

**TERRESTRIAL SMALL MAMMAL DIVERSITY AND MICROHABITAT  
ASSOCIATIONS IN SHADE COFFEE AGROECOSYSTEMS**

by

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## ABSTRACT

Microhabitats are proxies for resource availability and degree of predation risk. Small mammals respond to these cues by selecting for specific microhabitat characteristics. In agricultural systems, microhabitats are shaped by the management practices, in turn determining the distribution of local mammal communities and their persistence within the area. Coffee agroecosystems are acclaimed for their potential to conserve biodiversity, but little has been done to study the effects of different production methods on small mammals.

We compared the terrestrial small mammal communities between two coffee farms under differing management practices and tested for microhabitat associations for each species. Only five species of small mammals were trapped in the farms. Results indicate that while species richness did not differ between the two farms, the abundance of trapped individuals was significantly higher in the low shade coffee system as compared to the high shade system. Furthermore, ravines acted as pockets of habitats for local populations, with higher species diversity in areas closer to the ravines. Finally, no two small mammal species displayed the same set of microhabitat associations.

**Keywords:** Microhabitat, small mammal, diversity, coffee agroecosystems

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## INTRODUCTION

Three important trends define the current state of forests in the tropics - fragmentation, reduction in surface area and homogenization of floral and faunal communities (Horvath *et al.* 2001). One of the major causes of these trends is agriculture, which accounts for up to 90% of deforestation in the tropics (Benhin 2006). With the majority of the world's terrestrial biodiversity concentrated within these regions and threatened by deforestation, we cannot afford to lose any more species. Attempts have been made to conserve biodiversity by establishing forest reserves, but this method is largely insufficient given the rate of agriculture expansion and spillover effects from surrounding landscapes. Furthermore, the static nature of reserves provides no protection for organisms moving beyond the reserve boundaries (Daily *et al.* 2003; Caudill *et al.* 2014). Instead, the effectiveness of reserves would benefit from managing the surrounding agricultural matrix (Perfecto *et al.* 2009).

High-quality matrices provide cover for dispersal, support local populations and maintain resources for habitat and forage (Fahrig 2011; Perfecto and Vandermeer 2008). Diverse agroecosystems can be managed to provide for these functions. In well-managed agroecosystems, levels of biodiversity are comparable, if not higher than adjacent forest remnants due to the coexistence of forest specialists and edge-habitat generalists (Estrada *et al.* 1994; Mendellin and Equiha 1998; Daily *et al.* 2003; Weibull and Östman 2003). There may also be a shift of faunal community composition in agroecosystems to support rarer species. For example, Harvey and Villalobos (2007) found higher numbers of bats of conservation concern in cacao agroforests compared to neighboring forest reserves. In particular, coffee agroecosystems have garnered much attention due to their ecological and economical values (Perfecto *et al.* 1996; Jha *et al.* 2011, 2014).

Coffee is one of the most traded tropical commodities and supports 25 million families throughout the world (Bacon 2005; Daviron and Ponte 2005). The crop's ecological impacts stem from its cultivation in some of the most biodiverse regions of the tropics (Perfecto *et al.* 1996). In Mexico, coffee is grown with a variety of practices, ranging from high shade cover and vegetation complexity (e.g. traditional rustic coffee) to homogenized monocrop with no shade trees (e.g. sun coffee). The former is typically associated with low management intensity

practices such as reduced chemical applications and leaving the area unweeded during non- to low-production periods (Perfecto *et al.* 1996; Moguel and Toledo 1999). Within the study region, coffee is cultivated in farms (approximately 300 hectares) that are headed by a family owner who makes the decisions on farm management practices; hence adjacent farms may have markedly different production practices.

Of interest is the management of farms for biodiversity conservation purposes. While numerous studies have been done on avian taxa, arthropods and volant small mammals, little is known about terrestrial small mammals in coffee agroecosystems. Terrestrial small mammals have diverse feeding ecology and play important roles in tropical food webs. They act as predators, prey, and as disease vectors (Ellis *et al.* 1997; Alexander *et al.* 1998; Horváth *et al.* 2001; Daily *et al.* 2003; Jiménez-García *et al.* 2014). Many of them, such as the pocket mice *Heteromys* and *Liomys*, are seed dispersers that indirectly influence the composition of local plant communities via seed hoarding and discarding behaviors (Forget 1991; Brewer and Marcel 1999; Moguel and Toledo 1999; DeMattia *et al.* 2004; Klinger and Rejmánek 2010; Jiménez-García *et al.* 2014). Scat analyses have also found some mice species to consume and disperse arbuscular mycorrhizal fungi spores, which aids the growth of certain trees species (Mangan and Adler 2002). Additionally, terrestrial small mammals are sensitive to specific microhabitat features (Wells *et al.* 2004), and the presence or absence of certain species can be used as an indicator of local environment quality (Jiménez-García *et al.* 2014).

Microhabitats refer to the fine-scale environmental characteristics that are frequently used within an animal's home range (Moura 2005) that can otherwise act as cues for larger-scaled macrohabitat uses (Ellis 1997; Tew *et al.* 2004; Abreu and Oliveira 2014). That is, microhabitats provide consistent information for wildlife regarding the quality of a habitat. The preference for specific microhabitat features by small mammal reflects the species' or group's life history and behaviors. For example, mammals with small home range sizes such as *Heteromys desmarestianus* (Fleming 1974) home in on finer-scaled environmental characteristics during foraging and burrow-construction. These forest specialists are more abundant in areas of high structural complexity and spatial heterogeneity, whereas other generalists are frequently associated with more homogenized, disturbed environments. More importantly, factors such as predation risk, species coexistence and resource availability are functions of microhabitat

heterogeneity (Lagos 1995; Zollner *et al.* 2003; Harris *et al.* 2006), where higher heterogeneity is positively correlated to species diversity (Abreu and Oliveira 2014).

Despite these general trends, results have been mixed regarding the specific microhabitat features that influence small mammal diversity within agroecosystems (August *et al.* 1983; Williams *et al.* 2002). San-José *et al.* (2014) found yearly differences in the predictors for small mammal abundance in Neotropical rainforest fragments, with patch size in one year and basal area in the other. Not all microhabitats that are assumed to contribute to habitat heterogeneity are beneficial for the species. Caudill *et al.* (2014) found larger tree basal area and vegetation cover to be associated with higher abundance. However, in that study, the number of shade trees was negatively correlated with species richness. In some cases, none of the microhabitat characteristics measured had an impact on diversity (August *et al.* 1983; Fonseca and Robinson 1990). Given that microhabitats are shaped by agriculture practices, knowledge of beneficial microhabitats enable farm owners and managers to make crucial decisions about managing farms for biodiversity conservation.

Our study sets out to investigate how agricultural management can affect terrestrial small mammal communities. The objectives of the study are to (1) compare and contrast small mammal diversity (measured as species richness and abundance) in two coffee farms of differing management practices and (2) identify the microhabitat characteristics associated with specific species. We predict that the more traditional, shaded coffee farm will have a richer and larger small mammal community. Forest specialists will also be more abundant in the traditional, shaded farm due to structural similarity to the adjacent forest patch. In contrast, habitat generalists will be more abundant in the conventional farm, as they can exploit a wide range of resources. For objective 2, we predict that terrestrial small mammal communities will be positively associated with microhabitat heterogeneity, and negatively correlated with intensity of management practices such as an increase in coffee tree density.



