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Urban development in Costa Rica: the direct and indirect impacts on local and regional avian assemblages

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Urban development in Costa Rica: the direct and indirect impacts on local and regional avian assemblages

By

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A DISSERTATION

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ABSTRACT

Urban development, the pinnacle of human land use, has drastic effects on native ecosystems and the species they contain. For the first time in recorded history there are more people living in cities than in the rural areas surrounding them. Furthermore, the global rate of urbanization continues increasing; raising serious concerns for earth's tropical regions as they harbor a disproportionate amount of the earth's species, and where the impacts of urban development on natural communities are poorly known. Therefore, for my dissertation research I investigated the impacts of urban development on avian community structure and organization at both local and regional scales in Costa Rica.

To address this concern I followed a nested design and established survey sites following a complete development gradient that ran from the mature, interior forests of a large national park or reserve and into the urban core of a nearby city. Between both extremes I identified seven other key development steps and established 16 ha sites at each one. At each survey site I conducted annual surveys of the avifauna and characterized the local environmental conditions using remote sensing techniques. I identified three such development gradients within the drier habitats of Costa Rica's Pacific Northwest ecoregion, and three other development gradients in the wetter, Atlantic lowland ecoregion. In total, my 54 survey sites divided evenly across the two ecoregions, and spread across three replicate gradients in each, generated a dataset with over 27,000 observations representing over 36,000 individual birds and 328 species. With this dataset I could generalize the impact urban development had on the structure

and organization of local avian assemblages, and determine the key factors driving such patterns by running different analyses at different levels.

My first level of analyses was directed at the impact urban development has on avian diversity patterns, and discovered that urban development drives a monotonic loss of avian species at the local, 16 ha scale in both of the distinct ecoregions. Although somewhat predictable, such results suggested that alternative patterns such as peaks of species richness at intermediate levels of urban development are unlikely for the species rich Neotropics. Additionally, beta diversity in both ecoregions also decreased with an overall increase of urban development. Although local environmental conditions such as level of urban development or percentage of forest cover greatly influenced diversity patterns, they were dependent upon the ecoregion in which they were nested. For example, local alpha diversity was higher in the more species rich Atlantic ecoregion, and beta diversity did not decline as sharply in the Pacific Northwest. Furthermore, on a landscape scale the same level of urban development had a disproportionate effect on avian species richness near a large park or reserve than it did closer to the urban core. In the end, the results of this first level of analysis led to me to suggest particular management policies for avian species conservation along urbanization gradients for similar ecoregions of the Neotropics.

In my second level of analyses I took a closer look at the species composition and abundance of the 54 avian assemblages and how they were affected by increasing levels of urban development. I found that urban development did acts as an environmental filter and drove convergence of assemblage structure and organization. The biotic homogenization of urban avifaunas was strongly correlated with factors such as the level

of urban development and percentage of forest cover, but again within an ecoregional context. Within each ecoregion urban development acted as a deterministic filter since similarly developed sites from different cities or gradients were more often associated together from the results of multivariate analyses. The results of these multivariate analyses provided additional support for the management policies suggested in the first chapter. Not only did the results support the establishment of distinct management areas based on thresholds of urban development, they did so at an ecoregional scale given the similarity of results across the nested gradients.

Finally, I wanted to investigate the phenomenon that urban development also may have negative effects on native species conservation indirectly through social interactions in what is referred to as the "*extinction of experience*". In the first two chapters I clearly demonstrated a direct relationship between urban development, its impact on avian species, and the consequences for avian conservation in an urbanizing world. However less well known, but potentially more devastating, is the impact a lack of knowledge or awareness about nature could have on species conservation efforts. If we accept popular conservation paradigms that "we only save what we love and love what we know", then a lack of knowledge could be devastating to conservation efforts. Therefore, I established a survey-based outreach program to determine if 1) there is a lack of knowledge or a difference in perceptions across generations, and 2) outline the relationship of this knowledge with urban development in Costa Rica, a tropical, species-rich country well-known for its environmental awareness. In a survey of 310 upper-elementary students, their parents (n = 219) and grandparents (n = 83), the older generations outperformed the students on questions relating to knowledge of native and exotic species of birds.

However, more alarming were the results that students did better identifying exotic birds like penguins and ostriches from other continents than they did the national bird and other common backyard species. Furthermore, most students do not agree with their older relatives that the state of the environment is declining over the next 50 years, and a proportion of urban students actually believe the environment will improve.

Although my results from this last chapter may not be as straightforward as those investigated in the first two chapters, they were nonetheless informative about the conditions in which conservationists, urban planners, and to a large degree educators will need to operate in the coming decades. Using my comprehensive results from the direct impact urban development has on avian assemblages, I believe they can and should be used to establish the management practices put forward that would benefit species conservation well-into the areas where we live and work throughout the Neotropics. However, to what degree such plans will be accepted by the general populace will be much harder to determine.

I've been blessed with great teachers who fueled my interests in the natural world and turned regular classes into academic adventures that have shaped my way of life since high school (Jim Herget), through college (Edward H. "Jed" Burtt), and into graduate school (Bette Loiselle, Godfrey Bourne, and John Blake). They have been great mentors and good friends who in turn have been models I've attempted to emulate in my own teaching.

At one point or another most of the faculty in the Biology Department at UMSL provided some input into my graduate career, be it advice, an important reference paper, scores of knowledge, a critique or a question, either as part of a course or through formal and informal meetings. For this I thank Bob Marquis, Zuleyma Tang-Martinez, Toby Kellog, Bob Ricklefs, Jim Hunt, and Peter Stevens for helping me advance in my graduate career.

Additionally I would add a special thank you to the PI's of the MOSTEP program that not only provided valuable funding throughout my three years on campus, but gave me the opportunity to get back into the classroom where I feel most at home. Being a part of MOSTEP greatly enriched my graduate studies. Thank you, Charles Granger, Patrick Osborne, Patty Parker, Bette Loiselle, Joe Polman, and Jim Wilson. I would also like to thank the cooperating teachers of the MOSTEP program who opened their classrooms and shared their students as well as their collective experiences with me: Cathy Kane, Jack Bowles, and Resha Messick. Thank you for helping make me a better educator.

Special thanks goes to those individuals who were part of the research labs I was fortunate to be part of while at UMSL. All had a helping hand in the chapters that

follow. Thank you Godfrey for opening the door to graduate school, and to John and Bette for adopting me into your lab groups while Godfrey went to NSF. I was fortunate to be a part of four (MOSTEP included) different lab groups that gave me close interaction with dozens of students who provided valuable feedback, suggestions, hints, knowledge, and assistance with coursework, research ideas, and thesis development; but above all they formed a small army of allies that provided friendship and support throughout my time in St. Louis.

The department could not function without a few key staff members who greatly helped me, and other students navigate the course through graduate school; thank you Pat Hinton, and Kathy Burney-Miller. Maryann Hempen should receive additional praise for her knowledge of the intricate policies within the department and throughout the university is unmatched.

I am extremely grateful to have had the assistance of such a skilled, experienced, and personable thesis committee: Godfrey Bourne, Bette Loiselle, John Blake, John Marzluff, and Jed Burtt. They all provided important assistance in the development of my dissertation thesis from its incipient stages. Each has greatly helped me, the science teacher, retrain myself as an ecologist. From methodology, writing styles, analysis, and general tips (i.e., pivot tables!) I have greatly improved my skills as a scientist, and ultimately as a teacher as well.

Birds may grow in trees but money does not. Therefore my thesis would not have been possible without the generous support of three years of a MOSTEP graduate fellowship, The ICTE/Harris World Ecology Center, The Biology Department, and The Graduate School all at UMSL. In addition I was very grateful for a TWA Scholarship

every little advance over the past seven years. No one else lived the experience to the extent she did. She is the unsung hero and unofficial 6th member of my thesis committee, and the few words written here do little justice to the integral role she played in seeing this dissertation through to completion. I will forever be indebted to her for being an integral part of this process, and for ultimately making me a better person.

CHAPTER 1

Urban development in Costa Rica and local and regional avian diversity patterns

INTRODUCTION

Anthropogenic landscape change continues to be the leading cause of species loss worldwide (Wilson 2002), and urbanization may be the principal factor driving extinction this century (Czech et al. 2000, Marzluff et al. 2001). Despite decreasing birth rates, urbanization is increasing on a global scale (UNDESA 2009). More and more people are leaving rural, agrarian lifestyles and moving to the world's urban centers (Marzluff et al. 2001, Chamie 2007). As both a process and a level of development (Blair 2004), urbanization lies at the pinnacle of human induced changes, exerting long lasting effects on natural ecosystems when compared to other disturbances (McKinney 2002, Blair 2004). In fact, urbanization leads to entirely new human-dominated landscapes with emergent phenomena and distinct ecological properties (NSF 1998, Alberti et al. 2003, Olden et al. 2004, Kaye et al. 2006).

In the Neotropics, where species diversity reaches its highest levels for many taxa, such as birds (Stotz et al. 1996), the potential negative effects of increasing levels of urbanization proliferate as they are combined with continued high rates of human population growth (Cincotta et al. 2000). Costa Rica, one of the most species rich countries per unit area (Valerio 1999), has also witnessed an increase in its urban population from 33% to 62% over the past 50 years (UNDESA 2009). Many studies in

Costa Rica and throughout the Neotropics have already demonstrated the strong effects of anthropogenic land use, and the resultant habitat fragmentation on the composition and diversity of local avifaunas (Daily et al. 2001, Graham and Blake 2001, Sekercioglu et al. 2002, Lees and Peres 2006). However, few have examined how the remaining species respond within human-dominated urban environments in the Neotopics (Marzluff et al. 2001, Chace and Walsh 2006).

Recently, González-Urrutia (2009) and Ortega-Álvarez and MacGregor-Fors (2011) published much needed reviews of urban ornithology for Latin America. Their search only uncovered 109 peer reviewed works (i.e., approximately 6% of the known, global urban avifauna literature), a quarter of which are mere species lists for single cities or sites, and at least another quarter that come from temperate Latin America (González-Urrutia 2009, Ortega-Álvarez and MacGregor-Fors 2011). The remaining studies represent Neotropical avifauna and some address conservation issues as well as ecological patterns. However, the extreme variation in research objectives and approaches of each study generated problems when making direct comparisons among studies, and difficulty in building a consensus for the response of birds to urban development in this species rich region.

