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Guild-Specific Responses of Birds to Habitat Fragmentation: Evaluating the Effects of Different Coffee Production Systems in Colombia.

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Guild-Specific Responses of Birds to Habitat Fragmentation: Evaluating the Effects of Different Coffee Production Systems in Colombia

by

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Dedication

Dedicada con amor al eje fundamental de mi vida: Liliana, Gonzalo y Juan David, quienes han creído en mis sueños tanto o más que yo, y quienes me han apoyado incondicionalmente siempre. Sin su ejemplo de vida, amor y trabajo esta tesis no hubiera sido posible.

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Abstract

Guild-Specific Responses of the Avifauna Associated with Coffee Agro-Ecosystems to Habitat Fragmentation: evaluating the effects of different coffee production systems.

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Habitat loss and fragmentation are the main drivers of biodiversity loss, especially in the tropics, where the transformation of forested areas into agriculture is predicted to increase dramatically in the next five decades. Although several studies have elucidated the negative impacts of agriculture on biodiversity, recent work suggests that some agro-ecosystems, such as coffee plantations, are potential key environments for maintaining biodiversity and ecosystem services. This study evaluated the role of different coffee production types (sun-exposed, semi-shade and shade in polycultures or monocultures) on the bird communities associated with these agro-ecosystems in the tropical Andes of Colombia. It used a guild-specific approach and nonparametric statistical methods to identify the influence of particular environmental, ecological and landscape variables on the bird community assemblage and to assess potential changes in the species composition among management type. The potential responses of avifauna to fragmentation were studied from three different perspectives: i) from a patch-level point of view, evaluating the effect of local habitat factors (e.g. canopy cover, type of crop and crop management type); ii) from a species point of view, evaluating the role of species ecological traits (e.g. feeding habitat); and iii) from a landscape point of view, evaluating the effect of landscape configuration variables (e.g. patch area and perimeter length). The results indicated that polyculture and shade coffee crops host the most diverse avian communities and that guild representativeness varied among different coffee crop types. The type of coffee production type and the habitat characteristics associated with them seemed to have the greatest influences on families such as flycatchers, hummingbirds and wrens. Finally, coffee plantations can potentially contribute to the maintenance of bird diversity in anthropogenic landscapes; however these benefits are strongly influenced by the type of crop management. The maintenance of traditional coffee production (shade polyculture coffee) is recommended, and should be economically and socially encouraged.

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Chapter 1: Introduction

The tropical Andes Mountains contain several of the most biodiverse, as well as threatened ecosystems on Earth. Anthropogenic practices, such as agriculture, represent the greatest threat and are encroaching on these habitats (Perfecto et al. 1996, Myers et al. 2000). Although the negative effects of agriculture have been documented on most taxonomic groups (Andren 1994, Bruna et al. 2005, Vellend et al. 2006), recent findings have suggested some of these agro-ecosystems may serve as key ecosystems for biodiversity conservation (Ovenden et al. 1998, Swift et al. 2004, Perfecto et al. 2009). Examples of these habitats are coffee plantations, which are considered agroforest habitats in which crops are integrated with native trees and shrubs. These plantations have proven to be important habitats for several taxa, but in particular for birds and arthropods, by providing shelter, food and migratory stops (Moguel and Toledo 1999). Despite the potentially significant role that these areas play in biodiversity conservation, understanding of the factors (i.e. agriculture and development) and mechanisms (i.e. habitat fragmentation and habitat degradation) influencing natural communities' responses to anthropogenic practices remains incomplete.

Most research focus on species-specific responses to anthropogenic habitat changes, especially as related to habitat fragmentation, in which a large extent of natural vegetation is reduced into smaller and isolated patches, surrounded by a matrix of modified habitats, which ultimately will constitute the most extensive or dominant area (Forman 1995). Those studies adopt a patch-centered approach in forests (Villard et al. 1999, Fahrig 2002, McGarigal and Cushman 2002). This approach seeks only to measure species richness (alpha diversity) and places a heavy emphasis upon the response of forest species to changes in habitat configuration and on the spatial properties of the patches. Yet, this approach leaves out four important concerns:

i. What is the influence of species' ecology (foraging habits and species composition) on their response to habitat fragmentation?

ii. How does remnant habitat quality influence species' responses to habitat fragmentation?

iii. How do the matrix characteristics, such as matrix suitability, connectivity and heterogeneity influence species' responses to habitat fragmentation?

iv. How does biodiversity respond to habitat changes due to habitat fragmentation at a community level (e.g. changes in species composition)?

As a result, there is an urgent need to integrate the ecology, habitat quality and matrix characteristics in order to understand these agricultural landscapes and ecosystems, and how they can shape natural communities.

This thesis investigated the bird communities that inhabit coffee agro-ecosystems with different management and production systems. The main goal was to evaluate the role of different coffee crop management types on the bird communities associated these agro-ecosystems, by identifying the influence of particular environmental, ecological or landscape variables on the relative abundance of birds and their community composition. To accomplish this, I surveyed bird species and habitat characteristics in coffee plantations exposed to different management types. These data was examined using non-parametric analyses in order to explore potential associations of bird communities to particular habitats (coffee plantations).

Birds are a useful model group for an examination of the effects of habitat fragmentation on biodiversity conservation for three main reasons: first, they have shown to be a particularly sensitive group to anthropogenic habitat changes (Lee et al. 2005, Matthysen et al. 2008); second, their ecology is indirectly tied to other taxonomic groups (e.g. insects and plants) (Wilson et al. 1999); and finally, some of their natural history and behaviors, such as migration patterns and nest-location, are closely related to the phenology and structural characteristics of the crops.

Of particular relevance is the Tropical Andean avifauna, comprising at least 1,700 bird species (including approximately 600 world endemics and 66 regionally endemic genera). Moreover, at least 10% of the Tropical Andean bird species are currently threatened by anthropogenic practices, mainly due to habitat loss, as a consequence of agriculture and deforestation (Conservation International, 2010).

In addition to being a region with several global diversity hotspots, the Tropical Andean Mountains are also a vital agricultural area for many developing countries such as Colombia, for which food production is one of the main economic activities. In order to match human population growth and food demand projections, agricultural land use for food production over the next 50 years must dramatically increase (Tilman et al. 2001). These projections indicate that developing nations will likely prioritize social and economic concerns over biodiversity protection (Tilman et al. 2001). As a result, conservation strategies are forced to gradually overlap with agriculture and development, dismissing more common -- but less feasible -- conservation strategies, such as protected areas and natural reserves (Bruner et al. 2001). The idea that agricultural habitats can play a role as biodiversity refuges emphasizes the importance of understanding species use of agricultural landscapes and ultimately the species response to habitat fragmentation and degradation.

This thesis was inspired by the idea of connecting scientific knowledge about bird communities in fragmented landscapes to the current biodiversity scenarios in the Tropical Andes, using applied biogeographic and conservation perspectives. It was based on the belief that understanding the similarities regarding community composition between different elements of agricultural landscapes will facilitate the identification of areas that could potentially maximize regional biodiversity. It is my hope that this information may serve as the basis for future conservation and development projects, in regions of the world in need of strategies that account for both natural and societal demands.

Chapter 2: Literature Review

The next chapter will present an overview of current state of the art on habitat loss and fragmentation, and their effects on natural communities. First I will introduce some theoretical aspects that will be progressively linked to the current circumstances in the tropics, focusing especially on those aspects related to the role of agricultural landscapes on conservation of biodiversity. The second part of this chapter is an overall review of the latest ideas on the field of countryside biogeography, presenting the major findings about the positive, negative or neutral effects of agricultural development on natural communities. Finally, I will focus on the main target of this thesis and use the specific case of bird communities associated with coffee agro-ecosystems. This section will present all the background necessary to understand the use of different coffee production systems in Colombia and present the major findings regarding the management and conservation of avifauna in coffee landscapes.

2.1 Land Use and Land Cover Changes

Changes in land cover (the biophysical attributes of the earth's surface) and land use (the human purpose over those attributes) have been a prevalent phenomenon over hundreds, and in some places, thousands of years, mainly as a consequence of agriculture, grazing and timber production (Turner and Meyer 1994, Grau et al. 2003, Grau and Aide 2008, Vögeli et al. 2010). The negative impacts of land use and land cover changes (LULC) include the contribution to local, regional and global climate changes(Chase et al. 2000), soil degradation (Tilman et al. 2002, Foley et al. 2005), the impact on biodiversity loss and the alteration of ecosystem services (Meyer 1994, Vitousek et al. 1997, Sala and Chapin 2000). Most research on LULCC focuses on its environmental impacts such as global carbon cycle changes (Houghton 2003), surface energy and water balances (Carlson and Traci Arthur 2000, Costa et al. 2003) and lastly global climate changes (Bounoua et al. 2002). However, the role that land cover changes play in the amount of native habitat loss and degradation around the world has been only recently emphasized (Sala et al. 2000, Foley et al. 2005). Although the mechanisms throughout LULCC that alter ecosystems are countless, factors such as the degradation of soil and water, the overexploitation of native species and the loss, modification, and fragmentation of habitats are widely recognized as the main drivers of current biodiversity loss (Pimm and Raven 2000).

Although LULCC is a ubiquitous phenomenon around the world, particularly in the tropics, agricultural land use is growing at exponential rates, threatening some of the most biodiverse biomes in the world (Sala and Chapin 2000, Tilman et al. 2001, Foley et al. 2005). Given that the global tropics are important world regions of food production, current trends in population and consumption growth are predicted to increase the global demand for food for at least another 50 years, doubling the amount of land assigned for agriculture (Thomson et al. 2010). The global tropics are thus priority regions on research agendas for conservation and sustainable development around the world.

2.1.1 HABITAT FRAGMENTATION

A common consequence of land use and land cover changes is habitat fragmentation. This phenomenon is defined as the transformation of large extents of habitat by reducing native vegetation cover into smaller and isolated patches (Hobbs and Margules 1991, Haila 2002). In the most general scenario, a fragmented landscape is created after the original land cover has been cleared, leaving behind a number of smaller patches of native vegetation (remnant fragments), surrounded by a matrix of new atypical habitats (i.e. crops, roads, plantations or human settlements). Fragments would be located in different positions across the original landscape and differ in terms of plant community composition, ownership, and on their spatial characteristics (size, shape and insolation) (Saunders et al. 1991). The resulting scenario would depict significant amounts of habitat loss and a complex landscape composed of several remnants of original vegetation with different characteristics and vegetation types, which will be differentially affected by spatial and environmental variables.

Although habitat fragmentation is not strictly an anthropogenic process (Fagan 2002, Leisnham and Jamieson 2002) human use of the earth is responsible for a vast amount of habitat loss and fragmentation over the last centuries (Fahrig 2003). Land use and land cover changes have been mainly driven by the production of energy and industrial materials, agriculture and urban expansion. Today almost the Earth's entire surface is being used and transformed by humans in different degrees of intensity (Meyer 1994, Watson 2002, Fahrig 2003).

In the study of habitat fragmentation, fragments have been conceptualized as islands or patches, characterized by smaller proportions of suitable habitat, which are isolated from the mainland (original forest) and surrounded by an unsuitable habitat (the matrix) (Haila 2002). Accordingly, habitat fragmentation has been frequently analyzed based on the theory of island biogeography (MacArthur and Wilson 1967), where the species richness of a particular undisturbed and isolated place (an island) is given by immigration, emigration and extinction rates. At the same time, these rates depend on the physical and spatial characteristics of the "island" (or patch), such as distance from a source population (isolation effect) and the island's area, which determines the amount of available habitat that new species could occupy (area effect) (Haila 2002).

Although island biogeography theory and its applicability to conservation biology have contributed enormously to research in conservation science and conservation planning, over the last decades it was mainly limited to conceptual grounds (Turner 1996, Debinski and Holt 2000). New theoretical advances in other areas of biogeography, such as spatial theory (Tilman and Kareiva 1997), metapopulations (Hanski and Gaggiotti 2004), landscape ecology (Turner, 2004) and macroecology (Gaston et al. 2000), have given biogeographers a better understanding of how natural communities respond to habitat fragmentation.

The process of habitat fragmentation and modification may greatly change landscape structure and local ecosystem services (Kareiva and Wennergren 1995). Habitat fragmentation creates smaller and more isolated habitats, potentially leading to a decline in species richness and abundances, as well as changes in community structure (Holt et al. 1999, Connor et al. 2000, Debinski and Holt 2000, Steffan-Dewenter et al. 2002). Additionally, most of the ecological process and species interactions altered by spatial scales, therefore, it is important to link spatial patterns to ecological processes at both landscape and patch level to fully understand the effects of habitat fragmentation and degradation in natural communities (Gustafson 1998, Wiegand et al. 2005).

Ecological consequences of habitat fragmentation

The consequences of habitat fragmentation can be categorized into five clusters (Andren 1994, Didham 2001, Fischer and Lindenmayer 2007):

a) Area effects:

By definition, habitat fragmentation involves the loss of original habitat by progressively reducing the size of the native vegetation fragments (Haila 2002). It is expected that larger fragments will contain greater species richness, higher number of species per unit area and a wider range of habitats in comparison to smaller fragments. As a consequence, a considerable reduction of habitat area will lead to less original habitat, lower number of species and presumably, smaller patches will have smaller population sizes (Lomolino 2000). Finally, reducing the patch area limits resource availability alters reproductive success and imposes an intrinsic constraint on maximum population size, ultimately exposing populations to an increased risk of local extinction (Didham 2001, Hanski and Gaggioti 2004).

b) Isolation effects:

After fragmentation occurs, small fragments of original vegetation are created. These fragments are by definition disconnected from similar habitats decreasing the degree of habitat connectivity in the landscape. As habitat fragmentation increases, both time and distance of insolation also increase (Merriam 1991, Taylor et al. 1993, Bennett 1999). Remnant habitats can be scarce in providing resources and shelter, forcing species to move in order to find new suitable habitats. Consequently, the distance and quality of the matrix can represent a constraint for species movement, limiting dispersal, colonization and food availability, and threatening species persistence in a given habitat (Didham 2001, Ricketts 2001, Prugh et al. 2008).

c) Edge effects:

Edges are transitional zones between the patch's natural vegetation and the adjacent modified habitat (matrix), which contrast in structure and floristic composition due to changes in physical and ecological processes in fragments. Edges create changes in the microclimate conditions that can strongly affect native species (Ewers et al. 2007). As fragmentation occurs, the amount of edges found within natural vegetation increases, because small patches have a higher edge to area ratio, relative to larger blocks of natural vegetation. Edge effects have been proven to create unfavorable conditions for some species in fragmented forests (Fahrig 2003), though these same conditions may favor other species that are more likely to thrive in edge environments (Davies et al. 2000).

d) Matrix effects:

Despite the development of previous habitat fragmentation approaches, the study of fragmented landscapes has often been based on binary scenarios, considering only patches of suitable habitat against a matrix of unsuitable habitat. However, the matrix is more than just a portion of unsuitable habitat; it is the background cover type within a landscape, usually covering more than 50% of its area and can contribute to biodiversity by providing heterogeneity and connectivity (Turner et al. 2001). Therefore, the matrix has shown to have a great influence on species dynamics in fragmented landscapes (Ricketts 2001, Cunningham et al. 2002, Perfecto and Vandermeer 2002, Dunford and Freemark 2005, Vandermeer and Perfecto 2007).

Although it seems evident that similarities between patch and matrix habitats, habitat structure, floristic composition and microclimate conditions increase connectivity, it is not well understood which specific matrix characteristics play essential roles in determining species responses to habitat fragmentation. (Bennett 1999, Mesquita et al. 1999, Vandermeer and Perfecto 2007). In particular, the influence of the anthropogenic matrix on the bird communities that inhabit forest patches has been well documented (Soulé et al. 1992). Studies have shown that the matrix plays an important role in allowing the influx of species to forest fragments, increasing nest predation and parasitism (Andren 1994, Robinson et al. 1995, Stouffer and Bierregaard 1995) while also maintaining connectivity among patches.

In conclusion, habitat fragmentation has been subjected to great conceptual and theoretical debates (Van Dorp and Opdam 1987, Wiens 1995, Debinski and Holt 2000b, Haila 2002, Shanahan et al. 2010). These discrepancies have led to contrasting and disparate evidence on the effects of patch area, edge, isolation and the matrix. Some of the latest insights about the ecological effects of habitat fragmentation are in relation to the identification of scale- and species-specific responses, making difficult to interpret the current findings in the study of habitat fragmentation (Keitt et al. 1997, Steffan-Dewenter et al. 2002, Ewers and Didham 2006).

Species' Responses to Habitat Fragmentation

While habitat loss *per se* is well known as the principal cause of biodiversity decline (Tilman et al. 1994, Sala and Stuart Chapin 2000, Foley et al. 2005), the spatial arrangement of remnant fragments can also affect population dynamics and species persistence (Hanski et al. 2004). Species presence and permanence in a given habitat are influenced by its adaptations to a multidimensional arrangement of spatial, environmental, biological and ecological variables (niche concept *sensu* Hutchinson 1961). Habitat modifications can affect species, by limiting resource availability, changing environmental factors or altering species composition and dynamics (Forman 1995 Pereira and da Fonseca 2003, Travis 2003, Hollister, Webber and Bay 2005, Layman et al. 2007, Candolin 2009).