## METHODS

### *Study area*

The study took place from May to August 2015 in the coffee growing region of Soconusco, in Chiapas, Mexico. The area has distinct wet and dry seasons, lasting from May through September, and from October until April, respectively. Farms in the study area experience a constant year-round average temperature of 20-21°C and receive 4,500 mm precipitation annually (Armbrecht and Perfecto 2003).

The farms selected for the study were *Finca Irlanda* (15°10' North and 92°20' West) and *Finca Hamburgo* (15°10' North and 92°19' West). The former is a 300 hectare shaded organic coffee farm closely resembling a traditional polyculture (from now on referred to as high shade or HS) and the latter is a 300 hectare low shade system (from now on referred to as low shade or LS; Moguel and Toledo 1999). In Irlanda, mechanical removal of undergrowth occurred intermittently, but no agrochemicals were used. In Hamburgo, the majority of the shade tree species belong to the native nitrogen-fixing *Inga*, and are frequently pruned to reduce humidity and the probability of rust infection. Chemical herbicides are used to remove understory cover and suppress weed growth. The year our sampling took place, all of the coffee plants in Hamburgo were reduced to less than 0.7 meters for rejuvenation purposes. Dried coffee branches were piled in long rows approximately five meters apart - between every two rows of coffee - and small mammals and lizards were observed to use the branch piles for basking and refuge. Recovery of ground level vegetation was relatively rapid, within the span of two to three weeks. In both farms, farm workers occasionally returned to remove new undergrowth. All trappings and microhabitat measurements were conducted in between cycles of undergrowth removal to minimize the influences of human disturbances.

The two farms are separated by a forest remnant known as La Montañita. We also set up two grids in the forest for control purposes.

### *Mammal sampling*

Four 50 by 50 meter grids were established in each farm. An additional two grids were placed in the forest fragment for control purposes. Each grid consisted of six transects spaced ten meters apart. In each farm, two of the four farm grids were placed with corners partially in the ravines, as previous researches suggested higher small mammal activity in the ravines (Otero-Jimenez pers. comm.). All grids were located at least 250 meters apart to minimize dependence.

Each grid contained 36 stations spaced ten meters apart, and each station contained two 3x3.5x9" Sherman folding traps (H.B. Sherman Traps Inc., Tallahassee, Florida) (Fig. 1). The traps were baited with a one-part sunflower seed and two-part oat mix scented with vanilla extract. Traps were placed during the afternoon at 1300 to 1500 hour and checked in the mornings at 0600 to 0900 hour. They were placed strategically near fallen logs, under vegetation cover or adjacent to trees to increase chances of capture. Each grid was sampled for four nights with the exception of the first grid, which was sampled for six, yielding a total of 3,004 trap nights. Due to human disturbances, equipment malfunctions and inclement weather, 1,295 trap nights, 1,148 and 561 trap nights were recorded for *Finca Irlanda* (HS), *Finca Hamburgo* (LS) and the forest, respectively. Trapped individuals were weighed and identified based on external features using the Reid Field Guide (1997). A clip of hair was removed from captured individuals for mark-and-recapture purposes. All individuals were released at the site of capture.

### *Microhabitat surveys*

Ten microhabitat characteristics deemed important for small mammals were measured in each grid (Appendix I). The variables were: 1) number of shade trees, 2) number of shade tree species, 3) coffee density, 4) average basal area of shade trees, 5) vegetation density at 0.5 meter, 6) vegetation density at one meter, 7) percent groundcover, 8) canopy cover, 9) litter depth and 10) coffee height. Shade tree species were identified in the field with the help of a local assistant and picture guide. However, many of the trees in the forest were unidentifiable due to a lack of information on the tree species in the forest and difficulties in procuring leaf or branch samples. As such the forest data were excluded from the data analysis related to microhabitat characteristics.

## DATA ANALYSIS

We calculated the Shannon-Wiener Index and dominance of each species. The latter was obtained by taking the number of individuals of a species and dividing it by the total number of trapped individuals multiplied by a 100 to obtain a percentage value. We also used Nonmetric Multidimensional Scaling (NMDS) to explore the spatial clustering of sites in order to identify differences in community composition. Individual-based rarefaction curves were computed (EstimateS 9.1.0; Colwell 2013) to compare diversity between the sites.

To test the effect of farm management type and distance from the ravines, we performed two-way ANOVAs on species richness and abundance. Distance from the ravines was categorical (i.e. 'far', 'close'). Data were tested for normality and homoscedasticity of variance by examining the residuals and normal Q-Q plots. Where the assumptions were violated, data were square root transformed. We also ran a one-way ANOVA including the forest data for site against species richness and abundance. Distance from the ravine was not tested using the forest data because the forest is nested within a ravine.

### *Model construction*

We constructed generalized linear mixed effect models using Poisson distribution and loglink function for each species to test for microhabitat associations (Bolker 2008). The microhabitat variables were treated as fixed effects and sampling sites as random effects. All fixed effect data were standardized beforehand to remove scaling issues due to differing measurement units. A variance inflation factor (VIF) was used in conjunction with correlation plots to test for collinearity between microhabitat variables. Variables with  $VIF > 10$  were considered to have severe multicollinearity and were dropped from the model (Appendix II; Penn State Department of Statistics). Vegetation density at one meter, canopy cover, coffee height and the number of trees per plot were dropped due to high collinearity with multiple factors. After constructing the models, variables that were not statistically significant ( $p < 0.05$ ) were removed to better fit the models. We adhered to the rule of parsimony and lowest Akaike Information Criterion during model selection (Oehlert 2012).

In order to account for the potential effects of dropped variables, an index of management intensity was constructed (Mas and Dietsch 2003). This index followed the observations that higher management intensities were generally associated with lower values of the measured microhabitat characteristics. The only exception was coffee density, which increases with higher management. We calculated the index by first converting all sets of microhabitat variables to values between 0 and 1 through dividing the values by the maximum within the set. We then used the following equation to compute index value:

$$Index_{intensity} = R_1 + R_2 + \frac{R_3}{R_{max}} - R_4$$

where positive terms were terms associated with high management intensity (e.g coffee density) and negative terms were terms associated with low management intensity. Finally, we regressed the index against overall species diversity and the abundance of individual species.

All calculations were conducted using the softwares RStudio ver. 3.2.3, PAST 3 and EstimateS 9.1.0.

## RESULTS

### *Small Mammal Diversity*

We trapped a total of 319 animals and 235 individuals, equivalent to a 10.62% trapping success (Table 1). Six of the sites had a higher trapping success than the average recorded in Neotropical ecosystems (2.5-6.3%; Medellín and Equihua 1998). The small mammals trapped belonged to five genera of rodents and two families: *Heteromys goldmani* (also known as a subspecies of *H. desmarestianus*, *H. d. goldmani*; Goldman's spiny pocket mouse), *Oligoryzomys fulvescens* (northern pygmy rice rat), *Reithrodontomys sp.* (harvest mouse), *Handleyomys sp.* (rice rat) and *Peromyscus sp.* (deer mouse). The last three were not identified down to the species level due to difficulties with visual identification in the field (Reid 1997; Caudill pers. comm.) and inconsistencies in taxonomic assignments (Weksler 2006; IUCN 2008; San-Jose *et al.* 2014; Voss pers. comm.).

