seem to be important in influencing habitat use, including tree species, tree height, diameter at breast height, and percent canopy cover (Montgomery and Sunquist

1978, Castro-Vásquez et al. 2010). Few studies, however, have considered the influence of habitat characteristics on the distribution and habitat use of dispersal-limited species at multiple spatial scales. Determining which landscape and habitat features affect the spatial patterns of organisms at different scales is vital for assessing the impacts of land use change and informing conservation decisions.

Given the brown-throated sloths' low vagility and reliance on forest cover, they make an ideal model organism for which to investigate the effects of habitat and landscape context on the spatial ecology of dispersal-limited vertebrates. In this study, I examined how spatial elements and habitat features influence the distribution of brown-throated three-toed sloths (*Bradypus variegatus*) across multiple spatial scales. My objectives were to 1) relate sloth occurrence to local habitat structure within two countryside habitats: tree plantation and mixed-use areas, and 2) relate sloth occurrence to landscape composition and configuration at three spatial extents (*i.e.,* 0.5 ha, 2 ha, and 5 ha). Provided that brown-throated sloths are highly dependent on tree cover for survival and dispersal, I expected that sloths would be positively associated with countryside habitats that are 1) high in local habitat complexity and heterogeneity, and 2) adjacent to large patches of secondary forest. Thus, I expected that within patch effects would be important in determining the local distribution of sloths, but that the composition and configuration of the surrounding landscape would determine sloth distribution at a broader scale.

**METHODS**

*Study Area*

      The study was conducted in an area roughly 4 x 4 km (1,600 ha) within the community of San Juan de Peñas Blancas (10º23'N, 84º37'W), on the Caribbean slope of Cordillera de Tilarán in Costa Rica (refer to figure on page 11). The mean annual temperature is 23˚ C and the mean annual precipitation is roughly 4500 mm, with most rainfall occurring between May and December. The native vegetation of this region is classified as tropical premontane transitional cloud forest with elevations ranging from 275 – 465 meters above sea level. San Juan de Peñas Blancas consists of a mosaic landscape of forests and human-modified habitats. The landscape is primarily comprised of forests in different successional stages (59.5%), specifically secondary forests (45.5%), primary forests (11 %), and riparian forests (3%). The next dominant land uses are small-scale pasture and agriculture which cover 19% and 10% of the landscape, respectively. Plantations make up approximately 3.5% of the landscape, the majority of which are greater than 8 years old and contain both native and exotic species of trees. Mixed-use areas, which contain multiple land uses, comprise a smaller portion of the landscape (~1%), but are usually adjacent to pastures and agricultural lands and thus, may be important countryside habitats for biodiversity. Water and urban areas comprise the remaining 7% of the landscape.

*Data Collection*

    *Sloth Surveys*

Sloth presence or absence was determined from line transects surveyed in seven countryside habitats during May-August 2014 (refer to figure on page 13 and table on page 15). Of the seven total sites, four sites were located in tree plantations (9.5 ± 5.2 ha) and three sites were located in mixed-use areas (5.5 ± 3.2 ha). Among all sites, elevation changed < 175 m and daily mean temperatures were within 2°C so any variations in sloth abundance across sites were assumed to be related to differences in habitat features rather than abiotic factors.

Line-transect sampling has been applied to large fauna to understand complex relationships between animal species and environmental factors, including habitat structure and floristic composition (Haugaasen and Peres 2005, de Thoisy et al. 2008). Parallel line transects with an arbitrary first start point ensured uniform coverage and an element of randomization. Transects were walked at a relatively slow speed (*i.e.*, approximately 0.5 km/h) during peak sloth activity periods (0800 – 1600 h) to enhance my ability to detect sloths. Surveys were not carried out during periods of heavy rainfall because of the inactivity of sloths and lower detectability rates during stormy conditions.

It was possible to identify individual sloths based on markings on their fur. Certain individuals were resighted on multiple events, however, for this chapter I will only use information on sloth presence and absence. A sloth presence is signified by the occurrence of an individual sloth at a particular location, whereas a sloth absence is defined by a point within 5-ha (*i.e.,* the median home range size for *B. variegatus*) of a

sloth presence where, after extensive surveying, no sloths were observed. One precondition was that absence sites included a preferred tree species (*e.g., Cecropia spp.*) because brown-throated sloths are known to have a specialized diet and tend to favor certain trees for feeding (Vaughan et al. 2007, Mendoza et al. 2015). By including at least one favored food resource in every absence site, I sought to eliminate the potential influence of preferred tree species occurrence on brown-throated sloth occurrence.

### *Vegetation Structure of Different Habitats*

Structurally complex habitats generally possess multiple vegetation strata with dense foliage while more simple habitats have few vegetation strata. In contrast, habitat heterogeneity represents the horizontal variation in physiognomy of the habitat (August 1983). To characterize the structural complexity and heterogeneity of habitats within the study region, I established 28 vegetation plots, measuring 10 x 10 m (0.01 ha), in three different habitats types. Ten plots were carried out throughout mixed-use sites and 12 plots were conducted within tree plantations. Six vegetation plots were performed in mid-late successional forests, representing the most complex habitat type in the landscape, for the purpose of comparison.

The following variables were recorded within each plot: (1) diameter at breast height (DBH, cm) of all trees with a DBH $\geq$ 10 cm; (2) mean tree height of all trees with a DBH $\geq$ 10 cm using a clinometer and laser rangefinder (HEIGHT, m); (3) number of trees with a DBH $\geq$ 10 cm (NDBH); and (4) percent canopy cover (COVER, %) using a spherical densiometer following methods from Lemmon (1956).

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For each plot, a measure of total basal area (AREA, cm$^2$) was derived from the

DBH of all trees in the sample. A coefficient of variation for mean basal area

(CVAREA) was then calculated to capture a standardized measure of dispersion of the

variable AREA. Similarly, a coefficient of variation for mean tree height (CVHEIGHT)

was computed to obtain a measure of dispersion of the variable HEIGHT.

*Local-scale Habitat Characteristics*

The structural complexity and heterogeneity of habitats where brown-throated

sloths were present or absent were assessed to determine how the distribution of sloths

might be affected by local-scale habitat characteristics. Vegetation plots were centered

on sites where a new individual was observed (*i.e.,* presence), as well as sites where,

after exhaustive sampling, no sloths were detected (*i.e.,* absence). All vegetation plots

were conducted following the same methods described in the previous section. Several

of the variables that were measured, including average tree height, tree diameter, and

canopy cover, are considered to be important elements for habitat selection by three-toed

sloths (Montgomery and Sunquist 1978, Castro-Vásquez et al. 2010, Acevedo-Quintero

et al. 2011, Falconi et al. 2015).

*Landscape-scale Habitat Characteristics*

To characterize the landscape composition and configuration in my study region,

I conducted a manual habitat classification by digitizing aerial imagery. High-resolution

aerial imagery captured on March 20, 2012 with a spatial resolution of 0.5 meters was

obtained from Microsoft Bing Maps (Microsoft Corporation). The imagery was

georeferenced and registered to the UTM16 projection and WGS 1984 datum. Image

interpretation was performed on the imagery using manual digitization to classify the major land use types in the region. Manual habitat classification was favored over automated approaches to facilitate the accurate identification of fine-scale landscape features in a complex mosaic landscape. The following land use categories were digitized: primary forest, secondary forest, riparian forest, agriculture, pasture, water, tree plantations, mixed-use, urban, bare ground, and roads. Rivers were delineated based on contour lines from topographic maps of Costa Rica (Costa Rica Instituto Geográfico Nacional). Rivers were buffered out 15 meters to characterize riparian forests in accordance with the Costa Rican Forestry Act of 2006 (no. 7575), which mandates a protection area of 15 m on both banks of streams in rural areas (Stoner and Timm 2004).

I investigated the influence of landscape characteristics on brown-throated sloth presence or absence at a range of spatial scales. I established three circular buffers of 0.5-ha, 2-ha, and 5-ha (with radii of c. 40-m, 80-m and 126-m, respectively) around individual sloth presence and absence points, and quantified the composition and configuration of habitat types within these three extents. Brown-throated sloths rarely move more than 38-m per diel (Sunquist and Montgomery 1973), so I selected a 40-m radius for the smallest spatial extent to represent a sloths maximum daily movement. The largest spatial extent (area: 5-ha, radius: 126-m) corresponds with the median home range size of brown-throated sloths (Ramirez et al. 2011). An intermediate spatial scale was selected to determine whether sloths respond to landscape characteristics at a scale between their average daily movements and average home range size. The three scales

were nested hierarchies, in which the 5-ha buffers contained spatial features from the 2-ha and 0.5-ha buffers.

