The Conservation Ecology of Neotropical Tree Cavity Communities in Forest and Agro-Ecosystems in the Alexander Skutch Biological Corridor, Costa Rica

A Dissertation submitted to the Faculty of Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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Abstract

Shade coffee agro-ecosystems with a diversified canopy have been documented to provide quality habitat for a variety of vertebrates. For tree cavity dependent species however, shade coffee may be lacking critical habitat. I chose to investigate whether cavity abundance and the number cavity forming dead trees i.e., snags differed between shade coffee and other disturbed/undisturbed habitat types within the Alexander Skutch Biological Corridor (ASBC) in Costa Rica. I also chose to investigate whether artificial tree cavities could be used in ecological restoration projects for cavity-nesting species in agro-ecosystems like shade coffee. To accomplish these tasks, I first conducted a comprehensive survey of tree cavities and snags in 1) primary cloud forest (elevation 1100-1400m), 2) primary middle elevation old-growth rainforest (650-750m), 3) selectively logged secondary middle elevation rainforest (650-700m), and (4) shade coffee (900-1000m) and installed motion-sensor cameras across from selected cavities within each habitat to monitor/compare potential occupancy/use. I then installed artificial tree cavities constructed of bamboo in 3 of the 4 habitats with iButton temperature loggers to test the prediction that shade coffee artificial cavities would have a greater number of occupancy detections due to the low number of cavities in this habitat compared with other habitat types. My findings showed an almost complete absence of snags and tree cavities in shade coffee supporting the hypothesis that shade coffee does not provide habitat for cavity-dependent species. Consistent with my prediction, artificial bamboo tree cavities in shade coffee were occupied/used most relative to the other habitats, further supporting the hypothesis that habitat for cavity-nesting species is limited is this agro-ecosystem. This thesis provides evidence that tree cavity restoration through the use of artificial cavities and a change in the management practices of shade coffee farms should be a priority for those concerned with biodiversity in shade coffee agro-ecosystems. However, future research must be conducted over a broader geographic scale to show whether the lack of available habitat for cavity nesting species documented in this thesis is reflected in other areas.

Key Words: Agro-ecosystem, Artificial Tree Cavity, Conservation, Shade Coffee

Dedication

This thesis is dedicated to

Howard Daugherty, Paul Saker, and Andrea Storm-Suke.

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Chapter 1

General Introduction

The conversion of tropical forests to agricultural lands creates a mosaic of fragmented habitats across a landscape that vary in quality for many species and represents one of the largest threats to biodiversity on the planet (Gardner et al. 2009). In fact, habitat fragmentation is a central theme in tropical conservation literature as protected areas are becoming increasingly isolated from one another through processes of forest conversion to agriculture (Simberloff & Wilson 1969; Powell & Bjork 1995; Powell et al. 2000; Ellis & Porter-Bolland 2008). Some of the most influential and important work concerning the effects of habitat fragmentation was conducted by Robert MacArthur and E.O. Wilson in the 1960's. Their work established the field of "island biogeography" and attempted to address the various factors which control species richness in natural ecosystems. Though much of their work was focused on actual islands of land (mangroves) surrounded by water, island biogeography theory applies to any area of suitable habitat that is surrounded by a substantial area of unsuitable habitat, thus impeding biological movement in and out of the "island" (MacArthur & Wilson 1963; Simberloff & Wilson 1969). Island biogeography theory evolved into meta-population theory which models the movements of individuals between habitat patches and the resulting effects on population dynamics (Esler 2000).

One method of mitigating the problem of habitat fragmentation and providing connectivity between meta-populations is through the use of biological corridors which aid in the movement of organisms between habitats (Rosenberg et al. 1997). For example, the Alexander Skutch Biological Corridor (ASBC) located on the South Pacific slope of Costa Rica, named after a renowned ornithologist, helps to maintain regional ecological connectivity between Los Cusingos, a bird sanctuary composed of middle elevation rainforest once inhabited by Skutch, and the high elevations of Chirripo National Park and La Amistad Biosphere reserve (Figure 1.1 and 1.2). Collectively, the ABSC is recognized as an ecologically significant extension of the Mesoamerican Biological Corridor (MBC) that extends from Mexico to Panama (Daugherty 2005). The Pacific slope habitats found between 500m and 1500m are considered one of the most threatened ecosystems in Central America and are unfortunately, one of the least represented in the MBC (Powell et al. 2000). Not surprisingly, the ASBC is recognized as an ecologically significant area (Rapson et al. 2012).

Among the diverse matrix of agricultural land practices within the ASBC, sun coffee and shade coffee plantations are numerous. However, over a recent 10 year period, shade coffee plantations within the biological corridor were found to have decreased at the expense of more ecologically detrimental crops like pineapple, a trend seen throughout Costa Rica as global coffee prices have declined over recent years (Rapson et al. 2012). This is particularly concerning given that the function of a biological corridor is to improve biodiversity and connectivity within a fragmented landscape by facilitating animal movement and by providing important habitat for species affected by habitat loss/conversion. Unlike more ecologically damaging crops like pineapple, shade grown coffee can contribute to the effectiveness of corridors in contributing to biodiversity conservation (Znajda 2000; Daugherty 2002; Sanchez-Azofeifa 2002). A large body of ornithological literature already documents the high habitat quality of shade coffee farms, when certain environmental conditions, like a diversified tree canopy are in place (Greenberg 1997; Calvo & Blake 1998; Mas & Dietsch 2004;Tejeda-Cruz 2004; Perfecto 2005). In fact, shade coffee agro-ecosystems can provide important refugia for organisms displaced by deforestation and land use changes (Aguilar-Ortiz 1982; Wunderle & Waide 1993; Warkentin et al. 1995; Perfecto et al. 1996; Wunderle & Latta 1996).

Despite the documented utility of shade coffee plantations in providing suitable habitat for many displaced species, they may provide limited habitat for a community of species that depend on tree cavities for reproduction and protection. Tree-cavity communities can be large and diverse, and includes mammals, birds, amphibians, and reptiles, along with a range of invertebrates. Unfortunately, documenting the species using tree cavities is difficult given that these microhabitats harbour a wide range of diurnal and nocturnal species that require specialized technology and much time to identify (e.g., Koch et al. 2008; Luneau & Brandon 2010). In the ornithological world, this collection of species that depend on tree cavities for nesting, are referred to as “nest web” communities and are comprised of organisms whose interactions are centered on the availability of cavities for nesting (Martin & Eadie 1999). In shade coffee plantations, while the coffee trees themselves may provide roosting and foraging habitat for understory specialists (e.g., Antbirds, *Thamnophilidae*) and many songbirds (Greenberg et al. 1997), they provide few cavities of use for cavity nesting species.

Shade coffee plantations are often lacking “snags”, dead standing trees that most often provide cavities critical to the reproduction and protection of a variety of wildlife in several ecological systems (Mannan et al. 1980; Raphael & White 1984; Gibbs et al. 1993; Hutto 2006). In addition, as trees in shade coffee plantations reach profitable lumber size, they are almost always harvested so there are few (or no) large dead and dying trees. Furthermore, shade coffee maintenance practices encourage the removal of diseased tree limbs and imperfections, where under natural processes tree cavities would have been formed.

The reduction of tree cavities within shade coffee plantations is of considerable concern, especially given the potential benefits this type of agro-ecosystem was thought to provide to restoration and conservation efforts aimed at biodiversity. Instead, it appears that shade coffee agro-ecosystems may exhibit trends more similar to those found in a study of tree cavity abundance in a selectively logged sub-tropical forest; having only a few tree cavities compared to primary forest. The limited number of cavities in the selectively logged forest resulted in 17 times fewer active nests (Cockle et al. 2010). Similar to shade coffee, selectively logged forests had the largest, high quality trees removed which, under natural processes, often provide the greatest number of cavities. Given the special significance of the ASBC to the Mesoamerican Biological Corridor and the importance of maintaining biological diversity within its disturbed and fragmented landscape, the need is urgent for studies to investigate conservation strategies aimed at increasing the availability of cavities in shade coffee plantations.

The use of artificial nest boxes/cavities holds particular promise. Conservationists have often considered nest boxes the fastest and most suitable way of conserving cavity-dependent bird populations (Lindenmayer et al. 2009). For example, in areas where natural nest sites are limited for certain raptor populations, nest boxes are used almost exclusively for reproduction (Hakkarainen & Korpimaki 1996). Nest boxes have also been implemented in the conservation of a few arboreal marsupials including sugar gliders (*Petaurus breviceps*, Irvine & Bender 1997) and Leadbeaters possum (*Gymnobelideus leadbeateri*, Lindenmayer et al. 2003; Beyer & Goldingay 2006). In shade coffee agro-ecosystems, the use of artificial nest boxes/cavities may be of great conservation value. Unfortunately, few studies on nest box use and occupancy in disturbed landscapes exist outside of logged or selectively logged forests (e.g., Cockle et al. 2008; Cockle et al. 2010). However, a few studies have shown that nest box usage aids conservation in other agro-ecosystems including orange groves and agricultural fields (e.g., Barba & Gil-Delgado 1990; Meyrom et al. 2009).

Consequently, the objectives of this thesis were to (1) investigate how land use within a Neotropical biological corridor (ASBC) has affected the abundance of tree cavities and cavity forming dead trees (i.e., snags) and (2) investigate whether nest boxes/cavities can be used in ecological restoration projects of cavity-nesting species in a shade coffee agro-ecosystem. To accomplish these goals, a comprehensive survey of tree cavities and snags was conducted in four diverse habitats within the landscape matrix of the ASBC including primary cloud forest (elevation 1100-1400m), primary middle elevation old-growth rainforest (650-750m), selectively logged secondary middle elevation rainforest (650-700m), and a shade coffee plantation (900-1000m). Motion-sensor cameras were used to monitor potential cavity occupancy/use in the different habitat types (Chapter 2). In addition, artificial tree cavities were installed in a shade coffee agro-ecosystem to test the prediction that artificial cavities located in shade coffee would have greater occupancy/use compared with other less disturbed habitats, due to the greater shortage of cavities available (Chapter 3).

