Neotropical dry forest recovery and its impact on the avian community

by

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Abstract

Neotropical dry forests are severely threatened by human activities such as agricultural expansion, tourism, cattle ranching, logging, and an increase in human settlements. However, despite these trends, some countries have experienced forest recovery. Costa Rica is a clear example of this process, and dry forests in the country have recovered more than 50 % of their area in the last 50 years as a result of changes in socio-economic and conservation policies. Costa Rica currently holds the largest protected remnant of dry forest in Central America. Despite this success, information on the recovery of the forest structure, vegetation species composition, and fauna of successional forests (e.g. forests that are recovering or have recovered from the effects of clear-cutting and burning) is lacking. This Dissertation assessed the recovery of Neotropical dry forests and its impact on the avian community. Species composition of the bird community was evaluated in forests at different stages of recovery following the abandonment of cattle ranching in the largest protected tropical dry forest remnant in Central America (at the Santa Rosa National Park, Costa Rica). Chapter 2 described and compared tree species diversity and composition in three different dry forest successional stages (e.g. early, intermediate, and late), as well as the breeding systems and pollination and dispersal syndromes for the species. Findings showed that monoecy (e.g. having unisexual reproductive flowers on a single plant) was the most common tree breeding system, so tree species do not depend on specific fauna pollinators. Insects were very important tree pollinators for all successional stages, but the wind is the most important pollination and dispersal agent in open sites in early successional stages where animals are scarce. In contrast, birds and mammals are important seed dispersers in the intermediate and late stages of dry forest succession. Chapter 3 evaluated the influence of liana abundance on the avian acoustic community in tropical dry forests. Results showed that the avian community increases in diversity when the number of lianas at a site increases, suggesting that lianas provide important resources for birds (e.g. food and structure for shelter, nesting and roosting). Even though lianas have been reported to have a negative effect on the reproduction of tropical canopy trees, and probably on the species composition of forest faunas, a positive relationship between the occurrence of lianas and bird diversity was determined. This relationship is

important in dry forests due to the role of birds as tree pollinators and seed dispersal agents in areas where lianas have become highly abundant. Chapter 4 assessed changes in bird species richness and community composition in dry forests at different ages of recovery since abandonment (e.g. 20, 30, 40, and 60 years old). A similar species richness and avian community composition were observed in forests of different ages (e.g. 20, 30, 40, and 60 years). This probably reflects (a) the similarities in the structural characteristics of forests of different ages, and (b) the high variation in forest structure within each age group. As a result, birds can find suitable habitats and other key resources such as perches, nesting material, and food from all the different forest sites that were studied. This highlights a rapid recovery of bird species composition in the TDFs studied, and information generated from this study can be considered in bird conservation efforts in Neotropical dry forests.

Preface

Results generated from this research are the outcome of collaborative work; thus, this Dissertation contains journal articles co-authored with researchers from universities other than the University of Alberta as follows:

Chapter 2 of this Dissertation has been published as Hilje, B., Calvo-Alvarado, J., Jiménez-Rodríguez, C., & Sánchez-Azofeifa, A. (2015). Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica. Tropical Conservation Science, 8(1), 76-94.

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1 Introduction

Although Neotropical dry forests are highly threatened by human activities, in some countries such forests have experienced recovery. Tropical dry forests (TDFs) in the Neotropics are among the most threatened ecosystems worldwide due to the effects of anthropogenic activities such as agricultural expansion, tourism, and an increase in human settlement (Janzen, 1988; Sánchez-Azofeifa et al., 2005). The extent of TDFs in 2010 was estimated to be 519,597 km^2, with the largest area in South America (51%), followed by North and Central America (39%), and the Caribbean islands (9%) (Portillo-Quintero & Sánchez-Azofeifa, 2010). As of today, approximately 66% of the original extent of TDFs in the Americas has been converted to other land uses (Portillo-Quintero & Sánchez-Azofeifa, 2010). South America has the largest extent of dry forests, but the highest deforestation rate occurs also there.

Between 2001 and 2010, the highest rates of dry forest loss occurred in countries like Argentina, Bolivia, Paraguay, and Venezuela (Gasparri & Grau, 2009; Aide et al., 2013). This forest loss was mostly due to the conversion of forest into agricultural and pastures lands. However, despite dry forest loss in some countries, some other countries have experienced forest recovery during the same period of time. This was the case in Mexico and countries in Central America like Honduras, Costa Rica, and El Salvador, where an increase in woody vegetation has been attributed to a reduction in agricultural or grazing activities (Aide et al., 2013).

In the particular case of Costa Rica, TDFs were eliminated between 1950 and mid-1970's due to the expansion of the beef industry and land colonization programs promoted by the government which greatly reduced dry forest coverage (Janzen, 1988; Sánchez-Azofeifa et al., 2005; Calvo-Alvarado et al., 2009). However, by the mid-1980's, Costa Rica's TDFs started recovering due to changes in socio-economic policies and the implementation of forest conservation policies that allowed forests to recover (Calvo-Alvarado et al., 2009). The forests that emerged from this recovery now represent the largest protected remnant of dry forest in Central America (Portillo-Quintero & Sánchez-Azofeifa, 2010). As a result, there is currently a mix of successional dry forests that are in the process of recovery from clear-cutting and burning associated with such human activities as agriculture, cattle ranching, and logging (Janzen, 1973; Finegan, 1996; Foster et al., 1999; Aide et al., 2000).

The rate of forest structural recovery and the time required for full succession will depend on the degree of prior human disturbance (Chazdon, 2017; Ghazoul & Chazdon, 2017). As a result, disturbances of forest canopies will not have such a long-lasting effect on forest structure and species composition as disturbances that impact soils and above-ground vegetation (e.g. disturbance by agricultural and forestry machinery, heavy grazing, and fires) (Chazdon, 2003). With respect to the recovery of species composition, the proximity of a disturbed site to patches and remnants of undisturbed forest, and the nature of the surrounding landscape will be important factors to consider (Chazdon, 2003). Soils play also an important role in forest recovery, and there is an increase in soil carbon (e.g. organic matter) and matter decomposition as well as a higher mineralization when forests recover from pasture lands (Reiners et al., 1994).

Studies of successional processes in tropical wet forests in Puerto Rico showed that after 40 years of recovery following abandonment these forests have similar values for such structural parameters as tree density, tree basal area, and aboveground biomass as are found in forests > 60 years old. Tree species richness and diversity are also similar to those found in older forests (Aide et al., 1996; Aide et al., 2000). In Costa Rica, by 21-30 years after abandonment, successional tropical wet forests can achieve similar aboveground biomass to old-growth forests (Letcher & Chazdon, 2009). These forests can achieve similar tree species richness and composition to old forests since 30 years of abandonment. In Mexico, dry forests at intermediate ages of recovery following abandonment (e.g. 13-17 years) show a similar number of stems, individual plants, species, and tree basal area as forests more than 55 years old (Quesada et al., 2014). In Mexico, Venezuela, and Brazil, tree species richness peaks in the late successional stage, whereas in Costa Rica the highest richness is observed in the intermediate stage (Nassar et al., 2014; Espírito-Santo et al., 2014; Quesada et al., 2014).

Although tropical forests can recover after abandonment from human activities, the successional recovery of fauna species composition is poorly understood. Understanding the role of fauna in forest recovery is critical, but it is also important to understand the changes in fauna species composition that occur as the forest recovers. The length of the period of forest recovery since abandonment, the faunal group (e.g. arthropods, amphibians, reptiles, and mammals), and the surrounding landscape are the most significant factors that affect rates of faunal recovery in successional forests (Bowen et al., 2007). For example, 16-year-old successional wet forests in Costa Rica can hold amphibian communities with species richness and composition similar to those of communities found in old-growth forests (e.g. old forest with several years without significant disturbance that show unique biological features such as large live trees, and diverse forest structure and tree species composition) (Hilbert & Wiensczyk, 2007; Hilje & Aide, 2012). It has been observed that 25 to 30-year-old successional tropical wet forests in Puerto Rico can have ant communities with similar species composition to those found in old-growth forests (Osorio-Pérez et al., 2007). The recovery of ant arboreal communities in Brazil needed a similar amount of time of forest recovery (Neves et al., 2010). As for birds, species richness is generally positively related to the environmental heterogeneity of forests (e.g. it increases with foliage density and the occurrence of vegetation layers at different heights) (Mac Nally et al., 2002; Müller et al., 2010; Stein et al., 2014). This is because greater foliage density and multiple vegetation layers imply higher variation in forest structure, which in turn means an increase in niche availability for fauna in general (Mac Nally et al., 2002; Müller et al., 2010; Stein et al., 2014). Other studies have shown that bird species richness peaks in primary tropical forests, followed by secondary forests and plantations, respectively (Andrade and Rubio-Togler, 1994; Barlow et al., 2007). Yet, most of the research into the species composition of bird communities in successional tropical forests has been carried out in wet forests, and there is limited information for TDFs (de la Peña-Cuéllar et al., 2012; Nassar et al., 2013; Ávila-Cabadilla et al., 2014; Falcao et al., 2014; Santamaría-Rivero et al., 2016). To my knowledge, there are no published studies of fauna species richness and composition for the largest area of TDF succession in Central America - the Guanacaste Conservation Area (GCA), Costa Rica.

One of the most important sections of the GCA is the Santa Rosa National Park (SRNP) where the current forest cover is a mixture of successional stages developed on land formerly used for cattle ranching (Arroyo-Mora et al., 2005; Sánchez-Azofeifa et al., 2005). Because of this history, the SRNP has a very heterogeneous forest with a high diversity of forest types and biotic communities (Janzen, 1983). The forest has been categorized into three main successional stages (i.e. early, intermediate, and late) based on both vegetation indices calculated from satellite imagery, and ground-based measurements of vegetation structure (Arroyo-Mora, 2002; Kalacska et al., 2004a; Sánchez-Azofeifa et al., 2017).

The structural characteristics of these successional forest stages are understood to be as follows. Early stage forests have a single layer of vegetation with a dominance of deciduous trees. Intermediate stage forests have two layers of vegetation, with the presence of lianas and both deciduous and evergreen trees. Late stage forests have two layers of vegetation in which shade-tolerant tree species are present and evergreen species are dominant (Arroyo-Mora, 2002; Kalacska et al., 2004a; Kalacska et al., 2004b). More specifically, tree basal area and height, and vegetation indices (such as the presence of green leaves on trees), and the Leaf Area Index (LAI) - a descriptor of vegetation function and structure - show increasing values from early to late stages (Arroyo-Mora, 2002; Kalacska et al., 2005). The highest species richness is observed in the intermediate stage forests and the lowest in the early stage forests. Tree species composition is similar in the intermediate and late stages (Kalacska et al., 2004a). However, there is a lack of information on seed dispersal and pollination syndromes for all the successional stages, which limits our understanding of what controls the fauna species composition in these successional stages.

1.1 Thesis overview

The overall objective of this Dissertation is to assess the recovery of Neotropical Dry Forests in Costa Rica and its influence on the forest avian community. For this, bird species richness and community composition were evaluated in forests at different ages of recovery since the abandonment of cattle ranching in the largest protected remnant of Tropical Dry Forest in Central America, at the Santa Rosa National Park, Costa Rica. The relationship between the structural characteristics of forests at different stages of recovery and the species composition of the bird communities that occupy them was also assessed. As such, this Dissertation is divided into:

Chapter 2. *Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica.* This Chapter describes and compares the tree species diversity and composition in three different successional stages (e.g. early, intermediate, and late) of recovering tropical dry forests in Costa Rica. The breeding systems and pollination and dispersal syndromes of tree species found in these successional stages are also described. The main objective of this Chapter was to understand how the species composition, breeding systems, and pollination and dispersal syndromes of tropical dry forest trees change from early to old successional stages. These changes can influence the species composition of bird communities in the different successional stages.

Chapter 3. *Determining the relationship between liana abundance and the complexity of the avian community in tropical dry forests.* This Chapter evaluates the influence of liana abundance on the avian acoustic in tropical dry forests at the Santa Rosa National Park in Costa Rica. The objective of this Chapter is to understand the influence of lianas - which have become highly abundant in tropical dry forests - on birds, a very important faunal component in ecosystems. For this, forest sites with different levels of liana abundance were selected to set up autonomous sound recorders for data collection. The acoustic complexity index (ACI) was performed to determine the complexity of the avian acoustic community (Pieretti et al., 2011). Also, the ACI scores were related to the number of lianas in the forests as well as to such forest structural characteristics as tree basal area, plant area index and canopy height. ACI scores were validated with bird species detected from listening to recordings to determine whether sites with higher ACI scores had more species.

Chapter 4. *Bird community response to the recovery of tropical dry forests in Costa Rica.* This Chapter assesses changes in bird species richness and community composition in dry forests at different ages of recovery since abandonment (e.g. 20, 30, 40, and 60 years old) in the Santa Rosa National Park, Costa Rica. Associations between bird species and forests at different stages of recovery were also evaluated and related to such structural characteristics of the forests as tree basal area, canopy height, plant area index, canopy openness, the number of lianas, and Normalized Difference Vegetation Index (NDVI). The ages of different forest segments were categorized on the basis of satellite images. Structural characteristics of different forest sites were measured, and bird sounds were collected to identify the species using them and to obtain measures of species richness.

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2 Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica

2.1 Introduction

Among the world's most threatened ecosystems are the Tropical Dry Forests (TDFs) (Janzen, 1988; Ewel, 1999; Sánchez-Azofeifa et al., 2005a; Sánchez-Azofeifa et al., 2005b; Sánchez-Azofeifa et al., 2013; Hoekstra et al., 2005; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sánchez-Azofeifa & Portillo-Quintero, 2011. In the Neotropics, particularly in Mesoamerica, TDFs are heavily utilized and perturbed by human activities, and especially by agricultural expansion, tourism, and an increase in human settlements (Maass et al.,1995; Quesada & Stoner, 2004; Arroyo-Mora et al., 2005). However, in some countries such as Costa Rica, TDFs are experiencing a significant recovery due to changes in socio-economic conditions [12-15] (Calvo-Alvarado et al., 2008; Calvo-Alvarado et al., 2009; Calvo-Alvarado et al. 2013; Redo et al., 2012). Consequently, the TDFs in Costa Rica consists of a mosaic of secondary forests with varying ages and fragment sizes (Janzen, 1988; Arroyo-Mora et al., 2005; Janzen, 1986; Stoner & Timm, 2004; Kalacska et al., 2004). Currently, Costa Rica's TDFs are composed of deciduous and semi-deciduous trees with heights between 5 to 15 m (Kalacska et al., 2004; Bazzaz & Pickett, 1980; Hartshorn, 1983), organized mainly into two strata: the understory and the canopy (Kalacska et al., 2004). The understory contains more evergreen species, adapted to the low light conditions that occur during the wet season, than does the canopy layer (Kalacska et al., 2004; Bazzaz & Pickett, 1980; Hartshorn, 1983)

The species diversity and composition of the different successional stages of TDF are influenced and driven by natural and anthropogenic disturbances (Ewel, 1980; Brown & Lugo, 1990). Forest fires and the secondary effects of tropical storms (i.e. strong winds, extreme rainfall) allow the opening of canopy gaps and influence the natural forest succession. This disruption is described by the Intermediate Disturbance Hypothesis (IDH) (Wilson, 1994; Molino & Sabatier, 2001; Roxburgh et al., 2004), which argues that any ecological community in equilibrium is affected by disturbances that enhance species diversity by creating opportunities for species colonization and establishment (Townsend & Scarsbrook, 1997).

The presence or absence of a given species in a particular habitat can be determined by different factors (e.g. abiotic and biotic) (Turner, 2010). The mobility of plants, and their distribution within the landscape are determined by the seed dispersal strategies they use. For this reason, plants have adaptations that optimize seed dispersal by abiotic factors such as wind and water, or by biotic dispersers within the forest fauna. Biotic dispersal is especially common for fleshy colored fruits, and seeds with a food reward (Schaefer et al., 2003), although there is a debate about whether ripe-colored fruits offer a strategic defense against pests and act as an attractor of disperser species (Schaefer et al., 2003).

However, even when seeds succeed at colonizing a site, seed germination and seedling success require additional favorable conditions (e.g. soil humidity, light exposure or shade, amount of rain, and reduced competition with conspecifics and heterospecifics) (Belyea & Lancaster, 1999; Hargreaves & Eckert 2014). Plant reproduction is also important (Hargreaves & Eckert 2014) and is dependent on the actions of pollinators and seed dispersers (Vázquez et al., 2005). The variety of seed dispersal and pollination syndromes ranges from the very general (e.g., wind, water, gravity) to the very specific (e.g., particular species of fauna) (Waser et al., 1996). The success of each strategy is variable, but specialization depends highly on the activities of other organisms, which means that a pollinator or disperser species can be absent from or specific to a particular habitat. The presence or absence in a forest of pollinators and dispersers can also be affected by anthropogenic activities such as deforestation and forest fragmentation (Setsuko et al., 2013), by unusual climatic conditions, or by specific habitat characteristics such as seasonal flooding or drought conditions (Setsuko et al., 2013).

Studies on the ecology and dynamics of plant species in TDFs are mainly focused on a few particular species (Machado & Lopes, 2004; Leal et al., 2006; Machado et al., 2002). However, at the community level, differences in breeding systems, pollination, and seed dispersal syndromes in TDFs are not well understood or studied (Machado & Lopes, 2004). The types and frequency of breeding systems (e.g. monoecy and dioecy) have been studied mainly in Neotropical Rainforests, and there are a few such studies for TDF (Bawa, 1990; Machado et al., 2006; Bawa & Opler 1975). Sexual systems (e.g. monoecy and dioecy), pollination syndromes, and the characteristics of specific flowers and fruits can all influence the dynamics and successional processes of forests (Machado et al., 2006; Ibarra-Manríquez & Oyama, 1992). Thus, plant pollination and seed dispersal strategies can determine the plant community composition at a particular site (Du et al., 2009). Furthermore, the composition of the plant community can also influence the presence or absence of pollinators and seed dispersers, as well as the presence and abundance of certain plant species and breeding systems. Additionally, the nature of the vegetation cover, which varies with the different forest successional stages, can affect the presence, abundance, and species composition of pollinators and dispersers in the forest (Murali & Sukumar, 1994; van Schaik et al., 1993).

The characteristics of the remaining TDF fragments (size, shape and conservation status), underline the importance of the successional dynamics of the forest. Thus, it is critical to evaluate not only the tree species composition of the different successional stages (early, intermediate, and late) of the TDF, but also how plant breeding systems, and pollination and seed dispersal syndromes vary across the different successional stages. This makes it possible to determine whether these factors can restrict or enable the presence of particular plant species in each specific successional stage.

In this study, I describe and compare the breeding systems, and pollination and seed dispersal syndromes of tree species in three successional stages of the TDF in Guanacaste, Costa Rica. The comparisons are based on the species composition and diversity of the forest, and on the differences that occur between different successional stages. The main objective of this component of the thesis is to determine which reproductive traits influence the process of TDF recovery.

2.2 Methods

Study Area

The study area is located in the Santa Rosa National Park (SRNP), on the North-Western coast of Costa Rica (10°48'53" N, 85°36'54" W). This conservation area protects one of the largest dry forest remnants in Mesoamerica (Figure 1). The climate has a dry season of six months (December-May) and a highly variable annual precipitation that ranges from 915 mm/year to 2,558 mm/year due to periodical variation in winds and surface temperatures related to both El Niño–Southern Oscillation (ENSO) and La Niña (Figure 2) (Sánchez-Azofeifa et al., 2005b).

The current land cover is a mixture of successional forest stages and pasture areas, as the SRNP was created in 1971 from an old Spanish Hacienda (i.e., cattle ranching farm) (Quesada & Stoner, 2004; Arroyo-Mora et al., 2005; Kalacska et al. 2004). In addition, most of the current TDF at the SRNP is under intensive fire control, which involves a mix of suppression and controlled burns (Janzen, 1988). This creates a very heterogeneous forest with a high diversity of habitats and biotic communities (Janzen, 1983).

Data collection

Forest successional stages were selected based on their structure and composition as defined by Kalacska et al. (2004). These stages characterize the forest succession in the SRNP in terms of changes in forest structure: tree height, number of canopy layers, tree light tolerance, and plant functional types, using forest age as a descriptive characteristic of the forest development and not as a deterministic factor. Since the stages were categorized in 2004, for 2014 these categories were 31 years old (early stage), 42 y.o. (intermediate stage), and 100 y.o. or older (late stage) (Figure 3).

According to protocols described by Alvarez et al. (2008), nine permanent plots of 1,000 m^2 (50 x 20 m, three per successional stage) were established. The selection of forest patches was performed previously by Kalacska et al. 2004, who determined their random spatial distribution. The distance between plots ranged from 400 to 1,000 m. In each plot, all trees with diameters at breast height (DBH, i.e., 1.3 m) larger than 5 cm were measured and identified.

Tree species within the plots were classified according to its breeding system (e.g. monoecious or dioecious), and pollination and seed dispersal syndromes. Breeding systems, and pollination and seed dispersal syndromes were determined for each species primarily by reviewing literature on scientific articles and species monographs. The plant parataxonomists of the SRNP provided advice for some of the tree species pollination syndromes that were not well determined. Some of the syndromes were also corroborated in the field. Monoecious plants have male and female flowers on the same individual (tree), including perfect flowers. Dioecious plants have flowers of one sex, male or female on different individuals (Richards, 1997). The categories for pollination and seed dispersal syndromes were established according to Chazdon et al. 2003. The pollination syndromes were established as follows: entomophily (insects, including the Orders Coleoptera, Hymenoptera, Hemiptera, Diptera and other); lepidopterophily (Order Lepidoptera, moths, hawkmoths, and butterflies); anemophily (wind); chiropterophily (bats); and ornithophily (birds). Since some species can have more than one pollination system, the most important system observed for the species was used for the categories (Giovanetti & Aronne, 2011). Trees were classified according to the following seed dispersal syndromes: anemochory (wind); autochory (ballistic); barochory (gravity); chiropterochory (bats); mastochory (mammals other than bats); ornithochory (birds); and saurochory (reptiles). Tree species richness, species diversity, composition, and abundances were also determined for each successional stage.