Patch, class and landscape metrics were calculated for each sloth presence and absence point at each of the three broad scales using FRAGSTATS 4.2 (McGarigal et al. 2012). FRAGSTATS is a spatial pattern analysis program that quantifies the areal extent and spatial configuration of patches within a landscape. No single metric is capable of reflecting the entirety of landscape composition and pattern (Davidson 1998). I selected a range of metrics that would be most biologically relevant to brown-throated sloths and those that would directly relate to my hypotheses. Sixteen metrics were selected for analysis, representing five categories: 1) area/edge, 2) shape, 3) contrast, 4) aggregation, and 5) diversity. Brief descriptions of the metrics used in this study are listed in Table 3.

In several instances, there was only one habitat type occurring within a buffered circle, which prevented the calculation of Euclidean nearest neighbor distances, interspersion and juxtaposition indices, and coefficient of variation indices. Alternatively, other aggregation metrics (*e.g.,* patch density and contagion) and diversity metrics (*e.g.,* patch richness and Simpson's diversity index) were used to quantify landscape texture and composition.

**Table 3.** FRAGSTATS metrics* used to quantify landscape composition and configuration at each sloth presence or absence point.

| Variable | Description (units) |
|---|---|
| **Area/edge** | |
| AREA | Area of patch comprising sloth presence or absence point (ha) |
| GYRATE | Extent of patch comprising sloth presence or absence point (m) |
| PLANDSF | Percentage of secondary forest in the landscape (%) |
| AWMAREA | Mean area of all patches, weighted by patch area |
| AWMGYR | Mean extent of all patches, weighted by patch area |
| LPI | Proportion of landscape comprised by the largest patch (%) |
| TE | Total length of edge in the landscape (m) |
| | |
| **Shape** | |
| SHAPE | Shape complexity of patch comprising sloth presence or absence point |
| AWMSI | Mean shape complexity of all patches, weighted by patch area |
| | |
| **Contrast** | |
| ECON | Relative proportion of contrast along a patch perimeter (%) |
| CWED | Density of edge weighted by degree of structural contrast between adjacent patches, Approaches 0 when all edges are minimum contrast (m/ha) |
| | |
| **Aggregation** | |
| PD | Number of patches divided by total landscape area (no./100ha) |
| CONTAG | Proxy for fragmentation; approaches zero when patch types becomes increasingly disaggregated and interspersed (%) |
| | |
| **Diversity** | |
| PR | Number of different patch types present within the landscape |
| SIDI | Simpson's diversity index; Approaches 1 as PR increases and the distribution of area among patch types becomes more equitable |
| SIEI | Simpson's evenness index; Approaches 1 as the proportional distribution of area among patch types becomes more even |

*Complete descriptions and equations are provided in McGarigal and Marks (1995).

An edge contrast weight file containing user-defined weights of the dissimilarity between habitat types was input into FRAGSTATS for the calculation of certain metrics, such as contrast-weighted edge density and edge contrast index. Each unique pairwise combination of patch types was assigned an edge contrast weight ranging from 0 (no

contrast) to 1 (maximum contrast) based on sloth ecology, movement, and dispersal

(Table 4). For example, there is less contrast between a primary forest stand and a

secondary forest stand (*i.e.,* 0.25) than there is between a pasture and a secondary forest

stand (*i.e.,* 1).

Habitat isolation was measured as the Euclidean distance from the center of sloth

presence or absence to the nearest secondary forest patch ($\geq$ 10 ha) using ArcMap 10.2

(ESRI, 2014). Ten hectares was selected as the lower limit for forest patch area because

it is twice the size of brown-throated sloths' home range and more likely to serve as a

source population than forest fragments smaller than 10 ha. Sites that were located on

the border of secondary forest tracts greater than or equal to 10 ha were assigned a value

of zero for their degree of isolation. The Euclidean distances to nearest riparian forest

and road were also calculated.

**Table 4.** Edge contrast weights assigned to pairs of land use types. Values of 1 indicate high contrast boundaries, while values of 0 indicate no contrast between habitat edges.

|      | AG   | B    | MU   | P    | PF   | RF   | RD   | SF   | TP   | U    | W |
|------|------|------|------|------|------|------|------|------|------|------|---|
| AG   | 0    | 0.25 | 0.5  | 0.25 | 1    | 1    | 0.5  | 1    | 0.75 | 0.75 | 1 |
| B    | 0.25 | 0    | 0.5  | 0.25 | 1    | 1    | 0.25 | 1    | 1    | 0.5  | 1 |
| MU   | 0.5  | 0.5  | 0    | 0.75 | 0.75 | 0.75 | 0.5  | 0.5  | 0.5  | 0.25 | 1 |
| P    | 0.25 | 0.25 | 0.75 | 0    | 1    | 1    | 0.25 | 1    | 0.75 | 0.5  | 1 |
| PF   | 1    | 1    | 0.75 | 1    | 0    | 0.25 | 1    | 0.25 | 0.5  | 1    | 1 |
| RF   | 1    | 1    | 0.75 | 1    | 0.25 | 0    | 1    | 0    | 0.25 | 1    | 1 |
| RD   | 0.5  | 0.25 | 0.5  | 0.25 | 1    | 1    | 0    | 1    | 1    | 0.25 | 1 |
| SF   | 1    | 1    | 0.5  | 1    | 0.25 | 0    | 1    | 0    | 0.25 | 1    | 1 |
| TP   | 0.75 | 1    | 0.5  | 0.75 | 0.5  | 0.25 | 1    | 0.25 | 0    | 0.75 | 1 |
| U    | 0.75 | 0.5  | 0.25 | 1    | 1    | 1    | 0.25 | 1    | 0.75 | 0    | 1 |
| W    | 1    | 1    | 1    | 1    | 1    | 1    | 1    | 1    | 1    | 1    | 0 |

AG = agriculture; B = bare ground; MU = mixed-use; P = pasture; PF = primary forest; RF = riparian forest; RD = road; SF = secondary forest, TP = tree plantation; U = Urban; and W = Water.

*Data Analysis*

   *Data Processing*

   Prior to analyses, variables were transformed, when necessary, to achieve

normality and reduce heteroscedasticity in the data. Subsequently, I conducted four

separate principal components analyses (PCAs) for the local and landscape scale habitat

data to eliminate multicollinearity associated with the large number of predictor

variables (Riitters et al. 1995). For each set of predictor variables I conducted a PCA on

the correlation matrices and retained principal components (PCs) with eigenvalues

greater than one in place of the original variables, following the Kaiser-Guttman

criterion (Legendre and Legendre 2012). All PCAs were conducted using the package

'vegan' (Oksanen et al. 2013) in RStudio version 0.97.551 (RStudio 2012).

   *Vegetation Structure of Different Habitats*

   I tested for differences in vegetation characteristics and structural complexity

among secondary forest, plantation, and mixed-use areas using one-way analyses of

variance (ANOVA). The ANOVAs were followed by Tukey's range tests to clarify

specifically which groups differed significantly from the others.

   *Local-scale Habitat Characteristics*

   I performed a binary logistic regression via generalized linear modeling

(McCullagh and Nelder 1989) to model sloth presence or absence in relation to fine

scale habitat variables (*i.e.,* the PCs) across plantations and mixed-use habitats.

   Model selection was performed via backwards step-wise procedure, until the

removal of non-significant parameters significantly reduced the fit of the model to the

data. The optimal model possessed the lowest Second-order Akaike's Information Criterion ($AIC_c$). The $AIC_c$ should be used instead of AIC when sample size is small in comparison to the number of estimated parameters (Burnham and Anderson 2004). Furthermore, because individual AIC values contain arbitrary constants and are affected by sample size, they are not easily interpretable. It is necessary to rescale $AIC_c$ to $\Delta_i$ to facilitate interpretation as this transformation coerces the best model to have $\Delta_i = 0$, while the other models have positive values (Burnham and Anderson 2004). The larger the $\Delta_i$, the less probable it is for the fitted model $i$ to be the best approximating model in the set of candidate models. Subsequently, I calculated Akaike weights ($w_i$) to assist in the determination of the best model; $w_i$ values are interpreted as the probability that model $i$ is the best Kullback-Leibler model for the data (Burnham and Anderson 2004).