Furthermore, other studies have diverged from theoretical debates and started focusing on the ecological function of habitat patches and the species' ability to inhabit and use all the elements of the fragmented landscapes (Ferraz et al. 2007, Banks-Leite, Ewers and Metzger 2010, Ruiz-Gutiérrez, Zipkin and Dhondt 2010). Watson et al. (2005) conducted an extensive empirical study on bird community responses to habitat fragmentation by evaluating scale effects along an anthropogenic gradient (Watson et al. 2005). The aim was to identify bird communities' responses to habitat fragmentation and, to use empirical evidence to analyze the isolation effects in natural communities. They studied 127 remnants from three different landscape types (agricultural, peri-urban and urban) in southeastern Australia. Their results suggested that the type of landscape matrix may have considerable impact on how bird species are affected by fragmentation. All three types of landscapes showed a relationship between species and area of the patch, but the slopes of the curves, differed considerably among habitats. Moreover, habitat isolation effects were only significant in agricultural landscapes, and the probability of individual species' occurrence, when related to area and isolation, was highly variable across the anthropogenic gradient (Watson et al., 2005).

Ricketts (2001) similarly analyzed the contribution of the interpatch matrix to patch isolation, on butterfly communities from the Rocky Mountains in Colorado, comparing relative resistance of two matrix types (willow thicket and conifer forest) to butterfly movement. This study found that the surrounding matrix significantly influenced the "effective isolation" of habitat patches, and suggests that this effect can have a greater impact than distance among patches. Furthermore, Ricketts et al. (2001) studied tropical scenarios, analyzing moth species richness in forest fragments immerse in different anthropogenic matrices (e.g. coffee plantations, pastures, farms). His results showed that species richness in the matrix was strongly influenced by proximity to forest fragments, and but not by the matrix type (e.g. coffee plantations, pastures and farms). In conclusion, these two studies suggest that in addition to distance, the characteristics of the contiguous matrix can influence the effective isolation of habitat patches, but most importantly, this influence is different among taxa (Ricketts 2001, Ricketts et al. 2001).

Although the studies of habitat fragmentation effects on biodiversity have rapidly increased over the last 20 years (Laurance 2008), important aspects have been overlooked. For example, Ewers and Didham (2006) reviewed empirical work done on species responses to habitat fragmentation and uncovered some factors that could be misleading the insights about how species respond to habitat fragmentation. Among these they include the temporal scale and time lags in population responses, evidencing crowding effects and extinction debts (Bierregaard Jr et al. 1992, Tilman et al. 1994, Debinski and Holt 2000a), the synergistic effects with global environmental change (Thomas, Franco and Hill 2006, Tylianakis et al. 2008) and finally, the species ecological traits (e.g. trophic level, dispersal ability and degree of habitat specialization) (Steffan-Dewenter et al. 2002, Henle et al. 2004).

One of the factors influencing species responses to habitat changes is the species' guild. Guilds are groups of species that exploit the same class of environmental resources in a similar way (Simberloff 1991). Particular examples are feeding guilds that group species based on their dietary preferences. Studies suggested that species respond in different ways to habitat fragmentation depending on certain ecological preferences such as their feeding guild (Terborgh et al. 1997, Renjifo 1999, Ewers and Didham 2006). Rengifo (2001) evaluated the influence of three different matrices on the relative abundances of birds in Andean landscapes. He assigned bird species to different "response categories" based on their primary habitat associations, foraging strata, trophic level and taxon affinity, to identify particular species traits that will help predict the response to habitat fragmentation. Bird responses were largely species specific and independent of foraging strata, trophic group, and taxonomic affinities. Further studies showed that understory birds, specifically hummingbirds, are less affected by fragmentation and the surrounding matrix than other bird species, such as those associated with mixed-species flocks and understory insectivores (Bierregaard and Lovejoy 1989, Stouffer and Bierregaard 1995, Renjifo 1999, 2001).

Other studies have focused on analyzing the relationship between species responses and geographic scale (Lord and Norton 1990, Keitt et al. 1997, Steffan-Dewenter et al. 2002, Urban 2005). Habitat fragmentation can have consequences at both local and landscape scales demonstrating that perceived ecological relationships are partly determined by the scale at which spatial characteristics are measured (Doak et al. 1992, Andren 1994). Only a few studies have investigated the spatial aspects of fragmented grasslands and their influence on bird communities which established patch area as an important variable affecting habitat occupancy (Herkert 1994, Samson and Knopf 1994, Vickery et al. 1994, Cunningham and Johnson 2006, Ribic et al. 2009). This area effect has also been found when analyzing the distribution of bats (Gorresen and Willig 2004, Gorresen, Willig and Strauss 2005, Baessler and Klotz 2006) and bees (Steffan-Dewenter et al. 2002), suggesting that scale-dependent differential effects can change mutualistic plant–pollinator and plant-disperser interactions.

In conclusion, the study of habitat fragmentation is limited by two main constraints. First, even though habitat fragmentation is a landscape process, the majority of the studies are patch-centered, and do not consider a landscape perspective (Fahrig 2003). Additionally, the classical approach considers only binary situations where the habitat is either suitable or unsuitable (Wiegand et al., 2005, Ewers and Didham 2006). But the evidence shows that patches of fragmented habitats vary widely in suitability, and that these differences primarily affect the degree of connectivity among patches (Gobeil and Villard 2002, Castellon and Sieving 2006). Second, the study of habitat fragmentation is still under development and necessitates new approaches that will identify the key factors influencing species responses such as species ecological traits (Stouffer and Bierregaard Jr 1995, Gascon et al. 1999, Antongiovanni and Metzger 2005).

2.2 AGRICULTURE AND BIODIVERSITY

Agricultural landscapes are interesting examples of fragmented habitats, where the native vegetation has been replaced by crops and the original configuration/composition results in a mosaic of land crops and other anthropogenic land covers (Wunderle Jr 1999, Denevan 2003, Leyequién, De Boer and Toledo 2010). Furthermore, agriculture intensification has been widely considered one of the main drivers of biodiversity loss (Tilman et al. 2001). The effects of agriculture on natural communities can be observed at both local and landscape scales. At a local scale, practices such as tillage, drainage patterns, grazing and the use of pesticides and fertilizers can directly affect species presence in these areas (McLaughlin and Mineau 1995, Tscharntke et al. 2005a, Daily et al. 2001). At a landscape scale, intensive agricultural development leads to habitat fragmentation and converts complex natural ecosystems into simplified and homogeneous managed agroecosystems (Tilman et al. 2001, Benton et al. 2002, Robinson and Sutherland 2002, Benton 2003). As a result, agricultural practices can lead species to extinction by both deterministic (agricultural expansion) and stochastic processes (habitat fragmentation) (Benton et al. 2002).

The negative effects of agriculture have been documented for mammals (Chapin III et al. 2000), arthropods and flowering plants (Tilman et al. 2001) and more extensively in birds (Wilson et al. 1997, Perkins et al. 2000, Møller 2001). The consistent pattern found in these studies is a clear decline in the number of species associated with farmland landscapes. Of particular relevance are the studies by Donald et al. (2001) in European bird communities; Europe suffered from rapid expansion and intensification of agricultural activities during the postwar period, hence it constitutes a good case study about the effects of agriculture and the fate of native biodiversity (Donald et al. 2001, Loreau et al. 2001, Benton et al. 2002, Adams 2004). In particular, Donald et al (2001) found that the tripling of cereal yield during postwar periods, explained over 30% of the variation in the decline of bird populations in countries from the European Union. Another well-documented impact of agriculture intensification is the decline on insect populations, consequentially affecting insectivorous bird populations, mainly by altering food quality or quantity (Benton et al. 2002).

Despite the negative effects of agriculture intensification on biodiversity recent studies have suggested some agricultural systems as potential areas that contribute to regional or local scale biodiversity conservation (Vandermeer and Perfecto 2007). Given that land use does not necessarily mean habitat destruction, low-intensity agricultural management types can enhance not only ecosystem services (Daily 1997) but also biodiversity (Bignal and McCracken 1996, Perfecto et al. 1996). The beneficial effects of low intensity agriculture on biodiversity are based on the fact that agriculture increases land productivity and consequently food resources (i.e. plant biomass, fruits, and seeds) (Wunderle and Latta 1998b). These ideas are supported by studies that show that the level of agriculture intensification and agricultural system management can be associated with changes in the species richness of birds (Söderström et al. 2001), bats (Williams et al. 2010) and moths (Ricketts et al. 2001), which increased in recently cultivated areas, as opposed to a decline in old or abandoned fields among others.

In this regard, most of the conservation literature has focused on the fact that agricultural landscapes provide ecosystem services (Russell 1989, Daily1997). Most cases have been documented in Europe, where natural ecosystems are almost nonexistent and where the majority of natural reserves are managed for anthropogenic purposes (Tscharntke et al. 2008). The reality for the tropical regions is different. Despite the fact that agriculture in the global tropics has been undergoing a slow transition to more intense management systems (Grau and Aide 2008), small grower and low-intensity agriculture are still the most common production systems. These conditions offer planners, policy makers and conservation biologists a valuable opportunity to design proper conservation strategies relevant to these particular and local contexts. However, even when some of the beneficial effects of agriculture on biodiversity have been documented, the relative contribution of different management types to conservation is not fully understood yet.

Interesting examples of how the different management types of agriculture system can affect biodiversity are found among agroforestry systems (Huang et al. 2002). In these human modified ecosystems, common farming (of both crops and animals) are spatially interrelated with trees (Torquebiau 2000). Agroforestry systems have been considered important systems in the sense that they provide various ecosystem services such as increasing soil fertility, reducing erosion, improving water quality and sequestrating carbon (Jose 2009). Additionally, land changes associated with agroforestry systems, can maintain a good amount of the original vegetation, and have reduced the alteration of vegetation structure, hence, alleviating habitat loss and impacts on biodiversity (McNeely and Schroth 2006). Consequently, the amount of suitable and available habitat for local species, such as birds and insects, will depend on the intensity of the agricultural practices. These positive effects have been documented in various studies for several different regions of the world (McNeely and Schroth 2006, Harvey and González Villalobos 2007, Bhagwat et al. 2008, Jose 2009, DeClerck et al. 2010).

Most of the research related to biodiversity conservation done with agroforestry systems, has been done in large plantations of coffee, banana or cacao (Perfecto et al. 2003, Wilsey and Temple 2010). Noteworthy illustrations of agroforestry in the Neotropics are coffee plantations, important not only by its prevalence and its economic importance, but also because they have shown to offer promising contributions to biodiversity (Perfecto et al. 1996, Moguel and Toledo 1999). Nonetheless, among all the studies the role of smallholder agricultural systems was relegated until recent years (Perfecto et al. 2009)

Evidence supporting the importance of agroforestry systems in conservation of biodiversity has been shown by Daily (2001), who surveyed the avifauna of forest fragments and open-habitat sites in an agricultural landscape. Her study found that a substantial proportion of the forest native bird avifauna actually occurs in densely human populated areas and agricultural landscapes and even in places where original forest has been cleared for 50 years (Daily et al. 2001). However these results have serious implications and should not indicate that all agricultural types could offer habitat for bird species or that these areas can maintain sustainable populations (Tejeda-Cruz et al. 2010). The use of countryside by forest birds has been similarly reported by other studies, showing that non-forest habitats such as low-intensity agriculture systems, that incorporate fruiting trees as part of live fences or shade, would be beneficial to biodiversity conservation in Costa Rica, and may enable the regeneration of bird-dispersed rain forest plants (Luck and Daily 2003). These studies emphasized that appropriate management of agricultural systems may contribute to biodiversity conservation (Hughes et al. 2002, Luck and Daily 2003).

Conversely, evidence against the idea that smallholder agricultural systems can provide suitable habitat for biodiversity was presented by (Naidoo 2004), who compared both species richness and community composition of songbirds from three land use types associated with tropical forests in Uganda. Using generalized linear models he identified important habitat variables (e.g. tree density and distance to the nearest intact forest) that influence species richness and community composition in different land use types, and found that current smallholder agricultural practices did not contribute significantly to songbird biodiversity for this particular case (Naidoo 2004).

In conclusion, agricultural intensification has been indeed a main cause of native and farmland biodiversity losses over a long time. However, the factors influencing species responses to agriculture and the levels at which these responses occur is just recently being studied. Today it is clear that agroforestry systems offer an integrated approach to enhance biodiversity conservation in agricultural areas. However, few studies have assessed the degree to which smallholder agroforestry systems may contribute to local biodiversity. In this regard, ecologists, conservation biologists and environmental planners still have the challenge of identifying general and applicable solutions for small scale farming practices that will hopefully contemplate aspects that have previously left behind such as responses at the community level and the habitat quality of remaining patches (Bennett 1999, Tscharntke et al. 2005b).

Agriculture and Birds

In the past 50 years there has been seen across Europe a marked and progressive decline in countryside birds, which has been attributed by the scientific community to the intensification of agriculture during the twentieth century (Donald et al. 2006, BirdLife International, 2008). Some of the intensification practices that have been associated with bird declinations include increased mechanization, use of pesticides, changes in the species cultivated, farming methods and increased farm size. The intensification also leads to the elimination of original trees and changes the time of sowing or harvest and/or increased monocultures (Jones et al., 2005, Donald et al., 2006, BirdLife International,2008). The effect of these practices is usually indirect, for example, bird population declines in agricultural landscapes have been frequently associated with insect declines due to the use of pesticides, since it is well known that most of these birds base their diet on the intake of insects and other invertebrates (Benton et al. 2002).

In the case of the tropics, research on the patterns of functional diversity in different types of agricultural landscapes show that agricultural bird species have greater habitat and diet breadth than forest species in a study done by Tscharntke et al. (2008). Their study shows that agroforestry bird assemblages are composed in their majority of frugivorous and nectarivorous species and fewer insectivorous in comparison to forest habitats. This result suggested that agricultural transformation is disadvantageous for insectivorous species (Tscharntke et al. 2008).

These studies strongly support the idea that birds provide an excellent model to study the influences of agricultural habitats on natural communities. Birds can act not only as target species for conservation, but also as indicator groups of ecosystem health and providers of ecosystem services (Whelan, Wenny and Marquis 2008). Moreover, the behavioral, phonological and demographic patterns are closely associated with crop phenology and structure, influencing nest-site preferences, feeding habitats and migration patterns (Borg and Toft 2000, Brickle et al. 2000, Chamberlain et al. 2000).

Finally, birds are a charismatic group that brings together thousands of people, birdwatchers, NGO's and scientists from all around the world. The amount of data about birds' distributions is probably one of the best data sets of fauna worldwide (e.g. ebird.org, birdlife.org, and Aviabase.bsc-eoc.org). Birds represent one of the greatest opportunities humans have to understand natural communities in anthropogenic scenarios (Ormerod and Watkinson 2000).

2.3 Coffee Agroecosystems

Coffee crops are some of the agroforestry systems with the greatest potential to preserve biodiversity, partly due to the fact that coffee is produced in areas of high biodiversity. In Latin America, every country from Mexico to Bolivia are important global producers of coffee as well as hotspots for biodiversity, and particular, Colombia is regarded as having the world's highest diversity of biodiversity and is the second largest producer of coffee in Latin America (Botero and Baker 2002). The important role coffee plantations play in conservation is twofold (Perfecto et al. 2009): Coffee plantations offer important habitats for biodiversity, and second, coffee plantations are high quality elements of the matrix, facilitating dispersal and migration.

Coffee plants grew originally as understory vegetation, hence, initially coffee production took place in forests where the lower vegetation stratum was removed, and the canopy of the native vegetation was maintained. With time, this practice has been often replaced for more efficient and profitable techniques where canopy trees were replaced by new tree species that could be beneficial for the soils and therefore the coffee plantation (i.e. *Inga* sp) or species that will offer some kind of economic benefit for the small farmer (i.e. citrics, plantains, avocados). During the decade of the 1970's, a significant amount of the shade coffee plantations worldwide was eliminated from many regions for two main reasons: first, shade plantations create humid environments that facilitated the propagation of Coffee rust fungus (*Hemileia vastarix*) and other plagues, and second, there were economic reasons to eliminate the shade and increase the size of the yield (Perfecto et al 1996). As a result, coffee regions in Latin America have been undergoing a substantial agricultural transformation characterized by an increase in the number of hectares assigned for sun-exposed coffee, the elimination of shade trees and the increase of agrochemical input (Perfecto et al 1996, Moguel and Toledo 1999).

Coffee production systems used in Colombia

More than 70% of the original land cover in the Colombian Andes has been transformed into agriculture over the last 80 years (Guhl 2008). One of the main purposes has been the production of coffee, which currently represents around the 34% of the total area assigned for the use of permanent agriculture, making coffee the third most important product for exportation in this country and representing more than 1.8% of the GDP (Espinal et al 2005). Colombian coffee has become a national icon and has established itself as one of the best types in terms of quality and flavor.

In recent years, as in the rest of Latin America, coffee growing systems in Colombia have evolved significantly from low-density and highly diverse plantations (polycultures), into high density, monocultures with highly intensive agro-industrial production (Guhl 2008). These changes have not only had big economic implications, but also are well known for playing an important role in the maintenance of biodiversity and ecosystem services (Perfecto and Snelling 1995, Perfecto et al. 2005, Ibañez et al 2010).

The variety of edaphic, climatic and socioeconomic characteristics in which coffee can be grow in Colombia gives rise to a wide range of production systems. Variables such as the size of the coffee area, density, age, type of coffee, light, altitude, latitude, distinguish two general coffee production systems: sun-exposed coffee production or shade coffee production (agroforestry). Sun exposed coffee production thrives in areas with good soil fertility and with appropriate solar radiation and availability of water (with enough rainfall patterns and very good distribution throughout the year). These systems use high seeding rates, between 7,500 and 10,000 plants per hectare, resulting in a high productivity (2500-4000 kg dry parchment coffee per hectare). According to the National Federation of Coffee Growers (http://www.cafedecolombia.com), about 30% of Colombian coffee is grown in full sunlight. On the other hand, shade coffee production is an agroforestry system that uses trees to provide different levels of shade depending on the species and spatial arrangement. They are mainly used in areas where the climate is characterized by high solar radiation and extended dry periods, and physical conditions such as the soil erodability and steep slopes represent limitations for adequate crop growth. In these systems, the optimum planting density (2000-3000 plants per hectare) and productivity (500 -1000 kg dry parchment coffee per hectare) are lower than in sun-exposed coffee plantations.