Data analysis

Tree species diversity for each successional stage was estimated using the Shannon diversity index (H’) (Butturi-Gomes et al., 2014; Agrawal & Gopal, 2013), and then the index values were compared between successional stages using two sample two-tailed T-tests (Zar, 2010). A Jaccard’s coefficient of similarity (J) was performed to compare species composition similarities for the different successional stages. Values obtained from this analysis were used to perform a cluster (Real & Vargas, 1996). A Morisita Index ($C\lambda$) was performed based on plot species composition and their abundance, and a cluster analysis was performed using values from the Index (Golay et al., 2014). Both indices have been used widely to compare tree species composition between forest stages (Real & Vargas, 1996; Magurran, 2004; Pottier et al., 2013). The cluster analyses were performed using Neighbour-joining method. Finally, Chi-square tests were used to compare breeding systems among successional stages.

2.3 Results

Species Composition and Diversity

A total of 1,104 trees were measured in the nine successional plots. These trees were classified into 96 species and grouped into 41 families (Appendix 1). Tree species richness was highest in the intermediate successional stage (72 species), followed by the late stage (61 species), and then the early (32 species) stage (Appendix 1). Some endangered species such as Cocobolo (*Dalbergia retusa*) and Spanish cedar (*Cedrela odorata*), and species with high risk of extinction like Mahogany (*Swietenia macrophylla*) (CITES, 2014; IUCN, 2014), were found in low abundance in all three TDF successional stages (e.g. *Swietenia macrophylla* individuals' percentage per stage: early: 0.3%, intermediate 0.9%, and late 0.2%). The early forest stage was dominated by species well adapted to open habitats like Silk cotton tree (*Cochlospermum vitifolium*), Madero negro (*Gliricidia sepium*) and Yayo (*Rehdera trinervis*) (Appendix 1) (Janzen, 1983; Chavarría et al., 2001). These are also sun-loving species (heliophytes) that have anemochorous and autochorous dispersal syndromes. Molenillo (*Luehea candida*) and Guácimo (*Guazuma ulmifolia*) are the dominant species of the intermediate stage, and these are old tall trees that remain in forest patches. Mexican jumping bean (*Sebastiana pavoniana*) and Cancerina (*Semialarium mexicanum*) are shade tolerant species that prevail in the late stage.

A total of 20 families was represented in the early stage, 35 in the intermediate stage, and 36 in the late stage (Appendix 1). Tree species from the Fabaceae family were present in all the successional stages (Table 1) with abundances between 15-21% of the total individuals registered in each stage (early: 20.4%, intermediate: 18.5%, and late: 15.9%). However, this family is more dominant in the early and intermediate stages. Some families were highly dominant in only one successional stage such as Verbenaceae (29.5%) and Cochlospermaceae (18.2%) in the early stage, and Euphorbiaceae (20%) in the late stage (Table 1). Some families were only present, or at least more common, in specific stages such as Burseraceae in the late-stage, and Tiliaceae, Flacourtiaceae, Sterculiaceae and Boraginaceae in the intermediate stage (Table 1).

The intermediate stage is the most diverse ($H' = 3.89$), while the early and late stages have H' values of 1.90 and 3.31 respectively. The diversity indices showed differences among the three stages (late vs. intermediate, $t = 7.93$, $df = 784$, $p < 0.0001$; late vs. early, $t = 12.99$, $df = 609$, $p < 0.0001$; intermediate vs. early, $t = 19.30$, $df = 471$, $p < 0.0001$). Of the total of 96 species identified, 17 were common to all successional stages, while four species were exclusive to the early stage, 22 to the intermediate stage, and eight to the late stage (Appendix 1). Species similarity among successional stages was low: 26% species similarity between the early and the intermediate stages, 33% between the early and the late stages, and 44% between intermediate and late stages. Using Jaccard's similarity index, two major site groups were identified from a cluster analysis. One group associates the three early stage plots with an intermediate stage plot (I3) and a late plot (L2), and the second group links two intermediate and two late stage plots (Figure 4). The first group is based on the presence of four common species among the plots Yayo (*Rehdera trinervis*), Silk cotton tree (*Cochlospermum vitifolium*), Cancerina (*Semialarium mexicanum*), and Nance (*Byrsonima crassifolia*) showing a dominance of pioneer species. The second group is based on the presence of shade intolerant species like Molenillo (*Luehea candida*), Guácimo (*Guazuma ulmifolia*), and Madroño negro (*Guettarda macrosperma*) (Appendix 1). Most trees of these species are old trees that remain when forests become old.

The clustering based on the Morisita Index also showed two main groups (Figure 5). Plot similarities were very low, but two early stage plots (E1 and E2) had a high similarity (> 0.8) due to the high abundances of Yayo (*Rehdera trinervis*) (35% of the total trees) and Silk cotton tree (*Cochlospermum vitifolium*) (25% of the total trees) (Appendix 1). The plot with the lowest species similarity is from a late stage of succession (L1) and is characterized by the high dominance of Mexican jumping bean (*Sebastiana pavoniana*) (32% of the total trees) and Quina (*Exostema mexicanum*) (12%) (Appendix 1).

Breeding systems, pollination, and dispersal syndromes

Monoecy was the most common breeding system in terms of both the total number of individual trees and the total number of species ($X^2 = 920.41$, $df = 1$, $p < 0.0001$; X^2 yates = 135.91, $df = 1$, $p < 0.0001$, respectively), while dioecy was present in only a few individuals and species in each stage (Table 2). Five different pollination syndromes were identified in the three TDF successional stages at the SRNP (entomophily, lepidopterophily, anemophily, chiropterophily, and ornithophily). Entomophily was the most frequent syndrome in terms of both the number of individuals and number of species that used it, followed by lepidopterophily in all the successional stages (Table 3). Anemophily was important in terms of the number of trees pollinated, but only a few tree species are pollinated by the wind (Table 3). Chiropterophily and ornithophily were important syndromes for some trees, but only a few species rely on them. Some tree species are generalists and depend on more than a single pollinator (Appendix 1). Seven different dispersal syndromes were observed in all the TDF successional stages, wind and birds being the most important agents in terms of both the number of individuals and number of species dispersed (Table 4). Mastochory is also a very important syndrome in terms of the number of species dispersed for all three successional stages, and bats are important for some particular species such as Gumbo-limbo (*Bursera simaruba*), Nance (*Byrsonima crassifolia*), Ojoche (*Brosimum alicastrum*), and Jagua (*Genipa americana*). There are some tree species, such as Madero negro (*Gliricidia sepium*), Spanish cedar (*Cedrela odorata*), *Bernardia nicaraguensis*, and Casco de venado (*Bauhinia ungulata*) that do not depend on animals for seed dispersal (e.g. autochory and barochory) (Appendix 1).

2.4 Discussion

Species composition

The species richness and diversity of the TDFs evaluated in this study are consistent with the Intermediate Disturbance Hypothesis (IDH) (Catford et al., 2012), the intermediate stage being the most diverse and having the highest species richness. According to this hypothesis, intermediate successional stages at the SRNP have in general a level of recovery that results in a forest that is transitional in structure, physiognomy, microhabitats, and microclimates between young and old-growth forests (Catford et al., 2012). This transition makes the intermediate stage suitable for tree species that also reside in both young open habitats and old-growth forests. However, the intermediate stage shares more species with the late stage than with the early stage, suggesting that the transitional characteristics of the intermediate successional stage facilitate greater colonization by, and the establishment of, species that are more adapted to later successional stages. Pioneer tree species were found mostly in the early stage; these species are fast- growing and well-adapted to disturbed habitats with full sunlight exposure (Janzen, 1983; Barbosa et al., 2009).

Not surprisingly in this study, heliophitic plant families (e.g. Verbenaceae, Cochlospermaceae, and Fabaceae) were dominant in the early successional stage. The late successional stage has a more shaded understory and forest floor, and more humid soils (pers. obs.). This promotes tree species germination and growth and may explain why some species are restricted to this stage such as Huevos de caballo (*Stemmadenia obovata*), Mexican jumping bean (*Sebastiana pavoniana*), Quebracho (*Lysiloma divaricatum*), Canelo (*Ocotea veraguensis*), and Quina (*Exostema mexicanum*)). Low abundances of valuable timber species, Ron ron (*Astronium graveolens*), Cocobolo (*Dalbergia retusa*), Spanish cedar (*Cedrela odorata*), and Mahogany (*Swietenia macrophylla*) are likely related to selective pressure from logging in the past (CITES, 2014; IUCN, 2014; Chavarría et al., 2001; Jiménez-Madrigal et al., 2002; Flores-Vindas & Obando-Vargas, 2003). Some important dry forest pioneer species like Cocobolo (*D. retusa*) and Ron ron (*A. graveolens*), both wind-dispersed species, were absent from the early stage, which may be due to the local absence of mother trees (García & Di Stéfano, 2000; Guzmán & Cordero, 2013). The low species similarity among successional stages shows that the stages are very different in tree species composition, suggesting that the plots evaluated for each forest successional may have a particular history of species colonization and establishment (Figure 4). This is also supported by the cluster analysis based on species composition and species abundances (Figure 5). This is likely the result of a combination of species-specific habits (e.g. heliophytic, shade-tolerant) and the high abundance in the successional plots of particular species due to their dispersal syndromes. Two heliophytic wind-dispersed trees showed a high dominance in two early plots (E1 and E2) which had the highest species similarity. In contrast, one late successional stage plot with the lowest species similarity is dominated by two shade-tolerant species that exhibit anemochory (Quina (*Exostema mexicanum*)) and possibly autochory (Mexican jumping bean (*Sebastiana mexicanum))*, or an unknown dispersal syndrome (Saravy et al., 2003).

Breeding systems

Monoecy is the most common breeding system observed in this study in terms of both the number of individuals and the number of species. Monoecy is a basal evolutionary characteristic of flowering plants, and about 80% of the flowering tree species worldwide are monoecious (Renner & Ricklefs, 1995). Monoecy is present in tree species with small flowers and is not dependant on specific pollinators, while specific reliable pollinators are needed only for dioecious species to succeed (Bawa & Beach, 1981; Gross, 2005). Even though dioecious plants are found in relatively lower numbers, their out-crossing is much more effective than out-crossing of monoecious plants (Richards, 1997; Friedman & Barrett, 2009). Dioecy also avoids self-pollination and autonomous reproduction and increases genetic variability in unpredictable environments (Richards, 1997; Harder et al., 2000; Rea & Nasrallah, 2008). However, self-pollination can be important for monoecious tree species in TDF, particularly when conspecifics are few and/or located far away from each other (Rea & Nasrallah, 2008). Some scientific investigations have found that the ratio of monoecy:dioecy is 3:1 (20-25% of the trees are dioecious) for TDFs (Bullock, 1985; Gillespie, 1999), but surprisingly, in our study, only 4% of the trees are dioecious, indicating that in the dry forests of the SRNP trees are rarely dependant on specific pollinators, but rely mainly on generalist pollinators (e.g. insects and wind). This is supported by our findings for both pollination and dispersal syndromes, where the high frequency of strong winds allows tree species to take advantage of this particular climatic condition.

Pollination syndromes

Entomophily is one of the most common and important pollination syndromes in several biomes throughout the Neotropics (Machado & Lopes, 2004; van Dulmen, 2001; Meléndez-Ramírez et al., 2004; Gottsberger & Silberbauer-Gottsberger, 2006; Girão et al., 2007; Lopes et al., 2009; Kimmel et al., 2010).

Our results for the SRNP confirm this pattern, which is also reported for dry forests in Brazil (Machado & Lopes, 2004). Most of the tree species observed in our study have small inflorescences that seem to be adapted to pollination by small visitors such as insects. In addition, the SRNP has an enormous insect diversity of about 13,000 species with the potential to visit flowers and pollinate them. High insect diversity can define plant species composition in habitats, since insects are important seed predators and primary pollinators, and can, therefore, determine the presence/absence and abundance of different plant species in specific habitats (Janzen, 1987).

Wind pollination (anemophily) can be an important pollination agent in early stage forests (open and disturbed) where pollinators may be scarce due to their physical separation from less disturbed forests. I have observed few wind-pollinated tree species in the early stage forests, but one species was highly dominant there, Yayo (*Rehdera trinervis*) (Appendix 1). Also, wind does not completely prevent insects from visiting flowers. However, evaluating the success of these visits was not part of this study.

In this study, chiropterophily was a frequent syndrome in some tree species like Guapinol (*Hymenaea courbaril*) and Palanco (*Sapranthus palanga*), but again, most of the tree species surveyed in this study have small inflorescences that are better adapted for insect pollination. These particular species are highly dependent on chiropterophily due to their floral structures (Gentry, 1996; CATIE, 2004). Ornithophily is less common in TDF than in forests at higher elevations where there are higher amounts of mist and greater humidity (Stiles et al. 2007).

Dispersal syndromes

Wind is a very important dispersal agent, mainly in the early stage forests, where the majority of tree species have dry fruits (e.g. legumes, siliques, achenes, samaras, capsules) (pers. obs.). Plants with seeds and fruits adapted to wind-dispersal are less dependent on the presence of a specific disperser. This is very advantageous in the SRNP because the fruiting period of the majority of species is in the dry season, during which the trade winds are dominant and strong in the SRNP (Janzen, 1983).

Many tree species in the tropics, including the TDF, are either entirely or partially dependent on birds and mammals for seed dispersal (Howe & Smallwood, 1982; Jordano, 2000; Wikander, 1984; Peres et al., 1997). Fleshy fruits and dry indehiscent fruits are important food sources for birds (171 species of birds present in the SRNP) and mammals such as monkeys, agoutis and other rodents, white-tailed deer, peccaries, and others. However, the structure of the early successional stage forests (e.g. open short canopy) is not suitable for monkeys, though White-Faced Capuchin monkeys (*Cebus capucinus*) in the SRNP may visit early stages to feed on the fruit of Acacia trees (*Vachellia collinsii*), which are highly dominant in early successional stage forests (Young et al., 2008). The absence of a closed forest canopy can also limit bird visits, lengthening the time for tree species colonization and establishment in the early stages of forest development. On the other hand, seed dispersal by animals helps seeds to travel, and plants to colonize and establish themselves farther away from their parent trees, which reduces mortality by predation, pathogens, and intraspecific competition associated with parental proximity (Janzen, 1970). Autochory (ballistic) and barochory (gravity) are other important seed dispersal strategies in tree species that do not depend on any disperser (Wikander, 1984), such as those producing dry fruits, specifically dehiscent fruits like legumes and siliques. Even though a few tree species showed these dispersal traits, these were only very abundant in the early successional stage forests. These species included Guácimo de monte (*Helicteres baruensis*), Casco de venado (*Bauhinia ungulata*), and Madero negro (*Gliricidia sepium*) (Appendix 1). In the SRNP TDF, barochory is currently demonstrated by species with large heavy fruits, which used to be dispersed by extinct megafauna (Janzen & Martin, 1982).

Conclusions

This study describes the floristic composition of three successional stages of the dry forest of the SRNP in Costa Rica. This is one of the most significant and largest remnants of dry forest in Mesoamerica. Tree species in this region are related not only to abiotic factors such as soil humidity and canopy shade but also to biotic factors such as seed dispersers and proximity to seed mother trees, as well as to other biophysical soil properties (Powers et al., 2008). Many tree species common to Costa Rican TDF are missing from the early stage forests and, consequently, the species composition of these forests is different from that of the intermediate and late stages. Many tree species observed are restricted to the late stage forests, and some of these are very rare in Costa Rican dry forests in general.

This study describes for the first time the breeding systems and pollination and dispersal syndromes of a large number of tropical dry forest tree species that occur across a forest succession. This knowledge is critical in terms of conservation because it gives an idea of what species will colonize a perturbed place, and how long it takes for some other species to colonize and become established in older forests. A transition in species composition across a dry forest succession was observed, showing how species are replaced as the forest becomes older. In terms of pollination and dispersal agents, this study shows how syndromes vary across the dry forest succession and how some specific syndromes are restricted to certain forest age classes. The role of insects in this TDF remnant is important to consider due to their importance as key pollinators in TDFs. The SRNP dry forest fosters a high insect diversity that promotes pollination of many tree species. This information is crucial both for understanding how natural restoration occurs in a dry forest and for designing efforts to restore this highly endangered ecosystem in other countries in the Mesoamerican region.

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2.6 Tables and Figures

Table 2.1 Tree families with a percent of composition greater than 5% in three tropical dry forest successional stages in the Santa Rosa National Park, Guanacaste, Costa Rica.

Stage	Family	No of species	% Composition
Early	Verbenaceae	2	29,5
	Fabaceae	7	20,4
	Cochlospermaceae	1	18,2
	Hippocrateaceae	1	5,3
	Malphigiaceae	1	5,3
Intermediate	Fabaceae	12	18
	Tiliaceae	4	9
	Rubiaceae	4	9
	Meliaceae	6	8
	Flacourtiaceae	4	7
	Bignoniaceae	5	6
	Sterculiaceae	2	6
	Boraginaceae	2	6
Late	Euphorbiaceae	5	20,0
	Rubiaceae	6	14,5
	Hippocrateaceae	1	11,6
	Fabaceae	8	10,8
	Bignoniaceae	4	6,8
	Burseraceae	3	5,7

Table 2.2 Tree species richness and breeding systems observed in three tropical dry forests (TDFs) successional stages in the Santa Rosa National Park, Guanacaste, Costa Rica.

	Early		**Intermediate**		**Late**	
Breeding System	**#species**	**#individuals**	**#species**	**#individuals**	**#species**	**#individuals**
Monoecy	30	307	69	290	57	419
Dioecy	2	11	3	17	4	15
TOTAL	**33**	**318**	**72**	**307**	**61**	**434**

Table 2.3 Pollination syndrome by tree individuals and species observed in three tropical dry forest successional stages in the Santa Rosa National Park, Guanacaste, Costa Rica.

	EARLY		**INTERMEDIATE**		**LATE**	
Pollination Syndrome	**#species**	**#individuals**	**#species**	**#individuals**	**#species**	**#individuals**
Entomophily	24	292	55	227	46	370
Lepidopterophily	10	25	17	109	17	133
Anemophily	4	20	7	45	6	24
Chiropterophily	3	6	2	11	4	8
Ornithophily	0	0	1	1	2	4

Table 2.4 Seed dispersal syndrome by tree individuals and species observed in three tropical dry forest stages in the Santa Rosa, National Park, Guanacaste, Costa Rica.

	EARLY		**INTERMEDIATE**		**LATE**	
Dispersal Syndrome	**#species**	**#individuals**	**#species**	**#individuals**	**#species**	**#individuals**
Anemochory	12	184	21	100	19	159
Mastochory	12	30	21	97	24	126
Ornithochory	11	43	38	135	25	136
Autochory	4	62	5	23	6	26
Chiropterochory	3	19	5	21	4	29
Barochory	2	4	2	8	1	1
Saurochory	1	1	4	24	3	13

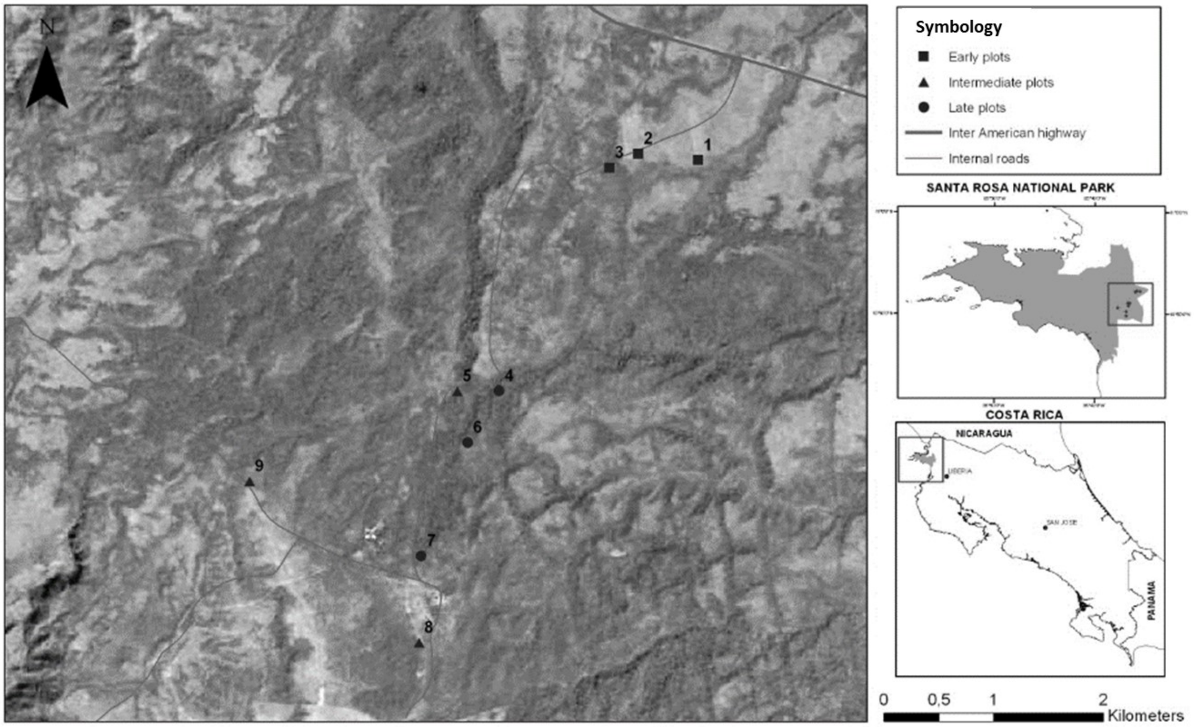


Figure 2.1 The Santa Rosa National Park map showing locations of the nine plots in the three TDFs successional stages, Guanacaste, Costa Rica.

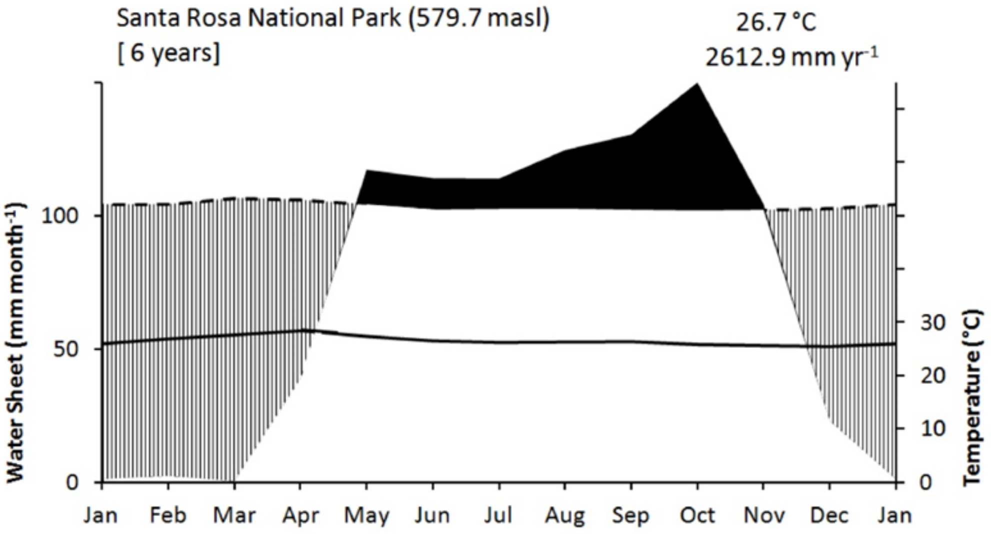


Figure 2.2 Climate diagram for the Santa Rosa National Park based on 6 years of meteorological data (2006-2011). It shows the monthly variation of wettest months (black solid area), evapo-transpirated water (white solid area), and water deficit (vertical lined area) defined by the potential evapotranspiration (dotted line) and temperature (solid line).