Subsequently, I performed ANOVAs to elucidate which of the variables on PCs are most associated with sloth presence or absence. While an ANOVA may detect significant differences in the means of the two groups (sloth presence *vs.* absence), it is important to note that all of the variables on the PCs will be correlated. Therefore, the ANOVAs will help to tease apart the driving factors, but it is not possible to definitively conclude which of the variables on a particular PC are affecting sloth presence or absence.

### *Landscape-scale Habitat Characteristics*

The potential relationships between the binary response variable, sloth presence or absence, and the broad scale habitat characteristics (*i.e.*, the PCs) were investigated by using logistic regression and a multi-scale approach (Gehring and Swihart 2003). A

binomial distribution was used to model sloth presence or absence, where sites with sloths present were assigned a value of one and those where sloths were absent were assigned a zero. In addition to the PCs, land use type was also incorporated into the analysis as an indicator variable.

Model selection was performed in the same manner as in the local scale section above. I also performed ANOVAs similarly as above, to clarify which of the variables on PCs are most correlated with sloth presence or absence.

**RESULTS**

The factor loadings for each PCs were examined to identify underlying associations with individual variables. For the local scale, six variables were reduced to three PCs, which described 85.4% of the variation in the original data (Table 5).

**Table 5.** Results of the principal component analysis (PCA) of local scale habitat descriptors for areas where brown-throated sloths were present or absent in San Juan de Peñas Blancas, Costa Rica, May – August 2014. Interpretations of the principal components (PCs) are based on component loadings > ± 1 (in bold).

| Interpretation of PCs | PC1 Habitat complexity | PC2 Habitat density | PC3 Habitat stage |
|---|---|---|---|
| **Loadings** | | | |
| *N* trees (NDBH) | -0.415 | **1.309** | -0.417 |
| Canopy cover (COVER) | **-1.083** | 0.182 | -0.033 |
| Basal area (AREA) | -0.966 | **1.020** | 0.116 |
| CV basal area (CVAREA) | **-1.299** | -0.684 | -0.076 |
| Tree height (HEIGHT) | -0.126 | 0.260 | **1.482** |
| CV tree height (CVHEIGHT) | **-1.301** | -0.669 | -0.006 |
| | | | |
| **Importance of components** | | | |
| Eigenvalue | 2.458 | 1.632 | 1.035 |
| Proportion Explained | 0.410 | 0.272 | 0.173 |
| Cumulative Proportion | 0.410 | 0.682 | 0.854 |

The first principal component (PC1: 41% variation) was interpreted as a proxy (negative) for structural complexity of a habitat, representing a gradient from high to low complexity. Sites positively associated with PC1 were less complex habitats with low coefficient of variation in tree basal area, coefficient of variation in mean tree height, and percent canopy cover. The second principal component (PC2: 27.2%) was interpreted as a proxy of habitat density, representing a gradient from low to high density. Sites positively correlated with PC2 contained a higher number of trees and total basal area. The third principal component (PC3: 17.3%) was interpreted as a proxy for successional stage, representing a gradient from early to late successional stages. Sites positively correlated with PC3 contained taller trees, on average.

Three separate PCAs were conducted for each of the landscape scales (5 ha, 2 ha, and 0.5 ha). At the 5-ha scale, 19 variables describing habitat composition and configuration were reduced to five PCs, which explained 89.5% of the variance in the original dataset (Table 6).

**Table 6.** Results of the principal component analysis (PCA) of the 5-ha scale habitat descriptors for areas where brown-throated sloths were present or absent in San Juan de Peñas Blancas, Costa Rica, May – August 2014. Component loadings > ± 1 are in bold.

| Loadings | PC1 | PC2 | PC3 | PC4 | PC5 |
|---|---|---|---|---|---|
| AREA | **1.367** | -0.320 | -0.055 | 0.063 | -0.330 |
| GYRATE | **1.090** | -0.360 | **-1.218** | 0.595 | 0.560 |
| SHAPE | -0.813 | -0.696 | **-2.107** | 0.770 | **1.573** |
| PLANDSF | -0.326 | **1.690** | **-1.713** | **-2.100** | -0.373 |
| PD | **-1.240** | -0.867 | 0.982 | -0.595 | -0.205 |
| LPI | **1.304** | -0.540 | -0.304 | -0.162 | 0.998 |
| TE | **-1.260** | **-1.053** | 0.213 | -0.760 | 0.825 |
| AWMAREA | **-1.325** | 0.276 | 0.747 | 0.149 | -0.641 |
| AWMGYR | **1.281** | -0.260 | **-1.010** | -0.727 | 0.761 |
| AWMSI | -0.891 | **-1.456** | **-1.781** | -0.158 | 0.657 |
| DIST_SF | 0.463 | **-1.780** | **1.502** | **1.400** | **1.109** |
| DIST_RF | 0.921 | -0.080 | -0.664 | **1.712** | **-2.435** |
| DIST_RD | 0.835 | 0.578 | **1.401** | 0.316 | **1.394** |
| CWED | **-1.220** | **-1.407** | -0.239 | -0.204 | 0.330 |
| ECON | -0.865 | -0.751 | **-1.193** | **2.011** | **-1.498** |
| CONTAG | -0.713 | **1.758** | -0.186 | **1.766** | **1.546** |
| PR | **-1.158** | -0.681 | 0.645 | -0.789 | -0.875 |
| SIDI | **-1.267** | 0.960 | 0.224 | 0.608 | 0.278 |
| SIEI | **-1.036** | **1.686** | -0.029 | **1.128** | 0.668 |
| | | | | | |
| **Importance of components** | | | | | |
| Eigenvalue | 10.358 | 2.466 | 1.650 | 1.487 | 1.057 |
| Proportion Explained | 0.545 | 0.130 | 0.087 | 0.078 | 0.056 |
| Cumulative Proportion | 0.545 | 0.675 | 0.762 | 0.840 | 0.895 |

At the 2-ha scale, 19 variables were reduced to three PCs (describing 83% of the variance; Table 7). At the 0.5-ha scale, 19 variables were reduced to two PCS (describing 81.6% of the variation; Table 8).

**Table 7.** Results of the principal component analysis (PCA) of the 2-ha scale habitat descriptors for areas where brown-throated sloths were present or absent in San Juan de Peñas Blancas, Costa Rica, May – August 2014. Component loadings > ± 1 are in bold.

| Loadings | PC1 | PC2 | PC3 |
|---|---|---|---|
| AREA | **1.243** | -0.053 | 0.715 |
| GYRATE | **1.078** | -0.373 | **1.215** |
| SHAPE | -0.976 | -0.518 | **1.097** |
| PLANDSF | -0.561 | **2.132** | 0.117 |
| PD | **-1.140** | **-1.151** | -0.366 |
| LPI | **1.286** | -0.329 | 0.433 |
| TE | **-1.195** | **-1.006** | -0.426 |
| AWMAREA | **1.310** | -0.112 | 0.296 |
| AWMGYR | **1.224** | -0.105 | -0.095 |
| AWMSI | **-1.158** | -0.836 | 0.328 |
| DIST_SF | 0.541 | **-2.042** | -0.102 |
| DIST_RF | 0.923 | 0.339 | **2.380** |
| DIST_RD | 0.733 | 0.218 | **-2.017** |
| CWED | **-1.193** | **-1.071** | 0.664 |
| ECON | -0.856 | -0.783 | **2.456** |
| CONTAG | -0.881 | **1.704** | 0.861 |
| PR | **-1.111** | -0.921 | -0.543 |
| SIDI | **-1.282** | 0.594 | -0.237 |
| SIEI | -0.976 | **1.741** | 0.364 |
| | | | |
| **Importance of components** | | | |
| Eigenvalue | 11.822 | 2.762 | 1.190 |
| Proportion Explained | 0.622 | 0.145 | 0.063 |
| Cumulative Proportion | 0.622 | 0.768 | 0.830 |