In regions outside the Neotropics, the effect of urbanization on birds is relatively well-studied; enough so that various authors have completed books (Marzluff et al. *2001*) meta-analyses (Clergeau et al. 2006b, McKinney 2006) or review papers (Chace and Walsh 2006). The majority of studies point to a decrease in species richness as levels of urbanization increase (Clergeau et al. 2001, Fernandez-Juricic and Jokimaki 2001, Marzluff 2001, Chace and Walsh 2006, Clergeau et al. 2006b, McKinney 2006). This

negative correlation of species richness with urban development is not only the most

prevalent in the literature (Marzluff 2001, Clergeau et al. 2006a), but it also follows a

habitat-loss or species-area model, one of the most widely supported patterns in ecology

(Rosenzweig 1995).

Yet, there are a few studies that found that avian species richness peaked at intermediate

levels of urban development (Blair 1996 and 2004, Crooks et al. 2004, McKinney 2002,

Marzluff 2005), and either invoke Connell's (1978) intermediate disturbance hypothesis

or increased habitat heterogeneity as the mechanism.

Most of the studies that focus on avian responses to urban development have

looked primarily at the change of local species richness, or alpha (α) diversity at varying

points along the urbanization gradient without explicitly looking at other measures of

diversity such as beta (β, species turnover or the degree of species compositional change

among sample sites) or gamma (γ, regional species richness) diversity. While alpha

diversity is important for establishing relationships of species richness with local

conditions, beta diversity may be the most useful of the diversity measures as it creates a

fundamental link between both local (α) and regional (γ) species richness (Rosenzweig

1995, Ricklefs 2004). Furthermore, beta diversity patterns are central to understanding

many ecological questions relating to the function or management of ecosystems and the

conservation of biodiversity (Legendre et al. 2005, McKnight et al. 2007).   This apparent

lack of beta and gamma diversity analyses in urban avian research may result from the

single city, single region approach prevalent in urban studies.

Therefore, the primary objective of this chapter is to determine if alpha diversity

(α) in Costa Rica follows a monotonically decreasing slope as urbanization increases, or

if it peaks at intermediate levels of development. Additionally, I calculate the degree of change in species composition or turnover (β diversity) among sites along the urban development gradients. Furthermore, I compare both alpha (α) and beta (β) diversity along urban gradients in distinct regions that varied in their regional or gamma (γ) diversity to determine if the pattern holds across different areas with distinct ecological properties. I also correlate the distribution of alpha species richness with environmental variables: forest cover, productivity (Normalized Difference Vegetation Index, NDVI), and habitat heterogeneity to generate better models for predicting the response of Neotropical avian species richness to increasing levels of urban development. Since most of the current data on avian responses to urban development come from studies conducted in temperate zones, from single cities or regions, and along incomplete development gradients; my goal is to provide a multi-region, multi-city approach along complete anthropogenic development gradients in tropical, species-rich Costa Rica that will not only provide the first comprehensive description of avian responses to urbanization for the Neotropics, but also establish a strong platform for future, similar studies in the region, and other areas throughout the tropics.

METHODS

Study area

I conducted my research along six anthropogenic development gradients evenly divided among two distinct ecoregions in Costa Rica (Fig. 1). Costa Rica is a small country of 51,000 km^2 in the Neotropics between 8° and 11° North latitude. As an ecologically rich country with a well-studied biodiversity (Valerio 1999), and having

doubled its urban population over the past 50 years with a predicted growth of 17.7% in the next 40 years (UN DESA 2009), it provided an ideal location for studying the effects of urban development on the distribution of avian species richness across local and regional scales in the Neotropics.

Site selection

Each gradient covered the full range of anthropogenic development from an urban core to the interior of a mature forest in a nearby national park or reserve. I chose three non-coastal cities below 1000 m elevation with human populations between 18,000 and 45,000 inhabitants, and selected the nearest park or reserve to anchor each end of the gradient in both ecoregions. Smaller cities (i.e., < 18,000 inhabitants) did not demonstrate clear urbanization gradients, nor were there any larger cities (> 45,000 inhabitants) with suitable replicates in each region. Each city selected in this study was large enough to demonstrate clear urban development gradients, but small enough to survey all sites in one day during each visit. The city-park gradients for the Atlantic ecoregion (ATL) were: Guapiles-La Selva (GuLS); Siquirres-Barbilla (SiBa); and Turrialba-Guayabo (TuGu). The gradients for the Pacific Northwest ecoregion (PNW) were: Liberia-Santa Rosa (LiSR); Canas-Palo Verde (CaPV); and Nicoya-Barra Honda (NiBH).

Along each gradient I used high resolution CARTA aerial images (PRIAS 2005) and a 16 ha grid overlay with 4 ha subdivisions in a GIS to estimate levels of urban development and natural cover within a 1.5 km buffer around each city and national park. I combined grid estimates with ground-truthing visits and established nine survey quadrats of 16 ha each (400 m x 400 m). Knowing that many avian species use human-

made environments (Johnston 2001), I took the *landscape level* approach (Figure 1b, Clergeau et al. 2006a) that urban areas constitute habitat and should not just be considered the disturbance matrix surrounding remnant vegetation (Rebele 1994, Pickett et al. 2001, Alberti et al. 2003).

Quadrats selected varied in their level of urban development and were classified as follows (Figs. 2-3): (A) *urban core*, a primarily commercial area with approximately 75% or greater of the available area developed and covered by impervious, urban structures (i.e., buildings, roads); (B) *commercial-residential transition*, typically close to the urban core where approximately 50-74% of the area has been developed for mixed residential and commercial use; (C) *high-density residential*, peripheral to the sites above and developed primarily with smaller, single-family homes (i.e., small lots with little space available for green areas) with an approximate 50-74% of the available area covered by impervious structures; (D) *low-density residential*, areas peripheral to sites A and B and approximately 15-49% developed with single-family homes on larger lots with ample gardens or green space, or smaller homes scattered among undeveloped lots; (E) *rural*, areas closer to the urban fringe dominated by agriculture, pasture, or large undeveloped sites with less than 14% of the available area covered by urban structures; (F) *forest fragment*, an area covered with at least 50% of remnant forest, of which at least 25% forms one continuous stand and less than 5% development (i.e., roads); (G) *rural settlement*, a small town or village near the park or reserve of each gradient, likely overlapping with quadrats "D-E" in terms of urban development; (H) *edge/succession forest*, advanced secondary or mature forest of a large park or reserve near its edge or bordering open areas where over 50% forms a continuous stand; and (I) *interior/mature*

forest, an area with at least 95% coverage by continuous forest and greater than 200 m from the nearest edge.

Of the nine quadrats in each gradient, six were associated with the city (A-F) and three were associated with the park (G-I). City quadrats A-E were randomly selected from a grid of available quadrats for each level of urban development, whereas quadrat G usually fit near the center of each rural village. Quadrats F, H, and I were chosen by their accessibility (e.g., with roads and trails) and where permission to the property was granted. Although rural settlement sites (G) actually represented a break or interruption in the development gradient, I included them in this study to compare how avian species richness varies between areas with similar levels of urban development, but different landscapes (i.e., urban vs. natural).

I subdivided each quadrat into four observation points for sub-sampling the avifauna and measuring environmental variables. The observation points in each quadrat were 200 m from their nearest neighbor to reduce the chances of double-counting individual birds in subsequent counts (Garafa et al. 2009). In a few cases I shifted or rotated quadrats and the observation points within to facilitate access within public property (e.g., alongside roads and trails), but never violated the 200 meter distance between neighboring points.

Avian surveys

Between June 10, 2008 and December 12, 2009 I made 14 visits to each site. To avoid seasonal biases I evenly divided the visits among two, six-month periods covering the peak months when North American migrants were either usually present (October-March) or absent (April-September, Stiles and Skutch 1989). During each visit I

surveyed birds at all observation points using variable circle point counts up to 100 m to reduce chances of counting the same bird in subsequent counts of nearby points. The start point for daily counts was randomly determined for both quadrat and sub-sample point using a random numbers table. I began counts approximately 20 minutes before sunrise (Blake and Loiselle 2000, Blake 2007) and all counts were usually completed within 5 hours. In the course of one morning I could reliably conduct surveys at all points associated with the city (i.e., quadrats A-F) or with the park or reserve (i.e., quadrats G-I). I conducted counts on days with little to no wind or rain, and delayed or suspended counts if conditions were unfavorable.

I identified all birds detected to species level using visual and aural cues. I measured their detection distance to the nearest meter with Leica 8x42 Geovid binoculars and digital rangefinder. Birds flying over the survey area were not included unless they were actively foraging (e.g., swallows) within the point count area. I recorded all counts with a Galaxy HDR2 digital recorder and two Sound Professional high-gain binaural omni-directional microphones clipped to my hat, one near each ear. This set-up allowed me to make high quality recordings for archival purposes that simulated conditions as they were heard in the field. I used both WAVEPAD 3.12 (NCH) and RAVEN PRO 1.3 (Cornell Lab of Ornithology) to manipulate sound files which later aided with data transcription and species identification when songs or calls in the field could not be identified immediately because of noise, incomplete vocalizations, low volume, or counts with a lot of activity.

Given the differences in rates of detection of birds across the different habitats of the urban development gradient (Table 1), I modified the duration of timed counts. For

all "urban" quadrats (i.e., A-E, G) I used 4 min count periods, whereas for all "forested"

quadrats (i.e., F, H, I) counts lasted 15 min.   In urban quadrats I limited the count time to

reduce the probability of re-counting individual birds as the rates of detection were

relatively higher and visual (50%, pers. obs.). In the forested quadrats the rates of

detection were lower and predominantly aural (84%, pers. obs.), of which only a limited

number could be attributed to a determined distance (Table 2). For surveys in forested

sites I increased the count length to sample more individuals. In all quadrats, birds seen

or heard near the sampling point upon approach were included, and I waited a few

minutes after arrival at each point to allow birds to settle before I began the count.

