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Assessment of Mammal Biodiversity in Coffee-Dominated Landscapes of India and Costa Rica

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ASSESSMENT OF MAMMAL BIODIVERSITY IN COFFEE-DOMINATED LANDSCAPES OF INDIA AND COSTA RICA

BY

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A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
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DOCTOR OF PHILOSOPHY DISSERTATION

OF

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ABSTRACT

The fate of many tropical wildlife species depends on the way in which human-dominated landscapes are managed. Conservation strategies that incorporate agricultural landscapes are imperative for the survival of native fauna. Coffee is a major cash crop worldwide and is grown in tropical regions of the world that are often designated as biodiversity hotspots. Shade coffee, an agroforestry system in which coffee is grown under the shade of intentionally managed and/or native tree cover, has shown promise to provide habitat and support the diversity of bird, bat, and insect communities, but few studies have focused on non-volant mammals living in and around coffee farms. Further research is needed to understand ecosystem dynamics within coffee-dominated landscapes and to evaluate the value of this landscape as habitat for wildlife. The objectives of my research were to assess the mammal diversity within coffee-dominated landscapes, quantify the habitat parameters that are important for mammals, and based on my findings, develop guidance and suggested management practices for ways to enhance mammal diversity on coffee farms.

I hypothesize that increased vegetation diversity within coffee farms leads to an increase in mammalian diversity. Additionally, I hypothesize that native forests support the highest amount of mammal abundance and diversity and that as vegetation complexity decreases within the coffee farms, the abundance and diversity of mammals also decrease.

I assessed mammal diversity within coffee landscapes in Kodagu, India and Turriabla, Costa Rica. In India, I investigated the effects of native and non-native shade trees on mammal diversity and vegetation structure within coffee farms. Twenty

farms, each with two 50- x 50-m trap grids, were sampled for five nights throughout the three rainfall zones in the region. Each farm also contained a grid with indirect sampling methods: track plates, hair traps, and camera traps.

In Costa Rica, I surveyed diversity and habitat preference of non-volant mammals across a broader coffee-forest landscape. Three 25-ha sites were selected that contained forest, shade coffee, and sun coffee habitats; and in two of the sites, a mix of other agricultural land uses were present. Each site was set with a 500- x 500-m trap grid, four camera traps, and four track plates. The sites were sampled in four sessions, each approximately two weeks in duration, totaling 46 sampling nights per site.

During the four-month study period in India, I captured 146 small mammals (129 individuals). Eleven species of mammals were detected, six species captured in small mammal traps and five detected from the track plates and camera traps. I found that neither abundance nor richness of small mammals was influenced by the composition of native or non-native trees within the site. On the plot level, small mammal abundances were higher at farms with higher amounts of low vegetation cover and basal area of shade trees, and lower numbers of shade trees within the farm; and species richness was positively associated with low vegetation cover. On a landscape level, the small mammal abundance increased as the distance to forest decreased. Although the amount of non-native trees was not related to mammal diversity, it was significantly related to vegetation structure and composition within the coffee farms. Overall, the coffee farms surveyed in India had relatively high levels of tree species richness and diversity but did not support a high diversity of mammals.

For the study in Costa Rica, I found that small mammals used a variety of agricultural habitats. I captured 1,258 mammals (597 individuals) during the seven-month study period. Sixteen species of mammals were found, thirteen were captured in the traps and camera trap yielded an additional three species. In general, I found the forest habitats had greater species richness and abundance of mammals than shade coffee, which in turn had more species and higher abundances than sun coffee habitats. Habitat type was significantly associated with mammal abundance and richness, but the distance to forest was not. Increased amounts of shade canopy and herbaceous ground cover within the habitats were shown to significantly increase the mammal abundance and richness for the study sites in Costa Rica. While there is no substitute for native forest, the abundance and richness of small mammals within shade coffee rivaled that of forest, whereas abundance and richness within sun coffee was much lower than both shade coffee and forest.

In the habitat preference analysis of five focal species found within the coffee-forest landscapes of Costa Rica, I found that all of the focal species preferred forest habitat over coffee habitats, except one species that had an equal preference for shade coffee and forest. Three species preferred shade coffee over sun coffee, while the remaining two species had no preference between the two coffee habitats.

My findings suggest that, although small mammals may be present in coffee habitats, most do not use shade coffee exclusively and may rely primarily upon forest habitat for survival. Small mammals may require forest tracts surrounding or intersecting coffee agriculture in addition to shade trees within the coffee farm. These habitat requirements should be included in conservation strategies for the promotion of biodiversity and sustainable agriculture. Our conservation strategies may need to be expanded to a broader-landscape scale that incorporates not only the management of shade trees and vegetation complexity within coffee farms, but also that includes forest habitats in the surrounding landscape.

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Twenty years from now, you will be more disappointed by the things you didn't do than by the ones you did do. So throw off the bowlines. Sail away from the safe harbor. Catch the trade winds in your sails. Explore. Dream. Discover. - Mark Twain

PREFACE

This dissertation is written in MANUSCRIPT FORMAT as specified by the University of Rhode Island Graduate School. The first manuscript on the mammal diversity in coffee farms in India conforms to the guidelines for submission to *Biodiversity and Conservation* was submitted on March 28, 2013. The second manuscript on mammal diversity in coffee-forest landscapes in central Costa Rica follows the guidelines of *Biological Conservation*. The third manuscript on the habitat preferences of five focal small mammal species in coffee-forest landscapes of Costa Rica adheres to the style of the *Journal of Mammalogy*.

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CHAPTER 1

Impacts of Native and Non-Native Shade Trees on Mammal Diversity and Vegetation Structure in Coffee Agroforestry in the Western Ghats, India

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Abstract Coffee agroforestry is a conservation strategy that has shown promise to support the diversity of bird, bat, and insect communities, but few studies have focused on non-volant mammals in coffee farms. We assessed mammal diversity within coffee agroforestry systems in Kodagu, India and investigated the impacts of native and non-native shade trees on mammal diversity and vegetation structure. Twenty farms, each with two trap grids, were sampled throughout three rainfall zones. We captured six species of small mammals, with indirect methods yielding an additional five species, during the four-month study period. Contrary to current ecological thought, we found that neither abundance nor richness of small mammals was influenced by the amount of non-native shade trees. Small mammal abundances were higher at farms with higher amounts of low vegetation cover and basal area of shade trees, and lower numbers of shade trees within the farm; and species richness was positively associated with low vegetation cover. Additionally, small mammal abundance was shown to increase as the distance to forest decreased. Although the amount of non-native trees was not related to mammal diversity, it was significantly related to vegetation structure and composition within the coffee farms. Overall, the coffee farms surveyed had relatively high levels of tree species richness and diversity but did not support a high diversity of mammals. We may need to expand our conservation strategies to a broader-landscape scale that incorporates not only the management and vegetation complexity on the farm level, but also that includes the surrounding landscape matrix.

Keywords small mammal diversity; coffee agroforestry; wildlife conservation; Western Ghats, India; coffee certification; sustainability

Introduction

There is no doubt that preserving forest reserves is necessary for wildlife conservation, but this strategy alone is not sufficient to provide a sustainable solution for biodiversity conservation. Forest reserves are often isolated, expensive to manage, and on their own, not a practical or sustainable solution in many parts of the world (Perfecto and Vandermeer 2008; DeClerck et al. 2010). Preservation of native forests must be coupled with other conservation strategies to ensure the protection of biodiversity. Management of shade trees and vegetation complexity within agricultural crops is one such strategy that has the potential to maximize biodiversity and provide wildlife habitat (Harvey and Villalobos 2007; Schroth and Harvey 2007).

Coffee is the second most heavily traded global commodity after oil and is the primary export in many developing countries (Taylor 2007). India is currently the fifth largest coffee producer in the world (International Coffee Organization 2012). A third of the country's coffee comes from the district of Kodagu in the state of Karnataka (Garcia et al. 2009), which lies in the eastern slopes of the Western Ghats mountain range. The Western Ghats hosts a high diversity of flora and fauna, including endangered flagship species such as tigers (*Panthera tigris*) and Asian elephants (*Elephas maximus*), and the region contains more than 30% of all plant and vertebrate species found in India (Das et al. 2006).

Traditionally, coffee is grown within the shaded canopy of native forests, and this is known as rustic coffee. In many parts of the coffee-growing world, there has been a trend to replace this system with a monoculture of coffee plants (often referred to as "sun coffee") (Perfecto et al. 2005). However, in India, virtually all coffee is grown under a tree canopy, and the recent trend has been to replace native shade tree species with a non-native species from Australia, *Grevillea robusta* (hereafter called *Grevillea*). *Grevillea* makes up 20% of the total number of trees in the Kodagu watershed (French Institute of Pondicherry 2012a) due to its multiuse as a fast-growing shade tree, a support for pepper vines, financially viable timber, and as a non-native tree species it lacks the regulatory restrictions attached to timber harvesting of native trees (Garcia et al. 2009).

Market-based approaches to conservation are a viable way to both protect wildlife habitat and provide financial incentives to coffee farmers. Coffee certifications created to promote biodiversity, such as Smithsonian Bird Friendly, UTZ Certified or Rainforest Alliance, have developed standards that offer management guidelines and include parameters to enhance wildlife habitat by maintaining or increasing the native vegetation complexity (Philpott et al. 2007; Rice 2010; Sustainable Agriculture Network 2010). Currently, there are no Bird Friendly certified farms in India and only 5% of UTZ Certified or Rainforest Alliance certified coffee farms are located in India (Smithsonian Migratory Bird Center 2012; Sustainable Agriculture Network 2012; Marie-Vivien et al. 2013).

The majority of research on the habitat value of coffee agroforestry has focused on bat, bird, and insect communities (e.g. Pineda et al. 2005; Williams-Guillén and Perfecto 2010; Philpott et al. 2012), with limited studies published that address non-volant mammals living in and around coffee farms (Gallina et al. 1996; Daily et al.

2003; Husband et al. 2007, 2009). Furthermore, there have been almost no studies to assess mammal diversity within coffee agroforestry in India (Bali et al. 2007; Molur and Singh 2009) and only one on small mammals in the Kodagu region since 1912 (Molur and Singh 2009). More research is needed on biodiversity and habitat, as it relates to coffee-dominated landscapes, to guide and inform conservation strategies for the protection of biodiversity and associated benefits to human health and livelihood, as well as ecosystem health, particularly for geographic areas and taxa such as mammals that have not been widely studied.

The objectives of our study were to: (1) Assess the impacts of native and non-native shade trees on the structure of mammal communities in coffee farms within three rainfall zones; (2) Quantify the habitat parameters associated with observed diversity and abundance of mammals; and (3) Develop guidance for ways to enhance mammal diversity in coffee farms while providing financial security for coffee farmers.

Materials and methods

Study Area and Design

Our study took place from February to June 2010 within the coffee-growing region of Kodagu, India (12° 08’- 12° 25’ N and 75° 33’- 75° 57’ E). The district of Kodagu, in the state of Karnataka, lies on the eastern slopes of the Western Ghats mountain range. The range blocks monsoon rains, thereby creating a precipitation gradient with averages of over 5000 mm/year on the western side to less than 1000 mm/year in the east (Garcia and Pascal 2006). The variation in rainfall allows for a diverse array of habitats from moist evergreen forests in the west to deciduous forests in the east.

We surveyed mammalian fauna and characterized the vegetation within coffee farms at 40 sites across three ecological zones: moist evergreen forest (high rainfall, 14 sites), transition forest (intermediate rainfall, 12 sites), and dry deciduous forest (low rainfall, 14 sites) (Fig. 1.1). The rainfall zones were delineated by average annual rainfall estimated by clustering rainfall data from a previous study conducted in the region 2009 (French Institute of Pondicherry 2012b). The sites have an average annual rainfall of approximately 4625 (±175) mm for the high rainfall zone, 2130 (±2) mm the transition zone sites, and 1400 (±65) mm for the low rainfall zone. To assess the impacts of shade tree composition on the structure of the mammalian community, we selected sites in the each of the three rainfall zones that contained varying degrees of exotic tree species: predominately native (0-20% *Grevillea*, 13 sites), mixed (21-50% *Grevillea*, 17 sites), and predominately exotic (>50% *Grevillea*, 10 sites).

Mammal Sampling

In each of 20 farms, we established two 0.25-ha (50- x 50-m) trap grids placed ≥ 50 m apart. This configuration yielded 40 independent sampling units. Plots were considered to be independent sites because tree species planted within plots on the farms were different; seven of the 20 farms surveyed fell within two different tree categories. Additionally, no individual mammal was captured in more than one site. Each of the trap grids contained 36 trap stations spaced 10 m apart with two small mammal traps (8 x 8 x 23 cm) at each station. For the majority of trap stations, both small traps were placed on the ground, however when low branches, fallen logs, or vines were available we secured one trap approximately 1 m above the ground. Two medium-sized mammal traps were placed within each trap grid: one measuring 69 x 43 x 45 cm and the other 90 x 43 x 45 cm. We baited all traps with homemade unsalted peanut butter and a mixture of 12 local seeds and pulses following Molur and Singh (2009).

We conducted mammal surveys throughout the sampling period from February to June 2010. Each site was sampled once for five consecutive nights with the exception of the first two sites that were surveyed for four nights. Our effort yielded a total of 14,256 trap nights during the dry season. Two to four sites were sampled at a same time. The time at which site surveys were conducted was ordered haphazardly with regard to logistics and permissions from farm owners, but we ensured that surveys of sites were spread out among the rainfall zones over the survey period. Traps were checked each morning and afternoon and baited daily as needed. All individuals captured were released at the point of capture after determining the species, taking standard measurements, and ear tagging each individual with a unique identification number.

At each farm, a third 0.25-ha grid employing indirect sampling methods was established >50 m from the two trap grids and these grids were checked each afternoon. Two track plates were placed in diagonal corners from each other, two hair traps in the opposite corners, and two digital camera traps in the center, ≥10 m apart facing opposite directions from each other, one with incandescent flash and the other with infrared photography. The flash camera (Trail Watcher Game Camera) was triggered by motion when an object broke an infrared light beam. The infrared camera (Bushnell Trophy Camera) with a passive infrared monitor was activated by heat and motion with an infrared flash not visible to the human eye. Photographs were identified to the species level, as possible.

We inserted track plates made of thin metal sheeting into wooden boxes (approximately 80 x 30 x 30 cm) with the back end closed. We placed bait at the back end of the track plate, contact paper in the middle, and copy toner at the front. Mammals that entered the box attracted by the bait would step in the copy toner and leave a track on the sticky contact paper next to the bait. As track reference guides specific to Indian mammals were not available, tracks were matched to track characteristics for that genus using Peterson Field Guides (Murie and Elbroch 2005).

We constructed hair traps made of wooden, triangular-shaped boards (approximately 14 x 60 cm) attached to a tree by ropes with the top and bottom open. The interior of the trap contained bait in the center with strips of glue on the sides to which hair would adhere. Hair samples were analyzed by the Centre for Ecological Sciences at the Indian Institute of Science, Bangalore, India.

Data obtained from indirect sampling methods are included as auxiliary information on species richness and not combined with the trap grid data for analysis.

Habitat Characteristics and Landscape Metrics

We quantified vegetation characteristics at each trap grid to assess possible factors that might influence mammal diversity. We measured the percent canopy cover at five locations within each 0.25-ha trap grid with a convex spherical densiometer. Two 50-

m line intercepts were recorded at four levels to categorize the percent of tree, high shrub and herbaceous vegetation (≥1 m), low shrub and herbaceous vegetation (5 cm to <1 m), and herbaceous ground cover (<5 cm). We measured the height, diameter approximately 10 cm from the ground, and dripline (circumference of the outer extent of branches) of each coffee plant within the grid. Additionally, we recorded the height, diameter at breast height, and species of each shade tree within the grid. Abiotic measurements such as spatial location, elevation, and daily temperature also were recorded for each site.

We calculated the distance to the nearest forest, waterbody, and rice paddy within a 500 m radius from the center of each trap grid using a land use land cover map developed by K.M. Nanaya for the Kodagu region. In this dataset, forest was defined as forest fragments >0.5 ha and waterbody as rivers, irrigation tanks, and ponds >0.05 ha. Distance from the site to the roadway was either measured in the field or using Google Earth imagery. All distance values were corrected if we took more exact measurements in the field.

We interviewed the owners at each farm (or farm manager in one case where the farmer was not available) to further understand their management practices, views on coffee certifications, and presence of and issues with mammals on their coffee farms. Interviews were based on 10 questions; five related to general management practices, three related to certifications, and two related to mammals. These interviews were conducted with each of the 20 farmers individually with the assistance of a translator, if needed.

Data Analysis

We analyzed mammal data as two dependent variables: abundance (number of individuals captured, not including recaptures) and richness (number of species) per site. We assessed the association of these dependent variables among tree composition and rainfall zone categories using contrasts within Poisson regression models. For multiple comparisons between treatment levels, the significance level was adjusted using the Bonferroni correction where the significance level is divided by the number of comparisons to maintain overall error rate. We used SAS Statistical Software version 9.3 (SAS Institute 2010) for all statistical modeling.

For the tree composition categories, we plotted the percent of *Grevillea* trees per total number of trees on each site. Natural breaks in the data occurred between 11 and 20% *Grevillea* and we considered a site with over 50% *Grevillea* to be predominately exotic, thus we created a categorical variable "tree composition" with three levels: "native," as 0-20% *Grevillea*; "mixed," as 21-50% *Grevillea*; and over 50% *Grevillea*, as "exotic." This categorical variable was used only for the contrasts and Kruskal-Wallis models and for comparison purposes in the tables. For all other statistical analyses, the continuous variable of percent *Grevillea* was used.