**Table 8.** Results of the principal component analysis (PCA) of the 0.5-ha scale habitat descriptors for areas where brown-throated sloths were present or absent in San Juan de Peñas Blancas, Costa Rica, May – August 2014. Component loadings $> \pm 1$ are in bold.

| Loadings | PC1 | PC2 |
|---|---|---|
| AREA | **1.203** | -0.193 |
| GYRATE | **1.137** | 0.268 |
| SHAPE | -0.932 | 0.031 |
| PLANDSF | -0.612 | **-2.708** |
| PD | **-1.099** | **1.233** |
| LPI | **1.228** | 0.040 |
| TE | **-1.195** | 0.680 |
| AWMAREA | **1.229** | -0.157 |
| AWMGYR | **1.198** | 0.169 |
| AWMSI | **-1.165** | 0.638 |
| DIST_SF | 0.572 | **2.416** |
| DIST_RF | 0.951 | -0.954 |
| DIST_RD | 0.611 | 0.181 |
| CWED | **-1.154** | 0.956 |
| ECON | **-1.039** | 0.432 |
| CONTAG | **-1.021** | **-1.277** |
| PR | **-1.110** | 0.615 |
| SIDI | **-1.227** | 0.615 |
| SIEI | **-1.060** | **-1.247** |
| | | |
| **Importance of components** | | |
| Eigenvalue | 13.683 | 1.817 |
| Proportion Explained | 0.720 | 0.096 |
| Cumulative Proportion | 0.720 | 0.816 |

*Use of Countryside Habitats by* B. variegatus

A total of 32 individual brown-throated sloths were present in plantation, mixed-use, and riparian forest habitats throughout May – August 2014 (Figure 6). A reasonably high number of sloths were observed in within mixed-use areas (n=22) compared to plantations (n=5) and riparian forest (n=5). The relatively low number of sloths observed in riparian forests compared to the mixed-use areas is likely attributable to the opportunistic sampling that occurred in those areas. If riparian forests were equally sampled, I would expect a higher relative density of sloths because of the greater diversity and abundance of preferred tree species (*e.g., Cecropia spp.)* in riparian fragments (Vaughan et al. 2007).
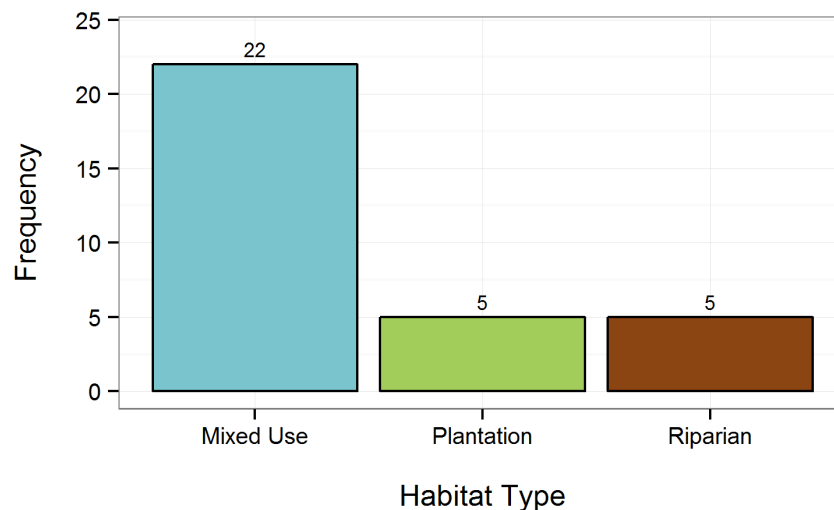


**Figure 6.** Histogram of brown-throated sloths in three different countryside habitats in San Juan de Peñas Blancas, Costa Rica during May – August 2014. Numbers above histograms indicate the number of individuals observed.

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Furthermore, a total of 15 points were determined to be devoid of brown-throated sloths after repeated sampling efforts were unable to detect any sloths at those locations. Three absence points were located in mixed-use areas, while 12 absence points were located throughout tree plantations.

The subsequent analysis and results are based solely on the presence or absence of brown-throated sloths. Therefore, if multiple sloths were observed using the same tree, only one of the individuals was included in the study. Additionally, local scale habitat data were unable to be collected for three mixed-use sloth presence points and one plantation presence point, thus those localities were also excluded from the analysis.

The local scale analysis was based on 18 presence and 15 absence points. The landscape scale analysis was based on the same 18 presence points, but comprised fewer absence points (n=7) to avoid issues related to spatial autocorrelation that were expected to occur with larger grain sizes. The 18 sloth presence points and 7 absence points that were used in the landscape-scale study are superimposed over a regional land use map in Figure 7.
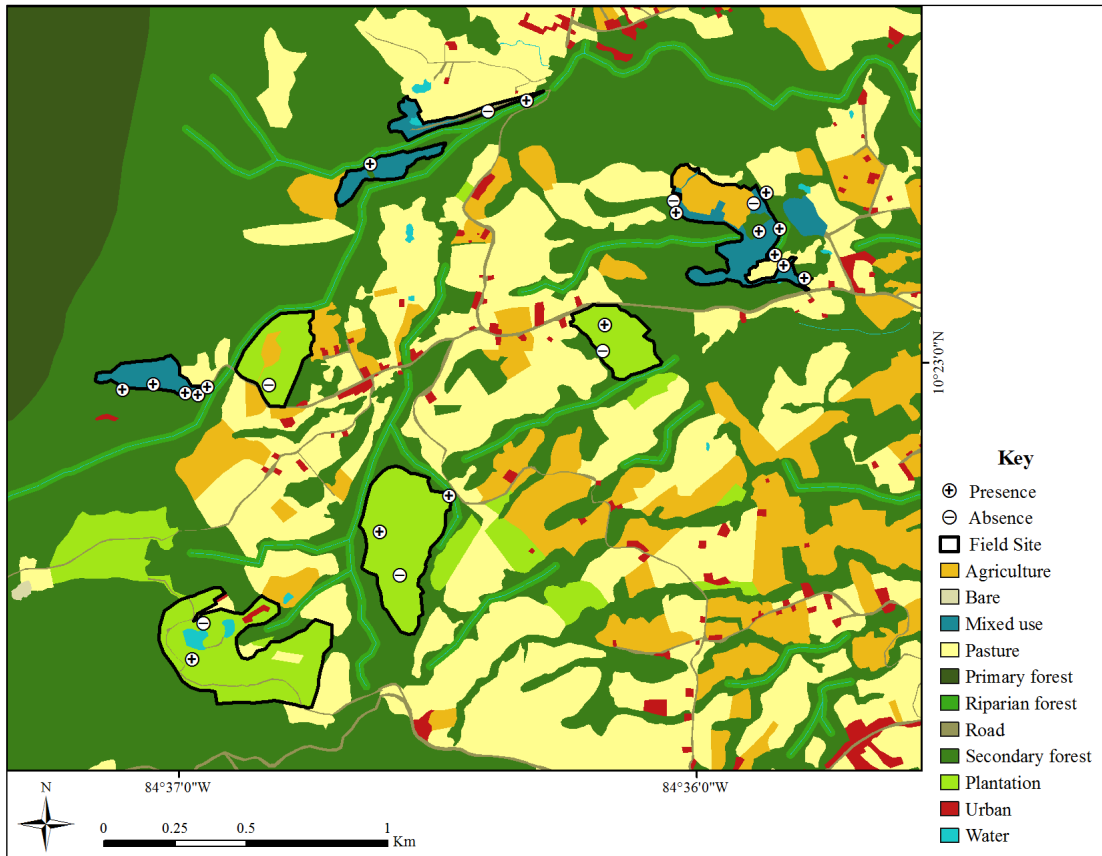
**Figure 7.** Brown-throated sloth presence (n = 18) and absence (n = 7) localities across countryside habitats in San Juan de Peñas Blancas, Costa Rica. Tree plantations are shaded in light green and mixed-use sites are shaded in dark blue. Survey sites are outlined in black.