Furthermore, the complexity of shade production systems varies widely. Within the shade coffee plantations, four particular production types have been defined in Colombia, depending on the degree at which the natural habitat, usually forest, has been altered. These categories are: i) rustic plantation, ii) traditional polyculture, iii) commercial polyculture, and iv) monoculture (Moguel and Toledo, 1999; http://www.cenicafe.org/).

Rustic coffee production, as mentioned before, was the former coffee production system and common during the first two thirds of the 20th century (Perfecto et al 1996). However, given the standards of quality and production coffee requires nowadays, this technique is no longer used in Colombia (Moguel and Toledo 1999). The second type is the traditional polyculture, where the forest canopy is transformed in small proportions. Some of the trees that make up the shade original shade are cut and new native or exotic species are introduced. These new tree species have usually a commercial value and hence farmers can obtain additional economic benefits, such as fruit trees, timber trees and medicinal species. The shade then will be made up by several of this species in a variety of proportions and arrangements, making traditional polycultures a real “natural garden” (Moguel and Toledo 1999). The third type is the commercial polyculture, where all the original canopy cover is removed and replaced by tree species beneficial to the coffee crops. In general, these species are *Inga* sp. (Guama) and *Erythrina* sp (Anacos), which provide considerable amounts of nitrogen to the soil, but they can also include fruit tree species. Finally, the fourth type is the monoculture, where only one species of tree provides the shade, and this is generally a leguminosae (*Inga* sp.). This last one is one of the most technified forms of production and its economic and the negative impacts on conservation of biodiversity can be comparable to the ones from sun exposed crop types (Moguel and Toledo 1999).

Coffee production Systems and Birds

Over the past 50 years, the transformation towards more sophisticated coffee production systems, such as monocultures and sun plantations, has increased at accelerated rates, contributing in a large extent to the loss of native vegetation cover and fauna (Perfecto et al., 1996). It has been increasingly shown that traditional shade coffee plantations provide an important refuge for biodiversity, especially when compared to more intense agricultural practices (Greenberg et al. 1997b, Moguel and Toledo 1999, Johnson 2000, Klein et al. 2002, Mas and Dietsch 2004). In conclusion, the social, economic and ecological set up of coffee producing systems in countries like Colombia have generated the urgent need to find conservation strategies that combined with the production of this national icon (Perfecto et al. 1996, Guhl 2008). On paper, coffee production systems in Colombia consist of rigorous schemes that ponder the socio-economic realities of the region, together with the implementation of high-tech agriculture, aiming to produce a strong and competitive coffee that in theory protects natural resources (Cenicafe, 2010). However, the study of economic and social inequalities associated with coffee production in Colombia goes beyond the scope of this thesis. Conversely, the implications that this different types of systems have on biodiversity is a main concern for this work.

Several studies have documented the importance of shade coffee plantations for a wide variety of fauna such as birds, frogs, arthropods, bats and other mammals (Gallina et al 1996, Greenberg et al 1997, Calvo and Blake 1998, Tejada et al 2004, Pineda et al 2005 Ambrecht et al 2005, Cruz et al 2005). The valuable characteristics that shade coffee plantations provide to biodiversity are related to higher crop diversity and vegetation complexity (i.e. traditional polycultures). Although the relative importance of different micro-environmental variables has not been deeply analyzed, it is suggested that these agroecosystems contributions to biodiversity rely on the high offer of food and habitats to forage and nest (Perfecto et al. 1996, Perfecto et al. 1997, Johnson 2000, Greenberg et al. 2000). In the same way, shade coffee plantations have been demonstrated to have animal and plant communities that are more similar to native forest communities than those communities hosted in sun-exposed plantations (Perfecto and Snelling 1995, Wunderle and Latta, 1996, Greenberg et al 1997c, Ambrecht et al 2005). In general, the scientific community has been suggesting that as the structural complexity of the shade increases, the community assemblage found in coffee plantations will be more interesting and valuable for conservation purposes (Greenberg et al 1997; Calvo and Blake 1998; Tejada et al 2004).

Coffee plantations have also shown to support high numbers of Neotropical migratory birds and this association has been shown depend on the floristic composition and the structural features of the vegetation within the coffee plantations (Bakermans et al. 2011). For example, plantations with a higher number of large trees (>38 cm dbh) and higher canopies are positively correlated with the densities of canopy forager species.

Additionally shade cover is positively correlated with understory forager species (Bakermans et al. 2011).

This work aims to investigate how bird species respond to habitat fragmentation in agricultural landscapes by answering the following questions:

1. Are bird communities associated with coffee agro-ecosystems affected by different small-holder coffee production systems?

2. What are the relative effects of particular environmental, ecological or landscape characteristics on the responses?

The specific goals were:

i. To assess the relationships between different coffee crop types and bird species' distributions.

ii. To identify the bird communities at each study site.

iii. To study bird – habitat associations

iv. To describe major micro-environmental conditions.

v. To analyze bird distributions in terms of the landscape structure.

Chapter 3: Methodology

3.1 Study Site

This study was conducted in the Municipality of Sasaima, Cundinamarca (4° 53' 53" N / 74° 26' 12" W), on the west slope of the Cordillera Oriental of the Colombian Andes, approximately 80 km NW from the capital city Bogota (Figure 1).

The area is classified as Sub-Andean forest or subtropical wet forest (*sensu* Holdridge, 1967), with an elevation between 1000-1200 m; annual precipitation ranges from 1200-1300 mm, and the mean annual temperature is 22°C (Instituto Geográfico Agustín Codazzi, 2002). The study area is representative of the regional landscape; dominated by pastures, agriculture (critics, plantain, and banana), coffee farms, and cattle fields. There are some small secondary forest patches associated with streams and exotic tree plantations and the closest primary forest patches found at a distance larger than 3km. The date in which human practices and habitat fragmentation began happening in this areas is not clear, though there is a broad idea that this process was originated 30-50 years ago (Renjifo 1999).These landscapes are composed by small holder farms of less than 1ha, hence, factors such as the land use of these small parcels and the management systems, create highly heterogeneous landscapes. Accordingly, the habitat characteristics of each one of these patches and farms could be playing an important role influencing the bird communities that can potentially inhabit and thrive in these patches.

The proximity of this study region to Bogota has led to a rapid increase in human population and development where agricultural, industrial and demographic processes represent a serious threat to biodiversity making the region one of the most degraded areas of the tropical Andes, with only 10% of the original habitats remaining (Conservation International, 2010). Consequently, the landscape heterogeneity of this region, allow it to be part of a natural experiment to locally assess the potential responses of bird communities to habitat fragmentation and compare the relative importance of different habitat types in conservation and planning programs. Given the absence of natural protected areas for biodiversity conservation in this area, adapting better agricultural production types can be key aspects for the avifauna conservation of this region.

Figure 1. Study Site (Sasaima, Cundinamarca - Colombia)

3.2 SAMPLING DESIGN AND SITE SELECTION

Bird communities were sampled in a total of 16 coffee plantations, comprising a total area of $5km^2$ (Figure 2 and Table 1).

The total number of sites selected for this study corresponds to the amount of sites I was able to visit during the 7 week period of field work, in June and July of 2010. Site selection criteria were firstly, the need to include coffee crops with different management types (shade, semi-shade and sun plantations), and secondarily to include sites that had a surface area of at least $100m^2$. Finally, due to budget limitations and the unavailability of a personal vehicle, the sites included need to be accessible using public transportation.

As seen in Chapter 1, landscape conceptualizations vary among the literature, for that reason and for the sake of clarity, the following concepts will be defined for this particular study (Fahrig 2003):

<u>Fragment:</u> Remnant of original habitat. For the purpose of this study, forest remnants are secondary forest associated with streams.

<u>Matrix:</u> Modified or cleared formerly forested habitat. For the purpose of this study, the matrix will consist of different crop types, pastures, roads and human settlements.

<u>Patch:</u> Small fragment of the original vegetation cover or the vegetation cover of interest, defined in terms of size, shape and type (e.g. coffee crop type). For this study, every sampling site constitutes one single patch of coffee plantation. For clarity, throughout the rest of this document, coffee patches will be called *sites.*

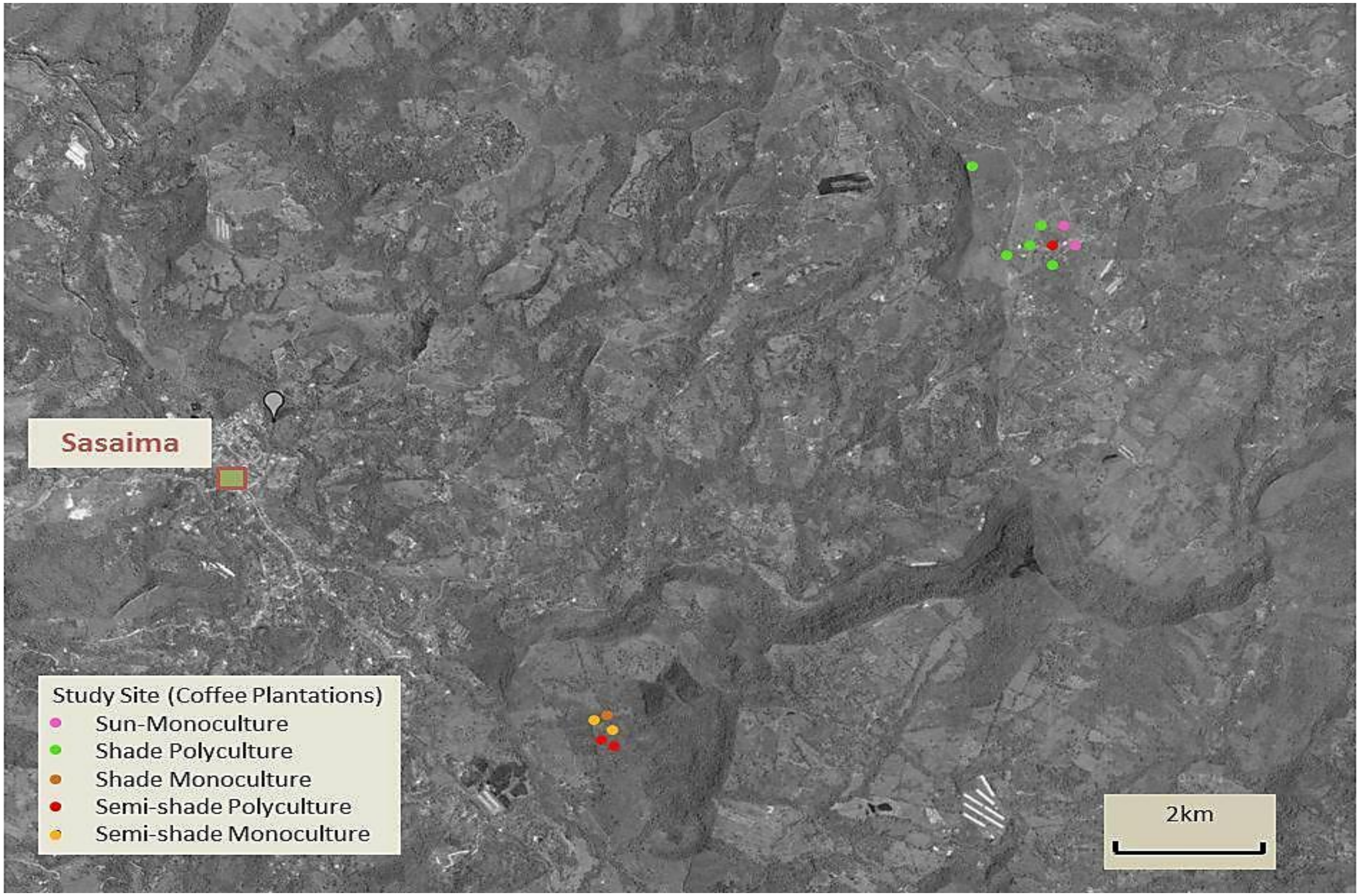


Figure 2. Sampling site locations.

Table 1. List of the sampled habitat types and correspondent sampling efforts.

Crop Type	Habitat Type	Habitat Code	No. of samples
Sun	Monoculture	SM	2
Semi-shade	Monoculture	SSHM	2
Semi-shade	Polyculture	SSHP	3
Shade	Monoculture	SHM	1
Shade	Polyculture	SHP	8

Photo 1. Landscape of the municipality of Sasaima, Cundinamarca (Colombia) and study sites.

The landscape in this study area is composed of smallholder farms, giving rise to a particularly heterogenic landscape mainly made up of a mix of crop types such as citrus trees, plantain, pastures and with a predominance of coffee (Figure 2, Photo 1).

This study focused on the relative influence of different coffee crop types in the community responses of the avifauna associated with these agro-ecosystems. Accordingly, coffee production systems were classified primarily based on the coffee crop type as: (1) Shade (2) Semi-shade or, (3) Sun-exposed coffee, and subsequently, based on the complexity of the vegetation providing the shade as (1) Polyculture, where more than two tree species provided shade to the coffee plants, or (2) Monoculture, where mainly one tree species provided the shade (Table 1, Photo 2-3)

Photo 2. Sun coffee plantation in Sasaima, Cundinamarca

Photo 3. Shade polyculture coffee plantation in Sasaima, Cundinamarca.

3.3 BIRD SURVEYS

In order to identify the understory bird community and its distribution in each coffee plantation, bird observations were conducted from 6 am to 11 am, and from 4 pm-6 pm, using 3 different methods:

1) Point count sampling: this popular method to sample birds, allows an efficient way to sample birds over broad areas at a moderately low cost, as well facilitating general evaluations of species-habitat relations. With this technique, all individuals heard and observed at each point station during 15 minutes were recorded. The distance between point stations varied according to the size of the fragment (50-100 meters). Additional information about group size, type of encounter (visual sighting, call, song, or flying), the sex of the individual birds (when possible), the height at which the bird was seen (ground, low, mid-strata or canopy), the activity (movements, foraging activity, foraging

behavior, and calls), and the type of habitat were also recorded (Rosenstock et al. 2002, Bibby 2000).

2) Systematic observations: given that in some mornings, birds are rather quiet, an additional hour of bird observations was done around the point counts, in order register species that were not detected during point counts and saturate the sampling. The data recorded was, when possible, the same data for point counts (Bibby 2000, Rosenstock et al. 2002) (Photo 4).

3) Mist netting: mist-netting is an effective way of recording quiet and cryptic species that inhabit the forest understory, which may not be recorded using other techniques. In order to compare this element of the avifauna, a minimum of 50 meters of mist nets was used as a standard method. The nets were open from 6 am-11 am and from 4 pm to 6 pm, in each sampling site for one day. Captured individuals were marked to exclude recaptured individuals from capture totals. Nets were checked at least every half hour, and were closed immediately during rain (Bibby 2000, Rosenstock et al. 2002) (Photo 5).

Only species making direct use of the coffee plantation were registered, this applied also for migrant species. Birds flying over the plantations or nocturnal were not considered in this study.

In order to evaluate the species ecological traits in this study, each bird species was assigned to one of 6 possible feeding guilds: Exclusively frugivore, frugivore/insectivore, granivore, insectivore, nectarivore or omnivore. This classification also applied for migrant species. See Table 2 for definitions and Photo 4 for examples.

Table 2. Feeding guilds definitions and examples.

Feeding Guild	**Definition**	**Examples**
Exclusively Frugivore (Frugivore)	Fruit eaters.	Parrots
Frugivore/Insectivore		Tanagers, Thrushes,
Granivore	Seed eaters	Sparrows, Finches
Insectivore	Understory and canopy insect eaters.	Antbirds, wrens, flycatchers, woodpeckers, Antshrike, spinetail
Nectarivore	Nectar	Hummingbirds
Omnivore	Mixed diet	Thrushes

Photo 4. Systematic observations.

Photo 5. Mist netting surveys.

a. *Forpus conspicillatus*

b. *Tangara cyanicollis*

c. Tiaris olivacea

d. *Synallaxis brachyuran*

e. *Chalybura buffoon*

f. *Turdus ignobilis*

Photo 6. Feeding guild examples: a. Frugivore; b. Frugivore/Insectivore; c. Granivore; d. Insectivore; e. Nectarivore; f. Omnivore.

3.4 HABITAT SURVEYS

To identify micro-environmental conditions that could potentially influence bird community composition associated with each crop type, habitat descriptions were made using standardized plots of 10 x 10 m where the percentage of canopy cover, the canopy height and the three most abundant tree shade species were recorded (Table 3) (Rengifo 2001). The canopy cover was calculated using an ocular estimation, measured with a plastic grid of 100 cm^2. The number of cells covered by foliage was recorded and is presented as the average percentage of canopy cover at each site (Korhonen et al. 2006). Canopy heights were estimated using distance-angle methods and were classified in 4 categories for the analyses, as follow: (1): 0-5 m, (2): 5-10 m, (3):10-20 m, (4): >20 m (Korning and Thomsen 1994). All observations were made by the same investigator to avoid observer bias. The patch area and perimeters were calculated using the GPS units.

Photo 7. Rapid habitat survey and descriptions by the author.

Table 3. Habitat and landscape variables used to characterize each site.

Variable	Possible values/units
Coffee Crop type	Shade (SH), Semi-shade (SSH), Sun (S)
Coffee habitat type	Monoculture (M), Polyculture (P)
Dominant shade species	Plantain, Citrus, Avocado,
2^{nd} Dominant shade species	Plantain, Citrus, Avocado,
3^{rd} Dominant shade species	Plantain, Citrus, Avocado,
% Canopy cover	0-100
Canopy height category : range (m)	1: 0-5 m, 2: 5-10 m, 3: 10-20 m, 4: <20 m
Patch Area	Square meters
Patch perimeter	Length in meters

Table 4. Explanation of the diversity indices used to characterize the bird communities in the coffee plantations.

