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**UNDERSTANDING THE INFLUENCE OF HABITAT ALTERATION
ON HUMMINGBIRD SPECIES USING A MULTI-LEVEL ANALYSIS APPROACH**

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Boris Tinoco

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Abstract of the Dissertation

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The tropical Andes, the richest region in the world in terms of biodiversity, faces widespread anthropogenic alteration of habitats. As a result, this region harbors one of the highest concentrations of threatened species worldwide. While there has been extensive research on the effects of habitat alteration on biodiversity, studies often focus on one level of ecological organization; however all levels are inherently linked. I investigated the influence of habitat alteration on biodiversity by studying hummingbird populations, the structure of hummingbird assemblages, and hummingbird – plant interactions in habitats with different land-use types that are the result of different human-induced alteration in the southern Andes of Ecuador. At the population level, I evaluated habitat specific demographic parameters of three hummingbird species, *Metallura tyrianthina*, *Eriocnemis luciani*, and *Coeligena iris*. Population growth rates of these species indicated that *M. tyrianthina* and *E. luciani* populations can likely persist in some altered habitat types; however, *C. iris* populations could be negatively affected by habitat alteration. At the assemblage level, I explored how landscape and local habitat characteristics influenced functional and taxonomic diversity of hummingbirds. Although there was little taxonomic change across landscapes with different types of alteration, functional diversity of hummingbirds decreased in more altered landscapes. At the level of hummingbird – plant interactions, I assessed variation in hummingbird’s diet specialization using a species interaction network approach, and explored how changes in specialization could be mediated by evolutionary factors (i.e., morphological traits) and ecological factors (i.e., resource availability). Results indicated that factors operating over short ecological time scales (i.e., variation in resource availability) may produce variation in the level of specialization of hummingbirds; however, I also found that the hummingbirds’ specialization was determined by morphological features (i.e., bill length) whose change occurs through evolutionary time. Hummingbirds were

less specialized in more altered habitat types. Overall my result showed that some aspects of hummingbird's biodiversity can be negatively affected by habitat alteration, which could have negative repercussion for biodiversity and ecosystem functioning in the tropical Andes. Moreover, this dissertation demonstrates that studying the effects of anthropogenic habitat alterations requires exploration of multiple facets of biodiversity, because each level of ecological organization contributes different insights about the on-going effects of human induced alteration.

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Chapter 1: Introduction

Study Species: Hummingbirds

Hummingbirds have a widespread distribution in the New World, and, with more than 320 species, represent one of the most diverse avian clades in the Neotropics (del Hoyo et al. 1999). The peak of hummingbird species richness is in the equatorial Andes (Rahbek and Graves 2000). This richness pattern is probably driven by the environmental complexity (in terms of climate and topography), the presence of stable refugia, and vicariance events promoted by the uplift of the Andes (Graves 1985, Bleiweiss 1998, Fjeldsa et al. 1999).

The reproductive biology of most hummingbird species is poorly known; however, certain generalities can be applied to the whole group (reviewed by Ortiz Crespo 2011). Male hummingbirds are polygynous and do not participate in parental care. Females lay two eggs, and can have more than one brood per year. Juveniles are reproductive after the first year. The life span of hummingbirds varies with body size, and ranges from about four years for the smallest species to six years in the largest species.

Hummingbirds depend on nectar availability to supply their energetic demands (Hainsworth et al. 1981, Powers and Conley 1994). Thus, the amount of nectar available influences several aspects of hummingbird biology and ecology, including timing of reproduction (Stiles 1980, Ortiz Crespo 2011), activity budgets (Wolf and Hainsworth 1971, Powers and McKee 1994), territory size (Hixon et al. 1983, Paton and Carpenter 1984), survival (Stiles 1992), and habitat selection (Baltosser 1989). Moreover, population size and seasonal migrations of hummingbirds also closely linked to the availability of nectar resources (Montgomerie and Gass 1981, Stiles 1992, Wethington and Russell 2003).

Hummingbirds have been used as a model system to learn about the factors that influence assemblage organization of vertebrates (e.g., Lack 1973, Wolf et al. 1976, Feinsinger and Colwell 1978, Brown and Bowers 1985). Intra and interspecific competition in hummingbirds promotes spatial and temporal displacement of subordinate individuals (Kodric-Brown et al. 1984, Pimm et al. 1985, Cotton 1998). Moreover, mutualistic interactions between hummingbirds and flowering plants can lead to high levels of specialization, where hummingbirds are pollen carriers and flowering plants provide hummingbirds with a nectar reward (Stiles 1981, Temeles and Kress 2003). Specialization in hummingbirds can set limits to the types of flowers visited by a species (Snow and Snow 1972, Lindberg and Olesen 2001, Temeles et al. 2006), and can thus influence habitat selection and foraging patterns of individuals (Stiles 1985, Arizmendi and Ornelas 1990, Dalsgaard et al. 2009).

Hummingbirds provide important pollination services in the Neotropics (Bawa 1990). They visit a particular spectrum of flowers that possess what is called the “hummingbird-pollination syndrome” (Bawa 1990, Fenster et al. 2004). These are flowers that have nectar with high sugar concentration, and corollas with long wavelength colors, and elongated shapes, and

exerted anthers and stigmas (Stiles 1981, Dalsgaard et al. 2009). Within the Neotropics, hummingbird pollination becomes particularly important in montane forests (Cruden 1972, Wolf et al. 1976). This is because hummingbirds are less vulnerable than invertebrate pollinators to harsh environmental conditions (i.e., abundant rain and low temperatures) prevalent in tropical mountains.

The decline of pollinator populations associated with anthropogenic habitat alteration has been documented in several parts of the world (Potts et al. 2010). These declines have caused decreases in the productivity of certain species of plants (Kremen et al. 2007). However, this evidence comes from studies of insect-flower pollination systems. Little is known about how habitat alteration influences hummingbird pollination systems (Wolowski et al. 2013). Thus, the study of hummingbirds and hummingbird pollinated plant interactions in altered habitats is relevant for understanding tropical ecosystem processes under the current threats posed by the widespread effects of anthropogenic habitat alteration.

Study region

The tropical Andes, one of the most biodiverse regions in the world (Myers et al. 2000), currently faces widespread anthropogenic habitat alteration (Foley et al. 2005). As a result, it harbors one of the highest concentrations of threatened species worldwide (Stattersfield et al. 1998, Pimm et al. 2006). My research was conducted in Cajas National Park and surrounding areas in Ecuador (~250 square km). More than 20 species of hummingbirds have been identified in this region (Tinoco and Astudillo 2007). Like elsewhere in the Andes, the region has been largely altered by different human activities (White and Maldonado 1991). Hummingbirds are an ideal study system because there is extensive knowledge about their functional traits, and the factors that influence the organization of assemblages (e.g., Stiles 1980; Collins 2008; Temeles et al. 2009). Based on this knowledge, it is possible to develop a hypothesis-testing framework to explore factors that might influence the distribution of hummingbirds across habitats that have been altered by human activities (Feinsinger and Colwell 1978, Graham et al. 2009). Moreover, in the tropical Andes, a large number of plant species depend on hummingbird pollination for sexual reproduction (Cruden 1972, Wolf et al. 1976). Given the current global concern for the decline of pollination services, it is imperative to understand the effects of habitat alteration on pollinators (Tylianakis et al. 2010, Winfree et al. 2011).

There are a range of land cover types in Cajas National Park and surroundings. Land cover in my study area mainly consisted of native vegetation, pastures and exotic tree plantations. Native vegetation is composed of high elevation native shrubs and forest. Pasture is composed of grasses for cattle and occasional hedgerows that have small shrubs. Exotic tree plantations are dominated by *Eucalyptus* and pines with some native plants. For my study I used a series of valleys that had different land cover types that ranged in elevation from 3000 to 3300 m above sea level. Valleys were relatively discrete areas between 2 and 5 square km, and were demarcated by native high elevation grasses at the top and pasture and housing at the mouth. I chose these valleys for several logistical and biological reasons. Logistical reasons included accessibility (e.g., a roads) and availability of long term data (e.g., mist-net data). From a biological perspective I wanted to capture the variation in land cover types in the region.

Given that I was interested in how land cover influenced diversity I chose valleys that varied in the proportion of the three major land cover types in the region: native vegetation, pasture and exotic tree plantations. In chapter 2 my choice of landscapes was dictated by the locations of long term mist-net study sites. I had two sites in a large valley. Within that valley, one mist-net site was dominated by exotic trees (referred to in Chapter 2 as introduced forest) and the other site by native vegetation (referred to in Chapter 2 as native forest). The last mist-net site was located in a valley that had a mixture of native vegetation and pasture (~20% pasture), and sampling was in an area dominated by native shrubs (referred to in Chapter 2 as native shrubs). In Chapter 3 I chose six valleys with different levels of human induced alteration. Finally, given that gathering network data on hummingbird-plant interactions is time-intensive, I restricted sampling to three valleys for chapter 4. One valley was dominated by native trees (referred to in chapter 4 as forest), one by native shrubs (referred to in Chapter 4 as shrubs) and one by active pasture lands (refer in Chapter 4 as cattle ranch).

Ecological effects of habitat alteration

While there has been extensive research on the effects of habitat alteration on the conservation of biodiversity, studies often focus on one level of ecological organization. Examples include population responses of a particular species (Peralvo et al. 2005, Tinoco et al. 2009), changes in the composition of assemblages (Latta et al. 2011, Leal et al. 2012), or dynamics of interacting species (host-parasite assemblages, mixed species flocks; Tylianakis, Tscharntke, and Lewis 2007, Knowlton and Graham 2011). However, all of these ecological levels are inherently linked, and any effect on one level of the system may influence a response in other levels (Chapin et al. 2000). Thus, a more holistic examination of ecological systems should include different levels of ecological organization to better understand the effects of land use change. Further, conservation biologists increasingly recognize that conservation efforts should include both the protection of single species and the maintenance of diversity and ecosystem functions (Naeem et al. 2009).

Anthropogenic alteration of habitats can negatively influence the population size of a species, which can result in local extinctions (Pulliam 1988). These changes in population size are mainly determined by demographic parameters such as survival probability of individuals in the population and offspring production, also referred to as productivity (Akçakaya et al. 1999). Land use change can affect survival and productivity rates of individuals in a population by altering factors such as, predation pressure, resource abundance, and density of competitors (Holmes et al. 1996, Oro 2008, Holt et al. 2013). Moreover, anthropogenic habitat alteration changes the composition and distribution of habitat types within a landscape (Fahrig 2003), which influences population dynamics (i.e., population fluctuation) of a species by decreasing habitat size and connectivity among habitats (Pulliam and Danielson 1991, Ruiz-Gutierrez et al. 2008). Therefore, information on habitat specific survival and productivity rates across habitats with different types of alteration is needed to understand how populations may fluctuate under continued land-use change.

Anthropogenic alteration of habitats can change the composition of species in an area (Chapin et al. 2000). Typically, the evaluation of compositional changes relies on variation in the taxonomic composition of assemblages across anthropogenic altered and non-altered habitat types (Lewis 2001, Latta et al. 2011). However, measuring taxonomic richness provides limited information about the ecological processes that may have influenced observed changes in species composition. An understanding of the ecological factors that influence the structure of assemblages in altered environments will benefit from the use of a trait based approach, especially for functional traits that affect organism-environment performance (McGill et al. 2006). For example, land use change can act as an environmental filter, and set the range and types of functional traits of species in an assemblage (Flynn et al. 2009). This type of information can be particularly important for conservation management because it may be possible to predict how species could respond to anthropogenic alteration of habitats based on their functional traits.

Species presence in a habitat is likely influenced by community level processes that include interactions with other species (Stanton 2003), like mutualistic pollination interactions. In the last decade, there has been increasing efforts to study pollinator-plant interactions using network approaches (Vazquez et al. 2009). Interaction network analysis can incorporate an ecological community context by identifying which species interact in a given community and exploring the ecological and evolutionary consequences of those interactions (Memmott 1999, Bascompte et al. 2006). Measuring particular properties of interaction networks may reveal how anthropogenic habitat alteration affects communities (Heleno et al. 2009, Tylianakis et al. 2010). For example, within mutualistic pollination networks, greater specialization of pollinators, defined as species that interact with a reduced number of partners (Vázquez and Aizen 2006), is important for pollination quality because it increases the likelihood of conspecific pollen transfer, which in turn increases plant reproductive success (Johnson and Steiner 2000, Vamosi et al. 2006, Brosi and Briggs 2013). These community level processes are impossible to capture by traditional studies that solely focus on taxonomic diversity and species richness metrics.

From a theoretical perspective, studying the ecological effects of the anthropogenic alteration of habitats has the potential to provide important insights into what factors regulate populations, communities, and ecosystem processes (Fukami and Wardle 2005, HilleRisLambers et al. 2013). For example, if land use change modifies the amount of native vegetation coverage in a landscape, landscapes with different amounts of native vegetation can be compared to evaluate how land use change influences population size, demography, and species interactions. Thus, land use change can provide the opportunity to understand fundamental ecological processes and fuel the development of ecological theory.

In this dissertation I investigated how co-occurring hummingbirds respond to habitat alteration, at the level of populations, assemblages, and species interaction networks. I first explored demographic parameters of three hummingbird species across three land use types (Chapter 2). Second, I evaluated the patterns of taxonomic and functional diversity of hummingbird assemblages across six landscapes with different land use types (Chapter 3). Third, I used network analyses to study how diet specialization of hummingbirds varied across a different land use types (Chapter 4). These chapters are briefly described below.

Chapter 2 – Knowledge of how habitat alteration influences the demography of populations is required to predict the long term effects of anthropogenic land use change on hummingbird populations. Most studies of species responses to human disturbance in the tropics only quantify variation in abundance of birds across altered and non-altered habitats (e.g., Graham and Blake 2001, Tinoco et al. 2009, Latta et al. 2011); however, abundance data may underestimate the effects of land use change if abundance is decoupled from other demographic parameters that influence population change, such as survival and reproduction (Van Horne 1983, Bock and Jones 2004). In this chapter, I evaluated demographic parameters of three hummingbird species across vegetation types with different types of anthropogenic habitat alteration using a seven year capture-recapture data set. I calculated survival, productivity, and population growth rates to examine the influence of anthropogenic habitat alteration on habitat quality for the selected species.

Chapter 3 – It is increasingly recognized that measures of functional diversity are an important complement to taxonomic diversity to reveal and predict the effects of land use change on biodiversity (Villéger et al. 2010, Cadotte et al. 2011, Mouillot et al. 2013). In this chapter, I used data collected in six landscapes with different land use types to explore how landscape and local characteristics influenced functional and taxonomic diversity of hummingbirds. Land use types included landscapes with different proportions of native vegetation, cattle ranching pastures, and exotic forests. I also used knowledge of hummingbird functional traits to test predictions about how these traits would influence species responses to land use change.

Chapter 4 – Recent development of analytical tools to study interacting species as part of complex ecological networks has led to a better understanding of the factors that regulate species specialization (Vázquez et al. 2009, Schleuning et al. 2012, Dalsgaard et al. 2013). In ecological networks, specialists are those species that interact with a limited number of partners (Vázquez and Aizen 2006). Specialization is influenced by a series of ecological (e.g., species abundance) and evolutionary (e.g., trait matching between interacting partners) factors that operate at different spatial and temporal scales (Futuyma and Moreno 1988, Carnicer et al. 2009). Anthropogenic habitat alteration can influence how these factors operate, and thus produce changes in the degree of specialization of hummingbird species. In this chapter, I assessed how hummingbird specialization varied among forest, shrub, and cattle pasture vegetation types and explored how these changes are mediated by morphological traits and resource availability.

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Chapter 2: Habitat-Specific Demography of Hummingbirds in Anthropogenic Altered Habitats in the Tropical Andes of Ecuador

Introduction

Detailed knowledge of how habitat alteration influences the demography of populations is required to predict the long term effects of anthropogenic land use change. This type of information is especially critical in areas that harbor high levels of diversity and endemism, such as the tropical Andes (Myers et al. 2000), where the loss of native forest is threatening the conservation of multiple species (Orme et al. 2005). Unfortunately, detailed demographic information from wildlife populations is difficult to obtain, making this type of data unavailable for most of the species in the tropics (Latta et al. 2005, Ruiz-Gutiérrez et al. 2012). Here I evaluate a unique data set from the tropical Andes of south Ecuador obtained by constant effort mist netting for seven years to determine the influence of habitat alteration on survival, productivity and population growth rates of three hummingbird species.

Most studies of species responses to human land use change, especially in the tropics, quantify variation in abundance across levels of degradation (Renjifo 2001, Lloyd 2008, Latta et al. 2011); however, abundance data may not reflect the effects of habitat alteration if it is decoupled from other demographic parameters that are influenced by habitat quality (Van Horne 1983). Habitat quality is defined as the ability of the environment to provide conditions appropriate for population persistence (Johnson et al. 2006, Mortelliti et al. 2010). Relative abundance is a relatively easy parameter to obtain for wildlife populations, and as such has been widely used as an indicator of habitat quality for many species (Holmes et al. 1996, Nevoux et al. 2011). The theoretical basis for the use of abundance as an indicator of habitat quality comes from Ideal Free Distribution models, which propose that individuals are able to detect differences in the value of habitats and will occupy those of better quality (Fretwell and Lucas 1970). As a consequence of this selection, it is expected that a greater abundance of individuals in high quality habitats compared to those of low value (Fretwell and Lucas 1970). Nevertheless, there are scenarios in which abundance is not correlated with demographic parameters that influence population trends, making habitat quality information based on abundance alone potentially biased. For example, the monopolization of high quality habitats by better competitors will force subordinate individuals to accumulate in low quality habitats (Pulliam and Danielson 1991). Likewise, an ecological trap will produce a large aggregation of individuals in low quality habitats due to a failure of individuals to distinguish critical differences in habitat quality among habitats (Robertson and Hutto 2006). These pitfalls of using abundance as an indicator of habitat quality demonstrate that detailed demographic data may be necessary to quantify the effects of anthropogenic habitat alteration on populations (Anders and Marshall 2005, Johnson et al. 2006, Mortelliti et al. 2010).

Two demographic factors that influence how populations change over space and time are survival and reproduction (Akçakaya et al. 1999). How these factors respond to habitat alteration will determine the balance between deaths and births in a population and define habitat quality for a species (Pulliam 1988). If the number of births exceeds the number of deaths, that habitat will be of high quality and is a population source; whereas a habitat where the number of deaths exceeds the number of births will be of low quality and is a population sink (Pulliam 1988). Identifying habitat specific demographic parameters is important for understanding

population trends because it is possible that each habitat will have a different contribution to population persistence in heterogeneous landscapes. Habitat specific information is highly valuable to target conservation priorities and management actions based on how different habitats in the landscape influence the long term probabilities of persistence of a population (Pulliam and Danielson 1991).

Hummingbirds are among the most species-rich and abundant groups of birds in the tropical Andes (Ridgely and Greenfield 2001) and play a key role in the ecosystem as pollinators of multiple species of plants (Cruden 1972). Therefore, studies of the effects of land use change on hummingbird populations are important for understanding ecosystem functioning, and conserving diversity. However, most of the ecological research about hummingbird – environment relationships in the tropical Andes focuses on community composition and organization (Abrahamczyk and Kessler 2010, Graham et al. 2012), and little is known about population dynamics of any species within this group. Considering hummingbirds' high metabolic rate, which imposes a high daily demand for energy (Powers and Conley 1994), they should be highly sensitive to changing environmental conditions (Stiles 1992). Nevertheless, species abundance and richness do not change significantly following forest degradation (Feinsinger et al. 1988, Stouffer and Bierregaard 1995, Renjifo 2001). Yet, because these evaluations are based on metrics of richness and abundance and provide limited information about the long term consequences of anthropogenic habitat alteration, more detailed studies of demographic responses to habitat change are warranted to confirm this finding.

Here I used a moderately long-term capture – recapture data set from the Ecuadorian Andes to determine how habitat specific demography of three hummingbird species, *Coeligena iris*, *Metallura tyrianthina* and *Eriocnemis luciani*, varies across three sites that have been altered by anthropogenic activities. These habitats include old second growth native forest, early successional native shrubs, and exotic forest plantation intermixed with native trees. To examine the influence of anthropogenic habitat alteration on habitat quality for the selected species, I obtained the population growth rate for each species in each habitat by combining individual survival and productivity (defined as offspring productivity) rates.

Methods

Study Area

This study was conducted in the western Andes in Cajas National Park and the contiguous Mazan Reserve (2°50'S, 79°15'W), Azuay province, Ecuador. The montane forest native to this region has been transformed by various anthropogenic activities, including agriculture, grazing and logging (White and Maldonado 1991). Today only the most inaccessible areas maintain mature native vegetation cover. Daily temperatures can show large fluctuations between 0 to 20 °C, but monthly averages do not present much variation and remain between 5 to 12 °C. Annual rainfall ranges from 1100 to 1800 mm, with a main rainy season from February - May, followed by a drier season from June – September, and a weak second wet season from October – November (Celleri et al. 2007).

In Cajas National Park I sampled hummingbirds in Llaviuco valley at 3150 m. Llaviuco is a U-shaped valley that was an active cattle ranch prior to 1996. This activity transformed the original montane forest vegetation such that only the steep slopes along the sides of the valley maintain mature native forest. My sampling area was located in early successional native shrubs which re-established naturally on the wide valley floor following the removal of cattle. This habitat was composed of shrubs of different species but was dominated by *Barnadesia arborea*, *Berberis lutea*, and *Salvia corrugata*. Canopy height ranged from 3-5 m, with a canopy cover <25%.

Mazan Reserve borders Cajas National Park and is also U-shaped valley of 2,640 ha. Mazan is managed for conservation under strict surveillance with only limited access afforded to researchers. The dominant vegetation in Mazan is high-elevation montane forest, which has been altered by selective logging before its declaration as a conservation area in 1986. Within Mazan I established two study sites: one in old second growth montane native forest (hereafter native forest), and the other in a forest with a large component of exotic tree species intermixed with remnant native tree species (hereafter introduced forest). The native forest was located at 3100 m. Tree species representative of this habitat included *Hedyosmum cumbalense*, *Symplocos quitensis* and *Myrcianthes* sp. The understory was represented by species such as *Salvia corrugata*, *S. hirta*, *Viola arguta*, and *Centropogon* sp. Canopy height reached 10 – 15 m, with a canopy cover >75 %. The introduced forest habitat was located at 3000 m, and was characterized by mixed stands of two species of mature exotic trees including *Eucalyptus globulus* and *Pinus patula*. Remnant native species occupied a dense understory composed of *Salvia hirta*, *Miconia* sp, and *Rubus floribundus*. Canopy height reached 15 – 20 m, with a canopy cover >75%. The spatial distances among study sites were 4.8 km between native shrubs and introduced forest, 0.6 km between introduced forest and native forest, and 4.7 km between native shrubs and native forest.