Figure 2.3 Forest successional stages early (top), intermediate (middle), late (bottom), dry season, Santa Rosa National Park, Guanacaste, Costa Rica.

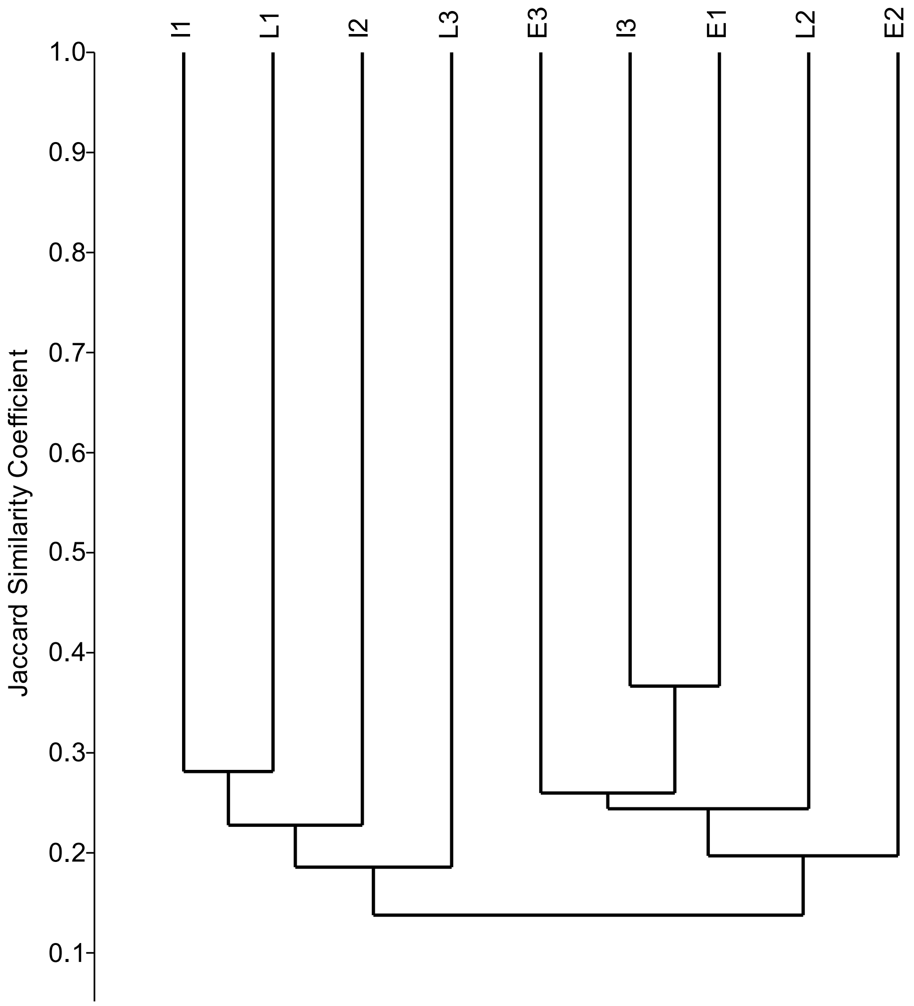


Figure 2.4 Cluster analysis for Jaccard Similarity Coefficient based on plot species composition in the Early (E1, E2, E3), Intermediate (I1, I2, I3), and Late (L1, L2, L3) successional stages of Tropical Dry Forests in the Santa Rosa National Park, Guanacaste, Costa Rica.

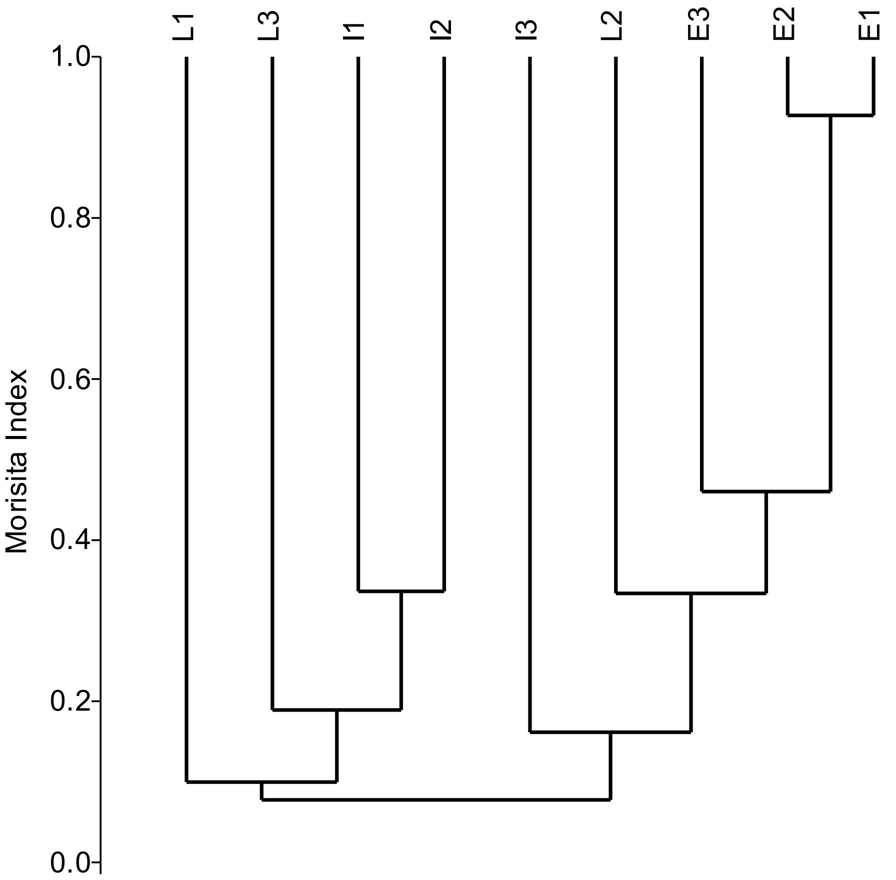
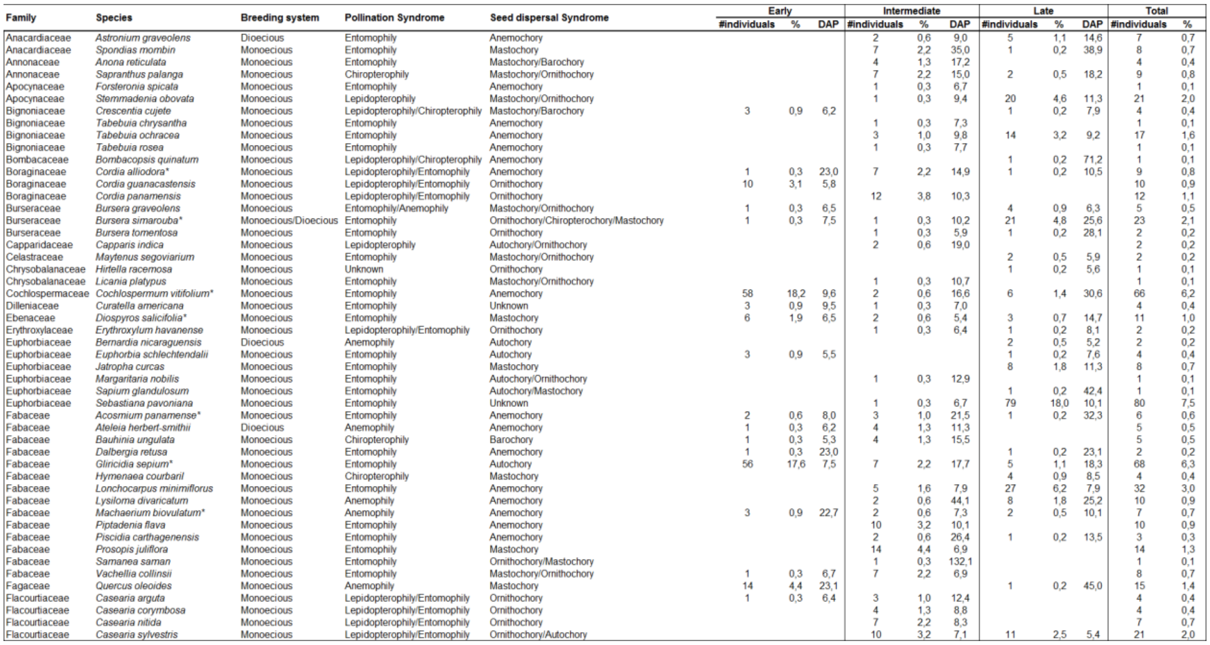


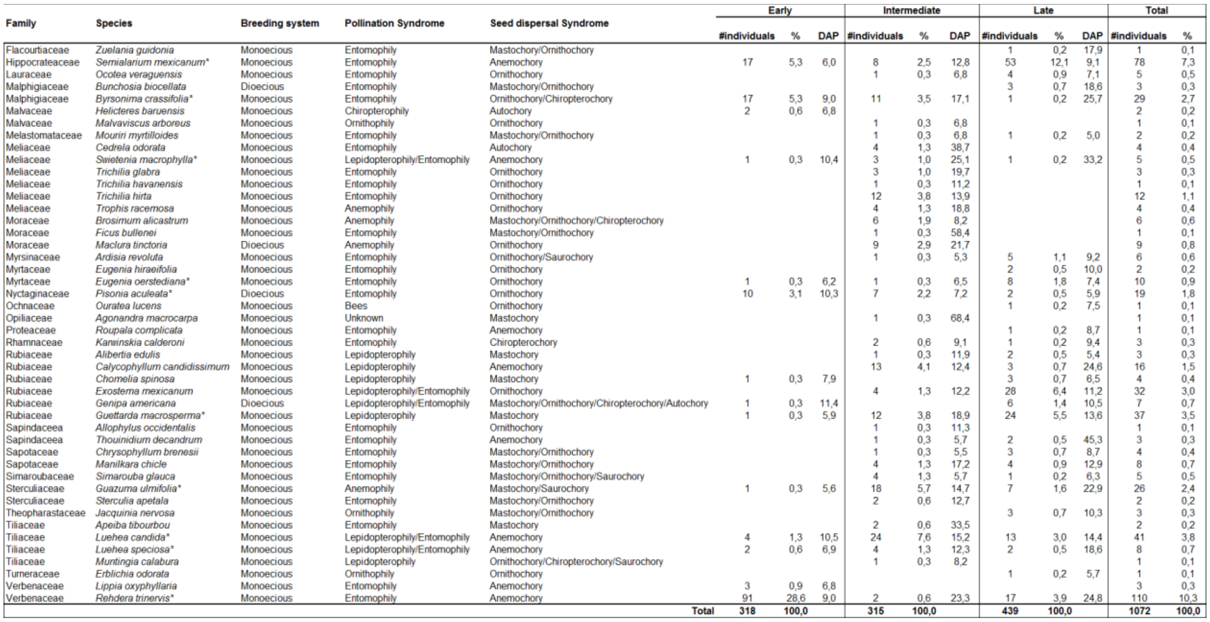
Figure 2.5 Morisita Index cluster analysis based on plot species composition in the Early (E1, E2, E3), Intermediate (I1, I2, I3), and Late (L1, L2, L3) successional stages of Tropical Dry Forests in the Santa Rosa National Park, Guanacaste, Costa Rica.

Supplementary Material

Supplementary Material 1.1 Tree species observed in numbers and percentages, including diameter at breast height (DBH), their breeding system, and pollination and seed dispersal syndrome in three tropical dry forest stages in the Santa Rosa, National Park, Guanacaste, Costa Rica.



Family	Species	Breeding system	Pollination Syndrome	Seed dispersal Syndrome	Early			Intermediate			Late			Total	
					#individuals	%	DAP	#individuals	%	DAP	#individuals	%	DAP	#individuals	%
Anacardiaceae	_Astronium graveolens_	Dioecious	Entomophily	Anemochory				2	0,6	9,0	5	1,1	14,6	7	0,7
Anacardiaceae	_Spondias mombin_	Monoecious	Entomophily	Mastochory				7	2,2	35,0	1	0,2	38,9	8	0,7
Annonaceae	_Anona reticulata_	Monoecious	Entomophily	Mastochory/Barochory				4	1,3	17,2				4	0,4
Annonaceae	_Sapranthus palanga_	Monoecious	Chiropterophily	Mastochory/Ornithochory				7	2,2	15,0	2	0,5	18,2	9	0,8
Apocynaceae	_Forsteronia spicata_	Monoecious	Entomophily	Anemochory				1	0,3	6,7				1	0,1
Apocynaceae	_Stemmadenia obovata_	Monoecious	Lepidopterophily	Mastochory/Ornithochory				1	0,3	9,4	20	4,6	11,3	21	2,0
Bignoniaceae	_Crescentia cujete_	Monoecious	Lepidopterophily/Chiropterophily	Mastochory/Barochory	3	0,9	6,2				1	0,2	7,9	4	0,4
Bignoniaceae	_Tabebuia chrysantha_	Monoecious	Entomophily	Anemochory				1	0,3	7,3				1	0,1
Bignoniaceae	_Tabebuia ochracea_	Monoecious	Entomophily	Anemochory				3	1,0	9,8	14	3,2	9,2	17	1,6
Bignoniaceae	_Tabebuia rosea_	Monoecious	Entomophily	Anemochory				1	0,3	7,7				1	0,1
Bombacaceae	_Bombacopsis quinatum_	Monoecious	Lepidopterophily/Chiropterophily	Anemochory							1	0,2	71,2	1	0,1
Boraginaceae	_Cordia alliodora_*	Monoecious	Lepidopterophily/Entomophily	Anemochory	1	0,3	23,0	7	2,2	14,9	1	0,2	10,5	9	0,8
Boraginaceae	_Cordia guanacastensis_	Monoecious	Lepidopterophily/Entomophily	Ornithochory	10	3,1	5,8							10	0,9
Boraginaceae	_Cordia panamensis_	Monoecious	Lepidopterophily/Entomophily	Ornithochory				12	3,8	10,3				12	1,1
Burseraceae	_Bursera graveolens_	Monoecious	Entomophily/Anemophily	Mastochory/Ornithochory	1	0,3	6,5				4	0,9	6,3	5	0,5
Burseraceae	_Bursera simarouba_*	Monoecious/Dioecious	Entomophily	Ornithochory/Chiropterochory/Mastochory	1	0,3	7,5	1	0,3	10,2	21	4,8	25,6	23	2,1
Burseraceae	_Bursera tomentosa_	Monoecious	Entomophily	Ornithochory				1	0,3	5,9	1	0,2	28,1	2	0,2
Capparidaceae	_Capparis indica_	Monoecious	Lepidopterophily	Autochory/Ornithochory				2	0,6	19,0				2	0,2
Celastraceae	_Maytenus segoviarium_	Monoecious	Entomophily	Mastochory/Ornithochory							2	0,5	5,9	2	0,2
Chrysobalanaceae	_Hirtella racemosa_	Monoecious	Unknown	Ornithochory							1	0,2	5,6	1	0,1
Chrysobalanaceae	_Licania platypus_	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	10,7				1	0,1
Cochlospermaceae	_Cochlospermum vitifolium_*	Monoecious	Entomophily	Anemochory	58	18,2	9,6	2	0,6	16,6	6	1,4	30,6	66	6,2
Dilleniaceae	_Curatella americana_	Monoecious	Entomophily	Unknown	3	0,9	9,5	1	0,3	7,0				4	0,4
Ebenaceae	_Diospyros salicifolia_*	Monoecious	Entomophily	Mastochory	6	1,9	6,5	2	0,6	5,4	3	0,7	14,7	11	1,0
Erythroxylaceae	_Erythroxylum havanense_	Monoecious	Lepidopterophily/Entomophily	Ornithochory				1	0,3	6,4	1	0,2	8,1	2	0,2
Euphorbiaceae	_Bernardia nicaraguensis_	Dioecious	Anemophily	Autochory							2	0,5	5,2	2	0,2
Euphorbiaceae	_Euphorbia schlechtendalii_	Monoecious	Entomophily	Autochory	3	0,9	5,5				1	0,2	7,6	4	0,4
Euphorbiaceae	_Jatropha curcas_	Monoecious	Entomophily	Mastochory							8	1,8	11,3	8	0,7
Euphorbiaceae	_Margaritaria nobilis_	Monoecious	Entomophily	Autochory/Ornithochory				1	0,3	12,9				1	0,1
Euphorbiaceae	_Sapium glandulosum_	Monoecious	Entomophily	Autochory/Mastochory							1	0,2	42,4	1	0,1
Euphorbiaceae	_Sebastiana pavoniana_	Monoecious	Entomophily	Unknown				1	0,3	6,7	79	18,0	10,1	80	7,5
Fabaceae	_Acosmium panamense_*	Monoecious	Entomophily	Anemochory	2	0,6	8,0	3	1,0	21,5	1	0,2	32,3	6	0,6
Fabaceae	_Ateleia herbert-smithii_	Dioecious	Anemophily	Anemochory	1	0,3	6,2	4	1,3	11,3				5	0,5
Fabaceae	_Bauhinia ungulata_	Monoecious	Chiropterophily	Barochory	1	0,3	5,3	4	1,3	15,5				5	0,5
Fabaceae	_Dalbergia retusa_	Monoecious	Entomophily	Anemochory	1	0,3	23,0				1	0,2	23,1	2	0,2
Fabaceae	_Gliricidia sepium_*	Monoecious	Entomophily	Autochory	56	17,6	7,5	7	2,2	17,7	5	1,1	18,3	68	6,3
Fabaceae	_Hymenaea courbaril_	Monoecious	Chiropterophily	Mastochory							4	0,9	8,5	4	0,4
Fabaceae	_Lonchocarpus minimiflorus_	Monoecious	Entomophily	Anemochory				5	1,6	7,9	27	6,2	7,9	32	3,0
Fabaceae	_Lysiloma divaricatum_	Monoecious	Anemophily	Anemochory				2	0,6	44,1	8	1,8	25,2	10	0,9
Fabaceae	_Machaerium biovulatum_*	Monoecious	Anemophily	Anemochory	3	0,9	22,7	2	0,6	7,3	2	0,5	10,1	7	0,7
Fabaceae	_Piptadenia flava_	Monoecious	Entomophily	Anemochory				10	3,2	10,1				10	0,9
Fabaceae	_Piscidia carthagenensis_	Monoecious	Entomophily	Anemochory				2	0,6	26,4	1	0,2	13,5	3	0,3
Fabaceae	_Prosopis juliflora_	Monoecious	Entomophily	Mastochory				14	4,4	6,9				14	1,3
Fabaceae	_Samanea saman_	Monoecious	Entomophily	Ornithochory/Mastochory				1	0,3	132,1				1	0,1
Fabaceae	_Vachellia collinsii_	Monoecious	Entomophily	Mastochory/Ornithochory	1	0,3	6,7	7	2,2	6,9				8	0,7
Fagaceae	_Quercus oleoides_	Monoecious	Anemophily	Mastochory	14	4,4	23,1				1	0,2	45,0	15	1,4
Flacourtiaceae	_Casearia arguta_	Monoecious	Lepidopterophily/Entomophily	Ornithochory	1	0,3	6,4	3	1,0	12,4				4	0,4
Flacourtiaceae	_Casearia corymbosa_	Monoecious	Lepidopterophily/Entomophily	Ornithochory				4	1,3	8,8				4	0,4
Flacourtiaceae	_Casearia nitida_	Monoecious	Lepidopterophily/Entomophily	Ornithochory				7	2,2	8,3				7	0,7
Flacourtiaceae	_Casearia sylvestris_	Monoecious	Lepidopterophily/Entomophily	Ornithochory/Autochory				10	3,2	7,1	11	2,5	5,4	21	2,0