Diversity index	Explanation
Shannon Index	Gives a measure of species numbers and the evenness of their abundance. Particularly useful when comparing similar ecosystems or habitats, as it can highlight one example being richer or more even than another (Krebs 1989)
Simpson Index	Represents the probability that two randomly selected individuals in the habitat will not belong to the same species. It takes into account the number of species present, as well as the relative abundance of each species (Krebs 1989).

3.5 Statistical Analysis

In order to examine the changes in the bird species composition across the different coffee crop types, community composition was analyzed with presence/absence data and species relative abundance. To estimate species richness, the total number of species detected at each site was counted, regardless of sample size differences among sites (Table 1).

Subsequently, using the Vegan package in R (http://www.r-project.org/), other diversity indices were calculated (Shannon index and Simpson's) and the rarefaction analysis was used, to minimize the subsampling bias on the dataset and correct differences in sampling effort. To estimate the relative abundance for each species at each study site, the total number of individuals per species was divided by the total number of individuals at a given site. This measure of abundance assumes that birds are recorded more often in areas where they are more abundant, and assumes that there are no significant differences in species detectability. This could potentially affect the absolute abundances approximations but not the relative abundance patterns.

Data about species and sites were organized in resemblance matrices in order to compare among-site community composition differences and their relationship with environmental and regional variables using the Bray-Curtis analysis of similarity. In these matrices, each cell contains a numerical measure of similarity or distance between a particular pair of sites for any variable of interest (Legendre and Legendre 1998); all matrices used in analyses were distance matrices, where higher index values indicated greater dissimilarity. This format has been used for comparing bird survey data to environmental variables when dealing with disparate types of spatial data (Wiens and Rotenberry 1985, Fleishman et al. 2003, Jankowski et al. 2009). Subsequently, bird incidence and habitat data were analyzed using a multivariate statistical approach which allowed addressing two main goals: (1) identify the general distribution of bird communities among the coffee crops, and (2) examine the general relationship between guilds and environmental variables. Differences among bird communities and species richness were statistically compared using non-parametric ANOVA (Kruskal-Wallis) and Tukey's multiple comparison tests (SPSS v.17.0.2, 2009).

For all the independent variables that were significantly correlated with variation in bird species compositions, a Non-metric Multidimensional Scaling (NMS) (Kruskal's Non-metric Multidimensional Scaling, R Mass Package) was used to sort samples (habitat types) and bird communities, to reduce dimensionality of the data and to identify major trends. This ordination technique (NMS) was chosen because contrary to other ordination techniques, NMS uses a small number of axes that are explicitly chosen prior to the analysis and the data are fitted to those dimensions, avoiding hidden axes of variation and ultimately, unlike other ordination methods, NMS makes few assumptions about the nature of the data (Minor and Urban 2010). The Steinhaus (Bray-Curtis) and Sørenson indices were used to estimate multivariate community composition distance for bird species and guilds (Minor and Urban 2010).

In order to graphically represent and identify the important environmental factors influencing families and guilds incidence, a classification and regression tree (CART) model was used. This analysis allows classifying community types by sub-setting the data and successively explaining smaller and smaller groups of the data (De'ath and Fabricius 2000). In particular for this study, CART analysis was selected because they are a nonparametric method that makes no assumptions about the nature of the response, and have been a popular way to graphically and hierarchically represent and explore complex ecological data, by describing and predicting ecological patterns and processes (O'Connor et al. 1996, De'ath and Fabricius 2000).

Chapter 4: Results

4.1 SPECIES RICHNESS

A total of 97 bird species (1670 individuals observed, 3 individuals not identified) were recorded among all the study sites (Appendix A). The 97 species belong to 21 families, representing all the six guilds defined previously. There was only one register of migratory species the Summer tanager (*Piranga rubra*), and this included a female, a male and a juvenile. Given the time of the year in which this study was carried out (July-August) neotropical migrants are not expected to be in the tropics yet, suggesting that this group was already established in this region, making use of the shade coffee plantation and is now a resident. No endangered species were recorded.

As seen in Figure 3, species richness varied among habitat types. Specifically, this study found that habitats characterized by shade or semi-shade coffee plantations under polycultures had the highest number of bird species (shade poly: 68; semi-shade poly: 67; Table 5), and that habitats characterized by shade or sun monocultures, had the lowest species richness (47 species). Shannon's and Simpson's diversity indices were similar among different habitats and showed no statistically significant differences (ANOVA Kruskal-Wallis, $P>0.05$). Even though the differences in diversity indices among sites were not statistically significant, there is a clear trend towards increased species richness and number of individuals, as the coffee plantations consists of more shade and where more than one tree species provide the shade (polycultures) (Figure 4, Figure 5, Table 5; ANOVA and Tukey's multiple comparison $P>0.05$).

The species accumulation curves based on the rarefaction analysis for each habitat type are shown in Figure 4 and illustrate that the sampling effort for polyculture habitats was sufficiently representative, collecting most of the species present in these habitat types, but did not reach the asymptote for monocultures. Additionally, the rarefaction results also indicate clear differences in bird species richness between different plantation types; the estimated total of species richness was greater in coffee plantations within Polycultures, for both shade and semi-shade types, and that Monocultures including Shade, Semi-shade and Sun plantations have the lowest species richness estimates. Shade and semi-shade polyculture plantations accumulated a highest number of species than any other production plantations. The curves also suggest that based on the estimated number of species in monoculture plantations, the sampling effort was not enough.

Table 5. Diversity indices among coffee habitat types.

Habitat type	Crop type	No. Families	No. Species	No. Individuals	Shannon's Index	Simpson's Index	Rarefaction
Shade	Mono	15	47	128	3.51	0.95	1.96
	Poly	17	68	844	3.43	0.95	1.95
Semi-shade	Mono	17	44	160	3.40	0.95	1.96
	Poly	20	67	435	3.45	0.94	1.94
Sun	Mono	18	41	103	3.47	0.96	1.97
P-Value Kruskal-Wallis Test		0.295	0.312	0.354	0.284	0.125	0.236

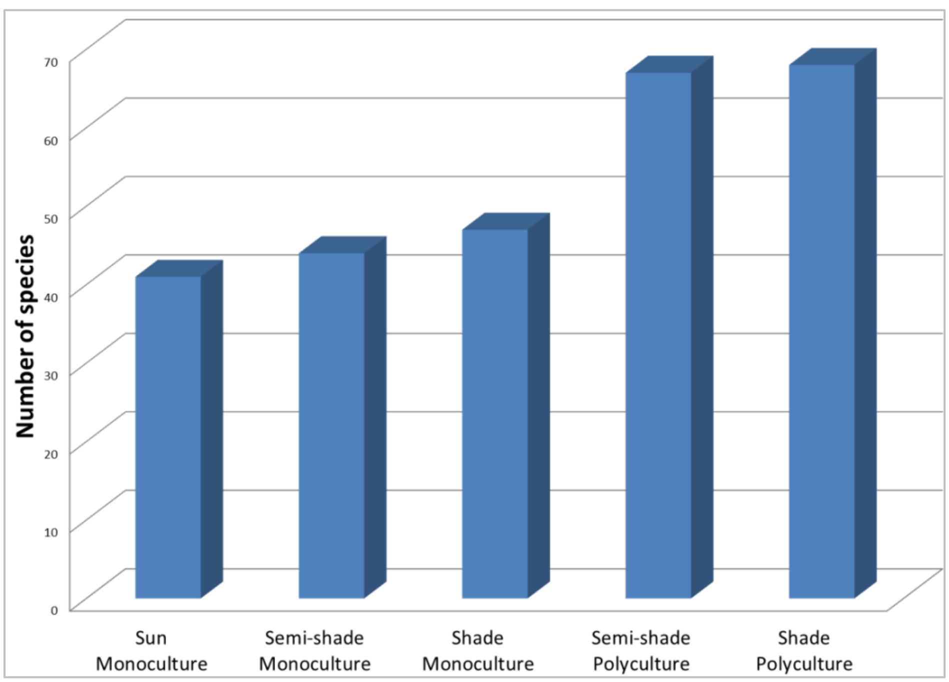


Figure 3. Species richness per habitat type.

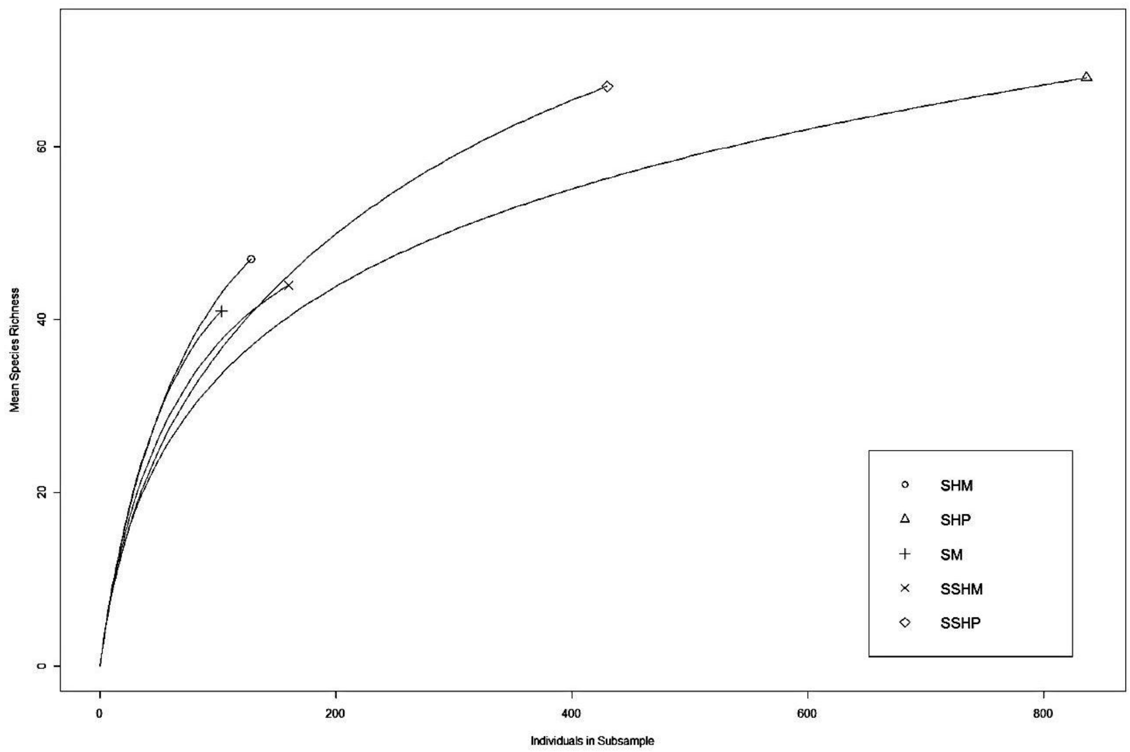


Figure 4. Species accumulation curves for all habitat types

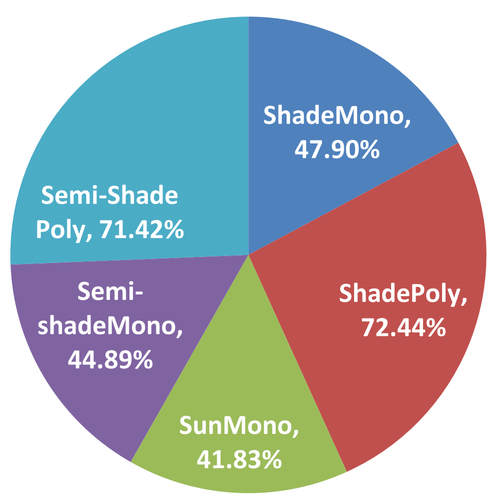


Figure 5. Contribution of each coffee production type to overall species richness (N= 97 species).

Species patterns

Different coffee farms studied share the same dominant species, despite their production type. Overall the most common and most abundant species recorded was the Crimson-backed Tanager *(Ramphocelus dimidiatus)* for all the habitat types (123 observations, 170 individuals) at all coffee plantations. Other common species were the Rufous-collared Sparrow (*Zonotrichia capensis*), the Bananaquit (*Coereba flaveola*) and the Streaked Saltator (*Saltator striatripectus*), all common species in anthropogenic landscapes of the tropical lowlands of the Andes (McMullan 2010).

The top 10 most common species for each habitat type are shown in Tables 7-12, and indicate that in general, seedeaters and tanagers were the most common groups among all habitats. There are no remarkable differences among these ranks, but it is worth noting that the granivorous guild was represented in different habitats by different dominant species; for example doves were very common on sun plantations and shade monocultures, but absent in polycultures, where the most common granivorous species was the Yellow-billed seed eater, absent in other types of plantations.

The majority of the species were generalist species that showed a high affinity for non-forest habitats. Some examples include genera like *Sporophila*, *Turdus*, *Tangara*, *Amazilia*, *Tiaris,* and *Thryothorus*. A second group of species were forest edge generalists, represented by genera like *Thraupis* and *Todirostrum*. There were no records for forest specialist species making use of any type of coffee plantation.

Table 6. List of the ten most abundant species in each site (shown as number of individuals per species).

Species	Shade Mono	Shade Poly	Sun Mono	Semi-shade Mono	Semi-shade Poly	Total
Ramphocelus dimidiatus	14	72	10	18	56	170
Thraupis episcopus	9	74	2	9	54	148
Coereba flaveola	3	45	2	15	24	89
Sporophila nigricollis	2	66	2	3	14	87
Turdus ignobilis	2	53	5	10	14	84
Basileuterus rufifrons	1	62	1	3	10	77
Zonotrichia capensis	2	51	7	2	3	65
Tangara cyanicollis	7	31	4	2	19	63
Thraupis palmarum	9	21	3	5	20	58
Carduelis psaltria	0	42	3	7	3	55

Family patterns

Family representativeness also varied among sites with different coffee plantations (Shade, Semi-shade and Sun). Figures 5-7 show the relative abundance of families for each habitat types and the number of species per family. The most abundant family for all habitat types was the Tanagers (Thraupidae), followed by Flycatchers (Tyrannidae) and Seedeaters (Emberizidae). Similarly, these families were the ones with highest representativeness, having between 7-14 species per family (Figures 5.b, 6.b, 7.b).

Major differences were found between crop types (monocoltures vs. polycultures), as seen in Flycatchers (Tyrannidae), hummingbirds (Trochilidae) and Wrens (Troglodytidae). Less abundant families, such as vireos (Vireonidae), thrushes (Mimidae and Turdidae), blackbirds (Icteridae) and ant-birds (Thamnophilidae) were evenly represented among crop types.

Table 7. Overall top ten of the most common species in this study.

Common name	Scientific name	Guild	No. Observations (Percentage)
Crimson-backed Tanager	*Ramphocelus dimidiatus*	F/I	123 (11%)
Blue-grey Tanager	*Thraupis episcopus*	F/I	78 (7%)
Yellow-bellied Seedeater	*Sporophila nigricollis*	G	65 (5.8%)
Bananaquit	*Coereba flaveola*	N	58 (5.2%)
Black-billed Thrush	*Turdus ignobilis*	O	52 (4.6%)
Rufous-collared Sparrow	*Zonotrichia capensis*	G	50 (4.5%)
Streaked Saltator	*Saltator striatipectus*	G	43 (3.8%)
Blue-necked Tanager	*Tangara cyanicollis*	F/I	43 (3.8%)
Palm Tanager	*Thraupis palmarum*	F/I	40 (3.6%)
Rufous-capped Warbler	*Basileuterus rufifrons*	F/I	38 (3.4%)

Table 8. Top ten most common species in Sun Monocultures.

Common name	Scientific name	Guild	No. Observations (Percentage)
Crimson-backed Tanager	*Ramphocelus dimidiatus*	F/I	9 (10%)
Rufous-collared Sparrow	*Zonotrichia capensis*	G	7 (7.8%)
Bar-crested Antshrike	*Thamnophilus multistriatus*	I	6 (6.6%))
Streaked Saltator	*Saltator striatipectus*	G	4 (4.4%)
Rufous-tailed Hummingbird	*Amazilia tzacatl*	N	3 (3.3%))
Ruddy Ground Dove	*Columbina talpacoti*	G	3 (3.3%)
Shiny Cowbird	*Molothrus bonariensis*	O	3 (3.3%)
Saffron Finch	*Sicalis flaveola*	I	3 (3.3%)
Blue-necked Tanager	*Tangara cyanicollis*	F/I	3 (3.3%)
Black-billed Thrush	*Turdus ignobilis*	O	3 (3.3%)

Table 9. Top ten most common species in Semi-shade Monocultures.

Common name	Scientific name	Guild	No. Observations (Percentage)
Crimson-backed Tanager	*Ramphocelus dimidiatus*	F/I	12 (10%)
Bananaquit	*Coereba flaveola*	N	8 (6.6%)
Streaked Saltator	*Saltator striatipectus*	G	7 (5.8%)
Slaty Spinetail	*Synallaxis brachyura*	I	7 (5.8%)
Black-billed Thrush	*Turdus ignobilis*	O	6 (5.0%)
Scrub Tanager	*Tangara vitriolina*	F/I	5 4.1(%)
Rufous-tailed Hummingbird	*Amazilia tzacatl*	N	4 (3.3%)
Lesser Goldfinch	*Carduelis psaltria*	G	4 (3.3%)
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*	I	4 (3.3%)
Palm Tanager	*Thraupis palmarum*	F/I	4 (3.3%)

Table 10. Top ten most common species in Semi-shade Polycultures

Common name	Scientific name	Gild	No. Observations (Percentage)
Crimson-backed Tanager	*Ramphocelus dimidiatus*	F/I	37 (11.6%)
Blue-grey Tanager	*Thraupis episcopus*	F/I	26 (8.2%)
Bananaquit	*Coereba flaveola*	N	19 (6.0%)
Streaked Saltator	*Saltator striatipectus*	G	17 (5.3%)
Blue-necked Tanager	*Tangara cyanicollis*	F/I	16 (5.0%)
Palm Tanager	*Thraupis palmarum*	F/I	15 (4.7%)
Yellow-bellied Seedeater	*Sporophila nigricollis*	G	11 (3.4%)
Scrub Tanager	*Tangara vitriolina*	F/I	10 (3.1%)
Black-billed Thrush	*Turdus ignobilis*	O	10 (3.1%)
Rufous-capped Warbler	*Basileuterus rufifrons*	I	9 (2.8%)

Table 11. Top ten most common species in Shade Monocultures.