Figures

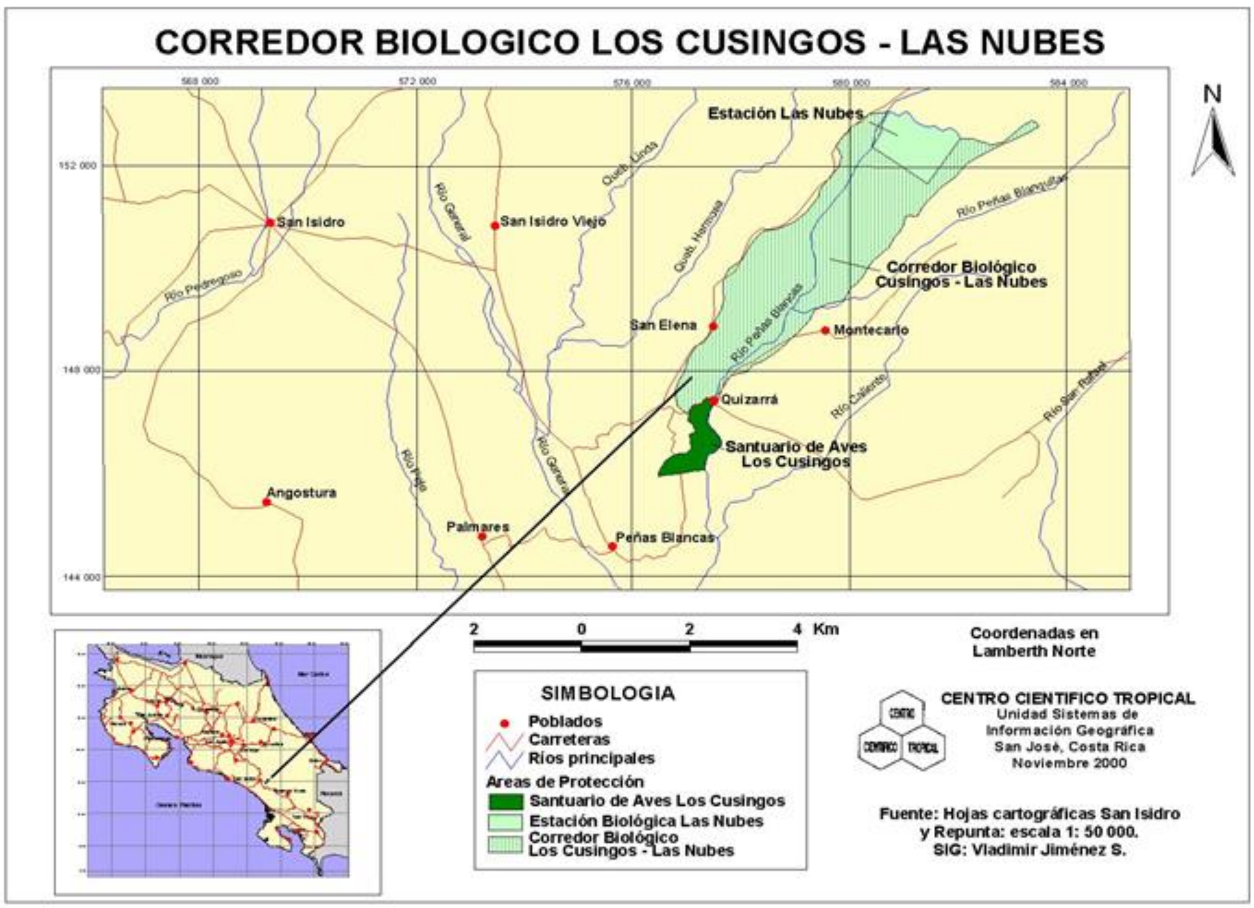

Figure 1.1 A map of the Alexander Skutch Biological Corridor (ASBC) which includes the Los Cusingos Bird Sanctuary and the Las Nubes Reserve. Map courtesy of Las Nubes: Centre for Neotropical Conservation and Research / Tropical Science Centre, 2007.

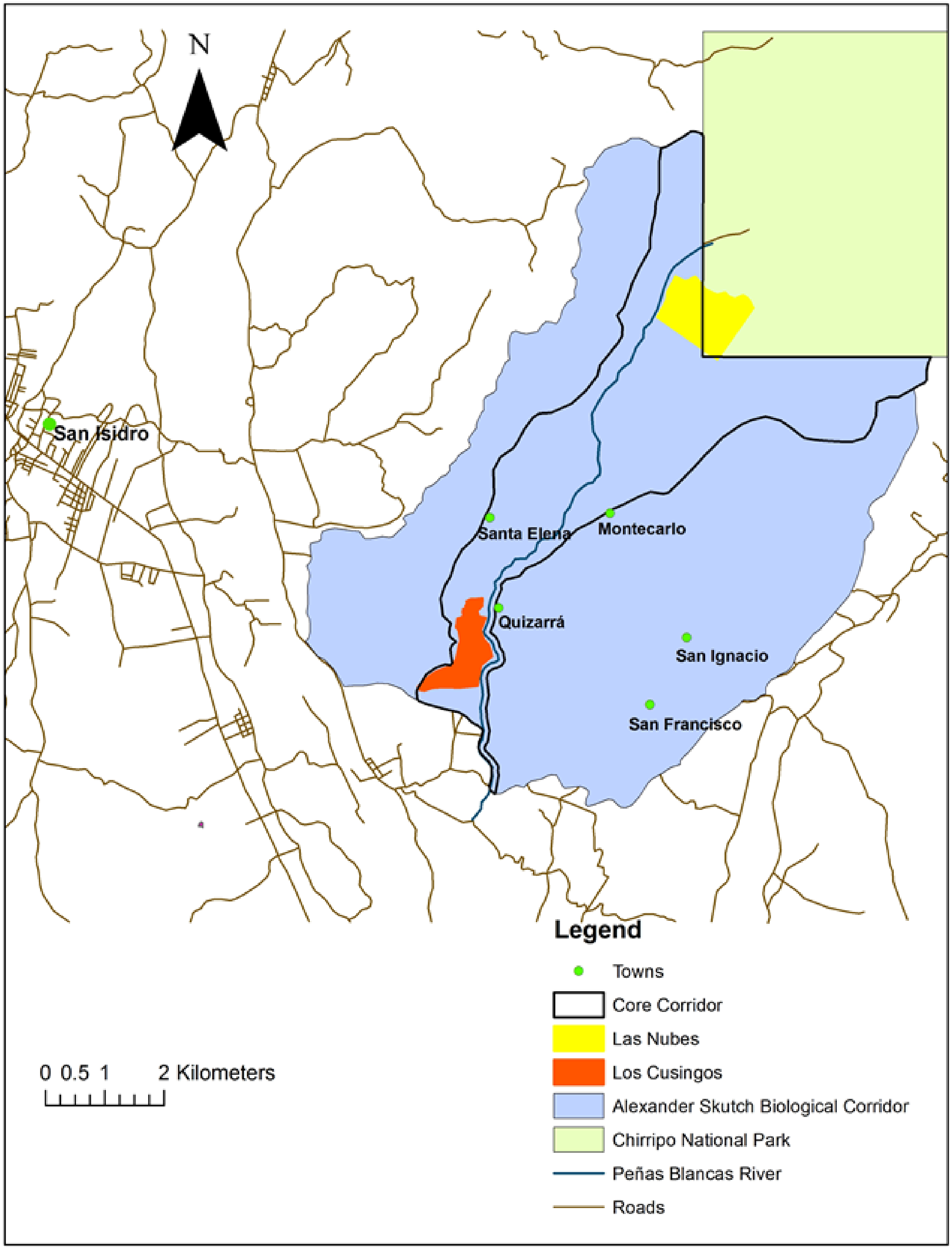

Figure 1.2 A close-up map of the Alexander Skutch Biological Corridor (ASBC) which includes the Los Cusingos Bird Sanctuary and the Las Nubes Reserve.

Chapter 2

Snag and tree cavity availability across habitats in a Neotropical biological corridor

Abstract

Tree cavities found in snags (i.e., dead or dying trees) are a critical resource for many animals but little is known regarding their abundance and characteristics in disturbed tropical habitats. This study investigated whether snag and tree cavity abundance and occupancy differed between four diverse habitat types within the Alexander Skutch Biological Corridor: primary cloud forest (elevation 1100-1400m), old-growth middle elevation rainforest (650-750m), selectively logged secondary middle elevation rainforest (650-700m), and shade coffee (900-1000m). An extensive survey of snags and tree cavities within each habitat was conducted and motion sensor cameras were used to detect tree cavity occupancy/use. The density of snags was found to differ significantly between habitat types. Secondary middle elevation rainforest had the highest density of snags (52/ha) compared with old-growth middle elevation (41/ha), primary cloudforest (27/ha), and shade coffee (1/ha). Old-growth middle elevation rainforest had the highest density of naturally occurring cavities whereas secondary middle elevation rainforest had the greatest density of excavated cavities. The number of cavity-using species detected by motion-sensor camera traps was low and totalled 18 mammals and birds. The low detection rates suggest that of the many cavities available, few were being used by cavity nesting species. The absence of naturally occurring snags and tree cavities

found in the shade coffee plantation of this study highlights the requirement for improved conservation management practices aimed at providing suitable habitat alternatives for cavity-dependent species. Of particular promise may be the use of nest boxes/artificial tree cavities in areas where snags and their cavities have been removed.

Introduction

Tree cavities are an important and highly coveted habitat for a wide range of fauna (von Haartman 1957; Short 1979; Newton 1994; Boyle et al., 2008; Czeszczewik 2008; Munks et al., 2009; Gottschalk et al., 2011; Ibarra et al.. 2014) forming a community known as a “nest web” (Martin & Eadie 1999). Combined with their ecological associations and impacts, tree cavities contribute significantly to ecological and biological diversity in forest habitats (von Haartman 1957; Skutch 1985; Newton 1994; Martin & Eadie 1999; Sandberger et al., 2010). Tree cavities in snags (e.g., dead and/or dying trees) are particularly important as sites for breeding and protection from predators by nest web communities, but have been highly reduced in abundance due to logging and deforestation (Cockle et al., 2010). In general, tree cavities have been highlighted as a limiting resource for nest-web communities, both in regards to their abundance and microhabitat characteristics, especially in modified forest landscapes (Newton 1994; Cockle et al., 2008; Cornelius et al., 2008; Remm et al., 2008; Banda & Blanco 2009; Politi et al., 2009; Cockle et al., 2010). In temperate climates, tree cavity abundance is highest in mature forests with no logging pressure whereas managed forests, and especially those managed for maximum wood production, have significantly reduced tree cavity abundance (Michel & Winter 2009). In addition to tree cavity availability, factors such as orientation, height, source of excavation, and tree diameter have all been shown to affect levels of cavity occupancy (Isaac et al., 2008; Campbell 2010). Despite much research on tree cavity ecology distribution and composition in temperate and a few subtropical forests (e.g., Braun 1988; Healey et al., 1989; Martin & Eadie 1999; Wiebe 2001; Aitken et al., 2002; Martin et al., 2004; Cockle et al., 2008; Ranius et al., 2009; Politi et al., 2010; Cockle et al., 2010), little is known of cavity ecology and distribution in tropical forests and disturbed tropical landscapes (Gibbs et al., 1993; Boyle et al., 2008). Unfortunately, temperate zone models for impacts of altered landscapes on cavity dwelling species are unlikely to apply directly to tropical communities (Michel & Winter 2009).

Gibbs et al., (1993) found a decrease in the number of snags and cavity-bearing trees present in tropical versus temperate forests. Coupled with the fact that there are approximately twice as many secondary cavity nesting bird species and relatively fewer cavity-excavating species throughout much of the tropics, cavities are likely to be a limiting resource in tropical ecosystems (Gibbs et al., 1993; Boyle et al., 2008; Cockle et al., 2010). These studies suggest that cavity-nesting species may be especially vulnerable to the high rates of tropical deforestation and land development observed (Wright & Muller-Landau 2006). For example, the Food and Agriculture Organization of the United Nations (FAO) estimated that 10.4 million hectares of tropical forest were permanently destroyed annually during 2000-2005 largely as result of conversion to agriculture (FAO 2006; Gibbs et al., 2010). This is of particular concern for keystone species, such as cavity-excavators in these tropical forest ecosystems (Stiles & Skutch 1989; Winkler & Christie 2002; Lammertink 2004; Cockle et al. 2011).