Hamburgo, the low shade (LS) farm, reported the highest total number of captures and individuals caught, followed by Irlanda, the high shade farm (HS) and the forest. The ordination plot found significant difference in community composition between the grids, particularly for the forest grids which were clustered further along the x-axis (Fig. 3). This was further illustrated by the inversion in pattern of dominance between the sites (Table 2). *Reithrodontomys sp.* was the dominant species in Hamburgo (43.97% of captures), but was one of the least common species found in Irlanda (6.49%). In contrast, there were only two incidences of *Handleyomys sp.* in Hamburgo (1.72%), whereas 31 individuals were trapped in Irlanda (40.26%). *H. goldmani*, *Peromyscus sp.*, and *O. fulvescens* shared similar dominance in both farms, the former of which was only trapped in small numbers in the farms but formed the dominant group in the forest (83.33%). This was not surprising, as *H. goldmani* is sometimes considered a subspecies of *H. desmarestianus*, a known forest specialist found in undisturbed areas (Horváth *et al.* 2001, Otero-Jimenez pers. comm.). Other species such as *Peromyscus sp.*, *O. fulvescens* and *Handleyomys sp.* were found in low numbers in the forest, and *Reithrodontomys sp.* was not trapped there at all. However, because the same set of species was caught in most of the grids, community diversity did not differ significantly between the sites (Fig. 4).

### *Effect of Farm Type and Distance from Ravine*

Species richness was not significantly different between the two farms ( $F_{1,30} = 0.9882$ ,  $p=0.3281$ ) since both farms contained the same set of five rodent species. However, distance from the ravines was a significant factor. This trend was particularly pronounced in Irlanda, where species richness increased closer to the ravines ( $F_{1,30}=7.1151$ ,  $p=0.0122$ ). Small mammal abundance was significantly different between the farms ( $F_{1,30}=6.4918$ ,  $P=0.016199$ ) and with distance from the ravines ( $F_{1,30}=11.1851$ ,  $p=0.002226$ ), where more individuals were trapped in Hamburgo and at sites closer to the ravines. The interaction between the two factors was significant ( $F_{1,30}=4.7774$ ,  $p=0.036775$ ; Fig 2.). When forest data were included into the analysis, neither species richness nor abundance were different between the sites ( $F_{1,30}=2.496$ ,  $p=0.0955$  and  $F_{1,30}=2.184$ ,  $p=0.126$ , respectively).

### *Microhabitat Associations*

On average Irlanda (HS) had a higher number of shade trees and shade tree species, vegetation density, herbaceous ground cover, canopy cover, litter depth and coffee height (Appendix III) than Hamburgo. That is, Irlanda had more microhabitat heterogeneity compared to Hamburgo (LS). Only coffee density was higher in Hamburgo. In a comparison of Hamburgo (LS) and Irlanda (HS), coffee density ( $t_{0.05(2),6}=2.6072$ ,  $P=0.04027$ ) was significantly higher in Hamburgo, whereas 0.5 meter ( $t_{0.05(2),6}=-4.9994$ ,  $P=0.002454$ ) and one meter herbaceous vegetation density ( $t_{0.05(2),6}=-6.8792$ ,  $P=0.0004653$ ), canopy cover ( $t_{0.05(2),6}=-15.928$ ,  $P=3.877*10^{-6}$ ), coffee height ( $t_{0.05(2),6}=-11.727$ ,  $P=2.32*10^{-5}$ ) and number of shade trees ( $t_{0.05(2),6}=-2.6098$ ,  $P=0.04013$ ) were significantly higher in Irlanda.

Microhabitat associations differ according to the species (Table 4). The overall abundance was positively correlated with shade tree richness and negatively correlated with distance from ravines, basal area, 0.5 m vegetation density and litter depth. In contrast, richness was negatively correlated with distance from ravines, although the correlation was only marginally significant ( $p=0.08$ ). Looking at individual species, we found *H. goldmani* did not have any associations with the microhabitat characteristics measured in the farm. This is probably because the species is predominantly a forest specialist, and there were very few individuals trapped within the farms. Furthermore, the microhabitats used to characterize the

farms may not be suitable measurements for a forest specialist. *Reithrodontomys sp.* was positively correlated with coffee density and the number of tree species, but negatively correlated with litter depth. The other small-sized rodent in the area, *O. fulvescens*, was also positively correlated with coffee density in addition to distance from ravines and herbaceous ground cover. On the other hand the larger-sized *Peromyscus sp.* decreased with distance from ravines and litter depth. Finally, we found the number of *Handleyomys sp.* to be higher in areas with higher ground cover.

Aside from *Reithrodontomys sp.* and *Handleyomys sp.*, none of the species were affected by the intensity of management (Table 5). *Reithrodontomys sp.* displayed a positive relationship with management intensity ( $R^2 = 0.1132$ ,  $p=0.02924$ ). On the other hand, the numbers of *Handleyomys* declined sharply with management intensity ( $R^2 = 0.1843$ ,  $p=0.00656$ ).

## DISCUSSION

### *Small Mammal Diversity*

We found a paltry small mammal community within the coffee farms and the forest fragment in the study site. Only five species of rodents were found in the area, compared to a range of eight to ten species observed in other lowland shade coffee plantations nearby in Loma Bonita, Chiapas, Mexico (Cruz-Lara L.E. *et al.* 2004). These five taxa represent only 22.73% of the total genera of rodents found in Chiapas (Retana and Lorenzo 2002). The taxa in our study are the same as the ones identified in a previous 1999-2000 study conducted on the same farms (Elisabeth Witt, unpublished), indicating that the terrestrial small mammal assemblage within the area has not changed drastically over time. Interestingly, *Reithrodontomys sp.*, *O. fulvescens* and *Handleyomys sp.* (previously referred to as *Oryzomys sp.*) were missing from the Hamburgo (LS) transects in the earlier study, whereas *Reithrodontomys sp.* and *Handleyomys sp.* were found in high numbers in the current study. However, due to different sampling designs, we were unable to perform any statistical comparisons between the current and previous study.

### *Effect of Farm Type and Distance from Ravine*

The two farms shared the same set of species, four of which were considered generalists. Two observations were surprising: (1) the more intensified farm had higher small mammal abundance compared to the organic farm, and (2) species richness was lowest in the forest. There are several potential explanations for the second observation. One postulate is that food resources may be higher in the forest; therefore the baits used for the traps may not be attractive enough for small mammals. While this is likely, we did not think this was the case as we still trapped a substantial number of *H. goldmani* individuals, indicating that the rodents considered the baits to be attractive, easy-to-access resources. A second, more likely postulate is that the forest supports a lower assemblage of terrestrial small mammals. We noted that the forest contains more structural complexity in terms of the density of lianas, number of canopy strata, shade tree height and an almost 100% canopy cover. Herbaceous ground cover was also lower in the forest (averaging 23.6%) compared to the two farms (36.6% to 54.1%). As such, the forest environment offered little protective covering for terrestrial species and may be more conducive



towards semi-arboreal and arboreal species that can exploit the vertical structures. This might explain why we did not trap any *Reithrodontomys sp.*, a semi-arboreal species, in the forest as Neotropical members of this genus were rarely trapped on the ground in mature forests (Reid 1997). Finally, we may simply not have sampled enough in the forest to detect other terrestrial species.