We used Poisson regression models separately for mammal abundance and species richness to examine the effects of 16 independent plot level habitat variables: number of coffee plants, % arabica coffee, coffee basal area, length of coffee leaf dripline, number of shade trees, % *Grevillea*, tree basal area (calculated from the tree diameter measurements), shade tree species richness, Simpson and Shannon indices of shade trees, average tree height, % canopy cover, % high vegetation cover, % low vegetation cover, % herbaceous ground cover, and rainfall zone as a categorical variable. Additionally, we analyzed the following landscape level variables to assess their effects on mammal diversity: distance to forest, rice paddy, waterbody, and roadways. Over or under dispersion in the data was adjusted by scaling for deviance. The variance inflation factor for each independent variable was examined for evidence of multicollinearity. We removed % arabica coffee and both indices of shade tree diversity from the models because they were highly correlated with number of coffee plants and % *Grevillea*, respectively.

The impact of *Grevillea* on the vegetation structure within the sites was assessed for each of the plot level habitat variables with the Pearson's correlation matrix after scatterplots of the variables were examined for linear relationships. Additionally, we analyzed the difference in vegetation variables with regards to tree composition and rainfall zone using non-parametric one-way Kruskal-Wallis models. Tukey's test of multiple comparisons was used for the variables that showed significant differences after they were log (+1) or square root transformed to meet the conditions of normality.

Results

Mammal Surveys

We captured 146 small mammals (129 individuals) during the four-month study period with an average trap success of 1.0%. While the average abundance per site tended to be higher for native and mixed farms compared to exotic, there was not a significant difference due to high variation among sites (Table 1.1). The capture success per site ranged from 0 to 3.89% with two or fewer individuals captured for 25 of the 40 sites (8 sites with 0, 9 sites only 1, and 8 sites with 2 individuals captured). No medium-sized mammals were captured during the study.

A total of six different small mammal species were captured: lesser bandicoot rat (*Bandicota bengalensis*), jungle palm squirrel (*Funambulus tristriatus*), little Indian field mouse (*Mus booduga*), common house mouse (*Mus musculus*), roof rat (*Rattus rattus*), and grey musk shrew (*Suncus murinus*). We followed Menon (2009) and Molur and Singh (2009) for identifications in the field. All species captured are native to India, with *F. tristriatus* being the only species that is endemic to the Western Ghats (Wilson and Reeder 2005). Fifty-six percent of all individuals captured were *R. rattus*, followed by *F. tristriatus* at 28%, *S. murinus* at 11%, and the remaining three species together making up the remaining 5%. For 95% of the sites, only 2 species or fewer of small mammals were captured.

We compared the dominant species captured within the three rainfall zones and within the three tree composition categories. We found that *R. rattus* was the dominant species captured in the mixed and native shade tree categories (54.8% and 67.4% of all captures, respectively) and a close second to *F. tristriatus* in the exotic tree category (33.3% for *F. tristriatus* and 27.8% for *R. rattus*). In terms of rainfall zones, *R. rattus* was dominant in the high and low rainfall zones with 68.0% and 57.3% of all captures, respectively, and again a close second in the transition rainfall zone with *R. rattus* consisting of 26.7% of all captures after *S. murinus* (33.3%).

We obtained a total of 92 track plate samples, 12 hair samples, and 40 images from the camera traps. The indirect methods provided valuable information, especially about the presence of medium-sized mammals in the area. At the farm level, the indirect sampling yielded an average of 1.5 (±0.2) additional species detected, with a range of 0 to 3 species at each site that were undetected by traps.

Five additional species were detected from indirect sampling grids. We were able to identify tracks to the genus level: *Mus, Rattus, Suncus, Canis* (photo of *Canis aureus* from camera trap), and civet species (most likely *Viverricula* as we obtained a photo from the camera trap).

No genetic information was able to be obtained from the hair samples. DNA was successfully extracted from 3 of the 12 samples, but the sequencing yielded no results.

Camera traps captured images of five additional mammal species that were not trapped: wild pig (*Sus scrofa*), golden jackal (*Canis aureus*), small Indian civet (*Viverricula indica*), common palm civet (*Paradoxurus hermaphrodites*), grey mongoose (*Herestes edwardsii*), in addition to *F. tristriatus* and *R. rattus* (Table 1.2). Additionally, images were recorded of domestic dogs, cats, fowl, and cattle which were excluded from the analysis. It is of interest to note that all the images of medium-sized mammals were captured by the infrared camera. We suspect that the incandescent flash being set off by leaves and branches moving in the wind could have been a deterrent for mammals at night.

Habitat Characteristics and Landscape Metrics

Overall, we found that the mean number of small mammals was higher in the low rainfall sites as compared to the sites in the transition (χ_1^2=17.0, *p*<0.001) and high rainfall zones (χ_1^2=21.22, *p*<0.001) with a mean number of individuals per site of 6.4

± 1.2 for the low rainfall zone, 1.3 ± 0.4 for the transition rainfall zone, and 1.8 ± 0.3 for the high rainfall. However, tree composition did not influence mammal abundance (χ_1^2=2.59, *p*=0.274). Neither rainfall zone nor tree composition had a strong association with species richness (rainfall: χ_1^2=1.76, *p*=0.414; tree composition: χ_1^2=0.12, *p*=0.941).

The Poisson regression models revealed that the abundance of small mammals increased with higher amounts of low vegetation cover (χ_1^2=4.43, *p*=0.035), larger basal area of shade trees (χ_1^2=7.50, *p*=0.006), and lower numbers of shade trees (χ_1^2=9.80, *p*=0.002), after adjusting for effects of the rainfall zone (χ_2^2=31.34, *p*<0.001). Species richness was found to be associated with a single variable, low vegetation cover (χ_1^2=4.76, *p*=0.029). *Grevillea* did not negatively affect small mammal abundance or richness in coffee farms, whether it was modeled either as a continuous or a categorical variable after being adjusted for the effects of the other variables. On a landscape level, we found that small mammal abundance increased as the distance to forest decreased (χ_1^2=7.34, *p*=0.007) after adjusting for the rainfall zone, but none of the variables were important in explaining species richness.

The coffee farms in Kodagu have remarkably high shade tree cover and tree diversity. One hundred and twenty-nine different tree species were identified in the study sites combined. The shade tree species richness ranged from 5 to 29 per site. On average, each site had 15 (± 0.8) different tree species. Mean canopy cover for all sites combined was 64.7% (± 3.8), although the average in the low rainfall zone was higher at 84.8% (± 2.6).

Interestingly, the percent of *Grevillea* per site was highly correlated with the calculated tree diversity indices (Shannon index: r=-0.859, p<0.001; Simpson index: r=0.897, p<0.001) and the tree species richness (r=-0.580, p<0.001) (Table 1.3). This indicated that as the percent of *Grevillea* on site increased, both the shade tree diversity and species richness decreased. *Grevillea*, a fast-growing tree, was also correlated with the basal area of shade trees (r=-0.544, p<0.001), as *Grevillea* on site increased, the basal area decreased.

There was a difference in mean shade tree richness, tree basal area, and shade tree diversity (p=0.001, 0.034, <0.001, respectively) for the tree composition categories of native, mixed, and exotic. The average tree species richness, basal area, and diversity were all highest on the native farms, followed by mixed, and then exotic; but not all the categories were significantly different from each other (Table 1.4). Although *Grevillea* did not show any direct relationship with mammal diversity, it did appear to have an influence on the vegetation structure and composition within the coffee farms in Kodagu.

Of the 20 farmers that we interviewed, five were not aware of coffee certification and two owned certified coffee farms; one UTZ certified (UTZ 2012) and the other certified organic by India’s Agricultural and Processed Food Products Export Development Authority. Seven farmers said they were interested in pursuing coffee certifications, four would be interested in finding out the benefits, and seven were not interested.

Almost all of the farmers that we interviewed used chemical fertilizers and Bordeaux mixture fungicide which is a calcium copper sulfate. Five of the 20 claimed not to use pesticides at all, although two discarded pesticide bags were found on two of those farms. Several farmers said that they had tried organic fertilizers, but they did not work well for coffee. Two of the farmers mixed manure with chemical fertilizers.

Although most farmers did not have problems with wildlife in their coffee farms, the following were listed as being potentially troublesome: elephants (*Elephas maximus*) were mentioned six times, civet cats (*Viverra* sp. or *Paradoxurus* sp.) mentioned three times, wild boars (*Sus scrofa*) mentioned twice, and rats (*Rattus* spp.), birds, flying squirrels and palm squirrels (*Petaurista* sp. and *Fundambulus* sp.), and cattle (*Bos* spp.) were mentioned once.

Discussion

We found remarkably high levels of tree species richness and diversity in coffee systems, but the coffee farms did not support a high diversity of mammals. Similar results of low mammal diversity have been obtained from other studies in India. Molur and Singh (2009) conducted a study of small mammal communities in various habitat types in the Kodagu region from 2004 to 2008. Nine species were captured in coffee and only five in forest habitats, although the abundance in forest habitats was more than twice the amount in coffee indicated by the trap success of 7.2% and 3.1%, respectively. Two other studies conducted on small mammals in Southern India also reported low species richness totaling only five and nine species in forest habitats, with a trap success of 4.9% and 5.6%, respectively (Chandrasekar-Roa and Sunquist 1996; Shanker and Sukumar 1998). The authors of these studies all reported *R. rattus* as the dominant species in their surveys. *R. rattus* is known as an aggressive, territorial, generalist species. Chandrasekar-Roa and Sunquist (1996) speculated that *R. rattus* could be excluding other small mammal species and therefore having an impact on the structure and diversity of small mammal communities in this area.

The species richness in both coffee and forest from these mammal studies in India is lower than those documented in coffee-growing regions of Costa Rica and Mexico. Studies of non-volant mammals in coffee farms in Costa Rica and Mexico revealed species richness as high as 11 (Husband et al. 2007, 2009), 16 (Daily 2003), and 24 species (Gallina et al. 1996). The species richness increased to 17 species for the studies that included trapping in forest that was contiguous with coffee agroforestry (both Daily et al. 2003; Husband et al. 2007, 2009). In 90% of our coffee study sites in India, only four species or fewer were found including the medium-sized mammal species detected from the camera traps.

The vegetation characteristics that we measured in the coffee farms in India are comparable and indeed often surpassed those measurements for cover percent, number of individual trees, number of tree species, and mean tree height as documented for coffee-growing regions in Mexico and Costa Rica (Philpott et al. 2007; Husband et al. 2007, 2009). It is likely that most of the farms in our survey would meet the requirements for the vegetation complexity, including shade tree cover percent, tree species richness, and number of native tree species, outlined in the coffee certifications that promote wildlife biodiversity, such as Smithsonian Bird Friendly and Rainforest Alliance (Philpott et al. 2007). For example, 77.5% of the sites in our study had greater than the standard of 40% shade tree cover and all of them had high tree species richness, with an average of 14.98 (±0.83 SE) compared to the standard of greater than 12 species for the Bird Friendly certification or Rainforest Alliance (Marie-Vivien et al. 2013).

Our results at the plot level indicated that small mammal abundance and species richness were higher at farms with greater amounts of low vegetation cover. This association may result from small mammals, which are often prey species, preferring areas with escape cover. We also found that mammal abundance increased with an increase in the basal area of shade trees and decrease in the number of shade trees. This indicates that the mammals in this study preferred farms with larger, more mature trees. Additionally, the abundance of small mammals, although not the species richness, is higher at farms that are closer to forested areas indicating that the surrounding landscape has an influence on the mammal community within the farms.

The disparity between the low mammal diversity in this study and those in other coffee-growing regions seems not to lie in the vegetation structure and characteristics within the coffee farms, but perhaps in other influential factors such as pesticide use, reduction of native habitats, management of neighboring farms, history of land use, and perhaps even the dominance of an aggressive species, such as *R. rattus*.

Historically, pesticides have been used for agriculture worldwide. Chemicals that are older, not patented, and more toxic, which are often banned in other countries, frequently continue to be employed in developing countries (Ecobichon 2001). Even if pesticides are banned, developing countries often do not have the manpower in place to enforce the regulations (Ecobichon 2001). India is the world’s twelfth largest user of pesticides and, as recently as the 1990s, 70% of pesticides used for agriculture there were either banned or severely restricted in other countries (Abhilash and Singh 2009).

Farmers reported that although they did not use pesticides that were banned in India, they know of neighboring farmers that do. Most of the farmers that we surveyed reported that they had not used highly toxic chemicals on the coffee plants for several years. We also noticed that even though chemicals might not be used for the coffee plants, they are sprayed adjacent to the coffee farm in areas where other crops such as ginger (*Zingiber officinale*) are grown. Small mammals may be highly susceptible to chemical uses in farms as they have limited home ranges (most less than 25-m in radius) and are ground foragers.

Currently, ecological thought is that non-native tree species negatively impact the native biodiversity of a region. While increasing presence of *Grevillea* did have an impact on the vegetation composition and structure including a reduction in tree species richness and diversity on the sites, our study did not find any relationship between the percentage of *Grevillea* within the coffee farms and mammal diversity. Several factors have influenced the shift in tree composition within the coffee farms. *Grevillea* is a fast-growing tree that is often used to support climbing pepper vines interspersed with the coffee plants (90% of the sites that we surveyed). Management decisions to plant *Grevillea* in this part of India are very much related to ownership rights. Farmers in this region do not necessarily have ownership rights over native trees on their estates. Depending on their individual ownership status, the native trees may be under the full control of the Karnataka Forest Department with no rights for farmers to harvest them or with farmers' ownerships but restricted rights to harvest them and having to pay a fee to fell, transport, and/or sell these native trees (Garcia et al. 2009). As *Grevillea* is not a native tree species, it does not fall under these same regulations, therefore farmers have unrestricted rights to these trees to sell for timber or otherwise use as they see fit. Although originally promulgated to protect native trees, the laws are now a major reason why farmers are shifting to growing a higher proportion of *Grevillea* on their land, thereby replacing native species.

Directions for Further Study

Habitat destruction threatens wildlife existence worldwide. While it is imperative that native forest be preserved to protect wildlife habitat, we also must develop and improve upon other conservation strategies to find a sustainable solution to conciliate agricultural development with wildlife conservation. Coffee agroforestry has shown promise to support wildlife biodiversity for birds, bats, and insects, but further research is needed to understand how to enhance this habitat for mammals.

Direction for further study could include examining the role that historical pesticide use, fragmentation of forested areas, and management of neighboring farms and intensive cropping systems such as *Z. officinale* has on mammal diversity. To what extent do these broader parameters influence biodiversity in comparison to the vegetation structure on the farm level and what can be done to incorporate them into conservation strategies such as coffee certifications? Is it fair to compare mammalian diversity across all coffee-growing regions? Our conservation strategies and research may need to be expanded to a broader-landscape scale that incorporates not only the management of vegetation complexity on the farm level, but also in the surrounding landscape matrix.

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Figures and Tables

Figure 1.1. Map of 2010 mammal study site locations in the Kodagu region delineated by rainfall zone and types of shade trees within the coffee farms. Each symbol represents a site location and the shading represents the shade tree category of the site (native, mixed, exotic as defined in Table 1.1 and text). The three rainfall zones are depicted in gray shades as labeled accordingly (high, transition, and low).

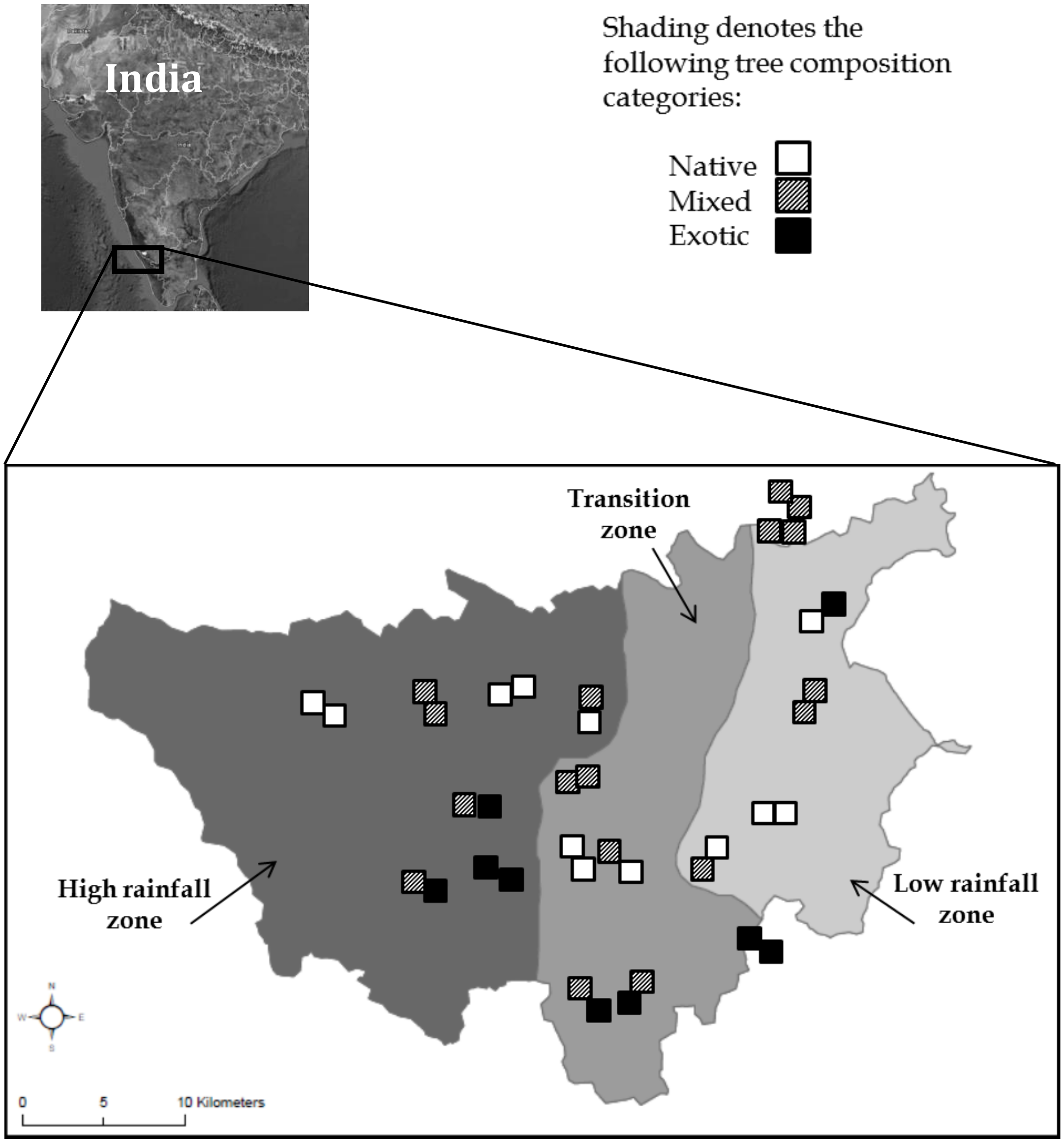

Table 1.1. Average abundance of small mammals captured per site and mammal species richness by tree composition category in Kodagu, India.