Counts were conservative (i.e., one detection = one bird), and multiple birds per detection

were only included if their number was visually confirmed, or by simultaneous aural cues

from different locations.   In order to eliminate observer bias I conducted all avian

surveys for this study.

Quantifying land cover

        To quantify the levels of development across the urbanization gradients and the

remnant vegetation structure I collaborated with Carlomagno Soto the GIS Lab Manager

at La Selva Biological Station and one of the technicians, Jose Martin Miranda. We used

remotely sensed hyperspectral HYMAP (PRIAS 2005) images in a geographic

information system and conducted a manual classification of the reflectance values for

the different spectral bands across all sites (Appendix I).   The HYMAP images used

were from March 2005 with a 15 m resolution and 108 different spectral bands. The

HYMAP images were georeferenced after atmospheric correction and superimposed with

high resolution (i.e., 1m) CARTA (PRIAS, 2005) images taken during the same flights as

the HYMAP images. All 216 sub-sample points from the 54 quadrats of the six urban development gradients were placed over both sets of images and surrounded by 100 m buffers.

Within each buffer we manually drew multiple polygons around known areas and classified them to the following land-use classifications: *urban*, non-vegetative areas covered with impervious surfaces like houses, buildings, and roads; *forest*, areas of continuous tree coverage; *grass*, areas of lawn or pasture; and *savanna*, areas of combined grass and trees with multi-strata vegetation (i.e., gardens or pastures with trees). For the Turrialba-Guayabo gradient we needed to include a coffee class to separate it from forest because of its similar reflectance score. However, coffee fields were only present at two sites and represented such a small proportion (i.e., less than 4%) of any one of the regional sites that the class was dropped from the analyses.

Half of the polygons chosen for each land-use class within each buffer were used as training data for the classification, and the remaining polygons were used for testing the final classification. The land-use classification was applied to all pixels within each buffer (n $\approx$ 139) using the image analysis program ENVI 4.6 (ITT) and the area totals for each land-use were exported as a text file. We calculated the total area of each land-use for all 54 sites by summing the four sub-samples or buffer scores, and converted these to percentages of the total sampled area. Pixel values not included in the classification polygons went unclassified. Only 11 of the 54 survey sites contained unclassified pixels and their average proportion was 4.33% of the total site area.

In addition to the image classification, which primarily quantified the level of disturbance, we also ran analyses within ENVI 4.6 (ITT) of the same hyperspectral

HYMAP images to quantify the available energy (i.e., productivity) as well as the habitat heterogeneity at each of the 54 sites. To calculate the level of productivity at each site we used NDVI scores calculated from the standard vegetation indices analysis as part of the ENVI program. As a measure of habitat heterogeneity my colleagues and I assumed the range or variation of pixel values from the HYMAP image within a given site would be a good proxy. We also assumed that pixel values within mature/interior forests or those within urban cores would show little variation because of their homogeneity of land-use, even if scores between them were expected to be quite different. Similarly, we thought that sites of intermediate development would show the greatest variability in pixel values as these sites would contain a mixture of the different land-uses. However, since each pixel contained 108 different values based on the level of reflectance for each spectral band, many of which were on different scales, we reduced all these values to three scores running a principal components analysis (PCA) on the original values. Of the three PCA values we chose the first for additional analyses, as the first PCA score usually retained the majority of the variation of the original pixel values. We calculated the coefficient of variation of the first PCA score to represent the variation in pixel scores (i.e., habitat heterogeneity) for each site.

Species richness and diversity calculations

In each survey site I totaled raw abundance data for each species across the four sub-sample points and both migrant seasons in a year-round species-by-quadrat matrix. I loaded the full species-by-quadrat matrix (i.e., 328 sp) into EcoSim 7.72 (Gotelli and Entsminger 2001) and using the species raw abundance totals calculated the species richness for all 54 survey sites. I selected individuals as the sampling unit and the

rarefaction curve for the randomization algorithm with 1000 iterations. I rarefied the

species richness calculations to 450 individuals for valid comparisons of species richness

across urban and forested quadrats that varied in point count duration (Gotelli and

Colwell 2001). The rarefied values for species richness and associated variance for each

16 ha site or survey site were used as the scores of local diversity, or alpha (α).

To calculate beta diversity (β), the turnover of species between sites, or the level

of difference in composition of avian assemblages across different survey sites, I used the

Sorensen/Bray-Curtis distance measure generated in PC-ORD 5.32 (McCune and

Mefford 2006). Although different measures of beta diversity exist (Koleff et al.2003),

the Sorensen/Bray-Curtis distance measure is both commonly used (Koleff et al.2003)

and also suggested for community analyses (McCune and Grace 2002). The

Sorensen/Bray-Curtis distance measure is a semi-parametric index that also allows for

proportional abundances as opposed to just presence or absence (McCune and Grace

2002). I began with the full year-round species-by-site matrix based on incidences of

observation. I removed those species observed less than three times throughout the entire

study as this removes the noise and reduces the size of the data set without losing much

of the pattern or relationships (McCune and Grace 2002). I used this reduced species-by-

site matrix and relativized the number of observations for each species using the general

relativization method for species totals in PC-ORD 5.32 (McCune and Mefford 2006). I

then generated a pairwise distance matrix among all 54 sites (n = 1431) using the

Sorensen/Bray-Curtis distance measure.

As a measure of regional species richness, or gamma diversity (γ), I used the

number of species observed across all sites and seasons within each ecoregion (McCune

and Grace 2002). For all comparisons of avian diversity patterns along urban
development gradients, I averaged values for replicate sites within each ecoregion to
control for spatial autocorrelation among sites. These composite site scores were
analyzed and used separately for each ecoregion, but graphed together to show how the
patterns of alpha and beta diversity vary along urban gradients in regions of differing
gamma diversity. I used JMP 8.0.2 (SAS) for the univariate analyses of alpha and beta
diversity values with urban development, and for multivariate correlations of species
richness with the environmental variables. All graphs were generated using Origin Pro
8.1 (Origin 2010).

RESULTS

Avian surveys

Across both ecoregions detection rates were lower in forested sites than in urban
sites (Table 1). Among most sites average detection distances were greater for visual
than aural cues (Table 2), and the average detection distances across all sites varied
between 30 and 40 m while the lowest average detection distances were from mature
forest interior (Table 2). Overall, I recorded a total of 27,639 detections representing
36,540 individual birds (Table 3), and I registered a total of 328 species (267 sp. ATL
and 154 sp. PNW, Appendix II). Less than 5% of the total birds detected could not be
identified to species level.

The mean number of birds detected in each site were quite similar across the two
ecoregions, 629 (PNW) and 661 (ATL). However, there were large ranges in the
numbers of individual birds observed across the 54 sites (PNW: 388-999, ATL: 403-

1149; Table 4).   Comparing avian abundances between forested and urban sites is

hampered by the increased sample effort in forested sites. However, comparing only

urban sites (i.e., A-E, G) the abundance patterns along the different gradients varied.

Averaging the abundance values across the three replicate sites of the different gradients

in each ecoregion revealed no overall trend of avian abundance along urban development

gradients in Costa Rica.

These birds represented median values of 37 species observed for the PNW

ecoregion (range 21-74) and 57 species observed for the ATL ecoregion (range 30-116,

Table 4). Removing rare species, or species observed less than three times throughout

the study (n = 60), yielded a total of 268 species, 217 from ATL and 144 from PNW

(Appendix III).

Land cover classification

The patterns of urban and vegetative land cover along anthropogenic development

gradients were similar across both ATL and PNW ecoregions (Fig. 4). As expected, the

level of urban development measured from remotely-sensed images decreased as one

moved from the city core towards the interior forests of a large national park or reserve.

The sharpest differences along the gradients of both ecoregions existed between the last

of the city sites (D and E) and the beginning of the forested sites (F), or between the

forested succession/edge sites (H) and the nearby rural settlement sites (G). Despite

small errors with our classification procedure (i.e., finding grass and savanna in interior

forest sites, or overlap between the coffee and forest classes of the TuGu sites), the

overall accuracy of image classification between training and testing pixels for the 11

images used was 73.55%.

Avian diversity

The regional avian species richness, or gamma diversity (γ) was higher in the ATL ecoregion (267 species) than in the PNW ecoregion (154 species), despite representing a smaller overall geographic area (Figure 1). Local species richness or alpha diversity (α) decreased as levels of urban development increased (Fig. 5). I found significant overlap in alpha diversity values both within and across regions (Table 4, Figure 5). Diversity in secondary/edge forest of the ATL region national park sites (i.e., H) was higher than those found in PNW (Tukey HSD post-hoc comparisons, see Table 4). Despite the monotonic loss of avian species along the urbanization gradients in both ecoregions (PNW: Welch's ANOVA, $F = 70.55$, d.f. = 8, $P < 0.0001$; ATL: Welch's ANOVA, $F = 71.97$, d.f. = 8, $P < 0.0001$), significant differences in avian species richness only occurred between the most heavily forested sites (F, H, and I) and the heavily urban or city sites (A, B, and C) (based on Tukey HSD post-hoc comparisons, see Fig. 5). Species turnover, or beta diversity (β), generally decreased between sites as urban development increased across both ecoregions (ATL: ANOVA, $F = 13.59$, d.f. = 7, $P < 0.0001$; PNW: ANOVA, $F = 8.22$, d.f. = 7, $P = 0.0003$, Figure 6), although there appeared to be a slight peak in species turnover between forested sites (i.e., F and H) and the nearby developed sites (i.e., E and G). Despite the differences in gamma diversity between the two ecoregions, I found no significant differences in beta diversity between homologous comparisons of the two ecoregions.

Local species richness and habitat associations along urbanization gradients

Urban development and the local species richness were found to be highly correlated (Table 5). I also found strong correlations between NDVI and forest cover

with avian species richness. Given the strong levels of correlation among the environmental variables (Table 5), and the fact that urban development already accounts for 91% of the variation in species richness along the ATL gradients and 93% of the variation in species richness along the PNW gradients (Table 5), I did not include other variables in regression analyses. Thus, patterns observed here are correlated with urban development but may be driven or explained better by other mechanisms.