Compared to Irlanda (HS), abundance of individuals was higher in Hamburgo (LS). This is attributed primarily due to the higher numbers of *Reithrodontomys sp.* and *O. fulvescens* trapped. For *Reithrodontomys sp.*, this pattern may be due to the absence of large, mature shade trees. *Reithrodontomys sp.* typically prefers vertical structures, which were lacking in Hamburgo. In the absence of large, mature shade trees, Reid (1997) noted that the species was primarily found in grassy areas; hence they likely were captured in higher numbers on the ground near Hamburgo. The open nature of Hamburgo's habitat is also favorable for species such as *O. fulvescens*, which is considered an edge species tolerant of open environments (Reid 1997).

A closer inspection also revealed that on average both species richness and abundance were significantly higher closer to the ravines, although the effect of distance from ravines on species abundance was minimal in Hamburgo (LS). It is possible that low resource availability in Hamburgo forces the small mammals to seek out the baits in the traps. We noticed that a large number of rodents were caught far away from ravines, suggesting that low food resources may increase the foraging range of the animals. Another explanation is that the removal of vegetation in Hamburgo also removed habitats for larger predators, freeing the rodents from predation pressure. We are cautious of this explanation as the removal of vegetation also exposes rodents to higher aerial predation (Orrock *et al.* 2004), which contradicts the observation that a large number of individuals were trapped in open areas far from the ravines. Nevertheless, the piles of dried coffee branches common in the Hamburgo site may compensate for aerial predation risk by serving as corridors for small mammals, as we observed released individuals to immediately dive for the dried coffee piles.

In general, the results of the study suggest that ravines act as pockets of refuge for small mammals within a human-modified landscape. More water tend to accumulate within the ravines, and in some cases ravines may even harbor brooks, which provides vital sources of water and higher food resources for rodents (Otero-Jimenez pers. comm.). More importantly,

anthropogenic disturbances were reduced near the ravines due to steep inclines. For example, coffee density was generally lower along the slopes of the ravines.

### *Microhabitat Associations*

Previous researches found small mammal diversity to be affected by herbaceous ground cover, presence of large shade trees, basal area, distance from natural patches, tree species richness and heterogeneity of local vegetation (Estrada 1994; Sanchez Cordero 2001; Williams *et al.* 2002; Bali *et al.* 2007; Horvath *et al.* 2010; Abreu and Oliveira 2014; Caudill 2014; San-Jose 2014). Our study found overall abundance of small mammals to be positively correlated with tree species richness, but negatively correlated with distance from ravines, basal area, vegetation density at 0.5m and litter depth. Shade tree species richness can be treated as a proxy for resource availability, which was one of the predominant factors in determining small mammal microhabitat use in a semiarid region in Chile (Lagos *et al.* 1995). Given that seeds and fruits constitute part of the diet for all species in our study, a higher variety of shade tree species offers more resources to sustain higher population numbers. We did not expect basal area and 0.5 m vegetation density to be negative correlates of species abundance. This pattern might be explained by the low numbers of *Reithrodontomys sp.* in Irlanda and high numbers of *O. fulvescens* found in Hamburgo, the low shade site. Because Irlanda contained higher amount of mature shade trees, it is likely that *Reithrodontomys sp.* used these resources; hence the lower number of individuals trapped on the ground in areas with large shade trees. For these two species, tree species richness and herbaceous ground cover were the important microhabitat characteristics.

Species richness was negatively impacted by distance from ravines. Many studies have also found distance from natural areas such as forest reserves to be the predominant factor in determining species richness for small mammals (Estrada *et al.* 1994; Bali *et al.* 2007; Williams-Guillén and Perfecto 2010). For example, in our study, more *Peromyscus sp.* were trapped near the ravines, as members of the genus prefer moist areas close to large bodies of water (Reid 1997).

No two species shared the same set of microhabitat associations. Interestingly *H. goldmani* did not respond to any of the microhabitat variables, suggesting that there are other environmental characteristics that determine the species' distribution. For example, *Heteromys*

*sp.* are known consumers of palm seeds (Martinez-Gallardo 1993), which were common in the forest but not on the farms. We also found seeds of *Schizolobium parahybum* in the pockets of captured *H. goldmani*. For this species, the presence of specific trees may act as better proxies for resource availability. As such, measuring the abundance and richness of fruiting trees and palm plants are more apt measurements for detecting this species. This demonstrates that because each species utilizes different resources, it can be hard to trap certain species without knowing beforehand species-specific behavior and resource usage.

It should be noted that most of the microhabitat variables related to structural complexity were removed from the models due to high collinearity. Numerous studies have found, however, that structural complexity is important for small mammals (August 1983; Williams *et al.* 2002; Horvath *et al.* 2010). Structural complexity is associated with higher resource availability, more habitat partitioning and increased obstruction for predators (Vasquez *et al.* 2002). When we included all the microhabitat variables in the management intensity indices, we did not detect any significant effects on small mammals except *Reithrodontomys sp.* and *Handleyomys sp.* (Table 5). Because *Handleyomys sp.* are not known climbers, they likely decreased in number due to loss of available ground cover as management intensity increased. The increase in *Reithrodontomys sp.* with management intensity is likely due to the abundance of individuals trapped on the ground when there were low tree resources.

Some caveats of the study were that it was restricted spatially and temporally in design. The current study only looked at terrestrial species or those that make use of terrestrial areas for foraging or dispersal. Other arboreal species such as opossums have been trapped by another researcher in the area. Squirrels were also commonly sighted amongst the canopies in Irlanda (HS) during the day. These species play equally important functions in seed dispersals and would be of interest to study as well. Moreover, we recognized that moon phases may have an effect on the daily activity of the nocturnal small mammals. Higher illumination is associated with lower activity due to increased detection by predators (Clarke 1983; Orrock *et al.* 2004). Looking at the calendar of moon phases, we noticed that full moon nights happened to fall on the nights that we trapped in Irlanda (HS), which might have contributed to a particularly low count in one of the sites. Finally, this study did not test for the effect of seasonality. Small mammals increase their reproductive efforts during wet seasons corresponding to higher resource availability (Sanchez-Cordero 2001; Tew *et al.* 2004; Wells 2004; Horvath *et al.* 2010). Cruz-Lara *et al.* (2004)

observed differences in species dominance between wet and dry seasons, where cotton rats dominated the mammal community in coffee plantations during the wet season but were replaced by little yellow-shouldered bats during the dry season. Understanding the fluctuations of small mammal composition during different season would provide us with a clue of available resources and species-specific resource usage.

