

# Effects of habitat disturbance on a montane bird community

By: Richard C. Stanley

A senior thesis presented to  
The Department of Organismic and Evolutionary Biology  
Harvard University  
Cambridge, MA

November 13, 2012

## Acknowledgements

*I would like to extend my sincerest thanks to:*

Jonathan Losos for his generous encouragement and support; Andrew Berry for his unfailingly sound advice; Scott Edwards and Tom Lovejoy for encouraging my interest in bird conservation biology; Brian Farrell for his mentorship and advice on audio recording technique; Ambika Kamath for her mentorship and help with statistics; Tom Gode, Linda Moskalyk and the staff of Cloudbridge Reserve for their hospitality; Jennifer Giddy for her dedication to cloud forest conservation; Gabby Salazar for her unwavering support and editorial assistance; Lisa Chen, John Stanley, Yan-Yee Lau, Claire Vincent, Olivia Kerns and Ali Brown for their assistance and camaraderie in the field; Bernal Morales for supporting my work in Chirripo; Talamanca Forest Reserve for access to their trails; my parents and Rubio del Castillo for encouraging my interests from an early age; Cagan Sekercioglu and Nathan Marcy for inspiring my study idea with their work.

*Funding:*

I am very grateful to the Harvard University Center for the Environment for supporting my fieldwork.

*Collaboration:*

I am indebted to Gabby Salazar, Lisa Chen, John Stanley, Yan-Yee Lau, Claire Vincent, Olivia Kerns and Ali Brown, who at various times provided invaluable assistance in the field, accompanying me on bird counts, operating the audio recorder, and taking down habitat measurements.

## Table of Contents

Abstract.....	4
Introduction.....	5
Methods.....	11
Results.....	22
Discussion.....	35
Conclusion.....	42
References.....	43
Appendices.....	49

## Abstract

My thesis research investigates the effects of habitat disturbance on a Costa Rican montane bird community. I collected my data at Cloudbridge Nature Reserve in the Talamanca Mountains, where I conducted point count surveys in four habitat types in different stages of ecological succession. I established 80 points—20 each in primary, secondary, young successional, and countryside habitats—and visited each point twice. I also collected data on the vegetation structure of the points. The objective of my study was to determine the conservation value of human-altered habitats by observing how bird species diversity, abundance, and composition change along a gradient of disturbance. I predicted that I would see a shift in community composition with increasing disturbance as well as a decline in species richness and diversity.

I found that contrary to expectations, richness and diversity did not decline in the more disturbed habitat categories; in fact, they increased slightly. As I predicted, I also found that community composition changed substantially with disturbance. Primary cloud forest sites contained a suite of species that were poorly represented or absent in other habitats. Forest birds declined sharply in richness and abundance in the more open habitats, while disturbance-tolerant species increased in numbers. Regional endemic species were also better represented in the forest. In this thesis, I report my findings on the effects of disturbance on all species of this highland bird community.

# Introduction

Anthropogenic habitat modification poses a global threat to bird populations, especially in the tropics (Bowen et al. 2007). Degraded tropical forests are a rapidly expanding habitat of great significance, although they have attracted limited interest from conservationists (Bowen et al. 2007). It is important to understand how avian community structure changes in disturbed habitats in order to establish conservation priorities and to predict the consequences of future habitat loss (O'Dea and Whittaker, 2007; Dunn, 2004).

Conservation biologists have traditionally focused their efforts on the study of primary tropical forests, because these ecosystems are among the planet's greatest repositories of biodiversity (Terborgh, 1999). Some conservationists have argued that if the goal of conservation is to preserve intact, ecologically functioning communities, one can settle for nothing less than pristine habitats (Terborgh, 1999). Recognizing the imperiled state of primary tropical forests, ecologists have sought to understand the effects of encroaching land clearance and habitat fragmentation on biodiversity (Bierregaard et al. 1992). Studies on birds have found declines in diversity with increasing fragmentation, and these declines can be related to island biogeography theory (Bierregaard et al. 1992).

Often, fragmentation studies categorize habitats in a binary fashion, as either suitable (the island habitat) or unsuitable (the matrix habitat). This approach tells only a part of the story, because it does not take into account the importance of partially degraded "gradient" habitats for biodiversity (Kupfer et al. 2006). Land use can create a mixture of habitats of intermediate suitability, including secondary growth, cultivated areas, and partially logged forest (Chazdon, 2003). Small-scale farming has also created a variety of countryside habitats that still retain trees

and hold potential conservation value (Hughes et al. 2002). Recently, interest in the conservation value of degraded habitats has risen substantially, although conservation biologists still disagree over the extent to which degraded habitats will curb the loss of biodiversity as pristine habitats are destroyed (Barlow et al. 2007b). While our understanding of the importance of disturbed areas is still incomplete (Bowen et al. 2007), studies have shown that high levels of bird biodiversity often persist in secondary forests (Blake and Loiselle, 2001) and even countryside habitats (Daily et al. 2001).

*What is the value of degraded habitats for conservation?*

Disturbed forests may be of great conservation value, and research has shown that bird species richness in secondary forest is often comparable with that of primary forest (Sodhi et al. 2005; Schulze et al 2004; Lawton et al. 1998; Andrade and Rubio-Torgler 1994). Barlow et al. (2007a) reviewed 11 studies comparing tropical bird communities in secondary forests (aged 17-30 years) with those of primary forests, finding that most studies recorded high species richness in both habitats. Only four studies documented lower richness in secondary forest (Raman et al. 1998; Bowman et al. 1990; Terborgh and Weske, 1969; Barlow et al 2007a). In another review, Bowen et al. (2007) evaluated 28 studies on birds and found that many of them documented high diversity in secondary forest. Some studies have even reported a peak in species richness in degraded habitats, including secondary forest (O'Dea and Whittaker, 2007, Blake and Loiselle 2001, Johns 1991) and selectively logged forest (Sekercioglu, 2002).

Agricultural landscapes can also be important for the conservation of bird diversity (Hughes et al. 2002). Many species inhabit the countryside, although richness is usually lower

than that seen in forest habitats (O'Dea and Whittaker, 2007, Posa and Sodhi, 2006). This is likely due to reduced vegetation cover, because countryside habitat has a far sparser canopy and a more open understory (Posa and Sodhi, 2006).

The capability of degraded habitats to support diverse bird faunas depends in large measure on their vegetation structure (Matlock and Edwards, 2006). Given the specificity of habitat requirements shown by many birds, there is a close relationship between the vegetation and the avian community composition, and even subtle changes in forest structure can have pronounced effects (Sekercioglu, 2002; Blake and Loiselle, 2001; Matlock and Edwards, 2006; Ansell et al. 2011). Percent canopy cover is frequently correlated with bird diversity, with species richness declining as canopy cover is reduced (Posa and Sodhi, 2006; Matlock and Edwards, 2006). MacArthur and MacArthur (1961) were among the first to find evidence that more layered vegetation also supports greater bird diversity, probably because it offers more foraging niches. More recent studies confirm this result, and the high foliage heterogeneity of young temperate forests may explain their elevated diversity (Keller et al. 2003). This research suggests that young temperate forest habitats with dense understories may support greater bird diversity than mature forests with open understories. Vegetation density has also been found to be important in tropical environments, where the removal of dense vines has decreased bird richness (Edwards, 2011).

The fact that high avian species richness is often observed in degraded habitats is not conclusive evidence that bird populations are resilient to disturbance. Barlow et al. (2007a) contend that many studies sample secondary forest in unsuitably close proximity to their primary forest controls, exaggerating their estimates of the species richness of degraded areas. Barlow et al. (2007a) attempted to minimize spillover in their work by sampling large, unbroken areas of

secondary forest in the Amazon, and they found lower richness in secondary forest and minimal species overlap between secondary and primary forest sites.

The conservation value of degraded habitats is also influenced by their community composition, which can vary significantly from that of primary forests. For instance, selectively logged forests in Uganda had distinctive bird communities even three decades after logging took place (Sekercioglu, 2002). Biologists must assess how well these altered habitats succeed in preserving the original community. Species are unevenly affected by disturbance, and conservationists have attempted to identify which groups of birds are most vulnerable (Thiollay, 1999). Although this will invariably depend on the features of each community (Reid et al. 2011), avifaunas in the tropics appear to show some broad patterns.

Gray et al. (2007) conducted a meta-analysis of avian guild composition in primary and degraded tropical habitats, defining degraded habitats as “selectively logged, burned, secondary or cultivated forests.” The authors found that insectivores and frugivores tend to respond poorly to high levels of disturbance, while granivores respond positively. Nectarivores in the neotropics appear more tolerant to disturbance than those in the old world tropics (Gray et al. 2011), while forest insectivores usually show a particularly negative response (Sekercioglu et al. 2002). Frugivores appear to show a mixed response, and some studies have shown that large frugivores do less well than small frugivores (Gomes et al. 2008).

Community composition in degraded habitats will depend upon whether species that naturally occur in the forest are able to shift their behavior to persist in a modified environment (Oostra et al. 2008). In tropical bird communities, there is strong segregation between forest and non-forest species (O’Dea and Whittaker, 2007). Based on observations in the field, Stotz et al. (1996) have classified neotropical birds by their habitat requirements and their expected



tolerance to disturbance, and these classifications have proven to be highly accurate (Matlock and Edwards, 2006). Unsurprisingly, those birds classified as disturbance-sensitive often decline when forest cover is reduced, while disturbance-tolerant birds increase in numbers. Dramatic turnover in species can occur even while the balance of general guilds represented remains similar (Blake and Loiselle, 2001). For example, with cloud forest insectivores in the Andes, a new suite of edge-tolerant species replaces primary forest species in secondary habitat (O'Dea and Whittaker, 2007).

Which species prove to be disturbance-sensitive may depend upon factors other than just foraging guild. Some species may have particular nesting needs that are only met in forest habitats. For example, species that only nest in tall trees decline in environments where forest cover is reduced (Posa and Sodhi, 2006). Also, there is evidence that some species' nests are more vulnerable to predation than others, and predation pressure may change with disturbance (Matlock and Edwards, 2006). Forest-dependent bird species may also include endemic and range-restricted species (Oostra et al. 2008) of particular conservation concern. It has been hypothesized that endemics might be exceptionally sensitive to disturbance, and some studies have supported this hypothesis (Posa and Sodhi, 2006; Oostra et al. 2008).

Whatever their importance for conservation, degraded tropical forests are a rapidly expanding habitat of great prominence (Bowen et al. 2007). Approximately 60% of the world's tropical forests are secondary, selectively logged, or burned (Chazdon, 2003). Montane cloud forests are among the most threatened habitats in the tropics (Doumenge et al. 1995), yet relatively few studies have looked at the effects of forest degradation on their avifaunas (O'Dea and Whittaker, 2007). Only a handful of studies have looked at disturbance and bird habitat

selection in the Talamanca cloud forests (Oostra et al. 2008; Gomes et al. 2008; Marcy unpublished).

My study looks at the impact of anthropogenic changes in vegetation structure on resident birds in the Talamanca Mountains. I chose to compare bird communities in primary forest, older secondary forest, young successional scrub, and countryside landscape. My study seeks to (1) determine how species diversity and abundance change along a gradient of disturbance, (2) quantify the differences in vegetation structure between the four habitats, and (3) identify the species and ecological groups that are adversely (or beneficially) affected. This will provide valuable information for establishing conservation priorities and understanding the ecological consequences of forest degradation in the Talamanca Mountains.