*Vegetation Structure of Different Habitats*

Five of the six local-scale habitat variables were significantly different among mid-late successional forest, plantation, and mixed-use habitats, suggesting that the three habitat types differ in their structural complexity (Table 9). Mid-late successional forests were the most complex habitats, with significantly taller trees (HEIGHT, $F_{2,25} = 5.69$, $p < .01$), higher tree basal area (AREA, $F_{2,25} = 15.11$, $p < .001$), greater canopy cover (COVER, $F_{2,25} = 5.54$, $p = .01$), and more variation in tree height (CVHEIGHT, $F_{2,25} = 19.6$, $p < .001$) than plantations and mixed-use areas.

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While mid-late successional forests and mixed-use areas had similar degrees of heterogeneity in tree basal area, trees in these habitats had significantly more variation in basal area than plantation trees (CVAREA, $F_{2,25} = 6.7, p < .005$). In addition, mixed-use areas had considerably more variation in tree height than plantations (CVHEIGHT, $F_{2,25} = 19.6$, $p < .001$), but the two habitat types did not differ significantly based on any of the other local-scale habitat variables (Figure 8). The relative abundance of trees was similar across the three land use types, and therefore was not an adequate gauge of the differences in vegetation structure among habitat types in this study (NDBH, $F_{2,25} = 0.75$, ns).

**Table 9.** Summary of ANOVAs of local habitat characteristics across three habitat types in San Juan de Peñas Blancas, Costa Rica, May – August 2014. Habitat types consisted of secondary forests (n=6), mixed-use areas (n=10), and plantations (n=12).

| Variable | Habitat Type | | | ANOVA | |
|---|---|---|---|---|---|
| | Forests | Mixed-Use | Plantations | $F$ | $p$ |
| $N$ trees (NDBH) | 5.5 [a] | 5.5 [a] | 7.5 [a] | 0.75 | 0.48 |
| Canopy cover (COVER, %) | 85.35 [a] | 71.26 [b] | 69.18 [b] | 5.54 | 0.010 |
| Basal area (AREA, cm$^2$) | 9995.6 [a] | 3756.3 [b] | 3697.2 [b] | 15.11 | < 0.0001 |
| CV basal area (CVAREA) | 1.22 [a] | 0.97 [a] | 0.57 [b] | 6.70 | 0.004 |
| Tree height (HEIGHT, m) | 26.05 [a] | 16.76 [b] | 17.69 [b] | 5.69 | 0.009 |
| CV tree height (CVHEIGHT) | 0.65 [a] | 0.40 [b] | 0.23 [c] | 19.6 | < 0.0001 |

[a] Group means of variables were tested with Tukey's range tests. Different letters represent significant differences at α = 0.05 among land use types where differences among sites were significant within analysis of variance.
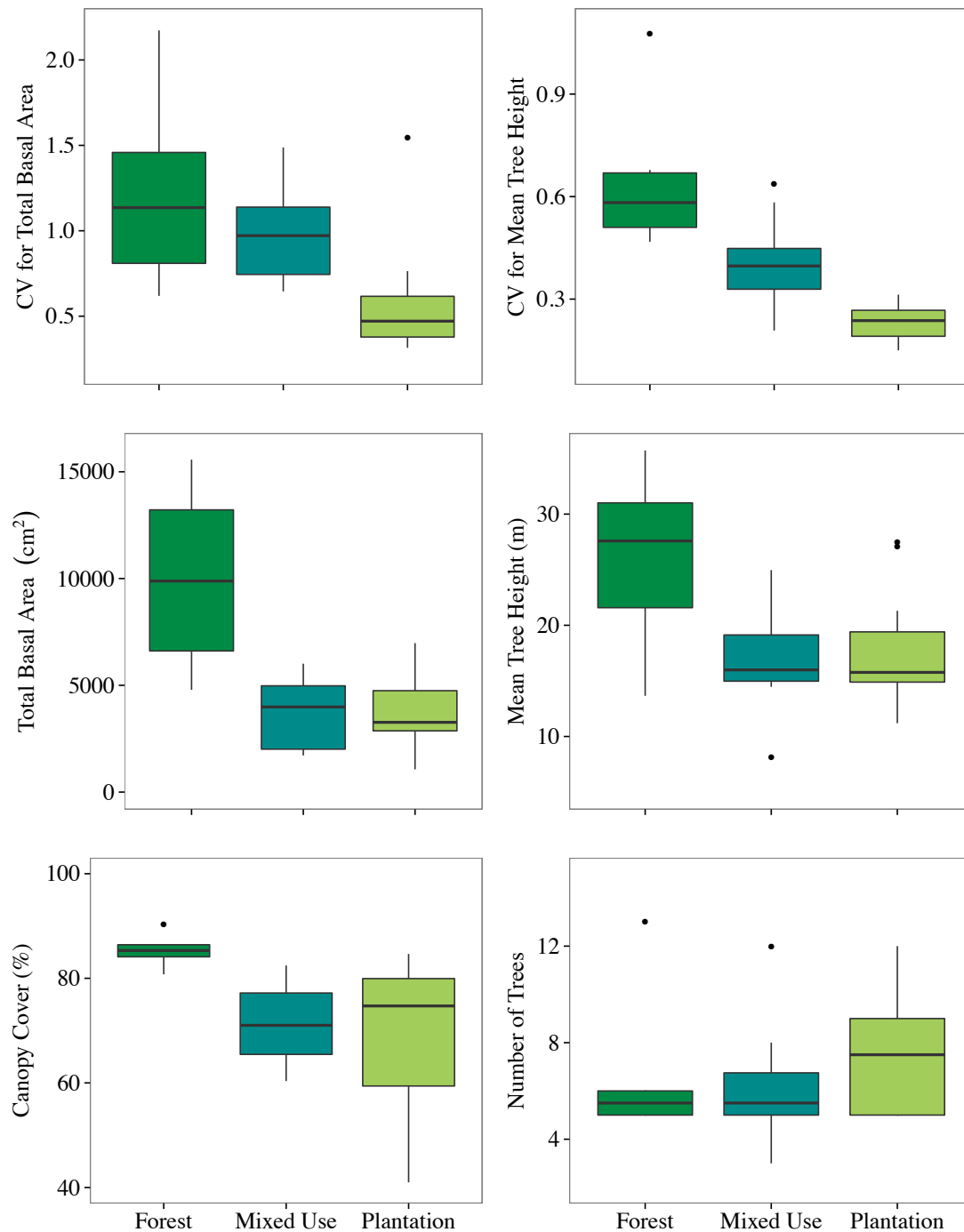
**Figure 8.** Box plot summaries of canopy cover, tree abundance, mean tree height, total basal area, coefficient of variation for mean tree height, and coefficient of variation for total basal area by land use type. Medians are represented by the bold horizontal bars, minimum and maximum values (excluding outliers) are represented at the ends of the vertical black lines, and outliers are represented by the points outside of the lower and upper limits. CV = coefficient of variation.

*Effects of Local-scale Habitat Features*

The best-fit model for describing the probability of brown-throated sloth presence or absence as a function of local habitat variables was selected based upon the lowest AICc value (Table 10). Based on this model, the local distribution and microhabitat use of brown-throated sloths was significantly influenced by aspects of fine-scale habitat complexity (Table 11). The model indicated that the probability of sloth presence was significantly correlated with PC1, the proxy for habitat complexity ($p$ < .01, Table 11). Predictor variables that loaded heavily on PC1 are also correlated with sloth occurrence. These variables include: coefficient of variation for basal area, coefficient of variation for mean height, and canopy cover.