Family	Species	Breeding system	Pollination Syndrome	Seed dispersal Syndrome	Early			Intermediate			Late			Total	
					#individuals	%	DAP	#individuals	%	DAP	#individuals	%	DAP	#individuals	%
Flacourtiaceae	_Zuelania guidonia_	Monoecious	Entomophily	Mastochory/Ornithochory							1	0,2	17,9	1	0,1
Hippocrateaceae	_Semialarium mexicanum_*	Monoecious	Entomophily	Anemochory	17	5,3	6,0	8	2,5	12,8	53	12,1	9,1	78	7,3
Lauraceae	_Ocotea veraguensis_	Monoecious	Entomophily	Ornithochory				1	0,3	6,8	4	0,9	7,1	5	0,5
Malphigiaceae	_Bunchosia biocellata_	Dioecious	Entomophily	Mastochory/Ornithochory							3	0,7	18,6	3	0,3
Malphigiaceae	_Byrsonima crassifolia_*	Monoecious	Entomophily	Ornithochory/Chiropterochory	17	5,3	9,0	11	3,5	17,1	1	0,2	25,7	29	2,7
Malvaceae	_Helicteres baruensis_	Monoecious	Chiropterophily	Autochory	2	0,6	6,8							2	0,2
Malvaceae	_Malvaviscus arboreus_	Monoecious	Ornithophily	Ornithochory				1	0,3	6,8				1	0,1
Melastomataceae	_Mouriri myrtilloides_	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	6,8	1	0,2	5,0	2	0,2
Meliaceae	_Cedrela odorata_	Monoecious	Entomophily	Autochory				4	1,3	38,7				4	0,4
Meliaceae	_Swietenia macrophylla_*	Monoecious	Lepidopterophily/Entomophily	Anemochory	1	0,3	10,4	3	1,0	25,1	1	0,2	33,2	5	0,5
Meliaceae	_Trichilia glabra_	Monoecious	Entomophily	Ornithochory				3	1,0	19,7				3	0,3
Meliaceae	_Trichilia havanensis_	Monoecious	Entomophily	Ornithochory				1	0,3	11,2				1	0,1
Meliaceae	_Trichilia hirta_	Monoecious	Entomophily	Ornithochory				12	3,8	13,9				12	1,1
Meliaceae	_Trophis racemosa_	Monoecious	Anemophily	Ornithochory				4	1,3	18,8				4	0,4
Moraceae	_Brosimum alicastrum_	Monoecious	Anemophily	Mastochory/Ornithochory/Chiropterochory				6	1,9	8,2				6	0,6
Moraceae	_Ficus bullenei_	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	58,4				1	0,1
Moraceae	_Maclura tinctoria_	Dioecious	Anemophily	Ornithochory				9	2,9	21,7				9	0,8
Myrsinaceae	_Ardisia revoluta_	Monoecious	Entomophily	Ornithochory/Saurochory				1	0,3	5,3	5	1,1	9,2	6	0,6
Myrtaceae	_Eugenia hiraeifolia_	Monoecious	Entomophily	Ornithochory							2	0,5	10,0	2	0,2
Myrtaceae	_Eugenia oerstediana_*	Monoecious	Entomophily	Ornithochory	1	0,3	6,2	1	0,3	6,5	8	1,8	7,4	10	0,9
Nyctaginaceae	_Pisonia aculeata_*	Dioecious	Entomophily	Ornithochory	10	3,1	10,3	7	2,2	7,2	2	0,5	5,9	19	1,8
Ochnaceae	_Ouratea lucens_	Monoecious	Bees	Ornithochory							1	0,2	7,5	1	0,1
Opiliaceae	_Agonandra macrocarpa_	Monoecious	Unknown	Mastochory				1	0,3	68,4				1	0,1
Proteaceae	_Roupala complicata_	Monoecious	Entomophily	Anemochory							1	0,2	8,7	1	0,1
Rhamnaceae	_Karwinskia calderoni_	Monoecious	Entomophily	Chiropterochory				2	0,6	9,1	1	0,2	9,4	3	0,3
Rubiaceae	_Alibertia edulis_	Monoecious	Lepidopterophily	Mastochory				1	0,3	11,9	2	0,5	5,4	3	0,3
Rubiaceae	_Calycophyllum candidissimum_	Monoecious	Lepidopterophily	Anemochory				13	4,1	12,4	3	0,7	24,6	16	1,5
Rubiaceae	_Chomelia spinosa_	Monoecious	Lepidopterophily	Mastochory	1	0,3	7,9				3	0,7	6,5	4	0,4
Rubiaceae	_Exostema mexicanum_	Monoecious	Lepidopterophily/Entomophily	Ornithochory				4	1,3	12,2	28	6,4	11,2	32	3,0
Rubiaceae	_Genipa americana_	Dioecious	Lepidopterophily/Entomophily	Mastochory/Ornithochory/Chiropterochory/Autochory	1	0,3	11,4				6	1,4	10,5	7	0,7
Rubiaceae	_Guettarda macrosperma_*	Monoecious	Lepidopterophily	Mastochory	1	0,3	5,9	12	3,8	18,9	24	5,5	13,6	37	3,5
Sapindaceea	_Allophylus occidentalis_	Monoecious	Entomophily	Ornithochory				1	0,3	11,3				1	0,1
Sapindaceea	_Thouinidium decandrum_	Monoecious	Entomophily	Anemochory				1	0,3	5,7	2	0,5	45,3	3	0,3
Sapotaceae	_Chrysophyllum brenesii_	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	5,5	3	0,7	8,7	4	0,4
Sapotaceae	_Manilkara chicle_	Monoecious	Entomophily	Mastochory/Ornithochory				4	1,3	17,2	4	0,9	12,9	8	0,7
Simaroubaceae	_Simarouba glauca_	Monoecious	Entomophily	Mastochory/Ornithochory/Saurochory				4	1,3	5,7	1	0,2	6,3	5	0,5
Sterculiaceae	_Guazuma ulmifolia_*	Monoecious	Anemophily	Mastochory/Saurochory	1	0,3	5,6	18	5,7	14,7	7	1,6	22,9	26	2,4
Sterculiaceae	_Sterculia apetala_	Monoecious	Entomophily	Mastochory/Ornithochory				2	0,6	12,7				2	0,2
Theopharastaceae	_Jacquinia nervosa_	Monoecious	Ornithophily	Mastochory/Ornithochory							3	0,7	10,3	3	0,3
Tiliaceae	_Apeiba tibourbou_	Monoecious	Entomophily	Mastochory				2	0,6	33,5				2	0,2
Tiliaceae	_Luehea candida_*	Monoecious	Lepidopterophily/Entomophily	Anemochory	4	1,3	10,5	24	7,6	15,2	13	3,0	14,4	41	3,8
Tiliaceae	_Luehea speciosa_*	Monoecious	Lepidopterophily/Entomophily	Anemochory	2	0,6	6,9	4	1,3	12,3	2	0,5	18,6	8	0,7
Tiliaceae	_Muntingia calabura_	Monoecious	Lepidopterophily	Ornithochory/Chiropterochory/Saurochory				1	0,3	8,2				1	0,1
Turneraceae	_Erblichia odorata_	Monoecious	Ornithophily	Ornithochory							1	0,2	5,7	1	0,1
Verbenaceae	_Lippia oxyphyllaria_	Monoecious	Entomophily	Anemochory	3	0,9	6,8							3	0,3
Verbenaceae	_Rehdera trinervis_*	Monoecious	Entomophily	Anemochory	91	28,6	9,0	2	0,6	23,3	17	3,9	24,8	110	10,3
				Total	**318**	**100,0**		**315**	**100,0**		**439**	**100,0**		**1072**	**100,0**

3 Determining the relationship between liana abundance and the complexity of the avian community in tropical dry forests

3.1 Introduction

Tropical dry forests (TDFs) are considered important sources of biodiversity and species richness given the wide variety of plant and animal species that have adapted to the unique habitats that are found exclusively in TDFs (Gillespie et al., 2000). Lianas are a structural group of plants that have received growing attention for their role in community structure and ecosystem function and are considered a key component of TDF ecosystems (Sánchez-Azofeifa & Castro-Esau, 2006). Lianas are defined as climbing plants that produce woody tissue and germinate on the ground. Eventually, these vines lose their ability to support their own weight and subsequently rely on external supports, such as trees, to aid their ascent into the forest canopy (Gerwing, 2006). As such, they are considered non-structural elements of a given forest. Unlike other plants that slow their growth during the dry season to preserve water, lianas have the competitive advantage of growing during times of drought due to an efficient vascular structure that allows for photosynthesis. As a result, liana abundance is often higher in TDFs than in other tropical forests (Schnitzer, 2005). In disturbed forests, an increase in liana abundance and biomass can help to restore the light environment, microclimatic conditions, and vegetation structure, creating habitat characteristics similar to those of the forest interior and thereby reducing the effects of forest fragmentation on birds (Michel et al., 2014).

Lianas provide important resources for fauna, particularly birds. These include both direct (e.g., fruit or nectar) and indirect resources (e.g., shelter, nesting sites, and arthropods for food) (Muller-Landau & Hardesty, 2005). Fruits and floral nectar are the main food resources that birds obtain directly from lianas; however, only 25% of liana species in the Neotropics have fleshy fruits, indicating that fruits are not the main food source for birds there. Thus, birds are not very dependent on lianas (Muller-Landau & Hardesty, 2005). Floral nectar is particularly important for some bird species, including hummingbirds, parrots, honeyeaters, and warblers (Fleming et al., 2005). As for indirect food sources, arthropods are the most frequent food item that birds obtain from lianas (Michel et al., 2014). Consequently, a few studies have shown that liana abundance can influence the avian abundance and species richness (Michel et al., 2014). For example, in rainforests recovering from logging, it has been observed that the liana abundance was positively correlated with the overall bird species richness, but negatively correlated with the presence and abundance of specific bird species (Ansell et al., 2011). Others have found that natural tree-fall gaps with dense lianas had greater total bird species richness than anthropogenic gaps with vine-cutting (Felton et al., 2008). Although lianas are key components of TDFs due to their abundance and biomass, there are no studies that evaluate the influence of lianas on fauna in TDFs (Robinson & Robinson, 2001).

The presence and activity of fauna can be evaluated using acoustic methods for those species that communicate or use sounds (Sueur et al., 2008; Aide et al., 2013). Acoustic tools include both sound recording in the field and analysis of the resulting sound recordings (Aide et al., 2013; Sueur et al., 2014; Towsey et al., 2014). Currently, several different acoustic indices are used for different purposes (Sueur et al., 2014). These include studies that use indices to monitor the presence, behavior, and activity of specific fauna, as well as indices that are used to evaluate acoustic richness, diversity, and complexity (Sueur et al., 2008; Farina et al., 2011; Pieretti et al., 2011; Depraetere et al., 2012; Pieretti & Farina, 2013; Gasc et al., 2013; Rodríguez et al., 2014). The Acoustic Complexity Index (ACI) is a tool that has been used as a general estimator of sound complexity, an estimator of the acoustic complexity of bird sounds (Farina et al., 2011; Pieretti et al., 2011), an indicator of ecosystem health (Buxton et al., 2016), and an indicator of change in avian communities (Farina et al., 2011). The ACI calculates the average of differences in sound pressure level between frequency bins and temporal steps in a spectrogram and uses sound intensities, rather than spectral features in a spectrogram, to characterize the acoustic environment (Pieretti et al., 2011). Analysis of spectral features in spectrograms can result in underestimation of the differences between frequency bins when two or more fauna sounds overlap within the same bin. This issue is addressed properly with the ACI which measures acoustic intensities instead of spectral features and reduces the likelihood of encountering two different organisms that produce the same sound intensity in the same frequency bin during the recording analysis. The ACI has been demonstrated to be a reliable index for characterizing avian communities (Farina et al., 2011; Pieretti et al., 2011). However, this is a recently developed index that has not been widely used in the Tropics.

This study assessed the relationship between liana abundance and the avian acoustic community of a TDF in Costa Rica. Eight intermediate forest sites with different levels of liana abundance were selected to evaluate the acoustic complexity as an estimator of the avian acoustic community. The goal of this is to determine whether the acoustic complexity could be used as more than an indicator of acoustic activity by additionally estimating bird species richness in TDFs. I used statistical tests to model the relationship between liana abundance, forest biophysical properties (such as tree basal area (BA), Plant Area Index (PAI), and canopy height (CH)) and the avian acoustic community. Since lianas provide important resources for birds, I hypothesized that liana abundance would influence the avian acoustic community in TDFs. I predicted that an increase in liana abundance would result in a more complex avian acoustic community within the TDF analyzed in this study.

3.2 Materials and Methods

Study Site and Experimental Design

This study was conducted at the Santa Rosa National Park (SRNP), Guanacaste, Costa Rica (10°48’53” N, 85°36’54” W) (Figure 1). This area is characterized by a dry season of six months and annual precipitation ranging from 900 to 2500 mm/year (Sánchez-Azofeifa et al., 2005). The SRNP land cover is a mixture of forest successional stages that developed during recovery from cattle ranching and use as pasture in the past (Quesada, M. & Stoner, 2004; Arroyo-Mora et al., 2005; Kalacska et al., 2004; Cao et al., 2015). These successional stages are very heterogeneous and contain a high diversity of habitats and biotic communities (Janzen, 1983; Hilje et al., 2015).

TDF successional stages were established based on their vegetation structure and tree species composition for individual trees with diameter at breast height (DBH) of more than 5 cm, according to Kalacska et al. (2004). Eight radial plots of 40 m diameter were set up within the intermediate TDF successional stage (radial plot total area = 1257 m^2). This successional stage has biophysical properties, like vertical forest structure, that can support liana coverage (Kalacska et al., 2005), and lianas can be observed throughout this successional stage at the SRNP (Figure 2). The total number of lianas above 5 cm of DBH was determined in each radial plot and this was standardized by dividing it by the total number of trees with diameters at breast height (DBH) of 10 cm or more (Figure 2). The minimum distance between radial plots was 150 m, and the maximum was 3000 m (Figure 1).

Forest Biophysical Properties

The DBH for all the trees with a diameter greater than 5 cm was measured in each radial plot and this information was used to calculate the tree basal area (BA). The BA was standardized by dividing the total tree basal area obtained for each plot by the radial plot area (total area = 1257 m^2) and dividing this value by the area of a Ha (i.e. 10000 m^2). Plant Area Index (PAI) was measured using a series of hemispherical photos taken in each radial plot. A cross was drawn inside each radial plot and hemispherical photos were taken at the cross center and 10 m away in each of the four cardinal directions to have a total of five photos per plot. Photos were captured at a height of 1.5 m above the forest floor using a fish-eye lens on a Nikon CoolPix 995 camera. The HPA Software program (Delta-T Devices, 1999) was used to calculate the PAI by determining the amount of vegetation, wood presence, and leaf angle position in each hemispherical photograph. Since PAI is affected by the angle of sun illumination, hemispherical photos were taken early in the morning and late in the afternoon to avoid the effect of direct sunlight at the solar zenith (Chen et al. 1991). Lastly, canopy height (CH) was measured by taking the average height of the three tallest trees inside each radial plot using a hand-held Blueskysea 600 M waterproof laser rangefinder.

The Avian Acoustic Community

An SM3 Songmeter automated sound recorder was deployed in the center of each radial plot between late July and early August 2014 (Wildlife Acoustics Inc. 2011). This period includes the peak of the breeding season of most dry forest birds (i.e. May through July) (Barrantes et al. 2016). In order to avoid sound overlap between plots, a minimum distance of 150 m was established between recorders. The sound was recorded using a “wav” file format at 16 bits per file, a minimum noise gain of -88 decibels (dB) and a sampling rate of 19.2 kHz. Three 15 min length recording sections from dawn (06:00–07:30) and three 15 min sections from dusk (16:00–17:30) were selected for each of the five days for the recording period (i.e., 450 min per forest site) because these are the hours with higher acoustic activity for birds in the SRNP.

The avian acoustic communities for the forest sites were obtained using Acoustic Complexity Indices (ACI) (Pieretti et al., 2011) determined from the recordings using the Soundecology package in R (version 3.3.2, R-Core-Team, Vienna, Austria) (Villanueva-Rivera & Pijanowski, 2016; R-Core Team, 2017). ACI has been correlated with the number of vocalizations produced by bird communities (Farina et al., 2011; Pieretti et al., 2011; Farina & Pieretti, 2014). ACI quantifies sound complexity from recordings based on the variability of the sound intensities present (Pieretti et al., 2011). It calculates the relative difference between two adjacent values of intensity in a single frequency bin (e.g. 0-1,000 Hz) and then adds together all differences included in that frequency bin (Figure 3a). Finally, it adds the differences for all the frequency bins to obtain a total ACI value for a recording (Pieretti et al., 2011). ACI was calculated using frequency bins from 0 to 10,000 Hz in the recordings and an amplitude default threshold of -50 dB relative to full scale (dBFS) was established. Since strong wind (39 km/h) and rainfall above -50 dB cover most of the frequency bands in the spectrograms (Figure 3b), only recordings with less than 15% of wind (e.g. 1.5 minutes) in the whole recording file were selected for the ACI analyses. Due to this, ACI analyses were performed on a total of 2360 recorded minutes for the forest sites evaluated. Using Songscope software (Wildlife Acoustics Inc. 2011), the ACI values were corroborated by clipping off the first minute of ten 15 min long recordings per forest site, performing ACI analysis on that minute and, finally, listening to this minute to determine the total number of bird species present.

Statistical Analysis

The relationship between ACI values and forest biophysical properties (e.g., BA, PAI, and CH) and the number of lianas was evaluated by using Generalized Linear Models (GLM). The Akaike's Information criterion was also used with a small sample size correction (AICc) and the AIC weights to select the best model (Burnham & Anderson, 2003; Burnham & Anderson, 2004; Sánchez et al., 2014). An Ordinary Least Squares (OLS) analysis was used to evaluate the relationship between the ACI values and the total number of bird species listened to in the first minute of ten recordings per forest site. The site was set as a categorical predictor for this analysis, and all the analyses were performed in R (version 3.3.2) (R-Core Team, 2017).

3.3 Results

The Avian Acoustic Community Relationship with Liana Abundance and Forest Biophysical Properties

The number of lianas present in the tropical dry forest segments evaluated ranged from 9 to 40 lianas per segment (mean = 20 lianas/plot). The mean ACI observed for the forest segments evaluated was 1831.85, with a minimum ACI value of 1784.21 and a maximum of 1970.46. The best model explaining the variation in ACI in the dry forests includes the number of lianas as a variable (Table 1 and Figure 4). The number of lianas explains 60 % of the variation when performing an OLS analysis ($F_{(1, 6)} = 11.44$, $p = 0.015$) (Figure 4). Other models that explain variation in ACI include the number of lianas combined with CH, BA, and PAI, respectively. However, each of these models has an AICc weight lower than 10%. (Table 1).

Acoustic Complexity Index as an Estimator of Bird Species Richness

A positive relationship was observed between the number of bird species detected in the first minute of the ten recordings per forest site and the ACI values ($F_{(8, 71)} = 6.383$, $p < 0.0001$, $R^2_{adj} = 0.353$) (Figure 5). This means that in recording files with high values of ACI more species of birds will be detected. A positive trend between the number of lianas and the bird species richness detected from the recordings was also observed (Figure. 6). However, this relationship was not significant ($F\ (1, 6) = 4.294$, $p = 0.083$, $R^2_{adj} = 0.32$). Some of the bird species recognized in the recordings included Thicket Tinamou (*Crypturellus cinnamomeus*), Crested Guan (*Penelope purpurascens*), Roadside Hawk (*Rupornis magnirostris*), Common Ground-Dove (*Columbina passerina*), Orange-fronted Parakeet (*Eupsittula canicularis*), Yellow-naped Parrot (*Amazona auropalliata*), Elegant Trogon (*Trogon elegans*), Barred

Antshrike (*Thamnophilus doliatus*), Northern Bentbill (*Oncostoma cinereigulare*), Long-tailed Manakin (*Chiroxiphia linearis*), Yellow-green Vireo (*Vireo flavoviridis*), White-throated Magpie-Jay (*Calocitta formosa*), Rufous-and-white Wren (*Thryophilus rufalbus*), Banded Wren (*Thryophilus pleurostictus*), Cabanis's Wren (*Cantorchilus modestus*), Long-billed Gnatwren (*Ramphocaenus melanurus*), Lesson's Motmot (*Momotus lessonii*), and Scrub Euphonia (*Euphonia affinis*).

3.4 Discussion and Conclusions

The Avian Acoustic Community Relationship with Liana Abundance and Forest Biophysical Properties

TDFs at the SRNP have recovered from a severe anthropogenic disturbance in the past, and high disturbance is key for the colonization and establishment of lianas (Michel et al., 2014). In this study, a broad range in the number of lianas was found in the intermediate forest sites. This finding allowed to evaluate how the avian acoustic community varied along a gradient of liana abundance.

Lianas abundance was positively related to the acoustic activity of TDF birds in this study, so an increase in liana abundance resulted in a more complex acoustic community than the one found in forest sites with fewer lianas. This suggests that lianas may provide important resources for birds. To refer back to the concept of direct resources that was discussed previously, lianas can provide birds with the structure for shelter in TDFs. The tangled stems that shape this shelter likely protect the birds from being seen and captured by predators during both the day and night. It is also likely that the lianas provide a structure for nesting and roosting (Michel et al., 2014), and there are reports of wrens in Costa Rica using lianas as roosting sites (Skutch, 1960). Lianas could also provide food in the form of fruits and flower nectar. However, this is not a reasonable explanation of the results presented here since this study was carried out during the wet season at the SRNP when the trees have no flowers or fruits.

When the indirect resources offered by lianas are considered, it is apparent that lianas provide an important source of food, such as arthropods that inhabit and/or use lianas (Michel et al., 2014). Research on seasonal forests in Panama has shown that the presence of lianas increases local arthropod diversity in canopies (Yanoviak, 2015). In these seasonal forests, about 150 species of beetles were associated with lianas and trees (Ødegaard, 2000), the abundance and diversity of hemipterans increased with the number of vines (Wolda, 1979), and ant species richness declined by 22% when lianas were removed from forests in an experiment (Yanoviak, 2015). Arthropods use lianas mostly for shelter, as a source of food, and for the physical connectivity that allows them to move through and between patches of vegetation (Michel et al., 2014; Yanoviak, 2015). Arthropods may be a significant indirect food source for birds at the SRNP since they are highly diverse and abundant (e.g., 13,000 species estimated) (Janzen, 1987). In addition, a literature review gathered information for 457 bird species in the Tropics and found that 150 species are known to use arthropods from lianas as their main food source (Michel et al., 2014).

Variation in the avian acoustic community was also explained by differences in the combination of the biophysical properties of each forest site (i.e., tree BA, CH, and PAI) and the number of lianas. The main goal of selecting TDFs from the intermediate successional stage was to control for similarities in the forest biophysical properties among forest sites. This allowed setting a range in liana abundance that could be used to assess its relationship with the avian community. The weights of these models were very low in comparison with those of the model that included only the number of lianas, suggesting that the forest biophysical properties had a limited influence on the diversity of the acoustic community.

Past research has shown the negative effect of liana abundance on reproduction by canopy trees in tropical forests. Not only do lianas affect the tree community composition, but they can also affect the species composition of the fauna using the forest (García León et al., 2017). However, a positive relationship was observed in this study, which suggests that birds may not use lianas as a direct food source but rather as a source of food and structural cover. This finding supports the prediction that as liana abundance increases in tropical dry forests, the avian acoustic community becomes more complex. Moreover, birds have a key role as flower-pollinators and seed dispersal agents in TDFs (Nassar et al., 2013), and they are particularly important in the SRNP since they are the main living seed dispersal agent (Hilje et al., 2015). This close relationship between lianas and birds appears to be critical in TDFs where lianas are becoming more abundant due to the level of forest disturbance (Michel et al., 2014) and where some bird species are endangered and/or restricted to this ecosystem (Gillespie et al., 2000).