# Methods

## Study Area Description

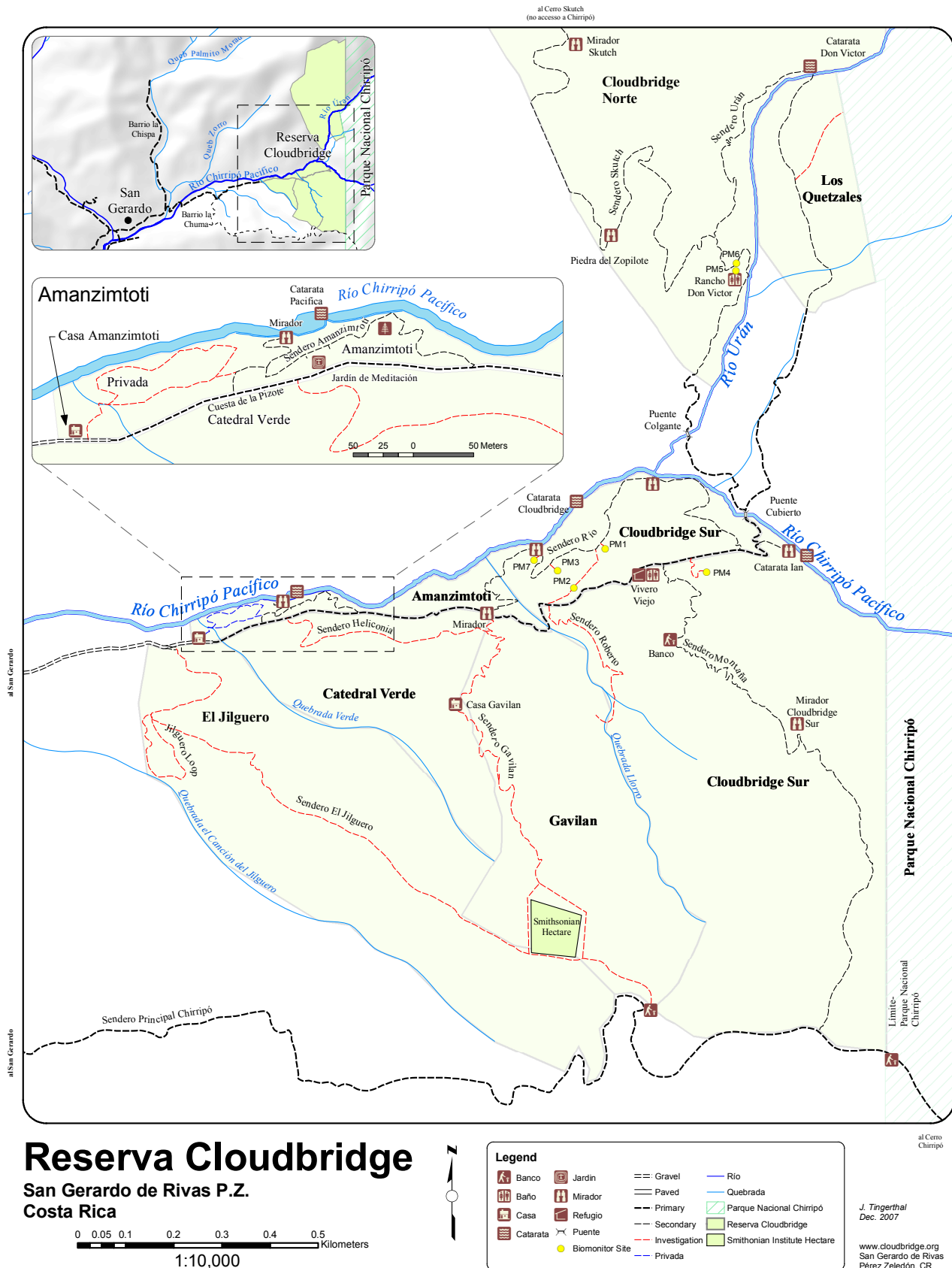
I conducted my research in the montane evergreen forests on the Pacific slope of the Talamanca Mountains from June 2<sup>nd</sup> to August 2<sup>nd</sup> 2012 (the wet season), a time of year when only resident bird species are present. My study area was located in the Perez Zeledon region and included Cloudbridge Nature Reserve, Chirripo National Park and the surrounding habitats. The area is a mosaic of primary forest, secondary forest, farmland and regenerating pastureland. Temperatures are generally mild, with a mean high temperature of 23.1 degrees Celsius and a mean low of 13.4 degrees Celsius (Spek, 2011). Rainfall is substantial at approximately 4300mm per year (Bol and Vroomen, 2008).

Bird-Life International has designated the cloud forests of Costa Rica and Panama an important “Endemic Bird Area” because they host 52 range-restricted species and eight endemic genera (Oostra et al. 2008). The largest tract of this forest occurs within the Talamanca Mountains, a major piece of the Meso-American Biological Corridor. Large-scale deforestation took place in the Talamanca region during the 1950s through 1970s; since then, the forest has been regrowing, although large areas have been reduced to a patchwork of degraded and secondary habitat (Gomes et al. 2008). The native vegetation is montane evergreen forest dominated by oaks. This habitat reaches its upper limit around 3400m at treeline and approaches its lower bound around 1500m, where it transitions into pre-montane forest (Kappelle and Juarez, 1995).

Cloudbridge Nature Reserve is a 700-acre private property on the Western border of Chirripo National Park. The Reserve is situated in a river valley and is divided into two segments: one on either side of the Uran River. Cloudbridge was founded as a private nature reserve in March 2002 (Spek, 2011). Before its purchase by Ian Giddy, much of the property was used for cattle grazing and subsistence farming, so the current vegetation is largely successional. Some of the reserve consisted of active pasture as recently as 2002, including segments of the Jilguero, Gavilan, Montaña, Principal and Quetzales trails. Other former pastureland now supports secondary forest that is over 25 years old, including segments of the Jilguero and Montaña trails. Some of the high-elevation areas in the reserve include primary forest that borders Chirripo National Park. The Cloudbridge trail system connects with the footpath that climbs Mount Chirripo, and a large amount of primary forest occurs on this trail. Another stretch of primary forest occurs at lower elevation in the Talamanca Reserve and Cloudbridge North on the opposite side of the Uran River.

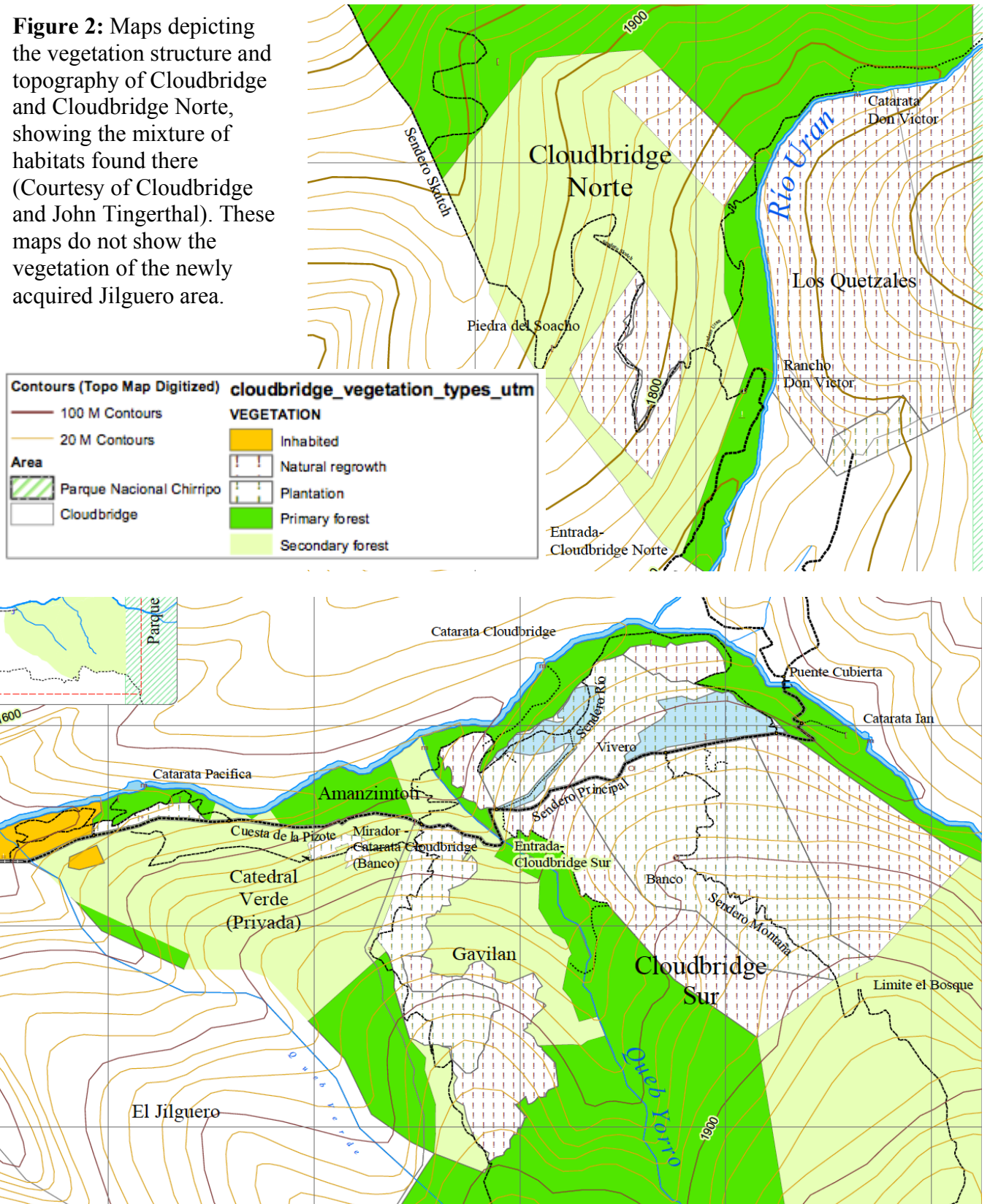
### **Selection of Point Count Sites**

To investigate the resilience of Talamanca's forest avifauna to habitat modification, I compared bird communities along a gradient of human disturbance. I divided the landscape into four categories: primary forest (PF), secondary forest (SF), young successional scrub (YS), and countryside habitat (CO). I assigned sites to these categories based on their ages and vegetation characteristics, informing my decisions with local knowledge (Gode, personal communication). I established 80 point-count stations, with 20 points in each habitat type, and I visited each site twice for a total of 160 surveys.



**Figure 1.** Map of Cloudbridge and Cloudbridge Norte, where the majority of my survey points were located. I also conducted surveys on the Chirripo trail (bottom) and inside the Talamanca Forest Reserve (trail not shown).

**Figure 2:** Maps depicting the vegetation structure and topography of Cloudbridge and Cloudbridge Norte, showing the mixture of habitats found there (Courtesy of Cloudbridge and John Tingerthal). These maps do not show the vegetation of the newly acquired Jilguero area.



Point-count stations were scattered throughout Cloudbridge and surrounding areas (Figure 1). Primary forest points were located on the Chirripo and Talamanca trails. All PF sites were at least 50 years old, with tall trees and a well-developed canopy. Oak trees were the dominant species, although the vegetation was floristically diverse. I sampled secondary forest on the Talamanca, Jilguero, Montaña and Chirripo trails. Secondary forest ranged from 25 to 50 years old and was characterized by a lower canopy than PF, and by smaller trees occurring at higher densities.

Young successional habitat occurred on various trails, including Gavilan, Jilguero, Quetzales, Uran, Chirripo and Principal. All YS sites were under 25 years old. They were characterized by an open canopy and by an often-dense terrestrial fern cover. Many of the YS sites consisted of 10-year-old scrub that began re-establishing when Cloudbridge was purchased. Cloudbridge has an ongoing reforestation project, so some of the YS sites have benefited from the restoration planting of native seedlings. Wild trees are quickly returning as well, and the plantation sites closely resemble natural sites at a more advanced stage of succession (Spek, 2011).

I sampled countryside sites predominantly on the Chispe, Principal, Chirripo and Los Angeles trails. This habitat type consisted of pastures, fields and homesteads. Unlike all other sites, CO points were over 50-percent cleared of vegetation, although individual large trees often persisted. CO differed from YS habitat in the presence of these large trees, and also in the sparseness of understory vegetation due to active clearing and grazing. However, this habitat was far from bare and homogenous: it supported a diversity of plants including both native and cultivated species.

When sampling these habitats, I systematically placed point-count stations along existing trails because the steep terrain made working away from the trail impractical. Points were spaced at least 150 meters apart “as the crow flies” for independence (Huff et al. 2000). I recorded the geographical coordinates of each point-count station using my Garmin GPS (see Appendix I for coordinates), and I marked the exact locations with flagging tape. All points were placed at least 50 meters away from habitat boundary zones (except in the case of a few CO sites, which sometimes graded into forested habitats). No sites were placed next to the river, because the noise of the river introduces biases in song detectability. The points spanned a large elevation range, from 1415m to 2468m. Within each habitat type, I sampled sites from both high and low elevations, and I scattered sites to avoid spatial correlations.

### **Point Count Surveys**

Upon arriving, but before beginning data collection, I spent two weeks familiarizing myself with the local birds. I used audio files downloaded from “<http://xeno-canto.org>” to learn the local bird vocalizations, and I consulted the field guides by Garrigues (2007) and Stiles and Skutch (1989) for visual identifications. By the end of this two-week introductory period, I had seen the majority of species that would appear in my study and I was proficient at identifications.

At each point, I recorded the number of species and individuals detected within a 50-meter radius (Ralph et al. 1995). Counts lasted 10 minutes and were conducted between 6:00 and 10:00 AM, during the peak period of bird activity. I ran an Olympus audio recorder for each 10-minute period, and dictated bird encounters into the recorder. Each recording was then analyzed at the end of the field season. This method allowed me to identify upon second listening any



birdsongs that I had failed to identify in the field. My competence at auditory identifications was better at the end of the field season than at the beginning; however, by revisiting the recordings, I was able to minimize this bias.

During each count, I identified the birds present, stated whether each detection was auditory or visual, and made a distance estimate (0-10m, 10-25m, 25-50m). Birds that flew overhead (such as vultures and swifts) were not counted, because these sightings did not indicate associations with the local habitat (Bibby et al. 2000). On most of the surveys, a field assistant accompanied me and held the audio recorder, leaving my hands free to use binoculars.

I surveyed multiple point-count stations during each morning hike along a trail transect. On repeat visits to these transects, I reversed the direction of travel to minimize time-of-day biases (Bibby et al. 2000). If on the first visit I had started at the nearby end of a trail, then on the second visit I rose earlier and began at the far end of the trail. I also attempted to separate transect visits temporally to minimize seasonal biases (see Appendix II for a complete schedule of counts). First visits of most sites occurred during the first half of the study, and second visits during the second half. For analyzing the data, I subsequently added together the two counts into a single species tally for each point.