Bird Sampling

In each habitat I sampled hummingbirds with 20 mist nets (12 m x 32 mm mesh), placed along or perpendicular to existing paths, and covering an area of ~ 510 m in native forest, ~ 575 m in introduced forest, and ~ 505 m in native shrubs. At each site, nets were opened for two consecutive days, from dawn to dusk of day 1, and dawn to 1100 hours of day 2. Within this time frame nets were closed during strong winds or rain. Each individual hummingbird captured was identified to species and sex was determined using information from Ridgely and Greenfield

(2001). I also determined the age of individuals (adult or yearling) by examining the extent of striations on the bill (Ortiz-Crespo 1972), as well as plumage and feather characteristics (Pyle 2001). All hummingbirds were banded with a unique numbered metal band for identification of recaptures. Because mist nets only sample a portion of the vertical strata, they provide potentially biased estimates of abundance if there are large differences in the structure of vegetation or differences in the vertical use of the vegetation by birds (Remsen and Good 1996). However, given that hummingbirds actively forage in the lower strata of the forest, it is not expected this would be problematic, and mist nets have been used as a reliable method to study hummingbird populations elsewhere (Feinsinger et al. 1988, Stouffer and Bierregaard 1995).

I sampled hummingbirds for seven years, from 2006 to 2012, employing three sampling sessions per year per site, resulting in 21 sampling sessions per habitat. The sampling sessions within years correspond with the climatic seasons present in the study area (Celleri et al. 2007), including main wet (sampled mid-March to early-May), dry season (sampled mid-July to late-August), and second wet seasons (sampled late-Oct to late-Nov). The number of days within sampling session varied across years, but overall they were around four months (mean number of days within sampling session was 118, SD \pm 6.23).

Study Species

I focused analyses on three species of hummingbirds, each with >150 total capture histories across this study: *M. tyrianthina*, *C. iris* and *E. luciani*. These species represent a range in size and behavior of hummingbirds present in the study area (Tinoco and Astudillo 2007).

Coeligena iris is a large hummingbird (7.07 gm \pm 0.23 SD, N= 7), with a long straight bill (27.42 mm \pm 1.03 SD, N = 19). It has a restricted distribution from central Ecuador to northern Peru, usually at elevations of 2000-3300 m (Ridgely and Greenfield 2001). In the study area, this species inhabited mature forest, secondary forest, and borders (Tinoco and Astudillo 2007). *Coeligena iris* is considered a trap-liner (*sensu* Feinsinger and Colwell 1978), because it uses foraging routes for feeding and does not defend particular flower patches (Tinoco and Astudillo 2007).

Metallura tyrianthina is a small hummingbird (3.82 gm \pm 0.34 SD, N= 25) with a short bill (11.45 mm \pm 0.65 SD, N = 77). It is widespread along the Andes from Colombia to Peru at elevations of 2300-3400 m (Ridgely and Greenfield 2001). This species occupies a series of habitat types that include mature forest, secondary forest, borders and clearings (Ridgely and Greenfield 2001). *Metallura tyrianthina* is a generalist species (Feinsinger and Colwell 1978), that often defends feeding territories depending on the availability of resources and the presence of competitors (Tinoco and Astudillo 2007).

Eriocnemis luciani is a medium sized hummingbird (6.11 gm \pm 0.39 SD, N= 10), with a medium-sized straight bill (20.00 mm \pm 0.97 SD, N = 11). It is distributed along the Andes of Colombia and Ecuador at an elevational range of 2700-3400 m (Ridgely and Greenfield 2001). This species occupies the understory of mature forest, secondary forest and borders. It is a territorial hummingbird (Feinsinger and Colwell 1978) that heavily defends preferred flowering plants (Tinoco and Astudillo 2007).

Data analysis

For each of the study species and in every habitat I calculated and compared habitat specific parameters that included abundance, survival, and productivity. I then used survival and productivity estimates to explore how population growth rate, which indicates habitat quality, changes across habitat types. For *E. luciani*, I was unable to include native forest in the data analysis due to low capture rates of this species in this habitat, but for all other species all three habitat types were included in the analyses.

Differences in relative abundances of hummingbirds among habitat types were evaluated by generalized linear models (GLM) using the number of individuals captured in each sampling session as the response variable, and habitat type as the predictive factor. I included the total number of mist net hours employed in each sampling session (1 net open for 1 hr = 1 mist-net hour) as an offset during model specifications (Zuur et al. 2009) to control for the possible influence of differences in sampling effort across sites. Given that I sampled hummingbirds in different climatic seasons, I also included season as a predictive factor in the models. In order to explore the potential for temporal autocorrelation in the data originating from multiple samples of the same sites across time, I used autocorrelation functions (ACFs). ACFs are plots of the coefficients of correlation between observations at different times, and is a valuable tool for exploring autocorrelation (Shumway and Stoffer 2010). Since I did not detect temporal autocorrelation for any of the species, I used every sampling period as an independent sample. I then followed Zuur et al. (2009) to construct the GLMs and validate the models. I used GLMs with a Poisson error structure and a log link. I evaluated for overdispersion of the models by dividing the residual deviance over the degrees of freedom. For all three species of hummingbirds I detected overdispersion in the models; therefore I corrected the standard errors by using quasi-GLMs (Zuur et al. 2009).

I estimated an index of productivity for each species at each site by dividing the number of yearlings captured by the total number of adults captured, a common method in ornithological studies that has served as a robust predictor of population fluctuations (DeSante and Geupel 1987, Peach et al. 1996, DeSante et al. 1999). Since I captured yearling individuals across all seasons in the year, I used data from every sampling session to obtain this index. I used GLMs with a Gaussian distribution of errors, and an identity link function, to detect significant variation in the productivity index among habitat types (Zuur et al. 2009). To account for the effects of climatic seasonality in productivity, I also included season as a predictor in these models. I included the total number of individuals captured each sampling session as weights in the models to account for the potential influence of differences in capture probabilities across sampling sessions.

All models were constructed in the software R (R development core team 2009 give version of R that you used). Statistical inference of the models was determined by deviance tests using an *F*-distribution (Zuur et al. 2009). I also assessed differences within the factor habitat using the Tukey HSD implemented in the R package multcomp (Hothorn et al. 2009).

To estimate survival rates of the three hummingbird species, I employed mark-recapture analysis by constructing Cormack-Jolly-Seber (CJS) open population models (Lebreton et al. 1992) in the software MARK (White and Burnham 1999). CJS models only provide estimates of apparent survival because mortality cannot be distinguished from permanent migration. I created capture histories for each individual of every species by considering captures and recaptures for

every sampling session. The total number of sampling sessions was 21, which represented 20 transitions within sessions. I set capture intervals to 1 in MARK, which in my case represented four months. I started by constructing models where survival varied across sampling periods, but due to sparse data for each of the study species, I decided to test a set of *a priori* simpler models that varied in their assumptions of apparent survival (ϕ). These models were: apparent survival differed by habitat type (ϕ_h), or apparent survival was constant across habitat types (ϕ). I also constructed time since marked models (TSM) (Pradel et al. 1997). In TSM models, ϕ differs between the first capture interval (ϕ^1) from survival during subsequent intervals (ϕ^2); this was to account for the potential influence of transient individuals, which are those birds who are just passing through a site, or juveniles that disperse from the natal sites, and as such they are no longer available for capture after the first interval (Sandercock 2006). I was unable to assess differences in survival between yearling and adult hummingbirds because too few individuals were captured as adult birds after being banded as yearlings in a previous sampling session. Recapture probabilities (p) were also constructed with or without constraints of habitat type.

To select the best models describing the data I used Akaike's Information Criteria corrected for small sample size (AICc) (Burnham and Anderson 2002). The goodness of fit of the data was evaluated by parametric bootstrap as described in (Cooch and White 2013). I did not detect overdispersion in any of the data for the species modeled, therefore, model selection was based on AICc values. Models with the lowest AICc were selected as the best fit models. Top models differing by < 2 were considered statistically equivalent, and, in those cases, more than one model was selected as the best supported model (Burnham and Anderson 2002). Survival rates in the literature are usually presented as annual survival rates; for comparisons with other studies, I raised my four-month survival rates to the third power to obtain an annual survival rate.

To determine the influence of the different habitat types on the population dynamics and habitat quality of each species, I estimated discrete population growth rates with a Leslie matrix that included my four month sampling intervals:

$$\begin{vmatrix} 0 & 0 & \text{Fec} = \phi \cdot \beta \\ \phi & 0 & 0 \\ 0 & \phi & \phi \end{vmatrix}$$

where Fec= fecundity, ϕ = survival rate, and β = productivity.

For this calculation I used the mean productivity across sampling sessions weighted by the number of individuals captured. Survival rates were taken from the top ranked CJS survival models that included habitat as a factor. The three columns of the matrix correspond to different age classes: 1) individuals < 4 months old; 2) individuals that are 4-8 months old; 3) individuals that were > 8 months old or are adults. I could not classify birds from the first two age classes in the field, but for the Leslie matrix calculations this was not necessary because my survival rate estimates were the same for every age class. In this matrix I assumed a pre-breeding census, that populations were at equilibrium, that only individuals that were more than eight months old

could reproduce, and that there was no senescence. I calculated the dominant eigenvalue of this matrix or lambda using the package popbio in R (Stubben and Milligan 2007). The resulting lambda value of this matrix predicts the rate of population change by sample interval (4 months in my case). Values equal to 1 indicate that the number of births and deaths are balanced in the population. Values > 1 indicate that there are more births than deaths, which corresponds to a source population. Values < 1 correspond to sink populations where the number of deaths exceeds the number of births.

Results

Abundance

I recorded 217 captures of *C. iris*. Variation in abundance of this species was explained by a habitat x season interaction (Table 2.1). The number of *C. iris* captured was greater in the native forest and introduced forest relative to the native shrub (Figure 2.1). I also found a greater number of captures of this species during the dry season, except in the introduced forest where the greatest number of captures occurred during the main wet season (Figure 2.1). Evidence of movement of individuals among my study sites was limited to one individual that was originally banded in introduced forest but later moved to native shrubs.

I recorded 472 captures of *M. tyrianthina*. I found an additive effect of habitat and season explaining the observed variation in the number of *M. tyrianthina* captures (Table 2.1). The habitat with the greatest number of captures was native shrubs (Figure 2.1). A greater number of individuals were captured during the dry season than in either rainy season, and this result was maintained across habitat types (Figure 2.1). Movement among habitat types was evidenced by one individual that was first captured in introduced forest but was later caught in native shrubs.

I captured 352 *E. luciani* individuals across the study period. I found a habitat x season interaction best explained the number of individuals captured of this species (Table 2.1). *Eriocnemis luciani* was most abundant in the native shrubs (Figure 2.1). The effect of season differed among habitats, but overall a greater number of individuals were captured during the dry season compared to other seasons (Figure 2.1). Evidence of movements of *E. luciani* individuals among habitat types was detected in two individuals: one was banded in native shrubs, but was later caught in introduced forest; a second individual was first banded in introduced forest but moved to native shrubs.

Productivity

I did not find differences in productivity of *C. iris* across habitat types (Table 2.2, Figure 2.2). For *M. tyrianthina* the models identified a habitat effect (Table 2.2). This species had higher productivity in native shrubs and the introduced forest than in the native forest (Figure 2.2). Lastly, for *E. luciani*, productivity did not differ across habitat types (Table 2, Figure 2.2).

Apparent Survival

Survival rates for *C. iris* varied among habitat types (Table 2.3). Survival was higher in introduced forest ($\phi = 0.76, \pm 0.04$) and native forest ($\phi = 0.69, \pm 0.07$) than in native shrubs ($\phi = 0.29, \pm 0.16$). Using these rates of survival across a four-month interval, the annual survival rate of this species was 0.44 for introduced forest, 0.33 for native forest, and 0.02 for native shrubs.

The best model of survival for *M. tyrianthina* was a time since capture model that included habitat as a factor (Table 2.3). The influence of habitat in this model was related to differences in survival during the first capture interval: ϕ 0.38 (± 0.1) in native shrubs, ϕ 0.31 (± 0.11) in introduced forest, and ϕ 0.19 (± 0.08) in native forest. Survival rates during subsequent captures also presented differences across habitat types: ϕ 0.74 (± 0.04) for native shrubs, ϕ 0.82 (± 0.06) for introduced forest, and ϕ 0.86 (± 0.07) for native forest. These latter estimates of

survival indicated annual survival rates of 0.40 in native shrubs, 0.55 in introduced forest, and 0.63 in native forest.

Model inference by AICc values for survival models for *E. luciani* ranked a model with no effect of habitat as the top model (Table 2.3). In this time since capture model survival was ϕ 0.39 (\pm 0.05) during the first capture interval, and ϕ 0.78 (\pm 0.03) during subsequent capture intervals across habitat types. These results indicated an annual survival rate of 0.45 for this species across habitat types and seasons. The best ranked model of survival containing habitats as a factor (Table 2.3) indicated survival rates of ϕ 0.78 (\pm 0.03) in the native shrubs and ϕ 0.79 (\pm 0.04) in the introduced forest.

Population growth rate

The Leslie matrix for *C. iris* indicated that population growth rate was positive in native and introduced forests ($\lambda = 1.15$, $\lambda = 1.07$ respectively), whereas in native shrubs growth rate was negative ($\lambda = 0.40$). For *M. tyrianthina* population growth across habitat types was positive (native forest $\lambda = 1.08$, native shrubs $\lambda = 1.06$, introduced forest $\lambda = 1.04$). Lastly for *E. luciani* growth rate in both native shrubs and introduced forest was close to 1 (native shrubs $\lambda = 0.98$, introduced forest $\lambda = 0.95$).

Discussion

A critical gap in knowledge for effective conservation of birds in the Neotropics is information on how land use change influences demographic parameters of bird populations, which is itself a requisite for evaluating the probabilities of long term persistence of a population (Johnson et al. 2006, Mortelliti et al. 2010). Here I contribute to the knowledge of population dynamics of Neotropical birds by exploring habitat specific demography of three species of hummingbirds in vegetation types with different types of habitat alteration in the tropical Andes. I found that *M. tyrianthina* and *E. luciani* populations can persist in some altered forests. These species had positive or nearly positive population growth rates in all habitat types sampled, including anthropogenic altered native shrubs and introduced forest. However, *C. iris* populations appear to be negatively affected by some types of habitat alteration; I found negative population growth rates for this species in the native shrub habitat.

Low sensitivity of hummingbirds to land use change has been reported elsewhere (Feinsinger et al. 1988, Stouffer and Bierregaard 1995, Renjifo 2001). Latta et al. (2011), also using data from native and introduced forest at the Mazan valley sites, explored variation in abundance of birds from 1994–95 to 2006–07. They found no temporal change in abundance estimates of *C. iris*, *M. tyrianthina* or *E. luciani*. My results support the population trends found by Latta et al. (2011), given that my population growth estimates predicted that native forest and introduced forest within Mazan reserve are population sources for the these two hummingbird species. For native shrubs I found a different result; while this habitat type is a potential source for *M. tyrianthina* and *E. luciani*, it is likely sink for *C. iris*. This suggests that source sink dynamics allow the maintenance of *C. iris* populations in native shrubs. Its persistence in this habitat depends on immigration of individuals from source habitats elsewhere. The generality of my results for *M. tyrianthina*, *C. iris*, and *E. luciani* should be confirmed with large scale studies in this region. Nonetheless, my results show that a better understanding of population trends of birds in the tropical Andes requires and evaluation of habitat specific demographic parameters because each habitat in the landscape likely contributes differently to the overall population dynamics of these species (Pulliam and Danielson 1991).

The low value of native shrubs as habitat for *C. iris* but not the other species shows that responses to land use change are not uniform across species and that some hummingbirds may be more negatively affected than others by anthropogenic activities. *Coeligena iris* is among the species with largest body mass, and longest bill length in the region (Tinoco and Astudillo 2007). These traits are associated with its trap-lining behavior for foraging on spatially distant flowers with long corollas (Feinsinger and Colwell 1978). High body mass and specialized diet in birds have been linked to negative effects of anthropogenic habitat alteration in many species (Gray et al. 2007), and thus may also be characteristics that influence responses of hummingbirds. While I only evaluated three species, my results are consistent with existing empirical results suggesting that information on body mass and specialization may be useful to predict which species are more likely to be affected by land use change.

The correspondence between survival and productivity estimates across habitat types might provide useful information about which demographic factors account for habitat-specific population growth rates (e.g., Holmes et al. 1996, Arlt et al. 2008). For example, for *M. tyrianthina* I found positive growth rates across habitat types, as well as habitat-specific trade-offs in productivity and survival estimates. The productivity index for this species was lowest in

native forest, but this same habitat presented the highest survival estimate among habitat types. Thus, high survival probabilities in native forest may have compensated the low productivity to realize a positive growth rate for *M. tyrianthina*. For *C. iris*, although I did not find differences in productivity among habitat types, I detected decreased survival in native shrubs. Thus, even though *C. iris* occupying native shrubs likely can recruit the same proportion of individuals as in other habitat types, a low survival rate produces a negative population growth rate for this species in this habitat types. Thus, these findings illustrate the need for combining different demographic parameters to understand habitat specific population dynamics of species and habitat quality (see also Arlt et al. 2008).

A mechanistic understanding of why demographic parameters vary requires studies of factors that regulate survival and productivity. For hummingbirds, the amount of nectar available is a key factor influencing population dynamics (Stiles 1980, 1992). Hummingbirds' high metabolic rate, expensive foraging strategies, and relative low capacity to store energy (Wolf and Hainsworth 1971, Powers and Conley 1994), result in immediate demands for resource acquisition (Powers and Conley 1994), and makes them highly sensitive to changes in availability of resources (Feinsinger et al. 1988, Baltosser 1989, Russell et al. 1994). For example, Russell et al. (1994) found that body weight and density of *Selasphorus rufus* in California's Sierra Nevada was positively correlated with the density of nectar resources. Therefore, it is possible that quantity and quality of resources available for each species can be an important determinant of habitat quality for hummingbirds. In this context, the amount of resources available in anthropogenic altered habitat types may positively influence habitat quality for hummingbirds. The production of nectar of flowering plants may increase in second growth vegetation because of greater light in these more open, less complex habitat types (Linhart et al. 1987, Feinsinger et al. 1988, Costa and Magnusson 2003). Unpublished data taken by us in 2012 on the abundance of resources for hummingbirds in the understory of the habitat types sampled here, support this hypothesis. Species richness and abundance of flowers possessing a hummingbird pollination syndrome (large corolla, bright colors and exerted anthers and stigmas, Fenster et al. 2004), were greater in native shrubs (mean richness of flowering plants: 17 ± 4.04 ; mean abundance of open flowers 2417.3 ± 440), compared to native forest (mean richness: 10.6 ± 1.7 ; mean abundance 1047 ± 114.02) and introduced forest (mean richness: 8.6 ± 1.3 , mean abundance 358.6 ± 153.5). Thus, high resource availability in native shrubs may explain the positive growth rates and the greater abundance of *M. tyrianthina* and *E. luciani* in this habitat compared to other habitat types. However, given the low habitat quality of native shrubs for *C. iris*, there are potentially species-specific resource requirements that influence habitat quality for hummingbirds. Similarly, the apparent high value of introduced forest for all three hummingbird species can be evaluated in the context of the potential resources available to them. This vegetation type was dominated by *Eucalyptus globulus* trees, which has long flowering periods and a mass production of flowers with abundant nectar (Montaldo 1984, Willis 2003). These characteristics likely had a positive influence on the amount of resources available for hummingbirds. Finally, the high habitat value of native forest, despite the low availability of resources here, suggests that there are other factors besides resource availability that might influence habitat quality for hummingbirds. For example, it has been found that predation rates are lower in forest habitats than in anthropogenically degraded habitat types (Robinson and Sherry 2012). Certainly, future studies should focus on the potential factors that influence productivity and survival (e.g., resources, predation, parasitism) to clarify the trade-offs and the mechanisms that influence the habitat-quality relationships reported here.

Inference about habitat quality requires information not just about the abundance of a species in a habitat, but data on population growth rates (Van Horne, 1983, Pulliam 1988). For example, given the relatively long timeframe of this study, we could assume that species are at equilibrium population sizes in their habitats, suggesting that they will be able to maintain populations in the long term in all the studied habitats. However, our results showed that there could be sink habitats where populations likely persist only because immigration of individuals from source habitats, such as the case of *C. iris* in the native shrubs. Attempts to indentify habitat quality, therefore, should be based on detailed knowledge of the demographic dynamics of a species across habitats.

Data on demographic parameters of resident Neotropical birds are scarce (Latta et al. 2005, Ruiz-Gutiérrez et al. 2012), therefore it is not possible to compare my results with other studies in the region. To my knowledge, these are the first estimates of survival rates for any bird species in the tropical Andes (see reviews by Blake and Loiselle 2008, Ruiz-Gutiérrez et al. 2012). I found only four other studies that report survival rates of hummingbird species in the Neotropics. Parker et al. (2006) presented estimates of survival for *Heliodoxa jacula* (0.44-0.70), *Adelomyia melanogenis* (0.42-0.48), and *Phaethornis baroni* (0.34-0.36) for a dry forest site in Ecuador. Blake and Loiselle (2008) found a survival rate of 0.53 for *P. malaris* in lowland rainforest in Ecuador, Stiles (1992) reported a survival rate of 0.57 for *P. superciliosus* in the lowland rain forest of Panama, and Ruiz-Gutiérrez et al. (2012) estimated a survival rate of 0.43 for *Colibri thalassinus* in a Mexican montane forest site. My estimates of annual survival rate, with the exception of *C. iris* in *native shrubs*, are similar to these values. However, survival estimates for the vast majority of hummingbird species are unknown, therefore generalizing survival rates among this large and diverse group of species is currently not possible.

I issue some caveats about my data analysis. First, transient individuals and seasonal movements across vegetation types and elevation gradients in hummingbirds could produce low site fidelity (Parker et al. 2006, Wilson et al. 2011). Site fidelity is the probability that an individual returns to the same sampling area and is available to be caught again (Sandercock 2006). Low site fidelity can be problematic for survival rate models because the models cannot distinguish true survival from permanent emigration, potentially causing underestimation of survival rates. However, I attempted to overcome this problem by using time since capture survival models (Pradel et al. 1997), which distinguish survival rates of resident individuals from transients. Likewise, the correspondence of the survival rate estimates presented here to those of other studies suggests that these estimations are robust. Second, the presence of transient individuals can also produce biased estimates of the productivity index (DeSante et al. 1999). In my GLM models of productivity, I included the factor season to account for the potential temporal influx of individuals that might affect the productivity index and found no effect of seasonality on productivity. However, my estimates of productivity could be underestimated because of this factor. Third, estimates of population growth rate were produced with the assumption that adult survival and juvenile survival are the same. Studies of other bird species have found that that survival of juveniles could be lower than survival of adults (Anders and Marshall 2005). Even though my data set covers a period of seven years, low recapture rates prevented us from constructing CJS models with age or sex structure. These difficulties highlight the challenge of obtaining survival rates for Neotropical resident birds. Certainly more data are needed to estimate survival rates of different age groups. Fourth, I did not test how density dependent mechanism influenced population growth rates estimates, and attributed all the

observed demographic rates to interactions of the species with the studied habitats. Increase densities in animal populations can produce negative feedbacks on survival and population growth rates (Akçakaya et al. 1999). Despite these caveats, all approaches to measuring demography of wildlife populations have limitations (Anders and Marshall 2005, Ruiz-Gutiérrez et al. 2012), but given the lack of information about demographic parameters for birds in the tropical Andes, any insights from field studies in this region have considerable value. Moreover, provided that my sampling effort and methods are equivalent among habitat types, my measures of demography should indicate if there are differences in the demographic parameters evaluated among the study habitat types.