## CONCLUSION

As demands for environmentally-friendly coffee grow, there are high hopes that coffee agroecosystems can also provide for biodiversity conservation. Our study indicates that terrestrial small mammals are relatively resilient to disturbances and make use of coffee systems. However, most populations are locally concentrated in areas of relatively low disturbance such as ravines. Managing the microhabitats for individuals to migrate between these patches is crucial for the maintenance of the species within the region. Based on our results, we make several tentative suggestions for coffee growers. Firstly, maintain some level of vegetative ground cover as corridors for small mammals to disperse between refuges. Secondly, maintain a variety of tree species to foster diversity of resources available for small mammals, particularly granivores that rely on seeds as their sole source of food. Finally, preserve existing forest patches and ravine vegetation to provide important habitats for forest specialists.

**Table 1. Trapping data in Irlanda, Hamburgo and the forest sites.**

|                                    | Irlanda (High Shade) | Hamburgo (Low Shade) | Forest |
|------------------------------------|----------------------|----------------------|--------|
| <b>Species richness</b>            | 5                    | 5                    | 4      |
| <b>Total individuals</b>           | 77                   | 116                  | 42     |
| <b>Total catches</b>               | 114                  | 160                  | 45     |
| <b>Capture success<sup>a</sup></b> | 8.80%                | 13.94%               | 8.02%  |
| <b>Trap nights</b>                 | 1,295                | 1,148                | 561    |

<sup>a</sup>Capture success is calculated as the total catches including recaptures divided by the total amount of trap nights.

**Table 2. Species abundance and capture in Irlanda, Hamburgo and the forest sites, including calculations of the percent dominance (number of individuals of a species/total number of individuals) of species within each site.**

|                                | Irlanda (High Shade) |                    | Hamburgo (Low Shade) |                    | Forest             |                    |
|--------------------------------|----------------------|--------------------|----------------------|--------------------|--------------------|--------------------|
|                                | Abun. <sup>a</sup>   | Capt. <sup>b</sup> | Abun. <sup>a</sup>   | Capt. <sup>b</sup> | Abun. <sup>a</sup> | Capt. <sup>b</sup> |
| <i>Heteromys goldmani</i>      | 5                    | 7                  | 8                    | 11                 | 35                 | 37                 |
| Dominance (%)                  | 6.49%                |                    | 6.90%                |                    | 83.33%             |                    |
| <i>Reithrodontomys sp.</i>     | 5                    | 9                  | 51                   | 60                 | 0                  | 0                  |
| Dominance (%)                  | 6.49%                |                    | 43.97%               |                    | 0%                 |                    |
| <i>Peromyscus sp.</i>          | 14                   | 20                 | 18                   | 36                 | 3                  | 3                  |
| Dominance (%)                  | 18.18%               |                    | 15.52%               |                    | 7.14%              |                    |
| <i>Handleyomys sp.</i>         | 31                   | 40                 | 2                    | 2                  | 3                  | 4                  |
| Dominance (%)                  | 40.26%               |                    | 1.72%                |                    | 7.14%              |                    |
| <i>Oligoryzomys fulvescens</i> | 22                   | 38                 | 37                   | 51                 | 1                  | 1                  |
| Dominance (%)                  | 28.57%               |                    | 31.90%               |                    | 2.38%              |                    |
| Total                          | 77                   | 114                | 116                  | 160                | 42                 | 45                 |

<sup>a</sup>Abundance of individuals trapped excluding recapture

<sup>b</sup>Captures including the sum of number of individuals and recaptures

**Table 3. Measurements of diversity using Shannon-Wiener index and measure of evenness. Higher values correspond to higher diversity and more evenly distributed species composition.**

|   | Irlanda (n=4)<br>(High Shade) | Hamburgo (n=4)<br>(Low Shade) | Forest (n=2) |
|---|-------------------------------|-------------------------------|--------------|
| <b>Species richness</b>                       | 5                             | 5                             | 4            |
| <b>Abundance</b>                              | 77                            | 116                           | 42           |
| <b>Shannon-Wiener Index (<math>H'</math>)</b> | 1.389                         | 1.269                         | 0.6179       |
| <b>Evenness (E)</b>                           | 0.8632                        | 0.7887                        | 0.4457       |



**Table 4. Generalized mixed linear models with only significant microhabitat variables (p<0.05) included.**

| Response variable                     | Microhabitat variables | Slope   | p-value                    |
|---------------------------------------|------------------------|---------|----------------------------|
| <b>Abundance (n=193)</b>              | Distance <sup>a</sup>  | -0.7367 | 0.000104***                |
|                                       | Tree richness          | 0.7183  | 2.94*10 <sup>-7</sup> ***  |
|                                       | Basal area             | -0.5727 | 4.47 *10 <sup>-5</sup> *** |
|                                       | 0.5 m vegetation       | -0.4145 | 0.000203***                |
|                                       | Litter depth           | -0.6856 | 1.85*10 <sup>-6</sup> ***  |
| <b>Richness (n=193)</b>               | Distance <sup>a</sup>  | -0.3911 | 0.0812.                    |
| <i>Heteromys goldmani</i> (n=13)      | --                     |         |                            |
| <i>Reithrodontomy sp.</i> (n=56)      | Coffee density         | 1.1813  | 0.000258                   |
|                                       | Tree richness          | 0.8557  | 6.51*10 <sup>-6</sup> ***  |
|                                       | Litter depth           | -1.1684 | 6.28*10 <sup>-6</sup> ***  |
| <i>Peromyscus sp.</i> (n=32)          | Distance <sup>a</sup>  | -1.7404 | 0.00129**                  |
| <i>Handleyomys sp.</i> (n=33)         | Ground cover           | 1.1875  | 3.56*10 <sup>-15</sup> *** |
| <i>Oligoryzomys fulvescens</i> (n=59) | Distance <sup>a</sup>  | 1.2894  | 0.002796**                 |
|                                       | Coffee density         | 1.1423  | 0.000376***                |
|                                       | Ground cover           | 0.9831  | 0.002750**                 |