## **Habitat Variables**

For each count, I recorded temperature, wind speed and relative humidity using a Kestrel 3000 Weather Meter. I also described the cloud cover using the following categories: cloudy (75-100% cloud cover), broken clouds (50-75%), scattered clouds (25-50%) or clear (0-25%). For each point count site, I measured the following quantitative habitat variables: elevation, canopy

cover, canopy height, tree density, shrub density, ground cover, and vertical vegetation density (Bibby et al. 2000). I also measured the following categorical variables: presence/absence of fruiting plants, presence/absence of flowering plants, steepness, and landform.

#### *Elevation:*

I recorded elevation in meters using a GPS unit that performed well even in dense forest cover.

#### *Canopy cover:*

I measured canopy cover using a convex spherical densiometer, a device common in forestry.

The final value was the average of four readings.

#### *Average canopy height:*

I measured canopy height by averaging four measurements with a compass clinometer. First, I selected four canopy trees. I measured the distance to each target tree using a Bosch DLR 130 laser measurer and measured the angle of view with my clinometer. Using trigonometry, I then calculated the height of each tree (adding two meters to each value to account for my height).

#### *Tree density:*

I measured tree density using the Point-Centered Quarter method (Cottam and Curtis, 1956). I identified the nearest tree (>10cm DBH) in each of the four quadrants of a circle centered on my point. Then, I measured the distance to each tree with my laser distance measurer. The four readings were averaged to calculate a mean point-to-tree distance; tree density was then

calculated (in individuals per square meter) using the following formula:  $Density = 1/(\text{mean point-to-tree distance}^2)$ .

*Shrub density:*

I counted the total number of woody shrubs with stems < 10 cm and height > 2m within a 5m radius around each point. Single plants with many stems I only counted once.

*Percent ground cover:*

I measured percent ground cover by pointing a “sighting tube” directly at the ground for a series of presence/absence readings for understory vegetation (Bibby et al. 2000). I took 20 readings, ten on either side of the trail, in order to create an estimate of percent ground cover.

*Vertical vegetation density:*

To investigate the vertical distribution of foliage layers, I visually scored vegetation density along an imaginary vertical line. The line was divided into six height brackets (0-2 meters, 2-5, 5-10, 10-15, 15-25, 25+); within each height bracket, I ranked the vegetation on a scale from zero to five—zero being the least dense and five being the densest. Then, I converted the foliage profiles into vertical vegetation density values using the Shannon-Weiner formula, treating each height bracket as a “species” (Sekercioglu, 2002). I took four readings per point and averaged them.

*Presence/absence of fruits and flowers:*

I recorded the presence/absence of any fruits and flowers that appeared likely to be food resources. Fruits and flowers that were obviously not food resources (eg. wind-pollinated flowers, inedible fruits) were excluded.

#### *Steepness and Landform:*

I classified each point as either steep (45-90 degree average incline) or sloped (0-45 degree incline). I also classified each point as either ridgetop, mid-slope, or valley.

### **Statistical Methods**

In order to extrapolate the total number of species present in each habitat, including the species that went undetected, I calculated three estimators of expected richness using the program EstimateS (Colwell, 2005). I chose to use non-parametric estimators (MMMean, ACE, and Chao 2), because these are recommended for diverse tropical avifaunas (Herzog et al. 2002). I also plotted species accumulation curves using EstimateS to assess the completeness of my sampling for each habitat and for the dataset as a whole. I compared diversity between habitats using the Shannon-Weiner, Simpson, and Fisher's Alpha diversity indices. I compared community similarity by conducting pairwise comparisons between habitats, using EstimateS to calculate Chao-Jaccard's index of similarity. I chose the Chao-Jaccard index because it takes abundance into account when calculating community similarity.

To assess how the four habitat categories differed in aspects of their vegetation structure, I tested for significance of difference of the habitat variable means in each habitat type using Kruskal-Wallis tests conducted in the program XLStat. I chose to use this non-parametric test because of the non-normal distributions of the data, and I performed pairwise comparisons

between each habitat type using Dunn's procedure with a Bonferonni-corrected significance level of 0.0083. For the categorical habitat variables (e.g., presence/absence of edible fruits), I tested for significant differences using Chi-squared tests.

In order to assess the impact of the birds' biology on their sensitivity to disturbance, I extracted descriptive data on each species from the literature. I gathered information on the elevational distribution and the indicator status of each bird species from Stotz et al. (1996). I grouped bird species into four categories based on their elevational distributions: low elevation species (0-1850m), very high elevation species (do not occur below 1500m), high elevation species (do not occur below 400m, but do occur below 1500m), and species with wide elevational ranges (0 to over 2000m). I gathered data on the diet of each species from Stiles and Skutch (1989), classifying species as insectivores, nectarivores, omnivores, frugivores, and granivores. I chose to exclude the carnivore guild from my analysis since so few individuals were detected. I classified birds into three categories by nesting preference (tree-nesters, shrub-nesters, and ground/bank nesters) based on descriptions by Stiles and Skutch (1989). I extracted data on the regional endemism of each species from Garrigues (2007), considering species to be Talamanca endemics if their ranges were restricted to Southern Costa Rica and Western Panama.

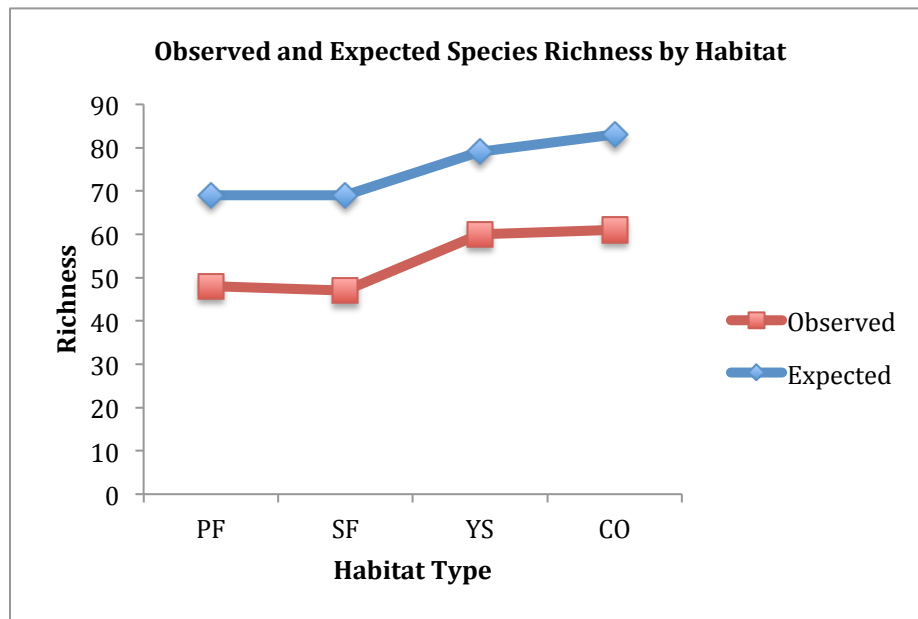
After sorting my data into subgroups based on these ecological characteristics, I tested for differences in mean observed richness and abundance for each ecological category using Kruskal-Wallis tests and Bonferonni-corrected pairwise comparisons. Using the same approach, I also tested for significant differences in the abundance of every species between habitats.

## Results

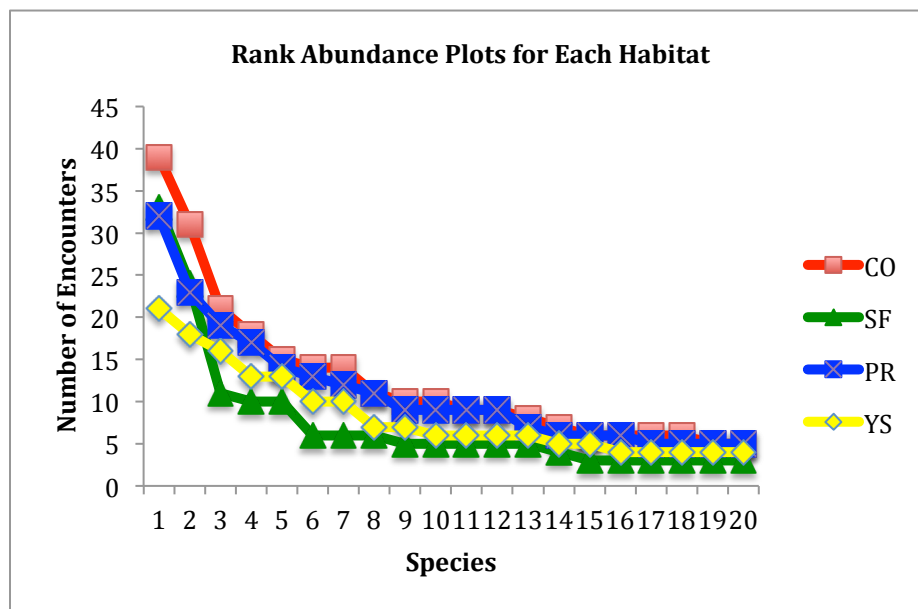
During 160 point-count surveys, I encountered a total of 1049 individual birds and 109 species, including 21 species that were regional endemics. I recorded 276 individuals of 48 species in PF, 192 individuals of 47 species in SF, 240 individuals of 60 species in YS, and 341 individuals of 61 species in CO. Species richness and diversity in the more disturbed environments was comparable to or higher than that in the forest. Mean observed species richness differed significantly between two of the habitats, with richness higher in CO than in SF. Mean Shannon Diversity showed the same pattern of statistical significance. Highest abundance of species occurred in PF and CO, which differed significantly from the lowest category, SF. Expected species richness estimators showed a broadly similar pattern to observed richness (Table 1 and Figure 3). Comparisons of the observed richness with the average expected richness indicate that my surveys detected about 70% of the species in PF, 68% of the species in SF, 76% of the species in YS, and 73% of the species in CO. For all habitats combined, I detected about 81% of the estimated total richness.

	PF	SF	YS	CO	All
<i>Observed Richness</i>	48	47	60	61	109
<i>Expected Richness</i>					
MMMean	60.17	67.35	88.89	81.22	124
ACE	62.45	63.67	72.7	74.65	129.42
Chao 2	84.75	74.56	73.92	91.73	147.89
Average, rounded	69	69	79	83	134
<i>Diversity</i>					
Shannon-Weiner	3.38	3.28	3.67	3.58	4.03
Simpson's	23.07	16.95	31.17	25.26	37.83
Fisher's Alpha	16.79	19.85	25.68	21.64	30.59

**Table 1:** Comparison of total observed richness (the raw number of species detected), three estimators of expected richness (the extrapolated total number of species present), and three diversity indices for the four habitats: primary forest (PF), secondary forest (SF), young successional scrub (YS), and countryside (CO).

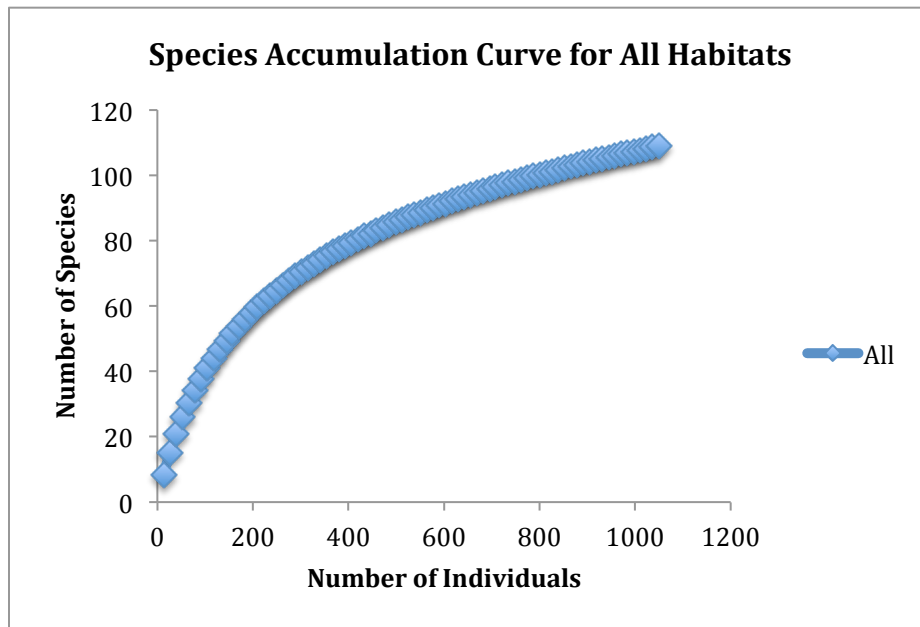


**Figure 3:** Expected richness (an average of the three richness estimators) compared with observed species richness.

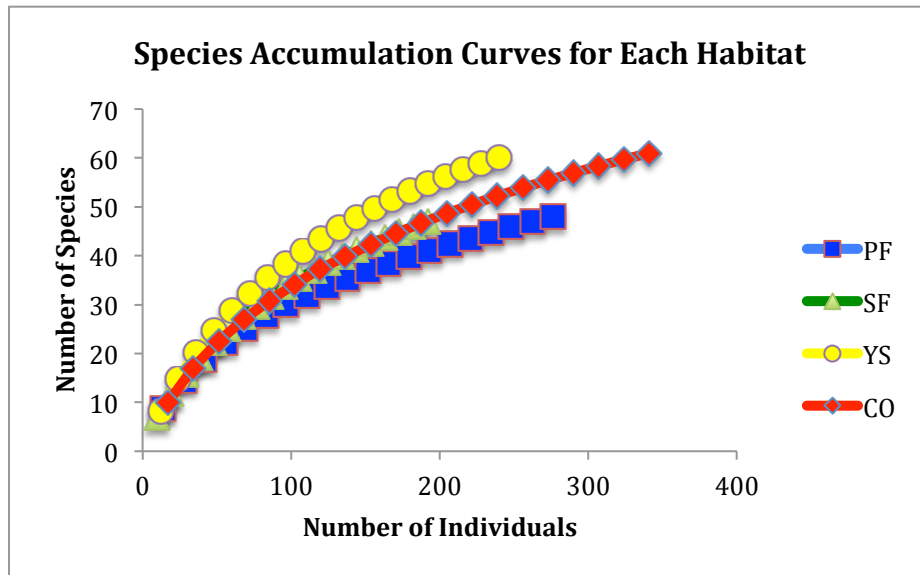


**Figure 4:** Number of encounters with the 20 most abundant species for each habitat (which species they are differs by habitat). A steep curve indicates a community dominated by a few common species (e.g. SF).