Conservation insights

National parks and protected reserves in the tropics have a key role in the maintenance of regional and worldwide biodiversity (Bruner et al. 2001). But, managers of the majority of these areas in the tropics do not have quantitative information about the status and population trends of the biodiversity they seek to protect (Chape et al. 2005). Here I contribute detailed demographic information about the status of populations of three hummingbird species in Cajas National Park and Mazan Reserve, important areas for bird conservation worldwide (Freile and Santander 2005). All three hummingbird species evaluated here had positive population growth rates inside these protected areas, reinforcing the importance of these reserves for the long term maintenance of populations of these species.

Native forest remnants in the south central Andes of Ecuador are scarce (Baquero et al. 2004), and are under constant pressure from human activities (White and Maldonado 1991). Therefore, it is important to assess the potential value of anthropogenically altered habitat types for the maintenance of biodiversity (Şekercioğlu et al. 2007, Chazdon et al. 2009). Two of the three hummingbird species evaluated here, *M. tyrianthina* and *E. luciani*, had positive growth rates, even in the anthropogenic altered shrubs; likewise, introduced forest appeared to be a relatively good quality habitat for each of the hummingbird species analyzed. These vegetation types are among the principle habitat types resulting from land use transformation in the Ecuadorian Andes (Baquero et al. 2004). As such, this study has wider regional application because these results suggest that these species may be able to maintain populations even under widespread effects of anthropogenic land use change. However, there are likely to be thresholds where habitat alteration beyond certain levels will result in negative effects on demographic parameters (Guénette and Villard 2005). In addition, it is likely that not all species of birds will respond as positively to habitat alteration as the hummingbird species reported here. Therefore, my finding that human-degraded vegetation types can be valuable for the studied species, but should not be extrapolated to other taxa or other types of habitat alteration.

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Tables

Table 2.1. Generalized linear model describing the effects of habitat (native forest, native shrubs and introduced forest) on the abundance of three hummingbird species obtained by captures with mist nets in constant-effort capture-recapture monitoring from 2006-2012 in the southern Ecuadorian Andes.

Species	<i>df</i>	<i>F</i>	<i>p</i>
<i>Coeligena iris</i>			
Habitat	2, 60	11.91	<0.001
Season	2, 58	4.79	0.01
Habitat x season	2, 54	2.57	0.04
<i>Metallura tyrianthina</i>			
Habitat	2, 60	30.73	<0.001
Season	2, 58	11.73	<0.001
Habitat x season	2, 54	0.52	0.71
<i>Eriocnemis luciani</i>			
Habitat	1, 40	89.95	<0.001
Season	2, 38	25.88	<0.001
Habitat x season	2, 36	5.15	0.01

Table 2.2. Generalized linear model describing the effects of habitat (native forest, native shrubs and introduced forest) on the productivity index of three hummingbird species. The productivity index was obtained by dividing the number of yearlings captured over the number of adults captured in each sampling session, from 2006-2012, in the Southern Ecuadorian Andes.

Species	<i>df</i>	<i>F</i>	<i>P</i>
<i>Coeligena iris</i>			
Habitat	2, 49	0.37	0.69
Season	2, 47	1.38	0.26
Habitat x season	4, 43	1.09	0.37
<i>Metallura tyrianthina</i>			
Habitat	2, 60	3.76	0.03
Season	2, 56	0.33	0.72
Habitat x season	4, 52	0.63	0.64
<i>Eriocnemis luciani</i>			
Habitat	1, 35	1.74	0.20
Season	2, 33	0.45	0.64
Habitat x season	2, 31	2.58	0.08

Table 2.3. Results of Cormack-Jolly-Seber models of apparent survival of three hummingbird species in three habitat types in the south Andes of Ecuador. Habitats included: native forest, introduced forest, and native shrubs. ϕ represents survival rate and p represents recapture probability. ϕ^1 and ϕ^2 represent “Time since marked” models which calculate different survival rates during the first capture interval (ϕ^1) from survival during subsequent intervals (ϕ^2).

Species	n	Top models	K	AICc	Δ AICc	w_i
<i>Coeligena iris</i>	176	$\phi(\text{habitat}) p(\cdot)$	4	315.63	0.00	0.74
		$\phi^1(\cdot) \phi^2(\cdot) p(\cdot)$	3	319.65	4.02	0.10
		$\phi^1(\text{habitat}) \phi^2(\text{habitat}) p(\cdot)$	7	319.74	4.11	0.10
		$\phi(\cdot) p(\cdot)$	2	320.57	4.95	0.06
<i>Metallura tyrianthina</i>	402	$\phi^1(\text{habitat}) \phi^2(\text{habitat}) p(\cdot)$	7	590.82	0.00	0.70
		$\phi^1(\cdot) \phi^2(\cdot) p(\cdot)$	3	594.01	3.19	0.14
		$\phi(\cdot) p(\cdot)$	2	594.06	3.24	0.14
		$\phi(\text{habitat}) p(\cdot)$	4	597.54	6.73	0.02
<i>Eriocnemis luciani</i>	219	$\phi^1(\cdot) \phi^2(\cdot) p(\cdot)$	3	642.23	0.00	0.86
		$\phi^1(\text{habitat}) \phi^2(\text{habitat}) p(\cdot)$	5	645.94	3.71	0.14
		$\phi(\cdot) p(\cdot)$	2	658.96	16.73	0.00
		$\phi(\text{habitat}) p(\cdot)$	3	660.86	18.62	0.00

Figures

Figure 2.1. Mean number of individuals captured (\pm SE) of three species of hummingbirds in three habitats and three climatic seasons in the southern Andes of Ecuador. Mean values were weighted by the number of individuals captured each sampling session. Letters indicate significant differences among habitat types ($p < 0.05$) calculated using Tukey Test.

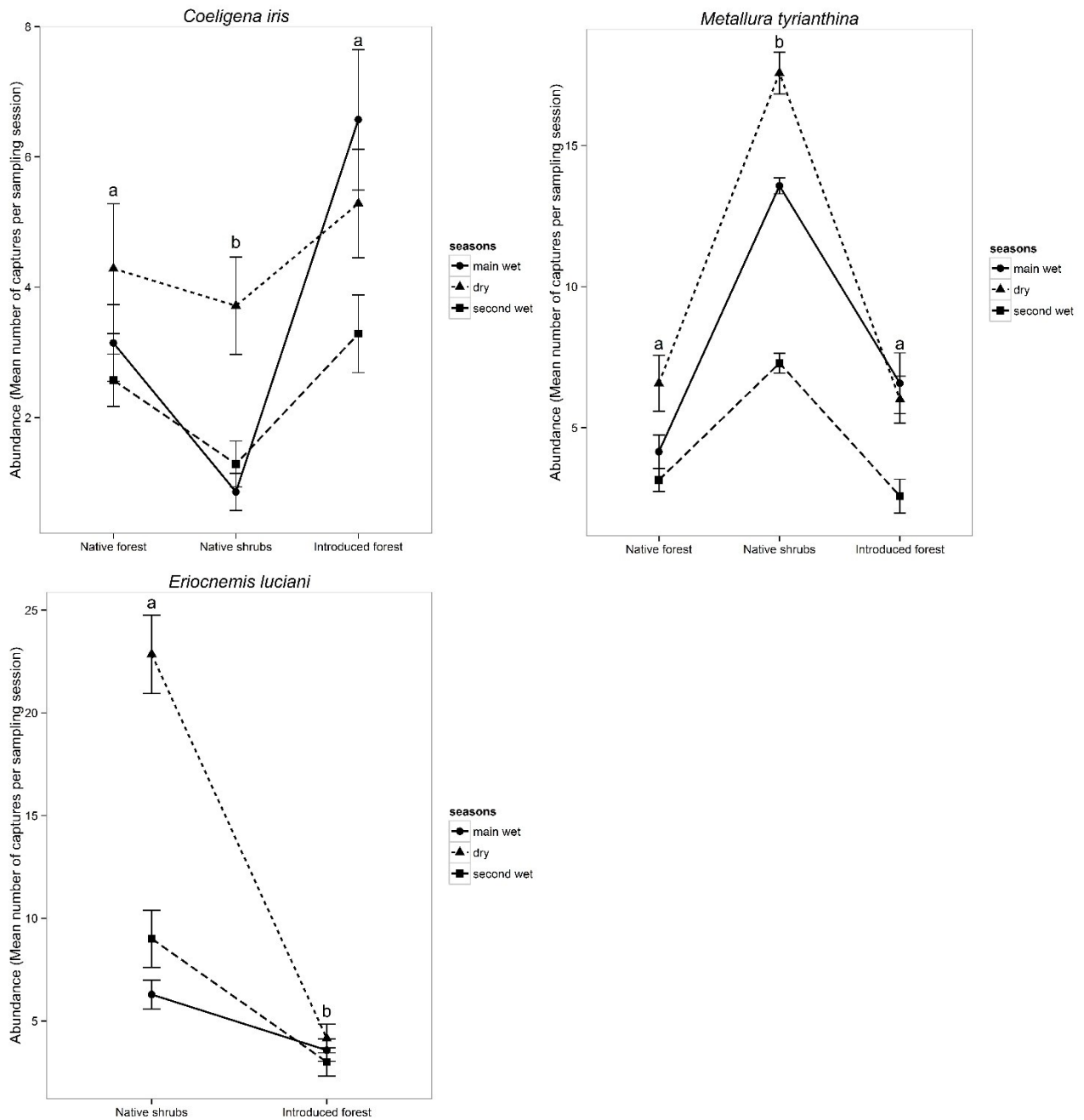
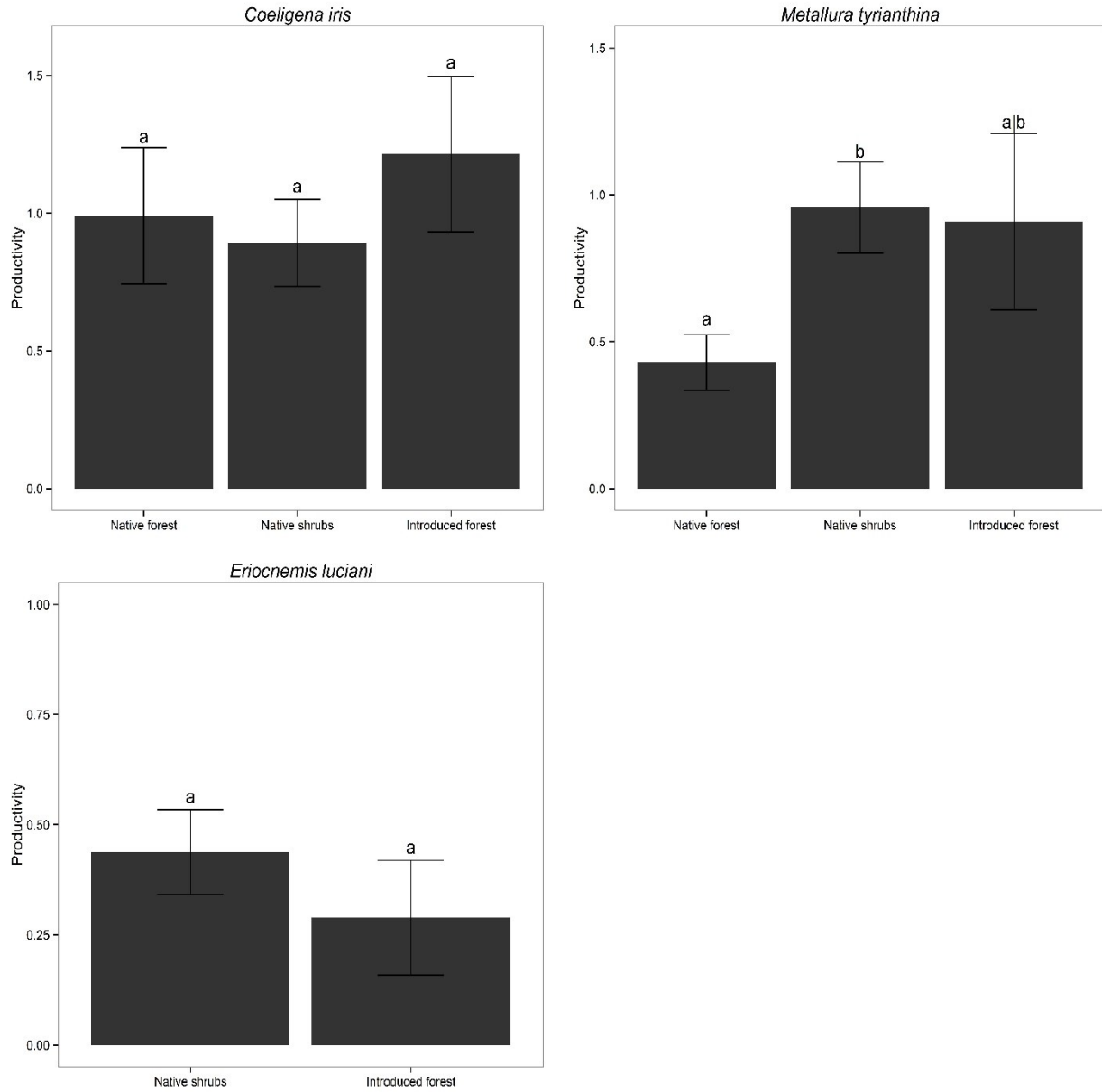


Figure 2.2. Mean productivity index (\pm SE) of three species of hummingbirds captured in three habitats in the southern Andes of Ecuador, 2006-2012. Mean values were weighted by the number of individuals captured each sampling session. Letters indicate significant differences among habitat types ($p < 0.05$) calculated using Tukey posthoc test.



Chapter 3: The Effects of Land Use Change on Tropical Hummingbirds Reveal Differences in Taxonomic and Functional Diversity

Introduction

Land use change is one of the most important drivers of species loss worldwide (Pimm et al. 2006). The negative effects of land use change are often studied in the context of taxonomic diversity, but they can also affect functional diversity (Villéger et al. 2010), which is the range of species functions in the ecosystem (Petchey and Gaston 2006). Species interact with the environment through their functional traits (i.e., any trait directly influencing organismal performance, *sensu* McGill et al. 2006). Thus, any alteration of environmental characteristics driven by land use change can potentially modify the types and ranges of functional traits represented in assemblages (Flynn et al. 2009, Mouillot et al. 2013). However, while ecologists have long acknowledged that factors influencing taxonomic diversity act at a variety of spatial scales – from local vegetation structure or resource abundance to the composition of vegetation in the broader landscape – studies of functional diversity have yet to be evaluated at multiple scales. I evaluated how taxonomic and functional diversity are affected by on-going land use change in the tropical Andes by considering how hummingbird assemblages respond to landscape-scale and local-scale characteristics in landscapes with different land uses.

Studies have demonstrated the value of measuring functional diversity across habitats impacted by human land use by showing that functional diversity does not always correlate with taxonomic diversity (Flynn et al. 2009, Cadotte et al. 2011). For example, if communities are structured by highly redundant species (i.e., species with similar functional roles), species loss will likely have a stronger negative effect on taxonomic diversity than on functional diversity, because functional diversity will be maintained (Flynn et al. 2009). A different scenario occurs in communities structured by a high number of species with unique functional roles. In these communities, the loss of a species can have greater consequences for functional diversity than for taxonomic diversity because the loss of a species could eliminate a functional role that is not replaced (Villéger et al. 2010). Therefore, a broader assessment of the effects of land use change on biodiversity requires multifaceted approaches to measure the consequences of environmental degradation on biodiversity.

Land use change modifies environmental conditions at multiple spatial scales which can cause variation in the composition of assemblages. At the local-habitat scale, a common result of the replacement of forest is the simplification of the vegetation structure of a habitat (in terms of the presence of large trees, a closed canopy cover, etc.), and changes in the types and abundance of resources (Breitbach et al. 2012, Albrecht et al. 2012). At the landscape scale, anthropogenic activities modify the types and distribution of habitats present in a landscape (Fahrig 2003). This results in a landscape mosaic with different landscape elements, each of which makes a distinct contribution to the maintenance of biodiversity (Chazdon et al. 2009). On the one hand, a decrease in the coverage of the original habitat in the landscape may affect the persistence of habitat specialists (Betts et al. 2007, Martensen et al. 2012). On the other hand, an increase in the number of habitat types in a landscape may sustain populations of other species that use the resources provided by the novel habitat types (Hendrickx et al. 2007, Haslem and Bennett 2008). While extensive work has documented how local and landscape factors

influence taxonomic diversity (Betts et al. 2007, Hendrickx et al. 2007, Tinoco et al. 2013), few studies have disentangled how environmental characteristics at multiple spatial scales affects functional diversity, especially in species-rich systems like the tropics (Tschardt et al. 2008).

Hummingbirds are particularly suitable for the study of the effects of land use change on biodiversity. They are among the most species-rich and abundant groups of birds in the tropical Andes (Rahbek and Graves 2000), and they play a key role in the ecosystem as pollinators of multiple species of plants (Cruden 1972, Stiles 1981). Hummingbirds vary in morphology, habitat requirements, and foraging roles (Feinsinger et al. 1988, Stiles 1995, Temeles and Kress 2003), resulting in high levels of functional diversity (Feinsinger and Colwell 1978). While hummingbird taxonomic diversity is often considered relatively insensitive to land use change (Feinsinger et al. 1988, Stouffer and Bierregaard 1995, Renjifo 1999), functional diversity of hummingbird assemblages has yet to be examined in this context.

Here, I use data collected in six landscapes in the Andes of Ecuador with different types of land uses that varied in the amount of coverage of native vegetation, cattle pastures and exotic tree plantations, to explore how local and landscape scale characteristics influenced functional and taxonomic diversity of hummingbirds. First, I assessed how local scale factors (i.e., vegetation structure, richness of flowering plants, nectar availability) and landscape scale factors (i.e., landscape diversity, edge density and coverage of native vegetation) influenced variation in hummingbird taxonomic and functional diversity. Second, using extensive knowledge of functional traits in hummingbirds, I developed a set of predictions for how these traits may influence a hummingbird's response to the transformation of native vegetation.

1) I predicted that hummingbirds with long bills would be negatively affected by land use change because they have greater levels of diet specialization than those with short bills (Snow and Snow 1972, Feinsinger et al. 1988) Chapter 4). Diet specialized species are more vulnerable to potential variation in the abundance of their restricted set of resources after anthropogenic alteration (Cleary et al. 2007, Bommarco et al. 2010).

2) I expected hummingbird body mass would be positively correlated with sensitivity of species to land use change. Larger animals tend to have smaller populations, larger home ranges, and higher energy requirements (Brown et al. 1978). These are characteristics that can increase the vulnerability of a species to the environmental modifications brought by land use change (Davidson et al. 2009, Newbold et al. 2013).

3) I predicted that hummingbirds with high wing loading (ratio of body mass to wing area) and broad wings would be at a disadvantage in highly altered habitats. Wing morphology influences flight behavior in hummingbirds, which affects their foraging strategy and territorial behavior (Altshuler et al. 2004, Stiles et al. 2005, Stiles 2008). Low wing loading and narrow wings facilitate fast flight, while high wing loading and broader wings increase maneuverability (Feinsinger and Chaplin 1975). Land use change should benefit species with traits that confer higher mobility because this should reduce the energetic cost of tracking resources through highly heterogeneous environments that could include low quality habitat types (Henle et al. 2004, Luck et al. 2012).

4) Lastly, tarsus length should influence how hummingbirds respond to land use change. This trait is associated with perching behavior in hummingbirds during feeding: species with longer tarsi tend to regularly perch on flowers for feeding (Stiles 2008). However, this behavior is also influenced by flower architecture, because perching in hummingbirds requires floral structures with landing platforms (Miller 1985). Therefore, any change in the types of flowers available could potentially alter the use of perching as a foraging option in hummingbird species.

Methods

Study area

I conducted this study in the western Andes of the Azuay province in southern Ecuador at elevations between 3000 and 3300 m above sea level (Figure 3.1). This area has a complex topography, mean annual precipitation ranging from 1100 to 1800 mm, and monthly mean temperatures that range from 5-12 C° (Celleri et al. 2007). At present, this area is mostly covered by cattle pastures, with remnants of Andean native forest confined to steep slopes (White and Maldonado 1991).

Study design

I chose six inter-Andean linear valleys within this study area, which varied in the amount that native vegetation had been transformed into other types of land use (Figure 3.1). Landscapes varied from an almost intact valley dominated by native vegetation to a highly modified valley with a mosaic of pastures and native vegetation remnants (Table 3.1). I chose valleys partially isolated from other areas by steep slopes (Figure 3.1), which likely restricts hummingbird movement to each valley, as evidenced by the fact that there have only been three captures of hummingbirds between valleys during eight years of systematic mist-netting (Chapter 2).

In each valley, I placed one plot of 2.2 km by 1 km (200 ha; I refer to these plots as landscape units or LUs). LUs were placed in the middle of each valley, with the restriction that they were within 3000 m to 3300 m in elevation (Figure 3.1). The dimensions of the LUs and their locations were chosen to fit the linear shape of the valleys. The elevation range was chosen because it corresponds to tropical high montane forest (following Baquero et al. 2004). Pairwise distances between each LU ranged from 2.5 km to 34 km (Figure 3.1).

Characteristics of Landscape Units

I used aerial photographs 1:5,000 of the study area provided by SIGTIERRAS - MAGAP (2010) to quantify land-cover types in each LU. Each photograph was manually digitized using ArcMap ver. 9.0 (ESRI 2011) and classified using the following land coverage types: native vegetation, pastures, and exotic forest. Native vegetation included both native forest and shrubs as the photos did not permit finer classification. However, differences in vegetation structure within the native vegetation were minor compared to the differences with the other land-cover types. The results of this classification were verified in the field.

To describe the structure of each LU, I obtained the following measures from the digitized photograph: 1) native vegetation coverage, 2) edge density, and 3) landscape diversity. Edge density was calculated as the amount of edge in the landscape divided by the total landscape area using Patch Analyst ver. 5 (Elkie et al. 1999). Landscape diversity was calculated using the Simpson index:

$$LandDiv = 1 - \sum_{i=1}^n P_i^2$$

LandDiv defines the probability that two equal sized patches of the landscape, selected at random, belong to different cover types (Nagendra 2002). P_i is the proportion of the landscape covered by the land use type i . LandDiv ranges from 0 to 1 where higher values represent greater landscape diversity. These three landscape characteristics were chosen because they describe the land use change in my study area. Compared to the highly used LUs, less used LUs had greater coverage of native vegetation, lower values of landscape diversity, and lower edge density. In addition, these three characteristics are relevant to birds, in general, and likely hummingbirds in particular. Bird species composition is often influenced by the amount and configuration of native vegetation; large blocks of native vegetation tend to harbor more forest species (Tinoco et al. 2013). Edge density is often related to resource availability, where fruits and flowers are more abundant at edges because of increased light (Hagen and Kraemer 2010). The characteristics of each LU are presented in Table 3.1.

Local habitat characteristics

I positioned 12 vegetation survey plots with a 20 m radius at 200 m intervals in the center of each LU (Figure 3.1). I quantified vertical vegetation complexity, canopy cover, abundance of shrubs, and number of trees in different diameter at breast height (DBH) classes following a protocol commonly used in bird studies (James and Shugart 1970). From the center point of the plot I established four 20 m long transects in each of the four cardinal directions. To obtain foliage-height profiles, I placed a 3 m pole at 4 m intervals along each transect and recorded the presence or absence of vegetation touching the pole at 0.5 m intervals from 0 to 3 m. Beyond 3 m, I visually estimated the presence or absence of vegetation at 1 m intervals to the top of the canopy. Using the foliage-height profiles, I calculated a Shannon diversity index to quantify vertical vegetation complexity in each plot (Hays et al. 1982). I visually estimated the canopy cover using a scale of 1 to 5 (1 = 0-19%, 2 = 20-39%, 3 = 40-59%, 4 = 60-79%, 5 = 80-100%). The foliage-height profile and canopy cover were averaged across all readings inside a vegetation plot ($n = 20$). The abundance of shrubs (plants with < 3 cm DBH) was obtained by counting the shrubs that contacted the extended arms of a person walking along each transect. Finally, all trees present in the plot were counted and assigned to one of four different DBH categories: 3-8 cm, 9-15 cm, 16-23 cm, 24-38 cm, and > 38 cm.