Tree composition[a]	*Number of sites*	*Average abundance*[b] *(SE)*	*Species richness of mammals captured*[c]	*Species richness including indirect methods*[d]
Native	13	3.77 (1.06)	5	9
Mixed	17	3.65 (1.01)	4	5
Exotic	10	1.80 (0.49)	6	9

[a] Native (0-20% *Grevillea*), mixed (21-50% *Grevillea*), and exotic (>50% *Grevillea*)
[b] Average number of individual mammals captured per site
[c] Species richness of mammals captured by small mammal traps within the tree composition category
[d] Species richness including results of track plates, hair traps, and camera traps

Table 1.2. Mammal species presence detected in each of the three tree composition categories in the coffee farms surveyed in Kodagu, India.

	Tree Composition Category[a]		
Species	*Native*	*Mixed*	*Exotic*
Rattus rattus	X	X	X
Funambulus tristriatus	X	X	X
Suncus murinus	X	X	X
Mus booduga	X		X
Mus musculus	X	X	X
Mus spp.[b]		X	
Bandicota bengalensis			X
Sus scrofa	X		
Canis aureus	X		
Viverricula indica	X	X	X
Paradoxurus hermaphrodites			X
Herestes edwardsii	X		X

[a] Native (0-20% *Grevillea*), mixed (21-50% *Grevillea*), and exotic (>50% *Grevillea*)
[b] Only evidence from track plate samples which are identified to genus level

Table 1.3. Relationship between measured vegetation characteristics and percent of non-native *Grevillea* shade trees within coffee farms surveyed in Kodagu, India.

Independent Variables	*Pearson correlation coefficient (r)*	*p*
Number of coffee plants	0.120	0.459
Arabica (% of total coffee plants)	0.120	0.461
Basal area of coffee plants (m^2 per 0.25 ha)	-0.252	0.117
Coffee dripline (% leaf cover)	-0.111	0.494
Number of shade trees per 0.25 ha	0.308	0.053
Basal area of shade trees (m^2 per 0.25 ha)	-0.348	0.027
Canopy cover (%)	-0.232	0.151
Tree height (m)	0.184	0.257
Tree species richness	-0.580	<0.001
Shannon index (H'_{ln}) – trees	-0.859	<0.001
Simpson index (D) – trees	0.897	<0.001
High vegetation cover (%)	-0.374	0.018
Low vegetation cover (%)	0.325	0.041
Herbaceous ground cover (%)	0.149	0.359

Table 1.4. Average values (± standard error) of vegetation characteristics by tree composition category in the coffee farms sampled in Kodagu, India.

	Tree Composition Category[*]		
Independent Variables	*Native* (n=13)	*Mixed* (n=17)	*Exotic* (n=10)
Number of coffee plants per 0.25 ha	336.9 ± 18.3	381.3 ± 38.4	396.6 ± 62.8
Arabica (% of total coffee plants)	2.8 ± 1.5	26.1 ± 10.3	13.4 ± 7.8
Basal area of coffee plants (m^2 per 0.25 ha)	3.4 ± 0.3	2.8 ± 0.3	2.5 ± 0.4
Coffee dripline (% leaf cover)	103.3 ± 6.2	96.8 ± 4.7	97.3 ± 15.8
Number of shade trees per 0.25 ha	59.1 ± 7.1	88.7 ± 9.5	94.3 ± 14.1
Basal area of shade trees (m^2 per 0.25 ha)	6.4 ± 0.6a,b	6.6 ± 0.6a	4.6 ± 0.6b
Total basal area of shade and coffee trees (m^2 per 0.25 ha)	9.8 ± 0.6a	9.4 ± 0.5a	7.1 ± 0.7b
Canopy cover (%)	67.5 ± 5.9	68.2 ± 5.6	55.4 ± 8.9
Tree height (m)	9.7 ± 0.5	9.9 ± 0.3	10.4 ± 0.6
Tree species richness	18.8 ± 1.4a	13.9 ± 1.0b	11.7 ± 1.2b
Shannon index (H'_{ln}) – trees	2.5 ± 0.1a	1.8 ± 0.1b	1.1 ± 0.1c
Simpson index (D) – trees	0.1 ± 0a	0.3 ± 0b	0.6± 0.3c
High vegetation cover (%)	82.2 ± 3.7a	77.3 ± 2.9a,b	66.2 ± 5.1b
Low vegetation cover (%)	0.1 ± 0.1	0.0 ± 0	0.6 ± 0.3
Herbaceous ground cover (%)	23.8 ± 5.3	25.0 ± 5.0	34.9 ± 6.7

*Numbers show mean ± SE and letters indicate significant difference in mean levels ($p<0.05$) per Tukey's multiple comparison test across the tree categories (native: 0-20% *Grevillea*; mixed: 21-50% *Grevillea*; and exotic: >50% *Grevillea*), same letter indicates no difference

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CHAPTER 2

Connecting Sustainable Agriculture and Wildlife Conservation: Does Shade Coffee Provide Habitat for Mammals?

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ABSTRACT

Shade coffee systems are reported to provide a refuge for biodiversity; however, few studies have focused on mammals living within coffee-dominated landscapes. In a survey of non-volant mammalian fauna in three coffee-forest landscapes in Costa Rica, we compared mammal abundance and richness across agricultural habitats with a particular focus on forest, shade coffee, and sun coffee. Each of the three sites contained a 500- x 500-m trap grid and was sampled in four sessions, totaling 46 sampling nights per site. We captured 1,258 mammals (597 individuals) of 16 species during the seven-month study period. We found forest habitats to have greater richness and abundance of mammals than shade coffee, which in turn had more species and higher abundances than sun coffee habitats. The species richness within shade coffee rivaled that of the nearby forested areas, suggesting that shade coffee may be a complement to, although not a substitute for, native forest for mammal diversity. Habitat type was significantly associated with mammal abundance and richness, but the distance to forest was not. Increased amounts of shade canopy and herbaceous ground cover within the habitats were shown to significantly increase the mammal abundance and richness. Within coffee habitats, higher amounts of canopy cover was associated with higher abundance and species richness of mammals. Our study indicated that mammals use coffee habitats and benefit from the increased canopy cover and vegetation complexity that shade coffee provides. Shade coffee does show promise as a conservation strategy to enhance wildlife habitat and protect biodiversity.

Keywords: small mammal diversity; coffee agroforestry; wildlife conservation; sustainable agriculture; coffee certification; mammal habitat; shade coffee

1. Introduction

Agriculture and biodiversity conservation are often viewed as opposing forces, competing for land use and management rights. While forest reserves are crucial to conservation goals, patches of forests alone are not a sustainable solution to ensure the protection of biodiversity. Recently, conservation strategies have begun to focus on a broader, landscape approach (Perfecto and Vandermeer, 2008) in which the dynamics of land uses within a region are taken into account. As human-managed landscapes, predominately used for agricultural, account for approximately 70% of terrestrial surface in the tropics (Perfecto and Vandermeer, 2008), the way in which agricultural lands are managed has significant influence on the level of biodiversity that a landscape can support.

Coffee is an important cash crop in Costa Rica and worldwide. Globally, it is the second most traded commodity next only to oil (Taylor, 2007). The livelihoods of millions of people are intertwined with this agricultural crop and 10 million ha of land are devoted to its production (Hergoualc’h et al., 2012).

Coffee is traditionally grown under a diverse shade canopy which provides wildlife habitat, fosters ecosystem services, and protects biodiversity (DeClerck et al., 2010; Moguel and Toledo, 1999). Over the past four decades, there has been a trend to move away from traditional coffee towards a monoculture of coffee plants or “sun” coffee aimed at higher yields (Perfecto et al., 2005) which, in addition to depleting the system of floristic complexity, requires higher levels of chemical inputs to replace the ecosystem services lost (Rice, 1999). Gobbi (2000) estimated that in Latin America 41% of shaded coffee has been replaced by minimally shaded or sun coffee. Coffee systems in Costa Rica exemplify this trend with approximately 60% of shade and the remaining 40% sun coffee (Hergoualc'h et al., 2012).

Conservation efforts to counteract this trend, such as biodiversity-friendly coffee certifications, provide financial incentives to coffee farmers to maintain or implement shaded systems for their coffee crops. Coffee certifications, such as Rainforest Alliance or Smithsonian Bird Friendly, provide standards to enhance biodiversity and wildlife habitat by requiring high levels of shade cover and native vegetation complexity within the coffee farm (Philpott et al., 2007; Rice, 2010; Sustainable Agriculture Network, 2010), as well as, reduction or elimination of agrochemicals. The importance of conservation strategies such as these have been internationally recognized and included in the recent Convention of Biological Diversity 2020 targets which incorporate biodiversity-friendly certification programs and sustainably managed agriculture as approaches to reduce the rate of biological diversity loss (GEO BON 2011).

Numerous benefits of shade coffee have been documented and include decreased water runoff and soil erosion, improved soil fertility and nutrient cycling, increased protection against coffee pests and insects, increased pollination and carbon sequestration, and improved coffee quality (Cannavo et al., 2012; Perfecto and Vandermeer, 2008; Rice, 2010). Shade trees also could be used as timber or sources of fruit to diversify farmers' incomes. The added floristic complexity of shaded coffee also has been shown to provide refuge for biodiversity; however, most studies have focused only on bat, bird, and insect communities (e.g. Gordon et al., 2007; Perfecto et al., 2003; Philpott et al., 2008) with only a handful of studies published that address non-volant mammals living in and around coffee farms (Caudill et al., 2011; Daily et al., 2003; Gallina et al., 1996; Husband et al., 2007, 2009). Furthermore, studies suggest that all taxonomic groups do not respond in the same way to gradients of shade cover within a forest-agriculture matrix (e.g. DeClerck et al., 2010; Perfecto et al., 2003; Pineda et al. 2005); therefore, a single taxonomic group cannot be used to indicate the quality of habitat for all wildlife. Further research is needed to guide and inform conservation strategies for the protection of biodiversity and habitat, particularly for taxa such as mammals that have not been widely studied.

We investigated the non-volant mammal abundance and diversity in three coffee landscapes in central Costa Rica. The specific objectives of our study were to: (1) Compare mammal abundance, richness, and composition in agricultural habitat types with a particular focus on forest, shade coffee, and sun coffee habitats; (2) Quantify the habitat parameters associated with observed mammalian fauna; and (3) Based on our findings, develop guidance and suggested management practices for ways to enhance mammal diversity on coffee farms. The results will offer another layer of sustainable conservation strategies for agricultural landscapes that would benefit both the biodiversity and economics of a region.

2. Methods and materials

Our study took place from August 2011 to February 2012 in the Turriabla region of Costa Rica (9°54’04” N and 83°41’04” W) which is located in the state of Cartago and falls within the Mesoamerican Biological Corridor (Figure 2.1). The land use around Turriabla is predominantly agricultural with coffee, sugar cane, and pastures interspersed with tracts of native forests.

We surveyed mammal abundance, richness, and composition and characterized vegetation within a 500- x 500-m (25-ha) sampling grid in each of the three sites in and around Turriabla. This sampling configuration provided a comprehensive view of how mammals use a mosaicked agricultural landscape. We selected sites that contained coffee plots surrounded or intersected by forest tracts and not interrupted by residential areas. Sampling grids were arranged to include the most coffee and forest habitats possible within the each site.

2.1 Study sites

Although the primary purpose of the study was to compare forest, sun, and shade coffee habitats, other agricultural habitats such as pasture, sugar cane, and tall grasses were included in Sites 1 and 2. Shade coffee was defined as coffee plots with at least 20% canopy cover and sun coffee as less than 20%. Pasture habitats typically had full herbaceous layer cover and sparsely planted trees. Sugar cane (*Saccharum* spp.) plots were a monoculture of tall sugar cane (1.5 to 2.5 m height) with little to no herbaceous cover and no shade trees. Tall grasses were characterized as grass species with a height of approximately 1.5 to 2.5 m and little to no herbaceous cover or shade trees.

Site 1 was located in Turriabla (9°48’50” N and 83°32’44” W) with an average elevation of 644 m. The site contained a mixture of agricultural habitats. The sampling grid configuration resulted in 54.8% of trap stations in forest, 18.7% in shade coffee, 14.5% in sun coffee, 5.4% in tall grasses, 5.4% in tree plantations, part of which was Klinki pine (*Araucaria hunsteinii*), and 1.2% in pasture.

Site 2, located in a neighboring community of Jicotea (9°52’49” N and 83° 39’52” W), had an average elevation of 965 m. This site had a mosaic of habitat types with 27.4% of traps in forest, 16.1% in shade coffee, 16.1% in sun coffee, 14.3% in sugar cane, 14.3% in pasture, 8.9% in pine groves, 1.8% in tall grasses, and 1.2% in land that was recently cleared.

Site 3 was located within a 673-ha coffee farm certified by Rainforest Alliance in the community of Aquiares, north of Turriabla (9°56’03” N and 83° 42’59” W). The average elevation was 969 m. The property is predominately coffee with a tract of forest running through the middle and riverine forest bordering the coffee to the south. The forest contained 25.1% of the traps, shade coffee had 40.1%, and sun coffee 34.7%.

2.2 Mammal survey

Two Sherman traps for small mammals were placed at 50-m intervals within the 500- x 500-m (25-ha) sampling area for each site. For the majority of trap stations, both small traps were placed on the ground, however when low lying branches or lianas were available we secured one trap approximately 1 m above the ground. The configuration resulted in a grid with 121 trap stations. In addition, for all but the first sampling rounds, three 30- x 30-m trap grids containing 16 traps stations were included within the larger grid in the habitat types of forest, shade coffee, and sun coffee. This scheme yielded 338 Sherman traps. Although we began the study with 12 Tomahawks distributed evenly throughout habitat types, due to theft, for most of the study only two to four Tomahawks were set per site. We divided the remaining traps equally between forest and coffee habitats.

Four sets of camera traps (one incandescent and one infrared) and track plates (e.g. Talancy 2005) were placed together within the grid, two sets in forest and two in coffee habitats. The incandescent flash camera (Trail Watcher Game Camera) was triggered by motion when an object broke an infrared light beam. The infrared camera (Bushnell Trophy Camera) with a passive infrared monitor was activated by heat and motion with an infrared flash not visible by the human eye. Photographs and tracks were identified to the species level, as possible (Reid 2009).

We conducted mammal surveys in four sampling sessions, two during the wet and two during the dry season. Each session was approximately two weeks in duration with one week in between the sessions from August 2011 through February 2012. We surveyed the sites sequentially as Site 1, Site 2, and then Site 3 for a total of 46 nights per site or 138 nights for the study period. After adjusting for theft of traps, our sampling effort for the entire study yielded a total of 42,306 trap nights.

We baited traps with a mix of peanut butter, bananas, vanilla, oats, seeds, and dry dog food. Traps were checked daily and baited as needed. All individuals captured were released at the point of capture after determining the species, taking standard measurements, and ear tagging each individual with a unique identification number. We followed Reid (2009) for identifications in the field.

Data obtained from Tomahawk traps and indirect sampling methods are included as auxiliary information on species richness and not combined with the trap grid data for analysis.

2.3 Habitat characteristics

We quantified vegetation characteristics during the first sampling session at each trap station to assess possible factors associated with mammalian fauna. We measured the percent canopy cover with a convex spherical densiometer. Ten-meter line intercepts at each trap station were recorded at three levels to categorize the percent of high shrub and herbaceous vegetation (≥1 m), low shrub and herbaceous vegetation (5 cm to <1 m), and herbaceous ground cover (<5 cm). Basal area of surrounding shade trees was recorded using a 10-factor wedge prism. We measured the diameter at breast height of the tree closest to the grid point. For the grid points within coffee habitats, we measured the height of the closest coffee plant. Spatial location, elevation, and habitat type were recorded for each grid point.

We created a land use map using Geographic Information Systems (GIS) based on the data recorded in the field and Google Earth imagery. Distance to forest was calculated for each of the trap stations.

We spoke to the owners or managers at each farm to further understand their management practices, views on coffee certifications, and presence of and issues with mammals on their coffee farms. Interviews were based on 11 questions; five related to general management practices, four related to certifications, and two related to mammals.

2.4 Data Analysis

We analyzed mammal data as two dependent variables: abundance (number of individuals captured, not including recaptures) and species richness per trap station per sampling session. We used Generalized Estimating Equations (GEE) regression models with a Poisson distribution and repeated measures since each site was revisited four times. We created five datasets for each model: all sites together with “site” as a categorical variable, each of the three sites individually, and all sites together with data from coffee habitats only. The GEE Poisson regression models were used to determine the effects of the measured habitat characteristics on mammal abundance and richness. An offset of trap nights (number of traps x sampling nights) was included in all models.

The following measured vegetation characteristics were modeled as independent continuous variables: % canopy cover, % high vegetation cover, % low vegetation cover, % herbaceous ground cover, tree basal area (m^2/ha), tree diameter (cm), and coffee height (m) for the coffee only dataset. Distance to forest was included in all models as a continuous independent variable.

All independent variables were included in the model and those shown not to be significant were removed one at a time by backwards elimination. We used contrasts within the GEE Poisson models (similar to Analysis of Variance for data with normal distributions) to compare each of the two dependent mammal variables across forest, shade, and sun coffee habitats as well as across sites. For multiple comparisons between treatment levels, the significance level is adjusted using the Bonferroni correction where the significance level is divided by the number of comparisons to maintain overall error rate.