a)



b)



**Figure 5:** Species accumulation curves depicting the rate of encounter of new species with increasing number of individuals detected for a) all habitats combined and b) each habitat type separately. Curves were generated in the program EstimateS with 50 randomizations.



## Community Composition

Comparisons of community similarity showed that there was a gradual turnover of species over the gradient of disturbance (Table 2). According to both the Chao-Jaccard Similarity index and the raw number of shared species, CO and YS had the most similar communities, while CO and PR had the least similar communities.

	PR	SF	YS	CO
PR		27	23	20
SF	0.627		31	22
YS	0.362	0.609		39
CO	0.227	0.336	0.702	

**Table 2:** Pairwise comparisons of community similarity among habitats, with Chao-Jaccard similarity (an abundance-based similarity index, below) and raw number of shared species (above).

In order to understand which groups of birds contributed to community turnover, I categorized species by their feeding behavior, disturbance tolerance, nesting behavior and elevational preference. I then compared the mean observed richness and abundance of each group between habitats (Tables 3, 4).

Composition of species by their indicator status (low, medium or high sensitivity) changed significantly between habitats ( $P < 0.0001$ ). High sensitivity species were better represented in the forest environments, showing significantly higher richness and abundance in PF than in CO (Figure 6). Medium sensitivity species also peaked in PF, demonstrating significantly higher richness and abundance there than in YS ( $P = 0.002$ ) and CO ( $P < 0.0001$ ). Low sensitivity species showed the opposite trend, having significantly higher richness and abundance in CO than in PF ( $P < 0.0001$ ).

Guild composition changed somewhat between habitats (Figure 8). Mean omnivore richness and abundance were significantly lower in SF than in CO ( $P=0.005$ ,  $0.003$ ), while mean nectarivore richness and abundance were significantly higher in YS than in CO ( $P=0.002$ ,  $0.001$ ). Richness and abundance of insectivores and frugivores did not show significant differences between the habitats. Granivores, however, were significantly more species-rich and abundant in CO than in all the other habitats ( $P<0.0001$ ).

Nest location preference (tree, shrub, and ground/bank) changed slightly between habitats (Figure 9). Tree nester richness was not significantly different between habitats. Shrub nesters were significantly more species-rich and abundant in YS than in PF ( $P=0.001$ ), while ground/bank nesters were more abundant and species-rich in CO than in SF and YS ( $P<0.0001$ ).

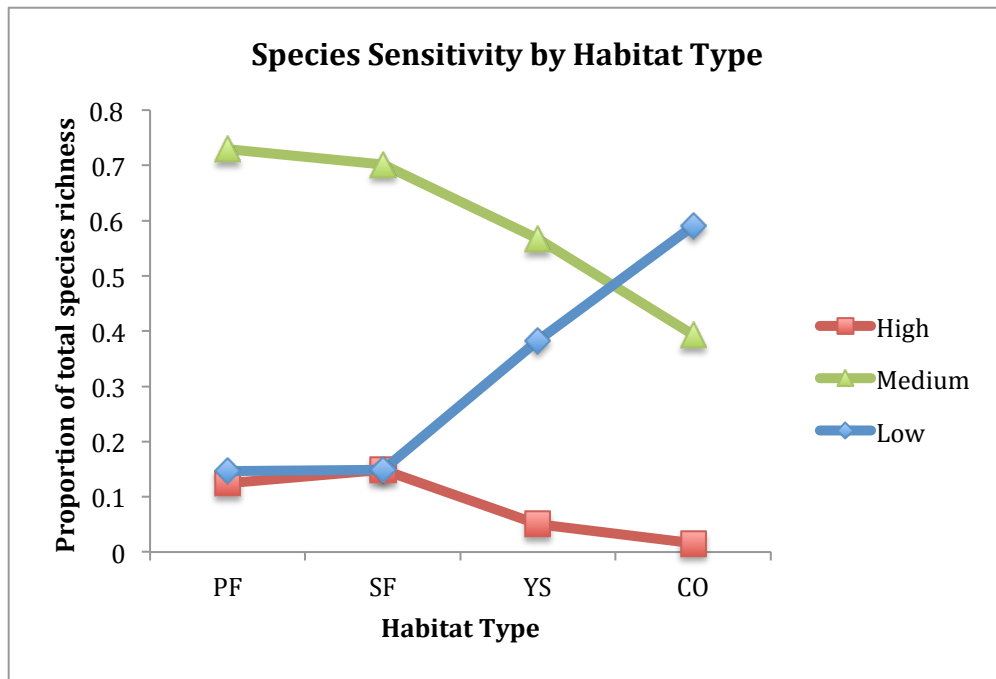
Composition of species by elevational preference changed between habitats, especially in CO, which supported a particularly high number of lowland species (Figure 7). Lowland species richness was significantly greater in CO than in PF or SF ( $P<0.001$ ,  $P<0.002$ ), while highland species richness was significantly lower in CO than in PF ( $P=0$ ). Extreme highland species were significantly more species-rich and abundant in PF than in SF and CO ( $P=0.001$ ). Species with wide elevational ranges were significantly richer and more abundant in CO than in the other habitats ( $P<0.0001$ ).

Mean observed species richness with standard deviations. Groupings resulting from pairwise comparisons denoted by superscripts a, b and c.						
Habitat Type	PF	SF	YS	CO	P-value	H Statistic
Total	8.7 ± 2.92 <sup>ab</sup>	6.85 ± 2.28 <sup>a</sup>	8.25 ± 3.28 <sup>ab</sup>	9.9 ± 3.09 <sup>b</sup>	0.008	11.71
<b>Disturbance Sensitivity</b>						
high sensitivity	0.85 ± 0.81 <sup>c</sup>	0.7 ± 0.80 <sup>bc</sup>	0.25 ± 0.44 <sup>ab</sup>	0.05 ± 0.22 <sup>a</sup>	0	18.77
medium sensitivity	7.05 ± 2.70 <sup>b</sup>	4.65 ± 2.32 <sup>ab</sup>	4.6 ± 2.91 <sup>a</sup>	2.8 ± 2.14 <sup>a</sup>	< 0.0001	22.39
low sensitivity	0.8 ± 0.77 <sup>a</sup>	1.5 ± 0.83 <sup>ab</sup>	3.4 ± 1.98 <sup>bc</sup>	7.05 ± 3.43 <sup>c</sup>	< 0.0001	49.87
<b>Feeding Guild</b>						
omnivore	2.85 ± 1.57 <sup>ab</sup>	2.05 ± 1.19 <sup>a</sup>	3.3 ± 2.18 <sup>ab</sup>	4 ± 2.25 <sup>b</sup>	0.026	9.3
nectarivore	0.45 ± 0.69 <sup>ab</sup>	0.55 ± 0.69 <sup>ab</sup>	1.15 ± 0.93 <sup>b</sup>	0.4 ± 0.94 <sup>a</sup>	0.01	11.4
insectivore	4.35 ± 2.09 <sup>a</sup>	3.75 ± 1.74 <sup>a</sup>	3.25 ± 1.89 <sup>a</sup>	3.9 ± 1.71 <sup>a</sup>	0.186	4.82
granivore	0 <sup>a</sup>	0.05 ± 0.22 <sup>a</sup>	0.15 ± 0.37 <sup>a</sup>	0.8 ± 0.7 <sup>b</sup>	<.0001	32.17
frugivore	1.05 ± 0.83 <sup>a</sup>	0.45 ± 0.69 <sup>a</sup>	0.4 ± 0.60 <sup>a</sup>	0.75 ± 0.910 <sup>a</sup>	0.03	8.94
<b>Nest Location</b>						
tree	4.45 ± 1.99 <sup>a</sup>	2.75 ± 1.71 <sup>a</sup>	3.45 ± 2.69 <sup>a</sup>	4.25 ± 2.25 <sup>a</sup>	0.05	8.28
shrub	1.75 ± 0.72 <sup>a</sup>	2.1 ± 1.12 <sup>ab</sup>	2.95 ± 1.15 <sup>b</sup>	2.7 ± 1.22 <sup>ab</sup>	0.003	13.88
bank or ground	1.8 ± 1.12 <sup>ab</sup>	1.3 ± 0.73 <sup>a</sup>	1.3 ± 0.87 <sup>a</sup>	2.8 ± 1.11 <sup>b</sup>	<.0001	21.29
<b>Elevation Range</b>						
lowland	1.2 ± 1.01 <sup>a</sup>	1.3 ± 0.66 <sup>a</sup>	1.8 ± 1.70 <sup>ab</sup>	3.5 ± 2.57 <sup>b</sup>	0.003	14.25
highland	5.2 ± 2.59 <sup>b</sup>	4.15 ± 2.13 <sup>ab</sup>	4.7 ± 2.06 <sup>b</sup>	2.4 ± 1.64 <sup>a</sup>	0.001	16.58
extreme highland	1.05 ± 1.19 <sup>b</sup>	0.1 ± 0.31 <sup>a</sup>	0.25 ± 0.45 <sup>ab</sup>	0.15 ± 0.49 <sup>a</sup>	0.001	16.14
wide	1.25 ± 0.79 <sup>a</sup>	1.3 ± 1.17 <sup>a</sup>	1.5 ± 1.36 <sup>a</sup>	3.85 ± 2.06 <sup>b</sup>	<.0001	22.22

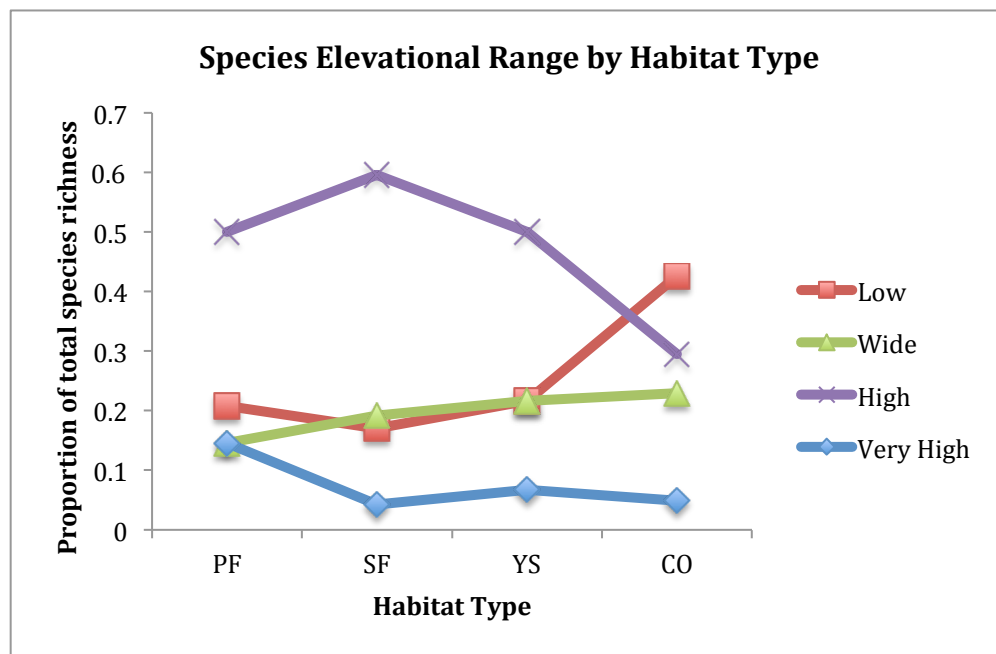
**Table 3:** Mean observed species richness per point for all species (top) and for various ecological groups, reported with one standard deviation. Significance of difference between habitats tested using a Kruskal-Wallis test, with the resulting P-values and H-statistics shown at right. Superscripts “a” through “c” denote groupings resulting from Bonferonni-corrected pairwise comparisons (a different letter denotes a significant difference, P<0.0083).