In order to obtain a composite description of the vegetation structure in each plot, I performed a principal components analysis (PCA) on all the vegetation structure variables measured in each plot (foliage vertical complexity, canopy cover, abundance of shrubs, and number of trees of five different DBH classes). Before performing the PCA, I checked for correlations among variables to avoid over-weighted eigenvalues (Jolliffe 2002). Only three Pearson correlation coefficients among all pairwise combinations of variables were in the range of 0.70 to 0.80. Therefore, I did not remove any variables in the PCA. The resulting principal components were used as new explanatory variables that represent the structure of the vegetation in each plot. Principal component one (PC1) and principal component two (PC2) accounted for 54.2 % and 20.9 % of the variation respectively, which together represented 75.1% of the variation of the original variables. PC1 represented a gradient with plots dominated by open vegetation to plots with closed vegetation (Table 3.2). PC2 depicted a gradient from plots with large numbers of large trees to plots dominated by shrubs (Table 3.2).

In each plot I also measured species richness and abundance of flowering plants during four survey periods per year during 2011 and 2012 (from February to August each year). LUs were sampled sequentially and in the same order during each survey period. I counted the number of open flowers of each plant species in each plot. When a complete flower count for a given plant was not possible, I estimated the total number of flowers by extrapolating the number of flowers in a sampled portion to the total plant area covered with flowers. I only included plant species that are known to be used by hummingbirds in the study area (Chapter 4). Mean sugar production per flower of each species was obtained from flowers that were bagged for 24-h to prevent access to hummingbirds, after which I extracted nectar with capillary tubes and recorded readings of sugar concentration with a handheld refractometer. Flowers were depleted of nectar before bagging (the number of flowers sampled and nectar produced per species are provided in Table 3.3). Sugar production was calculated as the product of nectar volume (ml) and sugar concentration (sugar mg /ml) following the table provided by (Kearns and Inouye 1993). Sugar production rates per point count and sampling period were obtained by multiplying the mean sugar production over 24 hours per flower with the total number of flowers available from the respective plant species in each plot. This measure is an indirect indicator of the amount of energy available for hummingbirds (Feinsinger and Colwell 1978; Feldman and McGill 2013). Abundance of flowers and nectar production were highly correlated ($r = 0.87$), so I only used sugar production for analysis. Although this is a crude measure of sugar availability, but it is a time-effective method for assessing community resource availability for pollinators and has been shown to be a more reliable measure of resource availability than direct flower counts (Potts et al. 2003, Ornelas et al. 2007).

Hummingbird sampling

In each of the 12 vegetation survey plots located in every LU, I censused hummingbirds using the point count method (Hutto et al. 1986). The censuses were performed during the same survey periods used to sample the richness and abundance of flowers. Each point count was surveyed for 10 minutes by two observers who identified and counted all hummingbird individuals visually or acoustically detected in a fixed radius of 30 m. Hummingbirds flying over the plot were excluded. All the point counts within a LU were sampled on the same day between 6h00 and 10h00, and on days without rain. The starting time of each point count was altered among survey periods to account for potential differences in detections among point counts due to the time of day

Species abundance was obtained using the double observer approach with the software DOBSERV (Nichols et al. 2000). For this method, two observers independently record study animals to provide detection probabilities by combining information about the individuals detected by one observer but not by the other (Nichols et al. 2000). Then, a joint detection probability for both observers during a survey is obtained:

$$P_{\text{joint}} = 1 - (1 - p_{\text{obs1}})(1 - p_{\text{obs2}})$$

where p_{obs1} and p_{obs2} are the detection probabilities of observer 1 and 2, respectively (see more details in Nichols et al. 2000). I used the joint detection probability to calculate corrected abundance estimates of each species for each point during every sampling period. A critical assumption of this method is the independent detection of birds by the two observers, which is hard to accomplish in the field when two observers are performing the census simultaneously.

Despite this limitation, the double observer approach is preferable to other methods for which detection probabilities of all species are assumed to be 1, as species detectability varies depending on behavior, size and plumage coloration (Nichols et al. 2000).

To determine whether the observed species richness in each LU was an accurate representation of total species richness in each valley, I evaluated whether sample-based rarefaction curves reached an asymptote. Curves were considered asymptotic if the last two values were within 2% of each other (Foggo et al. 2003). Rarefaction curves were constructed using the package *Vegan* in R (Oksanen et al. 2013). Overall, all rarefaction curves reached an asymptote (Appendix I) and I considered my observed species richness as accurate representations of total species richness at each LU.

Taxonomic and Functional diversity

I obtained taxonomic and functional diversity of hummingbirds at each point count using the annual mean abundance of each species. Taxonomic diversity was calculated by the Simpson index (Simpson 1949) as:

$$1 - \sum_{i=1}^s P_i^2$$

where P_i is the proportional abundance of the i th species. This index measures the probability that two individuals randomly chosen are two different species.

I considered three morphological functional traits in hummingbirds: body mass (weight of a live individual), culmen length (length of the bill from base to tip), and tarsus length (length from the outer bend of the tibiotarsal articulation to the base of the toes). In addition, I included wing aspect ratio (the quotient of twice the square of the wing length and wing area), and wing load (the ratio of body mass to wing area). Low wing loading represents a low body mass to wing area ratio, while a high aspect ratio denotes narrow wings. More details of how to obtain these measures can be found in (Stiles 1995). Functional diversity was represented by the Rao quadratic diversity index (Botta-Dukát 2005):

$$\sum_{i=1}^s \sum_{j=i+1}^s d_{ij} P_i P_j$$

where d_{ij} is the difference between the i th and the j th species. The distance d_{ij} was calculated from a species by trait matrix. Therefore, it is the sum of trait dissimilarity among all possible pairs of species, weighted by the product of species abundances. If $d_{ij} = 1$ for all $i \neq j$, the Rao index is reduced to the Simpson index, a property that facilitates comparison between taxonomic and functional diversity (De Bello et al. 2006). The Rao functional diversity index is sensitive to the influence of correlated traits (Lepš et al. 2006). Given that I was interested in measuring functional diversity beyond what is explained by body size correlations, I used the residuals from linear regressions of total culmen length and tarsus length against body mass as uncorrelated functional traits that represented relative culmen length and relative tarsus length, respectively. This approach is common for removing the effects of size in ecomorphological studies (Reist 1985). The Rao index was obtained using the package *FD* in R (Laliberté and Legendre 2010).

Data Analysis

I used linear mixed models fitted by maximum likelihood to examine how local scale factors (PC1, PC2, richness of flowering plants, sugar production) and landscape scale factors (landscape diversity, edge density, native vegetation coverage; Table 3.4) influenced species richness, taxonomic diversity, and functional diversity of hummingbirds. Richness of flowering plants, sugar production, edge density, and landscape diversity were all log-transformed because histograms of these variables revealed they were not normally distributed. After transformation, these variables were normally distributed. The random components of the models were landscape identity and year, to control for spatial-temporal correlations in the structure of the data (i.e., point counts sampled within a landscape and samples taken during the same year). The local scale and landscape factors were not significantly correlated; thus, I constructed models with all possible combinations of plot and landscape level factors, but did not include interactions because of too few degrees of freedom. I used multimodel inference to determine the most important factors influencing species richness, taxonomic, and functional diversity. Models were compared and ranked by Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) using the package MuMin in R (Barton 2011). I obtained model average coefficients from the top selected models with $\Delta AICc < 2$. Statistical significance of a factor was inferred when its 95 % confidence intervals (CI) excluded zero values (Burnham and Anderson 2002). Since the pairwise distances among LUs were not equal, I checked for spatial autocorrelation in the residuals of the models by assessing the significance of Morans' I values using the package spdep in R (Bivand 2013). None of the models revealed significant spatial autocorrelation.

To explore associations between hummingbird traits and environmental characteristics, I used RLQ analysis (Doledec et al. 1996). RLQ is a constrained ordination that maximizes the covariance between sites and species on the basis of environmental variables and species' traits. RLQ analysis employs three matrices, a matrix R ($n \times m$) describing the environment (m) in sites (n), a matrix L ($p \times n$) with information on species abundances (p) in sites (n), and a Q matrix ($s \times p$) describing characteristics of traits (s) for species (p). In my case, the matrices were composed of: R, environmental parameters at each plot (landscape and local habitat characteristics); L, species abundances at each plot; and Q, functional traits of each hummingbird species (body mass, relative culmen length, relative tarsus length, wing loading, and wing aspect ratio). I followed the procedure described in (Doledec et al. 1996) to perform this analysis. First, a correspondence analysis was done in the L matrix. Species with less than three records across the study period were excluded from this analysis. Second, the R and the Q matrices were analyzed by two independent PCA's. Third, the RLQ analysis was conducted on the cross matrix of R, L, Q. The analysis calculates an $s \times m$ matrix that contains a measure of the link between traits and environmental variables mediated by species abundances. An eigenanalysis of this new matrix creates a set of axes that maximize the covariance between R and Q matrices. The significance of the co-structure between R and Q matrices was obtained by 999 Monte Carlo permutations. This test performed permutations on the rows of the R and Q matrices, and compared the total inertia obtained by permutations with the observed total inertia. A probability of less than 0.05 of the observed inertia was considered as significant co-structure between R and Q matrices. RLQ was performed using the package ade4 in R (Dray and Dufour 2007).

To consider the spatial hierarchy in the structure of my dataset (local habitats embedded within landscapes), I performed RLQ analysis at two scales: a basic RLQ, including only landscape variables (coverage of native vegetation, landscape diversity, and edge density) on matrix R; and a partial-RLQ using only the variables measured at the local scale (PC1 and PC2 of the vegetation structure, richness of flowering plants, and nectar production) on matrix R. The partial-RLQ is a modification of RLQ that allowed us to explore the relationships within local scale factors and traits controlling for environmental differences at the landscape scale. In the partial-RLQ, R and L matrices were replaced by modified R and L matrices, which were constructed by the residuals of matrix regressions of variables that described the landscape against the original R and L matrices (Wesuls et al. 2012). The partial-RLQ implemented in the package ade4 (Dray and Dufour 2007), only uses categorical variables for the landscape variables; therefore, I include of each LU as a categorical variable in the analysis.

Results

I recorded 15 hummingbird species during my 576 point counts. The most abundant species across the study period were *Metallura tyrianthina*, *Eriocnemis luciani*, and *Coeligena iris* (Table 3.5).

There was large variation in the morphological traits of hummingbird species (Table 3.6). The species with the lowest body mass and culmen length were *Chaetocercus mulsant* and *Ramphomicron microrhynchum*, in contrast to other species that were up to almost 3 times heavier and had longer culmens, such as *Pterophanes cyanopterus* and *Ensifera ensifera*. Hummingbirds also presented large variation in wing morphology. Species with high wing loading included *C. mulsant* and *R. microrhynchum*; while species with low wing loading were *M. tyrianthina*, *Aglaeactis cupripennis* and *P. cyanopterus*. Species with narrow wings, indicated by a higher aspect ratio, were *E. luciani* and *M. baroni*; while the species with broad wings were *M. tyrianthina*, and *Lesbia nuna*. Culmen length and tarsus length were correlated with body mass (Table 3.7).

Hummingbird diversity

Several models explained differences in species richness of hummingbirds (Table 3.8). The only variable included in all of these models was richness of flowering plants (Table 3.8), and model averaging indicated that this variable was significantly associated with variation in species richness ($\beta = 0.12$, $SE = 0.05$). All top ranked models ($\Delta AICc < 2$) of taxonomic diversity of hummingbirds included the local scale factor richness of flowering plants and the landscape scale factors edge density and landscape diversity (Table 3.8). Richness of flowering plants was significantly positively associated with variation in taxonomic diversity ($\beta = 0.04$, $SE = 0.01$) (Figure 3.2a), however, there was large uncertainty in the relationship of edge density and landscape diversity with taxonomic diversity, as indicated by the large confidence intervals of their coefficients (Figure 3.2a).

Multimodel inference of functional diversity consistently selected the local scale factors, vegetation structure (PC1) and richness of flowering plants, together with the landscape scale, native vegetation coverage, edge density, and landscape diversity in the top ranked models ($\Delta AICc < 2$) (Table 3.8). Model averaged coefficients and confidence intervals supported the importance of all these factors as significantly associated with variation in functional diversity (Figure 3.2b). PC1 had a negative relationship with functional diversity ($\beta = -0.17$, $\pm SE = 0.05$), while richness of flowering plants, native vegetation coverage, edge density and landscape diversity ($\beta = 0.07$, $SE = 0.03$; $\beta = 0.48$, $SE = 0.05$; $\beta = 0.14$, $SE = 0.05$; $\beta = 0.30$, $SE = 0.14$ respectively) were positively correlated to functional diversity.

Trait-environment relationships

RLQ analysis indicated a significant relationship between landscape scale variables and species traits (Permutation test; $p = 0.002$). Axis I accounted for 95.3% in the RLQ analysis, while axis II only represented 2.77%; therefore I only interpreted loadings of the factors on the first axis. Important variables included, coverage of native vegetation with a positive loading, and landscape diversity and edge density, which had negative loadings. Thus, this axis depicted

landscapes with low levels of alteration, because high native vegetation coverage, and low values of landscape diversity and edge are all descriptors of less altered landscapes (Table 3.1). The positive loadings of body mass, wing aspect ratio, and relative tarsus length indicated an association of these traits with less altered LUs (Figure 3.3a). Species with positive loadings, and thus associated with characteristics of less altered LUs, were *E. ensifera*, *P. cyanopterus*, *C. iris* and *A. cupripennis* (Figure 3.3b); while species associated with the characteristics of more altered LUs included *M. tyrianthina* and *L. nuna*.

Partial-RLQ of local scale factors, which controlled for differences in landscape context, showed that at the local spatial scale the relationships between environmental characteristics and species were not significant (Permutation test; $p = 0.86$). Therefore, I did not evaluate the results from this analysis.

Discussion

On-going land use change in the tropical Andes influenced taxonomic and functional diversity differently. Functional diversity of birds was affected by land use change at a landscape scale, as indicated by the positive association between the amount of native vegetation coverage in a landscape and functional diversity of hummingbirds. However, measures of taxonomic diversity of hummingbirds did not vary across landscapes. Thus, the influence of land use change on biodiversity would have been obscured if only taxonomic diversity was evaluated. Moreover, I found that there are some traits, such as body mass, that appear to increase hummingbirds' sensitivity to land use change. Taken together, these results indicate that different components of diversity and environmental factors at multiple scales should be considered when evaluating how anthropogenic activities influence biodiversity and ecosystem functioning.

Hummingbird Diversity

Functional diversity of hummingbirds, but not taxonomic diversity, was influenced by the amount of native vegetation coverage in the landscape, landscape diversity and edge density. Different responses to anthropogenic habitat alterations between functional and taxonomy diversity have also been reported elsewhere (Flynn et al. 2009), demonstrating that trait differences among species in an assemblage do not always correlate with taxonomic diversity. In terms of coverage of native vegetation, taxonomic and functional diversity may be decoupled by land use change because altered environments can set limits to the types and ranges of traits of coexisting species, and thus constrains the amount of functional variation possible in assemblages (Díaz and Cabido 2001, Cadotte et al. 2011, Mouillot et al. 2013). In contrast, species richness often remains the same after land use change because, while some forest species may be lost, generalist species often colonize these altered habitats (Flynn et al. 2009). This process likely explains why functional diversity, but not species richness or taxonomic diversity, declined as the amount of native vegetation coverage in the landscape declined.

Unlike native vegetation coverage, it is less clear why landscape diversity and edge density influenced functional but not taxonomic diversity or species richness. Both of these variables can often promote high levels of taxonomic diversity by increasing niche availability and resources (Haslem and Bennett 2008, Mendoza et al. 2013). Niche and resource availability might promote species with unique functional roles, resulting in a greater increase in functional diversity compared to taxonomic diversity (Flynn et al. 2009). Thus, It is possible that landscape diversity and the amount of edges in a landscape are particularly beneficial for species with unique functional roles, which may use the additional niches available brought by these landscape characteristics.

At the local scale, I did not find any negative effect of habitat alteration on hummingbird diversity. In fact, within a given LU, hummingbird diversity was lower in 20 m plots with closed vegetation, as indicated by the negative relationship of functional diversity with PC1. Open vegetation can often provide high quality resources for pollinators because of the presence of plant species with flowers that produce abundant nectar (Hagen and Kraemer 2010). For example, in my study area, plant species such as *Oreocallis grandiflora*, and *Barnadesia arborea* are pioneer colonizers with flowers that attract many species of hummingbirds (Chapter

4). However, the strong association found between landscape characteristics and hummingbird functional diversity suggests that any relationship between local scale factors and hummingbirds might be largely dependent on the landscape context. This is to be expected if I consider that some hummingbirds have daily movements of more than 1 km (Hadley and Betts 2009). Therefore, any negative effect of land use change in the vegetation characteristics at small scales could be compensated by other environmental characteristics at larger spatial scales, as has been found elsewhere in the tropics (Haslem and Bennett 2008, Mendoza et al. 2013).

At the local scale, species richness of flowering plants was an important factor for explaining the variation in both taxonomic and functional diversity of hummingbirds. Niche partitioning of resources plays a major role in the structure of hummingbird assemblages (Feinsinger and Colwell 1978), and the richness of plant species is an important determinant of the total niche space available (Wolf et al. 1976, Stiles 1981, Gutierrez-Zamora Aquiles 2008). This is because plants with morphologically different corollas are used by different hummingbirds (Feinsinger and Colwell 1978, Kodric-Brown et al. 1984, Gutierrez-Zamora Aquiles 2008). Therefore, if an increase in plant species richness corresponds to an increase in species with morphologically different corollas, potentially more hummingbird species could coexist through niche partitioning. A positive correlation between plant species richness and pollinator species richness has also been reported in plant-insect pollination systems (Fründ et al. 2010, Weiner et al. 2011). However, some studies have found that the abundance of flowers could be a better predictor of hummingbird diversity than richness of flowers in lowland ecosystems (Cotton 2007, Abrahamczyk and Kessler 2010). Nonetheless, those studies were performed in non-disturbed environments, perhaps with less variation in plant species richness than that of the altered landscapes studied here. Studies are needed from multiple geographical regions and across different types of environmental gradients to be able to make generalizations about resource-consumer diversity relationships in tropical environments.

Trait – environment relationships

As predicted, landscapes that were more pristine tended to have heavier birds with longer culmens and longer tarsi than more altered landscapes. The positive association between body mass and environmental characteristics of more pristine LU's supports my prediction that this trait influences how hummingbird species respond to land use change. Heavier and larger hummingbirds have higher basal metabolic rates than smaller hummingbirds, and require access to flowers with high nectar yields (Brown et al. 1978). Therefore, changes in the types of resources available, which may result in reduced nectar availability, can negatively affect hummingbirds with large body size. In my study, *P. cyanopterus*, *E. ensifera*, and *E. luciani* are among those species with high body mass that responded negatively to land use change. Body mass could also indirectly increase the sensitivity of species to land use change because it is often correlated with other traits that can directly increase the likelihood of being affected by anthropogenic alteration, such as population size and home range size (McKinney 1997). In the same vein, heavier hummingbirds also had longer culmens, which is a characteristic that could increase hummingbirds' sensitivity to land use change. This is because hummingbirds with long culmens usually have high levels of diet specialization (Snow and Snow 1972), Chapter IV), which could limit species responses to land use change if their limited number of resources decline when habitats are altered (McKinney 1997, Newbold et al. 2013). Therefore, my finding

that hummingbirds with greater body mass could be particularly affected by land use change could be linked to the direct and indirect influence of this trait on the performance of hummingbirds. Finally, the positive association between relative tarsus length and more pristine LUs in hummingbirds could be related to the types of flowers available across the land use gradient. Hummingbirds with longer tarsi frequently perch on flowers for feeding (Stiles 2008), but this behavior is dependent on the availability of flowers with landing structures (Miller 1985). All of these associations among hummingbird traits and environmental characteristics support the utility of trait-based approaches to reveal patterns that could be used to identify the factors that influence species responses to the widespread effects of land use change.

There were some hummingbird functional traits that were not correlated with land use change as I had predicted. I predicted that species with high wing loading and broad wings would be negatively affected by land use change because these traits are related to low levels of mobility (Feinsinger and Chaplin 1975, Stiles 1995). The lack of correlations could be related to a weak influence of the functional traits evaluated and flying performance of hummingbirds. Studies by Altshuler et al. (2004) and Stiles et al. (2005) failed to find a clear relationships between wing loading and flying abilities of hummingbirds. They argue that the link between wing morphology and hummingbird behavior cannot be simplified to information provided by a single trait, because flying performance is defined by a complex group of parameters of wing morphology and flight kinematics. Alternatively, my failure to observe the predicted relationship between measures of wing morphology and land use change may be a result of my misinterpretation of trait – environment relationships in hummingbirds. Nectar resources in early secondary vegetation and edges could be spatially clumped and have less temporal fluctuations compared to resources in mature vegetation (Feinsinger et al. 1988, Hagen and Kraemer 2010). These are characteristics that could benefit less mobile hummingbirds whose broader wings would increase flying maneuverability and territorial defense over short distances (Stiles 1995). There is still much to learn about the ecomorphology of hummingbirds and future studies should assess how different functional traits of hummingbirds influence their performance across environments.

Conservation implications

The positive influence of native vegetation coverage on functional diversity of hummingbirds has important implications for conservation management, indicating that pollination services of hummingbirds might depend on the amount of native vegetation coverage in a landscape. Functional diversity of pollinators can increase fruit productivity in plants (Fontaine et al. 2006, Fründ et al. 2013); thus maintenance of functional diversity of pollinators might be key for sustaining high quality pollination services. Even though little is known about the relationship between functional diversity of hummingbirds and pollination services (Ornelas et al. 2004), considering the wide range of foraging strategies in hummingbirds it is reasonable to assume that reduced functional diversity of this group could be detrimental for the pollination services they provide. Given the widespread concern for the deterioration of pollination services worldwide (Potts et al. 2010), the exploration of changes in functional diversity of pollinators across land use gradients could provide valuable insights into the factors driving this decline.

My study points out the importance of the maintenance of native vegetation to promote high levels of functional diversity even landscapes used for cattle ranching. Cattle ranching is one of the main drivers of the reduction of native vegetation coverage in this region because of its importance as a major economic activity in the tropical Andes (Viña and Cavelier 1999). However, there are several management actions that could be implemented to both retain the commercial value of cattle ranching activities and improve conditions that maintain high levels of hummingbird diversity and the presence of species with unique functional roles. Activities such as the protection of native vegetation remnants, the incorporation of native vegetation hedgerows, the maintenance of native vegetation along rivers, and the use of native flowering plants on fences, are all important practices that could contribute to the conservation of hummingbirds' taxonomic and functional biodiversity, with little economic cost to cattle ranchers.