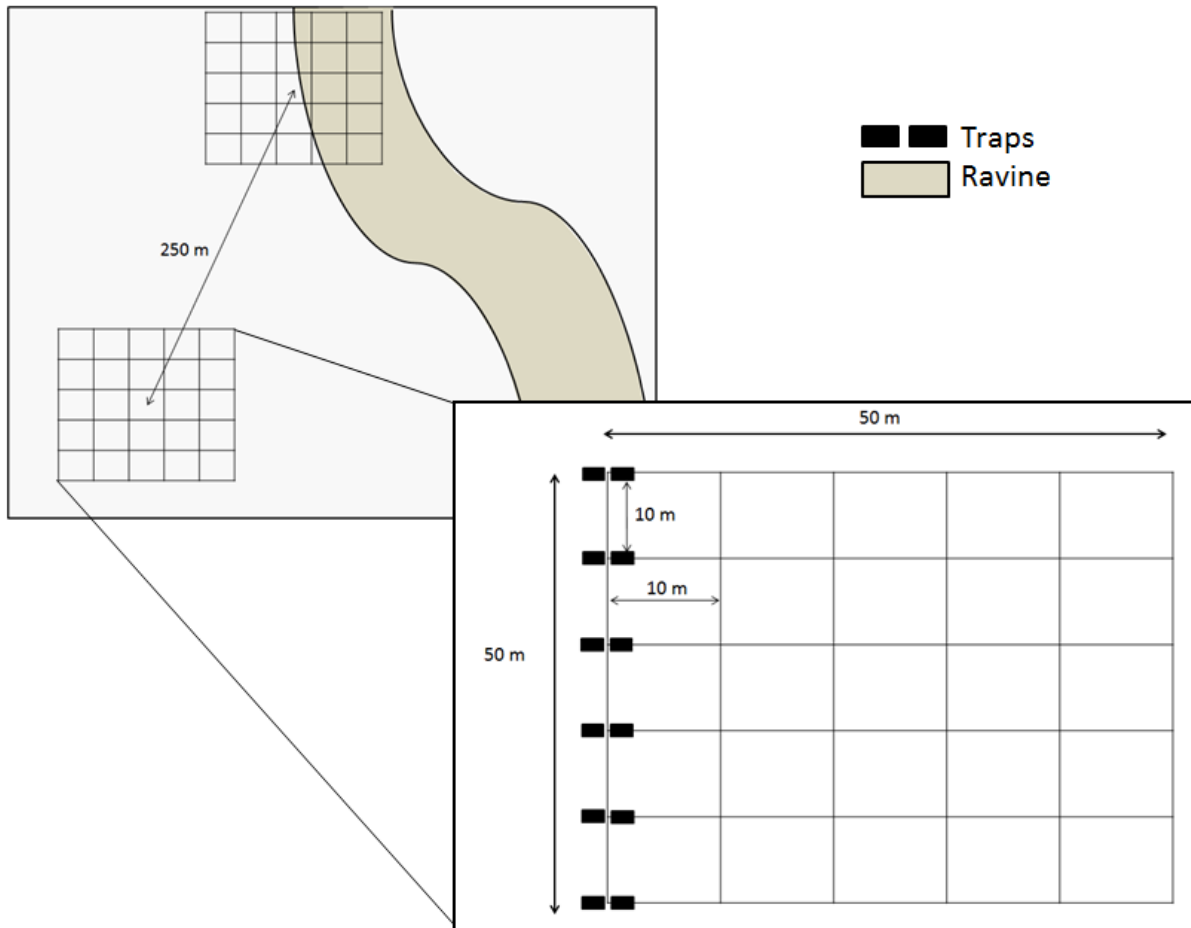
<sup>a</sup> Distance from the ravine categorized as 'close' and 'far'  
p-values significance: '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05

**Table 5. Linear regression of species diversity against index of management intensity.**

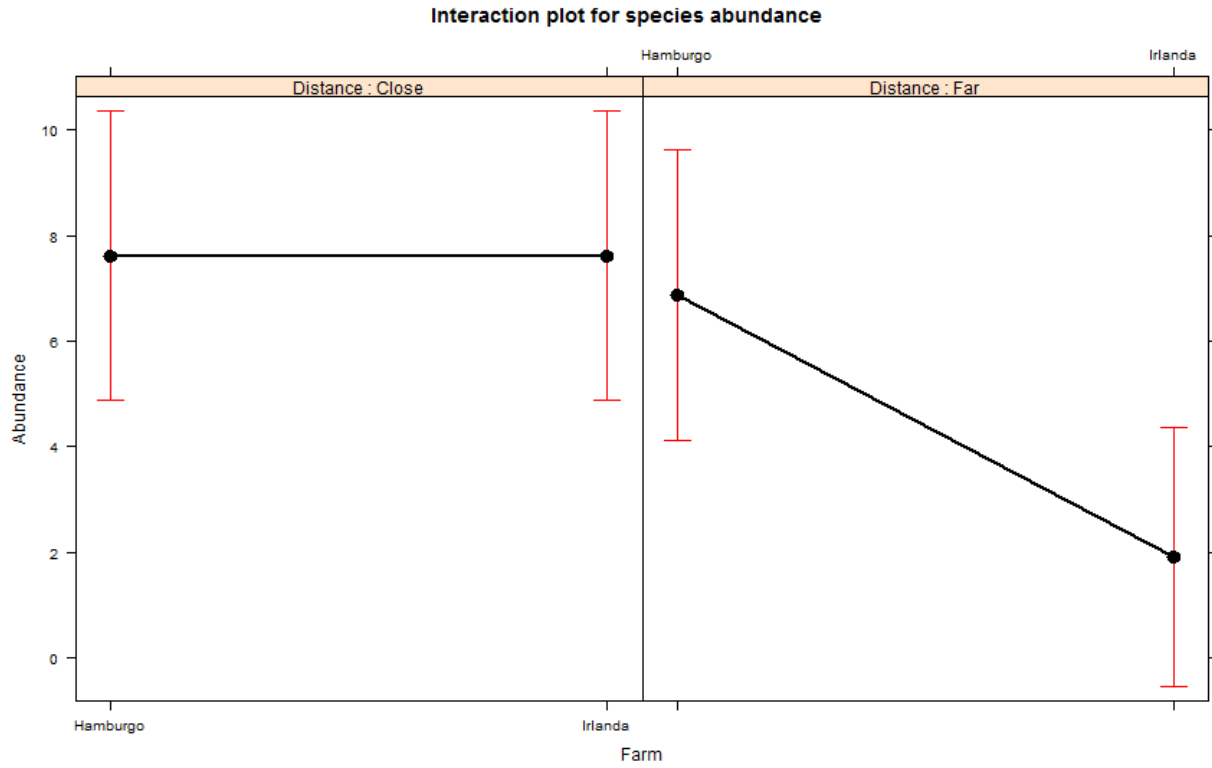
| Response variable              | Slope   | R <sup>2</sup> | p-value   |
|--------------------------------|---------|----------------|-----------|
| <b>Abundance</b>               | 0.57    | 0.0144         | 0.232365  |
| <b>Richness</b>                | 0.1145  | -0.001451      | 0.336     |
| <i>Heteromys goldmani</i>      | 0.05446 | -0.012         | 0.441     |
| <i>Reithrodontomys sp.</i>     | 0.6541  | 0.1132         | 0.02924*  |
| <i>Peromyscus sp.</i>          | 0.1431  | 0.007686       | 0.2708    |
| <i>Handleyomys sp.</i>         | -0.6634 | 0.1843         | 0.00656** |
| <i>Oligoryzomys fulvescens</i> | 0.3818  | 0.06311        | 0.08206   |