Acoustic Complexity Index as an Estimator of Bird Species Richness

The positive relationship between the number of bird species detected in recordings and the ACI suggests that dry forests with higher ACI values also have higher bird species richness. A few studies have successfully validated ACI, including one that was carried out in the Boreal forest of Alaska where the ecosystem is less complex than in tropical forests (Buxton et al., 2016). This study found a significant relationship between the presence of three bird species (e.g. Varied Thrush (*Ixoreus naevius*), Pacific Wren (*Troglodytes pacificus*), and Ruby-crowned Kinglet (*Regulus calendula*)) on the recordings and ACI, highlighting the use of this index as an indicator of healthy forests. Other studies that were carried out in coral reefs showed a positive relationship between ACI and fish species richness (Bertucci et al., 2016), highlighting that both ACI and fish communities are more complex in coral reefs inside marine protected areas (Bertucci et al., 2016). This study was carried out in TDFs that foster a higher biodiversity than boreal forests and coral reefs (Janzen, 1988), and thus, validation of the utility of the ACI as a measure of avian diversity is a more challenging process due to the more complex acoustic community (Farina & James, 1988). Before this study, there were no other studies that either validate the ACI or use it to estimate species richness in tropical forests. Findings here show that ACI could be used as a reliable metric to estimate relative bird species richness in TDFs, which have a complex forest structure, and highly diverse floras and faunas (Janzen, 1988).

This study determined that: (i) as the number of lianas in the forest evaluated increased, so did the ACI, and (ii) that ACI is positively related to the bird species richness. Based on this, it was tested whether the number of lianas influences the bird species richness, and a positive relationship was observed. Although this trend was not statistically significant, it was close to the significance level of rejection ($p = 0.083$), so it cannot be concluded confidently that the number of lianas does not influence the bird species richness at the SRNP. A significant positive relationship between liana occurrence and bird species richness was previously observed in tropical rainforests in Borneo, but this study was carried out in selectively logged forests which were under a different disturbance regime than the forests evaluated in our study (Ansell et al., 2011). Finally, it was observed that bird species richness is reflected in the avian acoustic community at the SRNP. Since the acoustic community is obtained through ACI, it is suggested a pre-processing effort applied to selected recordings that have a low effect from wind and rain, and also in an effort to evaluate the relationship between the ACI and bird species richness for a case where the study goal is to use the avian acoustic community as a representation of the real bird species richness.

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3.6 Tables and Figures

Table 3.1 General Linear Models of ACI related to liana abundance and forest biophysical properties (BA = tree basal area, CH = canopy height, and PAI = plant area index). Models are ranked using Akaike's Information Criterion for a small sample size correction (AICc). ΔAICc = delta AIC, AICcw = Akaike weights, NULL = ACI model without any parameter, K = number of parameters used in each model.

Model Rank	AICc	ΔAICc	AICcw	K
number of lianas	75.82	0	0.6352	2
CH + number of lianas	79.70	3.889	0.0908	3
number of lianas + PAI	79.77	3.954	0.0879	3
BA + number of lianas	79.80	3.984	0.0866	3
NULL	81.62	5.804	0.0348	1
BA + CH + number of lianas	83.64	7.822	0.0127	4
CH + number of lianas + PAI	83.68	7.864	0.0124	4
BA + number of lianas + PAI	83.77	7.953	0.0119	4
PAI	84.11	8.291	0.0100	2

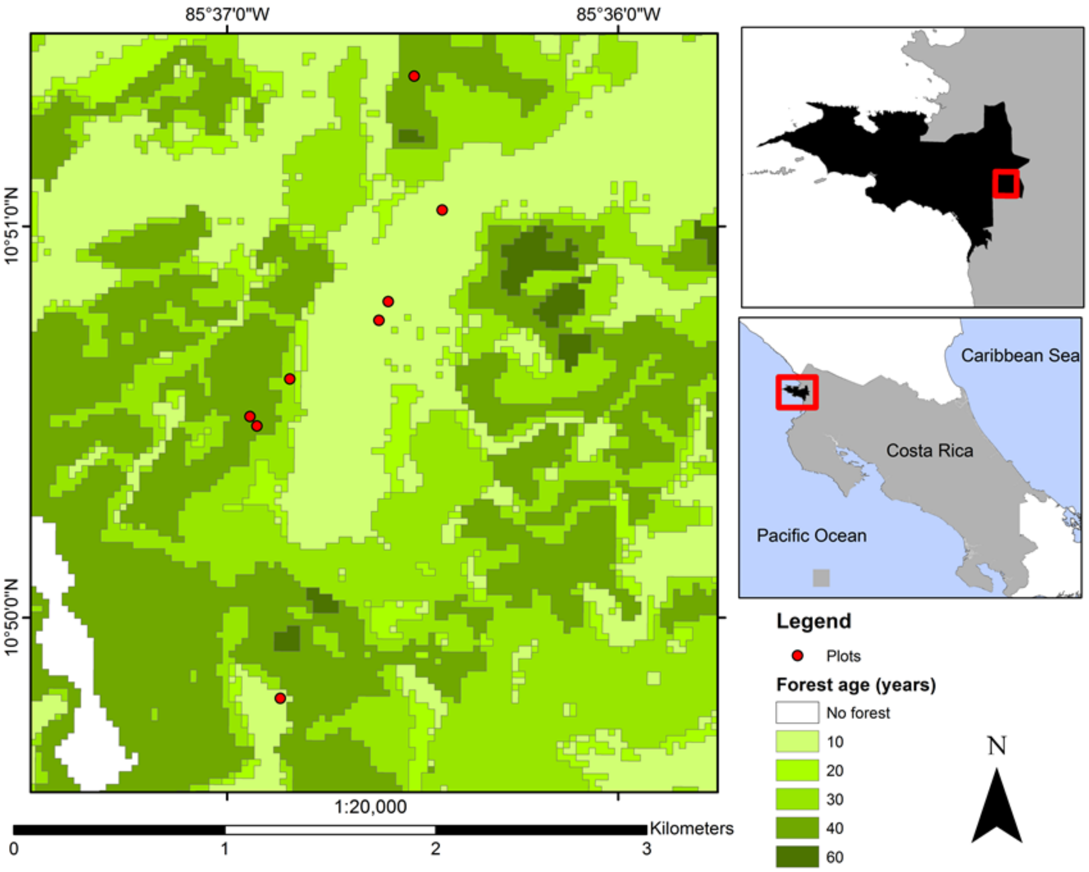


Figure 3.1 Location of the eight intermediate dry forest stages where radial plots were established at the Santa Rosa National Park, Guanacaste, Costa Rica (modified from Sánchez-Azofeifa et al. 2017).

Figure 3 2. Intermediate forest sites with few lianas (left) and forest sites with plenty of lianas (right).

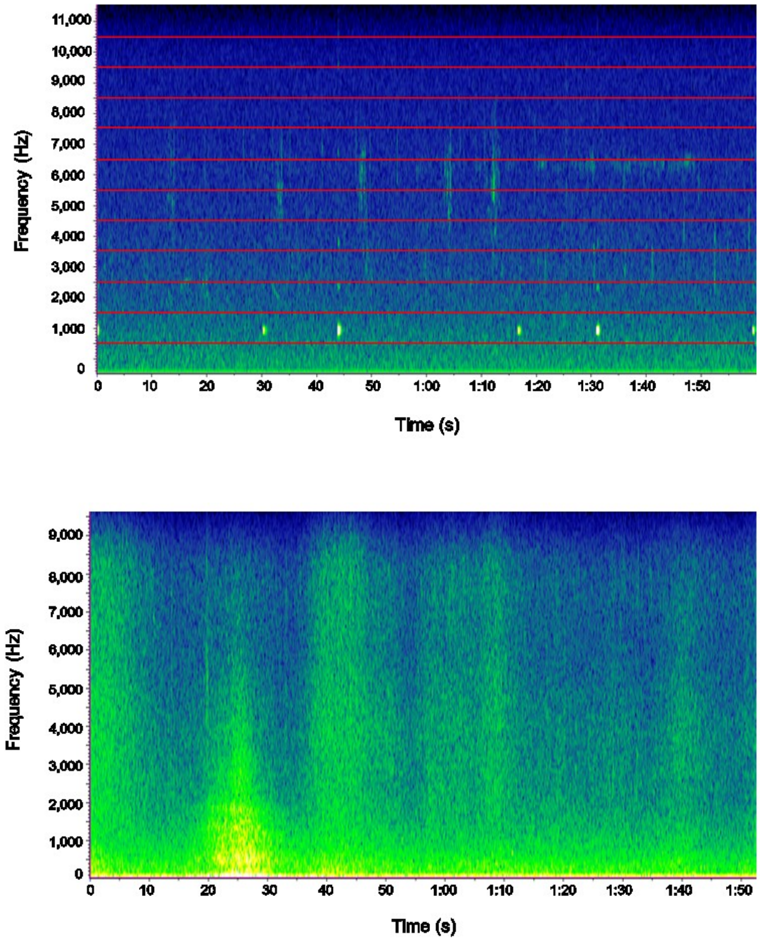


Figure 3.3 Spectrogram showing the frequency bins used by the acoustic complexity index (ACI) for the analysis (top), and spectrogram showing strong wind (39 km/h) covering all frequency bands (bottom).

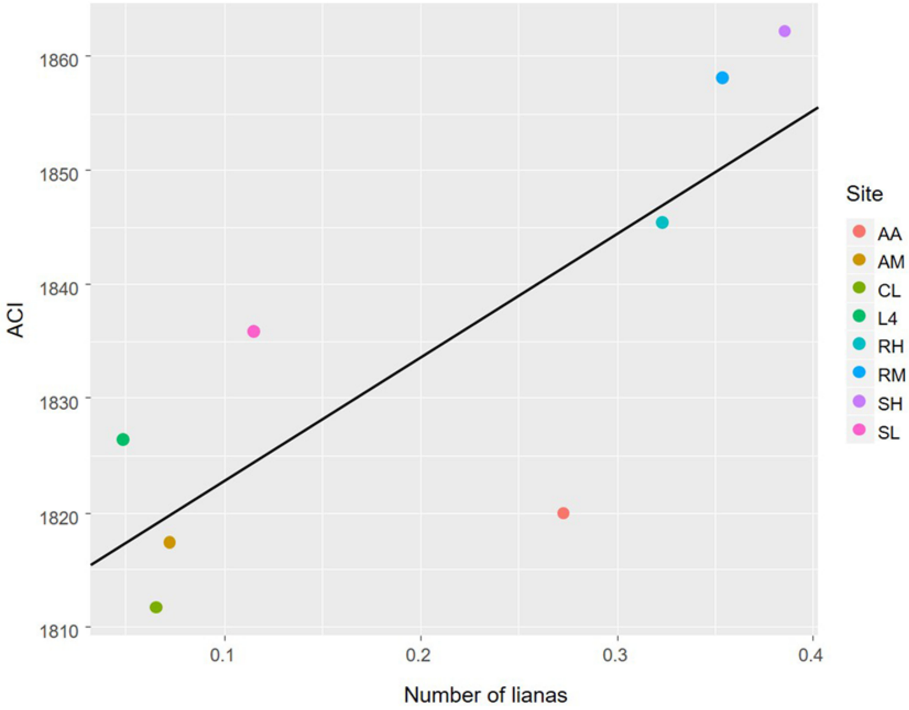
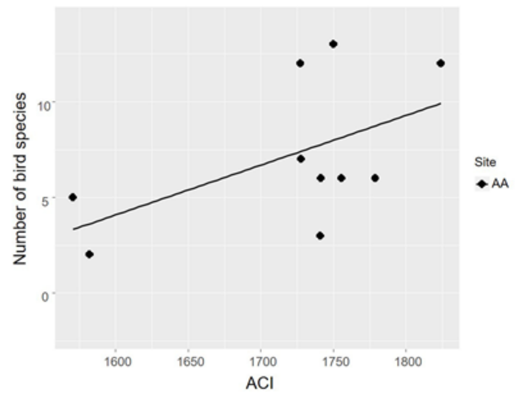
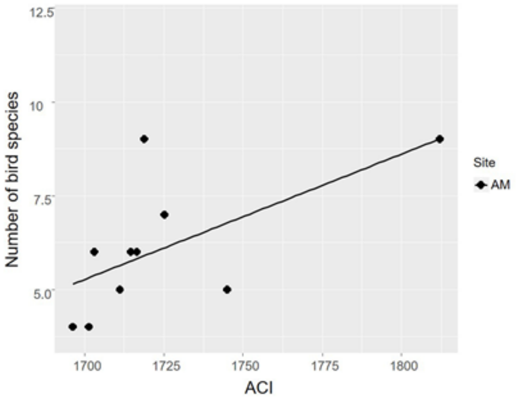
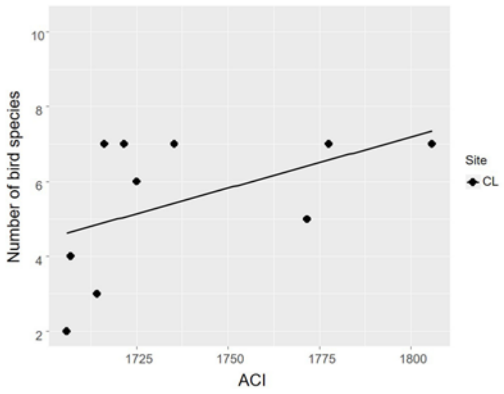
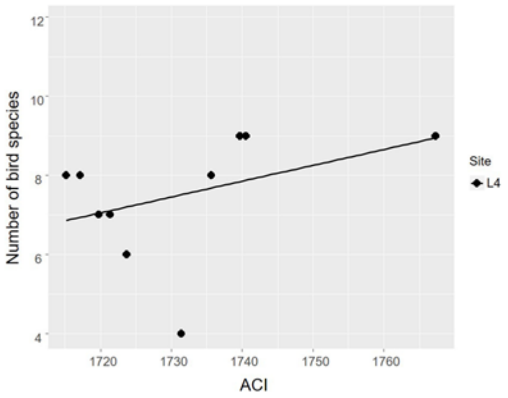


Figure 3.4 The relationship between the standardized number of lianas and the ACI values for different forest plots generated from the best model based on AICc values. The number of lianas explains 60% of the variation in ACI ($F_{(1,6)} = 11.44$, $p = 0.015$).


Number of bird species
10
5
0
1600
1650
1700
1750
1800
ACI
Site
AA


Number of bird species
12.5
10
7.5
5.0
1700
1725
1750
1775
1800
ACI
Site
AM


Number of bird species
10
8
6
4
2
1725
1750
1775
1800
ACI
Site
CL


Number of bird species
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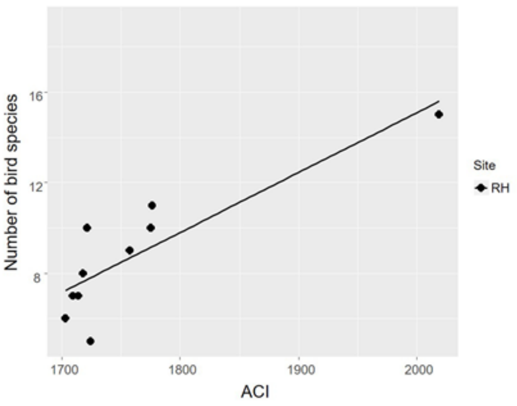
10
8
6
4
1720
1730
1740
1750
1760
ACI
Site
L4


Number of bird species
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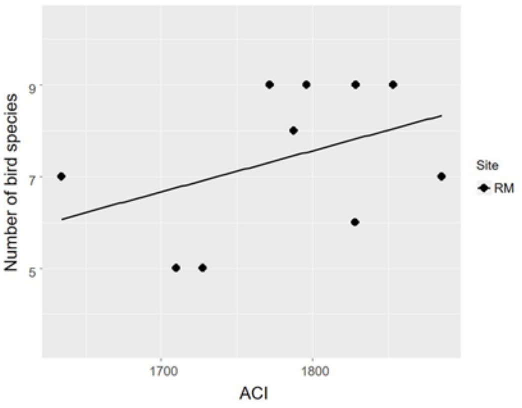
12
8
1700
1800
1900
2000
ACI
Site
RH


Number of bird species
9
7
5
1700
1800
ACI
Site
RM

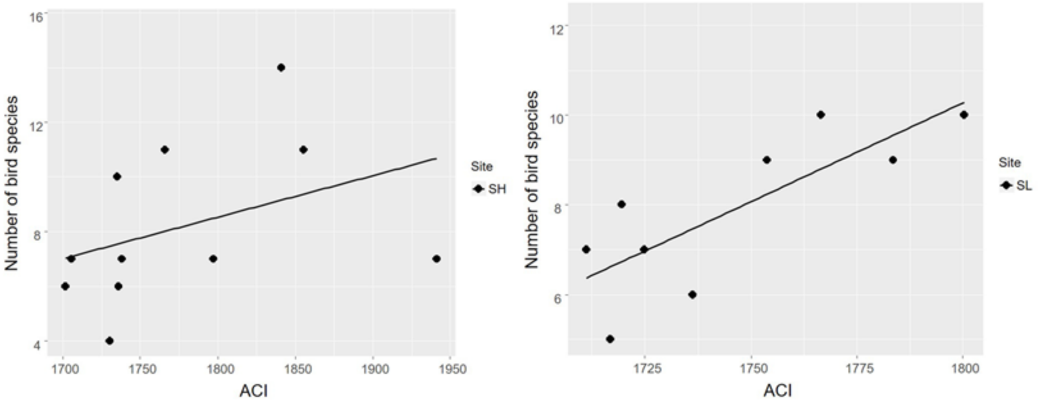


Figure 3.5 The relationship between the ACI values and the number of bird species detected in the first minute of ten recordings per forest site.

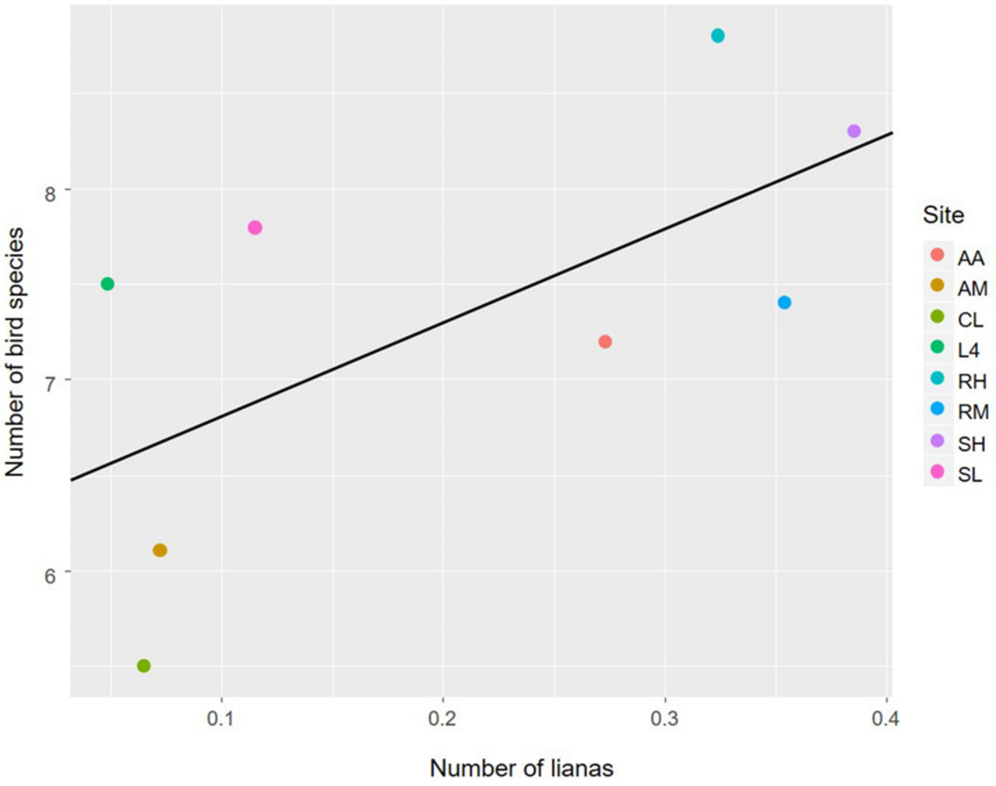


Figure 3.6 The relationship between the standardized number of lianas and bird species richness detected from recordings ($F_{(1, 6)} = 4.294$, $p = 0.083$, $R^2_{adj} = 0.32$).

4 Bird community response to the recovery of tropical dry forests in Costa Rica

4.1 Introduction

As of today, it is estimated that 60% of the world's tropical forests has been classified as degraded forests (ITTO, 2002). This degradation is mostly due to the effects of human activities such as logging, agriculture, and cattle ranching (Geist & Lambin, 2002). A similar pattern is observed in the tropical dry forests (TDFs) in the Neotropics that have seen 60% of their area converted to other land uses (Portillo-Quintero & Sánchez-Azofeifa, 2010). This process of environmental degradation has resulted in considerable reductions in biodiversity (Vié et al., 2009). Despite these trends, some countries like Costa Rica have experienced forest recovery as a result of changes in the country's economic and conservation policies (Sánchez-Azofeifa et al. 2007; Calvo-Alvarado et al., 2009). For example, TDFs in Costa Rica have recovered from cattle ranching over the past 45 years. Today, the TDF landscape is a mix of young and old forests of different ages (Janzen, 2002; Quesada & Stoner, 2004; Portillo-Quintero & Sánchez-Azofeifa, 2010). From this recovery, much is known about tree phenology (Lopezaraiza-Mikel et al., 2014), tree species composition (Kalacska et al., 2004; Hilje et al., 2015), pollination and dispersal syndromes (Hilje et al., 2015), and the structure of recovering dry forests of different ages (referred to here as forests in the early, intermediate, and late stages of recovery) (Kalacska et al., 2004). However, little is known about the relationship between the recovery of dry forests and the recovery of the fauna that inhabit them.

Faunal recovery has been studied in successional forests and results suggest that it is affected by factors such as the time elapsed since site abandonment, the age of the biome being studied, the nature of the surrounding environment, and the land use history of the area prior to abandonment and recovery. For example, a review by Dunn (2004) suggests that tropical forests that have been recovering for 20-40 years following abandonment can have similar ant and bird species richness to mature forests. This similarity is observed when fauna source populations are available nearby and when the intensity of the initial land clearance is relatively low. Osorio-Pérez et al. (2007) studying Puerto Rican forests found that the ant species composition was similar to that found in forests that had been recovering for 25-60 years since abandonment. Moreover, proximity and connectivity to forests have demonstrated to be important factors as a source of colonizing species (Gardner et al., 2007). These factors allowed for successional forests to recover to the point where amphibian species richness and composition are similar to those in older forests (Gardner et al., 2007; Ríos-López & Aide, 2007; Herrera-Montes & Brokaw, 2010; Hilje & Aide, 2012). The species richness of bats and other mammals can be quite similar in primary and secondary tropical forests (Barlow et al., 2007).