Lastly, I show that there are some traits associated with hummingbirds' sensitivity to land use change, such as body mass. Identifying functional traits that increase vulnerability to anthropogenic alteration is important in order to understand and predict the effects of the anthropogenic alteration of environments (Davidson et al. 2009, Newbold et al. 2013). This is particularly relevant in species-rich ecosystems, such as the tropical Andes, where the alteration of native vegetation is driving the decline of many species and the services they provide (Şekercioğlu 2012).

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Tables

Table 3.1. Description of landscape composition and structure of the landscape units where hummingbirds were sampled.

ID	Landscape composition			Landscape structure		Description of the type of anthropogenic alterations
	Native vegetation (%)	Pastures (%)	Exotic forest (%)	Edge density (m/Km ²)	Landscape diversity	
1	89.89	7.56	0.00	235.93	0.19	Native vegetation dominated
2	77.02	22.98	0.00	466.91	0.35	Native vegetation with pastures
3	76.62	18.45	4.93	521.25	0.38	Native vegetation dominated mosaic
4	60.86	39.14	0.00	772.95	0.48	Native vegetation dominated mosaic
5	54.63	38.08	7.30	361.27	0.55	Mixed used mosaic
6	34.67	65.33	0.00	601.00	0.49	Pastures dominated

Table 3.2. Principal components analysis of the vegetation structure of plots sampled across 6 landscapes in southern Ecuador. The highest factor loadings are in bold type.

Variables	PC1	PC2
Abundance of trees 9-15 cm DBH	1.44	-0.22
Abundance of trees 3-8 cm DBH	1.40	-0.59
Canopy cover	1.39	-0.30
Foliage height diversity	1.36	-0.46
Abundance of trees 16-23 cm DBH	1.33	0.18
Abundance of shrubs	1.23	-0.92
Abundance of trees 24-38 cm DBH	1.04	1.02
Average height of canopy	0.98	1.13
Abundance of trees > 39 cm DBH	0.76	1.18

Table 3.3. Nectar characteristics of all plant species used by the hummingbird species recorder across 6 landscapes in southern Ecuador.

Species	Nectar Volume ($\mu\text{l } 24\text{h}^{-1}$)		Sugar Concentration (%)		Nectar production sugar $\text{mg}^{-1} 24\text{h}$ per flower
	N	Mean ($\pm\text{SE}$)	N	Mean ($\pm\text{SE}$)	Mean
<i>Alloplectus peruvianus</i>	11	0.04 (± 0.02)	9	14.5 (± 2.4)	0.01
<i>Barnadesia arborea</i>	15	9.22 (± 1.5)	21	19.15 (± 0.6)	1.91
<i>Berberis lutea</i>	15	0.62 (± 0.04)	16	25.69 (± 1.7)	0.18
<i>Bomarea</i> sp	7	2.33 (± 0.89)	7	2.33 (± 0.4)	0.05
<i>Brachyotum confertum</i>	31	14.48 (± 3.13)	30	14.62 (± 0.7)	2.24
<i>Bromelia</i> sp2	9	1.5 (± 0.22)	16	10.63 (± 0.5)	0.17
<i>Bromelia</i> sp3	21	16.42 (± 2.58)	21	14.52 (± 1.2)	2.52
<i>Brugmansia sanguinea</i>	10	29.23 (± 10.17)	9	20.89 (± 1.8)	6.63
<i>Cavendishia bracteata</i>	18	0.14 (± 0.04)	7	16.31 (± 1.3)	0.02
<i>Centropogon</i> sp	10	6.14 (± 1.89)	10	12.2 (± 0.7)	0.78
<i>Fuchsia</i> cf. <i>vulcanica</i>	44	6.39 (± 1.74)	22	19.8 (± 1.4)	1.37
<i>Gaiadendron punctatum</i>	5	0.09 (± 0.01)	3	31 (± 1.4)	0.03
<i>Gaultheria erecta</i>	15	0.23 (± 0.05)	8	13.9 (± 1.8)	0.03
<i>Macleania rupestris</i>	46	10.81 (± 1.59)	39	17.5 (± 0.8)	2.02
<i>Mutisia lemanni</i>	13	34.7 (± 9.43)	21	19.5 (± 0.9)	7.30
<i>Oreocallis grandiflora</i>	48	18.69 (± 1.65)	42	14.8 (± 0.4)	2.93
<i>Palicuorea</i> sp	10	0.94 (± 1.33)	10	14.4 (± 0.6)	0.14
<i>Passiflora cumbalensis</i>	5	142.51 (± 29.45)	9	23 (± 1.4)	35.88
<i>Rubus floribundus</i>	5	2.44 (± 0.56)	1	50 ($\pm \text{NA}$)	1.50
<i>Salvia corrugate</i>	46	2 (± 0.33)	22	11.9 (± 1.8)	0.25
<i>Salvia hirta</i>	17	6.36 (± 1.78)	18	18.1 (± 1.2)	1.23
<i>Saracha quitensis</i>	14	13.29 (± 2.54)	19	12.5 (± 0.9)	1.74
<i>Tillandsia complanata</i>	9	1.49 (± 0.22)	9	10.6 (± 0.7)	0.17
<i>Tristerix longebracteatus</i>	30	4.56 (± 0.8)	18	18.9 (± 0.6)	0.93
<i>Verbesina latisquama</i>	15	0.69 (± 0.05)	18	22.1 (± 0.5)	0.17
<i>Viola arguta</i>	16	4.08 (± 0.73)	14	12.5 (± 1.1)	0.54

Table 3.4. Description of predictive variables at the local and landscape scales used to explore responses of hummingbirds across a land use gradient in southern Ecuador.

Variable name	Code	Variable definition	Units
<i>Local scale factors</i>			
Principal component I	PCI	From open to close vegetation	
Principal component II	PCII	From large trees to shrubs	
Richness of flowering plants	PRICH	Number of species of flowering plants use by hummingbirds	
Sugar production	SUGAR	Potential production of sugar in nectar or flowers	mg
<i>Landscape scale factors</i>			
Landscape diversity	LANDIV	Simpson index of landscape diversity	
Edge density	EDGE		m/m ²
Native vegetation coverage	NATCOV	Coverage of woody vegetation	%

Table 3.5. Hummingbird species recorded during the study period. Values represent annual averages of abundances per point count across all the landscapes.

Species name	Year	
	2011	2012
<i>Aglaeactis cupripennis</i>	0.25	0.40
<i>Chaetocercus mulsant</i>	0.03	0.02
<i>Coeligena iris</i>	0.62	0.49
<i>Colibri coruscans</i>	0.25	0.05
<i>Ensifera ensifera</i>	0.02	0.06
<i>Eriocnemis luciani</i>	0.51	0.74
<i>Eriocnemis vestita</i>	0.00	0.05
<i>Heliangelus viola</i>	0.25	0.28
<i>Lafresnaya lafresnayi</i>	0.36	0.41
<i>Lesbia nuna</i>	0.42	0.28
<i>Lesbia victoriae</i>	0.12	0.03
<i>Metallura baroni</i>	0.06	0.02
<i>Metallura tyrianthina</i>	1.92	2.03
<i>Pterophanes cyanopterus</i>	0.06	0.09
<i>Ramphomicron microrhynchum</i>	0.00	0.03

Table 3.6. Measures of functional traits of male hummingbirds in this study.

Species	Body mass		Total culmen		Wing aspect ratio		Wing loading		Tarsus	
	N	Mean (SE) gr	N	Mean (SE) mm	N	Mean (SE)	N	Mean (SE) g/cm ³	N	Mean (SE) mm
<i>Aglaeactis cupripennis</i>	21	8.21 (±0.14)	25	21.5 (±0.32)	17	7.79 (±0.10)	17	0.181(±0.01)	17	7.78 (±0.20)
<i>Chaetocercus mulsant*</i>	24	3.58 (±0.03)	24	19.5 (±0.15)	24	7.72 (±0.10)	24	0.368 (±0.01)	7	4.33 (±0.02)
<i>Colibri coruscans</i>	25	8.21 (±0.07)	34	28 (± 0.54)	25	7.82 (±0.05)	25	0.21 (±0.01)	25	6.22 (±0.28)
<i>Coeligena iris</i>	5	7.08 (±0.11)	7	31.81 (± 1.00)	3	7.39 (±0.51)	3	0.212 (±0.01)	8	7.44 (±0.15)
<i>Ensifera ensifera*</i>	4	9.68 (±0.27)	4	83.92 (± 1.33)	4	7.94 (±0.16)	4	0.254 (±0.01)	4	6.8 (±0.11)
<i>Eriocnemis luciani</i>	10	6.12 (±0.13)	14	24.98 (± 0.40)	1	7.9 (±NA)	1	0.233 (±NA)	13	7.79 (±0.20)
<i>Eriocnemis vestita*</i>	25	4.86 (±0.04)	25	21.38 (± 0.17)	25	7.14 (±0.05)	25	0.2 (±0.01)	25	5.7 (±0.05)
<i>Heliangelus viola</i>	12	5.63 (±0.11)	8	18.08 (± 0.78)	6	7.39 (±0.32)	6	0.246 (±0.01)	8	7.29 (±0.19)
<i>Lafresnaya lafresnayi</i>	19	5.69 (±0.07)	18	29.69 (±0.26)	19	7.63 (±0.05)	19	0.216 (±0.01)	18	5.62 (±0.01)
<i>Lesbia nuna*</i>	7	3.66 (±0.05)	7	12.66 (± 0.21)	7	6.82 (±0.06)	7	0.198 (±0.01)	7	5.64 (±0.08)
<i>Lesbia victoriae*</i>	11	5.29 (±0.05)	11	17.58 (±0.17)	11	7.44 (±0.07)	11	0.226 (±0.01)	11	6.25 (±0.07)
<i>Metallura baroni</i>	4	4.57 (±0.08)	3	17.77 (±0.62)	2	7.86 (±0.52)	2	0.248 (±0.01)	3	7.07 (±0.55)
<i>Metallura tyrianthina</i>	35	3.79 (±0.04)	42	14.83 (±0.15)	35	7.09 (±0.06)	35	0.161 (±0.01)	40	6.72 (±0.09)
<i>Pterophanes cyanopterus</i>	6	10.37 (±0.31)	6	36.45 (± 1.01)	6	7.55 (±0.09)	6	0.147 (±0.01)	6	7.84 (±0.14)
<i>Ramphomicron microrhynchum*</i>	15	3.67 (±0.06)	15	10.21 (±0.25)	15	7.5 (±0.10)	15	0.234 (±0.01)	15	6.07 (±0.04)

* symbol denotes species for which morphology data was obtained from Gary Stiles personal data base. Stiles contact information: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.

Table 3.7. Pearson correlation coefficients of the mean values of functional traits of hummingbirds in this study.

Traits	Traits			
	Total culmen length	Wing aspect ratio	Wing loading	Tarsus length
Body mass	0.71	0.49	-0.35	0.58
Culmen length		0.46	0.05	0.20
Wing aspect ratio			0.37	0.25
Wing loading				-0.55

Table 3.8. Top ranked models of linear mixed models that tested the effects of landscape scale and local scale factors on species richness, taxonomic diversity and functional diversity of hummingbirds. Only models with a $\Delta AICc$ of less than 2 were consider as top models. Codes of the variables are presented in Table 3.5.

Model	AICc	$\Delta AICc$	AICc weight
<i>Species richness</i>			
PRICH +PCII +LANDIV +SUGAR	74.70	0.00	0.05
PRICH +PCII +LANDIV	74.91	0.21	0.04
PRICH	75.35	0.65	0.03
PRICH +PCII	75.85	1.14	0.03
PRICH +PCII +LANDIV +PCI	75.96	1.26	0.02
PRICH +PCII +NATCOV +SUGAR	76.01	1.31	0.02
PRICH +PCII +NATCOV	76.08	1.38	0.02
PRICH +LANDIV +NATCOV	76.11	1.41	0.02
PRICH +LANDIV	76.13	1.42	0.02
PRICH +LANDIV +EDGE	76.16	1.46	0.02
PRICH +PCII +SUGAR	76.17	1.47	0.02
PRICH +PCII +LANDIV +SUGAR +PCI	76.30	1.60	0.02
PRICH +PCII +LANDIV +EDGE	76.31	1.61	0.02
PRICH +SUGAR	76.31	1.61	0.02
PRICH +PCII +NATCOV +PCI	76.32	1.61	0.02
PRICH +PCII +LANDIV +SUGAR +EDGE	76.39	1.68	0.02
PRICH +PCII +LANDIV +NATCOV +SUGAR	76.39	1.69	0.02
PRICH +PCII +LANDIV +NATCOV	76.52	1.82	0.02
PRICH +LANDIV +NATCOV +EDGE	76.57	1.87	0.02
<i>Taxonomic diversity</i>			
PRICH +EDGE +LANDIV +PCI	-168.17	0.00	0.11
PRICH +EDGE +LANDIV +NATCOV	-167.64	0.53	0.08
PRICH +EDGE +LANDIV	-166.85	1.33	0.06
PRICH +EDGE +LANDIV +NATCOV +SUGAR	-166.74	1.43	0.05
PRICH +EDGE +LANDIV +PCI+NATCOV	-166.49	1.69	0.05
PRICH +EDGE +LANDIV +PCI +SUGAR	-166.31	1.87	0.04
<i>Functional diversity</i>			
NATCOV +EDGE +LANDIV +PCI +PRICH	157.38	0.00	0.12
NATCOV +EDGE +LANDIV +PCI +PRICH +SUGAR	158.18	0.80	0.08
NATCOV +EDGE +LANDIV +PCI +PRICH +PCII	159.04	1.66	0.05
NATCOV +EDGE +LANDIV +PCI +SUGAR	159.06	1.68	0.05

Figures

Figure 3.1. Map of study area in the southern Andes of Ecuador. The map also depicts the two spatial scales considered in this study: local and landscape scale.

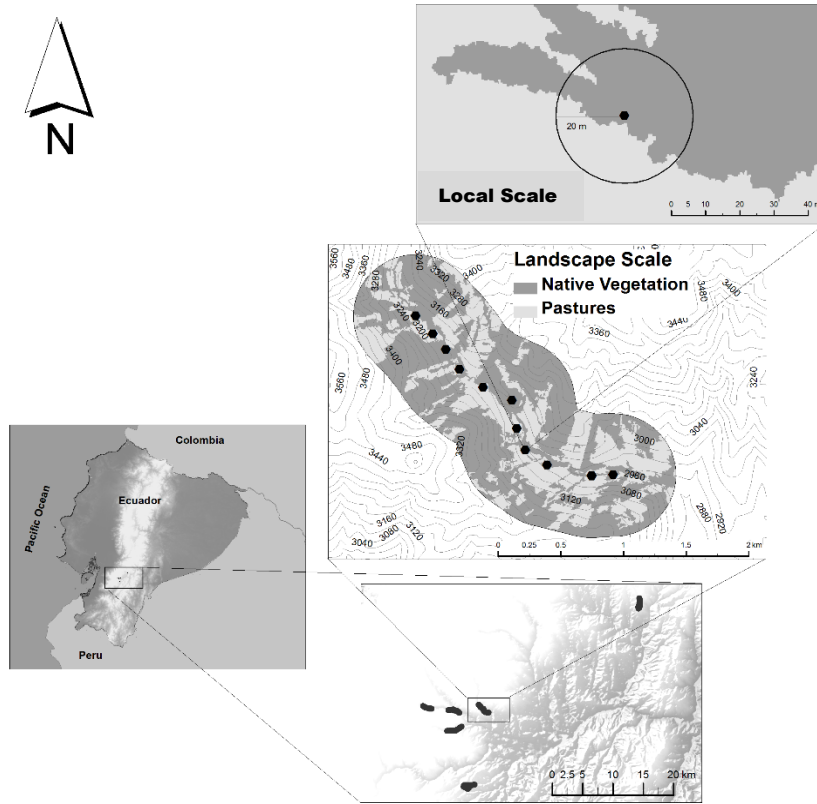


Figure 3.2. Model averaged parameters of local scale and landscape scale factors affecting taxonomic (a) and functional diversity (b) of hummingbirds obtained from linear mixed models. Depicted are standardized coefficients and 95% confidence intervals (CI). Code for factors are presented in Table 5.

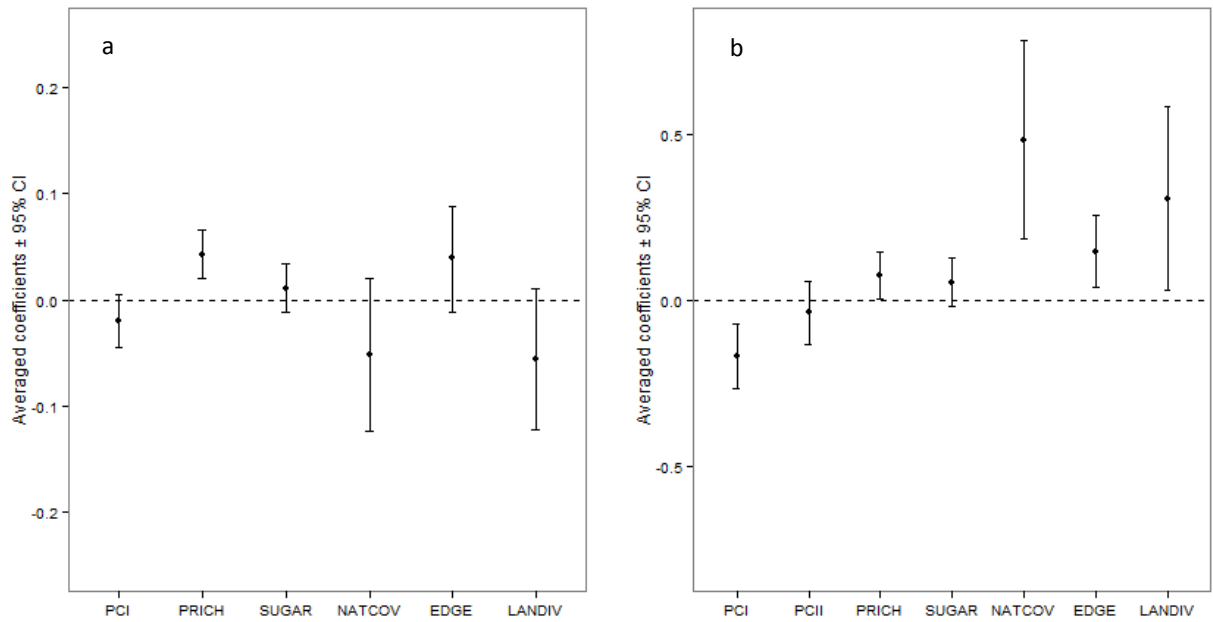
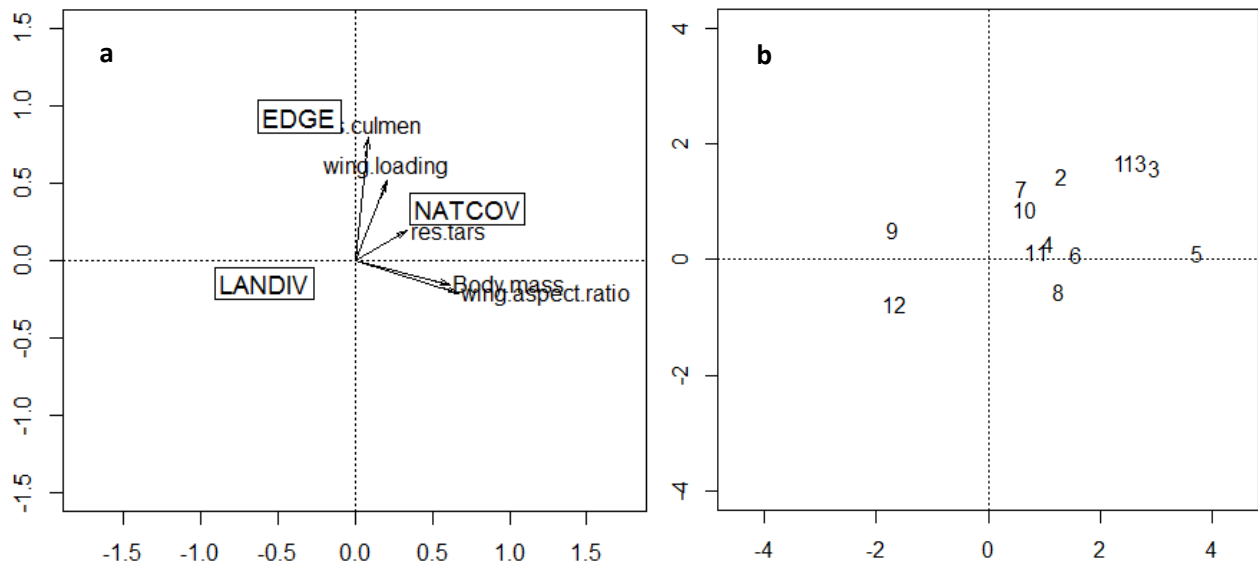
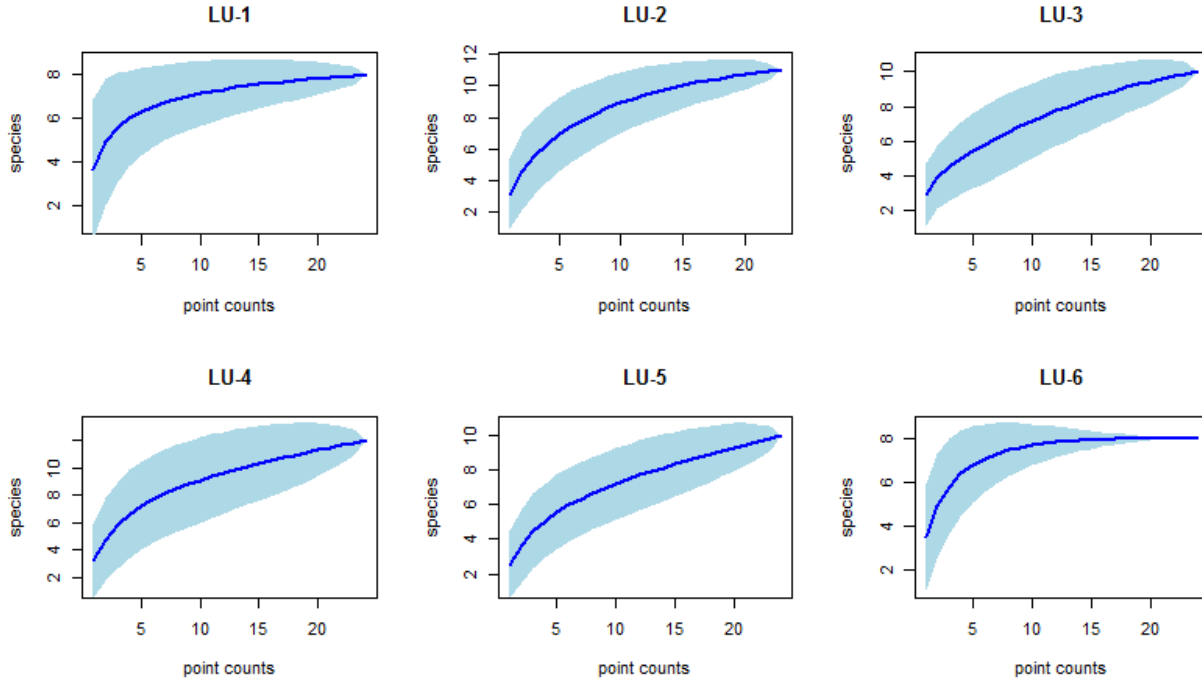


Figure 3.3. Graphical depiction of the RLQ analysis at the landscape scale. a) Functional traits (vectors), landscape scale environmental variable scores (boxes) along the first and second RLQ axis. Position of scores relative to the origin indicate their contribution to RLQ axis, and distances among scores represent close associations. Codes for factors are presented in Table 5. b) Species scores along the first and second RLQ axis. Species codes are: (1) *Aglaeactis cupripennis*; (2) *Chaetocercus mulsant*; (3) *Coeligena iris*; (4) *Colibri coruscans*; (5) *Ensifera ensifera*; (6) *Eriocnemis luciani*; (7) *Heliangelus viola*; (8) *Lafresnaya lafresnayi*; (9) *Lesbia nuna*; (10) *Lesbia victoriae*; (11) *Metallura baroni*; (12) *Metallura tyrianthina*; (13) *Pterophanes cyanopterus*.