DISCUSSION

Avian abundance

Some studies have found increased avian abundance with increasing levels of urban development (Clergeau et al. 2006a, Ortega-Álarez and MacGregor-Fors 2011); this pattern was not found in Costa Rica. Some greater abundances were associated with the urban cores (i.e., sites A) of the PNW, but ATL urban core sites were characterized by a reduced abundance of birds (Table 4). Although House Sparrows (*Passer domesticus*) and Rock Pigeons (*Columba livia*) were present, rarely did they reach the high densities known to be responsible for many of the abundance peaks in other studies. Furthermore, they were commonly found alongside other native Columbids and Emberizids. Most abundance peaks, especially among sites of the PNW gradients, were caused by early morning counts near roosts of the gregarious the Great-tailed Grackle (*Quiscalus mexicanus*), or from counts where many swallows (e.g., *Pygochelidon cyanoleuca* or *Progne chalybea*) were perched together on a wire. Additional spikes, especially near rural sites (i.e., E and G), may be due to the more open habitats where avian detections tended to be higher (Table 1). In studies that documented increased

numbers of synanthropic exotics, the pattern of increased avian abundance may possibly

be due to incomplete gradients, or small sample sizes (i.e., as represented by one or a few

cities of temperate regions). However, both Lim and Sodhi (2004) and Garaffa et al.

(2009) also found that avian abundance stayed the same or even decreased as the level of

urban development increased.

Avian diversity

Regionally, more avian species (gamma diversity) were observed in the Atlantic

(ATL) than Pacific Northwest (PNW) ecoregion. This particular pattern was not

influenced by area as the geographic extent of the PNW sites was approximately 1,200

km^2 greater than the geographic extent of the area covered by the ATL sites. However,

the larger gamma diversity of ATL may be, in part, a consequence of the greater

altitudinal extent of the ATL sites; Turrialba – Guayabo sites were all above 600m,

including the two park sites which were slightly above 1000 m in elevation. The median

elevation among PNW sites was 147 m (range 39-395 m), whereas for ATL the median

elevation (289 m, range 49-1084 m) was significantly higher (Wilcoxon rank sums test,

$X^2 = 8.3$, df = 1, $P > 0.004$). This is a potential problem given the mid-domain effect

(Colwell et al. 2004), since at middle elevations around 500-1000 m there is an altitudinal

band where the higher limits for lowland species and the lower limits for highland species

overlap (Stiles 1983).

Yet this likely had no effect on the alpha diversity comparisons. ATL sites still

had greater alpha diversity values than homologous sites in PNW found at the same

elevation. Furthermore, on the local scale, many of the higher elevation TuGu sites had

lower species richness, either observed or estimated, than did similar sites at lower

elevations along the GuLS or SiBa gradients (Table 4). Blake and Loiselle (2001) also found that rarefied species richness at their study sites along an elevation gradient on Atlantic slope of the Braulio Carillo – La Selva corridor changed little between 50 and 1,000m.

The overall decrease of beta diversity along urban development gradients in both ATL and PNW reinforced the pattern that urban development is driving biotic homogenization (Blair 2001, McKinney 2002, McKinney 2006). The apparent peak of beta diversity between forested sites and the nearby rural areas (i.e., F - E, or H – G, Figure 6) makes intuitive sense given that these steps represent large differences in habitat characteristics (Figure 4). The other stepwise comparisons were more subtle in their habitat differences as was the resultant decrease in species turnover (β diversity).

Response of avian species richness (alpha diversity)

The results of this study revealed a general loss of avian species as anthropogenic disturbance increased from the natural forested habitats of a large national park or reserve into the urban environments of a nearby city in both ecoregions. Such a habitat-loss or species-area model makes intuitive sense as increasing levels of urban development results in a decrease of forest cover (Er et al. 2005). Neotropical avifaunas are heavily influenced by species adapted to, or dependant upon forested habitats (Stiles 1983, Stotz et al. 1996), and Costa Rica has been dominated by forests over the past 3-5 million years (Stiles and Skutch 1989). Even up through the 1940's nearly 70% of Costa Rica was still covered by relatively undisturbed forest (Joyce 2006). The presence, size, and attributes (e.g., proportion of native vs. exotic species, structural layering) of remnant forest or vegetation patches have also been found to be positively associated with bird species

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richness and abundance across other urban areas of the tropics and Latin America

(Gonzalez-Urrutia 2009, Suarez-Rubio and Thomlinson 2009, Ortega-Ávarez and

MacGregor-Fors 2011).

This negative correlation between avian species richness and level of urban

development is the one presented in most studies (Marzluff 2001, Clergeau et al. 2006a),

it is common across a variety of habitats (Chace and Walsh 2006, Ortega-Álvarez and

MacGregor-Fors 2011), and covers a wide geographic range: from South America

(Caballero-Sadi et al. 2003, Garaffa et al. 2009), throughout North America (Stratford

and Robinson 2005, Donnelly and Marzluff 2006, Chapman and Reich 2007, Melles et

al. 2003), and across Europe (Palomino and Carrascal 2005, Clergeau et al. 2006b,

Sandstrom et al. 2006, Simon et al. 2007). For Latin America, Ortega-Álvarez and

MacGregor-Fors (2011) indicated, as a general pattern, that avian species richness

declines with an increase in levels of urban development. This same negative correlation

of bird species richness and urbanization holds across tropical Asia for montane species

(Soh et al. 2006) and mixed species flocks of Peninsular Malaysia (Lee et al. 2005), and

for all species across the island state of Singapore (Lim and Sodhi 2004).

One goal of this study was to determine whether or not species richness followed

a peaked, intermediate disturbance or habitat heterogeneity pattern suggested by some

authors (Blair 1996 and 2004, Crooks et al. 2004, McKinney 2002, Marzluff 2005).

Although species richness in both ecoregions of this study actually peaked at

secondary/edge forest sites (i.e., sites H in Fig. 5), this was expected (Stiles 1983, Blake

and Loiselle 2001). This is perhaps best viewed as the result of the increased habitat

heterogeneity (Tews et al. 2004) of this "semi-natural" habitat (e.g., succession forest

along anthropogenic trails or forest borders), as opposed to the result of differential colonization or competitive skills among species as suggested by the intermediate disturbance hypothesis (Connell 1978). Although different from natural disturbance regimes (e.g., fire, tree falls, hurricanes), urban development can fit the intermediate disturbance framework since biotic limitations (i.e., competition) are abundant at the more natural ends of the gradient, whereas physical limitations are greater at the more urban end (Blair 1996). If intermediate disturbance , or habitat heterogeneity, were the mechanisms driving the distribution of species richness along urban gradients in Costa Rica, I would have expected to see a peak of avian species richness somewhere between the rural sites (i.e., E) and the high-density residential sites (i.e., C). However, local species richness declined between these points on the gradient, and more so over the full extent from the natural, secondary/edge forest sites (i.e., H) through the urban core sites (i.e., A). Accordingly, my data, demonstrated a better fit to a habitat loss pattern (i.e., "percentage of area taken out of primary production", Blair 1996) as opposed to the intermediate disturbance hypothesis. There are many potential diversity-disturbance patterns (McDonnell and Hahs 2008), and Mackey and Currie (2001) reported that only 16% of studies found non-linear peaks of species richness along disturbance gradients as opposed to being found at either extreme. Therefore, more multi-region, multiple full-gradient studies are still required for the tropics; but it appears, that in most cases, a monotonic loss of avian species is to be expected with an increase in the level of urban development.

Avian diversity and habitat association

Forest cover was not as good as urban development as a predictor variable for the decline of avian species along urbanization gradients in Costa Rica (Table 5). Although level of urban development provided a strong predictor of avian species loss here and in other studies (Lim and Sodhi 2004), it should be thought of as an indirect gradient, or as a surrogate variable for the loss of forest (McDonnell and Hahs 2008), since forest cover was also strongly negatively correlated with urbanization (Table 5). NDVI also correlated strongly with species richness (Table 5), and is known as a good predictor of avian species richness patterns across different geographic regions and spatial scales (Hurlbert and Haskell 2003, Bino et al. 2008). While NDVI and forest cover are directly related to the available energy in an ecosystem, and provide shelter, food, and nesting sites which are directly related to the number of individuals or species of birds that can be supported in a given habitat; as predictor variables along an urban gradient they may not perform as well as the measure of urban development. Stiles (1983) warns against strict definitions of "forest" and "non-forest" birds since many of the "non-forest" species (which currently dominate anthropogenically modified areas, McKinney 2002) evolved in, and were dependent upon natural light gaps and edges as part of the dynamic forest habitat. Although more and more demographic research is being done (Reale and Blair 2005, Leston and Rodewald 2006, Shochat et al. 2006, Rodewald and Shustack 2008, Fokidis et al. 2009) there needs to be much more community and population level research, especially for the Neotropics, into whether urban habitats and the remnant vegetation patches they create act as sources or sinks, for which species, and the causal mechanisms that drive these responses.

Relationship between regional (gamma) and alpha and beta diversity

The similarity of both alpha and beta diversity values for homologous sites across the two ecoregions came as a surprise since Chase (2003) and Ricklefs (2004) indicated that an increase in regional species richness would also lead to increases in both alpha and beta diversity. However, these similarities, at least for alpha diversity, may be argued as a statistical similarity instead of a significant biological difference. For example, the mean of 33 species found in the urban cores (e.g., sites A) of the ATL ecoregion was approximately 50% greater than the mean of 19 species found in the urban cores of the PNW ecoregion. I suggest that such differences are biologically significant, if not statistically, since the addition of 9 or 10 species to the urban cores of Liberia, Nicoya and Cañas, would likely have a significant ecological impact on the avian assemblage already in place. Furthermore, the statistical similarity among alpha diversity values between homologous sites of the two ecoregions disappears when the replicate sites across the three gradients in each ecoregion are pooled and estimated with rarefaction curves in EcoSim (pers. obs.).