Common name	Scientific name	Guild	No. Observations
Crimson-backed Tanager	*Ramphocelus dimidiatus*	F/I	9 (9.4%)
White-tipped Dove	*Leptotila verreauxi*	G	6 (6.3%)
Blue-grey Tanager	*Thraupis episcopus*	F/I	6 (6.3%)
Palm Tanager	*Thraupis palmarum*	F/I	6 (6.3%)
Blue-necked Tanager	*Tangara cyanicollis*	F/I	4 (4.2%)
Black-headed Brush-finch	*Arremon atricapillus*	G	3 (3.1%)
Bananaquit	*Coereba flaveola*	N	3 (3.1%)
Grey-headed Tanager	*Eucometis penicillata*	F/I	3 (3.1%)
Tropical Kingbird	*Tyrannus melancholicus*	I	3 (3.1%)
Golden-faced Tyrannulet	*Zimmerius chrysops*	I	3 (3.1%)

Table 12. Top ten most common species in Shade Polyculture.

Common name	Scientific name	Guild	No. Observations
Crimson-backed Tanager	*Ramphocelus dimidiatus*	F/I	56 (9.7%)
Yellow-bellied Seedeater	*Sporophila nigricollis*	G	48 (8.3%)
Blue-grey Tanager	*Thraupis episcopus*	F/I	41 (7.1%)
Rufous-collared Sparrow	*Zonotrichia capensis*	G	37 (6.4%)
Black-billed Thrush	*Turdus ignobilis*	O	31 (5.3%)
Lesser Goldfinch	*Carduelis psaltria*	G	28 (4.8%)
The Bananaquit	*Coereba flaveola*	N	26 (4.5%)
Rufous-capped Warbler	*Basileuterus rufifrons*	I	24 (4.1%)
Scrub Tanager	*Tangara vitriolina*	F/I	20 (3.4%)
Blue-necked Tanager	*Tangara cyanicollis*	F/I	19 (3.2%)

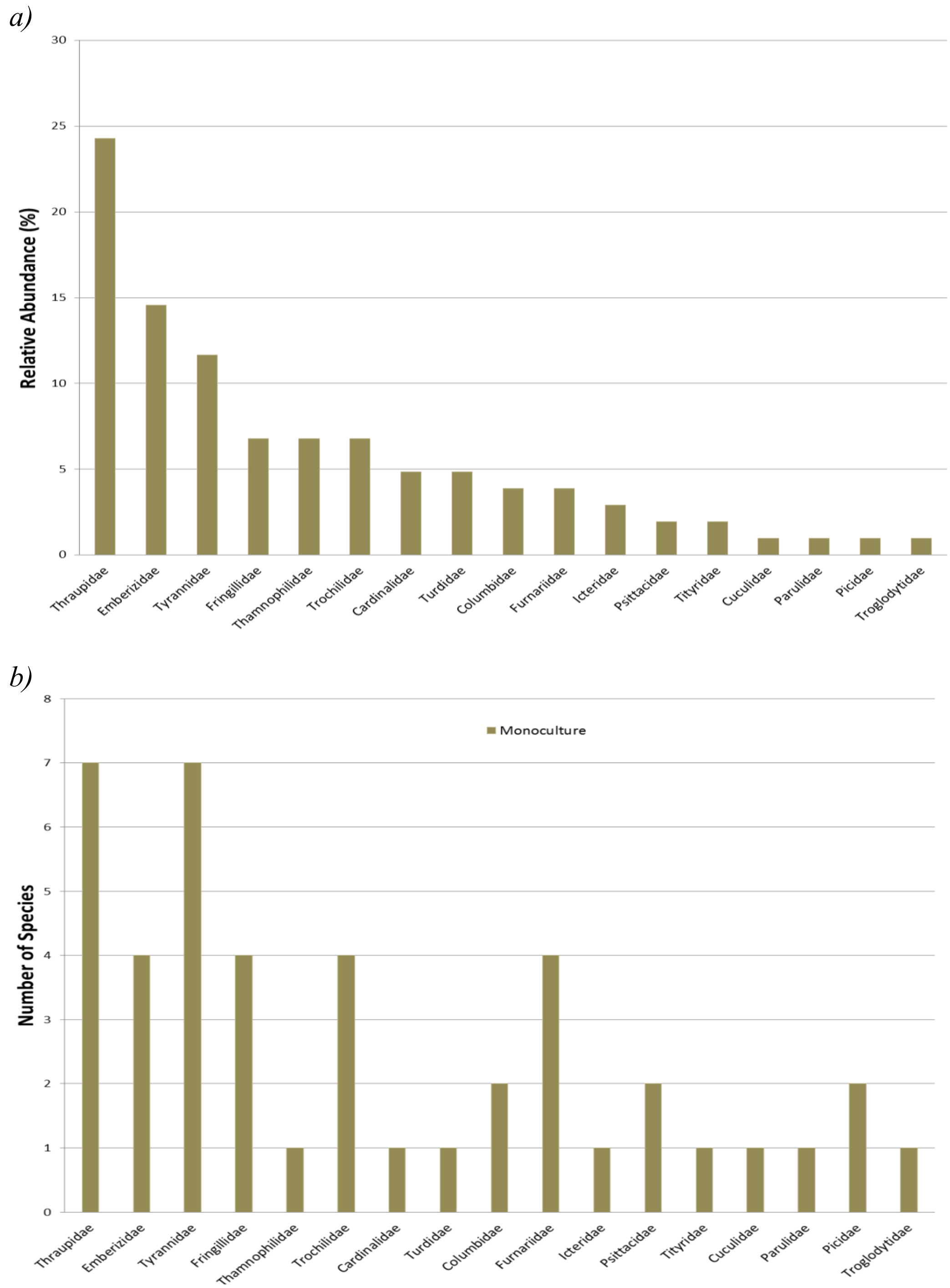


Figure 6. Relative abundances (*a*) and Species richness *(b)* of bird families in sun coffee plantations.

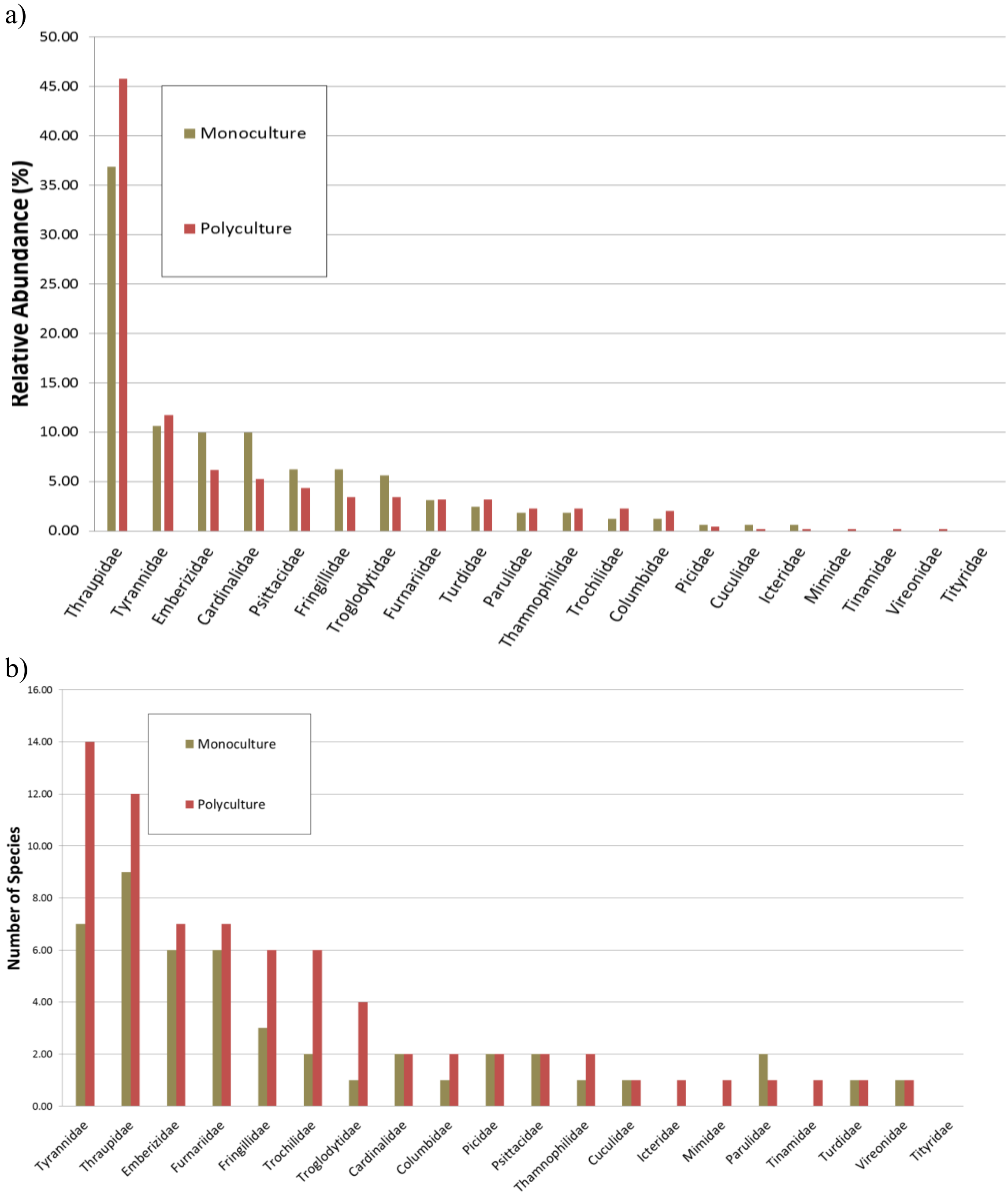


Figure 7. Relative abundances (*a*) and Species Richness (*b*) of bird families in Semi-shade coffee plantations.

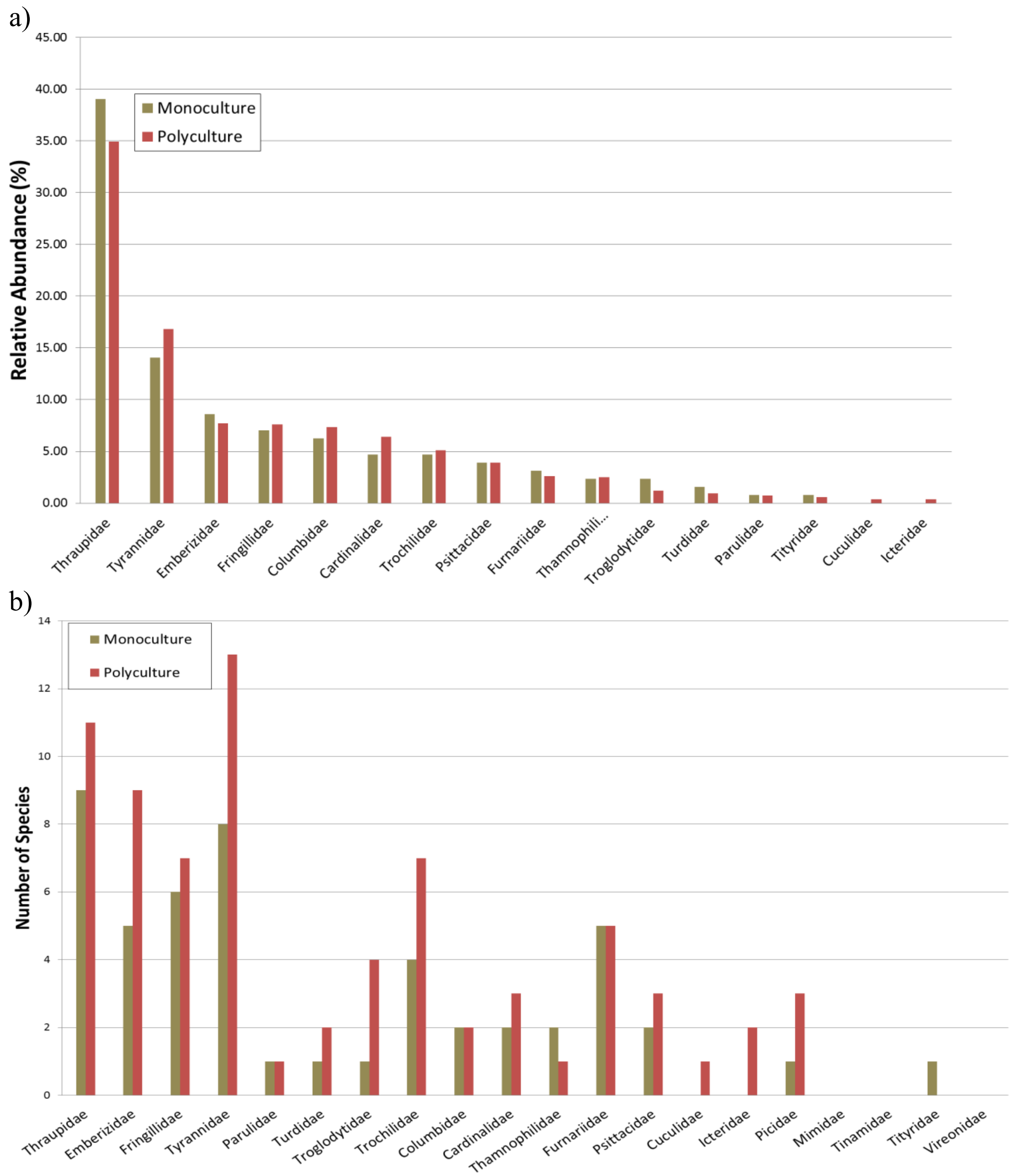


Figure 8.Relative abundances (*a*) and Species Richness (*b*) of bird families in Shade coffee plantations.

4.2 COMMUNITY COMPOSITION

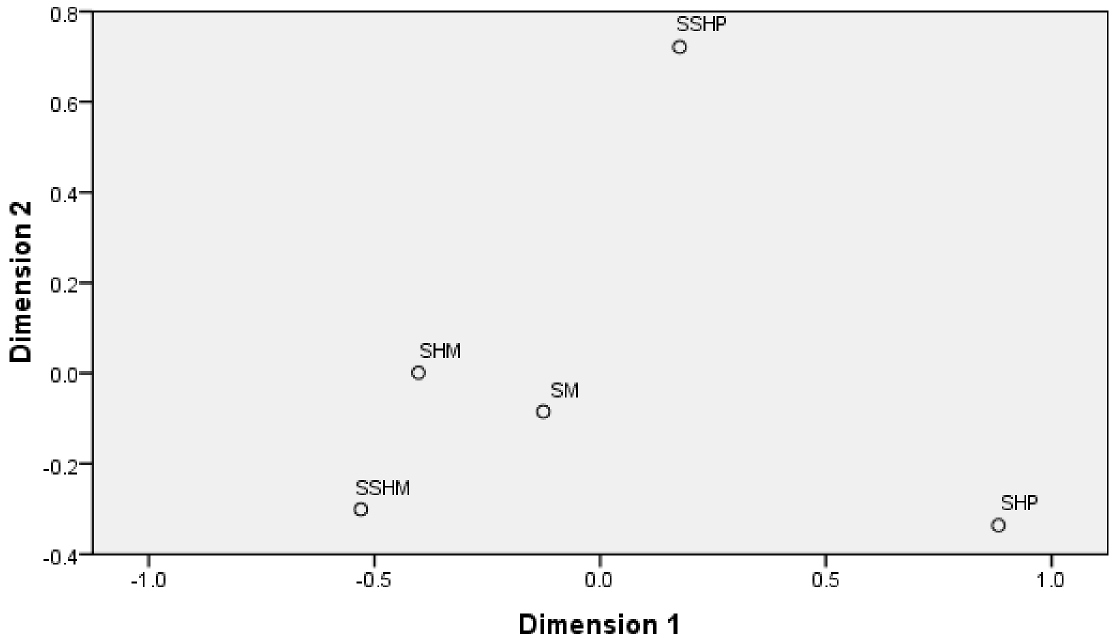
Based on the Non-metric Multi-dimensional scaling ordination, bird species composition varied among habitat types (Figure 9). Bird species assemblages from coffee plantations of polyculture habitat type (SSHP and SHP), are more distant from those from monoculture habitat types (SSH, SHM, SM), hence they share a lower proportion of species; this was true for all sites. The NMDS scores illustrate that the habitat characteristic that locates different species assemblages further apart is the presence of one or several tree shade species. In other words, the longest analytical distances found with the NMDS were between monocultures and polyculture (values of 1.413, 1.328 and 1.242. in Table 14 and 15), this supports the idea that coffee plantations under monoculture environments, host markedly different communities from those growing in polyculture environments. Semi-shade polycultures are the most different communities (most distant) from the other crop types, even from shade polycultures. However, Semi-shade, shade and sun plantations with monocultures cluster together, showing similar species compositions. Sun monocultures seem to have a mixed community composition that makes it hard to distinguish among other habitat types, and it is located in the center of the ordination, and all other habitat types.