**Table 10.** Results from stepwise logistic regression model selection for describing the relationship between brown-throated sloth occurrence and local habitat variables. Predictor variables PC1 and PC2, derived from principal components analysis, are characterized by habitat complexity and habitat density, respectively. The best fit model (in bold) was selected based upon the lowest AICc and $\Delta_i$ values.

| Model | AICc | $\Delta_i$ | $w_i$ |
| --- | --- | --- | --- |
| **PC1 + PC2** | **19.39** | **0.00** | **0.76** |
| PC1 + PC2 + PC3 | 21.99 | 2.59 | 0.21 |
| PC1 | 25.57 | 6.18 | 0.03 |

AICc = Akaike's Information Criterion with a correction for finite sample sizes*,*
$\Delta_i$ = $AIC_i$ − $AIC_{min}$, where $AIC_{min}$ is the minimum of the different $AIC_i$ values*,*
$w_i$ = Akaike weights

**Table 11.** Summary of the binary logistic regression analysis for predicting brown-throated sloth occurrence as a function of local-scale habitat characteristics. PC1 represents a proxy for habitat complexity and PC2 represents a proxy for habitat density.

| Variable | Parameter Estimate ($\beta$) | Standard Error | $p$ |
|---|---|---|---|
| Intercept | -0.465 | 0.956 | 0.626 |
| PC1 | -8.603 | 3.287 | 0.009* |
| PC2 | -7.583 | 4.162 | 0.068 |

The results from the ANOVAs revealed that of the three predictor variables highly correlated with PC1, only two of them were statistically different between sloth presence and absence sites. Although canopy cover loaded heavily on PC1, the results from the ANOVA were not significant ($F_{1,31} = 3.323$, *ns*). Brown-throated sloths demonstrated strong differential use of habitats that were more heterogeneous in tree basal area ($F_{1,31} = 95.34$, $p < .0001$) (Figure 9b). Overall, the coefficient of variation in basal area was significantly higher in areas where sloths were present ($1.94 \pm 0.41$) compared to areas where sloths were absent ($0.64 \pm 0.34$). When further divided by land use type it was apparent that, on average, mixed-use habitats contained a greater level of heterogeneity in tree basal area than plantations (Figure 9b). Moreover, even within a particular habitat type, brown-throated sloths were selecting microhabitats that had more variation in tree basal area. For example, in tree plantations sloths preferred trees that were more heterogeneous in basal area over trees that were uniform.

In a similar vein, the other predictor variable that was significantly different between sloth presence and absence sites was coefficient of variation for mean tree height (Figure 9c). Brown-throated sloths chose microhabitats that were significantly

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more heterogeneous in mean tree height ($F_{1,31}$ = 122.9, $p$ < .0001). In general, the coefficient of variation in mean tree height was significantly greater in areas where sloths were present (1.39 ± 0.17) in contrast to areas where sloths were absent (0.36 ± 0.31). When separated into habitat type, the trees in mixed-use areas were substantially more variable in height than in plantations (Figure 9d). Furthermore, when considering a single land use type, sloths seemed to prefer microhabitats that were more heterogeneous in tree height to areas that had mostly short trees, or mostly tall trees.

Brown-throated sloths appeared to be unresponsive to PC2 (*i.e.,* tree density; Table 11), which is contrary to other studies that have found tree density to be important in the habitat selection of maned three-toed sloths (Falconi et al. 2015). This disparity could be an artifact of the different methods by which the absent sites were selected. If absent sites were selected at random, as they were in previous studies (*e.g.,* Falconi et al. 2015), they could have been situated anywhere on the landscape, including pastures or croplands, where tree density would be dramatically different between presence and absence sites. Whereas with the selection method I used in my study, absence sites were required to be within the home range of a particular sloth and possess at least one tree species favored by brown-throated sloths. This selection process greatly reduced the possibility that absence points were located in areas that were not suitable habitat for sloths, such as the middle of an open pasture or body of water, but may have also been the reason that the the tree density was not significantly different across presence and absence sites in this study.
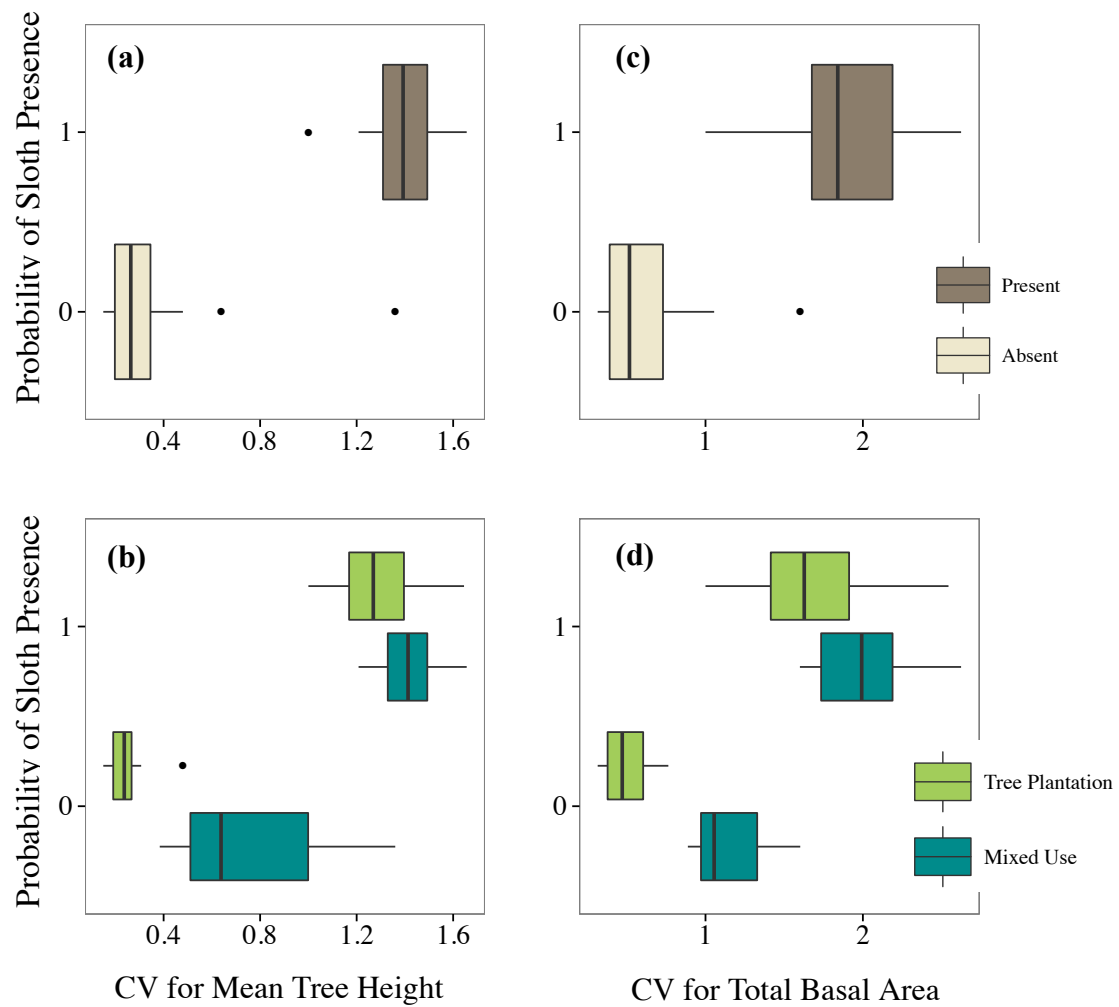
**Figure 9.** Box plot summaries of two local habitat variables, coefficient of variation for mean tree height and coefficient of variation for total basal area, by probability of sloth occurrence (a & c), and further separated by land use type (b & d). Medians are represented by the bold horizontal bars, minimum and maximum values (excluding outliers) are represented at the ends of the vertical black lines, and outliers are represented by the points outside of the lower and upper limits. CV = coefficient of variation.

*Effects of Landscape-scale Habitat Features*

The regional distribution and habitat use of brown-throated sloths was shaped by several elements associated with the composition and configuration of the surrounding landscape mosaic. However, the strengths of the associations differed as a function of scale. While landscape variables were unable to predict sloth presence or absence at the 0.5-ha and 2-ha spatial extents, sloths demonstrated significant responses to landscape characteristics at the 5 ha scale (Tables 12 and 13). At the 5-ha scale, logistic regression indicated that sloth presence was significantly correlated with PC4 ($p < .05$, Table 13). Consequently, variables that loaded heavily on PC4 were also correlated with sloth presence or absence. These variables include: percentage of secondary forest, distance to secondary forest (>10 ha), distance to riparian forest, edge contrast index, contagion, and Simpson's evenness index.