More than 80% of new farmland in the tropics in the last two decades of the 20th century has come at the expense of tropical forests (FAO 2006; Gibbs et al., 2010). The trend of converting forest to various forms of agriculture highlights the need to conduct conservation related research in agro-ecosystems in order to effectively develop and implement relevant management strategies and restoration efforts in response to tropical habitat loss. Progress on this front is owed largely to research on the potential of shade coffee in providing potential habitat for a variety of species when certain environmental conditions, such as a diversified canopy, are in place (Greenberg 1997; Calvo & Blake 1998; Mas 2004; Tejeda-Cruz & Sutherland 2004; Perfectoa 2005; Williams-Guillen 2006; Jha & Dick 2010). Currently, however, there appears to be no research focused on the value of shade coffee farms for providing habitat to resident cavity dwelling species specifically. Information of this kind is of particular importance for those cavity-excavating keystone species, like woodpeckers, who are likely to be increasingly displaced due to the continued development of tropical forest communities (Stiles & Skutch 1989; Lammertink 2004, 2007).

Given their ecological importance and specific conservation requirements, it is surprising that tree cavity communities in disturbed tropical habitats have previously received relatively little research attention (Martin & Eadie 1999; Boyle et al., 2008; Cockle et al., 2010). In order to maintain and/or restore tree cavity habitat in the Neotropics, particularly in disturbed or managed environments, more baseline information must be collected in order to determine the natural rates of tree cavity abundance, occupancy and tree-specific characteristics relating to age and rates of decay that are currently unknown (Boyle et al., 2008). Comparison of survey data of this kind from disturbed landscapes (e.g. secondary forests both directly after logging and ten years after) and ecologically relevant agro-ecosystems (e.g. shade grown coffee and timber plantations) can be compared with primary forest habitats (Boyle et al., 2008; Cockle et al., 2008; Cornelius et al., 2008). Several such studies in the Neotropics have found that disturbed landscapes reduce the abundance and variety of tree cavities available, thus negatively affecting cavity nest web communities (Cornelius et al., 2008; Cockle et al., 2008, 2010).

Consequently, this study investigated whether tree cavity abundance, occupancy, and orientation varied among four diverse habitats of varying elevation including primary cloud forest (elevation 1100-1400m), primary middle elevation old-growth rainforest (650-750m), selectively logged secondary middle elevation rainforest (650-700m), and a shade coffee plantation (900-1000m) in the Alexander Skutch Biological Corridor (ASBC) of southern Cosa Rica. It was hypothesized that the selectively logged forest and shade coffee farm would have fewer tree cavities per hectare and lower rates of occupancy compared to less disturbed habitats.

Methods

Tree Cavity Surveys

Beginning in late May 2011, four representative habitat types were chosen within the diverse landscapes and ecosystems present in the Alexander Skutch Biological Corridor, Costa Rica: 1) Primary cloud forest (elevation 1100-1400m), 2) Old-growth middle elevation wet rainforest (650-750m), 3) Selectively logged middle elevation wet rainforest (650-700m), 4) Shade-coffee plantation (900-1000) (Figure 2.1). Within each habitat, four 1 hectare (100m x 100m) quadrants were randomly established and marked via GPS, with each quadrant being separated from the others by at least 50m. To reduce edge effect, all quadrants were located at least 100m from any trails, roads or other habitat boundaries. Surveys for tree cavities as well as snags and dead standing trees, were conducted in each quadrant throughout all four habitats, totalling 16 hectares. Surveys were completed by late July 2011. Transects of each quadrant were spaced five metres apart and surveyed at an average pace of 3km/hr, measured by handheld GPS units. Each tree was examined from all sides for tree cavity presence with the use of binoculars from the ground. All snags and dead standing trees >10cm DBH (diameter at breast height) were surveyed and catalogued. The location of all tree cavities and snags were marked using a hand held Garmin GPS device. We measured DBH, estimated snag height, and assessed the overall condition of the tree. Tree cavities were placed into one of three categories: 'excavated' by a primary excavator as evidenced by bill markings on cavity and size, 'modified' by a mammal or bird as indicated by markings (e.g., scratch marks, teeth marks, additional material found in cavity, etc), and 'natural' cavities, those produced by weather and erosion. Feedings signs on the snags (i.e. excavation for insects) were placed into one of 4 categories including 'no signs', 'light' signs as indicated by having up 1/3rd of the trunk exhibiting signs of foraging (e.g., scaling, markings/scratches, digging, holes in trunk, etc), 'medium' signs by having 1/3rd to 2/3rds of tree indicating signs of foraging, and 'heavy' signs by having more than 2/3rds of the snag showing signs of foraging.

Cavity Occupancy-Camera traps

Upon completion of the tree cavity surveys, cavity monitoring for occupancy was initiated using motion detection camera traps (n = 8-13 cameras/habitat type). The selection criteria for cavity monitoring was driven by environmental factors (e.g., no obstructions in camera view, available trees to climb & mount cameras) and safety concerns (e.g., inability to climb rotten or dying trees, etc). Beginning mid-late August 2011 and ending in January 2012, remote motion-sensor cameras were installed. Cameras were set to capture 15 seconds of video with a 1 second interval between shots, including infra-red night-time video capture. Whenever possible, cameras were mounted at cavity level in adjacent trees < 5m distance from the cavity, for the most ideal angle of view.

Statistical Analyses

Prior to further statistical analyses, each dependent variable was tested for normality and homogeneity of variances. If the Kolmogorov-Smirnov and/or Levene's statistic were significant ($P < 0.05$), non-parametric statistical testing was used, otherwise parametric statistical analyses were performed. A Chi-Squared test was used to compare number of snags, and number of cavities among the four habitat types. A Kruskall-Wallis test was used to compare snag height and DBH among habitats and Mann-Whitney U tests were used to compare habitats in pairs to test for significant differences. Cavity height and cavity diameter were compared using a one-way ANOVA. Additionally, a chi-squared was performed to test whether the orientation of cavities and type of cavity differed between the different habitat types. Shade coffee was excluded from these cavity characteristic analyses because only one snag and cavity was found in that habitat. All analyses were performed in SPSS version 17 (SPSS Software, Armonk, New York).

Results

Snag Characteristics

The number of snags per habitat type differed significantly between habitat types (Chi-Squared test, $\chi^2 = 798.20$, $df = 3$, $P < 0.0001$). Secondary middle elevation rainforests had the greatest average number of snags/ha, followed by old-growth middle elevation rainforest and primary cloud forest (Figure 2.2a).

Similarly, the diameter at breast height (DBH) of snags differed between habitat types (Kruskal Wallis test, $\chi^2 = 7.484$, $df = 2$, $P = 0.02$). In general, snags of primary cloud forest had the largest DBH followed by snags of secondary middle and old growth middle elevation rainforest (Figure 2.2b). Primary cloud forest snags had significantly larger DBHs compared to old-growth middle elevation rainforest (Mann Whitney U = 7047.0, $N_1 = 179$, $N_2 = 117$, $P = 0.007$), and the DBH of old-growth middle elevation rainforest snags was nearly significantly different from secondary middle elevation rainforest (Mann Whitney U = 9718.5, $N_1 = 117$, $N_2 = 210$, $P = 0.06$). In contrast, for the subset of snags that held cavities, DBH did not differ between habitat types (Kruskal Wallis test, $\chi^2 = 2.71$, $df = 2$, $P = 0.258$).

The height of snags did not differ between habitat types (Kruskal Wallis test, $\chi^2 = 0.419$, $df = 2$, $P = 0.81$, Figure 2.2 c). Similarly, the height of snags with cavities was similar across habitat types (Kruskal Wallis test, $\chi^2 = 0.77$, $df = 2$, $P = 0.68$). The frequency of different feeding signs on snags was nearly significantly different between habitat types (Chi-square test, $\chi^2 = 12.82$, $df = 6$, $P = 0.05$).

Cavity Characteristics

The number of cavities in snags did not differ between habitat types (Chi-Squared test, $\chi^2 = 4.65$, $df = 3$, $P = 0.20$, Figure 2.2 a). Similarly, several cavity characteristics did not differ between habitat types including cavity height (Kruskal Wallis test, $\chi^2 = 0.842$, $df = 2$, $P = 0.66$), cavity diameter (Kruskal Wallis test, $\chi^2 = 4.81$, $df = 2$, $P = 0.09$), and cavity orientation (Chi squared test, $\chi^2 = 0.99$, $df = 2$, $P = 0.61$).

In contrast, the type of cavity (e.g., natural, modified, excavated) differed significantly between habitats (Chi-squared test, $\chi^2 = 13.31$, $df = 4$, $P = 0.01$). In particular, old-growth middle elevation rainforest had the highest number of natural cavities whereas secondary middle elevation rainforest had the largest number of excavated cavities (Table 2.2).

Cavity Occupancy

A total of 18 species of birds and mammals were detected by the motion-sensor camera traps monitoring of a total of 32 cavities, however the proportion of cavities occupied versus unoccupied did not differ between habitat types (Chi-square test, $\chi^2 = 3.452$, $df = 8$, $P = 0.903$, Table 2.3). A list of all identified species according to habitat type can be found in Appendix A.

Discussion

The almost complete absence of snags and tree cavities in the shade coffee habitat shows that current management practices in this type of shade coffee farm result in a nearly complete lack of tree cavity habitat for cavity dependent wildlife. In a previous study, Pale-billed Woodpeckers, *Campephilus guatemalensis*, the largest cavity excavating species in the corridor and known old-growth forest specialist, were found to be almost completely absent in shade coffee plantations (Saker 2007). This lack of naturally occurring snags and tree cavities highlights the requirement for improved management strategies aimed at providing suitable habitat alternatives for species displaced by shade coffee plantations and other agro-ecosystems. Of particular promise may be the use of nest boxes/artificial tree cavities in areas where snag/cavity density may be low. Due to the seed dispersal/pollinating benefits of many cavity nesting species (eg., Fiery-billed Aracari, *Pteroglossus frantzii*, Black-throated Trogon, *Trogon rufous*, Resplendant Quetzal, *Pharomachrus mocinno*, etc.), the use of nest boxes/artificial tree cavities could be an especially important and effective ecological restoration strategy in regenerating agro-ecosystems and forest habitats.

Although cavity density was far lower in shade coffee, it did not differ among the other habitat types. It was somewhat surprising to find no significant increase in the average DBH of snags surveyed in selectively logged middle elevation rainforest when compared to old-growth middle elevation forest. One possible explanation could be the increased presence of fast growing early successional species like those found in the logged forests compared to the slower growing species (e.g. Mahogany, *Swietenia* spp) found in old-growth forests. Quickly growing species such as Mayo Colorado, *Vismia guatemalensis*, or Targua, *Corton draco*, develop a relatively wide DBH in very few years, compared with many of the tree species associated with primary and old-growth forests. These trees also die and decay relatively quickly, providing snags and possible tree cavities in significant numbers. However, due to the especially soft nature of the wood, these early successional trees do not last long as standing snags after they die when compared with the slower rate of decay exhibited by hardwood trees found in old-growth forests (Cockle et al., 2011). I witnessed the destruction of Golden-naped woodpecker, *Melanerpes chrysauchen*, nests on two separate occasions, after they were excavated in a recently dead *Vismia* sp. located in disturbed, early succession forest patches. The rate of decay was so rapid that the snags broke off at the base and fell to the ground shortly after nesting began. In this way it is possible that early succession snags may even act as an ecological trap for cavity nesting species, i.e., by attracting species to a habitat with low quality snags. Further research on rates of tree decay and reproductive success of cavity nesters in old-growth trees versus early-successional snags would be necessary to test this hypothesis.