With beta diversity it is more difficult to make comparisons with Chase's (2003) and Ricklefs' (2004) predictions given the variety of ways beta diversity is calculated (Koleff et al. 2003). Most definitions of beta diversity refer to species *turnover* (Whittaker et al. 2001, Legendre et al. 2005), or as *divergence* in species composition between sites (McCune and Grace 2002, Chase 2003), and as such can be computed using dissimilarity matrices (Legendre et al. 2005). My data fit with McCune and Grace's (2002) characterization that species turnover *per se* is a special case of beta diversity as "changes in species composition along an explicit environmental gradients"

(i.e., urban development, McDonnell and Pickett 1990); and also fit Legendre et al.'s (2005) third level of abstraction since I am analyzing the variation of beta diversity among groups of sites (i.e., averaging beta values across similar sites of the three replicate gradients of each ecoregion, Figure 6). Nonetheless, even if I analyzed beta diversity as the variation in species composition between replicate sites of each ecoregion (the calculation of β diversity inferred from Chase [2003] and Ricklefs [2004]), then beta diversity is still not significantly higher in ATL than in homologous sites of PNW (Figure 7). However, both Figures 6 and 7 show that the decline of beta diversity along urban disturbance gradients is more pronounced in the more species rich ATL than in PNW.

Landscape effects

Results from this study were generated from relatively small urban centers (e.g., between 20,000-50,000 inhabitants), and whether or not my results apply to larger cities is an important question. Yet, at a local scale (i.e., 10-20 ha) I think my predictions will hold. Clergeau et al. (2006b) found that the size of 19 cities had no significant impact on avian species richness along a latitudinal gradient through Italy, France, and Finland,and Garaffa et al. (2009) found the same pattern in Argentina once the size of the urbanized area passed a threshold of 7,000 inhabitants or 1.6 km.

Additionally, it is the level of urban development and not the surrounding landscape that has the greatest impact on the alpha diversity or species richness. The rural settlement sites (i.e., G) had a greater overlap of species richness values with the more similarly developed sites of the distant cities within their region (i.e., E and D), than they did with the sites of the nearby national parks and reserves (i.e., I and H, Fig. 5). Even when species richness estimates were generated with pooled data among the

replicate sites within each region, the local species richness of the rural settlement sites (G) overlapped more so with the rural sites (E) and low density residential sites (D); and they were significantly lower than the species richness of the forest fragment (F) or the geographically much closer park sites (H and I, pers. obs.). Conversely, the local species richness of the forest fragment sites (F) near the cities of both ecoregions were similar to, or overlapped with the species richness values of the geographically distant forested park sites (H and I, Fig. 5). Although their results come from a mix of studies in Northern temperate, and boreal cities; Clergeau et al. (2001) also found that local, urban avian assemblages are independent of the species richness of adjacent landscapes as they are more greatly influenced by the level of local development.

Furthermore, despite their relatively low levels of urban development, rural settlement sites (i.e., G) had a greater impact on the average species loss in both ecoregions than did other development steps. Looking at Figure 5, the development step from the secondary/edge forest sites (H) of a park or reserve to the rural settlement (G) represented an approximate loss of 40% of the species found in H. These rural settlement sites fall within Hansen et al.'s (2005) *exurban* development framework as "low density housing within a landscape dominated by native vegetation" and are referred to as *rural residential* areas. Although less is known about the impacts of exurban development on native communities (Miller et al. 2001), preliminary results indicate the effects on biodiversity are disproportionately large relative to the area of development (Hansen et al. 2005), and therefore greater knowledge of its ecological consequences is required as part of the anthropogenic modification framework (Theobald 2004). As would be expected with increased species loss, exurban development (both *urban fringe*

development,F-to-E; and *rural residential development*, H-to-G; Hansen et al. 2005) also

led to some of the highest beta diversity values in both ecoregions (Fig. 6).

Urban development thresholds and management areas

Despite the *statistical* overlap of diversity values along the gradients (Figs. 5 and

6), we can still identify a few ecologically important development steps, or thresholds,

along the urbanization gradients in Costa Rica that mark distinct losses of species, and

significant changes to the structure of local avifaunas. Disregarding the changes or

differences between the avifauna of the mature, interior forest sites and the secondary,

edge forest sites as being natural (i.e., I-to-H); the first true development step appeared

with fragmentation (i.e., H-to-F). The literature on tropical forest fragmentation and its

impact on avian communities is quite extensive and will not be treated here.

Nonetheless, maintaining and protecting the largest remaining natural areas is the

principal goal of conservation. The second threshold appeared as the band of

development that included exurban development, both urban fringe (F-to-E) and rural

residential (H-to-G). As indicated in the previous section these small development steps

can have a disproportionate effect on species loss and turnover, more so if close to a

natural park or reserve. A third important area of development was the zone of rural to

urban transition (i.e., sites E/G-to-D). Approximately 26 – 45% of this area was

converted to urban infrastructure, but on average a full 40% of the species that could be

found in the nearby forest fragments were lost. Finally, as residential areas gave way to

commercial areas near the city core and surpassed the 50% mark of urban cover, the loss

of species began to level off. Although geographically and ecologically distant, Donnelly

and Marzluff (2006) also found a final threshold between 45 – 59% of urban cover where

most species tended to be absent.   Even if in PNW there is a significant drop in species richness from the high-density residential sites (i.e., C) and the urban core (i.e., sites A), I do not think an increase in urban development towards 75 – 80% in this region would result in much less than 18 – 19 species being present (Table 4).

Conclusion

Across two distinct ecoregions of tropical Costa Rica local species richness decreased as urban development increased, but with no appreciable increase or change in avian abundance. Furthermore, local species richness, or alpha diversity, of 16 ha urban sites tended to be higher in regions with greater gamma diversity or regional richness. Yet there was no appreciable difference in beta diversity, or species turnover, between homologous sites of the distinct ecoregions. On the local 16 ha scale the surrounding landscape may have little impact on alpha diversity when compared to the level of anthropogenic or urban development; but it does play an important role in species loss and species turnover, but in the latter case much depends on how species turnover, or beta diversity, is calculated (i.e., Figure 6 vs. Figure 7).

One of the reasons for my multiple gradients and multiple regions approach was to establish a framework of predictions that could be tested or applied to other regions of the species rich Neotropics and provide guidelines for avian conservation in these rapidly changing areas. Miller and Hobbs (2002) have called for an inclusion of urban areas into conservation strategies to increase connectivity and the availability of quality habitat for native species in order to mitigate to some degree the negative affects of anthropogenic development on natural ecosystems. This is even more important with the relatively recent realization that certain sectors or natural fragments within urban or anthropogenic

matrices can contain or harbor relatively high proportions of the regional, natural community (Clergeau et al. 1998, McKinney 2006, González-Urrutia 2009), especially in the species rich Neotropics (Daily et al. 2001, Suarez-Rubio and Thomlinson 2009, Ortega-Álvarez and MacGregor-Fors 2011).

For now, at least in Costa Rica, we can start using predictable thresholds along urbanization gradients to create distinct management units within the conservation framework and to help guide management decisions as the species-rich tropical landscape is continually developed anthropogenically.   Based on the results presented here I would : 1) limit urban development near large, protected natural areas; 2) regulate urban development in rural and low density residential areas; and 3) encourage further growth and development to be concentrated in high density residential and commercial areas. However, I would also encourage restoration and other environmentally friendly practices along all sectors of the urbanization gradient, especially as more rural lands become available with the expansion of urban populations from the rural exodus. What I propose is not radically different from current ecological and conservation practices, but I would extend them deeper into the anthropogenic realm. Odum (1969) made similar suggestions over 40 years ago with his combined successional view of ecosystem development and human ecology; to find … *"...a way to deal with the landscape as a whole*" since "…*it is not a supply depot but is also the oikos – the home in which we must live*."

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Table 1. The average and standard deviation for the number of observations and individual birds detected per minute within each region and across replicate survey sites.

Region - Quad	No. of Obs.	s.d.	No. of Birds	s.d.
ATL				
A	**1.44**	0.39	**2.05**	0.69
B	**1.76**	0.50	**2.82**	1.39
C	**1.80**	0.30	**2.55**	0.63
D	**1.87**	0.36	**2.46**	0.61
E	**2.22**	0.27	**2.70**	0.46
F	**0.84**	0.16	**0.99**	0.26
G	2.33	0.42	**2.89**	0.56
H	**1.15**	0.23	**1.35**	0.32
I	**0.78**	0.09	**0.87**	0.12
PNW				
A	**1.41**	0.37	**3.36**	2.26
B	**1.57**	0.35	**2.44**	0.99
C	**1.69**	0.28	2.31	0.46
D	**1.95**	0.30	2.79	0.71
E	**1.65**	0.31	2.56	0.75
F	**0.70**	0.20	**0.80**	0.28
G	1.79	0.34	2.50	0.82
H	**0.84**	0.18	**0.93**	0.19
I	**0.73**	0.11	**0.77**	0.12

Table 2.The number, and average detection distances by aural and visual cues for both

ecoregions. The total number of aural detections was higher as the numbers below only

include detections where the bird's location was revealed and the distance could be

determined with the range finder.

Region - Quad	Aural		Visual	
ATL	n	Avg.(m)	n	Avg.(m)
A	197	28.79	629	37.66
B	276	31.13	735	36.8
C	257	33.81	663	35.19
D	230	31.30	654	34.24
E	226	36.35	585	33.07
F	174	24.58	275	34.37
G	290	29.54	588	29.72
H	355	26.12	651	31.83
I	171	14.57	227	24.13
PNW				
A	166	31.46	700	40.17
B	196	34.95	678	37.98
C	266	32.73	656	37.16
D	274	34.04	753	35.43
E	229	42.14	496	40.46
F	203	29.90	260	31.48
G	238	36.77	419	35.30
H	217	18.72	221	21.79
I	126	16.08	127	16.06

Table 3. The number of detections, or observations, and the total number of individual birds observed across both regions and migrant seasons. Included in the totals are 1,702 birds that went unidentified to the species level. The total number of detections does not match the totals from Table 2 which only includes aural detections where distance could be determined.

DETECTIONS	ATL	PNW	TOTAL
Observations	*14,878*	*12,761*	*27,639*
Migrant	7,690	6,505	14,195
Non-Migrant	7,188	6,256	13,444
Individuals	*18,875*	*17,665*	*36,540*
Migrant	9,703	9,405	19,108
Non-Migrant	9,172	8,260	17,432

Table 4. The total number of individual birds and species identified in each survey site and the estimated species richness calculated by rarefaction curves based on 450 individuals. Only three of the 54 survey sites (shown with asterisks) were below this cut-off value for which their full data set was used to estimate species richness.