Appendix

Appendix I. Species rarefaction curves of hummingbirds sampled in point count stations in six landscapes in the southern Andes of Ecuador.



Chapter 4: Determinants of Hummingbird Specialization in Pollination Networks along Habitats with Different Alteration Levels

Introduction

Communities are structured in networks of interacting species that are important for the organization and maintenance of biodiversity (Bascompte et al. 2003, Montoya et al. 2006, Thébault and Fontaine 2010). The development of analytical tools to study interacting species within these complex ecological networks has yielded considerable insight into the general structure of species interactions within a community context (Bascompte et al. 2003; Tylianakis, Tscharnkte, and Lewis 2007; Olesen et al. 2011). However, there is still much to learn about the processes shaping species interactions and network structure (Stang et al. 2007, Vázquez et al. 2009a, Carnicer et al. 2009). Environmental variation occurring along land use gradients may provide insight into how different ecological and evolutionary factors influence species interactions within a network (Schleuning et al. 2010, Albrecht et al. 2013). Here, I explore how these different factors influence network structure, and specifically specialization of hummingbird pollinators, in habitats with different alterations in the tropical mountains of Ecuador.

In ecological networks, specialist are those species that interact with a limited number of partners (Vázquez and Aizen 2006). The degree of specialization of species in an assemblage has important implications in the structure of networks because it influences network robustness (Waser et al. 1996, Bascompte et al. 2006, Montoya et al. 2006). Robustness is measured by the number of species that will go extinct after one species is lost from the system (Dunne et al. 2002, Ives and Carpenter 2007). Low specialization of species should promote high network robustness because if a species is lost, there will be other species that have the same interactions as the species that was lost (Dunne et al. 2002, Bascompte et al. 2003, Memmott et al. 2004). Thus, in pollination networks, low specialization ensures that a plant will likely always have a pollinator. However, high specialization of pollinators can be important for pollination quality because it increases the likelihood of conspecific pollen transfer among plants, which ultimately benefits plant reproduction (Johnson and Steiner 2000, Brosi and Briggs 2013). Although recent studies have described macroecological patterns of specialization in pollination networks (Dalsgaard et al. 2011, Schleuning et al. 2012), there is little knowledge about the processes that drive specialization of species within networks (Stang et al. 2007, Vázquez et al. 2009a, Fründ et al. 2010), especially in species-rich networks from tropical ecosystems.

The level of specialization of species can be influenced by a series of ecological and evolutionary processes that operate at different temporal and spatial scales (Carnicer et al. 2009, Vázquez et al. 2009b, Thompson et al. 2013). One important ecological factor influencing species' specialization is resource availability, which generally varies on small spatial and short temporal scales (Kondoh 2003). For instance, competitive interactions driven by resource abundance can influence the degree of specialization of coexisting species (Laverly and Plowright 1985, Pimm et al. 1985, Graham and Jones 1996). In scenarios of low resource availability, interspecific competition among coexisting species is expected to increase specialization of species to reduce niche overlap (Pimm et al. 1985, Robinson and Wilson 1998). Recent field experiments of pollination networks have demonstrated higher levels of

specialization of pollinators when the number of coexisting pollinators in the network increases (Fründ et al. 2013, Brosi and Briggs 2013), as predicted by competition theory. On longer time scales, evolutionary processes can produce morphological and behavioral traits that influence which and how species interact (Futuyma and Moreno 1988, Kondoh 2003, Rezende et al. 2007). Accordingly, phylogenetic relationships among members of the network (Rezende et al. 2007), trait lability and trait matching between partners in mutualistic interactions (Stang et al. 2007, Olesen et al. 2011, Junker et al. 2013) are evolutionary factors that can affect interactions in networks and influence species' specialization. For example, Stang et al. (2007) showed that only insect species with long probosci visit flowers with deeply hidden nectar chambers. Thus, patterns of specialization of species are regulated by the relative importance of ecological and evolutionary factors influencing species interactions in a network.

Studying specialization across habitats with different types of alterations, presents a unique opportunity to unravel how the interplay between ecological and evolutionary factors influence patterns of interactions in hummingbird-plant networks (Kiers et al. 2010). Anthropogenic habitat alterations often occur over relatively small spatial and short temporal scales, influencing ecological factors, such as resource abundance. In birds such changes might influence behavioral responses resulting, for instance, in a change in the number of resources used (Futuyma and Moreno 1988, Agrawal 2001). Most morphological traits in birds are the result of long term evolutionary process, which might limit species' ability to respond to the sudden changes produced by anthropogenic alterations (Stockwell et al. 2003, Crispo et al. 2010). In particular, some foraging morphological traits (e.g., bill shape) show low levels of phenotypic plasticity (Jordano 1987, Böhning-Gaese and Oberrath 1999, Blomberg et al. 2003). Thus, it is expected that ecological factors, such as abundance of resources, may be more important in mediating changes in specialization in birds between altered and non-altered habitats than evolutionary factors. Evolutionary factors, such as morphological traits used for foraging, likely do not respond to habitat alterations and as a result have similar effects on specialization throughout different habitats (Levin 2004).

Hummingbird – plant pollination networks are well suited to explore the factors that shape specialization. Hummingbirds are highly dependent on nectar resources (Feinsinger and Colwell 1978), and there is a vast knowledge about hummingbird and flower traits that influence hummingbird visitation (Feinsinger and Colwell 1978, Kodric-Brown et al. 1984, Altshuler et al. 2004, Temeles et al. 2009). Here, I used a detailed data set containing independent measures of hummingbird abundance and resources (nectar), and measures of hummingbird traits to examine how resource availability and species' morphology influence the specialization of hummingbirds along habitats with different alteration types. I measured differences in resource availability, species traits and specialization of hummingbirds among forest, shrub and pasture habitats in the tropical montane forest of Ecuador. I predicted that (1) resource availability would differ among habitat types, (2) that hummingbird specialization will increase when resources are scarce, and (3) that hummingbird species-specific morphological traits will influence their level of specialization across all habitat types.

Methods

Study area

I conducted this study in the western Andes of Azuay province in southern Ecuador, at elevations between 3000 and 3200 m above sea level. This is an area of complex topography, with a mean annual precipitation that ranges from 1100 to 1800 mm, and monthly mean temperatures that vary from 5–12°C (Celleri et al. 2007). At present this area is mostly covered by pastures for cattle and remnants of Andean native forest are mostly confined to steep slopes in inaccessible areas (White and Maldonado 1991). I selected three valleys within the study area that have different disturbance histories. 1) A valley in Mazan was dominated by mature native forest (referred to as forest habitat; 2°52' S, 87°7' W). This area is a nature reserve managed for conservation under strict surveillance with access limited only to researchers. The native forest here was altered by selective logging before its incorporation under the administration of Cajas National Park in 1986. 2) A valley dominated by young secondary forest was located in Llaviuco – Cajas National Park (2°49' S, 79°10' W). This site was a cattle ranch before its inclusion in Cajas National Park in 1996. My sampling area in Llaviuco was located in early successional native shrubs (hereafter shrubs), which re-established naturally after the removal of cattle. 3) An area dominated by active cattle ranching was located in Nero Valley (hereafter cattle ranch) (2°56' S, 79°6' W). This valley was mostly dominated by pastures intermixed with hedgerows of native vegetation. Within each study area I characterized hummingbird – plant interactions.

Hummingbird abundance and traits

In each habitat type, I positioned one transect of 2.2 km containing 12 point count census stations at 200 m intervals. Two observers simultaneously identified and counted all hummingbird individuals detected in a fixed radius of 30 m during 10 min at each point count station. Hummingbirds flying over the station were excluded. All point counts within a transect were sampled on the same day between 6h00 and 10h00 and only on days without strong wind or heavy rain. I finished all sampling in a given valley and then moved to a different valley on consecutive days of sampling during each survey period. In total, I completed eight survey periods in each habitat type from February to August each year in 2011 and 2012.

Abundances of each species were estimated using data from the double observer approach with the software DOBSERV (Nichols et al. 2000). For this method, two observers independently record study animals to provide detection probabilities by combining information about the individuals detected by one observer but not by the other (Nichols et al. 2000). Then, a joint detection probability for both observers during a survey is obtained as:

$$P_{\text{joint}} = 1 - (1 - p_{\text{obs1}})(1 - p_{\text{obs2}})$$

where p_{obs1} and p_{obs2} are the detection probabilities of observer 1 and 2, respectively (see more details in Nichols et al. 2000). I then used the joint detection probability to calculate corrected abundance estimates of each species for each sampling period. A critical assumption of this method is the independent detection of birds by the two observers, which in practice is hard to accomplish in the field when two observers are performing the census simultaneously. Even considering this limitation, the double observer approach is preferable to those methods where

detection probabilities for all species are assumed to be 1 because species detectability varies depending on behavior, size and plumage coloration (Farnsworth et al. 2005).

I gathered information about functional traits (traits influencing performance, *sensu* McGill et al. 2006) of each hummingbird species from individuals captured in the study area with mist nets, complemented with data from G. Stiles (Stiles personal data base; Table 4.1). I obtained the following morphological traits related to foraging behavior: body mass (weight of a live individual), total culmen length (measured as the length of the bill from base to tip), tarsus length (measured as the length from the outer bend of the tibiotarsal articulation to the base to the toes), and wing chord (measured as the length of the closed wing from wrist joint to the longest primary feather). In addition, I calculated wing load (the ratio of body mass to wing area), and wing aspect ratio (the quotient of twice the square of the wing length divided by wing area). More details of how to obtain these measures can be found in Stiles et al. (2005). Body mass is related to competitive abilities; larger hummingbirds are competitively dominant over smaller birds (Kodric-Brown et al. 1984). Total culmen length influences resource use and efficiency of nectar extraction (Temeles and Kress 2003). Tarsus length is associated with perching behavior during feeding; species with longer tarsi tend to perch on flowers to feed (Stiles 2008). Wing load is related to the flight behavior of hummingbirds. Higher wing load favors maneuverability in territorial species and lower wing load is associated with slow speed movements along foraging routes (Feinsinger and Chaplin 1975; Kodric-Brown and Brown 1978, but see Altshuler et al. 2004). Wing aspect ratio is also related to flight ability. High aspect ratio denotes narrower and longer wings, which favor fast forward flight. Low aspect ratio indicates broader wings, and is associated with slow forward flight (Stiles et al. 2005, Stiles 2008). I only used morphological data for male individuals because I had a greater sample size for birds of this sex. Measures of traits of the hummingbird species are provided in Table 4.1.

Flower abundance

Plant species were identified by local experts from the Herbarium Azuay – Universidad del Azuay in Cuenca, Ecuador. In the first year of the study I included all flowering plants, with the exception of herbaceous Astereaceae, which are rarely visited by hummingbirds (Stiles 1981). During the second year, I focused my effort on plants that were visited by hummingbirds in the previous year. I sampled the abundance of flowers on the same day as the census of hummingbirds. In each habitat type, I placed three plots of 200 x 5 m to measure richness of flowering plants and flower abundance. Plots were placed at distances no closer than 500 m between each other, but overlapping with the point count transects. I measured the abundance of flowers in each plot by counting the number of open flowers of each plant species in the plot. In cases where a complete count was not possible, I counted the number of flowers in a portion of the plant and estimated the total number of flowers by extrapolating the number of flowers in the sampled portion to the total area of the foliage covered with flowers.

Flower abundance was used to estimate floral sugar production rates over 24-h for each sampling period and habitat type. Mean sugar production per flower of each species was obtained from flowers that were bagged for 24-h to prevent access by hummingbirds, after which I extracted nectar with capillary tubes and made readings of sugar concentration with a handheld refractometer. Flowers were depleted of nectar before bagging (the number of flowers sampled

and nectar production per species are provided in Table 4.2). Sugar production was calculated as the product of nectar volume in ml multiplied by sugar concentration measured in sugar mg/ml following the table provided by Kearns and Inouye (1993). Sugar production rates per habitat type and sampling period were obtained by multiplying the mean sugar production over 24 hours per flower with the total number of flowers available of the respective plant species in each plot. This measure is an indicator of the amount of available energy for hummingbirds (Feinsinger and Colwell 1978, Feldman and McGill 2014). To compute this measure, I included all the plant species visited by any hummingbird species across the study period. I am aware that this is a crude measure of sugar availability, but it is a time effective method for assessing community resource availability for pollinators and is proven to be a more reliable measure of resource availability compared to simply using direct flower counts (Potts et al. 2003, Ornelas et al. 2007).

Observations of hummingbird – plant interactions

I registered hummingbird - plant interactions by recording hummingbird visits to flowering plants in the same plots used to sample flower abundance. Observations in each plot were performed between 6:00 and 10:30 hours, on days without rain or strong wind. Interactions were recorded by two methods: 1) direct recordings by an observer wearing camouflage clothing to minimize the disruption of hummingbird behavior, and 2) video recordings with cameras mounted on tripods and focused on a focal group of flowers. If possible, flowers from multiple species were monitored within an observation period. I sampled each plot by dividing it into 10 x 5 m subplots, and then randomly choosing the order and segment of subplots to be monitored. Every flowering plant present in each subplot was sampled by either of the two methods for 30 min observation period. All plants, irrespective of their pollination syndrome, were observed with the exception of herbaceous Asteraceae. During the second year, I only monitored plant species that hummingbirds visited in the previous year. During each observation period, I recorded the frequency of legitimate hummingbird visits (i.e., visits where the hummingbird touched the reproductive parts of the flower) to open flowers from the ground level up to the vegetation canopy. I sequentially sampled plots placed within the same habitat type before moving to a different habitat type. This sampling protocol was used over the same sampling periods used for flower abundance.

Network analysis

I constructed quantitative interaction matrices by calculating the total frequency of visits of each hummingbird species to each plant species (the total number of flowers of each plant species visited by a hummingbird species). I constructed 8 interaction matrices per habitat type by pooling the information from the three plots placed in each habitat type for each of the 8 sampling periods. I did not pool networks across sampling periods due to potential changes in the phenology of plants and seasonal abundances of hummingbirds. By not pooling I avoided the appearance of “forbidden links” (Olesen et al. 2011) due to phenological mismatches.

I used the software package bipartite in R (Dormann et al. 2009) to calculate two different indices of specialization of hummingbirds, each of which measures a different aspect of specialization:

- 1) The degree of specialization d' (Blüthgen et al. 2006) is a measure of niche partitioning among species in a network. This index is based on information theory and is obtained by measuring the deviation of the observed frequency of resource use from the expected use. The expected use is determined by the availability of plant species. Species that are more abundant are expected to be visited more than those that are less abundant. d' also incorporates information about whether the resources are used by other consumers; thus, it is a reliable measure of niche partitioning among species in networks. I calculated resource availability as the abundance of flowers of each plant species in each sampling period. This metric is not biased by the number of observed links in a network (Blüthgen et al. 2006, 2008). Therefore, it is possible to compare specialization of species across vegetation types with different sized networks. d' ranges from 0 to 1, where 0 indicates high generalization and 1 high specialization. High levels of d' indicate low network robustness (Blüthgen et al. 2008).
- 2) Pollinator service index (PSI) (Dormann 2011) is a quantitative index derived from interaction strength (Bascompte, Jordano, and Olesen 2006). PSI is a measure of pollinator specialization, and is based on the assumption that it is disadvantageous to a plant if a pollinator carries a high heterospecific pollen load (Dormann 2011). Mathematically PSI is defined as:

$$PSI_j = \sum_i (P_{ij} \times P_{ji}^\beta)$$

P_{ij} is the proportion of visits by pollinator j over all visits to plant species i and is a measure of the dependence of plant i on pollinator j (Bascompte, Jordano, and Olesen 2006). P_{ji} calculates the proportion of all visits of pollinator j to plant i and is a measure of the reciprocal dependence of pollinator j on plant i . P_{ji} is associated with the amount of heterospecific pollen carried by pollinator j . The β coefficient takes into account the number of visits a pollinator has to make in order to pollinate a plant. I set the coefficient to 1 and assumed that the proportion of conspecific pollen deposited on a stigma is proportional to the number of visits, given that I lack in-depth information about pollen acquisition and transfer in these pollinators (Dormann 2011). This index is summed across all plant species present in the network to estimate the overall importance of pollinator j . PSI ranges from 0 to 1. A value of 1 indicates that all pollen is delivered to one plant species that completely depends on the visits of this pollinator, whereas 0 indicates that a pollinator is not important for the plant species. PSI is related to ecosystem functioning because it calculates the service of a pollinator for all plants in the network (Dormann 2011).

Statistical analysis

I explored changes in the community structure of hummingbirds across habitat types by analyzing the relationships among functional traits of hummingbirds and habitat types with a fourth corner analysis (Legendre et al. 1997, Dray and Legendre 2008) in the R package *ade4* (Dray and Dufour 2007). Fourth corner analysis tests for associations of species traits and environmental variables using three matrices (Dray and Legendre 2008): 1) matrix R, which contains information about environmental characteristics in each site; 2) matrix L, which contains data about species abundances in each site; and 3) matrix Q, which has information about trait values for each species. In my case, the R matrix was composed by the habitat types

in each sampled site as a categorical variable; in matrix L, I used the mean abundance of each hummingbird species in each site; lastly, in matrix Q, I used the mean trait values of each species of hummingbird as in Table 4.1. Then, a fourth corner statistic is calculated, which is a measure of the degree of the association between each pair of traits and environmental variables, taking into account the species abundances in each site provided in matrix L (Dray and Legendre 2008). Considering that in my case, the environmental variables were categorical, and the trait variables were quantitative, the degree of association was the correlation ratio (η^2), which is defined as the among-group sum of squares (groups denoted by the states of the categorical variable) divided by the total sum of squares (Dray and Legendre 2008). To test the significance of these associations permutation tests (9999 interactions) were carried out on the L matrix, by permuting the abundances for each species independently, keeping the number of habitats where each species occurs constant (Model 1 in Dray and Legendre 2008). This permutation model tests the null hypothesis that species are randomly distributed with respect to environmental characteristics of the sites.

Differences in resource availability among the three habitats were tested with linear mixed effects models (Bolker et al. 2009). I used two different metrics of resource availability as dependent variable in the models: (1) sugar production, represented by the production rate of sugar in 24 h per habitat (across all plant species visited by hummingbirds); and (2) richness of flowering plants, as a measure of resource diversity (only including plant species that were visited by hummingbirds). In these models, habitat type was used as fixed factor, and I specified the temporal replicates as random effects to control for temporal non-independence of data (Bolker et al. 2009). I also tested for changes in the sugar production of the most abundant plant species in each habitat type to explore the species-specific contribution to the overall variation in sugar production, using the same model structure as above.

I performed a series of analyses to explore whether specialization of hummingbirds changed across different habitat types and whether ecological (i.e., resource availability) and/or evolutionary factors (i.e., hummingbird traits) influenced variation in specialization using linear mixed models (Bolker et al. 2009). First, I tested for differences in network level d' and PSI among habitat types. I used habitat type as fixed factor and d' and PSI as response variables. Second, I analyzed species-specific changes in specialization among the three habitat types for the most common hummingbird species, using as response variables their respective values of d' and PSI. Third, I explored the relationships of evolutionary factors, represented by the hummingbird functional traits (all the measured hummingbird traits), and ecological factors, represented by resource availability (sugar production, resource richness), on network level d' and PSI with single predictor linear mixed effects models. Finally, I constructed multi-predictor models of the effects of evolutionary and ecological factors on d' and PSI. For the multi-predictor models, I only chose the variables with statistically significant influence in the single predictor models and calculated models for every possible combination of these predictor variables. For all the models described above, the random components were structured by hummingbird species identities, temporal replicates and network identities, with the exception of species-specific models where only the temporal replicates were considered. Including network identity as random component controls for non-independence of samples taken at the same place and time. Using the temporal replicate as a random component controls for temporal autocorrelation among networks located in different valleys but sampled during the same survey

period. The use of species identities as random component accounts for non-independent taxonomic responses of specialization. Moreover, I used abundance of each hummingbird species as a weight in the models to account for the potential influence of differences in data quality among species, given that rare species can potentially be under sampled in interaction networks (Dorado et al. 2010). Multi-predictor models were compared and ranked by Akaike's information criterion (AIC) corrected for small sample size (Burnham and Anderson 2002). Following Bolker et al. (2009), model comparisons were done on models fitted by maximum likelihood, but to obtain coefficients of predictor variables and their statistical significance, final models were fitted with a restricted maximum approach. Statistical significance of predictor variables was evaluated by P-values from Markov chain Monte Carlo sampling (MCMC). The variance explained by the final multi-predictor models (i.e., R^2) were obtained by the method proposed by Nakagawa and Schielzeth (2013). All analyses were conducted with R version 3.0.1 (R Development Core team 2013).

Results

Hummingbird abundance and community structure

The most abundant hummingbird species were the same across habitat types, and included *Metallura tyrianthina*, *Coeligena iris*, *Eriocnemis luciani*, and *Lafresnaya lafresnayi* (Table 4.3).

I found no association between traits of hummingbirds and habitat types with the exception of wing loading, which was marginally significant (Table 4.4). Thus, the structure of the hummingbird communities was similar in terms of hummingbirds' functional traits among habitat types.

Resource availability

The availability of nectar resources for hummingbirds differed among habitat types (Table 4.5). Nectar production and species richness of flowering plants were greater in the shrub and cattle ranch habitats than in the forest (Figure 4.1; Table 4.5). The most abundant plant species across habitat types had lower nectar production in the forest habitat than in the other two habitat types (Table 4.6).

Hummingbird plant pollination networks

The hummingbird–plant networks evaluated across the study period included 8 hummingbird species and 21 plant species in the forest (1298 interaction events); 12 hummingbird species and 19 plant species in the shrubs (3979 interaction events); and 9 hummingbird species and 19 plant species in the cattle ranch (2405 interaction events) (Fig 2). The Jaccard index indicated a high proportion of shared hummingbird species among networks (forest vs shrub: 0.71; forest vs. cattle ranch 0.63; shrub vs. cattle ranch 0.67), consistent with the similar functional structure of hummingbirds across habitats. The most frequent hummingbird visitors included: *Metallura tyrianthina*, *Lafresnaya lafresnayi*, and *Coeligena iris* in the forest; *Eriocnemis luciani*, *M. tyrianthina*, and *Ramphomicron microrhynchum* in the shrubs; and *M. tyrianthina*, *Aglaeactis cupripennis*, and *E. luciani* in the cattle ranch (Figure 4.2). The plant assemblages also presented high levels of similarity among networks (forest vs. shrub: 0.87; forest vs. cattle ranch: 0.88; shrub vs. cattle ranch: 0.87). Plants that attracted most hummingbird visits were: *Viola arguta*, *Macleania rupestris*, and *Palicourea* sp. in the forest; *Barnadesia arborea*, *Salvia hirta*, and *S. corrugata* in the shrubs; and, *Oreocallis grandiflora*, *Brachyotum confertum*, and *Gaultheria tomentosa* in the cattle ranch (Figure 4.2).