In the Neotropics, a general lack of quality cavities has already been shown to limit specific species of secondary cavity nesters, such as the Puerto Rican Parrot (Snyder et al., 1987), and the Great Green Macaw, *Ara ambiguus*, in Costa Rica, which relies on large, naturally eroded cavities and hollows in very large, old trees (Stiles & Skutch 1989). Scarlet Macaws, another large, secondary cavity nesting species disappeared from the Alexander Skutch Biological Corridor *(cira* 1970s) as the surrounding forests were cleared and selectively logged of all the largest trees (Skutch 1992). In addition, Chestnut-mandibled toucans, another large secondary cavity nesting species also became uncommon in the biological corridor around this time (Rojas *pers. comm*., 2012). Interestingly, the camera trap monitoring results from this study suggest that most tree cavities are not being used on a regular basis by cavity-nesting species supporting the possibility that tree cavities suitable for roosting and nesting, may be in even shorter supply than initially hypothesised (Gibbs et al., 1993; Boyle et al., 2008; Cockle et al., 2010), even in an intact forest ecosystem. This is strengthened by the fact that some of the cavities were used by a variety of species whereas other cavities were unoccupied. I observed competition between cavity-nesters outside of the study plots on several occasions, where Fiery-billed aracaris, *Pteroglossus frantzii*, usurped Pale-billed woodpeckers from occupied or freshly excavated cavities. Further research on cavity specific characteristics between occupied and unoccupied tree cavities is needed to determine species cavity preferences and to assess the extent to which suitable cavities are in short supply and limit local biodiversity of cavity-nesters.

The low cavity occupancy documented in this study, despite extensive monitoring, meant that it was not possible to create a ‘nest web’ to understand the ecological interactions among cavity-using species. Of course, it is possible that biodiversity in the corridor is suppressed by factors other than cavity availability, for instance due to low forest cover and forest fragmentation. Nest webs are expected to vary among habitat types in the tropics, because ecozones, forest type, and forest structure vary wildly, especially along elevational gradients (Richards 1996; Macdonald & Johnson 2000). With more sampling sites and direct elevational gradient sampling of biodiversity it would be possible to identify community specific micro-habitat requirements and limiting factors in regards to tree cavities and snag abundance and species occupancy. Such findings would be important in developing conservation and perhaps restoration strategies for cavity-using wildlife (Boyle et al., 2008; Cockle et al., 2008; Cockle et al., 2011). One important step would be controlled studies with nest boxes/artificial tree cavities in a variety of tropical habitats, including agro-ecosystems, such as shade coffee, which have been highlighted as important habitat for a wide array of wildlife in the tropics (Greenberg 1997; Mas 2004; Tejeda-Cruz & Sutherland 2004;

Perfectoa 2005; Williams-Guillen 2006; Cockle et al., 2008; Jha & Dick 2010; Cockle et al., 2011).

Tables & Figures

Table 2.1 The number and density of snags, cavities and camera trap occupancy detections from surveys (4 ha per habitat type) in different habitats in the Alexander Skutch Biological Corridor, Costa Rica

Habitat Type	Number of Snags	Number of Cavities	Camera Trap Occupancy
1° Cloud Forest	108 (27/ha)	28 (7/ha)	3 (0.75/ha)
Old Growth Middle Elevation Rainforest	163 (41/ha)	42 (11/ha)	7 (2/ha)
2° Middle Elevation Rainforest	207 (52/ha)	35 (9/ha)	7 (2/ha)
Shade Coffee	1 (0.25/ha)	1 (0.25/ha)	-

Table 2.2 The number of natural, modified, and excavated cavities in three different habitat types in the Alexander Skutch Biological Corridor, Costa Rica. 'Natural' cavities were formed by processes of weather and erosion; 'Modified' cavities were natural cavities with evidence of animal modification (i.e., scratch marks, teeth marks, additional material); 'Excavated" cavities were cavities excavated by cavity excavators (e.g., woodpecker spp.), indicated by bill markings on cavity trees, cavity size, etc.

Habitat Type	Natural	Modified	Excavated	Total
1° Cloud Forest	10	1	5	16
Old-Growth Middle Elevation Rainforest	20	17	6	43
2° Middle Elevation Rainforest	4	4	8	16
Total	34	22	19	75

Table 2.3 The number of species detected by motion-sensor camera traps, the number of cavities monitored, the total number of days monitored and the estimated rate of species detections per day for three habitat types monitored in the Alexander Skutch Biological Corridor. See Appendix A for a list of all species.

Habitat Type	Number of Species	Number of Birds	Number of Mammals	Number of Cavities Monitored	Total Number of Days Monitored	Rate of Species Detection (#/d)
1° Cloud Forest	3	2	1	10	976	0.003
Old Growth Middle Elevation Rainforest	6	3	3	13	1059	0.006
2° Middle Elevation Rainforest	9	6	3	12	851	0.011

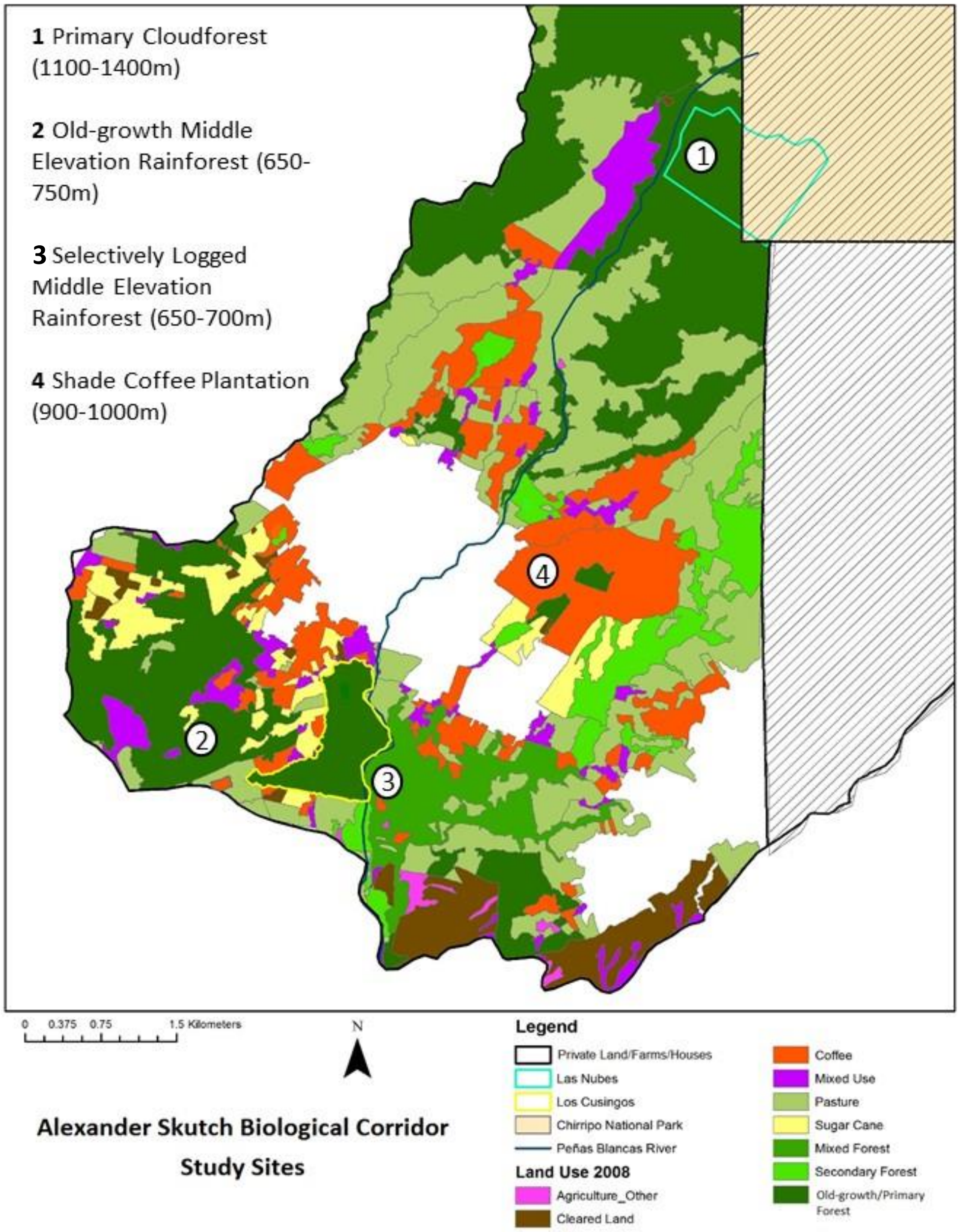

Figure 2.1 Map of study sites within the Alexander Skutch Biological Corridor, Perez Zeledon, Costa Rica.

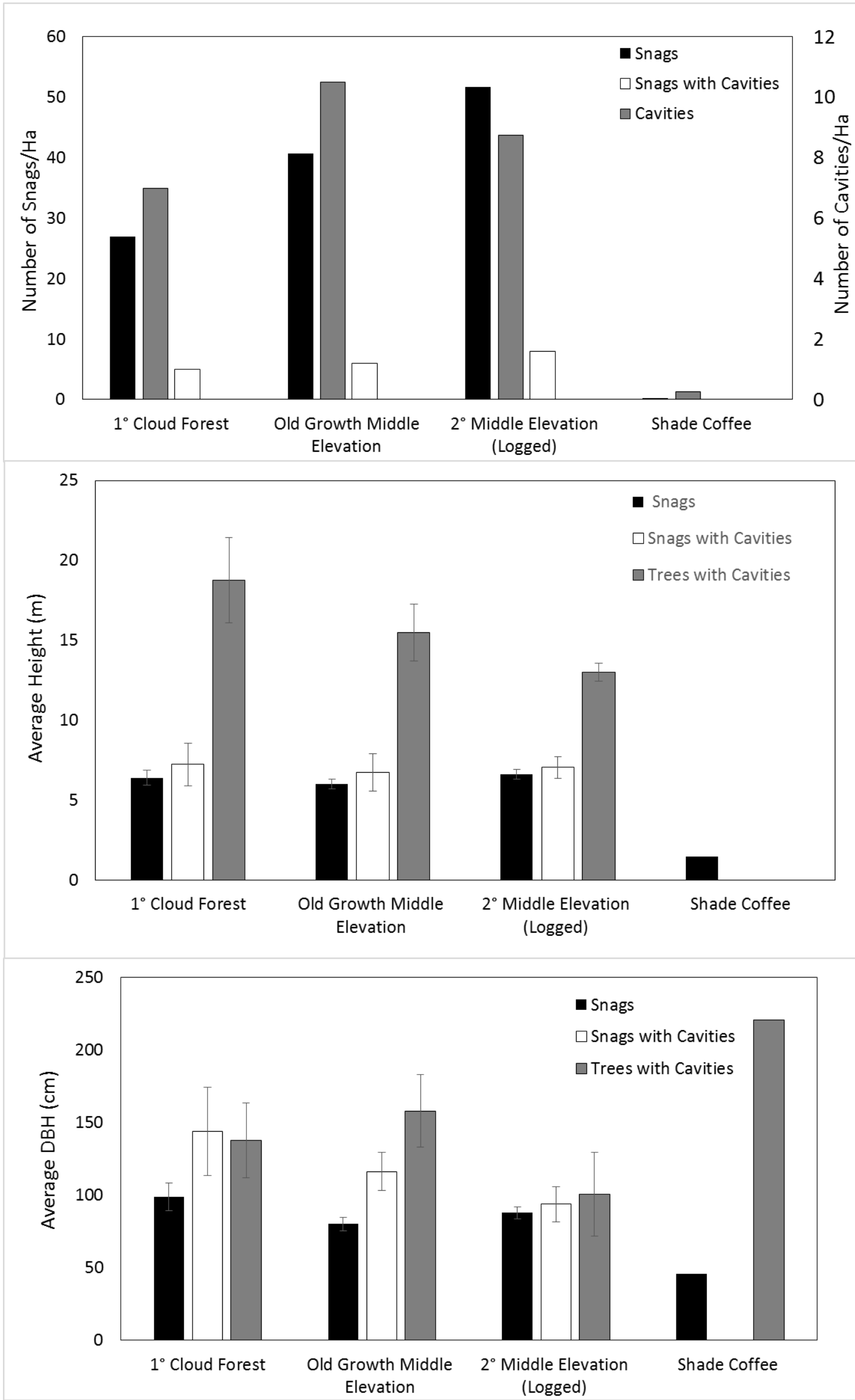

Figure 2.2 Tree cavity survey in primary cloud forest, primary middle elevation rainforest, secondary middle elevation (logged), and shade coffee showing (**A**) Number of snags/ha, number snags with cavities, and number cavities/ha (**B**) Average diameter at breast height (DBH) ± standard errors and (**C**) Average height. See Table 2.1 for sample sizes.