Mean abundance with standard deviations. Groupings resulting from pairwise comparisons denoted by superscripts a, b and c.						
Habitat Type	PF	SF	YS	CO	P-value	H Statistic
Total	13.8 ± 4.83 <sup>b</sup>	9.6 ± 3.73 <sup>a</sup>	12 ± 4.86 <sup>ab</sup>	17.05 ± 8.15 <sup>b</sup>	0.001	16.23
<b>Disturbance Sensitivity</b>						
high sensitivity	0.9 ± 0.91 <sup>b</sup>	0.85 ± 1.04 <sup>b</sup>	0.35 ± 0.67 <sup>ab</sup>	0.05 ± 0.224 <sup>a</sup>	0.001	17.3
medium sensitivity	11.75 ± 4.20 <sup>b</sup>	6.2 ± 3.49 <sup>a</sup>	6.8 ± 4.71 <sup>a</sup>	4.9 ± 4.29 <sup>a</sup>	<.0001	21.84
low sensitivity	1.15 ± 1.23 <sup>a</sup>	2.55 ± 1.43 <sup>ab</sup>	4.85 ± 2.81 <sup>bc</sup>	12.1 ± 7.56 <sup>c</sup>	<0.0001	47.46
<b>Feeding Guild</b>						
omnivore	4.5 ± 3.3 <sup>ab</sup>	2.75 ± 1.48 <sup>a</sup>	4.6 ± 3.07 <sup>ab</sup>	6.3 ± 4.29 <sup>b</sup>	0.047	7.93
nectarivore	0.5 ± 0.76 <sup>a</sup>	0.6 ± 0.754 <sup>ab</sup>	1.6 ± 1.47 <sup>b</sup>	0.45 ± 0.1 <sup>a</sup>	0.008	11.81
insectivore	7.1 ± 3.78 <sup>a</sup>	5.6 ± 3.03 <sup>a</sup>	4.95 ± 3.05 <sup>a</sup>	6.7 ± 2.89 <sup>a</sup>	0.127	5.71
granivore	0 <sup>a</sup>	0.05 ± 0.22 <sup>a</sup>	0.15 ± 0.37 <sup>a</sup>	1.8 ± 1.82 <sup>b</sup>	<.0001	34.12
frugivore	1.65 ± 1.66 <sup>a</sup>	0.6 ± 0.99 <sup>a</sup>	0.7 ± 1.26 <sup>a</sup>	1.75 ± 3.46 <sup>a</sup>	0.04	8.3
<b>Nest Location</b>						
tree	7.1 ± 2.95 <sup>b</sup>	3.5 ± 2.54 <sup>a</sup>	4.7 ± 3.73 <sup>ab</sup>	7.3 ± 5.68 <sup>b</sup>	0.002	14.37
shrub	2.55 ± 1.43 <sup>a</sup>	3.25 ± 1.48 <sup>ab</sup>	4.9 ± 2.34 <sup>b</sup>	3.85 ± 1.93 <sup>ab</sup>	0.006	12.45
bank or ground	3.05 ± 2.37 <sup>ab</sup>	2.05 ± 1.47 <sup>a</sup>	1.75 ± 1.16 <sup>a</sup>	5.7 ± 3.31 <sup>b</sup>	<.0001	21.79
<b>Elevation Range</b>						
lowland	1.8 ± 1.58 <sup>a</sup>	2.05 ± 1.05 <sup>a</sup>	2.95 ± 2.65 <sup>ab</sup>	5.75 ± 4.30 <sup>b</sup>	0.002	15.33
highland	8 ± 4.01 <sup>b</sup>	5.8 ± 3.47 <sup>ab</sup>	6.9 ± 3.16 <sup>ab</sup>	4.1 ± 3.42 <sup>a</sup>	0.004	13.24
extreme highland	2.05 ± 2.56 <sup>b</sup>	0.15 ± 0.49 <sup>a</sup>	0.5 ± 1.10 <sup>ab</sup>	0.25 ± 0.91 <sup>a</sup>	0.001	16.13
wide	1.95 ± 1.36 <sup>a</sup>	1.6 ± 1.64 <sup>a</sup>	1.65 ± 1.53 <sup>a</sup>	6.95 ± 4.89 <sup>b</sup>	<.0001	22.54

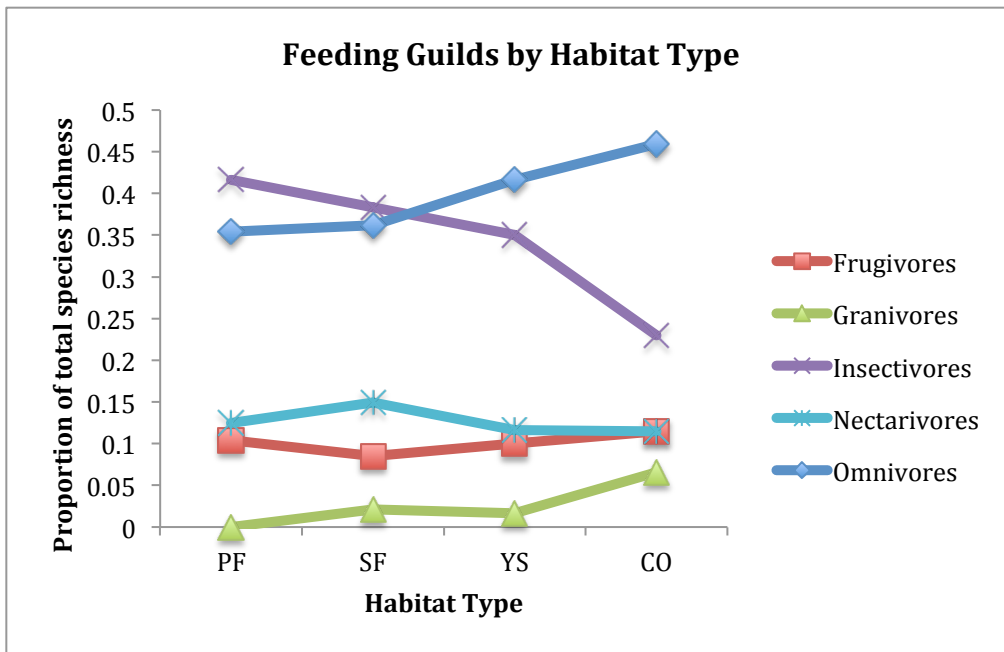
**Table 4:** Mean observed species abundance per point for all species (top) and for various ecological groups, reported with one standard deviation. Significance of difference between habitats was tested using a Kruskal-Wallis test, and the resulting P-values and H-statistics are shown at right. Superscripts “a” through “c” denote groupings resulting from pairwise comparisons (a different letter denotes a significant difference, P<0.0083)



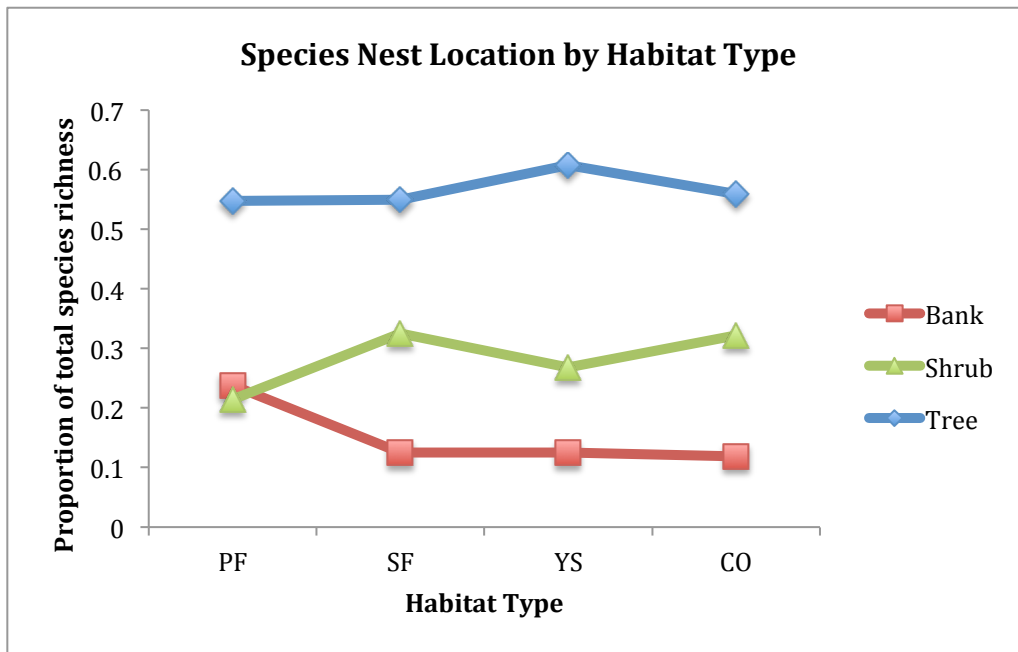
**Figure 6:** Proportion of species richness accounted for by species of three disturbance indicator levels, following the classifications of Stotz et al. (1996). High and medium sensitivity species richness declined with disturbance, while low sensitivity species richness increased.



**Figure 7:** Proportion of species richness accounted for by species of four different elevational ranges, following the classifications of Stotz et al. (1996). Low elevation species were better represented in the CO habitat.



**Figure 8:** Proportion of species richness accounted for by species of five different feeding guilds, following Stiles and Skutch (1989).



**Figure 9:** Proportion of species richness accounted for by species of three different nesting-preference categories, following Stiles and Skutch (1989).

**Table 5:** List of the 109 species detected during my point count surveys, arranged in taxonomic order following Stotz et al. (1996) Species that are endemic to the Talamanca region shown in bold. Species that showed a statistically significant difference in abundance between habitat categories (Kruskall Wallis,  $P < 0.05$ ) are marked with an asterisk.

Species abundances in number of individuals observed. Endemic species are in bold. (\*) denotes significant differences in abundance

Habitat Type		PF	SF	YS	CO	Total
Spotted Wood-Quail	<i>Odontophorus guttatus</i>			1	2	3
Laughing Falcon	<i>Herpetotheres cachinnans</i>					1
Ruddy Ground Dove	<i>Columbina talpacoti</i>					3
Ruddy Pigeon*	<i>Patagioenas subvinacea*</i>		5			5
Band-tailed Pigeon	<i>Patagioenas fasciata</i>				1	1
White-tipped Dove*	<i>Leptotila verreauxi*</i>				2	5
Chiriqui Quail-Dove	<b><i>Geotrygon chiriquensis</i></b>				1	1
Scaled Pigeon	<i>Patagioenas speciosa</i>					2
<b>Sulfur-winged Parakeet</b>	<b><i>Pyrrhura hoffmanni</i></b>		5	3	5	21
Green-fronted Lancebill	<i>Doryfera ludovicae</i>		1			1
Green Hermit	<i>Phaethornis guy</i>		2	1		3
Violet Sabrewing	<i>Campylopterus hemileucurus</i>			1		1
Green Violet-ear*	<i>Colibri thalassinus*</i>			1	13	1
Snowy-bellied Hummingbird	<i>Amazilia edward</i>		1	1		1
Rufus-tailed Hummingbird	<i>Amazilia tzacatl</i>				1	2
Purple-crowned Fairy	<i>Heliothryx barroti</i>			1		1
Striped-tailed Hummingbird	<i>Eupherusa eximia</i>		2		1	1
<b>White-tailed Emerald</b>	<b><i>Elvira chionura</i></b>		1			1
<b>White-throated Mountain Gem</b>	<b><i>Lampornis calolaemus</i></b>		3	6	1	10
<b>Scintillant Hummingbird*</b>	<b><i>Selasphorus scintilla*</i></b>				10	1
Green-crowned Brilliant	<i>Heliodoxa jacula</i>			1	2	3
Collared Trogon	<i>Trogon collaris</i>		1	2	4	7
Blue-crowned Motmot	<i>Momotus momota</i>		1	1	2	1
Red-headed Barbet	<i>Eubucco bourcierii</i>		3	1	2	6
Emerald Toucanet	<i>Aulacorhynchus prasinus</i>		4	4		2
Olivaceous Piculet	<i>Picumnus olivaceus</i>				1	2
Acorn Woodpecker	<i>Melanerpes formicivorus</i>		1			1
Red-crowned Woodpecker*	<i>Melanerpes rubricapillus*</i>					4
Hairy Woodpecker	<i>Picoides villosus</i>			1		1
Golden-olive Woodpecker	<i>Piculus rubiginosus</i>				2	1
Wedge-billed Woodcreeper	<i>Glyphorhynchus spirurus</i>		1			1
Spotted-crowned Woodcreeper*	<i>Lepidocolaptes affinis*</i>		11	6	6	23
Brown-billed Scythebill*	<i>Campylorhamphus pusillus*</i>		5	5		10
Red-faced Spinetail	<i>Cranioleuca erythrops</i>		6	5	2	10
<b>Ruddy Treerunner</b>	<b><i>Margarornis rubiginosus</i></b>		1			1
Spotted Barbtail	<i>Premnoplex brunnescens</i>			2	4	6
Buffy Tuftedcheek	<i>Pseudocolaptes lawrencii</i>		1			1
Lineated Foliage-gleaner	<i>Syndactyla subalaris</i>		1	2		3
Buff-fronted Foliage-gleaner	<i>Philydor rufum (rufus in book)</i>		1			1
Buff-throated foliage gleaner	<i>Automolus ochrolaemus</i>		4			4
<b>Streaked-breasted Treehunter</b>	<b><i>Thripadectes rufobrunneus</i></b>			1		1
Streaked Xenops	<i>Xenops rutilans</i>				1	1
Slaty Antwren	<i>Myrmotherula schisticolor</i>				1	1
<b>Silvery-fronted tapaculo</b>	<b><i>Scytalopus argentifrons</i></b>		5	3	3	11
Paltry Tyrannulet*	<i>Zimmerius vilissimus*</i>		23	11	7	9
Common tody-flycatcher	<i>Todirostrum cinereum</i>				2	2