Region Survey Site	Number of individuals observed	Number of species observed	Rarefied species richness	s.d.
PNW				
CaPV-A	999	23	19.18	1.41
CaPV-B	717	25	23.04	1.04
CaPV-C	609	27	25.63	1.01
CaPV-D	621	36	33.16	1.38
CaPV-E	789	50	43.97	1.81
CaPV-F	574	57	53.89	1.52
CaPV-G	710	37	34.68	1.27
CaPV-H	750	61	53.78	2.14
CaPV-I	614	56	53.57	1.35
LiSR-A	805	22	20.13	1.16
LiSR-B	592	22	21.08	0.87
LiSR-C	681	34	30.40	1.53
LiSR-D	891	35	31.35	1.57
LiSR-E	553	40	38.60	1.06
LiSR-F	513	49	48.04	0.89
LiSR-G	388*	37	36.69	0.53
LiSR-H	705	74	68.10	1.95
LiSR-I	506	70	68.00	1.33
NiBH-A	616	21	19.59	1.03
NiBH-B	476	35	34.53	0.66
NiBH-C	416*	27	26.68	0.55
NiBH-D	542	32	31.09	0.87
NiBH-E	529	54	51.97	1.37
NiBH-F	664	60	55.37	1.82
NiBH-G	730	38	34.51	1.58
NiBH-H	548	59	56.28	1.51
NiBH-I	467	44	43.45	0.73

Table 4. Continued

Region Survey Site	Number of individuals observed	Number of species observed	Rarefied species richness	s.d.
ATL				
GuLS-A	529	41	39.95	0.97
GuLS-B	492	32	31.24	0.85
GuLS-C	534	40	38.70	1.02
GuLS-D	535	53	50.17	1.56
GuLS-E	744	63	56.43	2.11
GuLS-F	652	91	84.94	2.08
GuLS-G	658	63	56.86	2.13
GuLS-H	955	116	95.56	3.19
GuLS-I	403*	57	56.59	0.60
SiBa-A	493	32	31.47	0.69
SiBa-B	661	36	33.07	1.42
SiBa-C	606	37	34.36	1.39
SiBa-D	588	52	49.47	1.35
SiBa-E	724	66	59.63	2.02
SiBa-F	983	101	85.24	2.97
SiBa-G	544	68	64.32	1.74
SiBa-H	791	106	92.57	2.90
SiBa-I	487	82	80.51	1.13
TuGu-A	467	30	29.82	0.41
TuGu-B	901	34	30.16	1.55
TuGu-C	694	32	28.83	1.47
TuGu-D	652	38	34.64	1.59
TuGu-E	449	55	54.03	0.94
TuGu-F	451	58	57.72	0.50
TuGu-G	856	57	49.78	2.11
TuGu-H	1148	112	88.82	3.32
TuGu-I	839	114	95.64	3.20

Table 5. The nonparametric correlation scores between the environmental variables and species richness estimates for the 27 sites of each region. Habitat heterogeneity was not included in the final analyses as there was no consistent pattern of values along the urbanization gradient. Asterisks indicate highly significant correlations.

Region	Variable	by Variable	Spearman ρ	Prob>$|\rho|$
ATL	Forest	Urban	-0.8964	<.0001*
	Grass	Urban	0.1509	0.4526
	Grass	Forest	-0.3905	0.0440*
	Savanna	Urban	0.1543	0.4423
	Savanna	Forest	-0.1934	0.3337
	Savanna	Grass	0.1899	0.3428
	NDVI	Urban	-0.9151	<.0001*
	NDVI	Forest	0.8490	<.0001*
	NDVI	Grass	-0.1838	0.3589
	NDVI	Savanna	-0.1261	0.5309
	Sp.Rich	Urban	-0.9138	<.0001*
	Sp.Rich	Forest	0.8860	<.0001*
	Sp.Rich	Grass	-0.2253	0.2586
	Sp.Rich	Savanna	0.0241	0.9050
	Sp.Rich	NDVI	0.9115	<.0001*
PNW	Forest	Urban	-0.7993	<.0001*
	Grass	Urban	-0.2741	0.1666
	Grass	Forest	-0.0830	0.6805
	Savanna	Urban	0.5847	0.0014*
	Savanna	Forest	-0.7175	<.0001*
	Savanna	Grass	-0.0718	0.7218
	NDVI	Urban	-0.8350	<.0001*
	NDVI	Forest	0.8065	<.0001*
	NDVI	Grass	0.1230	0.5409
	NDVI	Savanna	-0.4226	0.0281*
	Sp.Rich	Urban	-0.9268	<.0001*
	Sp.Rich	Forest	0.7741	<.0001*
	Sp.Rich	Grass	0.2641	0.1832
	Sp.Rich	Savanna	-0.5745	0.0017*
	Sp.Rich	NDVI	0.8791	<.0001*
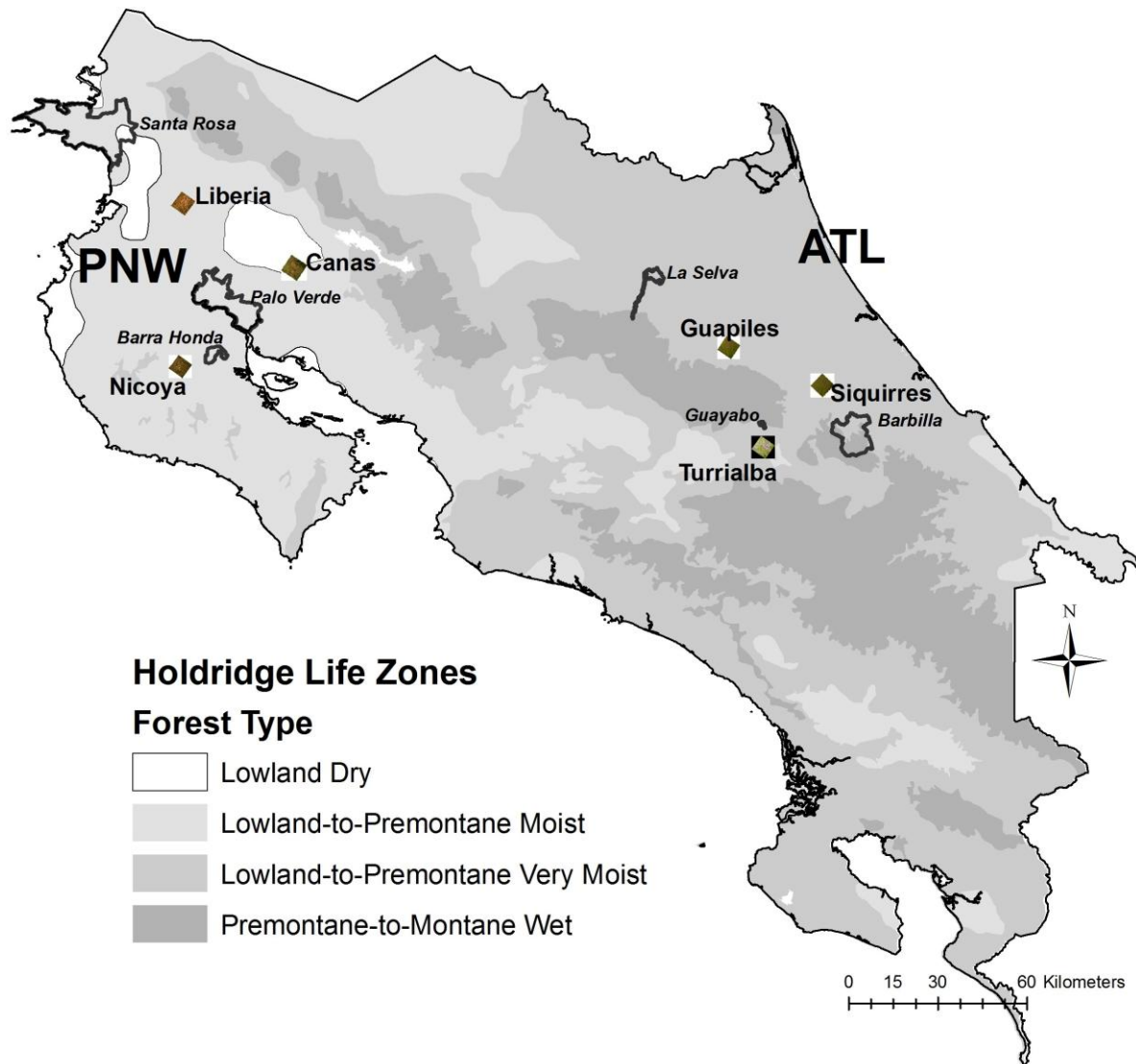
Figure 1. This map shows the two principal ecoregions in Costa Rica where I conducted my research and how they related to a condensed classification of the Holdridge life zones. The Atlantic (ATL) sites corresponded to the Isthmian Atlantic Moist-Forest ecoregion (National Geographic Society 2010) which is aseasonal and supported flora and fauna characteristic of the lowland and premontane, very moist to wet life zones. The Pacific Northwest (PNW) sites corresponded with the Central American Dry-Forest ecoregion (National Geographic Society 2010) which experienced a 4-6 month dry season; thereby supporting a distinct biological community better adapted to the lowland and premontane, dry to moist life zones. In each ecoregion I conducted avian surveys along three urban development gradients which extended from the core of a city into the interior forest of a nearby national park or reserve. ATL gradients were: Guapiles-La Selva (GuLS), Siquirres-Barbilla (SiBa), and Turrialba-Guayabo (TuGu). PNW gradients were: Liberia-Santa Rosa (LiSR), Canas-Palo Verde (CaPV), Nicoya-Barra Honda (NiBH). The PNW ecoregion covered a geographic extent of approximately 3,050 km^2 whereas the ATL ecoregion covered approximately only 1,800 km^2.
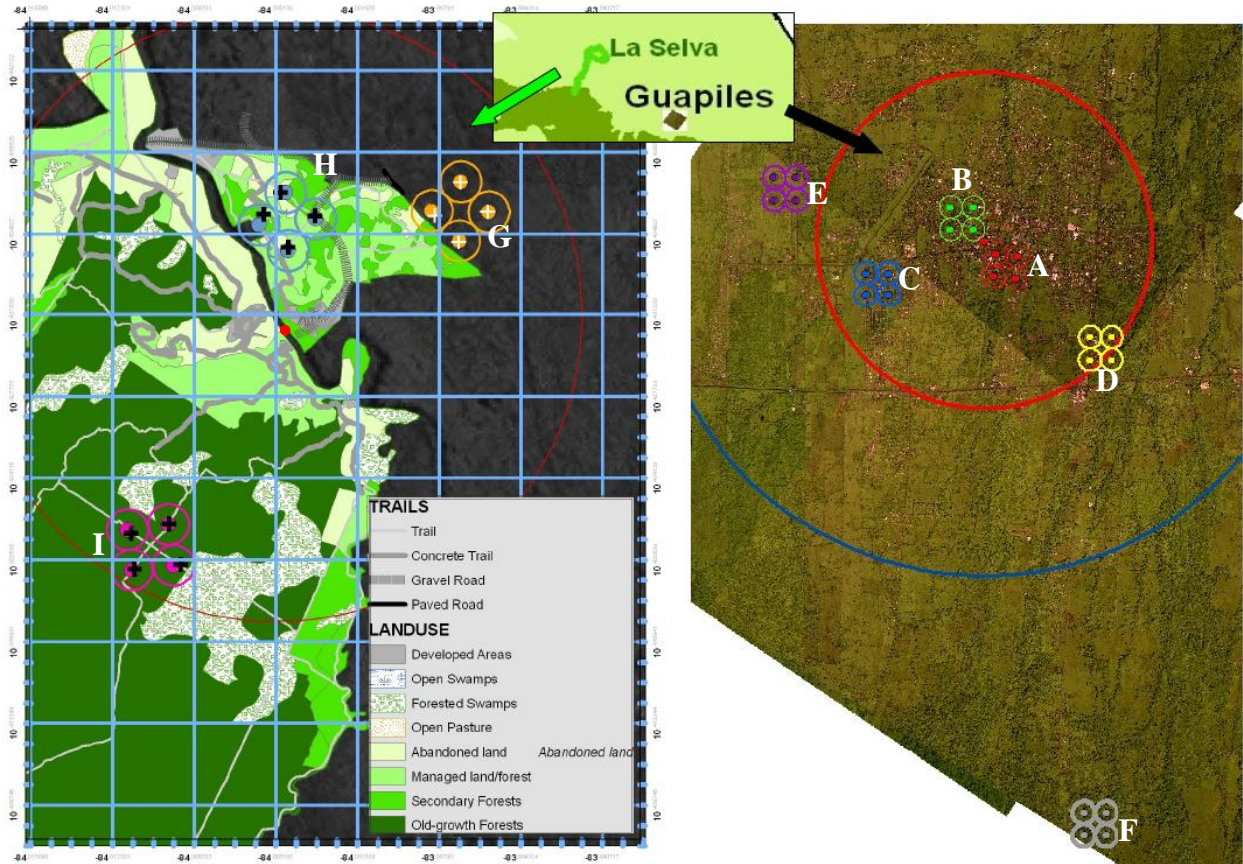
51