Chapter 3

Artificial Tree Cavity Monitoring In a Shade Coffee Agro-Ecosystem

Abstract

It is unknown to what extent the addition of nest boxes/cavities in tropical agro-ecosystems may aid in the conservation of cavity nesting species. This study compared bamboo artificial cavity use/occupancy in a range of undisturbed and disturbed habitat types including old-growth middle elevation rainforest, selectively logged secondary middle elevation rainforest, and a shade coffee plantation within the Alexander Skutch Biological Corridor (ASBC) of southern Costa Rica. Large and small bamboo cavities (large = 10 cm entrance diameter and 35cm depth, small = 4.5 cm entrance diameter and 25 cm depth) were installed and iButton temperature loggers used to infer occupancy. Artificial cavities successfully attracted birds and mammals to shade coffee in greater numbers compared to the less disturbed habitats, suggesting that biodiversity in this agro-ecosystem is limited by a shortage of tree cavities. A tropical screech owl (*Otus choleba*) and a house wren (*Troglodytes aegon*) with three eggs nested within large cavities located within the shade coffee along with another unidentified nesting bird species with three eggs. In addition, five woolly opossums (*Caluromys derbianus*) were found occupying large cavities within the shade coffee. iButton and observational evidence indicated a preference for large cavities relative to small. This study suggests that the use of artificial cavities/nest boxes holds great promise for the enhancement of shade coffee biodiversity and the conservation of cavity nesting species in the tropics.

Introduction

Currently, one of the most significant threats to remaining global forests is conversion to agricultural land. In fact, agriculture alone accounts for more than 70% of all deforestation across tropical and sub-tropical countries (Hosonuma et al., 2012). However, of the various forms of agriculture, shade coffee can provide critical habitat and enhance connectivity for local fauna between forest patches when managed correctly. For example, shade coffee agro-ecosystems have been found to provide important refugia for a wide range of organisms (Aguilar-Ortiz 1982; Wunderle & Waide 1993; Warkentin et al., 1995; Perfecto et al., 1996; Wunderle & Latta 1996). As a consequence, shade-coffee agro-ecosystems could be of particular importance to conservation efforts directed at increasing biodiversity and connectivity in disturbed tropical landscapes.

However, despite their potentially high value to conservation efforts, shade coffee plantations may not provide suitable habitat for cavity nesting species of birds and mammals. In particular, shade coffee plantations are lacking persistent dead standing trees (snags) which, in many other systems, are closely linked to the availability of suitable cavities for cavity nesting species (Hutto 2006; Gibbs et al., 1993; Boyle et al., 2008; *see* Chapter 2). Cavity nesting species play key roles in tropical forests as tree seed dispersers (Howe 1984; da Silva & Tabarelli 2000), and in the case of cavity excavating species (e.g., woodpeckers), can provide important habitat for a variety of secondary cavity nesters (e.g., toucans) who depend on cavities but cannot excavate them. Given that tree cavities are a keystone resource (e.g., Brightsmith 2005) the loss of this resource in the conversion of forest to shade coffee is of great concern. While a few studies have quantified the effects of shade coffee plantations on cavity nesting species of birds and mammals in sub-tropical and tropical areas (e.g., Cockle et al., 2010; Warakai et al., 2013), no studies have investigated the potential use of artificial nest boxes in shade coffee plantations in the Neotropics to help conserve populations of cavity nesting species. This is surprising given that artificial nest boxes are widely used for the conservation of cavity nesting species elsewhere (e.g., Newton 1994; Lalas et al., 1999; Katzner et al., 2005).

For example, artificial nest boxes have been successfully employed in many restoration efforts involving both cavity-nesting birds and mammals in a variety of temperate and subtropical environments (Beyer et al., 2006; Cockle et al., 2008; Isaac et al., 2008; Lindenmayer et al., 2009; Goldingay & Stevens 2009; Meyron et al., 2009). In addition, nest boxes have been used to bolster populations of endangered or near threatened cavity nesting species (e.g., Meyrom et al., 2009; Rodriguez et al., 2011). However, very few studies have been conducted in agro-ecosystems like shade coffee. One study, focused on orange groves in the Mediterranean forest region of eastern Spain highlighted the usefulness of nest boxes in this type of agricultural setting (Barba & Gil-Delgado 1990). In another study, a long-term investigation of Barn Owls (*Tyto alba*) in Israel demonstrated that the use of artificial nest boxes in various agricultural areas successfully increased population sizes (Meyrom et al., 2009).

The success of these studies relied on the construction of artificial nest boxes that met with the target species' cavity preferences. These preferences include the selection of cavities with specific qualities related to tree type and diameter (e.g., Schepps et al., 1999), entrance size diameter (e.g., Cockel et al., 2008), interior volume (e.g., Weibe & Swift 2001), cavity height (e.g., Li & Martin 1991) and orientation (e.g., Boyle et al., 2008). Presumably, these characteristics are selected by different species to optimize their reproductive success by limiting their susceptibility to predators, locating themselves close to available food sources and by providing a thermal environment that results in energetic benefits to the occupants (Sedgeley

2001). While it is difficult to define all of the characteristics that make up a ‘quality’ cavity due to the grand number of cavity using species and their diverse preferences, a few characteristics are similar among different species. For example, tree cavity heights for several different primary excavating species including Downy Woodpeckers (*Picoides pubescens*), Harry Woodpeckers (*Leuconotopicus villosus*), and Northern Flickers (*Colaptes auratus*) are similar and range between 12-16 m (Li & Martin 1991). Similarly, a cavity depth of 20 cm is often found for Tropical Screech-Owls (*Megascops choliba*) and Ferruginous Pygmy Owls (*Glaucidium brasilianum*) (Cockle et al. 2008). While cavity orientation preferences vary widely depending on habitat characteristics (e.g., canopy cover, sun exposure, etc), it has been found to be non-randomly selected by woodpeckers in tropical rainforests (Rico & Sandoval 2014). Despite these similarities, the construction of artificial cavities suitable to a wide range of cavity using species of birds and mammals may be challenging.

This study compared artificial cavity use/occupancy in a range of undisturbed and disturbed habitat types including old-growth middle elevation rainforest (650-750m), selectively logged secondary middle elevation rainforest (650-700m), and a shade coffee plantation (900-1000m) in the Alexander Skutch Biological Corridor (ASBC) of southern Costa Rica. In the construction of artificial cavities, cavity characteristics that accommodated the preferences of a wide variety of birds and mammals were used and included two sizes of artificial cavities (small and large), a cavity orientation facing North to reduce sun exposure and a height of 10 m in the tree. In contrast to traditional methods of cavity occupancy monitoring (e.g., Cockle et al. 2010), this study used iButton temperature loggers affixed to the inside of nest boxes to infer occupancy. The use of temperature-inferred monitoring allowed data collection during the daytime and nighttime simultaneously at different nest boxes over the same 9 month period. It was hypothesized that the shade coffee agro-ecosystems would have the highest levels of occupancy by cavity nesting species when compared with the other habitats.

Methods

Study Sites

Beginning in late May 2011, three representative habitat types were chosen to compare artificial tree cavity occupancy within the Alexander Skutch Biological Corridor, Costa Rica: 1) Old-growth middle elevation wet rainforest (650-750m); 2) Selectively logged middle elevation wet rainforest (650-700m); 3) Shade-coffee (900-1000) (*See* Chapter 2). A subset of the 1 hectare survey plots within each habitat type were selected for installation of artificial tree cavities (i.e., 2 plots each in old growth and selectively-logged middle elevation rainforest; 3 plots in shade coffee). To reduce edge effect, all quadrants were located at least 100m from any trails, roads or other habitat boundaries.

Artificial tree cavities

Cylindrical artificial tree cavities (N = 60) were constructed using bamboo with removable tops for access to the cavity (Figure 3.1). Cavities were either 'small' in diameter and cavity depth, measured from the base of the entrance hole to the base of the cavity (ie. total diameter = 10-12 cm, entrance diameter = 4.5 cm, depth = 23 cm) or 'large' in diameter and cavity depth (ie. total diameter = 18-22 cm, entrance diameter = 10 cm, depth = 35 cm). All artificial tree cavities were installed at 10 m height with iButton data loggers (Maxim Integrated, San Jose, CA) programmed to record internal cavity temperature (°C) every 15 minutes. In addition, all cavities had a plastic mesh affixed to the bottom of the interior over the bottom lip of the cavity entrance, and extended ~15cm down the exterior to provide grip on the bamboo. The ladder was attached using thumb tacks as well as steel construction wire looped through small holes drilled into the bamboo. All cavities had a handful of hay added to the bottom of each cavity as substrate.

During March 2012 to December 2012, 10 'small' and 10 'large' artificial tree cavities were deployed in each of the three focal habitat types. Nest boxes were placed at a height of 10m on the host tree and were spaced at least 50m apart from one another and at least 50m from the edge of the habitat type. Artificial tree cavities were installed on trees without naturally occurring tree cavities to avoid bias in attracting occupants. Artificial tree cavities were oriented in a North facing direction, to imitate woodpecker preference and to help control microclimatic conditions with decreased exposure to full sun (Boyle et al., 2008). All host trees had a diameter at breast height greater than 20 cm.

To examine whether occupancy (*see* below) differed on a seasonal basis (e.g., rainy: December to April, dry: May to November), the shade coffee habitat type was monitored for additional time including periods in August – October 2011, March – December 2012, and Jan – Feb 2013.