Specialization d' and PSI of hummingbirds

Specialization of hummingbirds (d' and PSI) at the network level differed among habitat types. d' and PSI were higher in the forest habitat than in shrub and cattle habitat types (Figure 4.3; Table 4.7). The most abundant hummingbird species, *M. tyrianthina*, *C. iris*, *E. luciani*, and *L. lafresnayi*, also showed variation in specialization (d' and PSI) among habitat types. In most of the cases these species showed higher levels of specialization in the forest habitat (Table 4.8).

Factors significantly associated with specialization d' of hummingbirds included a single variable related to hummingbird morphology, total culmen length, and the two factors describing resource availability, sugar production and species richness of flowering plants (Table 4.9). These same factors were included in the top ranked multi-predictor models ($\Delta AICc < 2$) of specialization of hummingbirds (Table 4.10). Specialization d' was positively related to total culmen length ($\beta = 0.13$, $SE = 0.02$, $P < 0.01$; Figure 4.4) and negatively to sugar production ($\beta = -0.05$, $SE = 0.01$, $P = 0.02$; Figure 4.5). Although d' was negative for richness of flowering plants, this relationship was not significant ($\beta = -0.03$, $SE = 0.02$, $P = 0.19$).

PSI levels of hummingbirds were unrelated to any of their functional traits, but were associated with sugar production (Table 9). PSI of hummingbirds increased with decreasing sugar production ($\beta = -0.07$, $SE = 0.02$, $P = 0.001$; Figure 4.5; Table 4.10).

Discussion

Environmental change produced by anthropogenic alteration of habitats offers the opportunity to learn about processes that can determine patterns of specialization in species interaction networks. Here I used two measures of specialization, d' and PSI, to explore how ecological and evolutionary processes, which may act at different time scales (Kondoh 2003), influenced hummingbirds' specialization among habitats with different types of alterations. Both specialization indices showed that factors operating at relatively short ecological time scales (i.e., variation in resource availability) influenced the foraging behavior of tropical hummingbirds that affected their levels of specialization. However, the finding that culmen length influences specialization d' of hummingbirds across habitats suggests that long term evolutionary factors can also produce species traits that set the background of potential interacting species (Rezende et al. 2007). These results support my prediction that both ecological and evolutionary processes can shape the level of specialization of species, but that changes in specialization among habitats with different types of alterations might be largely mediated by the influence of ecological factors such as resource abundance.

In general, my results are consistent with the studies of interaction networks of frugivorous birds. For example, Carnicer et al. (2009), and González-Castro et al. (2012), showed that temporal variation in the type of resources consumed by frugivorous birds can be determined by short term ecological factors (i.e., resource availability), but that frugivorous' capacity to switch between different resources can be influenced by relative long term evolutionary factors (i.e., beak shape).

Traits related with foraging activities in pollinator species can influence their level of specialization by limiting the range of visited flowers (Stang et al. 2009, Junker et al. 2013). I found a positive relationship between the culmen length of hummingbirds and specialization d' . Culmen length has been identified as a key factor determining the types of plant species used by hummingbirds (Stiles 1975, Feinsinger and Colwell 1978, Temeles et al. 2009). Although high levels of specialization in hummingbirds could be rare because the relationship between hummingbirds is likely the product of diffuse coevolution (Stiles 1981, Cotton 1998), hummingbirds with a long culmen tend to feed from a limited number of plant species that have flowers with long corollas (Snow and Snow 1972, Wolf et al. 1976, Gutiérrez et al. 2004). These patterns of increased specialization of hummingbirds with long culmen may arise because trait matching between hummingbird culmen and flower corolla can determine feeding performance of hummingbirds especially when the hummingbirds have extreme phenotypes (Temeles et al. 2009).

Specialization of hummingbirds in the network was lower in the shrub and cattle ranch compared to the forest habitat. These decreases in specialization could be a result of either the turnover in species across habitat types, where the presence or absence of species with different levels of specialization can drive network-wide changes in specialization, or differences in the foraging behavior of the same hummingbird species across habitat types. Considering that species composition and functional structure of hummingbird communities were both similar across habitat types, and that the most abundant hummingbird species, *C. iris*, *E. luciani*, *M. tyrianthina*, and *L. lafresnayi*, were more specialized in the forest habitat compared to the shrub

and cattle ranch habitat types, the differences in the levels of specialization d' and PSI across habitat types can be attributed to changes in the foraging behavior of these species.

My results indicate that the change in specialization of hummingbirds was mediated by differences in sugar production across habitat types. Resource abundance is an ecological factor that can vary on relatively short temporal and spatial scales (Blake and Loiselle 1991, González-Castro et al. 2012), and modify the level of specialization of species (Carnicer et al. 2009). Accordingly, the greater resource abundance in the shrub and cattle ranch habitat types may have resulted in a less specialized foraging behavior of hummingbirds in these habitat types. Because of increased light, second growth vegetation often contains plant species that produce large amounts of nectar that attract many pollinator species (Linhart et al. 1987, Feinsinger et al. 1988). I found that in the shrub and cattle pasture habitat types, hummingbirds disproportionately used a few plant species, such as *B. arborea* and *O. grandiflora* (Fig 2). These plant species produce large amounts of nectar (Table 2), have little morphological restriction to hummingbird visits and thrive in open areas (Young 2009). Thus, the use by many hummingbird species of “super-generalists plants”, like *B. arborea* and *O. grandiflora*, may have resulted in the lower levels of specialization of hummingbirds in the altered habitat types compared to the forest habitat.

Resource availability can also influence changes in the levels of specialization of species indirectly by affecting competitive interactions. For example, interspecific competitive interactions driven by a decrease in resource availability can result in an increase in specialization of species (Pimm et al. 1985, Graham and Jones 1996). Hummingbird assemblages are structured based on competition for nectar (Feinsinger and Colwell 1978; Brown and Kodric-Brown 1979). The lower availability of resources in the forest habitat compared to the other habitat types could have caused increased competition for limited resources resulting in greater specialization of hummingbirds in the forest habitat. Studies in temperate environments have identified the importance of interspecific competition on specialization by finding a positive correlation between the number pollinator species and specialization (Fründ et al. 2010, 2013, Brosi and Briggs 2013). Here I show that consumer specialization influenced by interspecific competition may not only be driven by the number of species that are part of the network, but that resource abundance may also play a role (Powers and McKee 1994). However, my result of an increase in specialization when resources in the system are low, is not consistent with recent studies of mutualistic networks of both seed dispersal (Albrecht et al. 2013, Chama et al. 2013) and insect pollination networks (Fontaine et al. 2008, Geslin et al. 2013), which have found an increase in specialization in situations of greater resource abundance. Those studies supported their findings by optimal foraging theory, which predicts that in situations of high resource abundance in the system consumer species should tend to specialized, benefited by a decrease in the foraging time for specific resource types and reduced competitive interactions (MacArthur and Pianka 1966). Strong interspecific competitive interactions among hummingbirds (Feinsinger and Colwell 1978), and/or high levels of co-evolution between hummingbirds and the plants they use in the tropical Andes (Stiles 1981) may explain the different results found here. Nevertheless, further work on this system should test the hypothesis that hummingbird specialization is driven by resource abundance by directly testing per capita resource availability across habitat types combined with measures of interspecific competition strength.

This study contributes to a better understanding of the factors that determine specialization in pollination mutualistic networks in the tropics and elsewhere. Particularly, my results shed light on the potential responses of hummingbird species to the continued modification of habitats in the Neotropics. My results indicate that behavioral plasticity of hummingbirds will play an important role in the capacity of species to occupy anthropogenically degraded habitat types (Agrawal 2001). However, foraging behavior may be constrained by species morphological traits (e.g., culmen length). This constraint may limit the ability of some species to respond to the environmental changes brought about by anthropogenic alteration of habitats (Crispo et al. 2010). Moreover, my results show that pollination functions of hummingbirds might be sensitive to alterations caused by land use change in the tropical Andes. A decrease in specialization of hummingbirds in the shrub and cattle ranch habitats might indicate high heterospecific pollen loads in degraded habitats, which may ultimately result in lower reproductive success of plants (Brosi and Briggs 2013). These possibilities should be tested with future studies aiming at exploring how changes in specialization of hummingbird species can have repercussions on plant reproductive success. Nevertheless, my findings are an example of how measuring the structure of networks can be an important tool providing evidence of potential impacts of land use change on biodiversity maintenance and ecosystem functioning.

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Tables

Table 4.1. Measures of morphological traits of male hummingbirds. Details of how to obtain this measures are provided in the text.

Species	Morphological Traits											
	Weigth		Total Culmen		Wing chord		Wing aspect ratio		Wing loading		Tarsus	
	N	Mean (SE) gr	N	Mean (SE) mm	N	Mean (SE) mm	N	Mean (SE)	N	Mean (SE)	N	Mean (SE) mm
<i>Aglaeactis cupripennis</i>	21	8.21 (±0.14)	25	21.5 (±0.32)	24	83.15 (±0.44)	17	7.79 (±0.10)	17	0.181(±0.002)	17	7.78 (±0.20)
<i>Chaetocercus mulsant</i> *	24	3.58 (±0.03)	24	19.5 (±0.15)	24	39.67 (±0.17)	24	7.72 (±0.10)	24	0.368 (±0.004)	7	4.33 (±0.02)
<i>Colibri coruscans</i>	25	8.21 (±0.07)	34	28 (± 0.54)	34	77.69 (±0.82)	25	7.82 (±0.05)	25	0.21 (±0.002)	25	6.22 (±0.28)
<i>Coeligena iris</i>	5	7.08 (±0.11)	7	31.81 (± 1.00)	10	78.18 (±1.33)	3	7.39 (±0.51)	3	0.212 (±0.012)	8	7.44 (±0.15)
<i>Ensifera ensifera</i> *	4	9.68 (±0.27)	4	83.92 (± 1.33)	4	76.83 (±0.72)	4	7.94 (±0.16)	4	0.254 (±0.007)	4	6.8 (±0.11)
<i>Eriocnemis luciani</i>	10	6.12 (±0.13)	14	24.98 (± 0.40)	14	70.26 (±0.37)	1	7.9 (±NA)	1	0.233 (±NA)	13	7.79 (±0.20)
<i>Eriocnemis vestita</i> *	25	4.86 (±0.04)	25	21.38 (± 0.17)	25	59.83 (±0.2)	25	7.14 (±0.05)	25	0.2 (±0.002)	25	5.7 (±0.05)
<i>Heliangelus viola</i>	12	5.63 (±0.11)	8	18.08 (± 0.78)	11	62.36(± 1.13)	6	7.39 (±0.32)	6	0.246 (±0.003)	8	7.29 (±0.19)
<i>Lafresnaya lafresnayi</i>	19	5.69 (±0.07)	18	29.69 (±0.26)	19	64.52 (± 0.31)	19	7.63 (±0.05)	19	0.216 (±0.003)	18	5.62 (±0.01)
<i>Lesbia nuna</i> *	7	3.66 (±0.05)	7	12.66 (± 0.21)	7	51.54 (±0.36)	7	6.82 (±0.06)	7	0.198 (±0.004)	7	5.64 (±0.08)
<i>Lesbia victoriae</i> *	11	5.29 (±0.05)	11	17.58 (±0.17)	11	59.75 (±0.33)	11	7.44 (±0.07)	11	0.226 (±0.004)	11	6.25 (±0.07)
<i>Metallura baroni</i>	4	4.57 (±0.08)	3	17.77 (±0.62)	5	57.7 (±1.22)	2	7.86 (±0.52)	2	0.248 (±0.003)	3	7.07 (±0.55)
<i>Metallura tyrianthina</i>	35	3.79 (±0.04)	42	14.83 (±0.15)	53	58.45 (±0.26)	35	7.09 (±0.06)	35	0.161 (±0.004)	40	6.72 (±0.09)
<i>Pterophanes cyanopterus</i>	6	10.37 (±0.31)	6	36.45 (± 1.01)	6	105.6 (±0.94)	6	7.55 (±0.09)	6	0.147 (±0.008)	6	7.84 (±0.14)
<i>Ramphomicron microrhynchum</i> *	15	3.67 (±0.06)	15	10.21 (±0.25)	15	49.85 (±0.41)	15	7.5 (±0.10)	15	0.234 (±0.003)	15	6.07 (±0.04)

* symbol denotes species for which morphology data was obtained from Gary Stiles personal data base. Stiles contact information: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.

Table 4.2. Nectar characteristics of all the plant species used by hummingbirds. Mean values of nectar volume include flowers with zero production of nectar. Nectar production was calculated as the product of nectar volume in ml multiplied by sugar concentration measured in sugar mg/ml following the table provided by Kearns and Inouye (1993).

Species	Nectar Volume ($\mu\text{l } 24\text{h}^{-1}$)		Sugar Concentration (% w/w)		Nectar production sugar $\text{mg}^{-24\text{h}}$ per flower
	N	Mean ($\pm\text{SE}$)	N	Mean ($\pm\text{SE}$)	Mean
<i>Alloplectus peruvianus</i>	11	0.04 (± 0.02)	9	14.5 (± 2.4)	0.01
<i>Barnadesia arborea</i>	15	9.22 (± 1.5)	21	19.15 (± 0.6)	1.91
<i>Berberis lutea</i>	15	0.62 (± 0.04)	16	25.69 (± 1.7)	0.18
<i>Bomarea</i> sp	7	2.33 (± 0.89)	7	2.33 (± 0.4)	0.05
<i>Brachyotum confertum</i>	31	14.48 (± 3.13)	30	14.62 (± 0.7)	2.24
<i>Bromelia</i> sp2	9	1.5 (± 0.22)	16	10.63 (± 0.5)	0.17
<i>Bromelia</i> sp3	21	16.42 (± 2.58)	21	14.52 (± 1.2)	2.52
<i>Brugmansia sanguinea</i>	10	29.23 (± 10.17)	9	20.89 (± 1.8)	6.63
<i>Cavendishia bracteata</i>	18	0.14 (± 0.04)	7	16.31 (± 1.3)	0.02
<i>Centropogon</i> sp	10	6.14 (± 1.89)	10	12.2 (± 0.7)	0.78
<i>Fuchsia cf. vulcanica</i>	44	6.39 (± 1.74)	22	19.8 (± 1.4)	1.37
<i>Gaiadendron punctatum</i>	5	0.09 (± 0.01)	3	31 (± 1.4)	0.03
<i>Gaultheria erecta</i>	15	0.23 (± 0.05)	8	13.9 (± 1.8)	0.03
<i>Macleania rupestris</i>	46	10.81 (± 1.59)	39	17.5 (± 0.8)	2.02
<i>Mutisia lemanni</i>	13	34.7 (± 9.43)	21	19.5 (± 0.9)	7.30
<i>Oreocallis grandiflora</i>	48	18.69 (± 1.65)	42	14.8 (± 0.4)	2.93
<i>Palicuorea</i> sp	10	0.94 (± 1.33)	10	14.4 (± 0.6)	0.14
<i>Passiflora cumbalensis</i>	5	142.51 (± 29.45)	9	23 (± 1.4)	35.88
<i>Rubus floribundus</i>	5	2.44 (± 0.56)	1	50 ($\pm \text{NA}$)	1.50
<i>Salvia corrugate</i>	46	2 (± 0.33)	22	11.9 (± 1.8)	0.25
<i>Salvia hirta</i>	17	6.36 (± 1.78)	18	18.1 (± 1.2)	1.23
<i>Saracha quitensis</i>	14	13.29 (± 2.54)	19	12.5 (± 0.9)	1.74
<i>Tillandsia complanata</i>	9	1.49 (± 0.22)	9	10.6 (± 0.7)	0.17
<i>Tristerix longibracteatus</i>	30	4.56 (± 0.8)	18	18.9 (± 0.6)	0.93
<i>Verbesina latisquama</i>	15	0.69 (± 0.05)	18	22.1 (± 0.5)	0.17
<i>Viola arguta</i>	16	4.08 (± 0.73)	14	12.5 (± 1.1)	0.54

Table 4.3. Average abundance across the sampling period of hummingbird species sampled by point counts in three habitat types (forest, shrub, cattle ranch) in the south central Andes of Ecuador. Abundance was corrected for detection probabilities using the double observer method.

Species	Forest	Shrub	Cattle ranch
	Mean (\pm SE)	Mean (\pm SE)	Mean (\pm SE)
<i>Aglaeactis cupripennis</i>			0.41 (\pm 0.32)
<i>Chaetocercus mulsant</i>		0.05 (\pm 0.23)	
<i>Colibri coruscans</i>	0.23 (\pm 0.28)	0.05 (\pm 0.23)	0.05 (\pm 0.23)
<i>Coeligena iris</i>	0.83 (\pm 0.12)	0.87 (\pm 0.17)	0.6 (\pm 0.22)
<i>Ensifera ensifera</i>	0.05 (\pm 0.23)	0.10 (\pm 0.23)	
<i>Eriocnemis luciani</i>	0.69 (\pm 0.56)	0.82 (\pm 0.56)	0.55 (\pm 0.18)
<i>Eriocnemis vestita</i>			0.05 (\pm 0.23)
<i>Heliangelus viola</i>	0.60 (\pm 0.31)	0.14 (\pm 0.22)	0.05 (\pm 0.23)
<i>Lafresnaya lafresnayi</i>	0.88 (\pm 0.22)	0.53 (\pm 0.27)	0.18 (\pm 0.21)
<i>Lesbia nuna</i>			0.05 (\pm 0.23)
<i>Lesbia victoriae</i>		0.10 (\pm 0.23)	0.09 (\pm 0.22)
<i>Metallura baroni</i>		0.19 (\pm 0.21)	
<i>Metallura tyrianthina</i>	1.98 (\pm 0.16)	2.07 (\pm 0.25)	2.35 (\pm 0.24)
<i>Pterophanes cyanopterus</i>	0.18 (\pm 0.31)	0.24 (\pm 0.29)	0.05 (\pm 0.23)
<i>Ramphomicron microrhynchum</i>		0.10 (\pm 0.23)	

Table 4.4. Results of a fourth-corner analysis of the relationships between hummingbird morphological traits and habitat types (forest, shrub, cattle ranch) in the south central Andes of Ecuador. Significance was obtained by a permutation that tests whether traits are randomly distributed across habitat types considering abundance of hummingbirds.

Morphology trait	F value	<i>P</i>
Body mass	0.17	0.68
Total culmen length	0.58	0.42
Wing chord	0.35	0.53
Wing aspect ratio	0.53	0.10
Wing loading	1.46	0.04
Tarsus length	1.25	0.14

Table 4.5. Models of testing for differences in resource availability for hummingbirds among three habitat types in the south central Andes of Ecuador. Given are standardized coefficients and their standard errors. P values come from Markov chain Monte Carlo sampling.

	β	SE	t	P
a) Flowering plant richness				
Forest vs shrub	0.17	0.06	2.88	<0.01
Forest vs cattle ranch	0.19	0.06	3.15	<0.01
Shrub vs cattle ranch	0.02	0.06	0.28	0.82
b) Nectar production (sugar mg per 24 h ⁻¹)				
Forest vs shrub	1.33	0.27	4.88	<0.01
Forest vs cattle ranch	1.41	0.27	5.17	<0.01
Shrub vs cattle ranch	0.08	0.27	0.30	0.84

Table 4.6. Mean sugar production across the study period of the most common plant species in the three habitat types. Pairwise comparisons were tested by linear mixed models considering a P value of less than 0.05 obtained from Markov chain Monte Carlo sampling. Pair-wise differences between groups were tested by switching the group specified as the intercept in the models.

Species	Forest		Shrub		Cattle Ranch		Pair wise comparison *
	Rank	Mean (SE)	Rank	Mean (SE)	Rank	Mean (SE)	
<i>Oreocallis grandiflora</i>	1	944.71 (±208.60)	1	2414.48 (±450.48)	1	7819.28 (±2024.84)	F<S,F<C,S=C
<i>Palicuorea sp</i>	2	861.66 (±733.30)					
<i>Verbesina latisquama</i>	3	572.61 (± 454.88)	3	1167.70 (± 389.39)			F<S
<i>Viola arguta</i>	4	142.88 (±24.18)	12	69.29 (± 40.35)	15	13.47 (± 3.08)	F>S, F>S ,S>C
<i>Salvia hirta</i>	5	129.07 (±11.04)	4	1046.66 (±190.38)			F<S
<i>Fuchsia cf. vulcanica</i>	7	78.66 (± 15.08)	5	465.42 (± 106.89)	5	77.43 (± 16.32)	F<S, F=C, S>C
<i>Barnadesia arborea</i>	16	27.95 (±4.96)	2	2047.11 (±682.03)	3	128.09 (±40.44)	F<S, F=C, S>C
<i>Brachyotum confertum</i>			6	460.27 (±195.99)	2	1647.56 (± 899.07)	S<C
<i>Berberis lutea</i>			15	36.27 (±14.56)	4	89.76 (±28.83)	S=C

* F, forest habitat; S, shrub habitat; C, cattle ranch habitat.

Table 4.7. Summary results of linear mixed effects models of the relationships between habitat type and a) specialization d' , and b) pollinator service index (PSI) of hummingbirds quantified from hummingbird – plant pollination networks in the south central Andes of Ecuador. Given are standardized coefficients and their standard errors. P values were derived by Markov chain Monte Carlo sampling.

	β	SE	t	P
a) Specialization d'				
Forest vs shrub	-0.13	0.03	-4.27	<0.01
Forest vs cattle ranch	-0.13	0.03	-4.08	<0.01
Shrub vs cattle ranch	-0.01	0.04	-0.03	0.90
b) PSI				
Forest vs shrub	-0.15	0.04	-3.86	0.01
Forest vs cattle ranch	-0.13	0.04	-3.24	0.02
Shrub vs cattle ranch	0.02	0.03	0.44	0.69

Table 4.8. Mean specialization d' (a) and pollinator service index PSI (b) of the most common hummingbird species across habitat types. Pairwise comparisons were tested by linear mixed models considering a P value of less than 0.05 obtained from Markov chain Monte Carlo sampling. Pair-wise differences between groups were tested by switching the group specified as the intercept in the models.

Species	Forest	Shrub	Cattle ranch	Pair wise comparison
a) d'				
<i>Coeligena iris</i>	0.49 (± 0.05)	0.41 (± 0.10)	0.30 (± 0.09)	F>S, F>C, S>C
<i>Eriocnemis luciani</i>	0.37 (± 0.09)	0.09 (± 0.02)	0.14 (± 0.03)	F>S, F>C, S=C
<i>Lafresnaya lafresnayi</i>	0.48 (± 0.13)	0.25 (± 0.08)	0.59 (± 0.01)	F=S, F=C, S=C
<i>Metallura tyrianthina</i>	0.15 (± 0.05)	0.09 (± 0.02)	0.12 (± 0.02)	F>S, F=C, S=C
b) PSI				
<i>Coeligena iris</i>	0.72 (± 0.09)	0.46 (± 0.10)	0.43 (± 0.09)	F>S, F>C, S=C
<i>Eriocnemis luciani</i>	0.44 (± 0.09)	0.57 (± 0.02)	0.34 (± 0.03)	F<S, F=C, S>C
<i>Lafresnaya lafresnayi</i>	0.58 (± 0.13)	0.46 (± 0.08)	1 (± 0.01)	F>S, F<C, S<C
<i>Metallura tyrianthina</i>	0.87 (± 0.05)	0.64 (± 0.02)	0.79 (± 0.02)	F>S, F>C, S<C

* F, forest habitat; S, shrub habitat; C, cattle ranch habitat.