**Table 12.** Results from stepwise logistic regression model selection for describing the relationship between brown-throated sloth occurrence and landscape habitat variables at the 5-ha scale. Predictor variables PC1 – PC4 are derived from a principal components analysis of the landscape scale variables. The best fit model (in bold) was selected based upon the lowest AICc and $\Delta_i$ values.

| Model | AICc | $\Delta_i$ | $w_i$ |
|---|---|---|---|
| **PC1 + PC2 + PC3 + PC4 + PC2:PC4** | **32.74** | **0** | **0.55** |
| PC1 + PC2 + PC3 + PC4 | 33.68 | 0.94 | 0.34 |
| PC1 + PC2 + PC3 + PC4 + PC1:PC4 + PC2:PC4 | 35.92 | 3.18 | 0.11 |

AICc = Akaike's Information Criterion with a correction for finite sample sizes,
$\Delta_i$ = AIC$_i$ − AIC$_{min}$, where AIC$_{min}$ is the minimum of the different AIC$_i$ values,
$w_i$ = Akaike weights

**Table 13.** Summary of the binary logistic regression analysis for predicting brown-throated sloth occurrence as a function of landscape-scale habitat characteristics. PC1 represents habitat complexity, whereas PC2 signifies habitat density.

| Model | Parameter Estimate ($\beta$) | Standard Error | $p$ |
|---|---|---|---|
| Intercept | 2.882 | 1.415 | 0.042* |
| PC1 | -1.244 | 1.174 | 0.298 |
| PC2 | 7.497 | 4.364 | 0.086 |
| PC3 | -2.943 | 3.418 | 0.389 |
| PC4 | -11.209 | 5.403 | 0.038* |
| PC2:PC4 | -28.015 | 16.098 | 0.082 |

The results from the ANOVAs suggest that of the six predictor variables highly correlated with PC4, only two of them were statistically different between sites where sloths were present versus absent. One of the two variables was the proportion of secondary forest within the 5-ha landscape surrounding each presence or absence point (Figure 10a). Brown-throated sloths exhibited strong differential use of habitats that were composed of a larger amount of secondary forest ($F_{1,23} = 6.29$, $p < .02$). On average, the proportion of secondary forest cover was significantly higher in areas where sloths were present (35.91 ± 13.76%) compared to areas where sloths were absent (21.04 ± 11.92%). When separated by land use type it became clear that, on average, mixed-use areas contained a higher proportion of secondary forest than plantations (Figure 10b). Furthermore, even within a given land use type, sloths appeared to be seeking out habitats that had a higher proportion of secondary forest in the immediate (within 5-ha) surroundings.
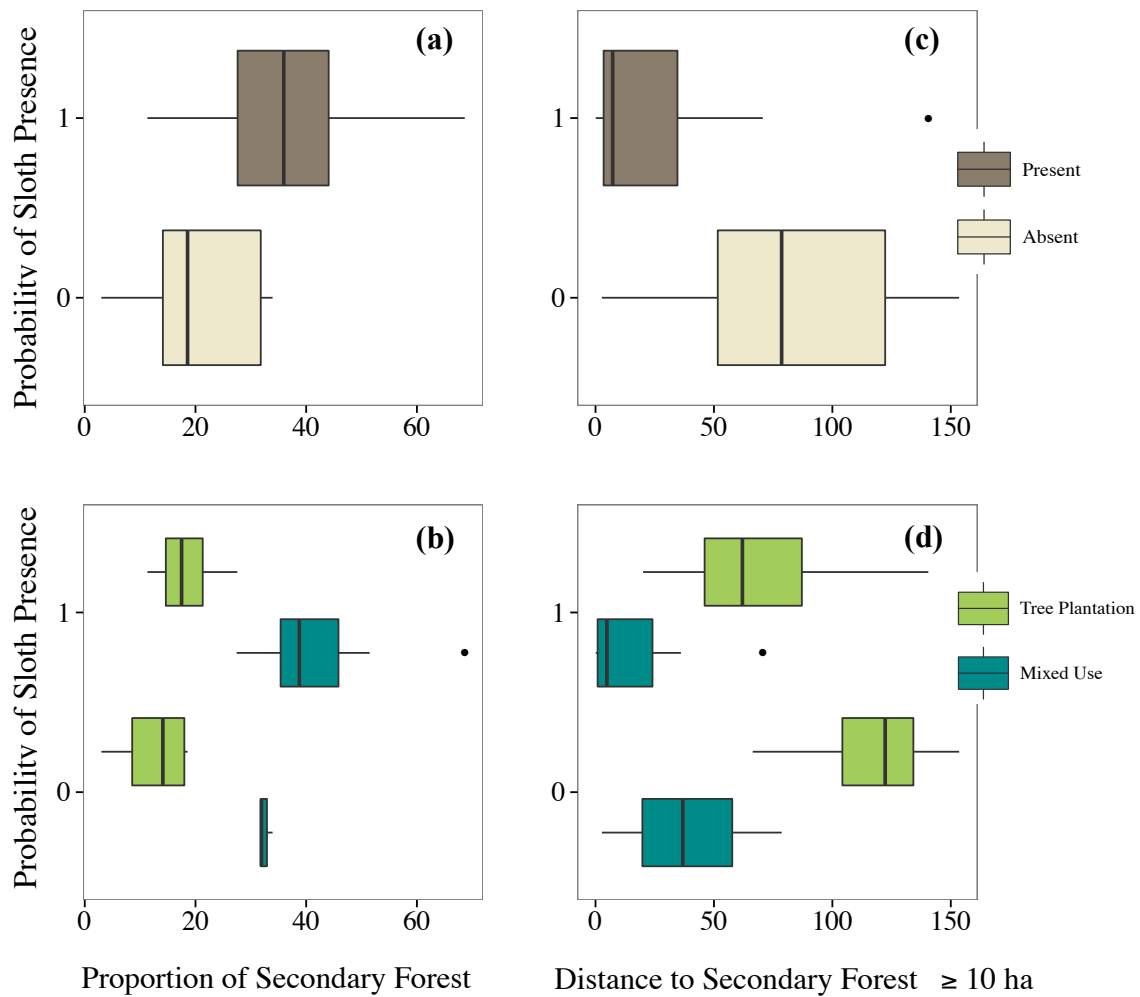
**Figure 10.** Box plot summaries of two landscape scale variables at the 5 ha scale, proportion of secondary forest and distance to secondary forest of at least 10 ha, by probability of sloth occurrence (a & c), and further separated by land use type (b & d). Medians are represented by the bold horizontal bars, minimum and maximum values (excluding outliers) are represented at the ends of the vertical black lines, and outliers are represented by the points outside of the lower and upper limits.

The other predictor variable that was statistically different between sloth

presence and absence sites was Euclidean distance to the nearest secondary forest patch

of at least 10 ha (Figure 10c). Brown-throated sloths selected habitats that were

significantly closer to large secondary forest tracts ($26.82 \pm 36.98$ m) than areas where

sloths were absent ($83.24 \pm 53.23$ m) ($F_{1,23} = 7.51, p < .02$). When further divided into

land use type it was evident that, on average, mixed-use areas were closer to large tracts

of secondary forest, while plantations were more isolated (Figure 10d). Additionally,

even within a given land use type, sloths appeared to be seeking out habitats that were

nearby large fragments of secondary forest.


**DISCUSSION**

Brown-throated sloths were observed using countryside habitats in this region,

albeit to varying degrees, and did not appear to be entirely dependent upon forest

fragments. My findings suggest that while countryside habitats are undoubtedly not a

substitute for protected forests, they may provide an opportunity for increasing the

viability of sloth populations in a region that will be facing land use changes of varying

intensities in the future.

Brown-throated sloths in this study favored habitats that comprised a high

proportion of secondary forest in the surrounding landscape. My results indicate that the

probability of a sloth being present is positively correlated with the amount of secondary

forest within a 5 ha area. These results are concordant with previous studies, which have

shown that the amount of available habitat is important in determining species distributions (Radford et al. 2005, Smith et al. 2011).

The spatial distribution of brown-throated sloths appears to be largely a function of physical connectivity and proximity to secondary forest ($\geq$ 10 ha). This result supports my hypothesis that brown-throated sloths are more likely to be associated with countryside habitats that are nearby large tracts of secondary forest. Given their high dependence on forest cover for survival and dispersal, it is not surprising that brown-throated sloths establish their home ranges in these areas over other areas that would be more isolated. The distance to forest is also of major importance for many other taxa (Fitzgibbon 1997, Ricketts et al. 2004, Watson et al. 2004). Isolation from nearby forest patches shifts species' distribution patterns and either prevents dispersal or coerces dispersing individuals to traverse a matrix habitat that separates suitable habitat fragments from each other. Susceptibility to increasing isolation is especially high for sedentary species, like brown-throated sloths (Ewers and Didham 2006). While isolation is commonly quantified by the Euclidean distance between habitat fragments, cost-distances may be a more realistic measure of isolation, especially for dispersal-limited species. Cost-distance analysis would take into account edge contrast and permeability (Adriaensen et al. 2003), which would likely influence sloth movement, and might provide a better understanding of the degree of isolation experienced by sloths in a landscape mosaic.