Occupancy Detections- Temperature loggers

To estimate cavity occupancy using iButton temperature loggers, the average cavity temperature per day was estimated separately for 'Daytime' (6am – 6pm) and 'Nighttime' (6pm – 6am) for each artificial tree cavity monitored, to allow detection of both diurnal and nocturnal occupants. Occupancy was defined as any detection, day or night, in which a given artificial tree cavity exceeded a 1°C difference when subtracted from the average per day or night temperature of all artificial cavities within the same study plot. Therefore, a given cavity with a temperature difference exceeding 1°C for 10 consecutive days would have counted as 10 detections of occupancy. To select 1°C as the threshold for occupancy, I compared average temperature differences across all habitat types and found that old-growth middle elevation had the lowest value of 1.2°C (Figure 3.2). To accommodate for the low average temperature difference in this habitat, 1°C was selected as the threshold for occupancy.

A Chi-squared analysis was used to estimate whether inferred occupancy differed between old-growth middle elevation rainforest, selectively logged middle elevation rainforest, and shade coffee during ‘daytime’ and ‘nighttime’. To estimate whether there were differences in occupancy between the rainy and dry seasons within the shade coffee habitat type, a chi-squared analysis was performed.

All analyses were conducted separately for large diameter cavities and small diameter cavities and were performed in SPSS version 17 (SPSS Software, Armonk, New York).

Observational Activity & Occupancy

During the same period as iButton temperature monitoring, visual observations of animal activity and occupancy were recorded. When possible, all animals observed or their leavings (e.g., feather, fur, etc) within the artificial cavities were identified as either a mammal, bird, amphibian, insects or spiders or marked as unknown. A Chi-squared test was used to estimate whether visual observations differed between old-growth middle elevation rainforest, selectively logged middle elevation rainforest, a shade grown coffee plantation.

Results

Occupancy Detections- Temperature loggers

To test for habitat differences in occupancy, I first controlled for both cavity size and time of day. For night monitoring, the frequency of occupancy differed significantly between habitat types for both large ($\chi^2 = 74.01$, $df = 2$, $P < 0.0001$) and small ($\chi^2 = 158.90$, $df = 2$, $P < 0.0001$) artificial tree cavities. The same was true for ‘daytime’ events for large ($\chi^2 = 237.76$, $df =$

2, $P < 0.0001$) and small ($\chi^2 = 37.04$, $df = 2$, $P < 0.0001$) cavities. Shade coffee had the greatest number occupancy detections at night (Figure 3.3a, c), while selectively-logged secondary middle elevation rainforest had the greatest number of occupancy detections during 'Daytime' (Figure 3.3b, d). The majority of artificial cavities had less than five detections each (Figure 3.4) however, in every habitat type except for old-growth middle elevation rainforest, certain cavities had detections that ranged from 15 to 70.

Visual Observations of Occupancy

A comparison of the observed number of mammals and birds did not differ between habitat types ($\chi^2 = 2.69$, $df = 2$, $P = 0.26$). While not statistically significant, shade coffee exhibited similar occupancy trends to those recorded by temperature loggers (Tables 3.1 & 3.2).

A total of four nest artificial cavities were found to have nesting species of birds (*see* Table 3.3 for species, Figure 3.5). Activity observed at the artificial cavities included hay being moved, removed or moulded, scratch marks or bill marks on the cavities interior or exterior, the presence of vegetation (e.g., leaves, seeds) found within the cavities, destruction of cavities by white-faced capuchin monkeys (*Cebus capucinus*), nesting, and/or the presence of feathers (Table 3.3.).

Seasonal and Within-Site Variation in Shade Coffee

To examine seasonal differences in artificial cavity occupancy, the shade coffee plantation was monitored for additional time relative to the old-growth and selectively logged habitats. Large and small artificial cavities in the rainy season had more occupants than the dry season (large: $\chi^2 = 12.08$, $df = 1$, $P < 0.001$; small: $\chi^2 = 5.172$, $df = 1$, $P = 0.023$).

Discussion

Shade coffee was found to contain a very low density of snags and cavities compared to old-growth and secondary-logged middle elevation rainforest, which could suppress biodiversity of cavity-nesters in shade coffee (Cockle et al. 2010; *see* Chapter 2). This study is the first to examine the differences in artificial cavity occupancy in a range of undisturbed and disturbed habitats in southern Costa Rica including middle elevation old-growth rainforest, selectively logged secondary middle elevation rainforest, and shade coffee. It is also the first study to my knowledge to use bamboo (Bambuseae) as the source material for the artificial cavities. Bamboo offers several advantages over traditional nest box materials (e.g., wood, PVC tubing) as it is a more sustainable and less expensive material that is easily accessible to farmers and conservation organizations interested in building artificial cavities without using traditional materials. Certainly, the greatest advantage of bamboo use is that unlike wood, it is not made from the material which also requires conservation.

The results from occupancy detections using iButtons were similar to those from visual/physical evidence, which suggests that the temperature-inferred occupancy detections were accurate. Consistent with the hypothesis that natural cavities are more limiting in shade coffee, shade coffee was found to have the greatest proportion of occupants in artificial cavities relative to the other habitat types. In general, large cavities were occupied more often than small nest boxes. These findings suggest that shade coffee agro-ecosystems are lacking suitable habitat (i.e. quality tree cavities) for many cavity nesting animals, including nocturnal species. Preliminary results suggest that the rainy season (i.e. December to April) had more occupancy detections than the dry season in the shade coffee plantation (i.e. May to November). While further long-term study is needed to clarify this finding, it is possible that the higher number of occupants during the rainy season was related to taking shelter during intense periods of precipitation, which in southern Costa Rica, can amount to 1350 mm during the rainy season (Coen 1983). Or, this could result from seasonality in breeding activity. From these findings, it is clear that the use of artificial tree cavities in shade coffee agro-ecosystems have potential for conserving cavity nesting species of birds and mammals and may be of great use in restoration efforts.

Observational evidence suggests that the presence of artificial cavities in the disturbed habitat types (i.e., secondary-logged rainforest, shade coffee) were particularly important to arboreal marsupials and cavity nesting birds. The Central American woolly opossum (*Caluromys derbianus*) was encountered most frequently during daytime monitoring but was notably absent from old-growth rainforest cavities, suggesting that quality cavities for this species were available in this habitat type (Figure 3.6a). Opossums are considered an important group of pollinating and seed dispersing species. Their presence in disturbed habitats offers a unique conservation/rehabilitation possibility whereby the use of artificial cavities could help improve opossum occupancy, which in turn may enrich the flora of disturbed landscapes thereby potentially accelerating restoration efforts (Medellin 1994; Tschapka & von Helversen 1999; Caceres et al. 1999). For shade coffee in particular, the presence of opossums may provide an opportunity to improve biodiversity of the understory plants, thereby potentially enhancing invertebrate diversities and consequently, may provide fodder for other wildlife e.g., bats, reptiles, birds, and amphibians.

The presence of cavity-nesting bird species was also greatest in the shade coffee plantation, relative to the other habitats (Table 3.3). Of the four nest boxes containing bird nests, three were found in shade coffee, while one nest was observed in secondary-logged rainforest and another was found in old-growth rainforest. House wren (*Troglodytes aegon*) and tropical screech owl (*Otus choleba*) nests (Figure 3.6b) were discovered in the shade coffee, each containing three eggs, while an unknown species nested in the secondary-logged forest and produced two chicks. Occupancy by a house wren in the shade coffee is not unsurprising given that they are a well-known habitat generalist species that thrive in a disturbed/edge environment. It is likely that this species was using the nest boxes opportunistically out of convenience as opposed to being limited by available cavities, especially given their penchant for nesting in the nooks and crevices of houses in urban areas. Similarly, the tropical screech owl is a common species (Stotz et al. 1996) that inhabits a range of habitat types including open woodland, second growth suburban areas with trees, black-water flooded forests (Borges et al. 2004) and coffee plantations (Stiles & Skutch 1989). While this study provides nine months of valuable monitoring data, longer-term studies of artificial nest boxes within shade coffee plantations may help to clarify the range of cavity nesting species able to inhabit artificial tree cavities within a disturbed landscape and determine the proportion of these species that are habitat generalists and/or specialists.

The diversity of species nesting in artificial tree cavities may also depend on the range of nest box sizes available for use. In the current study, the majority of occupancy detections occurred in large diameter nest boxes during the daytime regardless of habitat type (Figure 3.4). Similarly, observed activity/occupancy was greatest in large diameter nest boxes (Table 3.2). These observations and detections suggest that large diameter nest boxes were important for nocturnal mammals such as bats, marsupials, and/or roosting birds. In contrast, small diameter nest boxes had the most number of detections during the day within old-growth and secondary-logged rainforests, however, within shade coffee occupancy detections were greatest during the night (Figure 3.4). This finding suggests that small diameter cavities may also be of importance to diurnal cavity users. The use of two different nest box sizes within the shade coffee plantation clearly provided habitat for a variety of diurnal and nocturnal species. This is likely due to the lack of natural successional processes that create tree cavities in fully mature dead and dying trees within shade coffee. Consequently, the use of artificial tree cavities holds great promise for the enhancement of shade coffee plantations and conservation of cavity nesting species.

Tables & Figures

Table 3.1 The number of artificial nesting cavities (small versus large) in different habitat types that had at least one occupancy detection, as detected by iButton temperature loggers.

	Primary Middle		Secondary Middle (Logged)		Shade-Coffee Plantation	
	Small	Large	Small	Large	Small	Large
Unoccupied	11	12	12	10	9	5
Occupied	9	8	8	10	11	15

Table 3.2 The number of artificial nesting cavities (small versus large) in different habitat types where there was physical or observation evidence of occupancy by birds or mammals. Evidence and species involved, where known, is summarized in Table 3.3.

	Primary Middle		Secondary Middle (Logged)		Shade-Coffee Plantation	
	Small	Large	Small	Large	Small	Large
Unoccupied	16	16	15	14	16	2
Occupied	4	4	5	6	4	18

Table 3.3 The number of observed species and activities in artificial nest boxes within three different habitat types throughout the Alexander Skutch Biological Corridor, Costa Rica. The bolded number listed corresponds to large diameter artificial cavities. The second unbolded number corresponds to small diameter artificial cavities. Some individual cavities may be included more than once.

	Old-Growth Middle	Secondary Middle (Logged)	Shade Coffee Plantation
Birds			
Nesting Tropical Screech Owl (*Otus choleba*) with 3 Eggs	**-**	**-**	**1**
Nesting House Wren (*Troglodytes aegon*) with 3 Eggs	**-**	**-**	**1**
Unidentified species of nesting bird with 2 hatched chicks	**-**	**1**	**-**
Unidentified species of nesting bird with 2 eggs	-	**-**	1
Observed visitation by birds	**-**	**-**	**2**
Presence of Lineated Woodpecker (*Hylatomus lineatus*) feather	**-**	**-**	**1**
Presence of white-crowned parrot (*Pionus senilis*) feather	-	-	**1**
Presence of feathers (unidentifiable)	-	-	**4**, 1
Occupancy indications (e.g., hay modified, moulded, or removed)	**2**, 3	**5**, 2	**9**, 1
Scratch/bill markings	**-**	**1**	**-**
Presence of vegetation (i.e., seeds, plant material)	**1**	-	**2**
Mammals			
Rat species occupancy	-	-	**1**
Mouse species occupancy	**-**	-	**1**
Central American Whoolly Opossum (*Caluromys derbianus*) occupancy	**-**	**1**	**4**
Destruction by white-faced capuchin monkeys (*Cebus capucinus*)	**-**	**2**, 1	**-**
Amphibians			
Occupied by frog species	1	-	-
Insects			
Occupied by bee species	-	1	-
Occupied by large spider species	**1**	**-**	**-**
Occupied by termite species	1	**-**	**1**, 2
Occupied by ant species	**1**	**1**	**5**, 4

Figure 3.1 Artificial bamboo nest boxes used in this study. Dimensions of the large artificial cavity = 10-12 cm diameter, 4.5 cm entrance diameter, 23 cm depth. Dimensions of the small artificial cavity = 18-22 cm diameter, 10 cm entrance diameter, 35 cm depth.