Each dataset was modeled twice. The first model contained: all continuous vegetation variables and distance to forest; the categorical variable, season (wet, dry); the categorical variable, site (Site 1, Site 2, Site 3); and the categorical variable, habitat type (shade coffee, sun coffee, forest, and other as applicable). The second model contained all the same variables as the first model, but with the categorical variable of habitat type removed to allow for better understanding of the vegetation characteristics within each habitat type that were important. Variance inflation factors were examined for each independent variable but there was no evidence of multicollinearity. All data were standardized by sampling effort (number of traps and duration) to account for unequal numbers of traps per habitat type and trap theft.

We determined if there was a difference among the measured vegetation characteristics with regards to forest, shade coffee, and sun coffee habitat types using non-parametric one-way Kruskal-Wallis models. A Kruskal-Wallis-based post hoc test of multiple comparisons was employed for variables that showed significant differences (Ott and Longnecker 2010). We used SAS Statistical Software version 9.3 (SAS Institute 2010) for all statistical modeling.

3. Results

We captured a total of 1,251 small mammals in the Sherman traps and 7 medium-sized mammals in the Tomahawk traps during the study period, 597 of those were individuals. A total of 16 species were recorded, representing six families; 13 species were trapped, three additional species were detected only by camera traps, and track plate samples were duplicates of species trapped. Two species were captured in the Tomahawk traps: common opossum (*Didelphis marsupialis*) and gray four-eyed opossum (*Philander opossum*) although both of these species were also captured in the Sherman traps. For all sites together, 69.5% of individuals captured were from two species, dusky rice rat (*Melanomys caliginosus*) at 39.0% and Alfaro’s rice rat

(*Handleyomys alfaroi*) at 30.5% (although 89% of *H. alfaroi* were captured at Site 3). Roof rat (*Rattus rattus*) and house mouse (*Mus musculus*), with five individuals and one individual captured, respectively, were the only two non-native species captured (Table 2.1).

We obtained a total of 57 track plate samples and 30 images from the camera traps. The track plates yielded the same species that were detected by the small and medium-sized traps, while the camera trap yielded three additional species not detected by the traps: nine-banded armidillo (*Dasypus novemcinctus*), Northern raccoon (*Procyon lotor*), and rabbit (*Sylvilagus* spp).

3.1 Mammal composition

The overall mammal abundance per trap station varied significantly among the three sites (Site 1 vs. Site 2: χ^2=19.16, p<0.001; Site 1 vs. 3: χ^2=35.60, p<0.001; Site 2 vs. 3: χ^2=9.24, p=0.002). The abundance of individuals per 100 trap stations (± standard error) for all habitats and sampling sessions together was 18 ± 3 for Site 1, 51 ± 4 for Site 2, and 94 ± 8 for Site 3. Species richness also varied per site. Site 3 had the highest richness with 13 total mammal species detected, 9 species for Site 2, and 7 species for Site 1. Four species (*D. marsupialis*, *H. alfaroi, M. caliginosus, Oligoryzomys* sp.) were shared by all three sites. Site 1had no unique species, whereas Site 2 had one unique species and Site 3 had six species that were not detected in the other two sites (Table 2.2).

We were interested to understand the differences in mammal abundance, richness, and composition across the habitat types of forest, shade, and sun coffee. As expected, forest had the highest abundance and species richness, followed by shade coffee, then sun coffee when data from all sites was pooled together. For all three sites together, the total individuals captured per 100 grid points were 166 for forest, 134 for shade coffee, and 33 for sun coffee. Total species richness per land use type was 14, 13, and 6 for forest, shade coffee, and sun coffee, respectively.

We captured three unique species in the forest, two in shade coffee, and no unique species within sun coffee (Table 2.2). Six species were captured in all three habitats and five overlapped between shade coffee and forest. Interestingly, for mammal abundance and species richness for all sites combined, there was a significant difference between forest and sun habitats (abundance: $\chi^2=17.38$, $p<0.001$; richness: $\chi^2=15.68$, $p<0.001$) and between sun and shade coffee (abundance: $\chi^2=11.66$, $p<0.001$; richness: $\chi^2=12.34$, $p<0.001$), but no significant difference was detected between forest and shade coffee habitats (abundance: $\chi^2=0.70$, $p=0.590$; richness: $\chi^2=0.42$, $p=0.561$).

3.2 Habitat characteristics

We assessed the difference between the vegetation measurements within forest, shade coffee, and sun coffee habitats. There was a significant difference among canopy cover ($\chi^2=169.34$, $p<0.001$), basal area ($\chi^2=43.06$, $p<0.001$), shade tree diameter ($\chi^2=9.43$, $p<0.009$), high vegetation cover ($\chi^2=42.31$, $p<0.001$), and low vegetation cover ($\chi^2=41.76$, $p<0.001$), for these three habitat types, although not all habitats were significantly different from each other (Table 2.3).

Poisson loglinear regression models were used to examine the associations of the recorded habitat characteristics with the observed abundance and richness of mammals per trap station (summarized in Table 2.4). The first dataset is a compilation of all three sites together with all habitat types present. For models including the designation of habitat type, mammal abundance was shown to be associated with habitat type (χ^2=47.95, p<0.001), season (χ^2=3.91, p=0.048), and site (χ^2=51.94, p<0.001). Species richness also was associated with habitat type (χ^2=42.87, p<0.001), season (χ^2=5.36, p=0.021), and site (χ^2=44.35, p<0.001), and also herbaceous cover (χ^2=5.71, p=0.017). The dry season yielded higher abundances and species richness than the wet season in all models where season was shown to be significant.

For all sites together modeled with measured vegetation variables but not habitat type designations, increases in mammal abundance were explained by increased canopy cover (χ^2=27.53, p<0.001), season (χ^2=4.59, p=0.032), and site (χ^2=51.03, p<0.001); species richness increased with higher amounts of canopy cover (χ^2=15.37, p<0.001), season (χ^2=6.17, p=0.013), and site (χ^2=40.77, p<0.001) and also herbaceous cover (χ^2=4.44, p=0.035). Although interaction between canopy cover and site was tested for this model and found not to be significant (χ^2=5.78, p=0.056), individual comparisons between the three sites revealed that the relationship between canopy cover and Site 1 was significantly different than of canopy cover and Sites 2 and 3. Distance to forest was not significant in models for all sites together, although it should be noted that on average all points in the sites were within 59.5 ± 3.4 m of forest.

When each site was modeled separately with both vegetation parameters and designation of habitat type, the independent variables that affected mammal abundance and richness were similar for Sites 2 and 3, but not for Site 1. Habitat type was not significant for Site 1, but it was for both Sites 2 and 3. For Site 1, mammal abundance was associated with an increase in basal area (χ^2=4.15, *p*=0.042), a decrease in canopy cover (χ^2=9.10, *p*=0.003), and decreased distance to forest (χ^2=7.54, *p*=0.006). Mammal abundance for Site 2 was best explained by habitat type (χ^2 =18.15, *p*=0.020) and season (χ^2=6.90, *p*=0.009) and for Site 3 by habitat type (χ^2=18.59, *p*<0.001).

Habitat type also influenced species richness for Sites 2 and 3. For Site 1, species richness was shown to be associated with a decrease in canopy cover (χ^2=5.23, *p*=0.022) and decreased distance to forest (χ^2=7.25, *p*=0.007). Increases in species richness for Site 2 was best explained by habitat type (χ^2=18.07, *p*=0.020), increases in low vegetation cover (χ^2=4.80, *p*=0.028), and season (χ^2=9.02, *p*=0.003). For Site 3, the habitat type also best explained increases in richness for this site (habitat type: χ^2=17.90, *p*<0.001).

From the contrasts within the GEE Poisson models, we found that there were no significant differences between the habitat types of forest, shade, and sun coffee for either abundance or richness for Site 1. Forest and sun habitats were significantly different in terms of the number of species and individuals captured for Site 2 (abundance: χ^2=6.22, *p*=0.013; richness: χ^2=5.84, *p*=0.016), but there was no difference between shade and sun coffee or forest and shade coffee. For Site 3, abundance was significantly different between forest, shade, and sun coffee habitats (forest vs. shade: χ^2=10.09, p=0.002; forest vs. sun: χ^2=23.80, *p*<0.001; sun vs. shade: χ^2=15.92, *p*<0.001) and species richness varied significantly between sun and forest habitats and between sun and shade coffee habitats, however not between forest and shade coffee (forest vs. shade: χ^2=2.04, p=0.167; forest vs. sun: χ^2=14.27, p<0.001; sun vs. shade: χ^2=13.76, p<0.001).

When each site was modeled separately with measured vegetation features as the only independent variables (no habitat designations), mammal abundance was found to increase significantly with an increase in canopy coverage for Site 2 (χ^2=11.87, p<0.001) and Site 3(χ^2=18.35, p<0.001) and season was also significantly associated with mammal abundance for Site 2 (χ^2=7.56, p=0.006). Site 1 differed from the other two sites with the following variables found to be significantly associated with abundance: increase in basal area (χ^2=4.15, p=0.042), decrease in canopy cover (χ^2=9.10, p=0.003), and decrease in distance to forest (χ^2=7.54, p=0.006).

Increased amounts of canopy cover also were found to be positively associated with species richness for Sites 2 and 3, but negatively associated for Site 1. For Site 2, increases in canopy (χ^2=6.53, p=0.011) and low vegetation cover (χ^2=4.35, p=0.037) were found to be associated with species richness, with a significantly higher increase in the dry season than in the wet season (χ^2=9.89, p=0.002). For Site 3, species richness increased with increases in canopy cover (χ^2=9.73, p=0.002) and herbaceous ground cover (χ^2=4.08, p=0.044), while for Site 1 the species richness increased with a decrease in distance to forest (χ^2=7.25, p=0.007) and decrease in canopy cover (χ^2=5.23, p=0.022).

For the Poisson models of only coffee habitats, we found that shade coffee habitats were again found to have significantly higher mammal abundance than sun coffee habitats (χ^2=23.07, p<0.001), after adjusting for low vegetation cover (χ^2=3.94, p=0.047), coffee plant height (χ^2=4.88, p=0.027), and site (χ^2=15.45, p<0.001). Shade coffee also had significantly higher species richness than sun coffee (χ^2=23.01, *p*<0.001) after adjusting for coffee plant height (χ^2=5.60, *p*=0.018) and site (χ^2=14.88, *p*<0.001).

When the designations of sun and shade coffee were removed, the abundance was found to be positively associated with increases in low vegetation cover (χ^2=4.43, *p*=0.035), canopy cover (χ^2=6.63, *p*=0.010), and coffee height (χ^2=4.34, *p*=0.037); and species richness positively associated with canopy cover (χ^2=5.17, *p*=0.023), and coffee height (χ^2=4.91, *p*=0.027), after adjusting for site in both models (abundance: χ^2=16.30, *p*<0.001; richness: χ^2=17.04, *p*<0.001). Therefore, the results indicate that higher amounts of canopy cover within coffee farms leads to both higher abundance and species richness of mammals. As in the other models with data from all sites combined, the site was significant, whereas distance to forest was not. As all the sites contained forest, the average distance from sun coffee points to forest was 91.1 ± 7.5 m and shade coffee was 45.0 ± 4.6 m.

3.3 Interview Summaries

None of the farmers/managers reported having issues with mammals on their coffee farms. Combating leaf funguses such as *Hemileia vastatrix* (coffee rust) and *Cercospora coffeicola* (cercospora leaf spot or brown eyespot) were listed by all three farmers/managers as one of the main challenges to growing coffee in this region. Fungicides were used at Site 1 once a year and the farmer at Site 2 used an organic mixture for cercospora leaf spot. Pesticides, including endosulfan, a highly toxic chemical that is being phased out globally, were used once a year at Sites 1 and 3 to manage *Hypothenemus hampei* (coffee berry borer), an insect which destroys the coffee berries and impacts the quality of the coffee.

Chemical fertilizers were sprayed at Site 1 three times a year and herbicides approximately twice a year. Site 2 was privately owned by two small-scale farmers who used few chemicals because of cost, but herbicides including Round Up were sprayed. As a Rainforest Alliance certified site, Site 3 employed integrative pest management to reduce the amount of chemicals and fertilizers used. Herbicides were sprayed three times a year. An organic mixture of manure and coffee pulp was used as fertilizer. This property provides water to five surrounding towns; therefore a buffer around the water ways is required. The manager at Site 3 noted that the yield of the coffee where chemicals were used is 30 to 40 bags per hectare, whereas in the buffer zone about 10 bags per hectare.

4. Discussion

We found a thriving community of mammals in the coffee-forest landscapes of Turriabla, Costa Rica. We found forest habitats to have more species of mammals in greater numbers than shade coffee, which in turn had more species and higher abundances than sun coffee. The high richness and abundance in shade coffee habitats indicate that mammals benefit from the increased canopy cover and vegetation complexity that shade coffee provides. While sun coffee was not depauperate of mammalian fauna in these landscapes, the densities and species richness were significantly less than that of shaded coffee. The species richness within shade coffee rivals that of the nearby forested areas, suggesting as others have found that shade coffee may be a complement to, although not a substitute for, native forests (e.g. Harvey and González Villalobos, 2007; Pineda et al., 2005; Philpott et al., 2012).

The species richness and density of mammals varied significantly with habitat type but not distance to forest in this study. Although it is important to note because of the plot configuration that all traps for the study sites in our study were located less than 100 m from the forest edge. Other mammalian studies have found that coffee habitats contiguous with forest fragments are not significantly different than extensive forests in terms of species richness (Daily et al., 2003; Husband et al., 2007, 2009).

We found that both small mammal abundance and species richness were higher in the dry season than in the rainy season. It is likely that the activity level of the mammals is higher during the dry season than the rainy season which makes them more prone to being trapped during the dry reason. The species composition did not change between the two seasons, therefore we speculate that the increase in species richness during the dry season is also due to the higher activity level of the mammals leading to more captures of different species.

Overall, we found that higher amounts of canopy within these coffee-forest landscapes resulted in an increase of abundance and richness of mammals. Additionally, greater amounts of herbaceous ground cover were associated with higher species richness. Research on biodiversity in coffee has indicated that the common factor that influences habitat quality of a coffee farm is the complexity of vegetation, including tree richness and density and amount of canopy cover, as well as the use of agrochemicals (DeClerck et al., 2010; Perfecto and Vandermeer, 2008). Our study supported this finding for mammals, as increased canopy cover, greater amounts of low vegetation cover, and taller coffee plants were shown to result in higher levels of mammal abundance and diversity within coffee farms. These findings indicate that increased structural complexity of the vegetation is beneficial for mammal communities living in around coffee farms.

The general trend was the same for all three sites in our study: forest habitats hosted the highest density and most species of mammals, followed by shade coffee, and lastly sun coffee. The abundance and composition of mammals varied significantly among sites even though the vegetation measurements within each habitat type per site were similar. Sun coffee habitats yielded low richness and abundance for all three sites, but mammalian fauna did not respond the same in forest or shade coffee habitats across the sites.

Site 1 had the lowest species richness and captures of all the sites, significantly less than the other two sites. Only 69 individuals were captured for all habitat types during the entire study period. A previous mammal study conducted on this site yielded similar results (personal communication, DeClerck). There was no significant effect of habitat type on the mammalian fauna including no significant difference among forest, shade, or sun coffee for Site 1 which differed than that for Sites 2 and 3. Decreases in canopy cover and distance to forest were correlated with increased mammal abundance and richness at this site, whereas Sites 2 and 3 both included increased amount of canopy cover in the model. It may be that the tall grass habitat that bordered much of the forest in Site 1, with low amounts of canopy cover, could be influencing this model. Species richness was correlated to decreased amounts of canopy cover and decreased distance to forest. It is likely that habitats closest to forest have higher mammal abundances and richness, but it is unclear what role lower amounts of canopy cover have on mammal diversity for Site 1.

Both mammal abundance and richness in Site 2 were associated with type of habitat, but there was no significant difference between forest and shade coffee or between shade coffee and sun coffee. The pasture and sugar cane habitats yielded six species, the same number of species as forest in Site 2, all hosting predominately native species. This indicates that mammals were using these habitat types contrary to results reported from similar studies of agricultural landscapes in the tropics (Daily et al., 2003; Stevens and Husband, 1998). Sugar cane habitats are devoid of floristic complexity and have no shade trees, but the densely planted plots may provide extensive cover for small mammals.

Overall, Site 3 had the highest abundance and richness of the three sites. Over 50% of individuals captured for the study were from Site 3 and six unique species were detected. We have no definite answers as to why the observed mammalian fauna was different for the three sites during our study period. One possible explanation may be that Site 3 was managed to consciously support and enhance biodiversity. It is bordered by a riparian forest to the south however we captured small mammals throughout the study site. Site 2 was a mosaicked agricultural landscape, but the various habitat types seem to support some level of mammal diversity, most with greater success than in sun coffee. It is unclear why Site 1 did not support a higher level of mammal diversity. Opportunistically, we noted the most snakes and raptors at Site 1 while surveying the three sites. Predation could play a role, but there was no evidence to suggest that it did so at Site 1 more than the other two sites. Agrochemical inputs are known to influence habitat quality; however, agrochemicals were used at all sites albeit in varying degrees. Although the trend for all sites were the same, the difference among sites seems to indicate that more work is needed to further understand all the factors that may influence mammalian communities in coffee-forest landscapes.

This study provides evidence that shade coffee surpasses sun coffee in terms of habitat quality as mammals were found to benefit from the increased canopy cover and vegetation complexity that shade coffee provides. We hope that our findings will provide a foundation for further mammal studies in coffee-forest landscapes and contribute to the promotion of coffee agroforestry as a conservation strategy that enhances wildlife habitat and protects biodiversity.

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Figures and Tables

Figure 2.1 Map of 2011-2012 study sites for mammal survey in coffee-forest landscapes of central Costa Rica.