Bird species richness is usually higher in primary tropical forests, followed by secondary forests and then plantations (Andrade & Rubio-Togler, 1994; Barlow et al., 2007). The type of human disturbance and the amount of woody vegetation that remains after the disturbance influence the composition of bird communities in early successional forests (Warkentin et al., 1995; Borges & Stouffer, 1999). Still, most of the research into bird species richness and community composition in successional tropical forests has been carried out in wet forests, with little work in TDFs that hold high bird diversity. As an example, a total of 635 bird species have been reported to use TDFs in the Neotropics, of which 300 use the dry forest as their primary habitat, 173 species are endemic to it, and 109 species are migratory (Stotz et al., 1996; Hutto 1986). Yet, there is limited information on the changes in species richness and community composition that occur during dry forest succession following the abandonment of a different type of land use.

In general, forest structure recovers gradually during succession, which means that forests of different ages will have different structures (Finegan, 1996). Typically, young forests will have lower values of tree basal area (BA), higher density of stems, more open canopies, even canopy heights, and will lack tall trees (Aide et al., 1996; Clark, 1996; Guariguata et al., 1997; Montgomery & Chazdon, 2001). In contrast, when forests become older, they contain large trees (e.g. as defined by a higher BA), a lower density of stems, closed canopies, variable canopy heights, and tall trees (Aide et al., 1996; Clark, 1996; Guariguata et al., 1997; Montgomery & Chazdon, 2001). Consequently, the variation in forest structure observed across a forest succession can affect the richness and composition of the forest fauna (Wiens, 1989).

For birds, vegetation structure has been observed to be an important predictor of bird species richness and diversity (Macarthur & Macarthur, 1961; Karr & Roth, 1971; Wiens & Rotenberry, 1981; Thiollay, 1990; Poulsen, 2002) and, in general, forests with higher proportion of foliage at different heights will have more species of birds, and higher species diversity than forests with lower foliage height diversity (Macarthur & Macarthur, 1961; Wiens & Rotenberry, 1981; Thiollay, 1990). Moreover, since older forests have a greater structural complexity than young successional stages (Bu et al., 2014) they provide a greater availability of sites for nesting (Thompson et al., 1995), perching and roosting (Mcclanahan & Wolfe, 1993; Barlow et al., 2007), better protection from predators (Michel et al., 2014), more stable microclimatic environments (e.g. temperature and relative humidity) due to canopy closure (Muscolo et al., 2014; Fetcher et al., 1985; Laurance & Bierregard, 1997) and greater food availability (e.g. arthropods) (Kato et al., 1995).

Previous research into bird communities in successional dry forests in Mexico, Venezuela, and Brazil found that the greatest richness of fruit-eating birds was observed in the early successional stages from 3-5 years old (Nassar et al., 2013). This was explained by the high complexity of the vegetation in this stage in Venezuela, in contrast, in Mexico and Brazil, it was related to the availability of particular resources (e.g. insects, seeds, and fruits) that were present in early stage forests (Nassar et al., 2013). Another study for TDFs in Mexico found the highest species richness in the late-successional forests, while the early and intermediate successional forests had the most similar bird communities (Smith et al., 2001). Although forest structural characteristics are commonly used to classify successional forests, they have rarely been used to evaluate bird species assemblages and community composition in TDFs. In another successional TDF in Brazil, the species richness of bird flocks in young forests was lower than in late stage forests (Maldonado-Coelho & Marini, 2000). However, none of these studies explored the relationship between bird species composition and the structural characteristics of successional forests. These studies also focused on particular species and/or functional groups and did not evaluate the whole bird community.

In this context, the three main objectives of this study are: 1. to compare bird species richness and community composition in forests of different ages (e.g. 20, 30, 40, and 60 years old), 2. to establish the relationship between bird species richness, community composition, and forest structural characteristics, and 3. to determine the association between selected dry forest-dependent bird species and the structural characteristics of the forest. This study was conducted using autonomous recording units (ARUs) and remote sensing techniques to estimate bird species richness and community composition in successional forests. Based on the literature available, a higher bird species richness is expected in forests with intermediate stages (e.g. 40 years old) since these forests will have a mix of bird species that are primarily found in the early and late stage. Also, the biggest difference in bird community composition is expected between the early (20 years) and late forest ages (60 years) as the early stages will have the least complex forest structure (e.g. more open and shorter canopies, lower values for plant and vegetation greenness indices, thinner trees, and fewer lianas).

4.2 Methods

Study site

This study was carried out at the largest protected dry forest in Central America, namely the Santa Rosa National Park Environmental Monitoring Super Site (SRNP-EMSS) located in the province of Guanacaste, Costa Rica (10°48’53” N, 85°36’54” W) (Figure 1). The SRNP-EMSS covers an area of 390 km^2, and the climate has a dry season of six months (December-May) with a mean annual precipitation of

1,700 mm and a mean annual temperature of 25° C (Kalacska et al., 2004). The SRNP-EMSS current land cover is a mixture of forest successional stages that recovered from intense deforestation in the past 200 years due to human activities such as pasturelands for cattle ranching (Janzen, 1988a; Li et al., 2017). Current secondary forests are dominated by insect-pollinated and wind-dispersed tree species (Hilje et al., 2015). The SRNP-EMSS has a very heterogeneous forest that holds a high diversity of habitats and biotic communities (Janzen, 1983; Arroyo-Mora et al., 2005; Sánchez-Azofeifa et al., 2005).

Measurements of Dry Forest structural characteristics

Sixteen forest sites at different ages of successional recovery were selected. Forests were categorized in age classes of 20 (four sites), 30 (four sites), 40 (five sites), and 60 (three sites) years old on the basis of the date on which they were detected in aerial photographs and satellite images (Sánchez-Azofeifa et al., 2017). The minimum distance between two sites was 250 m and the maximum distance was 6,000 m (Figure 1). Forest sites were also characterized using forest structural characteristics measured in standardized 0.1 ha radial plot in each site based on Gentry's dataset (Phillips & Miller, 2002; Sánchez-Azofeifa et al. 2017). These included the percentage of canopy openness (CO) extracted from hemispherical photos; the plant area index (PAI) which is the area of foliage and wood (e.g. stems, twigs, lianas) present in a hemispherical photo; canopy height (CH) measured with a terrestrial laser scanner; tree basal area (BA) calculated from measurements of tree diameter at breast height (DBH) for all the trees observed in each plot (> 5 cm of DBH); and the liana-to-tree ratio (LR) (e.g. the total number of lianas in a site divided by the total number of trees) (see Table 1 for forest structural characteristics values used). A vegetation greenness index was used to collect information on the presence of green leaves on trees for each site (e.g. the Normalized Difference Vegetation Index (NDVI)). NDVI values were extracted from satellite images from MODIS collection 6 MOD13Q1 and MYD13Q1 from the Aqua (AM collection) and Terra (PM collection) instruments, respectively, which overpassed the SRNP-EMSS (ORNL DAAC, 2017). The spatial resolution for NDVI product is 250 m. NDVI values were collected in each site encompassed in a unique pixel for the same dates where the acoustic data collection was carried out.

Bird acoustic data collection and analysis

Autonomous recording units (ARUs) (SM3 Songmeters, Wildlife Acoustics Inc., 2011) were used for bird sound data collection. An ARU was deployed in each site for three consecutive days in May 2017, which is during the breeding period for most TDF bird species (Barrantes et al., 2016). Migrant species from North America are not expected in recordings by this time of the year. ARUs recorded for one full minute every 10 minutes during the peak period of avian acoustic activity at the SRNP-EMSS (0530-0630h) (Hilje et al., 2017). The file format used for recording was “wav” at 16 bits per file, with a minimum noise gain of -88 decibels (dB), and a sampling rate of 19.2 kHz. Recordings from 0530-0630h were selected for three days and listened to in order to determine the species present at each site. The software Songscope (Wildlife Acoustics Inc., 2011) was used for both aural and sound bird species identification from spectrograms. A total of approximately 22 recordings per site and 350 minutes in total were analyzed for the whole study area.

Statistical analysis

A Linear Discriminant Analysis (LDA) was performed to determine which forest structural characteristics best describe forest sites based on age classes (Izenman, 2013). A Multivariate Analysis of Variance (MANOVA) (Bray et al., 1985) was subsequently performed to determine differences in forest structural characteristics between the age classes. Both analyses were performed using the R package MASS (Venables & Ripley, 2002) in R version 3.4.3 (R-Core Team, 2018).

It was not possible to determine the recording radius for each ARU in the sites. This radius can be affected by sound attenuation and propagation related to forest structural characteristics (Charchuk & Bayne, 2018). To control for this, a rarified species richness estimation analysis was performed. This analysis assumes that each site sampled the same number of individual birds when assessing richness (Gotelli & Colwell, 2001; Charchuk & Bayne, 2018). The function *rarefy* from the *vegan* package in R was used for this analysis, taking a subsample size equal to the average species richness detected from recordings for all the sites (i.e. 31 species) (Oksanen et al., 2018). An Analysis of Variance (ANOVA) was performed to compare rarified species richness among age classes using each site as a replicate (Shahbaba, 2012).

The Indicator Value (IndVal) analysis was used to determine bird species-habitat associations for the different forest age categories (Dufrene & Legendre, 1997). This analysis compares the relative abundances and commonness of individual bird species detected from recordings among different forest ages. Since it was not possible to identify individuals from recordings, an abundance of one was used when the species was detected in recordings from day one. Therefore, abundances of two and three were used if a species was detected during two or three days in a site, respectively. As an example, there were four sites in forests of 20 years old where recordings for three consecutive days were collected in each site, so, if the species was detected every day in every site, its abundance would be 12. An abundance of

12 would be the maximum abundance for a species in this forest age. However, the IndVal analysis corrects for the number of sites per forest age in the case of forest ages of 40 and 60 years old which have five and three sites, respectively. A permutation test with 1,000 iterations was performed to obtain a p-value for each species-habitat association (De Caceres & Legendre, 2009; Roberts & Roberts, 2016). In addition, the relative indicator values were calculated to determine which species were preferentially utilizing the sites as a function of age. The R packages *indicspecies* was used for the IndVal analysis and *labdsv* for the relative abundance analysis (De Caceres & Legendre, 2009; Roberts & Roberts, 2016).

A meta multi-dimensional scaling (metaMDS) was performed to compare species assemblages in forests with different ages (Oksanen et al., 2018). For this, a dissimilarity matrix was generated using the Bray-Curtis index based on the number of recording files where the species were detected at each site. The optimal settings were established to be a 3-dimensional ordination at 500 iterations. The R packages *ecodist* and *vegan* were used for this (Goslee & Urban, 2007; Oksanen et al., 2018). A Multiple Response Permutation Procedure (MRPP) was used to test for differences in species composition between forest stages (Mielke, 1991). Using the R package *vegan,* 1000 permutations were calculated to establish exact p-values (Oksanen et al., 2018).

A Linear Mixed Model analysis (LMM) was performed to evaluate the relationship between forest structural characteristics (e.g., BA, PAI, CO, CH, LR, and NDVI) and bird species richness (Bates et al., 2014). The lme4 package in R was used for the analysis (Bates et al., 2014). An indirect gradient analysis using a non-metric multidimensional scaling (NMDS) was performed to determine the relationship between bird species composition and gradients in forest structural characteristics (e.g. CO, LAI, CH, BA, LR, and NDVI) for the 16 sites (Goslee & Urban, 2007). The forest structural characteristics were used as the independent variables and bird species frequencies as the dependent variable. A dissimilarity matrix using the Bray-Curtis index was generated based on the number of recordings in which a species was detected at each site. The R package *ecodist* was used for this analysis (Goslee & Urban, 2007).

Eleven bird species with distribution ranges restricted to dry forests were selected based on Stiles & Skutch, (1989), and information about the functional group of each species (e.g. frugivore, insectivore, or omnivore) was added according to Neotropical Birds 2018 (Table 2). The level of forest dependency was also included by grouping species in three categories: 1 = species that live and reproduce in extensive mature forest; 2 = species that require habitats with 40–50% of forest cover; 3 = species that inhabit open areas (Stiles & Skutch, 1989; Barrantes et al., 2016). A non-metric multidimensional scaling (NMDS) was performed to assess forest-dependent bird species composition among forests with different forest structural characteristics (e.g. CO, LAI, CH, BA, LR, and NDVI) (Goslee & Urban, 2007). For this, a dissimilarity matrix was generated using the Bray–Curtis index based on the number of recordings in which a species was detected at each site. The R package *ecodist* was used for this analysis (Goslee & Urban, 2007). Due to sample size constraints (i.e. 16 sites categorized in four age classes), a p-value of 0.1 of significance was used instead 0.05 to detect an effect from all the statistical analyses described above. The power of the analysis is determined by the number of groups (e.g. four age classes), the number of observations per group (e.g. four sites per age class), the effect size (e.g. the difference between two groups), and the significance level (e.g. Type I error probability) (Cohen, 1988). Therefore, by using a p-value of 0.1 both the power of the analysis and the probability of rejecting the Null hypothesis when is false is increased.

4.3 Results

Dry forest structural characteristics and forest age

Results from the LDA showed a trend in forest structure where forests from 20 years of age had a higher percentage of canopy openness, while forests from 60 years of age had closed canopies with higher values of NDVI and PAI (Figure 2). However, these age-dependent differences in forest structural characteristics are not significant ($F_{(3,12)} = 0.571$, $p > 0.1$). This suggests that the forest ages classes evaluated were not completely distinct and had a similarity in forest structural characteristics. From the LDA, the first axis explains 74.5 % of the total variance between forest ages for the structural characteristics evaluated, while the second axis explains 21.5 %.

Bird species richness and forest age and structural characteristics

A total of 65 species of birds was detected in the recordings from all the sites, with a range of 20-35 species at each site. From this total, 37 passerine species were detected, corresponding to 71 % of the species reported for the SRNP-EMSS forests (e.g. 52 species) (Stiles & Skutch, 1989; Barrantes et al., 2016). The species *Thryothorus pleurostictus* (Banded Wren), *Trogon elegans* (Elegant Trogon), and *Leptotila verreauxi* (White-tipped Dove) were detected in all the sites during the three days of sampling, while 13 species were detected in one or two sites in only one day of sampling. Based on this, only 52 species were included in the analysis (Table 3). There was a trend in rarified species richness where forests from 60 years of age had the highest richness, while forests from 30 years had the lowest (Figure 3). However, differences in species richness between age classes were not significant ($F_{(3,\ 12)} = 2.356$, $p = 0.1$). When evaluating species richness at a finer scale by regressing forest structural characteristics (e.g., BA, PAI, CO, CH, LR, and NDVI) against bird richness for each site using LMM, none of the characteristics explained bird species richness ($p > 0.1$).

Bird indicator species and forest age

From the 52 species evaluated using the indicator species analysis, two species were identified as significant indicators of a forest stage of 60 years old (e.g. *Ramphocaenus melanurus* (Long-billed Gnatwren) and *Pitangus sulphuratus* (Great Kiskadee)), one species as a significant indicator of forests of 40 years old (e.g. *Campephilus guatemalensis* (Pale-billed Woodpecker)), one species as an indicator of 30 years old forests (e.g. *Dendroica petechia* (Yellow Warbler)), and one species as an indicator of forest between 20 and 60 years old (e.g. *Penelope purpurascens* (Crested Guan)) (Table 3).

Bird community, forest age and forest structural characteristics

The four forest age classes had similar bird communities, and the communities of all stages overlapped in the metaMDS analysis ($F_{(3,\ 12)} = 0.805$, $p > 0.1$) (Figure 4). The NMDS for bird communities and forest structural characteristics showed that some species such as *Piaya cayana* (Squirrel Cuckoo), *Amazona albifrons* (White-fronted Parrot), *Polioptila albiloris* (White-lored Gnatcatcher), *Myiarchus tuberculifer* (Dusky-capped Flycatcher), *Euphonia affinis* (Scrub Euphonia), and *Attila spadiceus* (Bright-rumped Attila) were associated with forests with open canopies (Figure 5). On the other hand, *Polioptila plumbea* (Tropical Gnatcatcher) and *Thryothorus rufalbus* (Rufous-and-white Wren) are associated with forests with closed canopies and high PAI (Figure 5). The species *Archilochus colubris* (Ruby-throated Hummingbird), *Vireo flavoviridis* (Yellow-green Vireo), *Thamnophilus doliatus* (Barred Antshrike), and *Trogon elegans* (Elegant Trogon) were associated with forests with larger trees (e.g. BA). The number of lianas in forests is important for *Arremonops rufivirgatus* (Olive Sparrow), *Campylorhynchus rufinucha* (Rufous-naped Wren), *Penelope purpurascens* (Crested Guan), *Turdus grayi* (Clay-colored Thrush), *Dendroica petechia* (Yellow Warbler), and *Momotus lessonii* (Lesson's Motmot).

Forest-dependent bird species and forest structural characteristics

Of the eleven dry forest-dependent bird species selected, two species live and reproduce in mature forests, eight species require habitats with 40-50 % of forest cover, and one species inhabits open areas (Table 2). Regarding the functional groups, there were five insectivores, three frugivores, and three omnivores observed (Table 2). From the NMDS, there was not a clear association observed between forest-dependency categories or functional group, and forest structural characteristics for the eleven forest-dependent species. However, there were clear associations between some of the species and forest structural characteristics. For example, *Thryothorus pleurostictus* (Banded Wren), *Campylorhynchus rufinucha* (Rufous-naped Wren), and *Arremonops rufivirgatus* (Olive Sparrow) were associated with forests with a high number of lianas (Figure 6). The species *Myiarchus tyrannulus* (Brown-crested Flycatcher) was associated with forests with closed canopies; *Chiroxiphia linearis* (Long-tailed Manakin) and *Aratinga canicularis* (Orange-fronted Parakeet) were associated with forests with high values of PAI; *Amazona auropalliata* (Yellow-naped Parrot) was associated with forests with taller canopies, and *Trogon elegans* (Elegant Trogon) was associated with forests with higher BA. The species *Trogon melanocephalus* (Black-headed Trogon), *Eumomota superciliosa* (Turquoise-browed Motmot), and *Crypturellus cinnamomeus* (Thicket Tinamou) did not show any association with any of the forest structural characteristics evaluated (Figure 6).

4.4 Discussion

Dry forest structural characteristics and forest ages

Similar values of forest structural characteristics were found among the different forest age classes, indicating high variation in structure within forests of a given age (Figure 2). Similarities in forest structure among forests age classes can be explained by two possible reasons. First, forests regeneration processes at the SRNP-EMSS are not a deterministic phenomenon, and they showed a continuous stochastic phenomenon instead (Li et al., 2017). As a result, a smooth transition is observed between age classes in a successional gradient. Even so, young forest age class of 20-year-old forests tend to have a high percentage of canopy openness, and the oldest age class of 60 years tend to have closed canopies and high values of NDVI and PAI (Figure 2). Second, tree phenology and the presence of leaves on trees. Forests at the SRNP-EMSS are semi-deciduous and deciduousness decreases when forests become old across a succession. For example, the presence of deciduous trees species is very high in early stages and it decreases in intermediate and late stages, where evergreen tree species are dominant (Kalacska et al., 2004). Since this study was conducted during the peak of leafing intensity where trees have full leaves at the SRNP-EMSS (Lopezaraiza-Mikel et al., 2013), values of PAI and NDVI were high. Consequently, clearer differences in PAI and NDVI values among forest classes are not noticeable during this time of the year as they are observed during the peak of deciduousness, particularly between young and old age classes.

Bird species richness, forest age, and structural characteristics

Forests at intermediate age of recovery (e.g. 40 years old) were expected to have higher bird species richness, but similar species richness was found among all forest age classes. It was expected that forests of this age would have a combination of forest structural characteristics intermediate between those of early and late stage forests and that they would support more species. Instead, results showed that the four age classes are similar in structure. Since forest age classes cannot be classified according to forest structure, bird species presumably obtain similar resources from forests of different age; as a result, the differently aged forests have similar species richness.

When analyzing species richness at a finer scale by looking for specific relationships between species richness and forest structure, a relationship between structure and species richness was not established. This indicates that forests of all the age classes may have achieved a structure that allows them to support similar bird species richness. Forests of the age classes considered here appear to have a structure similar to that of the intermediate and late stages reported for the SRNP-EMSS, and forests of these stages harbor a high diversity of tree species (Kalacska et al., 2004; Hilje et al., 2015). Both forest structure and diversity of tree species seem to be important in determining bird species richness.

Three bird species were found in forests of each age class and these were very common within forests of each age. This confirms that all the sites provide highly suitable habitats for these generalist species by providing valuable resources. Since *Thryothorus pleurostictus* (Banded Wren) is a particularly territorial species, this means that it is actively defending places against intruders in all the study sites (Stiles & Skutch, 1989). The species *Trogon elegans* (Elegant Trogon) is an omnivorous species that inhabits forests with a suitable canopy cover (like the forests studied; Williams, 2011). The species *Leptotila verreauxi* (White-tipped Dove) is an omnivore that forages mostly on the forest floor (Stiles & Skutch, 1989).

Bird indicator species and forest age

The bird species identified in this study do not appear to prefer forests of any particular age class. These species can apparently obtain resources such as food, perches, and nesting sites from forests of all ages. This can be explained by both the proximity to and the transition observed between ages classes at the SRNP-EMSS (Li et al., 2017). As a result, age classes are not strictly isolated from each other, and bird species can move between forests of all ages where they can perch and search for food.

A few indicator species were observed. For example, *Ramphocaenus melanurus* (Long-billed Gnatwren), was very common in 60-year-old forests. Such forests could offer more prey for this strictly insectivorous species (Stiles & Skutch, 1989; Neotropical Birds, 2018). Although the *Pitangus sulphuratus* (Great Kiskadee) was an indicator of 60-year-old forests, this species cannot be considered as a resident of old forests. This species was also detected in a few sites that have open canopies and tall trees. This is an ideal habitat for perching and looking for insects and small vertebrates as food (Stiles &

Skutch, 1989). Sixty-year-old forests could provide ideal habitats with such a structure. The species *Campephilus guatemalensis* (Pale-billed Woodpecker) is a forest dweller that preys on wood-boring beetles and their larvae (Stiles & Skutch, 1989; Winkler & Christie, 2002). Forty-year-old forests could contain specific tree species that offer this food source. The species *Dendroica petechia* (Yellow Warbler) is an indicator of 30-year-old forests, suggesting that such forests may contain more areas of semi-open habitat where this species can look for insects on vegetation (Stiles & Skutch, 1989). The species *Penelope purpurascens* (Crested Guan) is a primarily frugivorous species that specializes on the fruits of certain species of trees such as *Spondias mombin* (Stiles & Skutch 1989; Gilbert & Schulenberg, 2013). Forests ranging from 20 to 60 years old could house individuals and patches of these tree species.