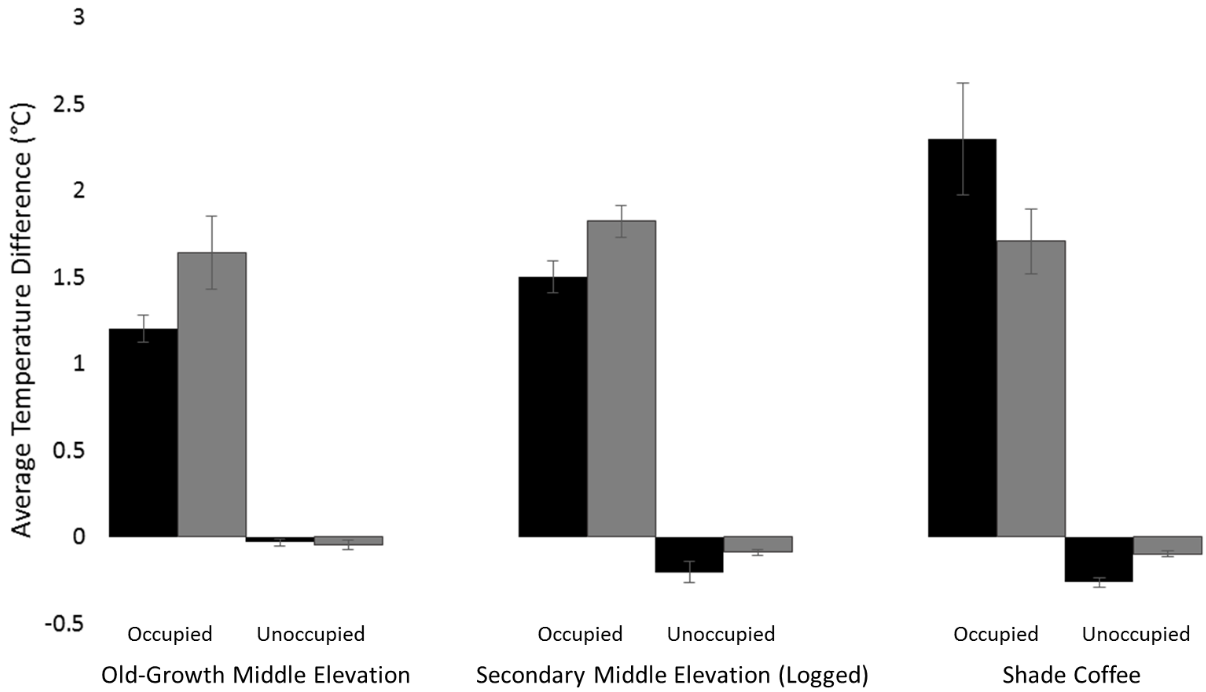

Figure 3.2 The average difference ± standard error between artificial cavity temperatures and the average plot temperatures for cavities that were occupied and unoccupied for large (black bars) and small cavities (gray bars) in three different habitat types.

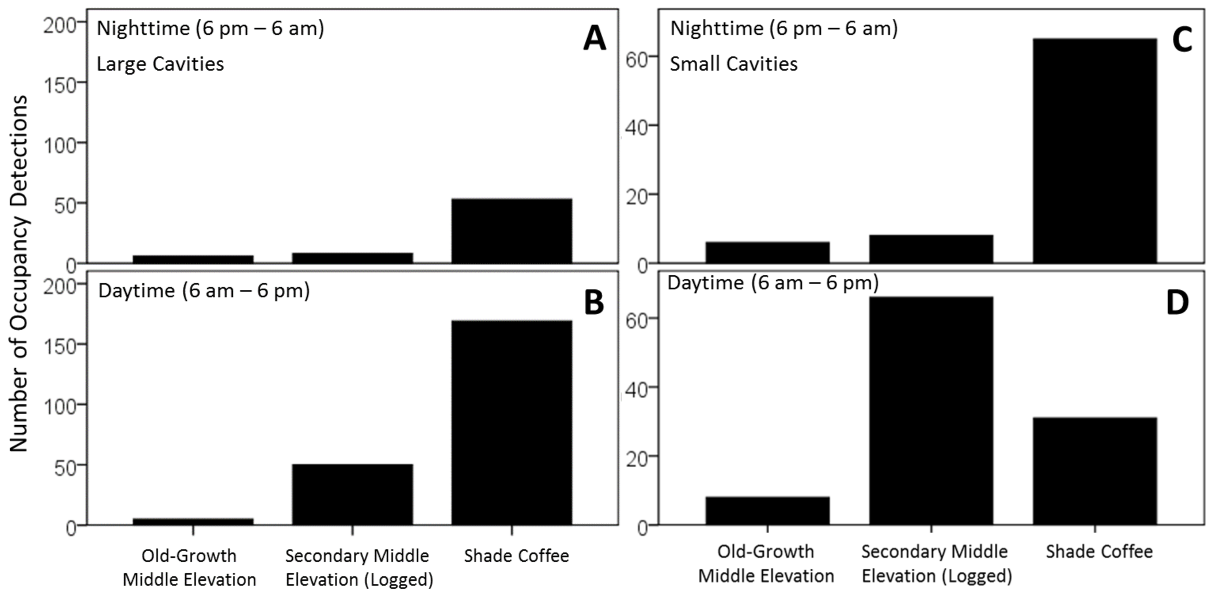

Figure 3.3 Number of occupancy detections recorded by iButtons in large and small artificial bamboo cavities placed in three different habitat types including old-growth middle elevation rainforest (large = 156 days, small = 203 days), selectively logged secondary middle elevation rainforest (large = 130 days, small = 127 days), and a shade coffee plantation (large = 146 days, small = 169 days). Number occupancy detections for large cavities at Nighttime (**A**) and Daytime (**B**) and for small cavities at Nighttime (**C**) and Daytime (**D**) are shown.

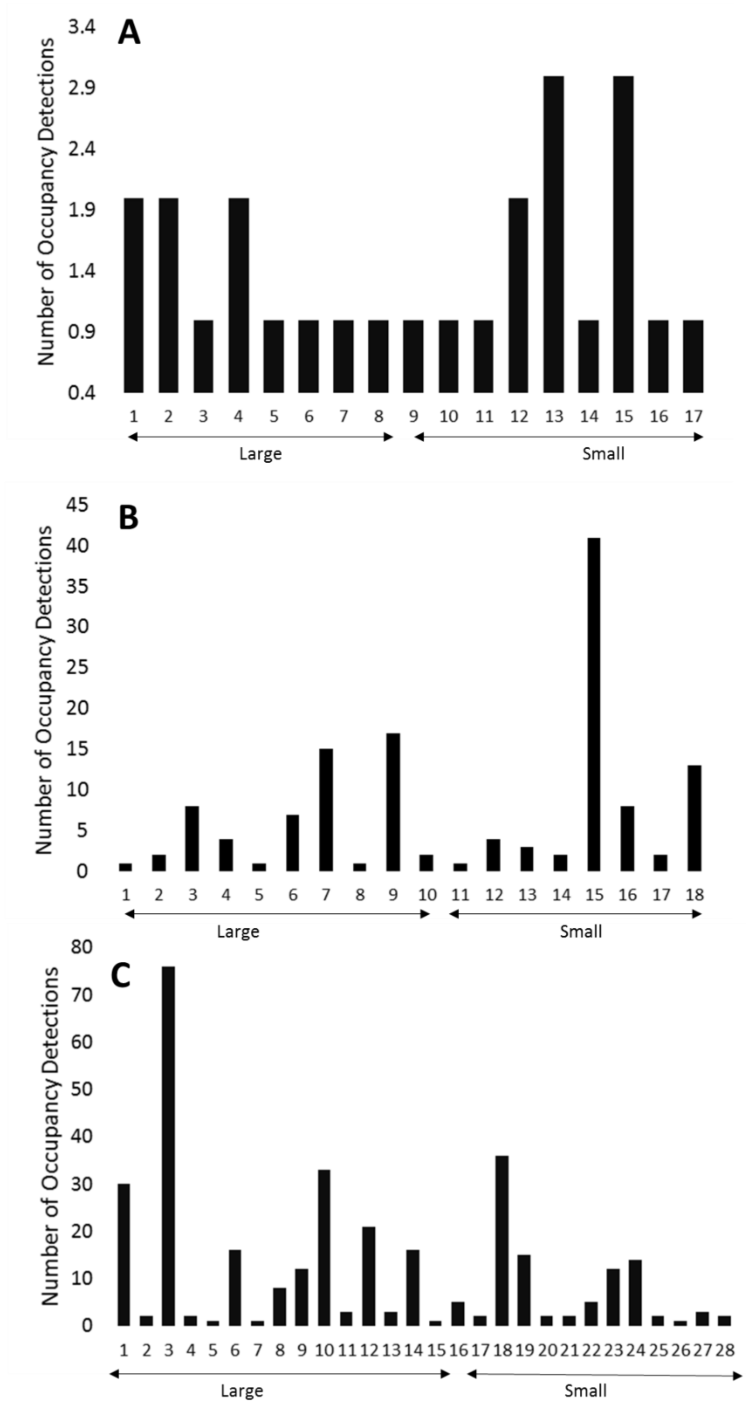

Figure 3.4 The frequency of occupancy detections for individual large and small artificial cavities in (**A**) old-growth middle elevation rainforest, (**B**) secondary middle elevation rainforest (logged), and (**C**) a shade coffee plantation.