Eye-ringed Flatbill	<i>Rhynchocyclus brevirostris</i>	1			1
White-throated Spadebill	<i>Platyrinchus mystaceus</i>	1			1
Tufted Flycatcher*	<i>Mitrephanes phaeocercus*</i>	13	5	2	20
Yellowish Flycatcher	<i>Empidonax flavescens</i>	6		2	8
Black Phoebe*	<i>Sayornis nigricans*</i>				6
Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>			1	2
Great Kiskadee	<i>Pitangus sulphuratus</i>				1
Boat-billed Flycatcher	<i>Megarhynchus pitangua</i>	1		2	9
Gray-capped Flycatcher	<i>Myiozetetes granadensis</i>				5
Golden-bellied Flycatcher	<i>Myiodynastes hemichrysus</i>		2	3	5
Tropical kingbird*	<i>Tyrannus melancholicus*</i>				5
Barred Becard	<i>Pachyramphus versicolor</i>		1	1	2
Masked Tityra	<i>Tityra semifasciata</i>				2
Plain Wren*	<i>Thryothorus modestus*</i>			4	15
Rufous-breasted Wren*	<i>Thryothorus rutilus*</i>		10	16	41
House Wren*	<i>Troglodytes aedon*</i>			2	20
<b>Ochraceous Wren*</b>	<b><i>Troglodytes ochraceus*</i></b>	<b>32</b>	<b>6</b>		<b>38</b>
Gray-breasted Wood-wren	<i>Henicorhina leucosticta</i>	19	24	18	70
<b>Black-faced Solitaire*</b>	<b><i>Myadestes melanops*</i></b>	<b>17</b>	<b>3</b>		<b>20</b>
Orange-billed Nightingale Thrush*	<i>Catharus aurantirostris*</i>			3	9
Ruddy-capped Nightingale-Thrush*	<i>Catharus frantzii*</i>	14	10	13	40
Slaty-backed Nightingale-Thrush*	<i>Catharus fuscater*</i>	5	5		10
<b>Black-billed nightingale thrush</b>	<b><i>Catharus gracilirostris</i></b>	<b>1</b>			<b>1</b>
Clay-colored Robin	<i>Turdus grayi</i>		3	1	12
Rufus-collared Sparrow*	<i>Zonotrichia capensis*</i>			4	43
Buff-throated Saltator	<i>Saltator maximus</i>		2	2	10
Common Bush Tanager	<i>Chlorospingus ophthalmicus</i>	9	5	10	28
Flame-colored Tanager	<i>Piranga bidentata</i>		3	5	11
White-winged Tanager	<i>Piranga leucoptera</i>			2	2
<b>Cherrie's Tanager*</b>	<b><i>Ramphocelus costaricensis*</i></b>			<b>6</b>	<b>20</b>
Blue-gray Tanager*	<i>Thraupis episcopus*</i>			2	12
Palm tanager	<i>Thraupis palmarum</i>				3
Elegant Euphonia	<i>Euphonia elegantissima</i>			4	5
<b>Golden-browed Chlorophonia</b>	<b><i>Chlorophonia callophrys</i></b>	<b>2</b>	<b>2</b>	<b>1</b>	<b>6</b>
<b>Spangled-cheeked Tanager</b>	<b><i>Tangara dowii</i></b>	<b>1</b>			<b>1</b>
Speckled Tanager	<i>Tangara guttata</i>				1
Bay-headed Tanager	<i>Tangara gyrola</i>			1	1
Silver-throated Tanager	<i>Tangara icterocephala</i>	2	3	6	18
Golden-hooded Tanager*	<i>Tangara larvata*</i>				5
Scarlet-thighed Dacnis	<i>Dacnis venusta</i>		1	3	9
<b>Slaty Flowerpiercer</b>	<b><i>Diglossa plumbea</i></b>			<b>4</b>	<b>6</b>
Tropical Parula	<i>Parula pitiayumi</i>		2	2	4
<b>Flame-throated Warbler*</b>	<b><i>Parula gutturalis*</i></b>	<b>9</b>			<b>10</b>
Slate-throated Redstart*	<i>Myioborus miniatus*</i>	12	33	21	80
<b>Collared Redstart*</b>	<b><i>Myioborus torquatus*</i></b>	<b>6</b>			<b>6</b>
Golden-crowned Warbler	<i>Basileuterus culicivorus</i>	4	3		12
<b>Black-cheeked Warbler</b>	<b><i>Basileuterus melanogenys</i></b>	<b>9</b>		<b>1</b>	<b>10</b>
Three-striped Warbler	<i>Basileuterus tristriatus</i>		1		1
Bananaquit	<i>Coereba flaveola</i>				2
<b>Yellow-winged Vireo*</b>	<b><i>Vireo carmioli*</i></b>	<b>7</b>		<b>1</b>	<b>9</b>
Brown-capped Vireo	<i>Vireo leucophrys</i>		3	6	12
Lesser greenlet	<i>Hylophilus decurtatus</i>	2			2
Blue Seedeater	<i>Amaurospiza concolor</i>		1		1
Yellow-faced Grassquit*	<i>Tiaris olivaceus*</i>			3	34
<b>Yellow-thighed Finch</b>	<b><i>Pseliophorus tibialis</i></b>	<b>5</b>	<b>2</b>	<b>7</b>	<b>17</b>
Chestnut-capped Brush Finch	<i>Buarremon brunneinucha</i>			2	2
Variable seedeater	<i>Sporophila americana</i>				1
Yellow-bellied seedeater	<i>Sporophila nigricollis</i>				3
White-naped Brush Finch	<i>Atlappetes albinucha</i>			2	4
Melodious blackbird	<i>Dives dives</i>				2
Lesser Goldfinch	<i>Carduelis psaltria</i>				1
<b>Silvery-throated jay</b>	<b><i>Cyanolyca argentigula</i></b>	<b>9</b>			<b>9</b>
Brown Jay	<i>Cyanocorax morio</i>	1	1	1	8

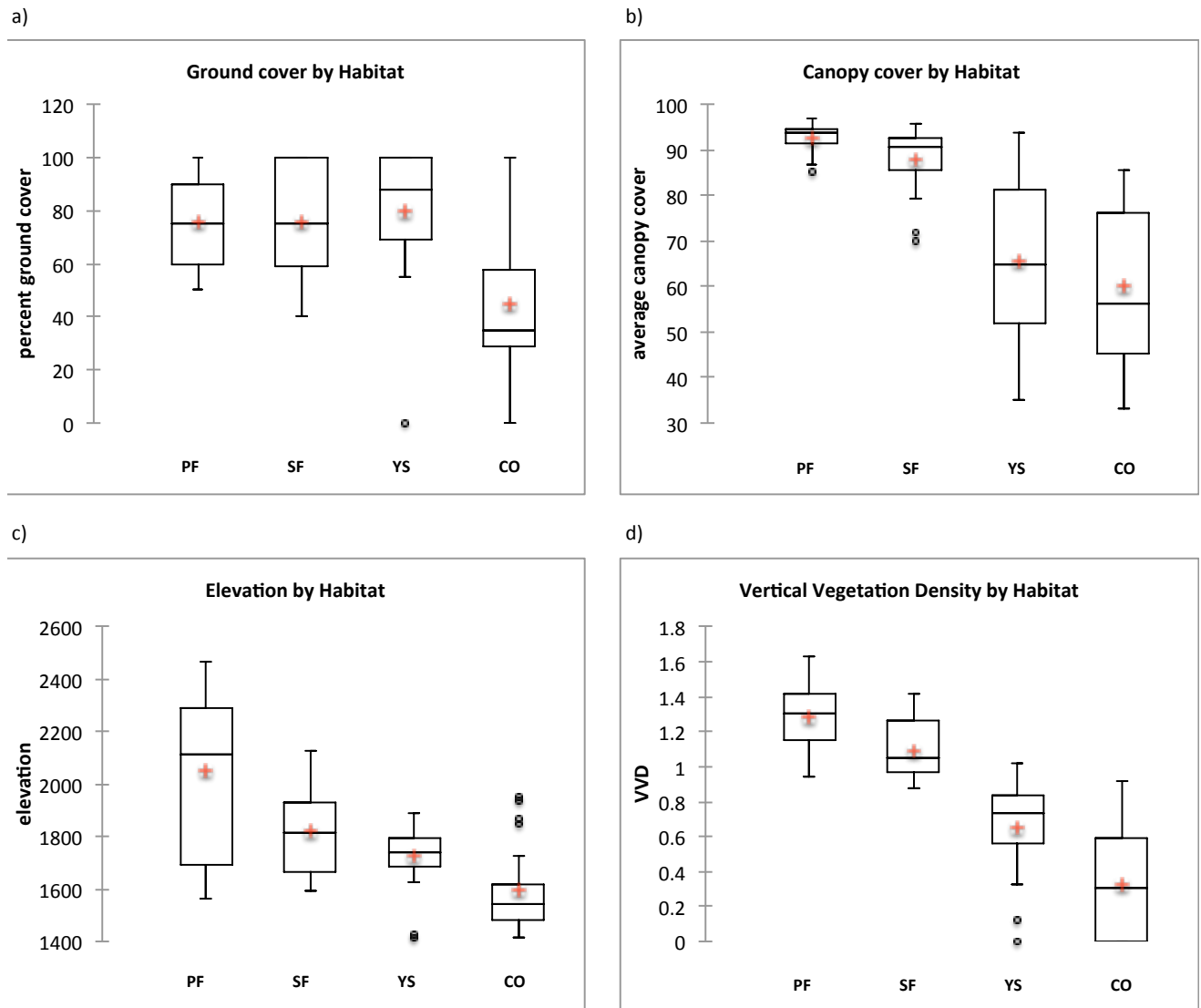


## Habitat Comparisons

All of the continuous habitat variables yielded statistically significant differences (Table 6, Kruskal-Wallis,  $P < 0.0001$ ). Four habitat variables differed significantly between the forest environments (PF and SF) and the non-forest environments (YS and CO): tree density, canopy cover, elevation and VVD were all significantly higher in the forest habitats. CO differed significantly from all other habitats in its low shrub density and ground cover. Canopy height was significantly higher in PF than in SF or CO, which in turn had significantly taller trees than YS. Three of the categorical habitat variables showed no significant difference between habitats (presence of fruits, presence of flowers, and landform), while slope type was significantly more often steep in primary forest.

Habitat variable means and standard deviations. Groupings resulting from pairwise comparisons denoted by superscripts a, b and c.						
Habitat Type	PF	SF	YS	CO	P-value	H statistic
tree density	$0.054 \pm 0.04^b$	$0.104 \pm 0.12^b$	$0.016 \pm 0.02^a$	$0.013 \pm 0.02^a$	<0.0001	22.97
VVD	$1.284 \pm 0.17^b$	$1.094 \pm 0.17^b$	$0.655 \pm 0.26^a$	$0.325 \pm 0.34^a$	<0.0001	62.42
shrub density	$0.243 \pm 0.11^b$	$0.276 \pm 0.12^b$	$0.224 \pm 0.13^b$	$0.129 \pm 0.09^a$	<0.0001	21.81
ground cover	$76 \pm 16.35^b$	$76 \pm 20.88^b$	$79.75 \pm 24.95^b$	$45 \pm 28.84^a$	0	18.84
elevation	$2049.45 \pm 305.99^c$	$1821 \pm 171.85^b$	$1723.25 \pm 126.37^{ab}$	$1597.9 \pm 169.83^a$	<0.0001	27.59
canopy height	$30.048 \pm 6.69^c$	$16.312 \pm 3.56^b$	$9.175 \pm 2.62^a$	$15.801 \pm 8.40^b$	<0.0001	50.95
canopy cover	$92.676 \pm 3.03^b$	$88.0715 \pm 7.16^b$	$65.489 \pm 18.65^a$	$60.014 \pm 18.25^a$	<0.0001	49.68

**Table 6:** Means of seven habitat variables reported with one standard deviation. Tree density and shrub density in trees per square meter, ground cover and canopy cover in percent, elevation and canopy height in meters. VVD (vertical vegetation density) is a Shannon diversity value representing the diversity in vertical layers of vegetation. Significance of difference between habitats was tested using a Kruskal-Wallis test, and the resulting P-values and H-statistics are shown at right. Superscripts “a” through “c” denote groupings resulting from Bonferonni-corrected pairwise comparisons (a different letter denotes a significant difference,  $P < 0.0083$ ).