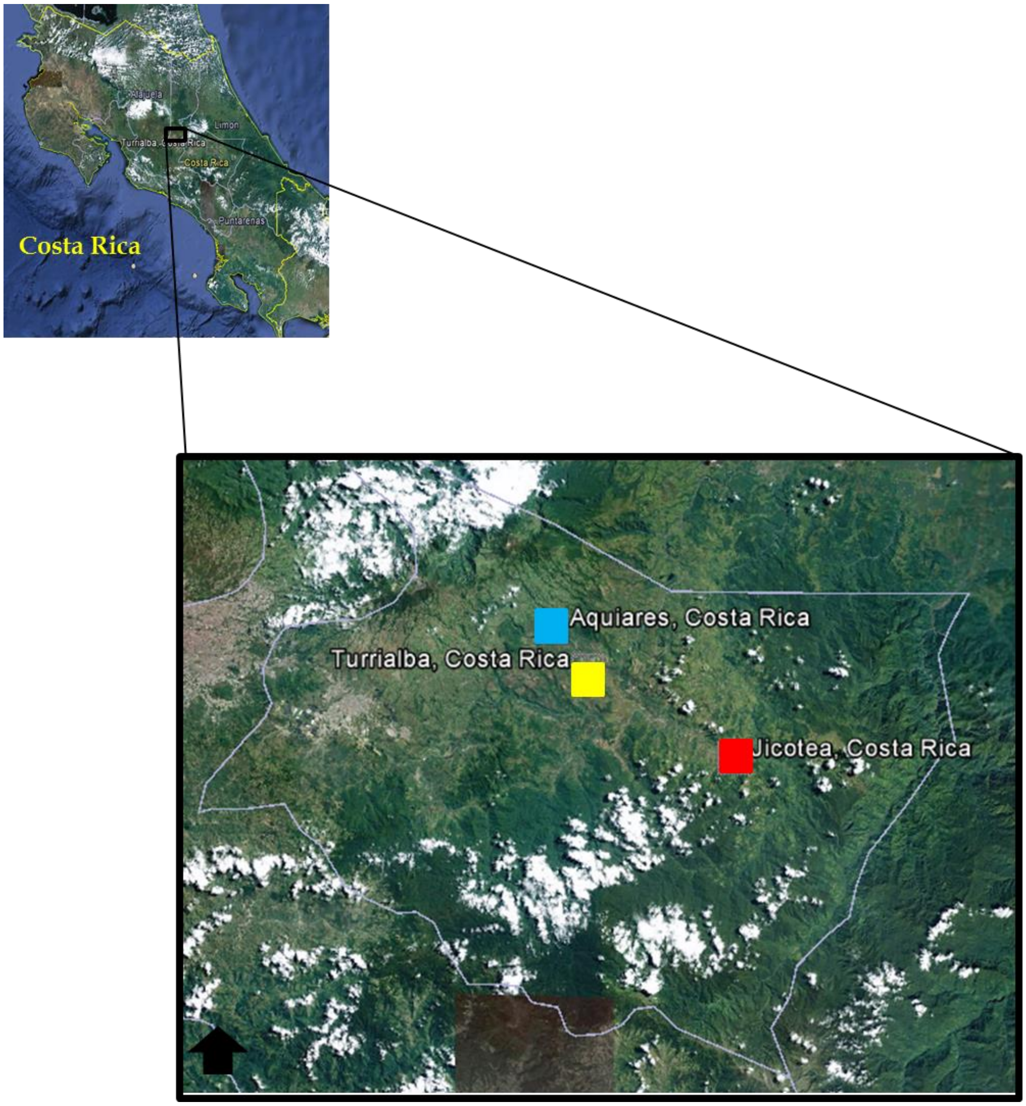

Table 2.1 - Abundance and percent of individual mammals (recaptures removed) trapped in small and medium-size mammal traps by site in 2011-2012 mammal study in coffee-forest landscapes in central Costa Rica. Each site was surveyed for a total of 46 nights.

	Abundance per site				Percent of species captured per site			
Species	**Total**	**Site 1**	**Site 2**	**Site 3**	**Total**	**Site 1**	**Site 2**	**Site 3**
Melanomys caliginosus	233	36	138	59	39.0%	52.2%	68.0%	18.2%
Handleyomys alfaroi	182	10	10	162	30.5%	14.5%	4.9%	49.8%
Peromyscus mexicanus	49	0	2	47	8.2%	0.0%	1.0%	14.5%
Oligoryzomys sp.	37	15	6	16	6.2%	21.7%	3.0%	4.9%
Heteromys desmarestianus	35	1	34	0	5.9%	1.4%	16.7%	0.0%
Marmosa robinsoni	30	0	0	30	5.0%	0.0%	0.0%	9.2%
Didelphis marsupialis	10	4	4	2	1.7%	5.8%	2.0%	0.6%
Unidentified rodents*	6	1	1	4	1.0%	1.4%	0.5%	1.2%
Rattus rattus	5	1	4	0	0.8%	1.4%	2.0%	0.0%
Philander opossum	3	0	0	3	0.5%	0.0%	0.0%	0.9%
Marmosa mexicanus	4	0	4	0	0.7%	0.0%	2.0%	0.0%
Sigmodon hispidus	2	1	0	1	0.3%	1.4%	0.0%	0.3%
Mus musculus	1	0	0	1	0.2%	0.0%	0.0%	0.3%
Total	597	69	203	325	100%			

*Five of the six unidentified rodents escaped before could be identified, but one at Site 3 appeared to be different than the other species captured for the study

Table 2.2 – Mammal species richness per habitat type detected by both small and medium-size mammal traps and camera traps for 2011-2012 mammal survey in three coffee-forest landscapes of central Costa Rica. The numbers in the habitat type columns indicate the site where species was detected and the X's indicate presence per site.

Species	Forest	Shade coffee	Sun coffee	Pasture	Tall grass	Sugar cane	Pine forest	Site 1	Site 2	Site 3
Dasypus novemcinctus [a]	2	3							X	X
Didelphis marsupialis	1,3	1,3	1,2,3	2		2		X	X	X
Handleyomys alfaroi	1,2,3	1,2,3	1,3	2				X	X	X
Heteromys desmarestianus	1,2	2		2		2		X	X	
Marmosa mexicanus	3	3								X
Marmosa robinsoni	3	3	3							X
Melanomys caliginosus	1,2,3	2,3	1,2,3	2	1,2	2	2	X	X	X
Mus musculus		3								X
Oligoryzomys sp.	1,3	1,3	1,3	1,2	1	2	2	X	X	X
Peromyscus mexicanus	2,3	2,3	3						X	X
Philander opossum	2	2				2			X	
Procyon lotor [a]	3	3								X
Rattus rattus	1			2		2	2	X	X	
Sigmodon hispidus	3			1				X		X
Sylvilagus sp.[a]		3								X
Unidentified rodent[b]	3									X
Total Species Richness	**14**	**13**	**6**	**7**	**2**	**6**	**3**	**7**	**9**	**13**
Percent of Traps per Habitat for All Sites Combined[c]	**37%**	**22%**	**17%**	**8%**	**3%**	**7%**	**4%**			

[a] Detected only by camera traps

[b] Five of the six unidentified rodents escaped before could be identified, but one at Site 3 appeared to be different than the other species captured for the study

[c] Remaining 2% of traps were located in tree plantation habitat of Site 1 where there were no captures

Table 2.3 – Median of vegetation measurements within habitat types of forest, shade coffee, and sun coffee for all three sites combined in 2011-2012 mammal study in coffee-forest landscapes of central Costa Rica.

Vegetation measured	**Forest**	**Shade coffee**	**Sun coffee**
Canopy cover (%)	98.9a	46.4b	5.2c
Basal area of trees (m^2/ha)	9.2a	2.3b	1.2c
Tree diameter (cm)	16.8a	17.2a	10.7b
High vegetation cover (%)	23.5a	51.0b	59.0b
Low vegetation cover (%)	15.0a	0.0b	0.0b
Herbaceous ground cover (%)	20.0	15.0	15.0
Coffee height (m)	NA	2.0	2.0

* Letters indicate significant difference between habitat categories (same letter indicates no difference) per Kruskal-Wallis-based post hoc test of multiple comparisons

Table 2.4 – Summary of Poisson regression model results with mammal abundance and richness as the dependent variables and measured habitat characteristics as independent variables[a] for 2011-2012 mammal survey in three coffee-forest landscapes of central Costa Rica.

	Abundance	Richness
1 - Models with vegetation measurements and habitat type designations (forest, shade coffee, sun coffee, other)		
All Sites Together	habitat, season[b], site	habitat, season, site, herb
Site 1	basal, (-)[c]ccover, (-)forest	(-)ccover, (-)forest
Site 2	habitat, season	habitat, low, season
Site 3	habitat	habitat
2 - Models with vegetation measurements only (no habitat designations)		
All Sites Together	ccover, season, site	ccover, season, site, herb
Site 1	basal, (-)ccover, (-)forest	(-)ccover, (-)forest
Site 2	ccover, season	ccover, low, season
Site 3	ccover	ccover, herb
3 - Coffee only: Models with vegetation measurements and habitat type (sun coffee, shade coffee)		
	habitat, low, coffeeht, site	habitat, coffeeht, site
4 - Coffee only: Models with vegetation measurements only (no habitat designations)		
	ccover, low, coffeeht, site	ccover, coffeeht, site

[a] Habitat=habitat type; season=wet or dry season; basal=shade tree basal area; ccover=% canopy cover; herb=% herbaceous ground cover; forest=distance to forest; low=% low vegetation cover; coffeeht=coffee height

[b] In models that include season, the dry season had significantly higher abundance and species richness than the wet season

[c] (-) Indicates a negative association

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CHAPTER 3

Habitat Use and Preference of Five Small Mammal Species in Coffee-Forest Landscapes of Costa Rica

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The fate of many tropical wildlife species depends largely on the way in which agricultural landscapes are managed. Coffee agroforestry has shown promise to provide wildlife habitat within these human-managed landscapes, however few have researched the habitat potential for non-volant mammals. In this study, we analyzed the habitat use and preference of 5 focal small mammal species within 3 coffee-forest agricultural landscapes in Costa Rica. Each of the 3 sites contained a mix of forest, shade coffee, and sun coffee; and in 2 of the sites a mix of other agricultural land uses was present. Each 0.25-ha site was set with a 500- x 500-m trap grid and sampled in 4 sessions, totaling 46 sampling nights per site. We calculated preference indices for each habitat based on the abundance of the species in each habitat type compared to the habitat availability. We found that small mammals occupied a variety of agricultural habitats. All 5 of the focal species preferred forest habitats to coffee habitats, except one that preferred forest and shade coffee equally. Three species preferred shade coffee to sun coffee (although for one of the species the trend appeared strong, but not statistically significant) and 2 species preferred shade and sun coffee equally. These finding suggests that although small mammals may be present in coffee habitats, most do not use shade coffee exclusively and may rely on forest habitat for survival. Small mammals may require forest tracts surrounding or intersecting coffee agriculture in addition to shade trees within the coffee plot. These habitat requirements need to be taken into account when devising conservation strategies for the promotion of biodiversity and sustainable agriculture.

Key words: coffee agroforestry, Costa Rica, habitat preference, habitat use, landscape, small mammals

Human-managed landscapes constitute approximately 90% of the terrestrial area of the world (Western and Pearl 1990). The way in which these landscapes are managed determines the fate of the wildlife species that depend on these lands for survival. Preserving native forest is one management strategy; however, this alone is not sufficient for wildlife conservation as forest reserves are often small, isolated, and expense to manage (DeClerck et al. 2010; Dietsch et al. 2004; Perfecto and Vandermeer 2008). Conservation strategies that incorporate agricultural landscapes are imperative for the survival of native fauna, particularly in tropical regions with fragmented landscapes (Perfecto and Vandermeer 2008). Agroforestry, the intentional management of shade trees within agricultural crops (Bhagwat et al. 2008), has shown promise to provide wildlife habitat and high-quality matrix within these human-managed landscapes (Harvey and Villalobos 2007; Schroth and Harvey 2007).

Coffee is the world’s most valuable tropical cash crop (International Coffee Organization 2012) and the second most important commodity in legal international trade after oil (O’Brien and Kinnaird 2003, Taylor 2007). It is grown in tropical regions of the world that are often designated as biodiversity hotspots (Cannavo et al. 2011). Over 10 million hectares of land have been converted to coffee production in over 50 countries worldwide (Hergoualc’h et al. 2012). As a result, coffee has the potential to greatly impact biodiversity, both negatively and positively.

The coffee producing country of Costa Rica had one of the highest rates of deforestation worldwide. Since the 1970s, however, there has been a national effort to conserve biodiversity with a network of national parks and biological reserves (Sánchez-Azofeifa et al. 2003). A recent assessment of Costa Rica's natural areas found that, while deforestation was negligible within the conservation areas and immediate buffer areas, significant clearing has taken place in larger buffer zones, thereby threatening to isolate forest habitats within the landscape (Sánchez-Azofeifa et al. 2003). Incorporating sustainable agriculture, such as coffee agroforestry, adjacent to forest buffer boundaries could provide wildlife habitat and connectivity among forested areas. Coffee agroforestry also has great promise to significantly contribute to the so-called "green infrastructure" of the landscape (Ahern 1995; Benedict and MacMahon 2006) by providing links among hubs of biodiversity.

Traditionally, coffee is grown under a diverse shade canopy, which provides wildlife habitat, fosters ecosystem services, and protects biodiversity (DeClerck et al. 2010; Moguel and Toledo 1999). Over the past 4 decades, there has been a trend to move away from traditional coffee towards a monoculture of coffee plants or "sun coffee" aimed at higher yields (Perfecto et al. 2005) which, in addition to depleting the system of floristic complexity, requires higher levels of chemical inputs to replace the ecosystem services lost (Rice 1999). The added floristic complexity of coffee agroforestry, or shade coffee, also has been shown to provide refuge for biodiversity. The research for coffee agroforestry as habitat has been dominated by avian and insect studies (e.g. Gordon et al. 2007; Perfecto et al. 2003; Philpott et al. 2008) with few studies conducted on the habitat potential of coffee agroforestry for non-volant mammal communities (e.g. Caudill et al. 2011; Daily et al. 2003; Gallina et al. 1996).

Small mammals play an important role in tropical ecosystems. In addition to being insectivores and seed dispersers, they constitute a large prey base for predatory mammals, birds, and reptiles. Alterations of small mammal communities can have a large influence on the ecosystem and higher trophic levels that small mammals support (Klinger 2006; Lambert et al. 2006). Habitat use and selection provides valuable knowledge into the structure of small mammal communities, resource use by different species, and knowledge of how communities coexist within an agricultural matrix (Holbrook 1979; Lambert et al. 2006; Poindexter et al. 2012). This information is vital to developing management guidelines for conservation strategies.

We analyzed the habitat use and preference of 5 focal species within 3 coffee-forest agricultural landscapes in Costa Rica: dusky rice rat (*Melanomys caliginosus*), Alfaro's rice rat (*Handleyomys alfaroi*), Robinson's mouse opossum (*Marmosa robinsoni*), Mexican deer mouse (*Peromyscus mexicanus*), and forest spiny pocket mouse (*Heteromys desmarestianus*). The specific objectives of our study were to: (1) Assess the habitat use and preference of each focal species within a coffee-forest agricultural mosaic; (2) Quantify the habitat parameters associated with each focal species; and (3) Provide suggestions on ways to maximize the benefit of coffee agroforestry for small mammals.

MATERIALS AND METHODS

Our 7-month small mammal survey took place in the Turriabla area of Costa Rica (9°54'04" N and 83°41'04" W) located in the state of Cartago (Fig.3.1). Turriabla is predominantly an agricultural region with coffee, sugar cane, and pastures interspersed with tracts of native forests. Three 25-hectare study sites were selected that contained coffee plots surrounded or intersected by forest tracts and were not in close proximity to residential areas to the best extent possible. Sampling grids were arranged to maximize the area of coffee and forest habitats within each site.

Mammal survey.–A 500- x 500-m (25-ha) sampling grid was set up at each site with two Sherman traps for small mammals placed at 50-m intervals. One trap was placed on the ground and the other secured to low-lying branches or lianas where available. We conducted mammal surveys from August 2011 through February 2012. Each site was sampled 4 times during the study, once at the end of the dry season (August 2011 to mid-September 2011), twice in the wet season (end of September 2011 to January 2012), and once at the beginning of the dry season (mid-January 2012 through February 2012). We surveyed the sites sequentially as Site 1, Site 2, and then Site 3. The first session was 9 nights in duration per site, the second and third sessions were both 13 nights per site, and the last session was 11 nights per site, totaling 46 nights per site or 138 nights for the study. After adjusting for theft of traps, our sampling effort for the entire study yielded a total of 42,306 trap nights.

Mark-recapture trapping was used to sample the small mammal community. Traps were baited as needed with a mix of peanut butter, bananas, vanilla, oats, seeds, and dry dog food and checked each morning. Small mammals were released at the point of capture after determining the species, taking standard morphologic measurements, and ear tagging each individual with a unique identification number. All research was conducted in accordance to American Society of Mammalogists guidelines (Sikes et al. 2011) and was approved by the University of Rhode Island's Animal Care and Use Committee. We followed Reid (2009) for identifications in the field. The five focal species selected for this analysis were found in abundances higher than 10 individuals at a site.

Study sites.–The primary purpose of the study was to compare forest, sun, and shade coffee habitats; however other agricultural habitats such as pasture, sugar cane, and tall grasses were included in Sites 1 and 2. A map depicting the habitat types for each site is included as Fig. 3.2.

Shade coffee was defined as coffee plantations with at least 20% canopy cover and sun coffee less than 20%. Tall grasses were characterized as grass species with a height of approximately 1.5 to 2.5 m and little to no herbaceous cover or shade trees. Pasture habitats typically had full herbaceous layer cover and sparsely planted trees. Sugar cane (*Saccharum* spp.) plots were a monoculture of tall sugar cane (1.5 to 2.5 m height) with little to no herbaceous cover and no shade trees and pasture-banana habitats were defined as lands with high amounts of herbaceous ground cover interspersed with banana trees.

Site 1 was located in Turriabla (9°48'50" N and 83°32'44" W) with an average elevation of 644 m. The site contained a mixture of agricultural habitats. The sampling grid configuration resulted in 63.6% of trap stations in forest, 12.7% in shade coffee, 6.8% in sun coffee, 7.6% in tall grasses, 7.6% in tree plantations, part of which was Klinki pine (*Araucaria hunsteinii*), and 1.7% in pasture. We added sun coffee points to the north of the original grid configuration (Fig. 3.2).