Moreover, my study validates previous empirical and theoretical findings that ecological patterns are dependent on scale (Gorresen et al. 2005, Lyra-Jorge et al. 2010).

I found that both local and landscape scale habitat characteristics influence the persistence of sloths in agricultural mosaics. The occurrence of brown-throated sloths depended not only on its context in the surrounding land mosaic (*i.e.,* percentage of secondary forest and degree of isolation from large fragments of secondary forest), but also on the local characteristics of the site (*i.e.*, degree of structural complexity).

As expected for an arboreal mammal of low vagility, structural elements associated with canopy connectivity and vegetation complexity were favored by brown-throated sloths. At a finer spatial scale, sloths selected habitats of greater structural complexity, even within a given habitat type. For example, within a tree plantation sloths sought out microhabitats that had closed canopies and were variable in tree height and basal area, and avoided areas that were more uniform in structure with a lower proportion of canopy cover. These elements have also been documented to influence the habitat use of other sloth species (Falconi et al. 2015, Acevedo-Quintero 2011).

The floristic composition of these areas likely plays a role in the habitat use and should be incorporated into future models. In all three countryside habitats in this study, sloths were often observed feeding and resting in pioneer tree species, such as *Cecropia* trees. Even when these species of trees were less abundant in a particular habitat, sloths still seemed to prefer them to other more common species.

At broader spatial extents, my findings suggest that sloths were selective only at the 5 ha scale, favoring countryside habitats high in secondary forest cover and close to tracts of secondary forest ≥ 10 ha. This spatial scale corresponds to the average home range size for brown-throated sloths, which may explain why they are responding most

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to this coarser spatial scale. These results indicate that models predicting species distribution based solely on local environmental attributes may be inadequate for sloths, in addition to other taxa (Mazerolle and Villard 1999, Urquiza-Haas et al. 2009).

This study complements previous research in highlighting the importance of considering multiple spatial scales when evaluating species-specific responses to fragmentation (Mazerolle and Villard 1999, Krawchuk and Taylor 2003, Panzacchi et al. 2010) and their utilization of human-modified habitats (Haslem and Bennett 2008). It is my hope that by understanding how organisms, specifically those of low vagility, are influenced by changes in habitat and at which scales this occurs, we will increase the efficiency of conservation strategies for mammals of low vagility.

*Conservation Implications*

Sloths' habitat requirements, as well as preferences, greatly depend on the structural complexity that is a consequence of specific land-management practices. The results from this study emphasize the capacity that individual landowners have to manage biodiversity and natural capital on their own land.

Land managers of mixed-use areas can incorporate more trees into their property to promote the movement of biodiversity, specifically species that rely on tree cover (Harvey et al. 2006a). Tree stands that are heterogeneous in basal area and height are of particular appeal to brown-throated sloths. If small-scale agriculture or pastures are present within mixed-use areas, they should incorporate patches of trees and retain as much structural complexity as possible.

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A number of approaches might be considered when designing and establishing tree plantations to promote the maintenance of biodiversity. First, native tree species should be favored over than exotic species (Hartley 2002) because larger patches of retained native vegetation within plantations generally support more species of vertebrates (Lindenmayer et al. 1999). Additionally, the growth of pioneer species (*i.e., Cecropia spp.)* should be permitted, rather than completely clearing understories. This would likely promote sloths, in particular, by increasing the structural complexity and the availability of preferred tree species.

While the potential for countryside habitats to function as supplemental resources for the conservation of sloths is promising, it is important to proceed with caution (Horner-Devine et al. 2003, Peery and Pauli 2014). The occurrence of brown-throated sloths in human-modified habitats does not necessarily indicate that they are able to maintain a stable population. Additionally, continuing intensification of land use may reduce sloth abundances in countryside habitats in the future (DeFries et al. 2005). Moreover, tree plantations are intended for eventual harvest, so the long-term contribution of tree plantations as potential habitat is unclear, however designed harvest rotations and patch geometry can maintain species diversity in managed forests (Goldstein et al. 2003). The extent and ecological qualities of countryside habitats will ultimately determine whether tropical forest species 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). Agricultural development and land use change does not necessarily imply that biodiversity is doomed (Daily et al. 2001). Provided that countryside landscapes retain forest fragments and areas of high structural complexity, many species can likely coexist with small-scale agricultural development (Harvey et al. 2006a, Faria et al. 2007). Although plantations and mixed-use areas are not surrogates for protected forests and are likely unable to maintain the region's biological diversity alone, these countryside habitats should be perceived as complementary to protected areas conservation planning.

# CHAPTER IV

## CONCLUSIONS

Throughout this thesis, I aimed to identify opportunities for conservation of the brown-throated three-toed sloth by investigating factors that influence the species' occurrence and distribution across multiple spatial scales. In addition to the weak dispersal potential of three-toed sloths, their sedentary lifestyle compounded by their low metabolic rate and reliance on forest cover make them especially susceptible to land use change (Moss et al. 2012). Given these characteristics of brown-throated sloths, it was important to examine the effects of habitat characteristics on brown-throated sloth occurrence at both the local and landscape scales.

In my first study (Chapter II), I used line-transect and point density surface mapping to compare brown-throated sloth densities across different habitats in a human-modified landscape. A total of 38 individual brown-throated sloths were observed during the three-month sampling season. I generated a point density surface map to determine how those 38 brown-throated sloths were distributed across the landscape and to what degree they were utilizing countryside habitats, with specific focus on tree plantations, mixed-used areas and riparian forests. From the point density surface map, two high-concentration areas of brown-throated sloths were identified. These areas were located within mixed-use areas and contained between 0.8 and 1.6 sloths per hectare. Several other areas with a moderate density of sloths were identified, which contained a density ranging from 0.61 to 0.8 sloths per hectare. This map is useful for efficient identification

of hotspot areas of brown-throated sloths in the study region and facilitates visual detection of patterns of habitat use by brown-throated sloths, enabling land managers to prioritize conservation initiatives in these locations. Future investigations may build upon this research by quantifying changes in brown-throated sloth distribution over time by comparing density surface maps from different seasons or years.

In my second study (Chapter III), I investigated how local habitat characteristics and landscape properties influence the presence or absence of brown-throated sloths in countryside habitats. At the local scale, I found that brown-throated sloths favored countryside habitats that were more heterogeneous in mean tree height and total basal area. Even within a particular land use type, it was evident that sloths were selecting sites that were more variable in tree height and basal area over sites that were more homogenous in these two variables. At the landscape scale, sloths were responsive to broad-scale factors at the 5-ha scale only, which corresponds with the species' median home range size. At the 5-ha scale, brown-throated sloths appeared to prefer countryside habitats that contained a higher proportion of secondary forest, and were closer to a forest tract of at least 10 ha. These land use types are fairly common in agricultural landscapes throughout Central America (Montagnini et al. 2005, Harvey et al. 2006a), making the results broadly applicable to similar landscapes across the region. These results indicate that models predicting brown-throated sloth distribution based solely on a single spatial scale may be inadequate for this species. Future work can expand upon my findings by sampling the same habitats during other seasons or by surveying other habitats in human-modified landscapes.

In summary, I conducted these two studies with the hope that by understanding how brown-throated sloths are influenced by changes in habitat and at which scales these effects occur, we will increase the efficiency of conservation strategies for brown-throated sloths, and perhaps, other mammals of low vagility. By studying how habitat elements influence the distribution of brown-throated sloths across multiple scales, my goal is to provide an understanding of the effects of land use change and fragmentation on the spatial patterns of species with low dispersal abilities. The analytical approaches I used can be applied to a wide variety of organisms, including other dispersal-limited species, as well as other landscapes experiencing a gradient of anthropogenic pressures.

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