**Figure 10:** Boxplots showing the means, medians, standard deviations and 95% confidence intervals for four habitat variables in each of the four habitats: a) ground cover (percent), b) canopy cover (percent), c) elevation (m), and d) vertical vegetation density index.

## Discussion

My study found a slight increase in bird species richness with increasing disturbance. Overall richness was highest in the non-forest habitats, although it only differed significantly between CO and SF. It is perhaps not surprising that there was no difference in richness between PF and SF, because these habitats were similar in vegetation structure, showing no significant differences in canopy cover, tree density, shrub density, and vertical vegetation density. In reviewing the literature on tropical bird faunas in secondary growth, Barlow et al. (2007a) found that a majority of studies detected comparable levels of species richness in secondary habitat, and my study was no exception. The high richness observed in YS and CO was more surprising, because these habitats differed markedly in vegetation structure from the forest. Both had significantly lower canopy cover, tree density, and vertical vegetation density, and therefore might have been expected to support lower bird diversity.

One possible explanation for the high number of species I recorded in YS and CO sites is that moderately disturbed habitats may genuinely have higher bird species richness in tropical cloud forests. Tropical montane faunas, O'Dea and Whittaker suggest (2007), may be naturally more resilient to disturbance than their lowland counterparts due to their continual exposure to a more intense disturbance regime. This peak in richness at disturbed sites seems to hold true for temperate bird faunas (Keller, 2003), and the idea that tropical highland faunas might share a higher tolerance for disturbance may be supported by my results.

The unexpectedly high species richness of the non-forest sites may be partially due their reasonably high remaining vegetation cover. While other studies sampled open fields devoid of any trees, or even sampled urban habitat (Posa and Sodhi, 2006), my most heavily altered

category was CO. This habitat still offered a considerable amount of vegetation on average, having a mean canopy cover of 60.06%. Although this was the least dense canopy of the four habitats, it was still much denser than that of a clear-cut landscape. If I had been able to add a fifth habitat class with no trees, I expect I would have found a dramatic decline in species richness.

Several confounding variables complicated my results. Elevation proved to be a strong confounding factor in this experiment, and the low elevation of most of my CO sites may have contributed to their higher richness. There is commonly a strong turnover of bird species at higher elevation as well as a decline in species richness (Terborgh, 1977). While I attempted to stratify sites by elevation, it was impossible to avoid this bias within my study sites on the mountainside. The forest habitats were significantly higher in elevation on average than the non-forest habitats, with CO being the lowest-elevation category. This meant that the elevation gradient mirrored the disturbance gradient in my experiment. A possible decrease in richness with disturbance may have been masked by a concomitant increase in richness at lower elevation. Other potential confounds include spillover effects from the nearby forest environments (Barlow et al. 2007a) and detectability biases (O'Dea and Whittaker, 2007). Birds are far more difficult to see in the forest, leading to a potential underestimate of richness. A strong reliance on auditory detection is desirable, because song detectability is less likely to be biased by habitat type (O'Dea and Whittaker, 2007). 49.95% of bird detections in my study were by ear exclusively, and this may have helped to minimize detectability bias.

## **Community Composition Changed Greatly with Disturbance**

While the overall number of species did not differ dramatically between habitats, species composition showed a very pronounced turnover. Only 20 of the 61 species (33%) observed in CO also occurred in PF. The community was quite different between PF and SF as well, with PF sharing only 27 of its 48 species with SF (56%). Chao-Jaccard abundance-based community similarity indices also showed low levels of similarity between most of the habitats.

*To what extent did elevation influence community turnover?*

Elevational turnover proved to be an important factor affecting bird community composition between habitats. High elevation species constituted a greater portion of the fauna in the less disturbed environments. 50 percent of the species in PF were high elevation species, versus only 29.5% in CO. By far the greatest change in elevation-related community composition occurred between YS and CO. There was not a significant change between PF, SF and YS, even though there was still a considerable turnover in bird species. This suggests that although elevational turnover was an important factor underlying species composition, it was not the only contributing factor.

*Does altered forest structure cause a decline in forest birds?*

In order to see whether the indicator classifications by Stotz et al. (1996) would explain species turnover, I looked at the richness and abundance of high, medium, and low sensitivity species in each habitat. Species classified as highly and moderately sensitive declined in richness and abundance from PF to CO (85.4% in PF to 41% in CO), while the remaining species—all

classified as low-sensitivity species—increased proportionally. While the proportion of disturbance-tolerant species hardly changed between PF and SF, it increased dramatically in the open-canopy habitats. These observations are consistent with the hypothesis that changes in forest structure cause avian species turnover; they are also consistent with the findings of other studies (Sekercioglu, 2002; O’Dea and Whittaker, 2007; Matlock and Edwards, 2006).

Three species classified as highly sensitive peaked in abundance in the forest environments: they were *Patagioenas subvinacea*, *Campylorhamphus pusillus*, and *Catharus fuscater*. Eight species classified as moderately sensitive had significantly higher abundance in the forest: *Lepidocolaptes affinis*, *Zimmerius vilissimus*, *Mitrephanes phaeocercus*, *Troglodytes ochraceus*, *Myadestes melanops*, *Parula gutturalis*, *Myioborus torquatus*, and *Vireo carmioli*. Two additional species that were categorized as moderately sensitive showed a statistically significant shift in abundance with habitat yet did not show a significant drop in abundance between the forest habitats and YS. These were *Catharus frantzii*, which showed similar abundance in PF, SF and YS, and *Selasphorus scintilla*, which peaked in YS.

Twelve species classified as low-sensitivity species had significantly higher abundance in the nonforest habitats, mostly peaking in CO. These were *Leptotila verreauxi*, *Sayornis nigricans*, *Tyrannus melancholicus*, *Thryothorus modestus*, *Troglodytes aedon*, *Catharus aurantiirostris*, *Zonotrichia capensis*, *Ramphocelus costaricensis*, *Thraupis episcopus*, *Tangara larvata*, *Melanerpes rubricapillus*, and *Colibri thalassinus*. Only two species that were classified as “low sensitivity” showed statistically significant abundance changes but did not peak in non-forest habitats: *Thryothorus rutilus* and *Myioborus miniatus*. These results support the findings of many studies that the classifications by Stotz et al. are highly accurate (Barlow et al. 2007a).

*Are endemic species vulnerable to disturbance?*

Of the 21 endemic species I recorded during the counts, seven of them showed a statistically significant change in abundance between habitat types. Although it is likely that additional species were affected, low encounter rates precluded any conclusions for many species. Five of the endemics had significantly higher abundance in the primary forest environment: namely, *Troglodytes ochraceus*, *Myadestes melanops*, *Parula gutturalis*, *Myioborus torquatus*, and *Vireo carmioli*. Only two showed a statistically significant increase in abundance in the disturbed habitats: *Selasphorus scintilla* and *Ramphocelus costaricensis*. Working at a slightly higher elevation than I did, Oostra et al. (2008) found that a majority of range-restricted bird species in the Talamanca Mountains appear to have higher population densities in forested environments. My results support this observation, and agree with their findings that *Myioborus torquatus*, *Myadestes melanops* and *Vireo carmioli* occur at significantly higher abundance in forest environments. However, my results differ from theirs with respect to two species: *Parula gutturalis* and *Troglodytes ochraceus*. While Oostra et al. (2008) report that these species show no strong habitat preference for either forest or nonforest environments, I found that they occurred at highest abundances in primary forest. In agreement with my observations, Daily et al. (2001) also found *Troglodytes ochraceus* to occur only in forest habitats. Species richness is not necessarily the key factor in determining conservation priorities, as species vulnerability can be equally important (Diamond et al. 1976). Because range-restricted endemics are arguably of greater conservation concern than more widespread species, my findings highlight the conservation importance of preserving primary forest in the Talamanca Mountains.

### *How does disturbance affect guild composition?*

Granivores responded positively to disturbance, consistent with the trend observed in many studies (O'Dea and Whittaker 2007, Blake and Loiselle 2001, Thiollay 1999). Granivores depend on a grassland-type habitat, and the open canopy and lack of herbaceous ground cover in CO proved most suitable for them. No granivores were observed in PF, and only one was observed in SF (a single encounter with *Amaurospiza concolor*). By contrast, 36 individuals of four species were recorded in CO—mostly *Tiaris olivaceus*—but also including *Sporophila americana*, *Carduelis psaltria*, and *Sporophila nigricollis*. Only *Tiaris olivaceus* was recorded in sufficient frequency to show a significant increase in abundance in the CO habitat.

Mean insectivore species richness and abundance did not change significantly between habitat types in my study. This is not consistent with the findings of the review paper by Gray et al. (2007), which suggests that insectivores often respond poorly to disturbance. However, my study did record a decrease in the proportion of insectivores and a change in insectivore species composition. Forest insectivores such as *Campylorhamphus pusillus*, *Lepidocolaptes affinis*, *Mitrephanes phaeocercus*, *Troglodytes ochraceus*, *Parula gutturalis* and *Myioborus torquatus* showed a peak in abundance in the forest environment, whereas a suite of new insectivores took over in the open habitats, including *Troglodytes aedon*, *Thryothorus modestus* and *Sayornis nigricans*. Forest insectivores are known to be very susceptible to disturbance (Sekercioglu et al. 2002), and the turnover in insectivore species I found is consistent with this observation.

Omnivores as a whole increased in diversity and abundance between PF and CO. While only 17 omnivore species were found in PF and SF, YS and CO harbored 25 and 28, respectively. The increase in omnivores largely reflected an influx of frugivore-insectivores such as tyrant flycatchers and a suite of tanagers.



Average nectarivore richness and abundance were significantly lower in CO than YS, but were similar in the other habitats. Previous studies have suggested that hummingbirds are resilient to disturbance, and my results partially support this finding. Feinsinger et al. (1987) argue that the higher availability of nectar in forest edge environments explains hummingbird distributions, with most hummingbirds favoring disturbed or edge habitats. While my study found no significant differences in the presence/absence of flowering vegetation between the habitat types, it is possible that I overlooked important patterns by failing to record the abundance of flowers. Gray et al. (2007) report that New World nectarivores (primarily hummingbirds) are resilient to disturbance, in contrast to Old World nectarivores. In my study, the low abundance of nectarivores in CO suggests that an intermediate level of regrowth may be ideal for hummingbirds.

Frugivores showed no significant change in richness or abundance in this study. Gomes et al., also working in the Talamanca Mountains, found that overall frugivore richness occurred at comparable levels in disturbed and primary sites. My results are in agreement with the findings of this study. My study did not find any significant differences in the presence/absence of edible fruits between habitats, and this may have contributed to the even distribution of frugivore richness.

## Conclusion

My study documented a diverse avifauna in successional and countryside habitats in the highlands of Costa Rica. My results emphasize the high conservation value of degraded habitats in the Talamanca Mountains, suggesting that small-scale agriculture and intermediate disturbance may be compatible with the maintenance of high levels of tropical montane bird diversity. Nonetheless, my results show that the avifauna that persisted in altered habitats was highly distinct from that seen in primary habitats, and endemic species of the Talamanca Mountains appeared to be relatively intolerant of habitat modification.

In order to conserve the full spectrum of bird species native to the Talamanca Mountains, conservationists should see the protection of partially degraded and secondary forest habitats as complimentary to the conservation of primary forest. Private reserves like Cloudbridge Nature Reserve have embraced this approach, preserving primary forest in addition to former pastureland. The reestablishment of native vegetation on fallow at Cloudbridge has created a variety of successional habitats, contributing to a high avian beta-diversity. Apart from their intrinsic value, birds serve as an ecotourism attraction and also provide valuable ecological services such as a pollination and seed dispersal (Posa and Sodhi, 2006).

As human populations grow and habitat loss increases, national parks and reserves may be insufficient to preserve biodiversity. To establish conservation priorities in the future, additional research should examine the ability of cloud forest birds to persist in degraded environments so that conservationists can better understand the value of successional landscapes for avian conservation.

## References

Andrade GI, Rubio-Torgler H. 1994. Sustainable use of the tropical rain-forest – evidence from the avifauna in a shifting- cultivation habitat Mosaic in the Colombian Amazon. *Conservation Biology* 8(2): 545–554.

Ansell FA, Edwards DP, Hamer KC. 2011. Rehabilitation of logged rain forests: Avifaunal composition, habitat Structure, and implications for biodiversity-friendly REDD+. *Biotropica* 43(4): 504-511.