p-values significance ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05

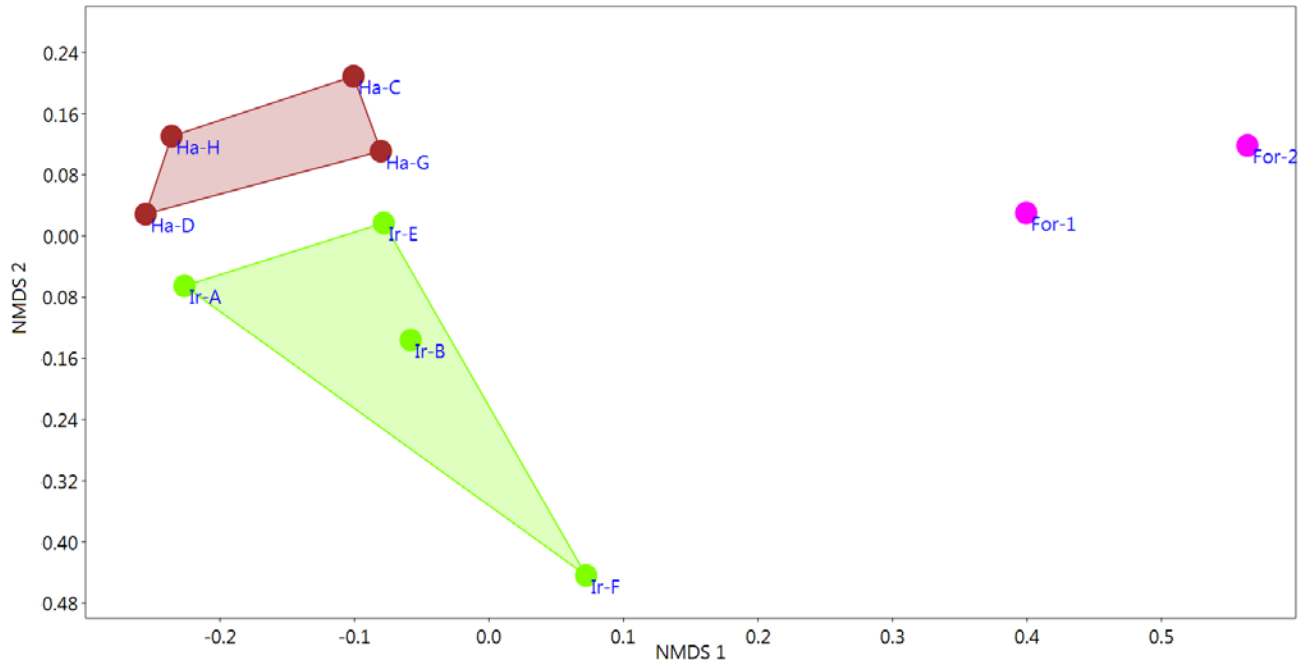
**Figure 1. Four 50 meter x 50 meter grids were placed in each farm, two of which were close to a ravine and two far away. Each grid contained six transects spaced ten meters apart. In each transect, two Sherman live traps baited with sunflower seeds, oats and vanilla extract were placed on the ground at every ten meters. Grids were placed at least 250 meter away from one another to minimize dependence. Trapping was done for four consecutive nights on each grid.**



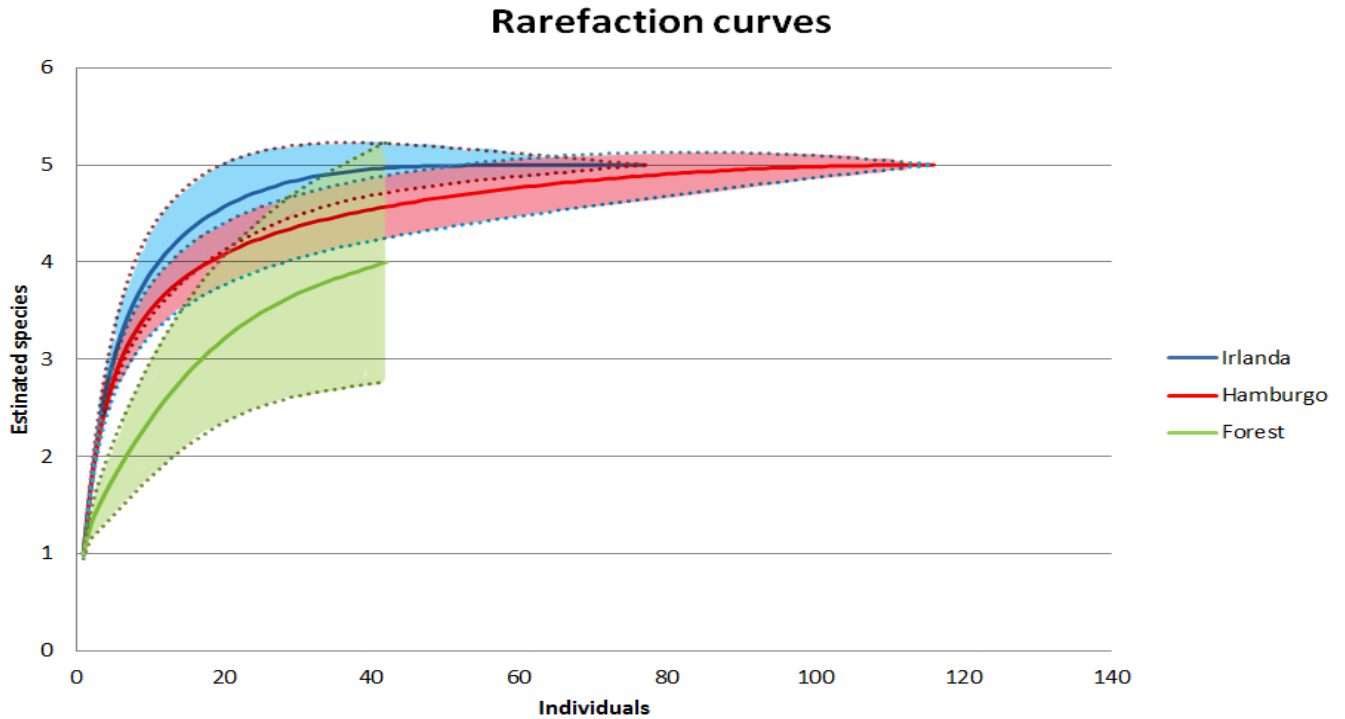
**Figure 2. There was a significant interaction between distance from ravine and farm type ( $F_{1,30}=4.7774$ ,  $p=0.036775$ ) when testing for the effect of the two factors on species abundance. Distance from ravine had a pronounced effect on the average number of individuals trapped in Irlanda (HS), with significantly more individuals trapped near the ravines.**



**Figure 3. NMDS (Non-Metric Multidimensional Scaling) of the Irlanda (Ir), Hamburgo (Ha) and Forest (For) grids. The forest grids were significantly different in community composition compared to the two farms. In addition, the Irlanda and Hamburgo grids were clustered in two separate clusters, suggesting different compositions between the grids.**



**Figure 4. Individual-based rarefaction curves for all three sites without extrapolation. Based off the overlapping 95% confidence intervals, none of the sites had significantly different terrestrial small mammal community diversity. For Irlanda (LS) and Hamburgo (HS), the curves had already reached an asymptote, suggesting that we have trapped majority of the terrestrial small mammals in the sites.**



### Appendix I. Detailed descriptions of the microhabitat variables measured

| Microhabitat variables                        | Description   |
|---|---|
| Number of shade trees                         | Count of shade tree individuals within a 50 x 50 m grid   |
| Number of shade tree species                  | Count of number of shade tree species within a 50 x 50 m grid   |
| Coffee density                                | Count of coffee plants within a randomly selected 10 x 10 m plot  |
| Circumference at breast height of shade trees | Diameter and basal area values (m) were calculated from circumference measurements using stoichiometric equations                                     |
| Vegetation density at 0.5 m                   | Number of 'hits' by 0.5 m tall herbaceous plants recorded at one meter increments along three of the six transects (n = 50 measurements per transect) |
| Vegetation density at 1 m                     | Number of 'hits' by 1 m tall herbaceous plants recorded at one meter increments along three of the six transects (n = 50 measurements per transect)   |
| % ground cover                                | Percentage of herbaceous ground cover in a 0.5 x 0.5 m quadrat at every trap station (n = 36 readings per grid)                                       |
| % canopy cover                                | Percentage of canopy cover reading taken with a densiometer at every trap station and averaged across the grid (n = 36 readings per grid)             |
| Litter depth                                  | Depth of litter measured at every trap station  |
| Coffee height                                 | Estimated coffee height using marked one-meter poles taken for 18 randomly chosen coffee plants within the plot                                       |