Figure 2. This series of images shows the nine sites along the Guapiles-La Selva (GuLS) urban development gradient. Letters correspond to specific sites and different levels of urban development (see Methods for details) along the gradient. For scale, the large red circles refer to a 1.5 km buffer extending from the city core and the park station. The blue circle is a 3 km buffer. Light blue grid lines show a 400 m by 400 m grid overlay (i.e., the size of each survey site). Each randomly selected survey site is divided into four, sub-sample sites with 100 m buffers.

Figure 3. This figure shows photos of the nine quadrats, or survey sites, from the Canas–Palo Verde (CaPV) urban development gradient. Moving left-to-right, then top-to-bottom the sites decreased in their respective levels of urban development, or anthropogenic disturbance. Letters correspond to the development classifications outlined in the text.
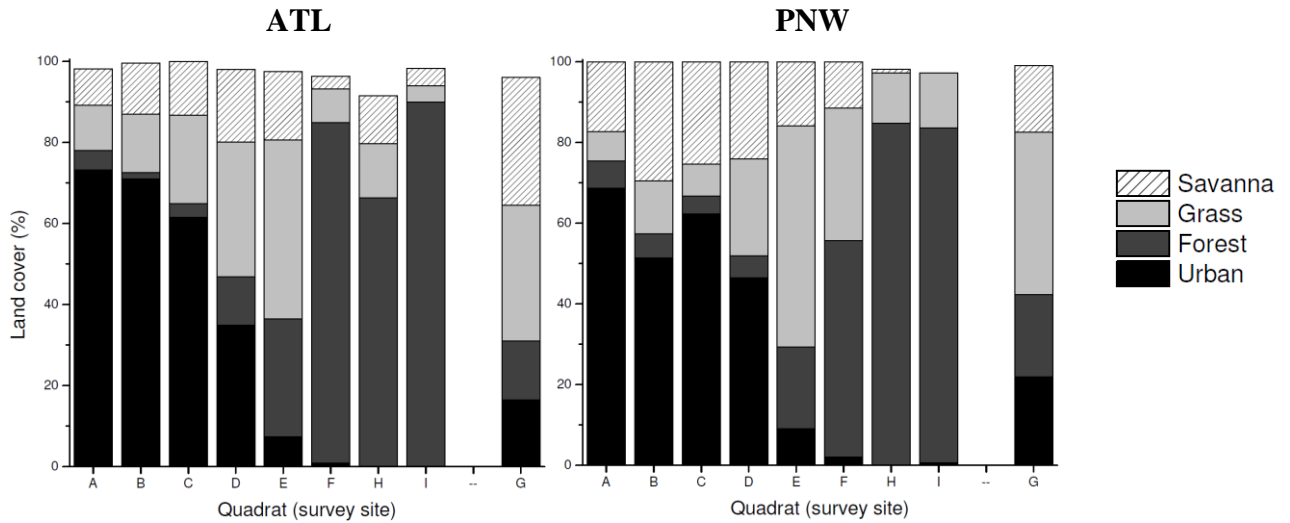
Figure 4. Bar charts showing the average percent of the four, main land cover types for each level of urban development in the ATL and PNW ecoregions. The letters along the x axis refer to nine sites or different development levels along each gradient (see Methods for details). The more urban sites are towards the left of each graph and the more forested sites are towards the right. The rural settlement sites (G) are set apart in each graph as they represent a break in the development gradient. These rural settlement sites are more similar in land cover characteristics to sites associated with the city (intermediate between sites D and E), than they are to the geographically closer sites of the national park or reserve (H and I).
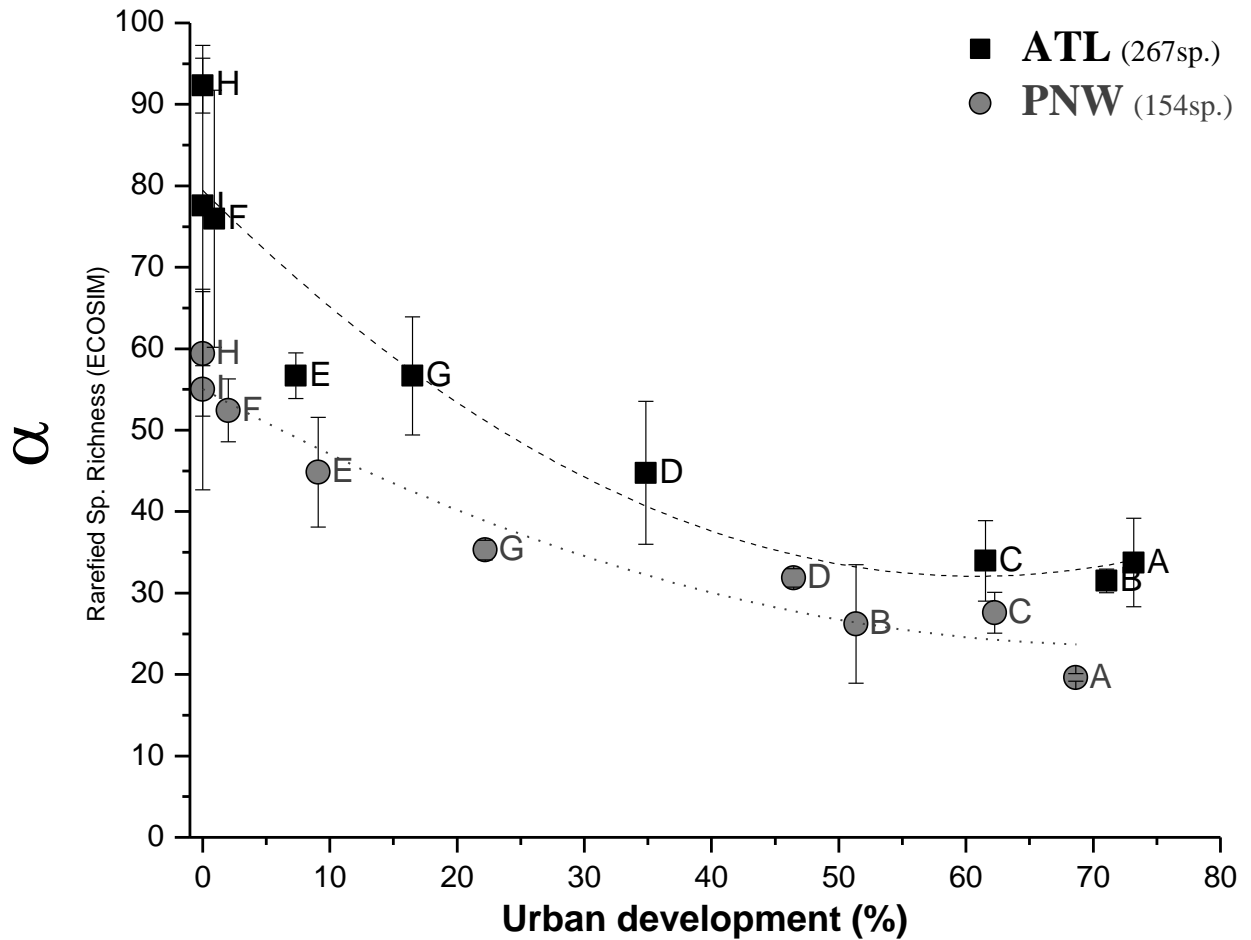
Figure 5. Patterns of avian species richness across the gradient of urban development in two distinct ecoregions of Costa Rica (ATL: $\alpha = 79.46 - 1.56(\text{Urban}) + 0.013(\text{Urban})^2$, n = 9, Adj. $R^2 = 0.88$, $P = 0.0006$; PNW: $\alpha = 55.07 - 0.86(\text{Urban}) + 0.006(\text{Urban})^2$, n = 9, Adj. $R^2 = 0.93$, $P < 0.0001$). Letters correspond to the development classifications outlined in the Methods. Points represent the mean estimated species richness based on rarefaction analysis for each level of urban development across the three replicates within each region (error bars represent the standard deviation). Polynomial lines of best fit (ATL = dashed line, PNW = dotted) were generated with Origin Pro 8.1 (2010). The residuals for both species richness and urban development fit a normal distribution.
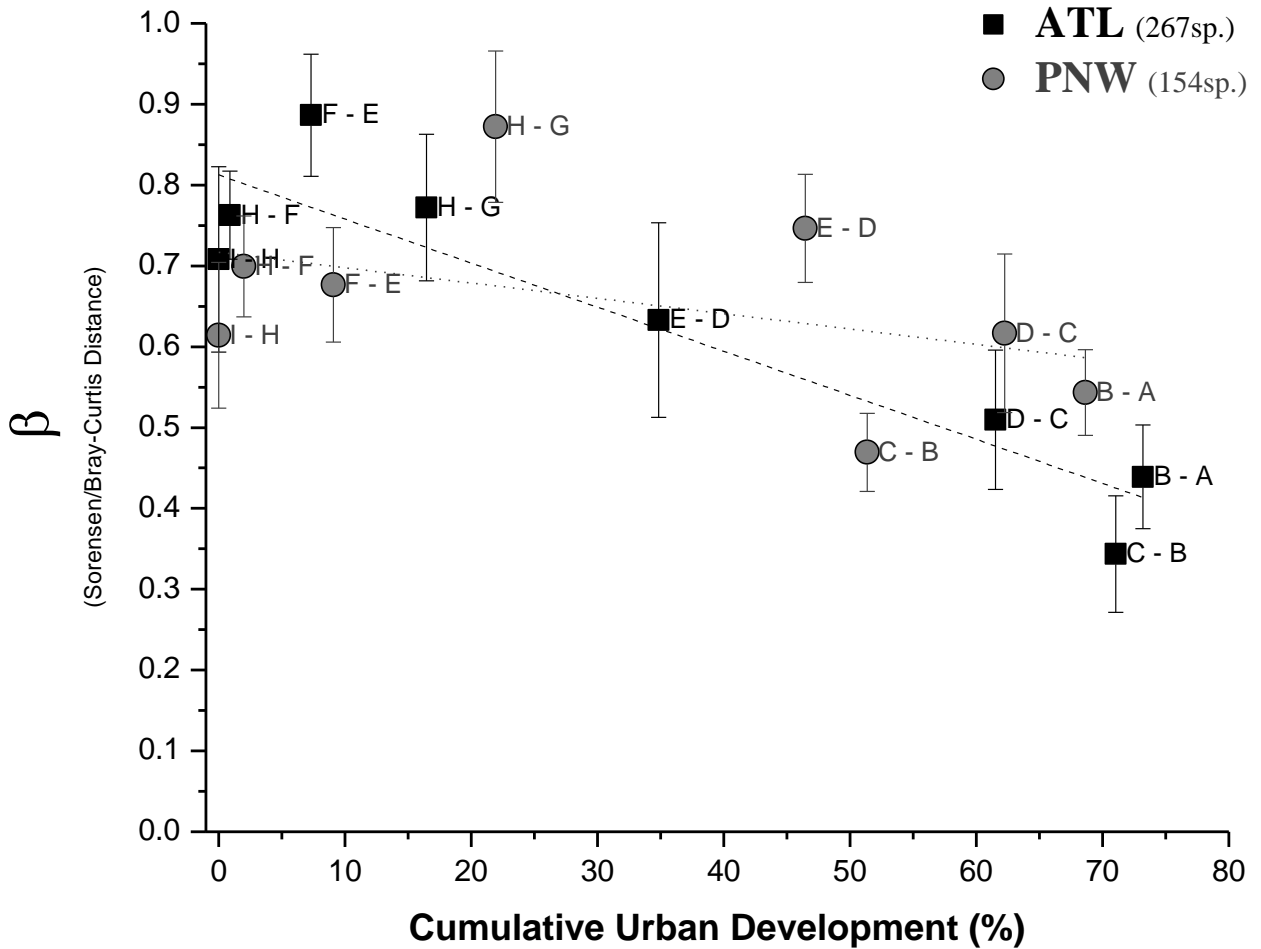
Figure 6. Changes in β diversity in two distinct ecoregions of Costa Rica along a generalized