The results for the Bray-Curtis analysis of similarity test reveal significant differences among all pairs of habitats and are shown in Table 13. These values indicate that the more distinct communities are those from semi-shade monocultures (SSHM) and shade polycultures (SHP). Conversely, the more similar bird assemblages are shade monocultures (SHM) and semi-shade polycultures (SSHP). This analysis supports that probably, the main differences among community compositions are related to the use of more than one tree shade species, and increasing complexity of vegetation, the main differences between monocultures or polycultures in coffee plantations.

Table 13. Bray-Curtis percent of similarity among habitat types.

	SHM	SHP	SM	SSHM
SHP	0.373 (3)			
SM	0.318 (6)	0.321 (5)		
SSHM	0.296 (8)	0.410 (1)	0.364 (4)	
SSHP	0.280 (9)	0.259 (10)	0.314 (7)	0.387 (2)

SHP: Shade polyculture; SM: Sun Monoculture; SSHM: Semi-shade Monoculture; SSHP: Semi-shade Polyculture. Rank of similitude in parenthesis: 1: Most different, 10: most similar communities.



SHP: Shade polyculture; SM: Sun Monoculture; SSHM: Semi-shade Monoculture; SSHP: Semi-shade Polyculture (Stress 0.00031. Tucker's coefficient of congruence 0.9998[1]).

Figure 9. Non-metric multidimensional scaling of habitat types based on bird species relative abundance.

[1] Tucker's coefficient of congruence takes values between 0 and 1 and is similar to the correlation coefficient, where a value of 0 indicates no similarity and 1 high similarity Lorenzo-Seva, U. & J. M. F. Ten Berge (2006) Tucker's congruence coefficient as a meaningful index of factor similarity. *Methodology: European Journal of Research Methods for the Behavioral and Social Sciences,* 2**,** 57-64..

Table 14. NMS Distances among habitat types based on their species presence/absence.

	SHM	SHP	SM	SSHM	SSHP
SHM	0				
SHP	1.328	0			
SM	.290	1.039	0		
SSHM	.328	1.413	.458	0	
SSHP	.924	1.272	.861	1.242	0

SHP: Shade polyculture; SM: Sun Monoculture; SSHM: Semi-shade Monoculture; SSHP: Semi-shade Polyculture

Table 15. Proximity matrix based on their species presence/absence.

	SHM	SHP	SM	SSHM	SSHP
SHM	1				
SHP	.917	1			
SM	.917	.910	1		
SSHM	.951	.923	.903	1	
SSHP	.977	.912	.862	.956	1

SHP: Shade polyculture; SM: Sun Monoculture; SSHM: Semi-shade Monoculture; SSHP: Semi-shade Polyculture

4.3 GUILD RESPONSES

Another approach to analyze how bird communities respond to different coffee production systems was a guild approach, where each species recorded in the study was assigned to particular feeding guilds (Table 2, Appendix A). In this regard, the abundance of each guild was different between habitat types (Figure 10, Table 9-11). The most abundant guild in all habitat types was the Frugivorous/Insectivorous, with the exception of Sun Plantations, where granivorous were the most abundant species. The second most abundant guild was Insectivorous in semi-shade and sun plantations, and Granivorous in Shade plantations. The least abundant guild for all the habitat types was "exclusively" Frugivorous (Figure 10). The patterns of guild abundances among habitat types are generally the same as for species richness, with the highest abundances and guild representativeness in Shade and Polyculture plantations, and the lowest in Sun plantations. The NMDS scores illustrate that the habitat characteristic that locates different guilds further apart is the presence of one or several tree shade species. In other words, the longest analytical distances found with the NMDS were between monocultures and polyculture (values of 1.568, 1.236 and 1.107. in Table 16), this supports the idea that coffee plantations under monoculture environments, host markedly different communities from those growing in polyculture environments.

In terms of species richness the dominant guild was Insectivore in all habitats, contributing between 40-45% of the species and the individuals present in each habitat type. The second most represented guild was the Granivore (26-36% of the species), the third Frugivore/Insectivore (18-21% of the species); the Nectarivore, Omnivore and Frugivore represent less than the 10% of the total number of species present in these habitats, contributing with one to 3 species (Figure 11). These patterns were the same for all habitats, and there were no significant differences among Shade, Semi-shade or Sun coffee plantation or monoculture or polyculture crop types (Figure 11; ANOVA and Tukey's multiple comparison test P.0.05).

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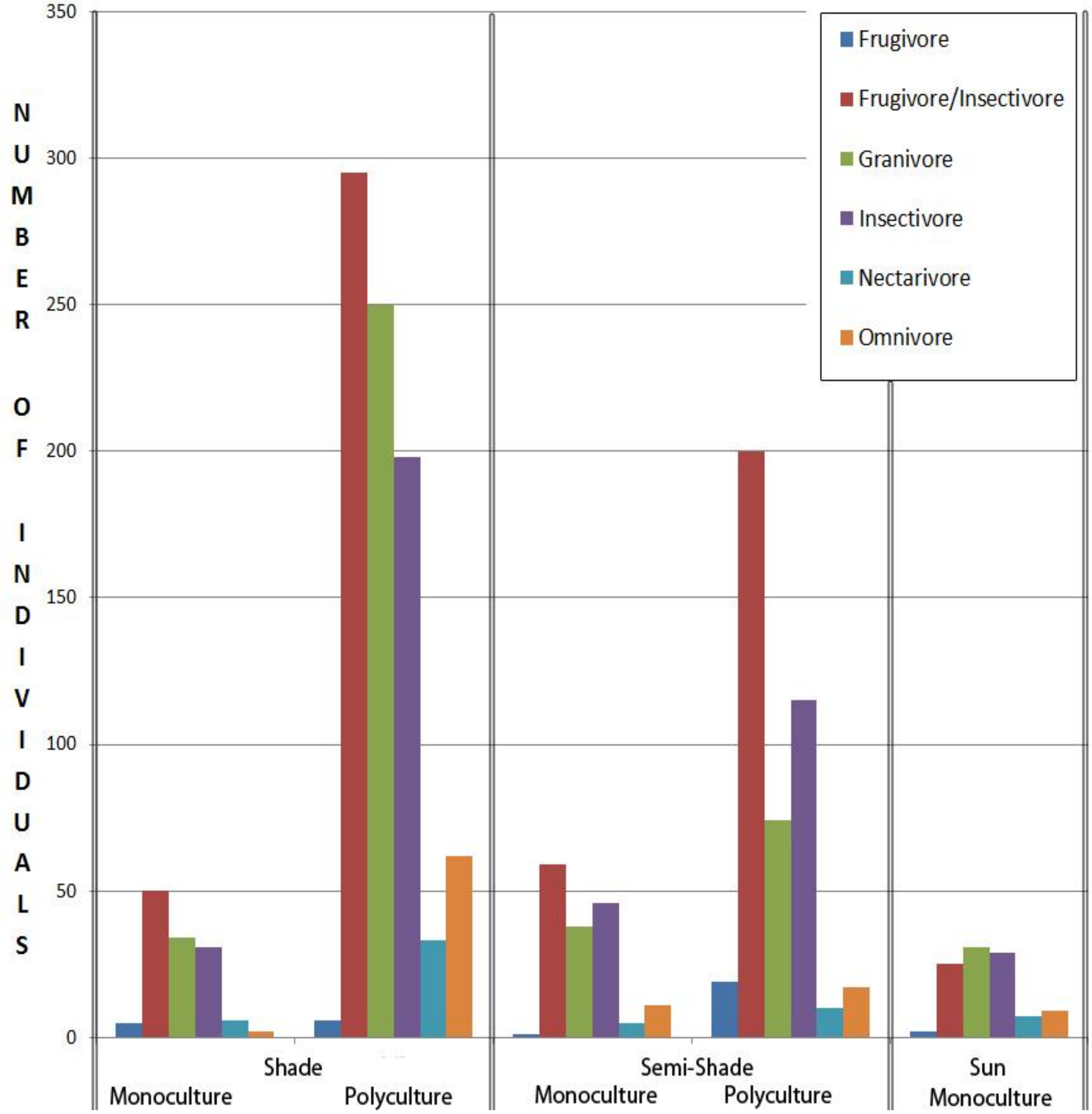

Figure 10. Guild representation (relative abundances) per habitat type.

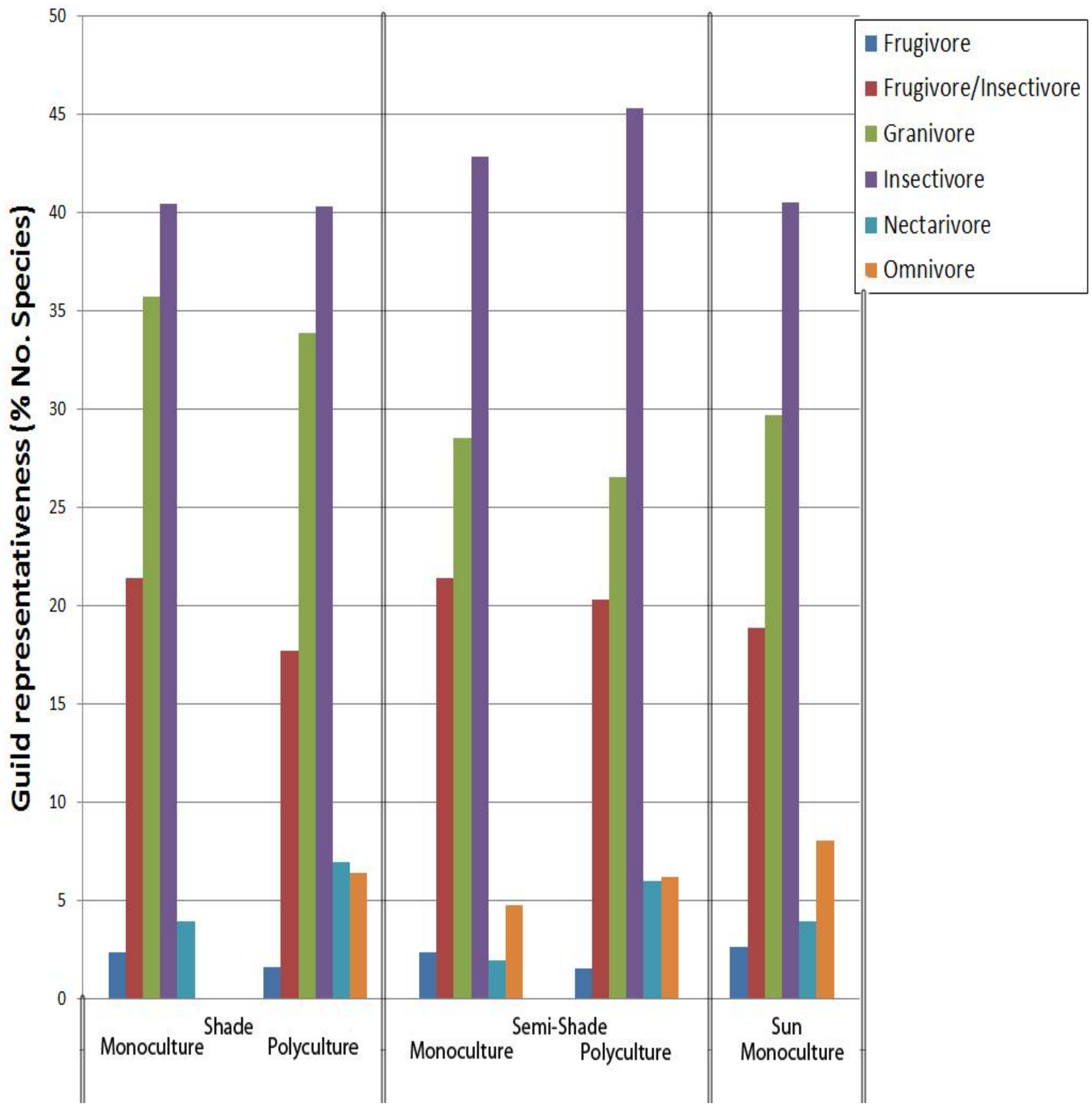

Figure 11. Species richness for each feeding guild.

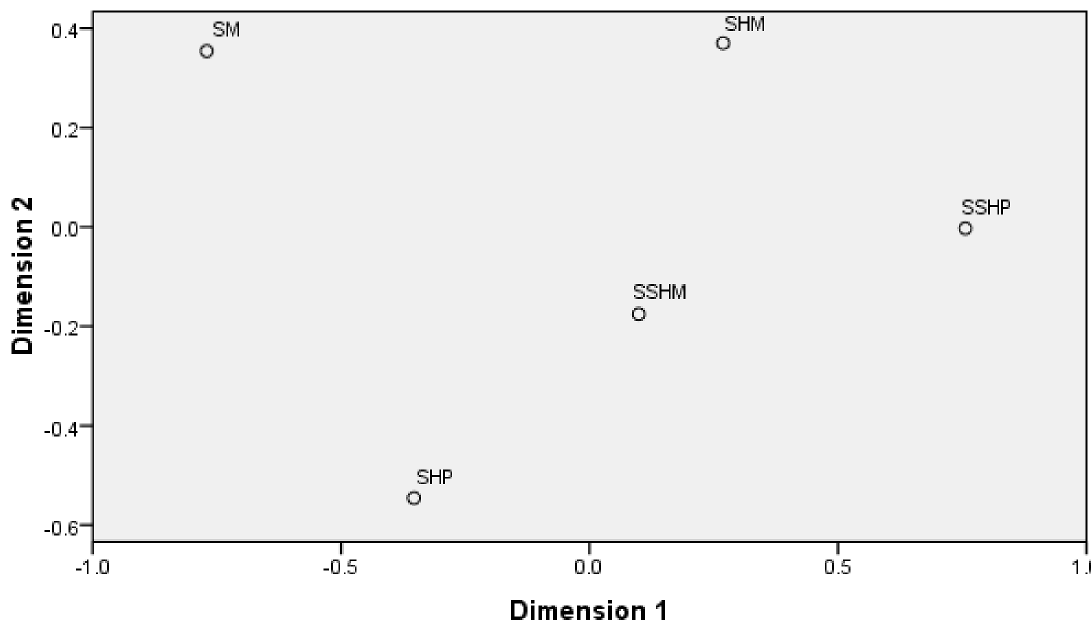

Figure 12. Non-metric multidimensional scaling of habitat types based on species guilds relative abundances. (Stress 0.01797; Tucker's coefficient of congruence 0.990).

Table 16. NMS Distances among habitat types based on the relative abundance of feeding guilds

	SHM	SHP	SM	SSHM	SSHP
SHM	.000				
SHP	1.107	.000			
SM	1.040	.992	.000		
SSHM	.571	.585	1.018	.000	
SSHP	.614	1.236	1.568	.679	.000

SHP: Shade polyculture; SM: Sun Monoculture; SSHM: Semi-shade Monoculture; SSHP: Semi-shade Polyculture

4.4. LANDSCAPE AND HABITAT INDICATORS OF AVIAN DISTRIBUTIONS

Classification and regression tree (CART) analysis was used to create hierarchically organized models of the distribution of bird guilds across sites with different coffee production systems. After the NMS analysis, it was not clear which particular variables might be influencing the community composition at each site hence the CART analysis was done to identify the relative importance of the explanatory variables. The relative abundance of bird species grouped by guild was used as response variable, and explained using five habitat and landscape characteristics (Table 3), in order to understand the abundance patterns. No pruning was performed for three reasons: first, the primarily interest of this study was to explore the relationships between different habitats and the bird communities, and pruning is mostly used to make models that are less overfit to the data and more appropriate for prediction. Second, this study aimed to visualize the role of every possible explanatory variable, regardless of the power of the branch, hence the pruning of branches would have leaded to fewer explanatory variables and finally, the complexity of the dataset did not require it.

The results of the CART analyses for each of the six guilds are shown in Figures 13-18. The results indicate that the presence of each guild is differentially influenced by the explanatory variables. For example, the <Shade species> variable was the most important variable influencing the abundances of all the guilds studied, except frugivores. DBH and Canopy height were other two important explanatory variables. A detailed interpretation of the CART results can be found in the discussion section.