**Appendix II. VIF values (<10) for the microhabitat variables used in the initial model.  
Distance from ravine was omitted due to the variable being categorical than continuous.**

| Microhabitat variable       | VIF      |
|-----------------------------|----------|
| Coffee density              | 6.460805 |
| Tree species                | 4.994956 |
| Basal area                  | 4.178569 |
| Vegetation density at 0.5 m | 2.955754 |
| Ground cover                | 3.005184 |
| Litter depth                | 5.048140 |



**Appendix III. Average microhabitat characteristics of each site (mean  $\pm$  SE). Except coffee density and basal area, all other microhabitat variable values were higher in Irlanda (HS) than Hamburgo (LS), indicating that Irlanda is a more heterogeneous and complex system.**

|                         | Irlanda (n=4)<br>(High Shade) | Hamburgo (n=4)<br>(Low Shade) | Forest (n=2)     |
|-------------------------|-------------------------------|-------------------------------|------------------|
| Coffee density          | 34.5 $\pm$ 4.87               | 48.5 $\pm$ 2.25               | 0                |
| Number of shade tree    | 40 $\pm$ 4.24                 | 28.5 $\pm$ 1.19               | 59 $\pm$ 1       |
| Tree species richness   | 10.25 $\pm$ 1.89              | 7.5 $\pm$ 1.66                | --               |
| Basal area              | 0.092 $\pm$ 0.02              | 0.096 $\pm$ 0.02              | 0.15 $\pm$ 0.008 |
| 0.5m vegetation density | 440.5 $\pm$ 38.28             | 170.25 $\pm$ .38.17           | --               |
| 1m vegetation density   | 155.25 $\pm$ 12.25            | 40.25 $\pm$ 11.38             | --               |
| Herbaceous ground cover | 54.1 $\pm$ 8.97               | 36.6 $\pm$ 3.70               | 23.5 $\pm$ 1.3   |
| Canopy cover            | 83.5 $\pm$ 1.77               | 32.47 $\pm$ 2.67              | 94.67 $\pm$ 0.14 |
| Litter depth            | 2.02 $\pm$ 0.34               | 1.52 $\pm$ 0.13               | 1.85 $\pm$ 0.21  |
| Coffee height           | 2.768 $\pm$ 0.18              | 0.66 $\pm$ 0.01               | --               |

**Appendix IV. Tree species found in both farms and the proportion of each species relative to the total.**

| <b>Tree species</b>             | <b>% of each species recorded from eight plots in the farm (n=274)</b> |
|---------------------------------|--|
| <i>Inga micheliana</i>          | 40.51  |
| <i>Inga vera</i>                | 7.30   |
| <i>Yucca sp.</i>                | 7.30   |
| <i>Trema micrantha</i>          | 5.84   |
| <i>Alchornia latifolia</i>      | 4.74   |
| <i>Conostegia xalapensis</i>    | 4.74   |
| <i>Terminalia Amazonia</i>      | 4.38   |
| <i>Inga rodrigueziana</i>       | 4.38   |
| <i>Apidosperma megalocarpum</i> | 2.55   |
| <i>Cordia stellifera</i>        | 2.55   |
| <i>Cestrum nocturnum</i>        | 1.82   |
| <i>Tabebuia sp.</i>             | 1.46   |
| <i>Inga lauriana</i>            | 1.09   |
| <i>Schizolobium parahybum</i>   | 1.09   |
| <i>Nectandra siuata</i>         | 1.09   |
| <i>Apidosperma cruentum</i>     | 1.09   |
| <i>Cecropia sp.</i>             | 0.73   |
| <i>Cedrela odorata</i>          | 0.73   |
| <i>Veronia deppeana</i>         | 0.73   |
| <i>Escobillo</i>                | 0.73   |
| <i>Citrus sinesis</i>           | 0.36   |
| 'Arbusto'                       | 0.36   |
| <i>Bursera simaruba</i>         | 0.36   |
| <i>Virola guatemalensis</i>     | 0.36   |
| <i>Spathodea campanulata</i>    | 0.36   |
| <i>Erythrina chiapasana</i>     | 0.36   |
| <i>Persia Americana</i>         | 0.36   |
| <i>Cupania glabra</i>           | 0.36   |
| <i>Unknown 1<sup>a</sup></i>    | 1.46   |
| <i>Unknown 2<sup>b</sup></i>    | 0.36   |
| <i>Unknown 3<sup>c</sup></i>    | 0.36   |

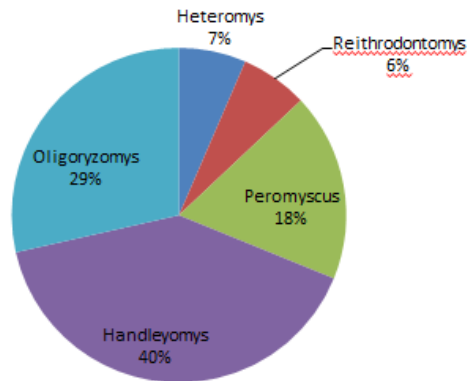
<sup>a</sup> Present only in the *La Lucha* plot

<sup>b</sup> Present only in one of the Irlanda plots far from the ravine

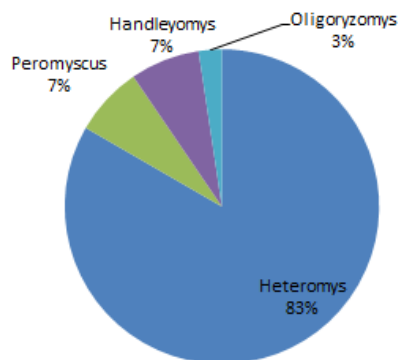
<sup>c</sup> Present only in one of the Hamburgo plots close to the ravine

**Appendix V. Pie chart of the species composition and dominance in all three sites. *Handleyomys sp.* was the dominant species in Irlanda, but least common in Hamburgo. This was opposite of what was found for *Reithrodontomys sp.* in the farms. In comparison, the forest was dominated by *H. goldmani*, a known forest specialist.**

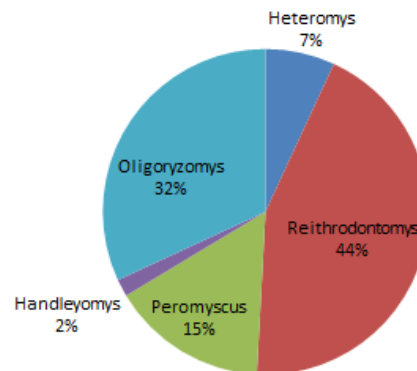
**Irlanda Small Mammal Composition**



**Forest Small Mammal Composition**



**Hamburgo Small Mammal Composition**



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