Barlow J, Mestrec AM, Gardner TA, Peres CA. 2007. The value of primary, secondary and plantation forests for Amazonian birds. *Biological conservation* 136(2): 212–231

Barlow, J., Gardner, T. A., Araujo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., ... & Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences*, 104(47), 18555-18560.

Bibby CJ, Burgess ND, Hill DA, Mustoe S. 2000. *Bird Census Techniques*, Second Edition. San Diego, CA: Academic Press.

Bierregard RO, Lovejoy TE, Kapos V, Augusto dos Santos A, Hutchings RW. 1992. The biological dynamics of tropical rainforest fragments. *BioScience* 42(11): 859-866.

Blake JG and Loiselle BA. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *The Auk* 118(2): 304-326.

Bol, Matthijs and Vroomen, Dennis. 2008. The succession of pastureland towards original cloud forest in the pre-montane area of Costa Rica. (<http://cloudbridge.org>).

Bowman D, Woinarski JCZ, Sands DPA, Wells A, McShane VJ. 1990. Slash-and-burn agriculture in the wet coastal lowlands of Papua-New-Guinea – response of birds, butterflies and reptiles. *Journal of Biogeography* 17: 227–239.

Bowen ME, McAlpine CA, Housec APN, Smith GC. 2007. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biological Conservation* 140 (3-4): 273–296.

Chazdon RL. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6(1-2): 51-71.

Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.

Cottam, G., & Curtis, J. T. (1956). The use of distance measures in phytosociological sampling. *Ecology*, 37(3) 451-460.

Daily GC, Erlich PR, Sanchez-Azofeifa GA. 2001. Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* 11(1): 1-13.

Doumenge C, Gilmour D, Perez M, Blockhus J. 1995. Tropical montane cloud forests: conservation status and management issues. In: *Tropical Montane Cloud Forests. Ecological Studies* 110, L.S. Hamilton, J.O. Juvik, J.O. and F.N. Scatena (eds). Springer Verlag, New York, pp. 24-37.

Dunn RR. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18(2): 302-309.

Feinsinger P, Beach JH, Linhart YB, Busby WH, Murray KG. 1987. Disturbance, pollinator predictability and pollination success among Costa Rican cloud forest plants. *Ecology* 68(5): 1294-1305

Garrigues R. 2007. *The Birds of Costa Rica: A Field Guide*. Ithica, NY: Cornell University Press.

Gomes LGL, Oostraa V, Nijmanb V, Cleefa AM, Kappellec M. 2008. Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological conservation* 141(3): 860–871.

Gray MA, Baldauf SL, Mayhew PJ, Hill JK. 2007. The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology* 21(1): 133–141.

Herzog, S. K., Kessler, M., & Cahill, T. M. (2002). Estimating species richness of tropical bird communities from rapid assessment data. *The Auk*, 119(3), 749-769.

Huff MH, Bettinger KA, Ferguson HL, Brown MJ, Altman, B. 2000. A habitat-based Point count protocol for terrestrial birds, emphasizing Washington and Oregon. Portland OR: United States Department of Agriculture.

Hughes JB, Daily GC, Ehrlich PR. 2002. Conservation of tropical forest birds in countryside habitats. *Ecology Letters* 5: 121-129.

Johns AD. 1991. Responses of Amazonian rain-forest birds to habitat modification. *Journal of Tropical Ecology* 7(4): 417–437.

Kappelle, M., & Juárez, M. E. (1995). Agro-ecological zonation along an altitudinal gradient in the montane belt of the Los Santos Forest Reserve in Costa Rica. *Mountain Research and Development*, 19-37.

Keller JK, Richmond ME, Smith CR. 2003. An explanation of patterns of breeding bird species richness and density following clearcutting in northeastern USA forests. *Forest Ecology and Management* 174: 541-564

Kupfer JA, Malanson GP, Franklin SB. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*. 15: 8-20.

Lawton J.H, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond P, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72–76.

Marcy, N. 2004. Avifauna at Cloudbridge. (<http://cloudbridge.org>).

Matlock RB and Edwards PJ. 2006. The influence of habitat variables on bird communities in forest remnants in Costa Rica. *Biodiversity and Conservation* 15(9): 2987-3016

MacArthur RH and MacArthur JW. 1961. On bird species diversity. *Ecology* 42(3): 594-598.

O’Dea N and Whittaker RJ. 2007. How resilient are Andean montane forest bird communities to habitat degradation? *Biodiversity and Conservation* 16(4):1131–1159

Oostra V, Gomes LGL, Nijman V. 2008. Implications of deforestation for the abundance of restricted-range bird species in a Costa Rican cloud-forest. *Bird Conservation International* 18(1): 11–19.

Posa MRC, Sodhi NS. 2006. Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines. *Biological Conservation* 129: 256–270

Ralph C, Droege S, Sauer J. 1995. Managing and Monitoring Birds Using Point Counts: Standards and Applications. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149.

Raman TRS, Rawat GS, Johnsingh AJT. 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north- east India. *Journal of Applied Ecology* 35: 214–231.

Schulze CH, Waltert M, Kessler PJA, Pitopang R, Veddeler D, Muhlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I, Tschardt T. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* 14: 1321–1333.

Sekercioglu CH. 2002. Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biological Conservation* 107: 229–240.

Sekercioglu CH, Loarie SR, Brenes FO, Ehrlich PR, Daily GC. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology* 21(2): 482-494.

Sekercioglu CH, Ehrlich PR, Daily GC, Aygen D, Goehring D, Sand RF. 2002. Disappearance of insectivorous birds from tropical forest fragments. *PNAS* 99 (1): 263–267.

Sodhi NS, Koh LP, Prawiradilaga DM, Tinulele I, Putra DD, Tan THT. 2005. Land use and conservation value for forest birds in Central Sulawesi (Indonesia). *Biological Conservation* 122(4): 547–558.

Spek, Michiel. 2011. Cloud Forest Recovery: evaluation at Cloudbridge Nature Reserve, Costa Rica. (<http://cloudbridge.org>).

Stotz DF, Fitzpatrick JW, Parker, TA, Mostovits DK. 1996. Neotropical birds: Ecology and conservation. Chicago, IL: University of Chicago Press.

Stiles FG, Skutch AF. 1989. A guide to the birds of Costa Rica. Ithaca, NY: Cornell University Press.

Terborgh J and Weske JS. 1969. Colonization of secondary habitats by Peruvian Birds. *Ecology* 50(5): 765–782.

Terborgh J. 1999. *Requiem for Nature*. Washington, DC: Island Press.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology*, 58(5):1007-1019.

Thiollay JM. 1999. Responses of an avian community to rain forest degradation. *Biodiversity and Conservation*. 8(4) 513-534.



## Appendix I

GPS Coordinates and Elevation of Points. Points labeled by trail: P- Principal; C- Chirripo; HL- Heliconia; G- Gavilan; J- Jilguero; He- Hectare; U-Uran; Q- Quetzales; T- Talamanca; A- Los Angeles; M-Montana; Ch- Chispe

### Primary forest points:

C-1: 9.28.088, 83.35.102, 1615  
 C-8: 9.27.815, 83.34.267, 2019  
 C-9: 9.27.874, 83.34.206, 2059  
 C-10: 9.27.847, 83.34.128, 2103  
 C-11: 9.27.889, 83.34.057, 2130  
 C-13: 9.27.869, 83.33.897, 2166  
 C-14: 9.27.804, 83.33.849, 2204  
 C-15: 9.27.736, 83.33.804, 2241  
 C-16: 9.27.670, 83.33.757, 2284  
 C-17: 9.27.598, 83.33.726, 2295  
 C-18: 9.27.563, 83.33.649, 2361  
 C-19: 9.27.561, 83.33.560, 2401  
 C-20: 9.27.536, 83.33.480, 2446  
 C-21: 9.27.562, 83.33.403, 2468  
 T-2: 9.28.504, 83.34.399, 1699  
 T-3: 9.28.473, 83.34.478, 1677  
 T-4: 9.28.462, 83.34.558, 1653  
 T-5: 9.28.421, 83.34.628, 1633  
 T-8: 9.28.404, 83.34.874, 1560  
 He-1: 9.27.973, 83.34.262, 1975

### Secondary forest points:

HL-1: 9.28.339, 83.34.549, 1608  
 HL-2: 9.28.343, 83.34.469, 1642  
 HL-3: 9.28.344, 83.34.386, 1696  
 A-1: 9.27.931, 83.35.136, 1649  
 J-1: 9.28.020, 83.34.371, 1929  
 J-2: 9.28.068, 83.34.439, 1870  
 J-3: 9.28.117, 83.34.503, 1837  
 M-3: 9.28.217, 83.33.997, 1937  
 M-4: 9.28.164, 83.33.933, 2012  
 M-5: 9.28.091, 83.33.903, 2078  
 M-6: 9.28.019, 83.33.936, 2109  
 M-7: 9.27.937, 83.33.941, 2127  
 C-4: 9.27.877, 83.34.960, 1763  
 C-5: 9.27.833, 83.34.891, 1791  
 C-6: 9.27.872, 83.34.816, 1844  
 C-7: 9.27.879, 83.34.740, 1877  
 U-4: 9.28.744, 83.34.072, 1786  
 T-1: 9.28.498, 83.34.290, 1668  
 T-6: 9.28.403, 83.34.709, 1593  
 T-7: 9.28.416, 83.34.791, 1604

### Young successional points:

G-A: 9.28.163, 83.34.309, 1885  
 G-1: 9.28.242, 83.34.357, 1824  
 P-0: 09.28.434, 083.34.070, 1744  
 P-1: 09.28.410, 083.34.170, 1736  
 P-2: 09.28.372, 083.34.245, 1708  
 P-3: 09.28.353, 08.34.325, 1690  
 P-11: 9.28.134, 83.35.340, 1428  
 P-12: 9.28.129, 83.35.424, 1415  
 J-4: 9.28.152, 83.34.578, 1784  
 J-5: 9.28.206, 83.34.639, 1711  
 J-6: 9.28.237, 83.34.715, 1671  
 J-7: 9.28.283, 83.34.647, 1626  
 M-1: 9.28.362, 83.34.108, 1774  
 M-2: 9.28.294, 83.34.062, 1886  
 C-2: 9.28.007, 83.35.109, 1648  
 C-3: 9.27.943, 83.35.022, 1703  
 U-5: 9.28.826, 83.34.065, 1788  
 Q-1: 9.28.888, 83.34.011, 1824  
 Q-2: 9.28.805, 83.33.986, 1841  
 Q-3: 9.28.723, 83.33.980, 1829

### Countryside points:

Q-A: 9.28.510, 83.34.040, 1724  
 P-4 new: 9.28.322, 83.34.736, 1558  
 P-5: 9.28.307, 83.34.817, 1562  
 P-6: 9.28.283, 83.34.926, 1543  
 P-7: 9.28.215, 83.35.015, 1537  
 P-8: 9.28.233, 83.35.122, 1501  
 P-9: 9.28.224, 83.35.203, 1460  
 P-10: 9.28.179, 83.35.273, 1448  
 Ch-1: 9.28.150, 83.35.508, 1415  
 Ch-2: 9.28.292, 83.35.568, 1452  
 Ch-3: 9.28.397, 83.35.609, 1462  
 Ch-4: 9.28.476, 83.35.627, 1491  
 Ch-5: 9.28.653, 83.35.584, 1548  
 A-2: 9.27.880, 83.35.267, 1585  
 A-3: 9.27.822, 83.35.325, 1545  
 A-4: 9.27.791, 83.35.402, 1522  
 C-A: 9.27.894, 83.34.656, 1846  
 C-B: 9.27.884, 83.34.576, 1871  
 C-C: 9.27.830, 83.34.438, 1938  
 C-D: 9.27.828, 83.34.346, 1950

## Appendix II

### Schedule of point count visits:

June 15: Principal going down: P-4 through P-8 plus C-1  
June 17: Montana going up: P-3, P-1, P-2, M-1 through M-7  
June 19: Chirripo going up: C-2 through C-9  
June 20: HL-1 through HL-3, G-1 and G-2, J-1 and J-2  
June 21: J-7 through J-1, He-1  
June 23: P-0, U-1 through U-5  
June 24: P-8 through P-4  
June 30: C-10 through C-19  
July 1: He-1, J-1 through J-7  
July 2: Q-5 through Q-1  
July 5: C-20, C-21  
July 7: P-9 through P-12, Ch-1 through Ch-5  
July 8: T-1 through T-8  
July 9: C-A through C-D  
July 10: A-1, A-2, A-3, A-4, C-1  
July 11: Q-A  
July 12: M-7 through P-2  
July 13: G-1, P-3, Hl-1, Hl-2, Hl-3  
July 15: C-21 through C-17  
July 18: Q-A, Q-1 through Q-3  
July 19: C-16 through C-10  
July 21: G-A  
July 22: Ch-5 through Ch-1; P-12 through P-10  
July 23: T-8 through T-1  
July 25: C-D through C-A, C-9 through C-5  
July 26: A-4 through A-1, C-4 through C-2, P-9  
July 28: U-5, U-4  
July 29: G-A, P-4 new  
July 30: P-4 new, P0