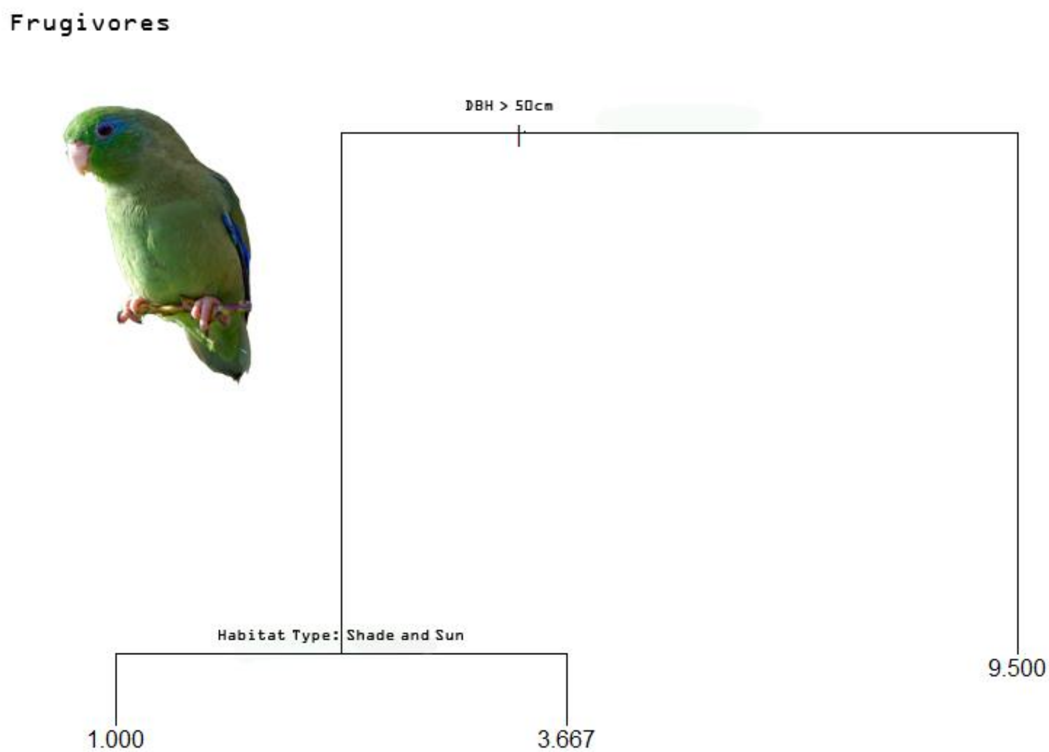

Figure 13. Classification and regression tree (CART) model for Frugivore presence across sites. The split variable and its threshold value is shown in each branch at each node

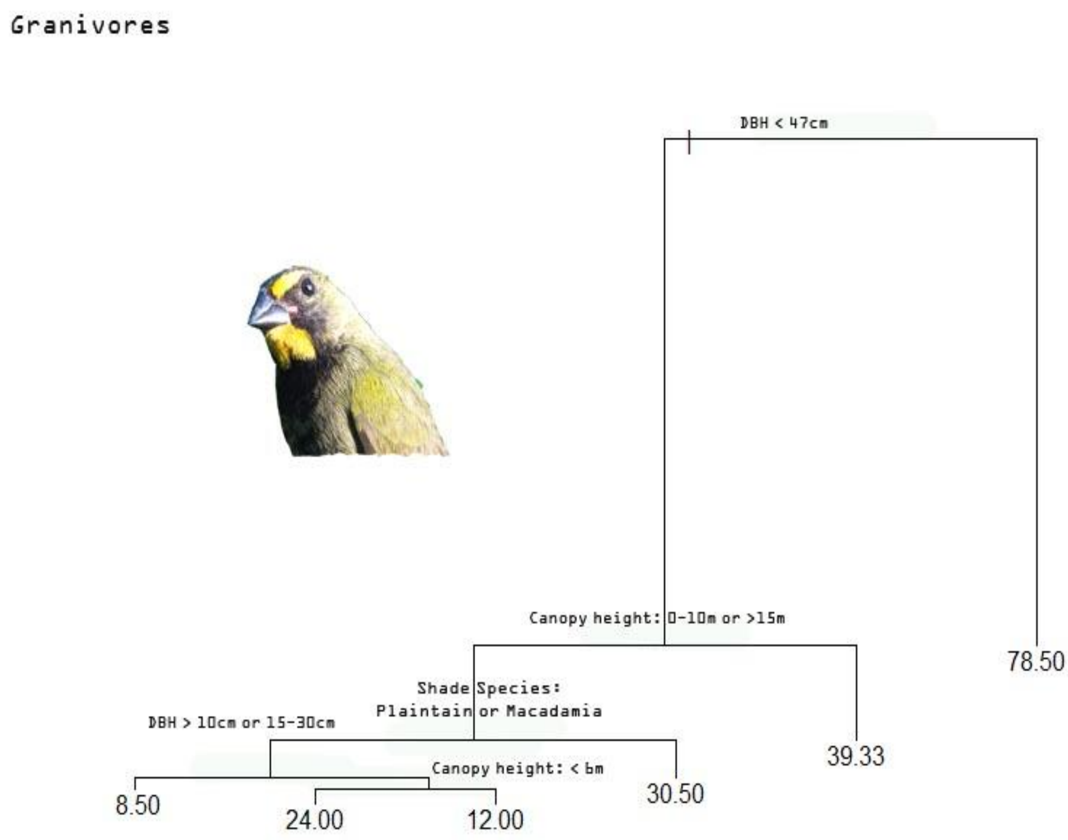

Figure 14. Classification and regression tree (CART) model for Granivore presence across sites. The split variable and its threshold value are shown in each branch at each node.

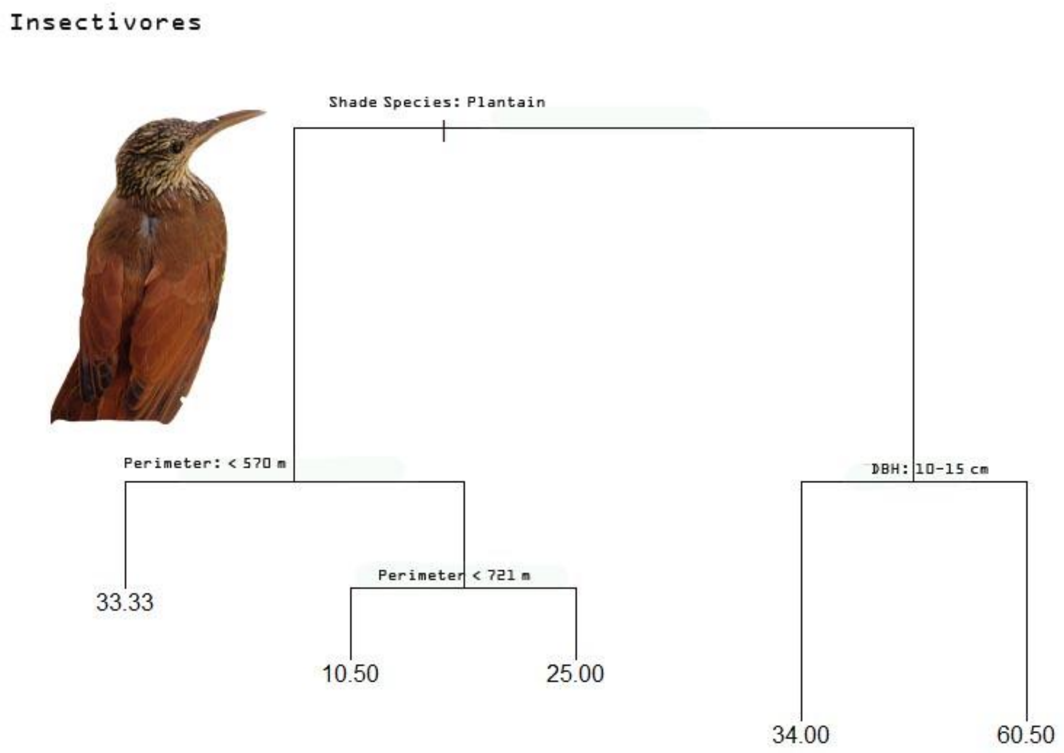

Figure 15. Classification and regression tree (CART) model for Insectivore presence across sites. The split variable and its threshold value are shown in each branch at each node.

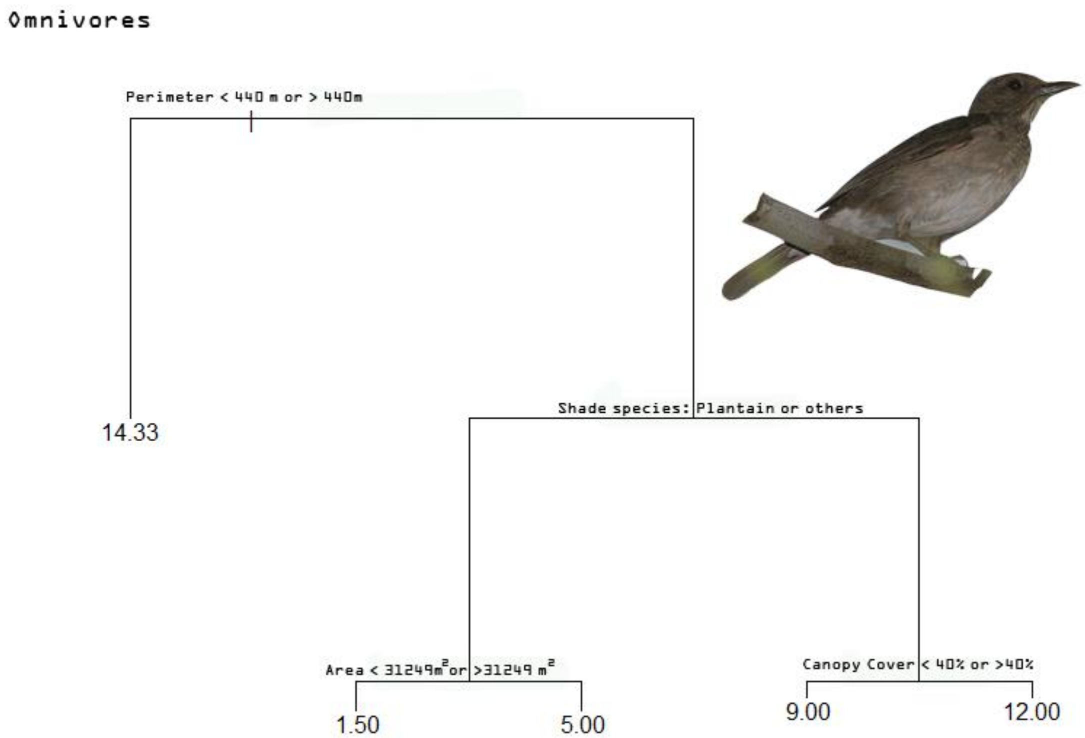

Figure 16. Classification and regression tree (CART) model for Omnivore presence across sites. The split variable and its threshold value are shown in each branch at each node.

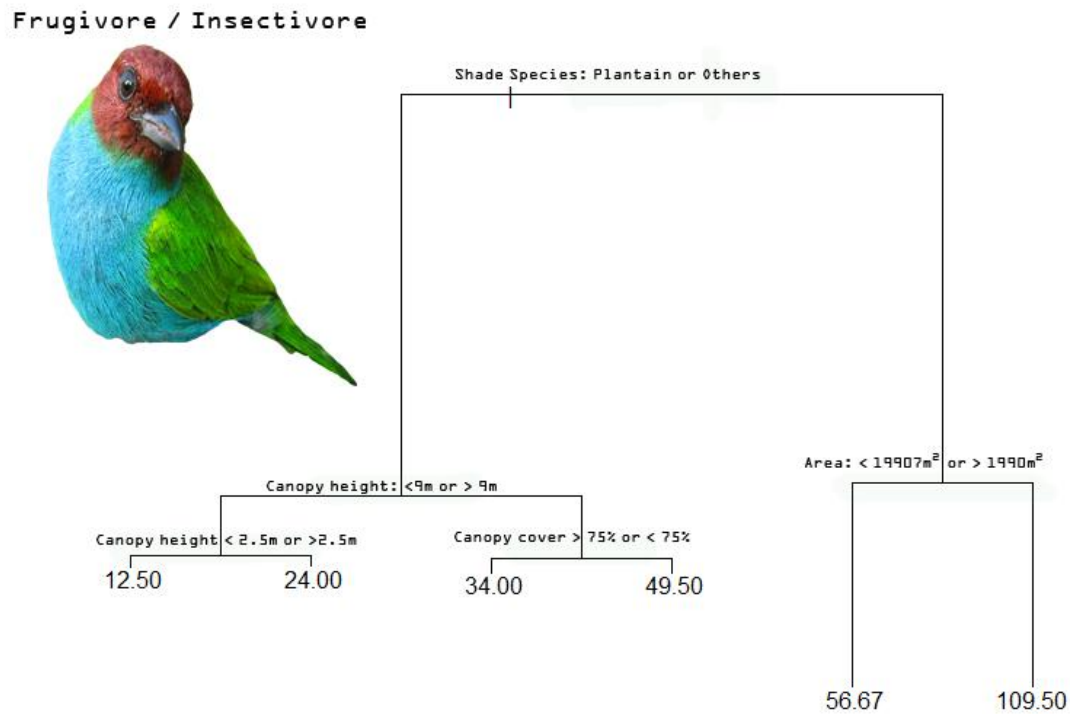

Figure 17. Classification and regression tree (CART) model for Insectivore/Frugivore presence across sites. The split variable and its threshold value are shown in each branch at each node.

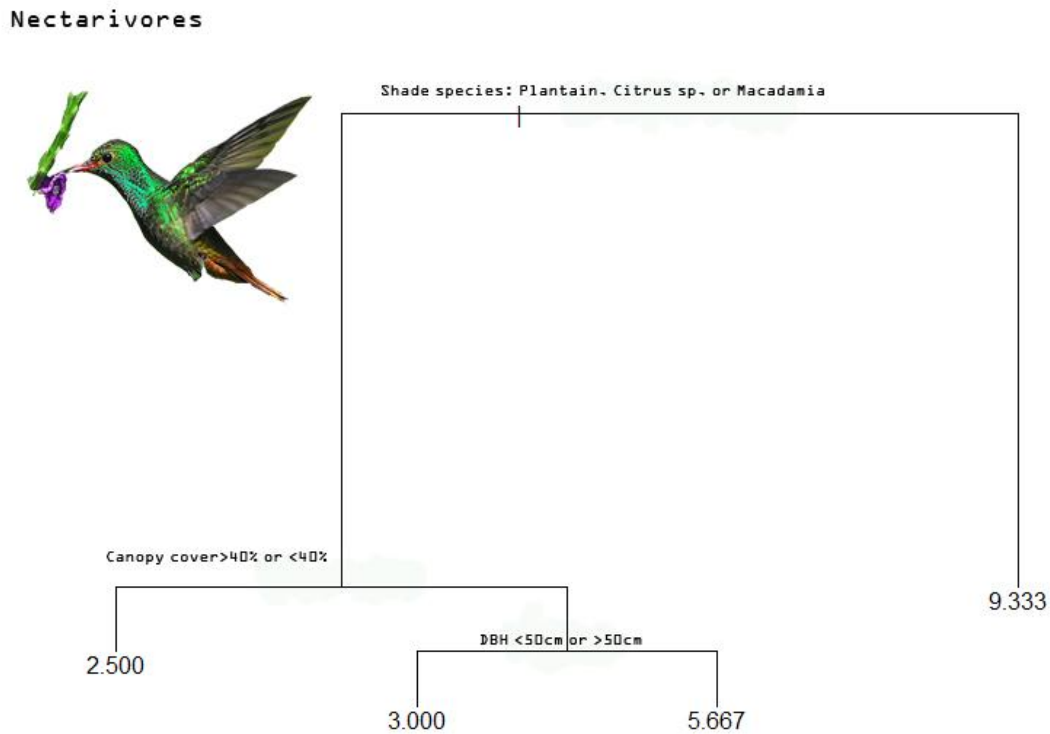

Figure 18. Classification and regression tree (CART) model for Nectarivore presence across sites. The split variable and its threshold value are shown in each branch at each node.

Chapter 5: Discussion

Smallholder coffee plantations in Sasaima, Cundinamarca have diverse bird communities and can be considered important habitats for avifauna in highly modified, human landscapes. This study found 97 species, representing 6% of the total avifauna diversity in Colombia (McMullan 2010), and is a close approximation to the 10% total number of species estimated to inhabit this agroecosystems in this country (Juan P. Gomez, Unpublished data).

As reported in earlier studies, the results of this thesis indicate that coffee production systems characterized by shade and semi-shade polycultures, harbor the highest avian diversity. This is consistent with the results found by other studies on the use of shade coffee plantations as potential habitats for avifauna conservation (Perfecto et al. 1996, Perfecto et al. 2009). However there are remarkable differences on species and guild compositions between this work and previous studies done in Central America and the Caribbean (Perfecto et al. 1996, Greenberg et al. 1997a, Greenberg et al. 1997b, Wunderle and Latta 1998b, Moguel and Toledo 1999, Perfecto et al. 2003, Tejeda-Cruz and Sutherland 2004) and these ones will be discuss in depth in following sections.

5.1 Species Patterns

The species richness among different coffee plantations varied widely. Shade and semi-shade polycultures showed the highest number of species (68 and 67 respectively), followed by shade and semi-shade monocultures (47 and 44 respectively) and the lowest number of species richness was recorded for sun monoculture plantations (41). This relative lower number of species in sun and monoculture plantations has also been documented in other coffee estates in Mexico and Guatemala with single or no canopy layer, and where shade coffee plantations were reported to have bird diversity levels similar to, or even higher than, natural forest (Greenberg et al., 1997a,b, Tejada-Cruz and Sutherland 2004). These differences in species richness have been attributed to the differences in vegetation structure and the floristic composition of the plantations (Perfecto et al. 1996, Wunderle 1999, Backermans et al. 2011).

Species composition varied across different coffee production types, however all the communities were characterized by the absence of forest specialist species. Although this absolute absence of forest specialists in shade coffee plantations has never been documented in other studies, significantly lower numbers of these group has been frequently reported in these agroecosystems (Greenberg et al. 1997, Tejeda-Cruz and Sutherland 2004). Consequently most of the species present in all the sites in the study area were characteristic species of open agricultural habitats (generalists). Similar results were found for other coffee agroecosystems in Guatemala (Greenberg et al 1997), Dominican Republic (Wunderle and Latta 1998b) and Mexico (Moguel and Toledo 1999, Greenberg et al. 1997a, Greenberg et al. 1997b), all reporting high diversity of second growth and edge bird species in shade plantations of *Inga* and *Gliricida,* and specialized forest species almost absent. Contrary to those results, Petit and Petit (2003) found that coffee plantations in Panama are important habitats for forest specialist and forest generalist, when compared to other 10 natural and human-modified habitats in Panama and assessed the importance of those habitats for species of different vulnerability to disturbance.