Bird community, forest age and forest structural characteristics

The bird community was similar among forests of different ages, indicating that no specific forest age class hosts a particular community of birds. Although noticeable differences in bird communities between forests 20 and 60 years old were expected due to bird species specialized in forests of low and high complexity, respectively, the results did not show that. Finding similar bird communities in the different age classes supports the idea that forests cannot be categorized on the basis of their structural characteristics when dealing with birds due to high variation in structure within ages. Also, this finding suggests that young forests of 20 years old have reached similar species composition to 60-year-old forests at the SRNP-EMSS. This can be explained by both the proximity to and the transition between ages classes that allow birds to move easily between forest patches to look for different resources (e.g. perches, nesting sites, and food) (Sekercioglu et al., 2002; Li et al., 2017). Even though some species were associated with forests of a specific age, it is difficult to determine whether there is a real preference for these since forests of different age have such similar structures that vary significantly within and between forests of the same age.

However, when analyzing species associations at a finer scale using forest structural characteristics some species were associated with open habitats. While some species like *Piaya cayana* (Squirrel Cuckoo) and *Amazona albifrons* (White-fronted Parrot) inhabit open areas within semi-deciduous and deciduous forests (Stiles & Skutch, 1989; Neotropical Birds, 2018), other species like *Polioptila albiloris* (White-lored Gnatcatcher), *Myiarchus tuberculifer* (Dusky-capped Flycatcher), *Euphonia affinis* (Scrub Euphonia), and *Attila spadiceus* (Bright-rumped Attila) use open habitats to actively or steadily look for food (e.g. insects and arthropods) (Stiles & Skutch, 1989; Neotropical Birds, 2018). Strictly insectivorous species such as *Polioptila plumbea* (Tropical Gnatcatcher) and *Thryothorus rufalbus* (Rufous-and-white Wren) are associated with forests with closed canopies and a high density of leaves, in which they feed on insects found on the vegetation (Stiles & Skutch, 1989; Neotropical Birds, 2018). Other species are associated with forests with larger trees (e.g. BA), but it is not clear whether this is related to habitat preferences or to a preference for specific food resources obtainable from sites with larger trees (e.g. *Archilochus colubris* (Ruby-throated Hummingbird): nectarivore, *Vireo flavoviridis* (Yellow-green Vireo), and *Thamnophilus doliatus* (Barred Antshrike): insectivores, and *Trogon elegans* (Elegant Trogon): omnivore) (Stiles & Skutch 1989; Neotropical Birds, 2018).

In addition, some species are associated with forests containing a higher number of lianas, but they are using the lianas differently. The species *Campylorhynchus rufinucha* (Rufous-naped Wren) and *Dendroica petechia* (Mangrove Warbler) are insectivores that complement their diets with nectar from flowers from a specific liana species (e.g. *Combretum farinosum*) (Schemske, 1980). Both could be looking for sites where this liana is present. There are no previous reports of the species *Arremonops rufivirgatus* (Olive Sparrow), *Penelope purpurascens* (Crested Guan), *Turdus grayi* (Clay-colored Thrush), and *Momotus lessonii* (Lesson's Motmot) associated with forests with lianas. However, these species could be benefiting from food, nesting and roosting perches, protection from predators, movement, and song or display perches provided by the 15 species of lianas reported for the SRNP-EMSS (Michel et al., 2014; Gillespie et al., 2000). This bird-liana association is very important in dry forests, where liana abundance is increasing due to both anthropogenic factors (e.g. logging) and natural disturbances (e.g. tree fall gaps) (Wright et al., 2004; Schnitzer & Bongers, 2011), and because lianas may also thrive during seasonal drought at the SRNP-EMSS (Kalacska et al., 2005).

Forest-dependent bird species and forest structural characteristics

The categories of forest dependency are not related to any specific structural characteristic of the forest. This indicates that species that need 40-50 % of forest cover are not associated with any forest structural characteristic. A similar pattern was found for other forest dependency categories. Regarding functional groups, associations between insectivores, frugivores or omnivores could not establish with any of the forest structural characteristics. These findings suggest that each species is using specific and different structural resources from the dry forests.

As a result, associations with specific forest structural characteristics become more obvious when each species is considered separately. For example, the species *Thryothorus pleurostictus* (Banded Wren), *Campylorhynchus rufinucha* (Rufous-naped Wren), and *Arremonops rufivirgatus* (Olive Sparrow) are associated with forests with a higher number of lianas, suggesting that they can obtain resources directly from lianas (such as food (e.g. nectar), structure for shelter, nesting and roosting, protection from predators provided by tangled stems, and dormitory sites in the case of the wrens (Michel et al., 2014; Skutch, 1960). The presence of lianas also increases arthropod diversity in seasonal forests (Yanoviak, 2015), and there is a high diversity of arthropods at the SRNP-EMSS (e.g. 13,000 species, Janzen, 1987). Thus, insectivorous species could obtain arthropods as a food source from lianas.

The species *Chiroxiphia linearis* (Long-tailed Manakin) and *Aratinga canicularis* (Orange-fronted Parakeet) were associated with forests with high values of PAI. *Chiroxiphia linearis* prefers forests with shaded understories where they used branches for elaborate courtship displays (Stiles & Skutch, 1989). Higher values of PAI found in forests could be related to the presence of suitable branches for display. *Aratinga canicularis* could select forest patches with a specific tree species composition as a source of food, and these patches can have higher values of PAI. Not surprisingly, the species *Amazona auropalliata* (Yellow-naped Parrot) and *Trogon elegans* (Elegant Trogon) are associated with forests with taller canopies. The parrot is reported to perch in tall trees where it feeds on fruits and seeds (Stiles & Skutch, 1989), while the trogon inhabits dense and tall dry forests (Stiles & Skutch, 1989).

4.5 Conclusions

Tropical dry forests with different recovery times since the abandonment of cattle ranching support similar bird species richness and communities. Twenty-year-old forests provide equally suitable habitat for birds as 60 year old forests, suggesting a rapid recovery of bird species composition at the SRNP-EMSS. The structural characteristics of the forests are similar across all forest ages, suggesting that forests of all ages are an important source of perches for roosting and mating displays, material for nesting, and a direct or indirect source of food. These results suggest that similarity of forest age classes is critical to achieving similar species richness and community composition. This is an important finding to consider in bird conservation efforts for both the Guanacaste region and other neotropical dry forests. Associations at a fine scale were found between certain bird species that are resident in tropical dry forests and forest structural characteristics. This information is valuable for understanding the presence, abundance, and distribution of these species in dry forests and for anticipating how these will respond to changes in forest structure that can be expected to occur as the forests become older through a natural recovery process.

4.6 References

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4.7 Tables and Figures

Table 4.1 Forest structural characteristics recorded for the sites used by Sánchez-Azofeifa et al. 2017. CO: the percentage of canopy openness, PAI: plant area index, CH: canopy height, BA: tree basal area, LR: the liana-to-tree ratio, and the Normalized Difference Vegetation Index (NDVI)

Forest age	CO (%)	PAI	CH (m)	BA (m^2)	LR	NDVI
20 years	8.26 - 20.23	2.02 - 2.7	10.6 - 18.5	6 - 33.1	0 - 0.083	0.800 - 0.857
30 years	7.71 - 24.27	1.38 - 2.96	11.7 - 25.3	12.6 - 38.3	0.017 - 0.336	0.816 - 0.869
40 years	7.18 - 23.64	1.36 - 3.21	18.1 - 35.5	7.9 - 29.3	0.056 - 0.378	0.828 - 0.874
60 years	9.97 - 12.6	2.49 - 3.26	12.5 - 28.2	17.7 - 35.6	0.045 - 0.113	0.818 - 0.957

Table 4.2 Selected bird species and their functional group and forest dependence category according to Stiles and Skutch 1989, Barrantes et al. 2016, and Neotropical Birds 2018.

Species	Latin name	Species Code	Functional Group	Forest Dependency
Thicket Tinamou	*Crypturellus cinnamomeus*	THTI	Omnivore	habitats with 40-50% of forest cover
Orange-fronted Parakeet	*Aratinga canicularis*	OFPA	Frugivore	habitats with 40-50% of forest cover
Yellow-naped Parrot	*Amazona auropalliata*	YNPA	Frugivore	habitats with 40-50% of forest cover
Elegant Trogon	*Trogon elegans*	ELTR	Omnivore	live and reproduce in extensive mature forest
Black-headed Trogon	*Trogon melanocephalus*	BHTR	Omnivore	habitats with 40-50% of forest cover
Turquoise-browed Motmot	*Eumomota superciliosa*	TBMO	Insectivore	open areas
Brown-crested Flycatcher	*Myiarchus tyrannulus*	BCFL	Insectivore	habitats with 40-50% of forest cover
Long-tailed Manakin	*Chiroxiphia linearis*	LOTM	Frugivore	habitats with 40-50% of forest cover
Banded Wren	*Thryothorus pleurostictus*	BANW	Insectivore	habitats with 40-50% of forest cover
Rufous-naped Wren	*Campylorhynchus rufinucha*	RNAW	Insectivore	habitats with 40-50% of forest cover
Olive Sparrow	*Arremonops rufivirgatus*	OLSP	Insectivore	live and reproduce in extensive mature forest

Table 4.3 Indicator values for 52 species for the different forest ages (e.g. 20, 30, 40, and 60 years old). Relative indicator values for each species for each forest age (out of 100%) are shown. Significant indicator species and P-values <0.1 indicated in bold.

Species	Latin Name	Species Code	20	30	40	60	Habitat Indicator	P-value
Banded Wren	*Thryothorus pleurostictus*	BANW	25.5	23.4	25.5	25.5	20,30,40,60	>0.1
Barred Antshrike	*Thamnophilus doliatus*	BAAN	19.5	27.3	21.9	31.3	60	>0.1
Black-headed Trogon	*Trogon melanocephalus*	BHTR	22.3	22.3	25.5	29.8	60	>0.1
Boat-billed Flycatcher	*Megarynchus pitangua*	BOBF	23	26.9	24.6	25.6	30	>0.1
Bright-rumped Attila	*Attila spadiceus*	BRAT	23.1	0	46.2	30.8	40	>0.1
Brown-crested Flycatcher	*Myiarchus tyrannulus*	BCFL	32.5	14.8	33.1	19.7	20	>0.1
Canivet's Emerald	*Chlorostilbon canivetii*	CAEM	0	29.4	70.6	0	40	>0.1
Clay-colored Thrush	*Turdus grayi*	CCTH	21.4	21.4	0	57.1	60	>0.1
Crested Guan	*Penelope purpurascens*	CRGU	45.5	0	9.1	45.5	**20,60**	**0.06**
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	DCFL	35.7	35.7	28.6	0	20,30	>0.1
Elegant Trogon	*Trogon elegans*	ELTR	23.4	25.5	25.5	25.5	30,40,60	>0.1
Great Kiskadee	*Pitangus sulphuratus*	GKIS	0	0	23.1	76.9	**60**	**0.06**
Inca Dove	*Columbina inca*	INDO	23.8	0	76.2	0	40	>0.1
Ivory-billed Woodcreeper	*Xiphorhynchus flavigaster*	IBIW	45.5	0	54.5	0	40	>0.1
Laughing Falcon	*Herpetotheres cachinnans*	LAFA	28.6	14.3	28.6	28.6	20,40,60	>0.1
Lesser Greenlet	*Hylophilus decurtatus*	LESG	30	30	0	40	60	>0.1
Lesson's Motmot	*Momotus lessonii*	LEMO	19.2	19.2	35.9	25.6	40	>0.1
Long-billed Gnatwren	*Ramphocaenus melanurus*	LBGN	26.4	4.4	28.2	41.1	**60**	**0.04**
Long-tailed Manakin	*Chiroxiphia linearis*	LOTM	18.7	18.7	32.8	29.9	40	>0.1
Northern Barred-Woodcreeper	*Dendrocolaptes sanctithomae*	NOBW	21.7	29	20.3	29	30,60	>0.1
Olive Sparrow	*Arremonops rufivirgatus*	OLSP	22.4	29.9	17.9	29.9	30,60	>0.1
Orange-fronted Parakeet	*Aratinga canicularis*	OFPA	12.9	12.9	31	43.1	60	>0.1
Pale-billed Woodpecker	*Campephilus guatemalensis*	PBIW	34.1	11.4	54.5	0	**40**	**0.06**
Red-billed Pigeon	*Patagioenas flavirostris*	RBPI	30.2	37.7	12.1	20.1	30	>0.1
Ruby-throated Hummingbird	*Archilochus colubris*	RTHU	29.4	39.2	31.4	0	30	>0.1
Rufous-and-white Wren	*Thryothorus rufalbus*	RAWW	18	25.2	23.1	33.7	60	>0.1
Rufous-capped Warbler	*Basileuterus rufifrons*	RCWA	25.3	23	24	27.6	60	>0.1
Rufous-naped Wren	*Campylorhynchus rufinucha*	RNAW	28.1	25.7	24.3	21.8	20	>0.1
Scrub Euphonia	*Euphonia affinis*	SEUP	19.2	19.2	61.5	0	40	>0.1
Slate-headed Tody-Flycatcher	*Poecilotriccus sylvia*	SHTF	37.5	62.5	0	0	30	>0.1
Squirrel Cuckoo	*Piaya cayana*	SQCU	52.6	26.3	21.1	0	20	>0.1
Steely-vented Hummingbird	*Amazilia saucerrottei*	SVHU	0	0	47.4	52.6	60	>0.1
Streak-backed Oriole	*Icterus pustulatus*	SBAO	78.9	0	21.1	0	20	>0.1
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*	SHWO	13.4	23.4	32.1	31.2	40	>0.1
Stripe-headed Sparrow	*Peucaea ruficauda*	SHSP	17.9	53.6	28.6	0	30	>0.1
Stripe-throated Hermit	*Phaethornis striigularis*	SRTH	35.4	21.2	5.7	37.7	60	>0.1
Summer Tanager	*Piranga rubra*	SUTA	7.8	23.4	37.5	31.3	40	>0.1
Tennessee Warbler	*Oreothlypis peregrina*	TEWA	62.5	20.8	16.7	0	20	>0.1
Thicket Tinamou	*Crypturellus cinnamomeus*	THTI	23	23	26.6	27.3	60	>0.1
Tropical Gnatcatcher	*Polioptila plumbea*	TRGN	28.7	18.3	25.1	27.9	20	>0.1
Turquoise-browed Motmot	*Eumomota superciliosa*	TBMO	21.4	17.1	27.4	34.2	60	>0.1
White-fronted Parrot	*Amazona albifrons*	WFPA	22.7	22.7	9.1	45.5	60	>0.1
White-lored Gnatcatcher	*Polioptila albiloris*	WLGN	33.6	26.9	21.5	17.9	20	>0.1
White-throated Magpie-Jay	*Calocitta formosa*	WTMJ	39.9	11.4	18.3	30.4	20	>0.1
White-tipped Dove	*Leptotila verreauxi*	WTDO	25.5	23.4	25.5	25.5	20,40,60	>0.1
White-winged Dove	*Zenaida asiatica*	WWDO	7.4	37.1	35.6	19.8	30	>0.1
Yellow Warbler	*Dendroica petechia*	YWAR	28.5	31.7	10.1	29.6	**30**	**0.03**
Yellow-green Vireo	*Vireo flavoviridis*	YGVI	20	26.7	26.7	26.7	30,40,60	>0.1
Yellow-naped Parrot	*Amazona auropalliata*	YNPA	23.6	30.4	18.9	27	30	>0.1
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	YOFL	23.1	23.1	25.9	27.8	60	>0.1
Yellow-throated Euphonia	*Euphonia hirundinacea*	YTEU	48.9	16.3	13	21.7	20	>0.1
Yellow-throated Vireo	*Vireo flavifrons*	YTVI	28.8	28.8	23.1	19.2	20,30	>0.1

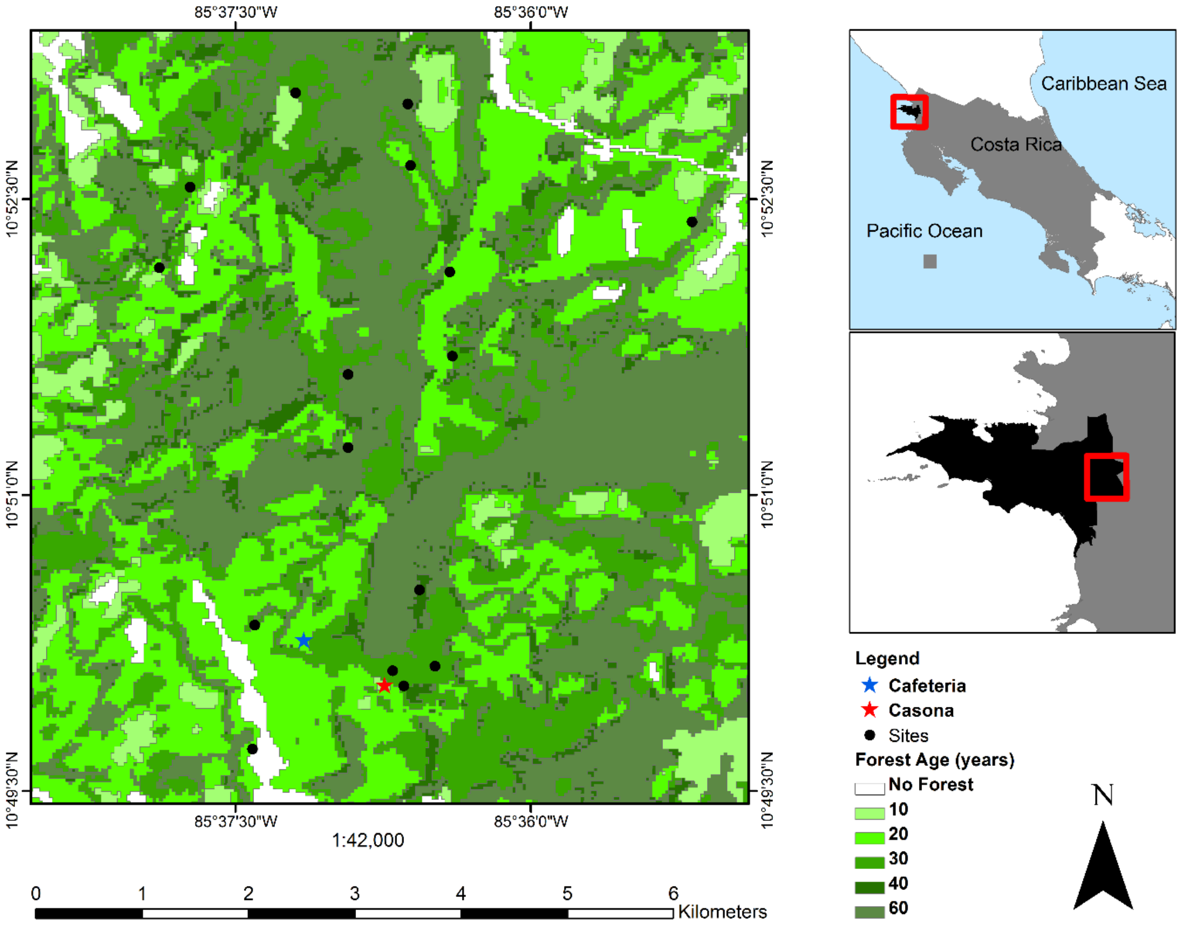

Figure 4.1 Location of the 16 dry forest study sites at the Santa Rosa National Park, Guanacaste, Costa Rica (modified from Sánchez-Azofeifa et al. 2017).

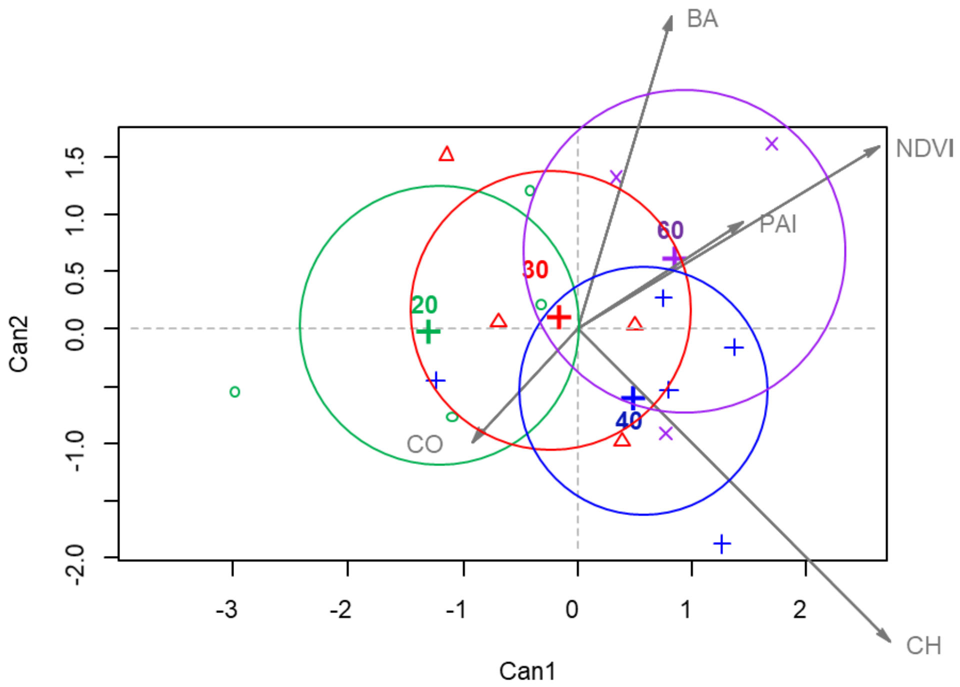

Figure 4.2 Linear Discriminant Analysis (LDA) for the different forest ages (e.g. 20, 30, 40, and 60 years old) and forest structural characteristics (tree basal area: BA; percentage of canopy openness; CO; plant area index (PAI); canopy height: CH; and Normalized Difference Vegetation Index: NDVI). Axis 1 (Can1) explains 74.5 % of the variance and Axis 2 (Can2) explains 21.5 %.