Site 2, located in a neighboring community of Jicotea southeast of Turriabla (9°52’49” N and 83° 39’52” W), had an average elevation of 965 m. This site had a mosaic of habitat types with 25.0% of traps located in forest, 9.2% in shade coffee, 9.2% in sun coffee, 20.0% in sugar cane, 16.7% in pasture, 12.5% in pine groves, 5.0% in pasture-banana, and 2.5% in tall grasses (Fig. 3.2).

Site 3 was located within a 673-ha coffee farm certified by Rainforest Alliance in the community of Aquiares, north of Turriabla (9°56’03” N and 83° 42’59” W). The average elevation was 969 m. The property is predominately coffee with a tract of forest running through the middle and riverine forest bordering the coffee to the south. The forest contained 21.9% of the traps, shade coffee had 42.9%, and sun coffee contained 35.3% of the traps (Fig. 3.2).

Habitat characteristics.–We quantified vegetation characteristics at each trap station to assess possible habitat parameters associated with the abundance of each focal species. We measured the percent canopy cover with a convex spherical densiometer. Ten-meter line intercepts at each trap station were recorded at 3 levels to categorize the percent of high shrub and herbaceous vegetation (≥1 m), low shrub and herbaceous vegetation (5 cm to <1 m), and herbaceous ground cover (<5 cm). Basal area of surrounding shade trees was recorded using a 10-factor wedge prism. We measured the diameter at breast height of the tree closest to the grid point. Spatial location, elevation, and habitat type were recorded for each grid point.

Data Analysis.–A data set was created for each focal species per site where its abundance was greater than 10 individuals. The 7 data sets were as follows:

M. caliginosus for Site 1, 2, and 3; *H. desmarestianus* for Site 2; *Handleyomys alfaroi* for Site 3; *M. robinsoni* for Site 3; and *P. mexicanus* for Site 3. All means given in the results are accompanied by one standard error.

We examined habitat use and preference using 2 scales: microhabitat and neighborhood analysis. For the microhabitat scale, we determined the habitat type based solely on the habitat parameters in which the trap was located. For the neighborhood analysis, we created Thiessen polygons around each of the trap stations using Geographic Information Systems (GIS). Land use maps were created for each site based on data recorded in the field and Google Earth imagery. A 25-m buffer was created around the outside boundary of the outermost traps. We determined the acreages of each habitat type within the trap catchment area (Thiessen polygon), which measured approximately 0.25 ha. Site 1 had a total of 6 habitat types: 18.26 ha of forest, 3.95 ha of shade coffee, 2.32 ha of sun coffee, 0.53 ha of pasture, 2.05 ha of tall grass, and 2.39 ha of tree plantation. Site 2 had a total of 8 habitat types: 7.89 ha of forest, 2.84 ha of shade coffee, 1.51 ha of sun coffee, 4.98 ha of pasture, 0.40 ha of tall grass, 1.31 ha of pasture with banana, 3.63 ha of pine grove, and 6.83 ha of sugar cane. Site 3 contained only 3 habitat types: 6.57 ha of forest, 12.50 ha of shade coffee, and 9.79 ha of sun coffee. These areas include the 25-m buffer around the trap grid.

Habitat preference was assessed as the number of individuals per species that occupied each habitat type. For the neighborhood analysis, if there was more than one habitat type within the catchment area, the number of individuals captured was weighted by the proportion of area per habitat type within the catchment area. The preference index was calculated as the percent of use of each habitat type divided by the percent of availability of each habitat type per site (Krebs 1999). This ratio gave an indication of habitat preference for each focal species per site and allowed us to rank each species' habitat preferences. A preference index of greater than one indicates a preferred habitat, as the use of the habitat type is greater than its availability on site. Habitat availability for the microhabitat analysis was calculated as the percent of trap stations per habitat type out of the total number of trap stations and for the neighborhood analysis as the percent of each habitat type out of the total site area. A chi-squared test (Manly et al. 1993) was used to determine if there were significant differences in preference for the habitat types for each focal species. For multiple comparisons, the significance level is adjusted using the Bonferroni correction where the significance level is divided by the number of comparisons to maintain overall error rate (Krebs 1999). It is assumed the entire site is available to each species. This assumption is confirmed for this study as each of the focal species was captured throughout each of the sites where they were present.

The grid configuration allowed us to track movements for individuals in each of these 5 focal species, as each was marked with a unique identification number. These data are included to demonstrate the way in which the small mammals used this agricultural mosaic, in addition to which habitat types were preferred.

We used Poisson loglinear regression to determine the association of the measured habitat characteristics with the abundance of each focal species per trap station per site for the study period. Over or under dispersion in the data was adjusted by scaling for deviance. The following 6 vegetation characteristics measured at each trap station were modeled as independent continuous variables: % canopy cover, %

high vegetation cover, % low vegetation cover, % herbaceous ground cover, tree basal area (m^2/ha), and tree diameter (cm). Variance inflation factors for each independent variable were examined, but there was no evidence of multicollinearity. All data were offset by sampling effort to account for unequal numbers of traps per habitat type and trap theft. We used SAS Statistical Software version 9.3 (SAS Institute 2010) for all statistical modeling.

RESULTS

Melanomys caliginosus.–We captured 440 *M. caliginosus* (233 of those were individuals) in all 3 sites for the study period. Of those, 15.4% were found at Site 1, 59.2% at Site 2, and 25.3% at Site 3. *M. caliginosus* was captured at the full range of elevations for all 3 sites, from 626 to 1010 m. If an individual was captured in more than one trap location, 64.9% of the time it was within the same habitat type. The average distance traveled of those captured in more than one trap was 104 ± 15 m, although we recorded one adult male that traveled 682 m in 9 days through tall grass and forest at Site 1; and a juvenile female that traveled a distance of 438 m in 8 days through pasture, coffee, and sugar cane at Site 2.

Overall, we found that *M. caliginosus* preferred tall grasses, forest, pastures with banana trees, and pine groves (Table 3.1 and 3.2). For Site 1, *M. caliginosus* was the dominant species making up 52.2% of all small mammals captured. Tall grass was the most preferred habitat for *M. caliginosus* at Site 1. In the microhabitat analysis, tall grass was significantly preferred over forest (χ_1^2=17.11, p<0.001) and forest was significantly preferred over all the other habitat types, which had preference indices of zero (χ_1^2=56.57, p<0.001). In the neighborhood analysis, tall grass again was preferred significantly over forest (χ_1^2=10.71, p<0.001), and although there was a significant difference between the preference for forest and shade coffee (χ_1^2=9.46, p=0.002), there was not a difference between forest and sun coffee (χ_1^2=2.91, p=0.088, as compared to Bonferroni's adjusted α=0.007 for multiple comparisons for this site). The increase in the preference index of sun coffee in the neighborhood analysis compared to the microhabitat analysis indicates that although there were no captures of *M. caliginosus* in sun coffee at Site 1, sun coffee was included in the catchment areas where this species was trapped (Table 3.3).

Out of all small mammals captured at Site 2, 68.0% were *M. caliginosus*. This species was captured in all 8 habitat types at this site and showed a preference for tall grasses, forest, pastures with banana trees, and pine groves in both the neighborhood and microhabitat analyses (Table 3.1 and 3.2). Although tall grasses were shown to be preferred over other habitats by a margin of at least 2 to 1 from the microhabitat analysis (Table 3.3), the neighborhood analysis revealed that there was no significant difference between the preference for tall grass and forest, pasture-banana, or pine groves (tall grass vs. forest: χ_1^2=3.66, p=0.056; tall grass vs. pasture-banana: χ_1^2=2.89, p=0.069; tall grass vs. pine: χ_1^2=4.16, p=0.041, compared to α=0.003 for multiple comparisons at this site). Forest was significantly preferred over both shade and sun coffee for the microhabitat analysis (forest vs. shade: χ_1^2=48.02, p<0.001; forest vs. sun: χ_1^2=73.91, p<0.001), but there was no difference between shade and sun coffee habitats in terms of preference (χ_1^2=1.03, p=0.311). For the neighborhood analysis, as well, forest was preferred over both coffee habitats (forest vs. shade: χ_1^2=15.61, p<0.001; forest vs. sun: χ_1^2=53.82, p<0.001) and although shade coffee had a higher preference ranking than sun coffee, the preference for the 2 habitats was not shown to be significantly different (χ_1^2=4.57, *p*=0.033 compared to α=0.003 for multiple comparisons at this site).

In Site 3, *M. caliginosus* mainly used forest habitats and occasionally shade and sun coffee habitats. From the neighborhood analysis, forest habitats were shown to be preferred over shade and sun coffee (forest vs. shade: χ_1^2=38.98, *p*<0.001; forest vs. sun: χ_1^2=46.31, *p*<0.001), and shade coffee was preferred over sun coffee at this site (χ_1^2=18.49, *p*<0.001) (Table 3.1). The micro level habitat analysis confirmed that *M. caliginosus* preferred forest to coffee habitats (forest vs. shade: χ_1^2=358.15, *p*<0.001; forest vs. sun: χ_1^2=371.71, *p*<0.001), but it showed no difference in preference between sun and shade coffee (χ_1^2=0.14, *p*=0.711) (Table 3.2). The difference in the preferences between the 2 scales for shade and sun coffee at this site indicates that although *M. caliginosus* was not often trapped in shade coffee, the catchment area around the traps where this species was trapped included higher amounts of shade coffee than sun coffee (Table 3.3).

Handleyomys alfaroi.–We captured *H. alfaroi* at all three sites with a total of 398 captures (182 individuals) from elevations ranging from 630 to 1018 m. Approximately 89% of all individuals were found at Site 3 with fewer than 10 individuals at Sites 1 and 2; therefore only data for Site 3 were used for this analysis. *H. alfaroi* showed a preference for both forest and shade coffee habitats in both the microhabitat and neighborhood analysis (Table 3.1 and 3.2). Although there was no significant difference between these 2 habitats in the neighborhood analysis (χ_1^2=0.17, *p*=0.684), in the microhabitat analysis forest was preferred over shade coffee

(χ_1^2=10.69, p=0.001). This indicates that although *H. alfaroi* was most often caught in traps within the forest, many of the catchment areas also contained shade coffee (Table 3.3). Shade coffee was significantly preferred over sun coffee for this species in both the microhabitat (χ_1^2=202.06, p<0.001) and neighborhood analysis (χ_1^2=205.13, p<0.001). This was the only focal species that showed a strong preference for shade coffee in both the microhabitat and neighborhood analysis.

Individuals found in more than one trap station were trapped within the same habitat type approximately 66% of the time. We recorded one juvenile female that traveled 630 m in 2 days within forest and shade coffee habitats, but the average distance traveled for those individuals captured in more than one location as 85 ± 9 m.

Marmosa robinsoni.–We found *M. robinsoni* to occupy the full elevation range of Site 3, from 914 to 1018 m. We captured 72 *M. robinsoni*, 30 of those individuals, only at Site 3. For those found in more than one trap station, 92% of the time it was within the same habitat type. The average amount traveled of those found in more than one location was 92 ± 11 m. One adult male, captured 12 times, routinely traveled 50 m in one day between trap locations within forested habitats and on one occasion traveled 100 m in one day. A lactating female was captured in shade coffee then 2 days later at a forest point 368 m away.

Forest habitats were shown to be preferred in both the neighborhood and micro level habitat analysis, although both coffee habitat types were used regularly by this species (Table 3.1 and 3.2). The microhabitat analyses indicated that *M. robinsoni* significantly preferred forest habitats over both shade and sun coffee habitats (microhabitat analysis forest vs. shade: χ_1^2=14.34, p<0.001; forest vs. sun: χ_1^2=9.44, *p*=0.002). While the preference index was higher for forest than sun coffee, there was not a significant difference between these 2 habitats in neighborhood analysis (χ_1^2=3.47, *p*=0.063), indicating that *M. robinsoni* was captured in traps where sun coffee habitats were present within the catchment areas (Table 3.3). We found that there was no difference in preference between shade and sun coffee (microhabitat analysis χ_1^2=1.80, *p*=0.179; neighborhood analysis χ_1^2=0.80, *p*=0.372).

Peromyscus mexicanus.–*P. mexicanus* was captured 183 times at Site 3, 47 of those were individuals, yielding at high recapture rate of 75%. We also captured 2 individuals at Site 2, but these data were not included in the analysis. We captured *P. mexicanus* throughout Site 3 from elevations of 914 to 1018 m. For individuals captured in more than one trap location, 95% of the time they were captured within the same habitat type and the average amount traveled was 115 ± 29 m. We recorded an adult female that traveled 486 m in 4 days within shade coffee and another traveled 412 m in 9 days in forest and shade coffee habitats.

We found *P. mexicanus* preferred forest habitats significantly more than shade coffee (microhabitat χ_1^2=48.67, *p*<0.001; neighborhood χ_1^2=74.90, *p*<0.001), and preferred shade coffee significantly more than sun coffee (microhabitat χ_1^2=12.11, *p*<0.001; neighborhood χ_1^2=18.84, *p*<0.001) for both the neighborhood and microhabitat analyses (Table 3.1 and 3.2). *P. mexicanus* was captured approximately 3 times more in forest than in shade coffee, which in turn had approximately 4.5 times more captures than sun coffee (Table 3.3). Additionally, we noted that 2 of the 3 sun coffee points where *P. mexicanus* was trapped were close to or under the sparse shade trees within that area.

Heteromys desmarestianus.–We found *H. desmarestianus* at Sites 1 and 2 from elevations of 653 to 1072 m. Sixty-six captures of this species of 34 individuals occurred at Site 2 and only one individual was captured at Site 1; therefore, this analysis is based on Site 2 only. Only 2 of the 35 individuals were found at different trap points; one traveled 69 m in 2 days and the other, a lactating female, traveled 50 m in one day.

The ranking of the habitat preference indices from the neighborhood and microhabitat analysis differed for this species. The neighborhood analysis indicated that *H. desmarestianus* had a preference for both forest and pasture with banana habitats, with no difference in preference between the 2 habitats (χ_1^2=0.36, p=0.550) which were both significantly higher than shade coffee, sugar cane, pasture, and sun coffee for which there was no significant preference difference (Table 3.1). While the microhabitat analysis indicated that forest was the most preferred, followed by shade coffee and then pasture-banana, the latter 2 had approximately equal preference values (Table 3.2). For both analyses, forest habitats were significantly preferred over shade coffee (microhabitat χ_1^2=12.71, p<0.001; neighborhood χ_1^2=9.29, p<0.001) and sun coffee (microhabitat χ_1^2=93.6, p<0.001; neighborhood χ_1^2=16.12, p<0.001), but there was no significant difference between the preference of shade or sun coffee habitats (microhabitat χ_1^2=4.5, p=0.034; neighborhood χ_1^2=0.67, p=0.412, compared to α=0.006 for multiple comparisons for this site) for *H. desmarestianus*.

Habitat Characteristics.–In general, the focal species were found in habitats where the vegetation cover was at least the same or higher than the average for the site (Table 3.4). For Site 1, high vegetation, herbaceous, canopy cover, and tree diameter were higher than average for the site where *M. caliginosus* was found, although the basal area was much lower. At Site 2, both focal species were found in habitats with higher than average amounts of low vegetation cover, canopy cover, basal area, and tree diameter for the site. All 4 focal species at Site 3 were present where the low vegetation cover, canopy cover, and basal area were higher than the site average.

From the Poisson regression analysis, we found that at Site 1, the only vegetation parameter found to be associated with abundance of *M. caliginosus* was an increase in high vegetation cover ($\chi_1^2=6.04$, $p=0.014$) which could be indicative of this species' preference for tall grass. Increased canopy coverage was associated with the abundance of *M. caliginosus* for Site 2 ($\chi_1^2=4.83$, $p=0.028$), while at Site 3 increased amounts of herbaceous ground cover ($\chi_1^2=10.80$, $p=0.001$), low vegetation cover ($\chi_1^2=34.17$, $p<0.001$), and canopy cover ($\chi_1^2=13.81$, $p<0.001$) were found to be significant for the abundance of this species.

At Site 2, the abundance of *H. desmarestianus* was associated with increases in canopy cover ($\chi_1^2=39.91$, $p<0.001$) and decreases in herbaceous ground cover ($\chi_1^2=10.82$, $p=0.001$). These vegetation characteristics may describe generally the forested habitat on this site for which it showed a preference.

For Site 3, increased amount of canopy cover was positively associated with *H. alfaroi* abundance ($\chi_1^2=28.24$, $p<0.001$). This result correlates with the preference analysis that *H. alfaroi* preferred forest and shade coffee habitats, but avoided coffee habitats with low amounts of canopy cover. The vegetation variable significantly related to abundance of *M. robinsoni* was an increase in canopy cover ($\chi_1^2=5.75$, $p=0.017$), which reflects its preference for forest habitats; although the preference index for both shade and sun coffee was relatively high. An increase in basal area (χ_1^2=16.58, p<0.001) was found to be related to the abundance of *P. mexicanus*, which could correspond to forested habitats on Site 3. Canopy cover was not shown to be significantly related to the abundance of *P. mexicanus*, although the average percent of canopy cover where this species was present is higher than the average for the site (Table 3.4).

DISCUSSION

The small mammals in our study occupied a variety of agricultural habitats. We found that all 5 of the focal species preferred forest habitats to coffee habitats, except one that preferred forest and shade coffee equally. Three species preferred shade coffee to sun coffee (although for *H. desmarestianus* the preference difference was not statistically significant) and 2 species preferred shade and sun coffee equally.

Reid (2009) reported *H. alfaroi* to be found in and near forests, and near streams or fallen logs. She also noted that this species was uncommon, however, *H. alfaroi* was the most abundant species found in our study, although predominately at Site 3. It was the only species that we found to favor shade coffee equally to forested habitats.

Out of the 5 focal species in this study, *M. robinsoni* was the only species to use sun coffee in nearly the same proportion as the habitat was available. *M. robinsoni* is arboreal in addition to terrestrial and likely used branches in the dense rows of coffee plants as pathways for locomotion. Other field studies have indicated that this species in found in a variety of habitats, but prefers secondary forest and disturbed farmlands to undisturbed areas (O’Connell 1983).