Table 4.9. Single predictor models of the effects of morphological traits of hummingbirds and resource availability on a) specialization d' , and b) pollinator service index (PSI) of hummingbirds quantified from hummingbird – plant pollination networks in the south central Andes of Ecuador. Given are standardized coefficients and their standard errors. P values were derived by Markov chain Monte Carlo sampling.

	β	SE	t	P
a) Specialization d'				
<i>Hummingbird morphological traits</i>				
Body mass	0.03	0.02	2.06	0.10
Total culmen	0.01	0.01	6.44	<0.01
Wing chord	0.01	0.01	1.08	0.34
Wing aspect ratio	0.05	0.24	0.23	0.91
Wing load	1.53	0.81	1.90	0.12
Tarsus length	-0.02	0.04	-0.56	0.61
<i>Resource availability</i>				
Richness of flowering species	-0.02	0.01	-2.54	0.05
Nectar production (in sugar mg 24 h ⁻¹)	-0.06	0.02	-3.95	<0.01
b) PSI				
<i>Hummingbird morphological traits</i>				
Body mass	-0.04	0.02	-2.34	0.12
Total culmen	0.01	0.01	0.24	0.82
Wing aspect ratio	0.09	0.32	0.27	0.91
Wing load	0.72	1.14	0.63	0.73
Tarsus length	-0.03	0.05	-0.60	0.44
<i>Resource availability</i>				
Richness of flowering species	-0.01	0.00	-1.50	0.41
Nectar production (in sugar mg 24 h ⁻¹)	-0.08	0.02	-5.18	<0.01

Table 4.10. Comparisons of different models explaining a) specialization d' and b) pollinator service index (PSI) of hummingbirds obtained from hummingbird – plants pollination networks in south central Andes of Ecuador. Factors included in the models are: Sugar production (sugar mg 24 h⁻¹), richness of flowering plants, and total culmen length in mm of hummingbird species. R² marginal represents the proportion of variance explained by the fixed factors alone, and R² conditional represents the proportion of variance explained by both the fixed and random factors.

Model description	AICc	Δ AICc	AICc weight	R ² marginal	R ² conditional
a) specialization d'					
Sugar production + total culmen	47.00	0.00	0.56	0.37	0.43
Sugar production + total culmen + flowering plants richness	48.00	1.01	0.34	0.38	0.43
Total culmen + flowering plants richness	51.50	4.50	0.06	0.35	0.42
Total culmen	52.50	5.45	0.04	0.32	0.40
Sugar production	60.10	13.04	0.00	0.08	0.24
Sugar production + flowering plants richness	60.80	13.83	0.00	0.08	0.24
flowering plants richness	64.10	17.10	0.00	0.03	0.22
~ 1	65.30	18.26	0.00		0.20
b) PSI					
Sugar production	97.72	0.00	0.98	0.08	0.32
~ 1	105.80	8.05	0.01		0.27

Figures

Figure 4.1. Effects of habitat type on sugar production and richness of flowering plants used by hummingbirds in south-central Andes of Ecuador. Sugar production was estimated as the total production of sugar mg in 24 h by the total number of flowers available in each habitat. Letters over the bars represent differences in groups tested by linear mixed models considering a P value of less than 0.05 obtained from Markov chain Monte Carlo sampling. Pair-wise differences between groups were tested by switching the group specified as the intercept in the models.

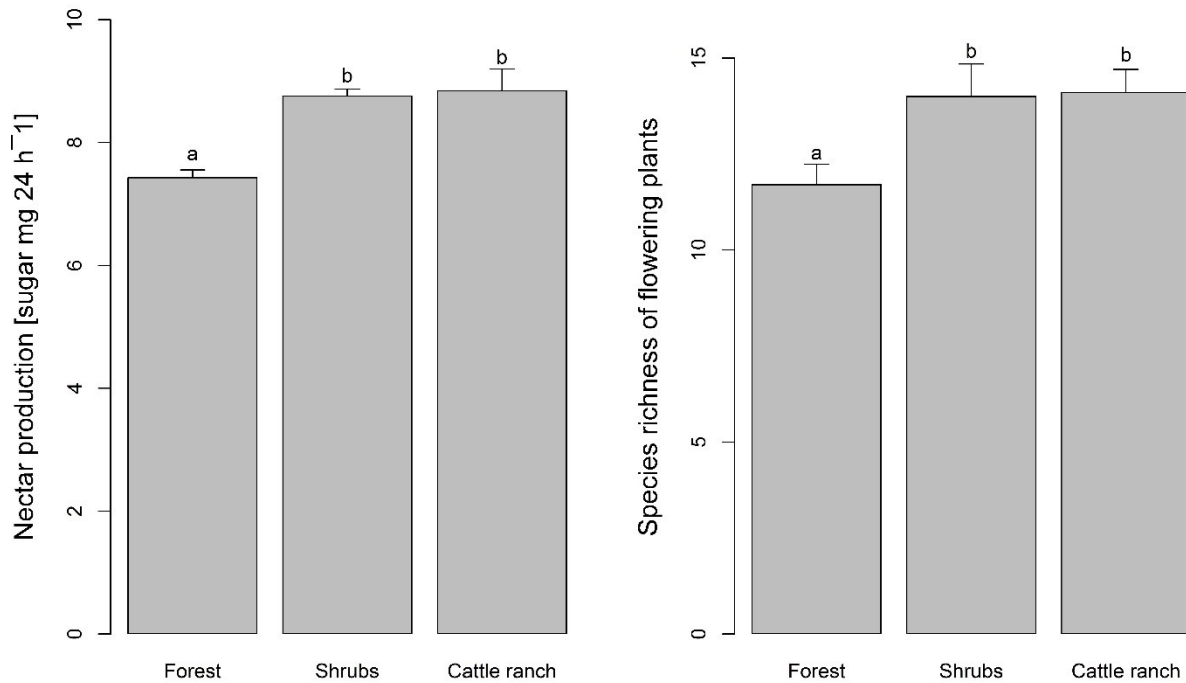


Figure 4.2. Bipartite pollination networks of hummingbirds (top) and plants (bottom) in the south central Andes of Ecuador. Figure depicts networks of three habitats: a) forest, b) shrub, and c) cattle ranch. For the figures data were pooled from 10 observation periods from February 2011 to August 2012. The width of the top and bottom bars represent the number of visit frequencies of each species within the network.

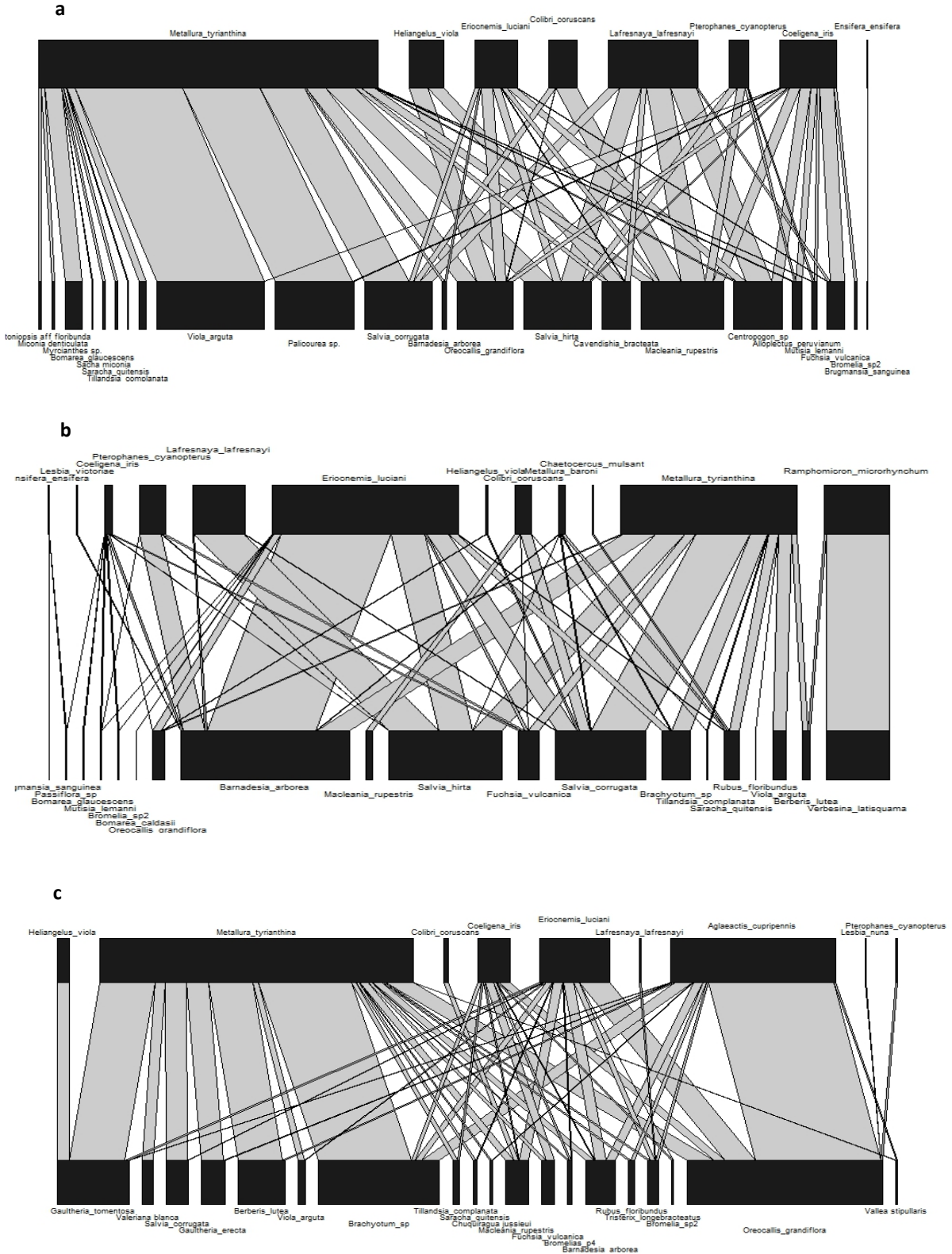


Figure 4.3. Effects of habitat type on specialization (d') and pollinator service index (PSI) of hummingbirds calculated from hummingbird – plant pollination networks in south-central Andes of Ecuador. Figure shows mean values and standard errors weighted by the abundance of each hummingbird species across ten sampling periods. Letters over the bars represent differences in groups tested by linear mixed models considering a P value of less than 0.05 obtained from Markov chain Monte Carlo sampling. Pair-wise differences between groups were tested by switching the group specified as the intercept of the models.

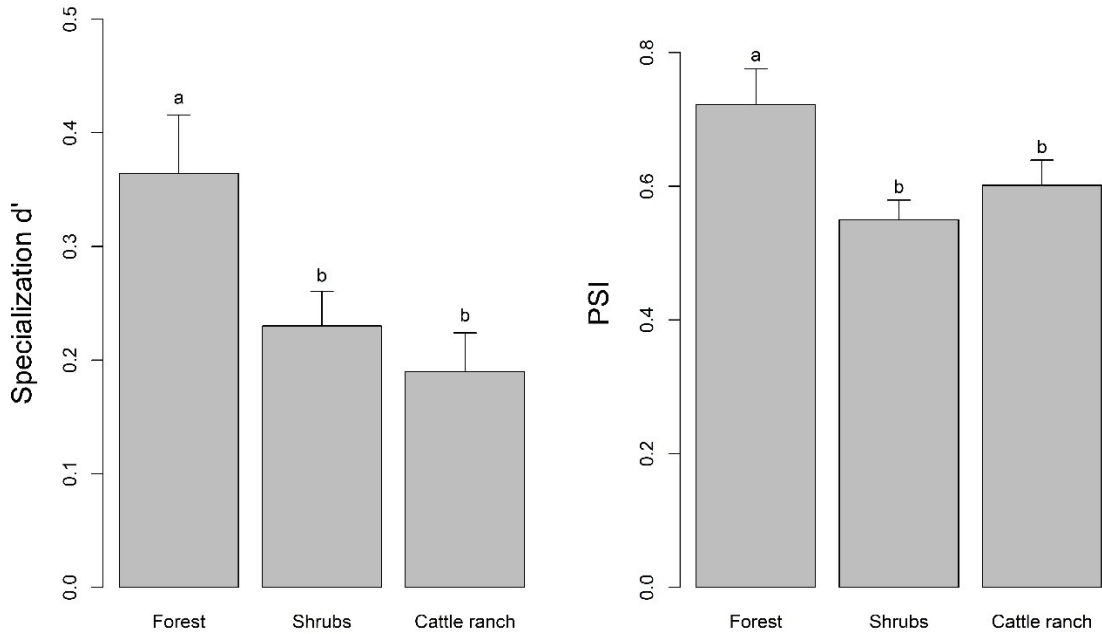


Figure 4.4. Effects of culmen length on specialization d' of hummingbird pollinators calculated from hummingbird – plant networks in south-central Andes of Ecuador. The values of d' represent fitted values from linear mixed effects models. d' depicts mean values weighted by the abundances of hummingbird species. Culmen length is represented on a log scale. Black dots represents species from forest habitat, gray dots represent species from shrub habitat, and open squares were built from species in cattle ranch habitat.

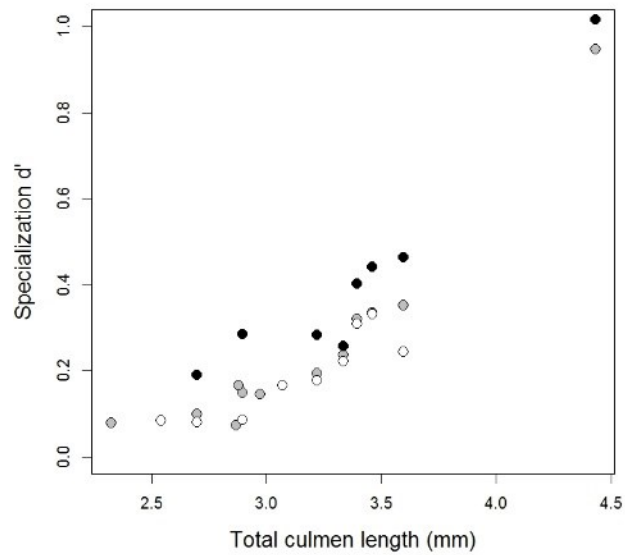
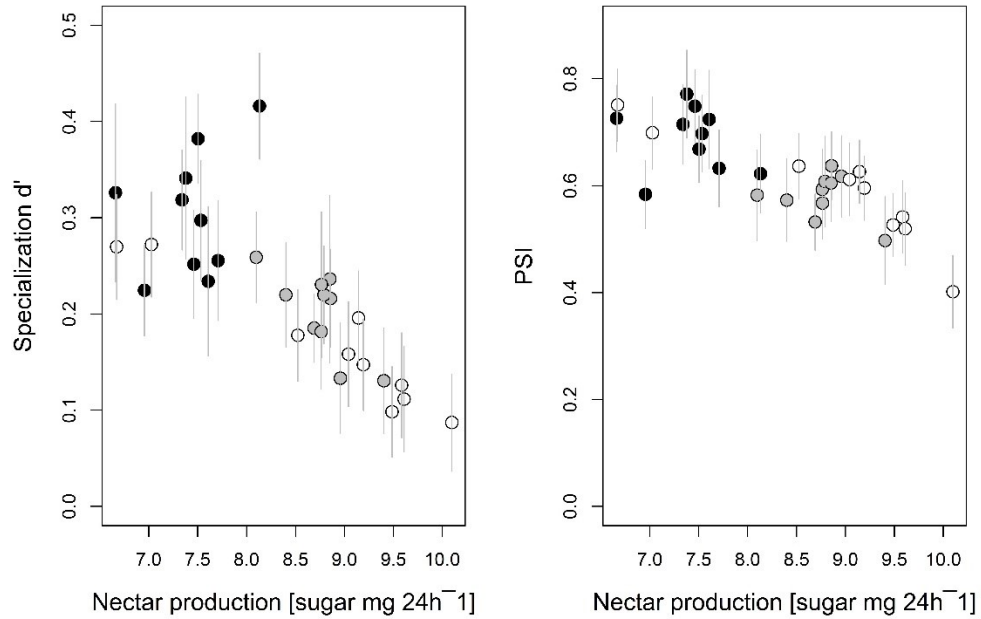


Figure 4.5. Effects of resource availability (measured as total production of sugar mg in 24 h of available flowers) on specialization d' and pollinator service index (PSI) of hummingbird pollinators calculated from hummingbird – plant networks in south-central Andes of Ecuador. The values of d' and PSI of hummingbirds represent fitted values from linear mixed models of networks obtained in three different habitats: Black dots come from forest habitat, gray dots represent shrub habitat, and open squares were built from cattle ranch habitat. d' and PSI' depict mean values and standard errors weighted by the abundances of hummingbirds species.



Chapter 5: Conclusion

The tropical Andes have one of the highest rates of deforestation on earth (Sodhi et al. 2008, Asner et al. 2009). This poses significant threats to the conservation of biodiversity and the maintenance of ecosystem services in this region (Myers et al. 2000, Orme et al. 2005). In this dissertation I contributed to the knowledge base of how anthropogenic habitat alterations affect the biodiversity of the tropical Andes by studying hummingbird responses to habitat alternation at different levels of ecological organization: populations, assemblages, and community (plant-animal interactions). I also discussed the applied and theoretical implications of my findings.

In chapter 2, I used a seven-year capture-recapture hummingbird dataset to study the effects of habitat alteration on demographic parameters. I showed that populations of some hummingbird species (*Metallura tyrianthina* and *Eriocnemis luciani*) were likely to persist in anthropogenically altered habitats; however, populations of other species (*Coeligena iris*) could be negatively affected by this alteration. My results also indicated that population growth rates of these species are likely influenced by a trade-off between survival and the number of offspring produced (productivity). Future studies should focus on the factors that directly influence survival and productivity (e.g., resources, predation, parasitism), and dispersal rates among populations. To my knowledge there are no published demographic estimates of native birds in the tropical Andes, and hence this work provides new information to help determine how anthropogenic alteration effects biodiversity in this region. Detailed demographic data are necessary to understand and predict the long term consequences of habitat alteration for the local persistence of a population.

In chapter 3, I evaluated changes in hummingbird assemblages across landscapes with different land uses, from landscapes dominated by native vegetation, to a landscapes with reduced native vegetation coverage dominated by cattle pastures. I found that taxonomic diversity showed little variation among landscapes; however, functional diversity was negatively affected by the loss of native vegetation cover in the landscape. These results suggest that anthropogenic alteration of habitats can act as an environmental filter, allowing only species with particular traits to occupy these habitats. This process can produce decoupled responses of taxonomic and functional diversity to environmental gradients (Flynn et al. 2009, Cadotte et al. 2011). Therefore, the exclusive use of taxonomic diversity to study the effects of land use change can mask negative responses on other facets of the diversity of an assemblage, such as functional diversity. This is troubling, given the close association between functional diversity and ecosystem processes (Tilman et al. 1997, Fründ et al. 2013, Brosi and Briggs 2013).

To better understand hummingbird-environment relationships in altered habitat types, I used knowledge about the functional role of different hummingbird traits to make a series of predictions about how these traits influenced hummingbird's responses to land use change. Ordinations were used to relate hummingbird functional traits to land use change. These relatively new methods proved valuable for identifying traits that might determine species' sensitivity to land use change. In particular, large body size is a trait that may increase the sensitivity of hummingbird species to land use change because I found a positive association of this trait and the amount of native vegetation in a landscape. This information is important in

order to predict which species may be at high risk given the ongoing transformation of native vegetation in the tropical Andes (e.g., Davidson et al. 2009, Newbold et al. 2013).

In chapter 4, I used network analysis to explore the effects of habitat alteration on hummingbird-plant interactions. Network analysis is a useful tool for quantifying species interactions because interactions can be studied in a community context (Memmott 1999, Jordano et al. 2003, Carnicer et al. 2009). I assessed how the levels of specialization of hummingbirds changed across forest, shrub and cattle ranch habitats. Specialists in ecological networks are those species that interact with a reduced number of partners (Vázquez and Aizen 2006). I evaluated how changes in specialization across habitats might be mediated by ecological factors (i.e., variation in resource abundance), and evolutionary factors (i.e., morphological traits). The level of specialization in hummingbirds was greater in the forest habitat compared to the more altered habitat types (shrub habitat and a cattle ranch). Variation in resource abundance among habitat types likely influenced the level of specialization. Moreover, specialization of hummingbirds was positively associated with culmen length across all habitat types, which might be related to co-adaptive process between long billed hummingbirds and flowers with long corollas (Stiles 1981). From an applied perspective, lower levels of specialization of hummingbirds in more altered habitats could diminish hummingbirds' role as pollinators, because this could translate to pollen loads with increased pollen diversity (Brosi and Briggs 2013). Evaluating how pollen loads influence plant reproduction is an interesting area of research about the impacts of habitat alteration on the role of hummingbirds as pollinators.

An important challenge in biodiversity studies is to understand how ecological responses at one level of ecological organization (e.g., populations) can scale up and influence responses at other levels (e.g., assemblages, communities, etc.) (Chapin III et al. 2000). The use of functional trait approaches to study biodiversity could be a promising way to integrate ecological responses at multiple levels of organization (McGill et al. 2006, Polly et al. 2011). My analysis of demographic parameters of hummingbird populations showed that *Coeligena iris* could be sensitive to anthropogenic alterations of habitats (Chapter 2). Among the three hummingbird species evaluated, *C. iris* has the largest body mass and the longest culmen length. In Chapter 3, I found that the body size and culmen length of a hummingbird can increase its sensitivity to land use change. At the network level (Chapter 4), my results indicated that culmen length of a hummingbird influences their level of specialization and thus affects pollination interactions in a community. Taken together these results across levels of organization could indicate the lower survival of birds with long culmens and large body sizes might scale up and effect the distribution of hummingbird species in different habitat types. Accordingly, the distribution of culmen lengths among hummingbirds present in a habitat could determine which pollination interactions are possible in a community. However, these process are not unidirectional, and factors operating a higher levels of ecological organization could also impact responses at lower levels (Martín González et al. 2010, Polly et al. 2011). These results highlight the value of studying functional traits of organisms across environments to learn about the interplay of process that operate at different levels of ecological organization.

While my research has broad conservation and management implications I also evaluated several theoretical ideas. I showed that tradeoffs between survival and productivity can regulate population growth rates in altered habitats. Further, by comparing taxonomic and functional

responses to a land use gradient, I showed that environmental filtering may be one factor determining the assemblage of communities in landscapes subjected to anthropogenic alteration. Finally, my study of hummingbird-plant interaction networks identified important factors, such as availability of resources and feeding morphological traits, which might regulate species interactions within ecological networks.

Taken together, my results demonstrate that determining the effects of habitat alteration on biodiversity requires exploring different levels of ecological organization. As shown here, each level can contribute different insights about the consequences of habitat alteration on biodiversity conservation and ecosystem functioning. My results have important implications for conservation and management in the region, because they show that effective conservation practices in a region will require approaches that consider various levels of ecological organization. Only this will ensure the conservation of both species and ecosystem function (Dyer et al. 2010, Hegland et al. 2010).

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