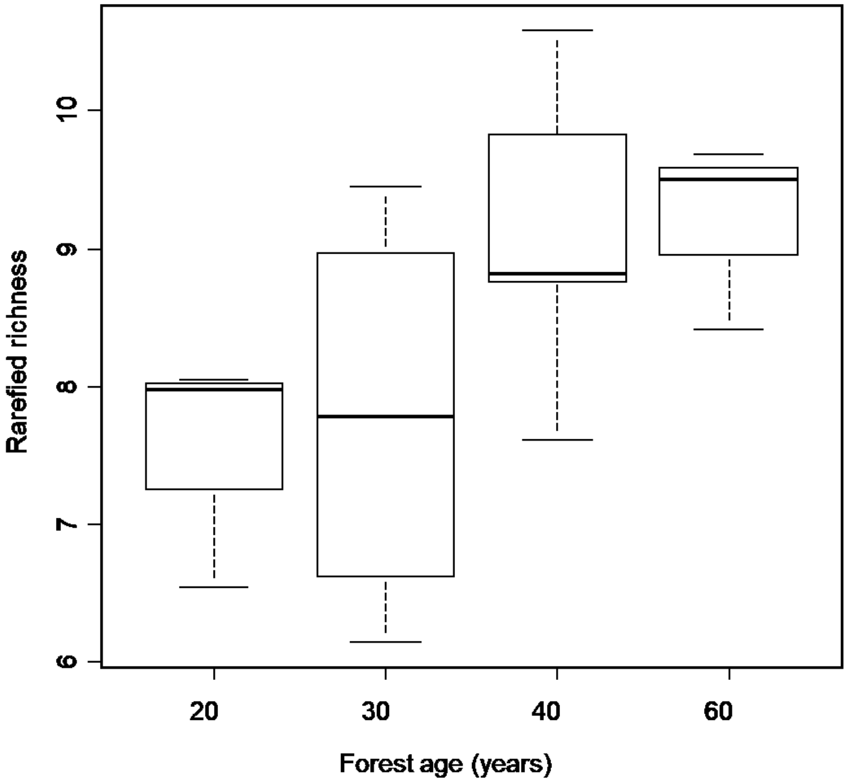

Figure 4.3 Box plot showing rarefied bird species richness for the forest age classes.

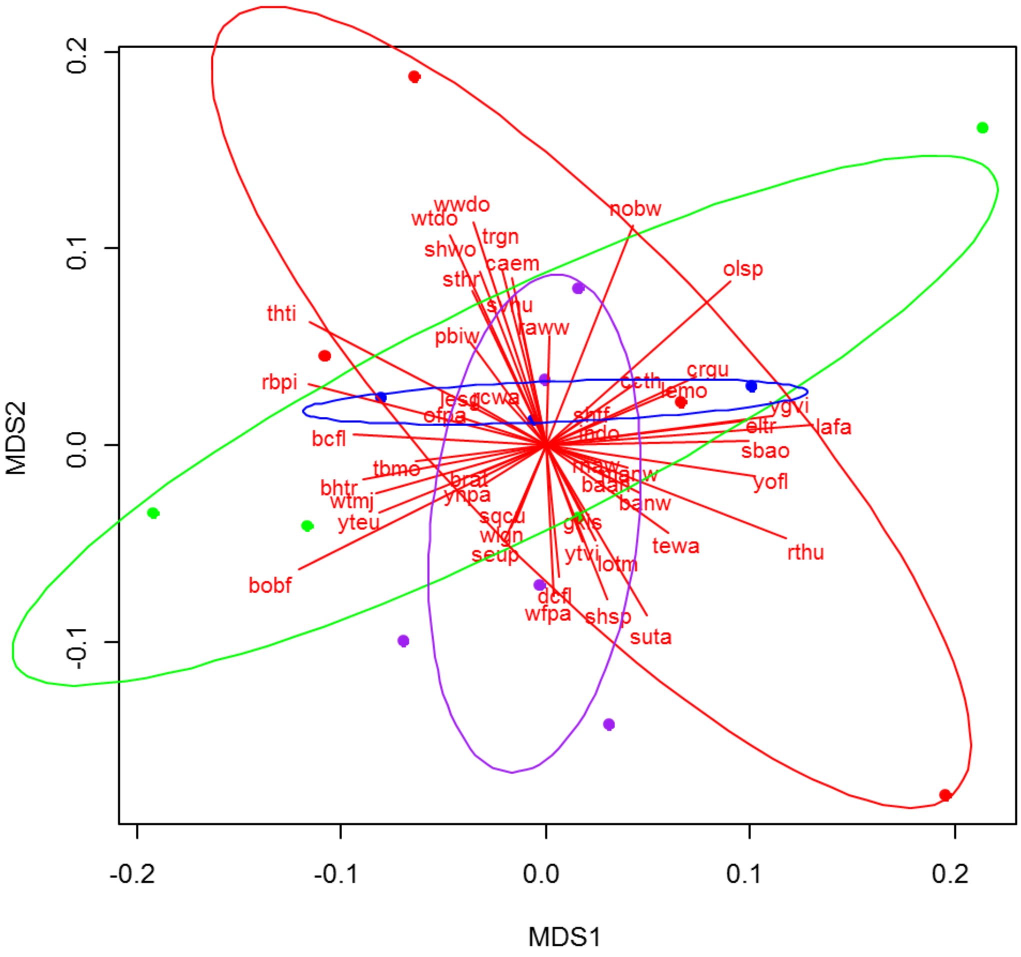

Figure 4.4 Meta multidimensional scaling (metaMDS) ordination plot performed on forest ages by species matrix data. Stress and model complexity were optimized at k= 3 and n = 500 iterations, distance matrix calculated using the Bray-Curtis index. Ellipse colors, green: forests of 20 years old, red: forests of 30 years, purple: forests of 40 years, and blue: forests of 60 years. Species four letter codes indicated in Table 1.

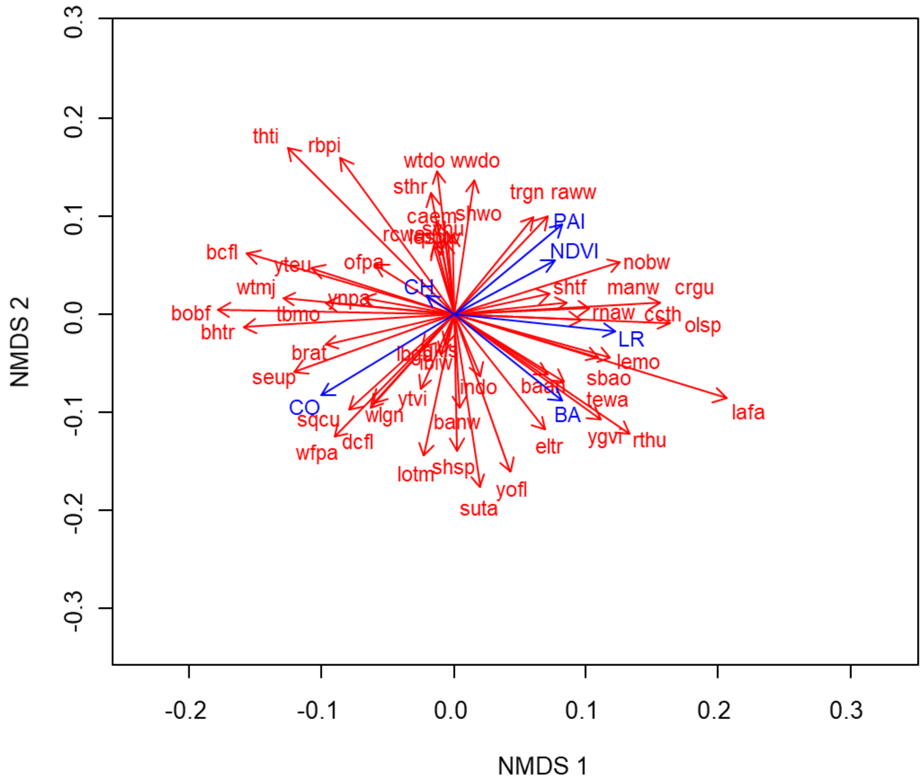

Figure 4.5 Non-metric multidimensional scaling (NMDS) ordination performed on forest sites by species matrix data. Forest structural characteristics were used as independent variables and bird species frequencies as the dependent variable. Distance matrix calculated using the Bray-Curtis index. Forest structural characteristics evaluated shown in blue (CO: canopy openness, PAI: plant area index, CH: canopy height, BA: tree basal area, LR: liana ratio, and NDVI: Normalized Difference Vegetation Index). Species four letter codes indicated in Table 1.

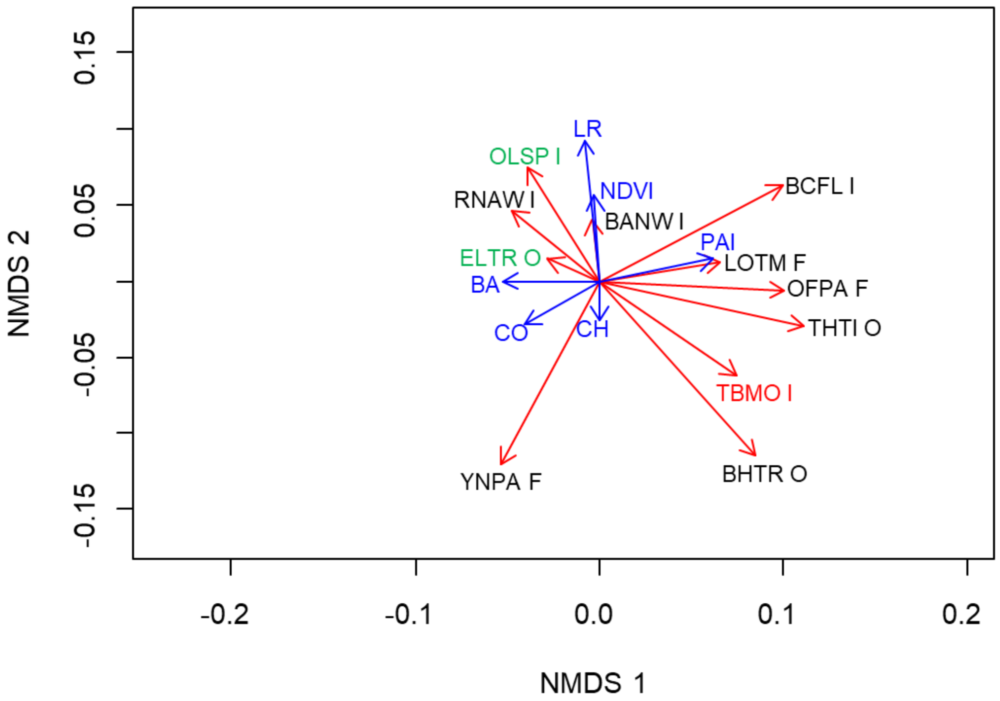

Figure 4.6 Non-metric multidimensional scaling (NMDS) ordination performed on forest sites by species matrix data. Forest structural characteristics were used as independent variables and bird species frequencies for the 11 species as the dependent variable. Distance matrix calculated using the Bray-Curtis index. Forest structural characteristics evaluated shown in blue (CO: canopy openness, PAI: plant area index, CH: canopy height, BA: tree basal area, LR: liana ratio, and NDVI: Normalized Difference Vegetation Index). Species shown in red. Species four letter codes indicated in Table 1. Species names in green color live and reproduce in extensive mature forest, names in black require habitats with 40-50% of forest cover, and species in red live in open areas. Functional group letter code: F: frugivore, I: insectivore, and O: omnivore.

5 Synthesis

5.1 Conclusions

The objective of this Dissertation was to evaluate the relationship between the recovery of tropical dry forests (TDFs) from cattle ranching abandonment and the nature of the avian communities found in different successional stages at the Santa Rosa National Park (SRNP). To date, studies of successional processes associated with the recovery of dry forests following cattle ranching abandonment have focused mainly on characterizing the structure of different successional stages of the forest (Arroyo-Mora, 2002; Kalacska et al., 2004a; Kalacska et al., 2004b; Kalacska et al., 2005; Sánchez-Azofeifa et al., 2017). Based on these studies, the general successional pattern for recovering TDFs in Mexico, Costa Rica, and Brazil is an increase in the structural complexity of the forests as succession proceeds and the forests mature. This means an increase in tree size (e.g. DBH) and height, tree basal area, and stem density as forest age increases (Kalacska et al., 2004; Quesada et al., 2014; Carvajal-Vanegas & Calvo-Alvarado 2013). However, there is limited information about how forest age and forest structural characteristics affect the diversity and composition of the fauna in successional dry forests in the Neotropics.

Differently from findings from previous studies mentioned above, the results of this Dissertation demonstrated that bird species richness and community composition are similar in forests at different stages of recovery following the abandonment of cattle ranching. Forests of different ages were similar in terms of such structural characteristics as tree basal area, the percentage of canopy openness, canopy height, plant area index, the abundance of lianas, and the amount of green vegetation. This suggests that even forests that have been developing for 20 years since abandonment can provide suitable habitat and resources for birds. The proximity of forests of different ages was likely an important factor in explaining the similarities in bird species richness and communities in forests with different ages at the SRNP (e.g. the minimum distance between forests was 250 m). When bird species associations are analyzed at a finer scale, it is apparent that the presence and abundance of a few bird species are related to specific structural characteristics of the forests. The observation that bird species richness and community structure vary little between forests of different ages is an important finding in relation to the question of how natural processes of vegetation succession may affect the presence, abundance, and distribution of bird species in TDFs. This is important for bird conservation in TDFs in the Neotropics, where bird diversity is high and birds play an important role in forest function due to their roles as plant pollinators, seed dispersers, and a controlling influence on populations of herbivores in these forests (Sekercioglu et al., 2002; Sekercioglu 2006).

There are two important aspects to consider in this Dissertation. One is that the successional forests established by Kalacska et al. (2004) were clearly different among them in terms of forest structural characteristics. The early stage used to have the lowest values for tree basal area and height, NDVI and PAI. However, findings from this Dissertation showed that currently these successional stages have reached similar forest structural characteristics (e.g. BA, CO, PAI, NDVI, and LR), and that successional stages cannot be categorized based on these characteristics. Findings from previous studies could not establish differences in forest structural characteristics such as BA, PAI, and LAI between the early and the intermediate stage at the SRNP (Sánchez-Azofeifa et al., 2017). This Dissertation showed that early forests from 20 years old have also similar forest structural characteristics to late forests of more than 60 years old.

The second aspect to consider is the statistical power for the analyses, particularly for Chapter 4. In this Chapter, 16 sites were selected and categorized into four age classes based on aerial photographs and satellite images. Bird species richness and composition were evaluated in these age classes and related also to forest structural characteristics. A power analysis performed using four sites for each of the four age classes, with a significance level of 0.05, and a medium effect size of 0.5 -suggested as an acceptable effect by Cohen, (1988)- results in a power of 0.3. Values between 0.8-0.9 for the power analysis are considered high and desirable to increase the probability to reduce type II error (e.g. failing to reject a false null hypothesis) (Champely et al., 2018). Based on this, a p-value of 0.1 was used for all the analyses performed for this Chapter, and this generated a power analysis score of 0.4, which is still low. An ideal number of observations of 10 for each stage was obtained from a power analysis when using a power of eight and a p-value of 0.1. This number of observations per each class involves some important limitations to consider. First, it is not possible to select 10 sites for each age class that meet the criteria of the minimum distance between sites to place the recorders for the acoustic data collection (i.e. 250 m) to avoid autocorrelation of the species detected from recordings. Second, 10 sites per forest age class involves a substantial effort in terms of equipment for acoustic data collection during the same days for the sites; and third, it also implies a large person/effort to carry out the field work. This statistical limitation should be acknowledged for this Chapter.

5.2 Contributions and significance

Chapter 2 described and compared the diversity and composition of tree species found in three successional stages of tropical dry forests in Costa Rica. A total of 1,072 trees of 96 species were identified. Contrary to findings from studies of dry forests in Mexico, Venezuela, and Brazil, where species richness was higher in late successional stages, species richness and diversity were higher in the intermediate stage of dry forest succession in Costa Rica. This was also observed by Kalacska et al., 2004 for other successional sites within the SRNP. This implies a transition in forest structure, microhabitats, and microclimates that promotes suitable habitat for tree species that can survive in both early stage open forests and old-growth forests, and, therefore, accounts for the fact that the highest tree species richness is found in the intermediate stage forests (Catford et al., 2012).

The breeding systems and pollination and dispersal syndromes of tree species present in different successional stages were described for the first-time for dry forests at the SRNP. Monoecy was found as the most common breeding system. Consequently, most of the tree species and individual trees followed this system, in which tree species do not depend on specific pollinators (e.g. fauna). This is important for the SRNP since self-pollination is advantageous when conspecifics are scarce or located far apart from each other (Rea & Nasrallah, 2008). Regarding pollination syndromes, insects are extremely important pollinators since several tree species at the SRNP have small inflorescences that are an adaptation to being pollinated by small visitors. In early stage open forests, however, the wind is the most important pollination agent, and this is a useful syndrome in open sites where pollinators may be scarce. While wind is the most important disperser in early stage forests, the importance of birds and mammals as dispersal agents increases when forests increase in age across a succession. This is because a number of tree species produce fleshy fruits and dry indehiscent fruits that are the main food sources for a number of bird and mammal species.

Chapter 3 evaluated the influence of liana abundance on the avian acoustic community in tropical dry forests in Costa Rica. Findings showed that as the number of lianas at a site increases, so too does the diversity of the avian acoustic community. Thus, a more complex acoustic community is found in forest sites with more lianas. This suggests that lianas provide important resources for birds in dry forests (e.g. structure for shelter, nesting and roosting, and both direct and indirect food sources) (Michel et al., 2014).

Lianas have been shown to have a negative effect on the reproduction of tropical canopy trees and it has also been suggested that they have an adverse impact on faunal species composition (García León et al., 2017). Results showed a positive relationship between lianas and bird diversity which can be mostly related to the importance of the arthropods that live in lianas as a source of food for birds. This relationship is particularly important in Neotropical dry forests where birds have a key role as flower-pollinators and seed dispersal agents, and where lianas have become highly abundant (Schnitzer, 2005; Michel et al., 2014; Hilje et al., 2015).

Another important contribution of this Dissertation was to demonstrate, for the first time for tropical forests, that acoustic diversity indices can be related directly to measures of species richness derived by listening to recordings. Previous studies that related acoustic diversity indices to species diversity were carried out in Boreal forests, oceans, and on coral reefs (Bertucci et al., 2016; Buscaino et al., 2016; Buxton et al., 2016). This study is the first to address the challenging task of validating acoustic diversity indices in highly bird-diverse tropical forests. This validation was possible due to the observed similarities between the forest sites studied in terms of Plant Area Index, and the tree height and basal area. On the basis of this validation, the differences observed between the avian acoustic communities of the SRNP forests correspond to differences in the actual bird communities.

Chapter 4 assessed how the bird species richness and bird communities in dry forests changed during the course of forest recovery following the abandonment of cattle ranching at the SRNP, Costa Rica. Similar forest structural characteristics were observed in forests with different ages (e.g. 20, 30, 40, and 60 years) due to a high variation in forest structure within each age. As a result, forest structure could not be used to classify forests based on their age and length of the period of recovery. These similarities in forest structure among forests age classes can be mostly explained by a continuous forest regeneration that results in a smooth transition between classes. The similarities in forest structure between forests of different ages are consistent with the similarities in bird species richness and community composition in forests of different ages.

Birds use the same suitable habitats and other major resources (e.g. perches for roosting and mating displays, material for nesting, and food) in the different forest sites. The proximity of forests of different ages as well as the transition between classes were critical factors to the occurrence of similar bird species richness and community compositions and this is a key factor to consider in bird conservation efforts in Neotropical Dry Forests. The presence and abundance of some bird species were associated with specific structural characteristics of the forests, suggesting that even when bird communities are similar among forests of different ages, there are vital associations that become important when analyzing the occurrence of different bird species at a finer scale.

5.3 Future research

The avian acoustic community is more diverse in dry forest sites with a higher number of lianas. This finding highlights an influence of lianas on the bird communities of a tropical dry forest. Future research should evaluate this relationship at a finer scale by identifying the associations between species of lianas and species of birds. For this, both lianas and birds should be identified to species level. Ideally, acoustic surveys would be complemented by bird visual surveys (e.g. point counts). Future research should evaluate what resources lianas provide to birds by checking whether they use lianas to collect material for nesting, as sites for nesting, perching or roosting, or as sites for feeding on nectar, flowers, seeds, or fruits, or on arthropods that live on lianas. It would also be interesting to understand whether bird-liana associations are permanent throughout the year or if the species visiting lianas change based on liana phenology (e.g. the presence of leaves, flowers, and fruits) related to seasonality. Finally, it would be interesting to determine bird-liana association for migrant species related to seasonality.

This Dissertation assessed the differences in the structural characteristics of forests that had evolved over different periods of time following the abandonment on cattle ranching and evaluated how these affected the richness and composition of bird communities in TDFs. A similar bird species richness and community composition were observed in forests with different age classes, and this is due to similarities in the habitats and main sources offered by the different forest ages. This is an interesting finding that supports the idea that the bird species richness and community composition in a dry forest can recover in only a few years after cattle ranching abandonment. TDFs of 20 years old can provide suitable habitat and sources for birds as 60 year old forests, indicating a rapid recovery of bird species composition at the SRNP. However, the proximity between forests is also an important factor to consider. Future research should include studies of even younger successional forests, including those dating from only 5 years since abandonment, which may include pastures with isolated trees. This would clarify the processes underlying the transition in bird species composition that is associated with the change from very simple habitats to young forests that is evaluated here. This is not an easy task, however, since the remaining pastures at the SRNP are located adjacent to forests, and the birds that inhabit those forests can be detected in recordings from pastures (pers. obs.).

The main objective of this Dissertation was to generate information on the bird communities of TDFs, but for future research, it would be interesting to evaluate the role and influence of forest structural characteristics on insectivorous birds that use the forest understorey. This functional group is particularly affected by changes in forest structure due to disturbances by human activities (Sekercioglu et al., 2002). It would be interesting to focus future research on this group, which includes less mobile and highly territorial species such as wrens, as well as more mobile species such as antshrikes, woodcreepers, and flycatchers. This would generate information on what TDFs structural or food resources these species depend on. It would also be interesting to determine how extended periods of drought due to the frequency of El Niño Southern Oscillation (ENSO) could affect these resources and, therefore, affect and threat insectivorous bird species.

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