Tall grass habitat was the highest preferred habitat of *M. caliginosus* at both Sites 1 and 2 where tall grass was available. *M. caliginosus* occupied all 8 agricultural habitat types present at Site 2. This wide use of agricultural habitats is consistent with other studies where *M. caliginosus* was found to favor overgrown fields and brushy second growth (Reid 2009) and use a variety of agricultural and disturbed habitats (Gardner 1983). The neighborhood analysis showed that *M. caliginosus* in Site 3 favored shade coffee habitats to sun coffee, whereas in the other 2 sites, there was not a distinguishable preference between the 2 coffee habitats.

It has been reported that *H. desmarestianus* is a generalist in terms of habitat use and diet (Fleming 1983; Klinger 2006). This species has been found in forested areas and second growth and favors areas with abundant palms (Reid 2009). We found *H. desmarestianus* in this study to favor pastures with banana trees as well as forest. Although there was not a significant difference detected between *H. desmarestianus'* preference for shade or sun coffee, shade coffee was ranked second in terms of habitat preferences for the microhabitat analysis and third for the neighborhood analysis. In the shade coffee areas where it was trapped, banana trees shaded 3 of the 4 trap stations.

P. mexicanus is common and abundant within a variety of habitats including coffee farms (Reid 2009). We found this species to prefer forested areas to shade coffee, and shade coffee to sun coffee habitats. Coffee beans have been reported to be cached near *P. mexicanus'* borrows in Mexico (Reid 2009), although it is unclear if that is a consistent part of this species' diet.

We found increased amounts of canopy cover to significantly increase the abundance of 4 of the 5 focal species. *H. desmarestianus* abundance was significantly related to lower amounts of herbaceous ground cover which may be associated with the fact that this species burrows into the ground near trees or fallen logs. *M. caliginosus*, which do not burrow were found to have higher abundances with increased amounts of herbaceous ground and low vegetation cover at Site 3. Higher basal areas also were found to be positively related to *P. mexicanus* abundance, which corresponds with its preference for forest habitats. High vegetation cover indicative of tall grass habitats was found to be positively related to *M. caliginosus* at Site 1.

The trap grid configuration that we devised allowed us to better understand the habitat use of the small mammal community across this coffee-forest agricultural landscape. The microhabitat analysis took into account only the habitat type where the trap was located, while the neighborhood analysis included the habitat types within the surrounding 50- x 50-m area. The combination of the 2 scales provided a more comprehensive picture of how these species use a mosaicked agricultural landscape.

For most of the focal species, both the neighborhood and microhabitat analyses yielded similar results; although for *H. desmarestianus* in Site 2, the shade coffee had a much higher preference index in the microhabitat analysis than in the neighborhood analysis. The habitat availability was the same in both analyses. The percent as area of shade coffee on the site is approximately the same as the percent of the traps located in shade coffee for the site, 9% and 10% respectively. In a closer examination of the data, in the 4 shade coffee traps where *H. desmarestianus* was found, 2 were adjacent to forested areas, one was adjacent to pasture-banana habitat, and the fourth was adjacent to sun coffee. Therefore, this indicates that although *H. desmarestianus* was captured in traps in shade coffee, there were other habitats within the surrounding catchment area that it may have been exploiting or from which it emanated.

The results were influenced by the availability of each habitat type for both methods. Ideally, each site would have similar amounts of available habitat, although for a 25-ha site in an agricultural landscape, this is not often the case. If there were captures in habitats with low availability, this habitat may have registered a high preference ranking because the species is selecting that habitat, even though it is not widely available. For example, on Site 2 there were only three traps and 1.4% of the site acreage in tall grass habitats, however 12 *M. caliginosus* were captured in that habitat which seems to be strong evidence that the tall grass was a preferred habitat as the analysis indicated.

Similarly, the analyses showed that *H. desmarestianus* had a preference for pasture-banana habitats. There were 2 individuals for the study period captured in this habitat type, which comprised approximately 4 % of the area and 5% of the traps for Site 2, therefore the microhabitat results indicated a preference for this habitat. Both individuals were captured in one trap location in which the catchment area was predominately pasture-banana habitat, but also included portions of sugar cane. The neighborhood habitat analysis confirmed this preference for pasture-banana. Four of the other catchment areas where *H. desmarestianus* was found included pasture-banana habitat although the trap itself was not located there but within forest and shade coffee habitats. Using these 2 preference analysis methods in tandem allows us to have a greater understanding of how these species are using this agricultural landscape and provides a way to verify the accuracy of our findings.

Few studies have been conducted to determine the influence of coffee-forest landscapes on mammals and even fewer on mammals and varying degrees of shade tree cover and vegetation complexity within coffee habitats. Gallina et al. (1996) surveyed medium-sized mammals in coffee landscapes and found species richness to be related to vegetation diversity. They recommended high tree diversity within coffee farms to provide food and protection for the mammals. Husband et al. (2007, 2009) found that, although small mammal species were detected in shade and sun coffee, each represented a very different species composition.

Previous research on these 3 sites reveals that forest habitats have the highest abundance and species richness, followed by shade coffee, then sun coffee (Caudill et al. 2013). Shade coffee rivals forest habitats in terms of species richness with 14 and 13 species recorded, respectively, but sun coffee is much lower with only 6 species. These results indicate that while no substitute for native forest, shade coffee provides habitat value for some mammals, whereas sun coffee provides very little. The habitat preference and use for the 5 focal species in this study supported the previous findings. However, the current results reveal that, although small mammals may have been present in shade coffee habitats, it was not a highly preferred habitat for most of the species. More research is needed to understand if shade coffee alone can support this diverse community of small mammals or if shade coffee needs to be in close proximity to forest, as in these study sites, to support mammal communities.

There have been 2 studies that involve coffee habitats and distance to forest, although one took place in India where the difference in species richness and composition for small mammals may preclude us from making direct comparisons and the other studied coffee farms that would be considered sun coffee, or at least not coffee with structurally diverse shade canopy (Daily et al. 2003). In shade coffee farms in India, Caudill et al. (2013) reveal that abundance of small mammals significantly increases as distance to forest decreases, although there is no relationship between species richness and distance to forest. Daily et al. (2003) report a significant difference in species richness or composition in coffee farms sparsely shaded with banana trees close to or far from extensive forest (<1 km and ≥5 km, respectively) in Costa Rica. In both of these studies, proximity to forest did not significantly influence the species richness, although the richness is noted as being generally low within the coffee habitats. Rocha et al. (2011) indicate that forest corridors as narrow as 4 m provide habitat and support high species richness within a coffee-forest matrix in Brazil. The vegetation structure for the coffee matrix is not described in their work, but again it is assumed to be of low vegetation complexity, similar to the sun coffee in our study.

More research is needed to determine if coffee agroforestry can act as a refuge for mammalian wildlife on its own, or if shade coffee must be in close proximity to forested areas. Forest tracts surrounding or intersecting coffee agriculture may be required in addition to shade trees within the coffee plot for small mammal communities to survive in coffee-dominated landscapes. These habitat preferences and requirements should be included in conservation strategies for the promotion of biodiversity and sustainable agriculture and employed to inform management guidelines to the farmers to enhance mammalian habitat within coffee landscapes.

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FIGURES AND TABLES

FIG. 3.1. – Location map of the three study sites for 2011-2012 mammal survey in coffee-forest landscapes in Cartago, Costa Rica.

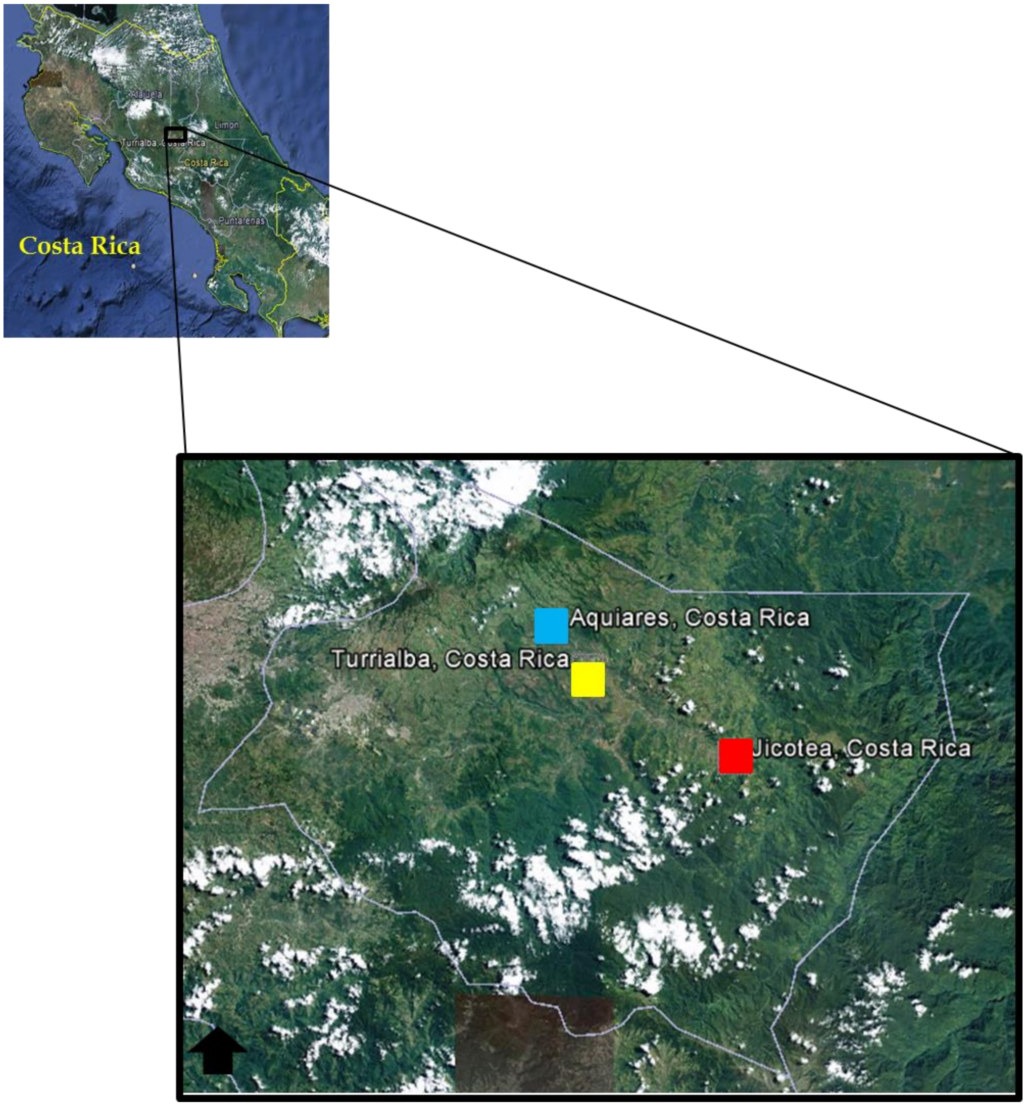

FIG. 3.2. – Habitat maps of 2011-2012 mammal study sites in three coffee-forest landscapes of Cartago, Costa Rica.

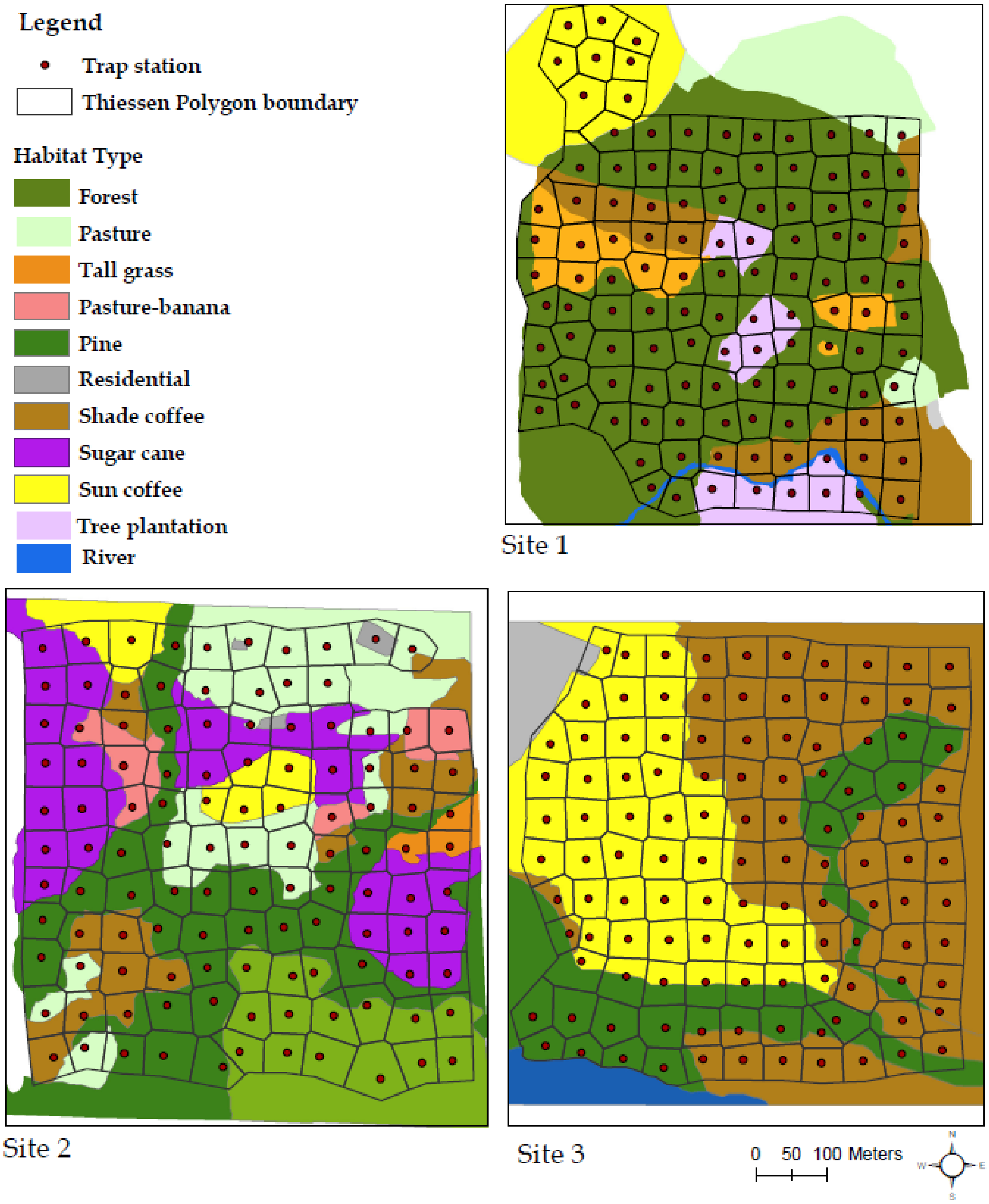

Table 3.1.–Habitat preference indices for neighborhood analysis (0.25-ha catchment area) for focal species in coffee-forest landscapes in Costa Rica. Indices were calculated as percent of use for each species divided by percent of habitat availability per site. Percent availability of each habitat type is listed per site.

	Habitat type								
Species	**Forest**	**Shade Coffee**	**Sun Coffee**	**Pasture**	**Tall Grass**	**Tree Plantation**	**Pasture-banana**	**Pine Groves**	**Sugar cane**
Site 1	**62%**	**13%**	**8%**	**2%**	**7%**	**8%**	**NA***	**NA**	**NA**
Melanomys caliginosus	1.00b	0.27c	0.39b,c	0.15c	4.24a	0.24c			
Site 2	**27%**	**10%**	**5%**	**17%**	**1%**	**NA**	**4%**	**12%**	**23%**
Melanomys caliginosus	1.51a,b	0.63a,c,d	0.13a,d	0.59a,c,d	3.14a		1.04a,b	1.30a,b	0.80a,c
Heteromys desmarestianus	2.22a	0.82b	0.32b	0.46b	0.00b		1.67a,b	0.00b	0.69b
Site 3	**23%**	**43%**	**34%**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Melanomys caliginosus	2.11a	0.97b	0.30c						
Handleyomys alfaroi	1.45a	1.41a	0.17b						
Marmosa robinsoni	1.53a	0.76b	0.95a,b						
Peromyscus mexicanus	2.47a	0.90b	0.16c						

* NA - Habitat type not available for that site and letters indicate significant difference in mean levels per chi-squared multiple comparison test across habitat types

Table 3.2.–Habitat preference indices for microhabitat analysis for focal species in coffee-forest landscapes in Costa Rica. Indices were calculated as percent of use for each species divided by percent of habitat availability per site. Percent availability of each habitat type is listed per site.

	Habitat type								
Species	**Forest**	**Shade Coffee**	**Sun Coffee**	**Pasture**	**Tall Grass**	**Tree Plantation**	**Pasture-banana**	**Pine Groves**	**Sugar cane**
Site 1	**64%**	**13%**	**7%**	**2%**	**8%**	**8%**	**NA***	**NA**	**NA**
Melanomys caliginosus	0.96b	0.00c	0.00c	0.00c	5.10a	0.00c			
Site 2	**25%**	**9%**	**9%**	**17%**	**3%**	**NA**	**5%**	**13%**	**20%**
Melanomys caliginosus	1.52a	0.21c,d	0.07d	0.83b	3.14a		1.44a	1.36a,b	0.69b,c
Heteromys desmarestianus	2.89a	1.21b	0.00b	0.33b	0.00b		1.11b	0.00b	0.28b
Site 3	**21%**	**43%**	**35%**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Melanomys caliginosus	3.69a	0.23b	0.27b						
Handleyomys alfaroi	1.69a	1.38b	0.12c						
Marmosa robinsoni	1.91a	0.62b	0.92b						
Peromyscus mexicanus	2.38a	0.89b	0.28c						

* NA - Habitat type not available for that site and letters indicate significant difference in mean levels per chi-squared multiple comparison test across habitat types

TABLE 3.3. –Proportion of focal species found within each habitat type per site in coffee-forest landscapes in Costa Rica for both microhabitat[a] and neighborhood[b] scales. Note that these values do not incorporate the habitat availability which varies per habitat type.