The aforementioned results may suggest that the coffee agroecosystems of this particular study have a low conservation value for forest specialist species, however this result can be attributed to particular aspects of the landscape configuration rather that to the habitat quality offered by the shade and semi-shade coffee plantation, since it is well supported that high taxonomically and structurally diverse canopy of shade coffee plantations are invaluable habitat characteristics for the avifauna (Wunderle 1999). It is important to consider that the surveyed plantations of this study occurred at a considerable distance from forest patches (>3km). As shown by Petit and Petit (2003), proximity and connectivity between forest and coffee plantations, two important aspects of the landscape configuration, are key variables that increase the conservation value of these human-modified landscapes. In conclusion, the absence of forest specialist species in the coffee plantations of this study should not discourage conservation initiatives in coffee agroecosystems or diminish their conservation value. Instead, these results suggest that one single factor, of great conservation importance, such as a structurally complex vegetation and canopy, could be significantly enhanced by increasing connectivity with forest habitats (Rengifo 2001, Perfecto et al. 2003).

The overall species composition of this study is consistent with previous ones, showing that the great diversity of shade plantations results from a high number bird species common in edge, open and second growth habitats, as can be seen in Tables 6-12, where the most common and abundant species was the Crimson-backed tanager (*Ramphocelus dimidiatus*) representing between 10-11% of all the observations. The other 9 species of the top 10 ranks, added up to the 50% of the species found at each site, were also a common group of species that are residents of agricultural landscapes (Hilty and Brown 1986, McMullan 2010).

5.2 Guild Patterns

The feeding guild composition of bird communities was very similar between all the types of coffee production systems. The majority of birds belong to the

Frugivore/Insectivore guild, followed by Granivore and then Insectivore. Although the dominance of frugivorous has been reported in shade coffee plantations in Mexico, Guatemala, Dominican Republic and Costa Rica, (Perfecto et al. 1996, Greenberg et al. 1997a, Greenberg et al. 1997b, Wunderle and Latta 1998b) the higher abundances found for insectivorous in this study is uncommon. Since food availability is one determining factor of the guild composition, it is expected that the diversity of shade tree species will highly influence this patterns. Shade species provide not only an important structural complexity within the coffee plantations, but also a wide supply of flowers and fruits (Wunderle 1999, Harvey and González-Villalobos 2007). Only Wunderle and Latta (1998) found a preponderance of insectivory in coffee plantations (50% of the species recorded). The differences in guild representativeness between this and other studies might be due to the fact that the canopy of the shade and semi-shade polyculture coffee plantations of this study were mainly composed of fruit trees, which attract higher numbers of arthropods.

The consistent presence and representativeness of insectivorous birds throughout the different production types, was only different in monocultures of shade and sun plantations, suggesting that the availability of arthropods, especially in the understory is limited in monoculture coffee plantations, as previously found in southern Mexico and Dominican Republic (Wunderle and Latta 1998, Tejeda-Cruz and Sutherland 2004). For this particular case, and based on conversations with the owners and managers of the plantations studied, these two crop types (shade monoculture and sun monoculture) were the ones with highest intensities of management practices, which included more frequent pruning and the use of pesticides. This suggested the importance of including an analysis of other management variables that could influence the presence of insectivorous birds in this plantations (i.e. use of pesticides). For example Monterrey et al (2011) showed that the incidence of certain insect pests such as leaf miners (*Leucoptera coffeell*) is influenced by the intensity of the shade management. Similarly, Johnson (2000) observed a predominance of insectivorous birds in shade monoculture coffee in dense, unpruned areas and the upper canopy layers, suggesting once again the influence of other management techniques in the distribution and abundances of insectivorous birds. Although this study does not possess field data to explore these aspects, based on previous studies (Perfecto et al. 1997), it can be speculated that the elimination of trees with their foliage, fruits, flowers, and nectaries results in a dramatic decrease of arthropods, from both canopy and ground.

5.3 INDICATORS OF BIRD COMMUNITY COMPOSITION

As seen in the NMS analyses, the bird communities were clearly differentiated by habitat types (Figure 12). The use of CART analyses was an asset of this study. These classification trees helped to explain in a simple and meaningful way the variation in the presence of each guild with several habitat and landscape variables. The CART process repeatedly divides the set of observation units into groups, choosing the best available explanatory variable at each decision point. The first variable split the sample into two subgroups, each more homogenous than possible with any other split; each of these subgroups was split in turn, continuing until stopping criteria were satisfied (O'Connor et al. 1996).

The results of the CART analysis are shown in Figures 13-18. Based on these, the <Shade species> variable was the most important, showing influence on the abundances and distributions of all 6 guilds, and being especially important for Insectivorous, Frugivorous/Insectivorous and Nectarivorous guilds. This could suggest that coffee plantations alone do not provide satisfactory resources and habitat to host these groups, probably because of the absence of flowers and fruits that attract insects (e.g. flowers with nectar, rotten fruits). Conversely, the <Shade species> tree variable was not explanatory of the granivorous species presence. Instead, DBH and Canopy height were the most important explanatory variables for this guild. Moreover, DBH was the second most common explanatory variable for the incidence of the guilds among all habitats, except for the Frugivorous/Insectivorous species. These results are consistent with the literature supporting the idea that polyculture shade coffee plantations are important foraging sites for insectivorous (Wunderle and Latta 1998).

Nectarivorous species have been usually reported as a common group on shade polyculture plantations (Greenberg et al 1997, Tejeda-Cruz and Sutherland 2004). Contrastingly, this group was remarkably uncommon in this study. These discrepancies can be attributed to the influence of the canopy species. As seen in Figure 18, the shade and semi-shade plantations of this study had canopy covers that constituted mainly of fruit trees. This was a fundamental difference between the present and the aforementioned studies, in which the canopy covers of those Mexican and Guatemalan coffee plantations were constituted by *Inga* sp. and *Erythrina* sp. trees; both tree species are key food resources for hummingbirds and other nectarivorous species (Bruneau 1997)

Landscape effects

The landscape context is considered an important factor that can affect bird species composition and abundance (McGarigal and McComb 1995, McGarigal and Cushman 2002, Fahrig 2003, Klingbeil and Willig 2009). In this study the area and perimeter of each plantation were used as explanatory variables of the abundance and presence of guild species, as seen in the CART analyses. In this regard, only the

Insectivorous and Frugivorous/Insectivorous species seemed to be affected by these landscape variables. Most of the literature on the effect of landscape variables on the bird communities of agroecosystems has been done in temperate regions, however the small but growing evidence in the tropics suggests that birds are sensitive to the area of the plantations (patch size) (Ferraz et al. 2007, Sekercioglu 2007, Gavin and Dhondt 2008, Suarez-Rubio and Thomlinson 2009, Banks-Leite et al. 2010, Morrison et al. 2010, Cerezo et al. 2010).

Additionally, species richness is also likely to be affected by the landscape context, including patch size, perimeter, distance to forest patches, connectivity and others. This study did not analyze all these other landscape variables due to the unavailability of imagery to perform land cover analyses. Nevertheless, personal observations suggest that the presence of live-fences and remnant vegetation can contribute to the species richness of these coffee plantations. These results strongly support Leyequién et al. (2010)'s, who found that plot- and landscape-level variables significantly explained the bird community composition best across all scales, and were significantly correlated with the abundance of the dietary guilds.

Habitat effects

The relatively high species richness found in shade and semi-shade polyculture plantations can be attributed to the increase in structural complexity of the vegetation. This characteristic translates into additional habitat and resources for birds to feed, nest and mate (Wunderle and Latta 1998, Somarriba et al. 2004). Although it was not measured in this study, it has been shown that shade coffee plantations also have a higher number of epiphytes, creating a variety of microhabitats and increasing canopy cover and biomass (Nadkarni 1994, Cruz-Angon and Greenberg 2005). Other important resources for birds are flowers, nectar, fruits, invertebrates and small vertebrates; these habitat characteristics are not necessarily offered by the coffee plants, therefore the importance of having diverse tree species within the plantations that could potentially act as keystone resources in coffee plantations (Somarriba 2004). By using CART analyses, it was also possible to clarify that height and coverage of the canopy were also important explanatory variables for Granivorous, Frugivorous/Insectivorous and Nectarivorous guild species. This indicated that the distribution and abundance of the foliage can influence the foraging patterns and the abundance and nest success of birds (Cruz-Angon and Greenberg 2005)

In the same way, these results suggest that coffee plantations with one canopy layer particularly dominated by a single species provide poor habitat for birds. Previous studies showed that in cases were the shade has been provided for a single species (i.e. *Erythrina poeppigiana*), the frequency of pruning for shade regulation increases and was suggested to affect foliage, flowers and fruit distribution, consequently influencing the foraging patterns abundances and nesting sites and success of birds (Calvo and Blake 1998).

5.4 IMPLICATIONS FOR CONSERVATION

The coffee plantations studied in this thesis were smallholder plantations surrounded by diverse crops that include *Citrus* sp., *Persea americana* (Avocado) and *Musa* sp. (Plantain). These small and low intensity farms had an area below 1 hectare, and were surrounded by grasslands, abandoned crops and very few and small patches of secondary forest associated with streams. These landscape practices create highly heterogeneous habitats, a key factor to conserve biodiversity in farmlands (Benton et al. 2003). Additionally, this study further supports the fact that shade coffee plantations are a particularly important type of human land use that provides important assistance and habitat for biodiversity. Furthermore, this study indirectly proposes that the importance of shade coffee plantations for biodiversity does not only rely on their capability to support high numbers of bird species, but that there are complementary factors that should be integrated into conservation planning in agricultural landscapes (Perfecto and Vandermeere 2009). In particular, landscape and metacommunity approaches are encouraged, since it is clear that coffee plantations are not merely suitable patches for bird diversity but that they might be the key factor for building suitable and biodiversity friendly matrices in agricultural landscapes.

Conclusions and Recommendations

A total of 97 species of birds were found in the 14 plantations studied in this study, indicating that the coffee plantations of the region of Sasaima Cundinamarca have a potential to harbor and conserve a high biodiversity of birds. However there were no records of specialist species suggesting that coffee plantations by themselves are not sufficient to maintain the avian communities of these agricultural Andean regions. Although lacking in forest specialist bird species, shade and semi-shade coffee plantations in Sasaima provide habitat for a large number of tropical lowland species. By understanding the similarities and differences regarding community composition between different elements of agricultural landscapes, this study facilitates the identification of areas that could potentially maximize regional biodiversity.

The influence of different coffee crop management types on the bird communities associated to these habitats was evident. Coffee plantations under shade and semi-shade polycultures seem to be the most suitable for avian biodiversity, indicating that bird species can augment in number by increasing the number and diversity of canopy food trees. Similarly, this study highlights the influence of particular habitat variables (e.g. canopy cover, canopy height, shade species) on the relative abundances of birds, which in turn indicate that more structurally complex coffee plantations (shade or semi-shade polycultures) harbored the greatest abundance and diversity of individuals. These suggest that improving the structural quality of the coffee plantations will play an important role in providing additional resources and habitat for birds. Conservation efforts should therefore promote the diversification of sun exposed and monoculture coffee plantations to be more similar to shade and Semi-shade polyculture coffee plantations that ensure more structurally complex habitats.

A wide variety of insectivorous and frugivorous/insectivorous species was found in shade and semi-shade polycultures which indicates that these ecosystems are key foraging sites for insectivorous birds of both the canopy and the understory. However, these species and habitat associations need to be explored deeper through vegetation surveys to recognize particular relationships. This study provides a good starting point for understanding when and where high avian biodiversity in coffee plantations can be expected.

Although it was not directly measured in this study, the absence of forest specialist species suggests that the distance of these coffee plantations to forest patches might be influencing the species composition in the plantations. Future research should incorporate connectivity and proximity to forest patches to coffee plantations

For the first time in coffee and biodiversity studies, the CART analyses proved to be a useful method to organize the influence of ecological variables. They provided an easy graphical interpretation of the results and possible interactions and helped understand the effect of combined and particular habitat characteristics of the coffee plantations for each guild. Future research should incorporate other environmental and landscape variables, including landscape structure as well as the plant composition of each patch.

These results highlight two main ways in which coffee plantations may contribute to conservation efforts. First, by increasing the structural complexity of the shade canopy, and by adding diverse layers of vegetation to the plantations. Second, by incorporating landscape characteristics (e.g. area, perimeter and proximity to forest) into the analyses and into management plans, since this study has proved that coffee plantations can significantly contribute to the overall heterogeneity of the agricultural landscapes in the tropical Andes.

Recommendations and future research

Two important analyses are recommended for future studies: a landscape structure analysis and a vegetation composition analysis. Even when the results found in this study show differences among the different types of coffee production types, clarifying the associations of species and habitat types, through vegetation surveys, and the influence of connectivity and proximity to forest patches, is key, since it has been demonstrated in other studies that the local species richness is reduced in small patch sizes and in habitats that are at a greater distance from fragments.

Structurally complex, smallholder coffee plantations have the potential to maintain highest abundances and species richness of birds in the coffee region of Sasaima, therefore it is important to find alternative ways to incorporate additional species of trees to improve the structural quality of the plantation. A complementary priority, then, is to identify ways in which careful management can enhance the conservation value of these areas. This will be of particular importance in those areas where little or no native vegetation remains.

Coffee plantations in general should have the greatest structural and floristic diversity and at the same time provide economically viable returns to coffee farmers. Hence it is important that shade trees have a commercial value like fruits or timber. The promotion of these multistrata coffee production systems will lessen the dependence of small farmers on a single cash crop and have the secondary effect of improving coffee farms and habitats for birds and other organisms. The adoption of these types of coffee agroecosystems could represent a viable economic solution in particular for small holder

/small scale coffee farmers that are suffering most of the impact of the global coffee market fluctuations. Additionally, it would be interesting to study the possibility to incorporating a system of payment for environmental services and other initiatives, not commonly used in Colombia, to help promote more complex structural coffee agroforestry systems that favor the presence of avifauna.

One last important point should be to explore the alternatives for biodiversity conservation offered by organic and friendly coffee certifications and a market based strategy. These certification programs have grown over the past ten years and are considered to provide higher quality habitat for biodiversity. In spite of good intentions and an increasing market, little consensus exists on whether current criteria can successfully identify coffee farms of conservation significance and little is known about their true contribution to the biodiversity of agricultural landscapes.

Appendix

Apendix 1. List of species present in each coffee production type.

Species	Shade		Semi-shade		Sun
	Mono	Poly	Mono	Poly	Mono
Amazilia cyanifrons		X		X	X
Amazilia tzacatl	X	X	X	X	X
Anthracothorax nigricollis		X		X	X
Arremon atricapillus	X		X	X	
Arremon nigricollis		X	X		
Arremonops conirostris		X		X	
Basileuterus rufifrons	X	X	X	X	X
Camptostoma obsoletum		X		X	
Campylorhamphus trochilirostris				X	
Campylorhynchus zonatus	X	X	X	X	
Carduelis psaltria		X	X	X	X
Chalybura buffonii	X		X	X	
Chlorostilbon gibsoni		X			
Chlorostilbon poortmani		X			
Coereba flaveola	X	X	X	X	X
Coerebidae sp				X	
Colaptes punctigula		X	X		
Columbina talpacoti	X	X		X	X
Cranioleuca curtata	X		X	X	
Crotophaga ani		X	X	X	X
Crypturellus soui				X	
Cyclarhis gujanensis			X		
Dysithamnus mentalis	X			X	
Elaenia flavogaster	X	X	X	X	X
Elaenia frantzii	X	X		X	
Eucometis penicillata	X			X	
Euphonia concinna	X		X		X
Euphonia flavigaster	X	X			
Euphonia laniirostris	X	X	X	X	X

Species	Shade		Semi-shade		Sun
	Mono	Poly	Mono	Poly	Mono
Euphonia xanthogaster		X			
Forpus conspicilatus		X			
Hylophilus flavipes				X	
Icterus chrysater		X			
Lepidocolaptes souleyetii	X	X	X	X	X
Lepidocolaptes sp			X		
Leptotila verreauxi	X	X	X	X	X
Mecocerculus leucophis		X			
Phaethornis guy	X	X		X	
Pheugopedius sclateri		X			
Picumnus olivaceus		X	X	X	X
Piranga rubra		X			
Pitangus sulphuratus	X	X		X	X
Poecilotriccus sylvia	X	X		X	X
Pyrocephalus rubinus		X			X
Ramphocelus dimidiatus	X	X	X	X	X
Rhodinocichla rosea	X	X	X	X	X
Saltator albicollis		X		X	
Saltator maximus	X		X		
Saltator striatipectus	X	X	X	X	X
Sicalis flaveola	X	X	X	X	X
Sporophila intermedia	X	X		X	X
Sporophila luctuosa		X			
Sporophila minuta		X	X		
Sporophila nigricollis	X	X	X	X	X
Sporophila sp		X		X	
Synallaxis albescens				X	X
Synallaxis brachyura	X	X	X	X	
Tachyphonus rufus		X		X	
Tangara cyanicollis	X	X	X	X	X
Tangara gyrola	X	X	X	X	X
Tangara sp		X		X	
Tangara vitriolina	X	X	X	X	
Thamnophilus multistriatus	X	X	X	X	X
Thraupis episcopus	X	X	X	X	X

Species	Shade		Semi-shade		Sun
	Mono	Poly	Mono	Poly	Mono
Thraupis palmarum	X	X	X	X	X
Tiaris bicolor	X			X	
Tiaris olivacea				X	
Tiaris olivaceus		X			X
Todirostrum cinereum	X		X	X	X
Trochilidae sp	X	X		X	X
Trogloditidae sp		X		X	
Troglodytes aedon		X		X	X
Turdus ignobilis	X	X	X	X	X
Turdus leucomelas		X			
Tyrannus melancholicus	X	X	X	X	
Tyranulus eleatus				X	
Volatinia jacarina		X	X		
Zimmerius chrysops	X	X	X	X	X
Zonotrichia capensis	X	X	X	X	X

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