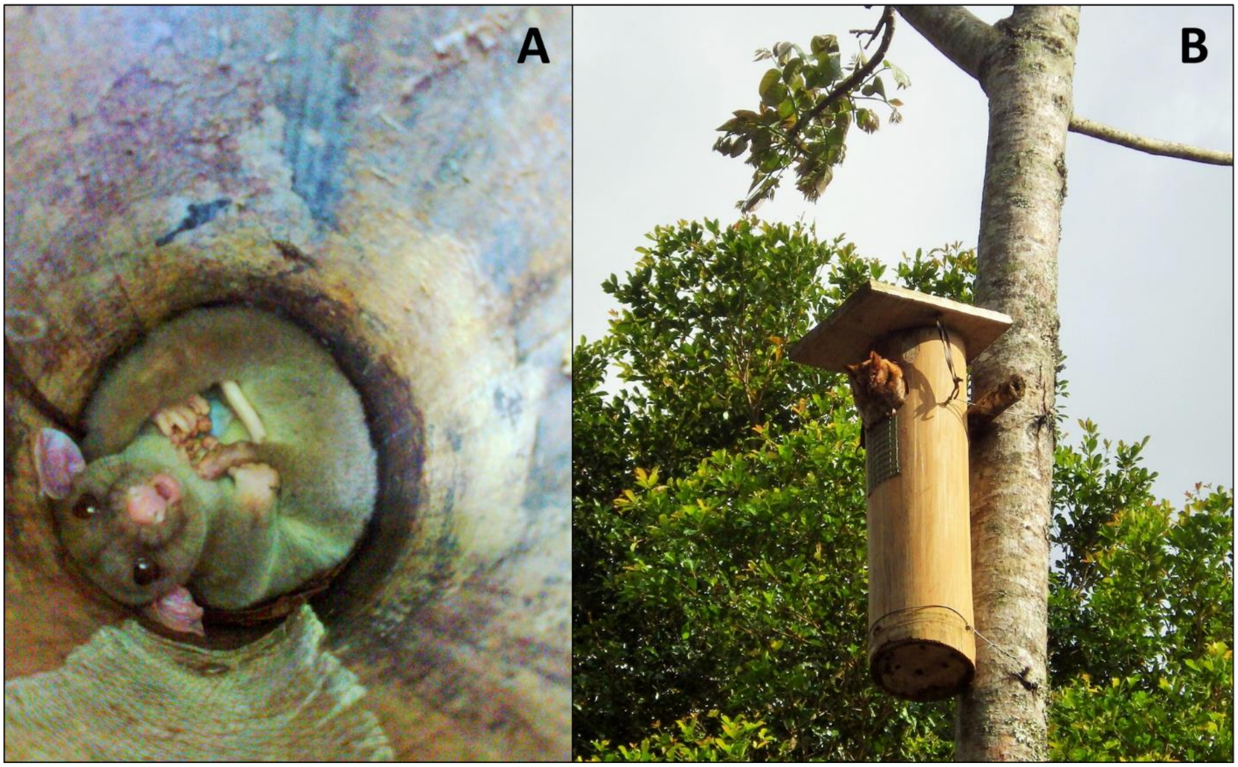

Figure 3.5 Occupants of bamboo nest boxes observed in the shade coffee plantation (**A**) Central American Woolly Opossum (*Caluromys derbianus*) (**B**) Tropical Screech Owl (*Otus choleba*)

Chapter 4

General Discussion

Fragmentation and loss of tropical ecosystems due to agricultural expansion is a problem that for the most part is left unchecked (FAO 2006; Geist & Lambin 2002; Rudel et al. 2005; Gibbs et al. 2010). Even within the Alexander Skutch Biological Corridor (ASBC) over a 10-year period, forest cover declined 19% with a corresponding reduction in forest patch sizes (Rapson et al. 2012). Shade coffee, which is a relatively ecologically sensitive crop, has also decreased at the expense of pineapple plantations, which are responsible for the greatest loss of forest within the corridor (Rapson et al. 2012). These changes in land use and corresponding deforestation rates are alarming, especially given that the ASBC is intended to protect biodiversity by linking forest fragments and by practicing sustainable land use management. It is clear that appropriate action must be taken to prevent further forest loss and the cultivation of less ecologically sensitive forms of agriculture e.g., pineapple within the corridor, while attempting restoration efforts to support and sustain the corridor's biodiversity.

Shade coffee plantations have been documented as providing suitable habitat for species affected by forest loss and conversion (Greenberg 1997; Mas 2004; Perfecto 2005; Tejeda-Cruz 2004). In the ASBC, shade coffee farms help provide connectivity between intact forest patches and protected areas that are separated by various forms of anthropocentric land use. While their habitat/connectivity value to a variety of taxa cannot be argued, shade coffee plantations do appear to lack critical habitat for cavity nesting/using species. In Chapter 2, I reported on my extensive survey of tree cavities and snags within four habitat types of the ASBC that included primary cloud forest (1100-1400m), old-growth (650-750m) and secondary-logged middle elevation rainforest (650-700m), and a shade coffee plantation (900-1000m).

I found an almost complete absence of snags and tree cavities in shade coffee. While it is well known that tree diversity is important for biodiversity in shade coffee plantations (e.g., Greenberg 1997; Mas & Dietsch 2004; Perfecto 2005; Tejeda-Cruz 2004) snags are also very important. Without fully mature, dying, and dead standing trees, in various states of decay, it is almost impossible to imagine a nest web of tree cavity specialists surviving in these agro-ecosystems. The existing model of shade coffee farm management may benefit greatly if processes of natural succession could occur for a subset of trees within a shade coffee plantation. Ideally some trees would be allowed to fully mature, die, and become snags thereby leading to the formation of some naturally eroded tree cavities. This process would provide micro-habitats for invertebrates, and subsequently provide some foraging material for woodpeckers, as well as other wildlife. However, further research is first needed. To start, future surveys of tree cavity/snag occurrence in several different shade coffee plantations across a much broader geographic scale will help clarify the extent to which my findings and recommendations can be generalized and applied to other areas.

In Chapter 2, I also reported on my detections of cavity use through the use of motion detection cameras. In general, detections of cavity use were low. It is possible that these results reflect the relatively limited number of cavities monitored in this study and its relatively short temporal scale. Future studies with a large number of cameras monitoring tree cavity use across a range of disturbed and undisturbed landscapes over several years could help elucidate whether quality cavities in the tropics are in fact limited (i.e., Gibbs et al. 1993; Boyle et al. 2008).

In Chapter 3, I used artificial bamboo cavities to assess their potential for providing suitable tree cavity habitat for cavity nesting species in shade coffee. I chose to compare occupancy/activity within artificial cavities between old-growth, secondary-logged middle elevation rainforest and shade coffee. In contrast to traditional methods of tree cavity monitoring, I used digital temperature loggers to detect occupancy in nest boxes. Occupancy detections and observations highlighted that nest boxes in shade coffee were used more often and by a wider variety of species compared to the less disturbed habitats investigated. The findings of this chapter provides evidence that the addition of artificial tree cavities to shade coffee plantations may be of great benefit for increasing local biodiversity. However, there is also the possibility that the addition of nest boxes creates an ecological trap for certain species. Future studies that monitor the different species using artificial tree cavities and their reproductive success in shade coffee and/or other agro-ecosystems are needed to determine the extent to which artificial tree cavities benefit species that are affected by habitat fragmentation/loss thereby increasing local biodiversity.

Based on my findings, the simultaneous use of artificial nest boxes with natural successional processes in shade coffee would be of benefit in restoration and conservation efforts directed at increasing biodiversity. One means of encouraging compliance with this type of successional model for shade coffee farms, would be through the use of coffee certification programs such as Smithsonian Bird Friendly Coffee and the Rainforest Alliance. These programs aim to foster more ecologically sensitive agricultural practices in coffee plantations and should consider forest micro-habitat such as tree cavities within their certification criteria given the broad diversity of taxa dependent on cavities and the already limited supply in primary and old-growth tropical forests (Cornelius et al. 2008).

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Appendix A

Table 1A Identified species detected by motion-sensor camera traps located throughout the Alexander Skutch Biological Corridor, Costa Rica according to habitat type. An additional three mammals and three birds were documented but could not be identified to species.

Habitat Type	Mammal Species	Bird Species
1° Cloud Forest	Squirrel Spp. (*Sciuridae spp.*)	Brown-billed Scythe Bill (*Campylorhamphus pusillus*)
	Vesper Rat (*Nyctomys sumichrasti*)	Buff-throated Foliage Gleaner (*Automolus orchrolaemus*)
	Rodent Spp. (*Rodentia spp.*)	Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*)
1° Middle Elevation Rainforest	Squirrel Spp. (*Sciuridae spp.*)	Chestnut-mandibled Toucan (*Ramphastos swainsonii*)
	Mammal Spp. (*Mammalia spp.*)	Woodcreeper Spp. (*Dendrocolaptidae* Spp.)
		Tawny-winged Woodcreeper (*Dendrocincla anabatina*)
		Pale-billed Woodpecker (*Campephilus guatemalensis*)
2° Middle Elevation Rainforest	Squirrel Spp. (*Sciuridae spp.*)	Fiery-billed Aracari (*Pteroglossus frantzii*)
	Mammal Spp. (*Mammalia spp.*)	Vermiculated Screech Owl (*Otus guatemalae*)
		Black-throated Trogon (*Trogon rufus*)

Table 2A GPS co-ordinates including the longitude and latitude (decimal degrees) of cavities surveyed in primary cloud forest.

Latitude	Longitude	Cavity Number
9.328408	-83.6225	1
9.384599	-83.5908	2
9.384608	-83.5909	3
9.384626	-83.5914	4
9.384686	-83.5947	5
9.384736	-83.5947	6
9.384758	-83.5905	7
9.384908	-83.5948	8
9.384961	-83.5906	9
9.385096	-83.5944	10
9.38511	-83.5914	11
9.385202	-83.5911	12
9.385239	-83.5914	13
9.385243	-83.5914	14
9.385312	-83.5906	15
9.385314	-83.5943	16
9.385324	-83.5943	17
9.385332	-83.5907	18
9.385345	-83.5906	19
9.385487	-83.5942	20
9.385489	-83.5942	21
9.385519	-83.5945	22
9.385524	-83.5945	23
9.385588	-83.5947	24
9.386075	-83.5927	25
9.386137	-83.5927	26
9.386331	-83.5927	27
9.386372	-83.593	28

Table 3A GPS co-ordinates including the longitude and latitude (decimal degrees) of cavities surveyed in primary middle elevation rainforest.

Latitude	Longitude	Cavity Number
9.334328	-83.6403	1
9.332765	-83.6417	2
9.3326	-83.6417	3
9.336325	-83.6461	4
9.338637	-83.6498	5
9.336106	-83.6451	6
9.338416	-83.649	7,8
9.334154	-83.6404	9
9.335002	-83.6404	10
9.334103	-83.6404	11,12
9.334087	-83.6401	13
9.334868	-83.64	14
9.334819	-83.6402	15
9.334319	-83.6402	16
9.334733	-83.6405	17
9.334967	-83.6404	18, 19
9.332784	-83.6419	20
9.333052	-83.6416	21
9.33313	-83.6415	22
9.333131	-83.6415	23
9.332993	-83.6411	24
9.333128	-83.641	25
9.332192	-83.6415	26, 27
9.332702	-83.6412	28
9.332606	-83.6414	29
9.332702	-83.6414	30
9.332715	-83.6415	31
9.332755	-83.6417	32
9.333106	-83.6415	33
9.335768	-83.6455	34
9.335995	-83.6456	35,36,37,38,39,40
9.336028	-83.6451	41
9.336067	-83.6451	42

Table 4A GPS co-ordinates including the longitude and latitude (decimal degrees) of cavities surveyed in selectively-logged secondary middle elevation rainforest.

Latitude	Longitude	Cavity Number
9.32518	-83.622848	1
9.32526	-83.622686	2
9.32528	-83.622854	3
9.325287	-83.622393	4,5,6
9.325331	-83.622487	7
9.325545	-83.622239	8
9.325744	-83.623021	9
9.325825	-83.622753	10
9.325828	-83.622086	11
9.325902	-83.623065	12
9.326098	-83.622505	13,14
9.327077	-83.620554	15
9.327095	-83.620626	16
9.327145	-83.620505	17
9.327554	-83.622699	18
9.327559	-83.622768	19
9.32765	-83.622583	20
9.327719	-83.620403	21
9.327856	-83.623345	22
9.327884	-83.623172	23
9.328017	-83.622724	24
9.328082	-83.623116	25
9.328199	-83.622714	26
9.328241	-83.622748	27
9.328355	-83.622556	28, 29
9.328357	-83.622458	30, 31
9.328365	-83.622632	32
9.328419	-83.622904	33,34
9.328448	-83.622438	35