	Habitat type								
Species	Forest	Shade Coffee	Sun Coffee	Pasture	Tall Grass	Tree Plantation	Pasture-banana	Pine Groves	Sugar cane
Microhabitat Scale									
Site 1							**NA**[c]	**NA**	**NA**
Melanomys caliginosus	61%	0%	0%	0%	39%	0%			
Site 2						**NA**			
Melanomys caliginosus	38%	2%	1%	14%	8%		7%	17%	14%
Heteromys desmarestianus	72%	11%	0%	6%	0%		6%	0%	6%
Site 3				**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Melanomys caliginosus	81%	10%	10%						
Handleyomys alfaroi	37%	59%	4%						
Marmosa robinsoni	41%	26%	32%						
Peromyscus mexicanus	52%	38%	10%						
Neighborhood Scale									
Site 1							**NA**	**NA**	**NA**
Melanomys caliginosus	62%	4%	3%	0%	29%	2%			
Site 2						**NA**			
Melanomys caliginosus	40%	6%	1%	10%	4%		5%	16%	18%
Heteromys desmarestianus	59%	8%	2%	8%	0%		7%	0%	16%
Site 3				**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
Melanomys caliginosus	48%	42%	10%						
Handleyomys alfaroi	33%	61%	6%						
Marmosa robinsoni	35%	33%	32%						
Peromyscus mexicanus	56%	39%	5%						

[a] Percent of microhabitat use is calculated as number of individuals per species captured in traps within that habitat type out of total traps in site.

[b] Percent of neighborhood use is calculated as a number of individuals captured weighted by proportion of area per habitat type within catchment area out of total site area.

[c] NA- Habitat type not available for that site

Table 3.4. –Average values of vegetation characteristics for trap stations where focal species were present in coffee-forest landscapes in Costa Rica. Standard errors are in parenthesis.

	High Vegetation Cover (%)	**Low Vegetation Cover (%)**	**Herbaceous Ground Cover (%)**	**Canopy Cover (%)**	**Basal Area (m^2/ha)**	**Tree diameter (cm)**
Site 1						
Melanomys caliginosus	47.4 (8.3)	18.0 (6.1)	42.0 (8.9)	86.0 (4.4)	2.1 (0.3)	28.8 (5.5)
Total Site 1	**38.1 (3.1)**	**18.0 (2.5)**	**34.8 (3.4)**	**82.4 (2.6)**	**9.4 (0.7)**	**26.2 (2.0)**
Site 2						
Melanomys caliginosus	34.3 (5.2)	18.3 (3.6)	58.4 (4.9)	56.4 (4.9)	6.9 (0.9)	13.9 (1.6)
Heteromys desmarestianus	33.5 (6.7)	19.0 (4.5)	43.6 (8.6)	72.0 (6.5)	7.1 (1.4)	15.7 (3.6)
Total Site 2	**33.5 (3.4)**	**13.3 (1.9)**	**57.3 (3.4)**	**46.0 (3.4)**	**5.5 (0.5)**	**11.5 (1.1)**
Site 3						
Melanomys caliginosus	38.1 (7.6)	23.7 (6.3)	39.1 (7.0)	69.2 (7.2)	6.1 (1.5)	22.3 (4.6)
Handleyomys alfaroi	51.1 (3.9)	10.7 (2.3)	22.4 (2.9)	55.9 (4.4)	4.8 (0.7)	24.6 (3.2)
Marmosa robinsoni	57.3 (6.2)	9.7 (2.9)	22.3 (5.3)	52.9 (6.9)	4.9 (1.2)	23.8 (5.8)
Peromyscus mexicanus	48.9 (6.7)	13.5 (3.5)	19.0 (5.5)	66.1 (7.0)	6.6 (1.3)	21.3 (5.2)
Total Site 3	**55.4 (2.6)**	**9.4 (1.4)**	**22.5 (2.1)**	**45.0 (3.3)**	**4.0 (0.5)**	**26.6 (3.6)**

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APPENDICES

A. INTRODUCTION AND REVIEW OF THE PROBLEM

Agriculture and conservation are often viewed as opposing forces, competing for land use and management rights. While preserving tropical forests is a necessity for biological conservation, this must be coupled with other conservation strategies. Forest reserves are often isolated, expensive to manage, and on their own, not a practical or sustainable solution in many parts of the world (DeClerck et al. 2010, Perfecto and Vandermeer 2008). Recently conservation strategies have begun to focus on a broader, landscape approach (Perfecto and Vandermeer 2008) in which dynamics of land uses within a region are taken into account.

Agroforestry, defined as "intentional management of shade trees within agricultural crops" (Bhagwat et al. 2008), plays an important role in this landscape matrix as studies have shown that it has the potential to maximize biodiversity, minimize environmental degradation, and provide wildlife habitat and environmental services (Harvey and Villalobos 2007, Schroth and Harvey 2007). Agroforestry also supports local farmers and the economy through profits gained from agroforestry crops such as coffee and cacao, as well as, potential payments for the environmental services that are provided. Understanding the ecosystem dynamics within agroforestry landscape matrices would promote best management practices not only for local farmers, but also for those interested in conserving and improving wildlife habitat.

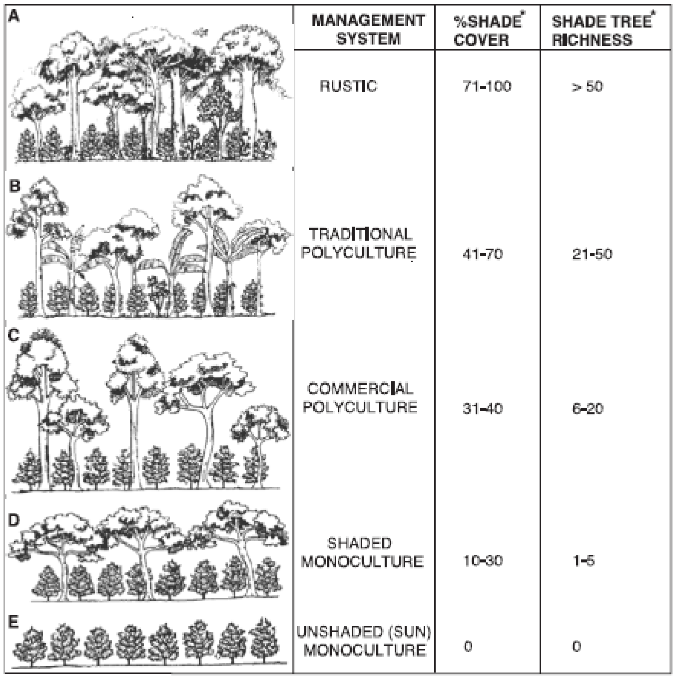
Coffee is an agroforestry crop that shows promise to enhance habitat value and ecosystem services, while increasing profit margins for the farmers. Coffee is the second most traded commodity in the world after oil and in many developing countries, the primary export (Taylor 2007). There are approximately 25 million coffee farmers and workers in over 50 countries involved in producing coffee. The way in which coffee is grown has a significant influence on the level of biodiversity that a landscape matrix can support and the environmental benefits that it may provide.

Traditionally, coffee is grown within native forest, an approach that provides wildlife habitat, fosters ecosystem services, and protects biodiversity (DeClerck et al. 2010). Over the past four decades, there has been a trend to move away from the traditional or "rustic" coffee towards coffee that is more intensively managed (Perfecto et al. 2005) which, in addition to depleting the system of floristic complexity, requires higher levels of chemical inputs to replace the ecosystem services lost (Rice 1999). In the early 1990s, several factors caused the price of coffee to plummet, giving rise to what many call "the coffee crisis" (O'Brien and Kinnaird 2003). This led many farmers in Latin America to replace traditional coffee systems and native forests on their lands with a monoculture of coffee plants to increase coffee yields, while farmers in India planted non-native tree species to be harvested and sold as timber products; both in hopes of being able to financially support themselves and their families.

Vegetation Structure in Coffee Farms

In the coffee growing regions of Latin America, there are gradients of coffee production systems, characterized by management intensity and vegetation structure. The lowest management intensive system, rustic coffee is grown within native forests (A in figure). The highest managed system, as depicted by E in the figure, is sun coffee, which is a monoculture of coffee plants with no other tree species. Between these two systems are coffee farms with varying degrees of management intensity and abundance and diversity of shade tree species.

The vegetation structure within coffee farms in India differs from Latin American farms. In India, although most coffee is no longer grown within the native forests, there are no management systems employing full sun coffee. The trend in India has been to replace native tree species with a non-native tree species, *Grevillea robusta* (Silver Oak) within coffee farms. There are protection laws that prohibit farmers from harvesting native trees as forest products, but these laws do not apply to the non-native Silver Oak (Vaast personal communication). Additionally, Silver Oak has a straight trunk, is fast growing, and therefore useful for supporting pepper vines that are often intermixed with coffee plants.



	MANAGEMENT SYSTEM	%SHADE* COVER	SHADE TREE* RICHNESS
A	RUSTIC	71-100	> 50
B	TRADITIONAL POLYCULTURE	41-70	21-50
C	COMMERCIAL POLYCULTURE	31-40	6-20
D	SHADED MONOCULTURE	10-30	1-5
E	UNSHADED (SUN) MONOCULTURE	0	0

Modiefied from: Moguel and Toledo, 1999; Rain Forest Allience.

* *Figures for percent shade and tree species richness are approximates based on studies cided by Moguel and Toledo, 1999 and our own reserach (Perfecto et al., 2003).*

Socio-economics of Coffee

Coffee farmers everywhere are faced with challenging management decisions in determining how to maximize profit from their crops, protect crops from coffee pests and disease, and at the same time maintain the ecosystem health and services for their farms. The impact of their decisions is far reaching, affecting their farm and family and also workers, wildlife, ecosystems, and their local community. Research is needed to provide best management practices to the farmers to assist them in making educated, sustainable decisions from which they can profit financially.

Market-based approaches to conservation are a viable way to both protect wildlife habitat and provide financial incentives to coffee farmers. Several coffee certifications are on the market that provide a guarantee that coffee is grown in an environmentally sustainable way such as organic labels, a socially conscious manner such as fair trade, and/or promote protection of biodiversity and wildlife habitat such as shade grown under the Bird Friendly or Rainforest Alliance labels (Philpott et al. 2007a). Farms that are certified not only yield a higher premium for the coffee, but the farmers, their families, and workers also receive improved health conditions with the reduction in agrochemicals as required by most certifications.

Although shade grown coffee has the potential to protect wildlife habitat and promote biodiversity, the certifications that promote it are still in their infancy and more research is needed to evaluate their effectiveness. There are concerns that promoting shade grown coffee could lead to the conversion of primary forests to shade coffee plantations. It has also been noted that shade coffee is not a substitute for native forests in terms of habitat for wildlife (Daily et al. 2003). Additionally, there can be a wide range of vegetation composition and management intensity within shade coffee farms (Philpott and Dietsch 2003, Rappole et al. 2003). Further research is needed on biodiversity and habitat, as it relates to coffee-dominated landscapes, to guide and inform shade certification requirements to ensure that biodiversity and habitats are protected.

Coffee Agroforestry as Wildlife Habitat

Although research has shown that coffee agroforestry may produce valuable habitat for various wildlife species, most studies have focused on bird and insect diversity (e.g. Gordon et al. 2007, Mas and Dietsch 2003, 2004, Perfecto et al. 2003, Philpott et al. 2007, Pineda et al. 2005) with few studies published that address the mammals living in and around coffee farms (Daily et al. 2003, Gallina et al. 1996, Husband et al. 2007, 2009). The common factor that influences habitat quality of a coffee farm is the complexity of vegetation, including tree richness and density and amount of canopy cover, as well as, the use of agrochemicals (DeClerck et al. 2010, Perfecto and Vandermeer 2008). However, studies suggest that all taxonomic groups do not respond in the same way to the various habitat gradients within a forest-agriculture matrix (DeClerck et al. 2010, Perfecto et al. 2003).

It has been reported that mammalian species richness is similar in coffee farms that are adjacent to small forest remnants as compared to extensive forests, but less in coffee, pasture, and pasture adjacent to forest (Daily et al. 2003). Husband et al. (2007, 2009) found that there was no significant difference in mammalian species richness between shade and sun coffee habitats in Costa Rica, although coffee supported a very different species composition than forest remnants. Butterfly and ant species richness generally decreases as tree canopy cover within coffee farms decreases (Perfecto et al. 2003). Perfecto et al. found that avian species richness correlates with distance to forest (Perfecto et al. 2003), but most studies have shown that the number of bird species decreases with an increase in management intensity (Gordon et al. 2007, Mas and Dietsch 2004, Philpott et al. 2007a, Pineda et al. 2005) with coffee agroforestry supporting higher levels of birds and forest dependent bird species than full sun coffee. Additionally, the values for the species richness of butterfly, ant, and bird species are not correlated with each other (Perfecto et al. 2003); therefore a single species cannot be used to indicate the quality of habitat for all biodiversity.

The literature shows that shade coffee supports birds, ants, and butterflies, but such evidence is not apparent for mammals (Gordon et al. 2007, Mas and Dietsch 2003, Mas and Dietsch 2004, Perfecto et al. 2003, Philpott et al. 2007, Pineda et al. 2005, Gallina et al. 1996, Husband et al. 2007, 2009). Mammal communities may be more dependent on forest corridors and therefore require forest remnants adjacent to the coffee farms. More research is needed at both the farm and landscape scale to understand the response of different species in this coffee-forest matrix, in particular those species such as small mammals for which studies seem to indicate that the addition of shade trees alone may not improve habitat.

B. DISCUSSION

The overall results of this dissertation research indicate that although mammals may be found in coffee habitats, most do not use coffee habitats exclusively and may rely on nearby forest habitats for survival. Eighty percent of the study sites in India were greater than 500 m from forested areas. We found the highest abundances of mammals in sites closest to the forest. Additionally, most of the medium-sized mammals detected through our camera traps were from farms in close proximity to forested areas. Regression models indicated that the small mammal numbers increased in coffee farms with high amounts of low vegetation cover and with large, mature trees, while species richness increased with high amounts of low vegetation cover. It is important to note that all of the sites in India had very high amounts of shade tree cover because sun coffee is not grown in India. There was little variation in the canopy cover percentage among farms; therefore it is not surprising that this variable was not included in any of the models explaining mammal abundance or richness. The species richness of the shade trees in the coffee farms in India was remarkably high. Even with high tree diversity and amounts of canopy cover, the coffee farms in India did not support a high level of mammal abundance and species richness. These results led me to consider a broader-landscape scale to understand the impacts that the surrounding landscape may have on mammal communities in and around coffee farms.

My research in Costa Rica incorporated coffee farms and the surrounding landscape. All of the sites included tracts of forested areas surrounding or intersecting shade and sun coffee. I found that shade coffee rivaled forest habitats in terms of mammal abundance and species richness. The mammals in these coffee-forest landscapes were present in shade coffee and to a lesser degree sun coffee, as well. Regression models indicated that high amounts of canopy cover led to higher abundances and that canopy cover and herbaceous ground cover led to higher species richness for mammals. For coffee habitats only, we found that mammal abundance was positively associated with canopy cover, low vegetation cover, and coffee height and species richness was associated with only canopy cover and coffee height. The coffee farms for this study in Costa Rica seem to support a high level of mammal abundance and species richness.

The habitat preference analysis allowed us to understand not only if mammals were using coffee habitats, but how the mammals used the habitats in this agricultural matrix. We analyzed the habitat preferences for the five most dominant species in the study. We found that all highly preferred forest to coffee habitats in the landscape, except for one that preferred shade coffee and forest equally. Two of the focal species did not have a preference between shade and sun coffee, while the remaining three species preferred shade to sun coffee according to the calculated preference indices (although for one of these there was no statistical difference between the two coffee habitat preferences). Although mammals may be using coffee habitats in this coffee-forest landscape, coffee is not a preferred habitat for most of the mammals in this study.

This study was devised to test the following null hypothesis:

Mammalian diversity within coffee farms does not change regardless of changes in the diversity of the plant community. It is hypothesized that increased vegetation diversity within coffee farms leads to an increase in mammalian diversity.

In India, we found that the coffee farms with native trees were significantly higher in terms of vegetation diversity than coffee farms with non-native and mixed tree compositions. From our study, there was not enough evidence to reject the null hypothesis as the mammal diversity was not significantly different among the coffee farms with predominately native tree species, non-native tree species, and mixed tree composition.

However, the results for the Costa Rica study did show that shade coffee with increased vegetation diversity has significantly higher mammal abundance and diversity than sun coffee; therefore we reject the null hypothesis. We found as hypothesized that native forests supported the highest amount of mammal abundance and richness and as vegetation complexity decreased within the coffee farms, the abundance and richness of mammals decreased.

C. MANAGEMENT IMPLICATIONS

The results of this study indicate that coffee farms may need to be in close proximity to forested areas to support a diverse mammal community. It is not clear that coffee agroforestry alone provides a refuge for mammalian fauna. The resources that they need for survival might not be found in coffee farms exclusively. Our results shows that providing shade trees, higher amounts of canopy cover, and low vegetation cover within the coffee farms is beneficial for mammal communities and may help to provide a high quality matrix for the mammals, even if it is not used as their primary habitat.

Suggested management guidelines for coffee farms to achieve these habitat requirements would include the following:

- Incorporate forested areas within the coffee farms.
- Include shade trees and maintain high amounts of canopy cover within the coffee farms.
- Retain low vegetation cover (<1m tall) on the ground.

In addition to shade tree species intermixed with the coffee plants, preserving or replacing forested areas around the perimeter or intersecting coffee farms may provide more connectively among forest patches. Maintaining low vegetation cover within the coffee farms would provide cover for small and medium-sized mammals and would also reduce exposure to herbicides that are often sprayed on ground vegetation within the farms. These habitat requirements should be included in conservation strategies for the promotion of biodiversity and sustainable agriculture to enhance mammal diversity on coffee farms.

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