disturbance gradient from the interior, mature forest of a national park to the urban core of a city

(ATL: $\beta = 0.81 - 0.005$(Urban), Adj. $R^2 = 0.82$, $P = 0.001$; PNW: $\beta = 0.71 - 0.002$(Urban), Adj. R^2

$= 0.043$, $P = 0.295$). Letters correspond to the development classifications outlined in the Methods

and the graphed values represent the average β scores and the average cumulative percentage of

urban land cover at each consecutive level of development from the three stepwise comparisons

within each region. The error bars represent the standard deviation. Note that two different

developmental steps are shown from the secondary/edge forest of the national park (i.e., H) to: i) a

nearby rural settlement or village (i.e., G), or ii) a forest fragment (i.e., F). Graphs and lines of best

fit (ATL = dashed line, PNW = dotted) were generated with Origin Pro 8.1 (2010). The residuals

for both beta diversity and urban development fit a normal distribution.   56
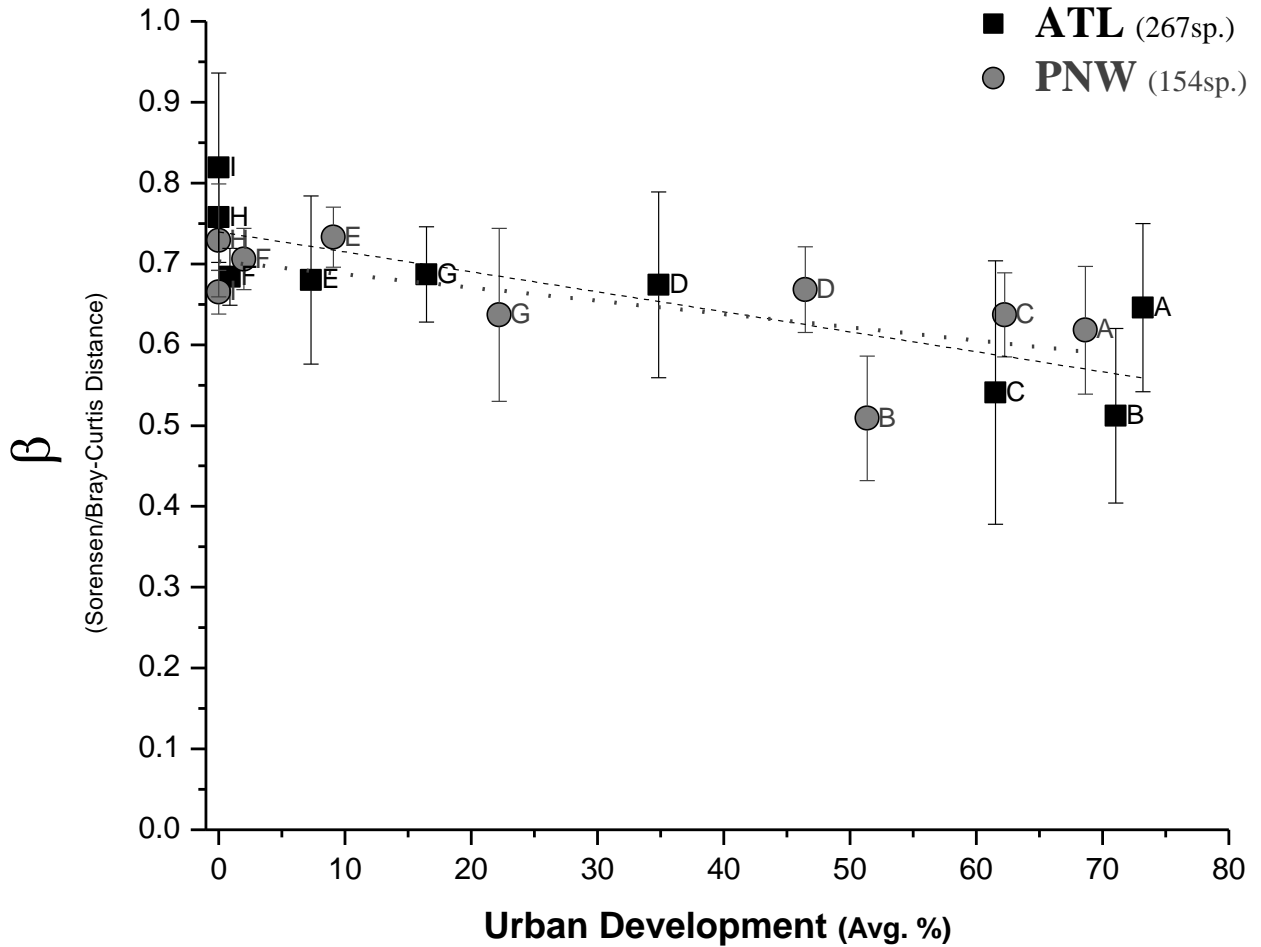
Figure 7. Another scatterplot showing how β diversity in two distinct ecoregions of Costa Rica changed along an urban disturbance gradient from the interior, mature forest of a national park into the urban core of a city (ATL: β = 0.74 − 0.002(Urban), Adj. R^2 = 0.62, P = 0.007; PNW: β = 0.70 − 0.002(Urban), Adj. R^2 = 0.37, P = 0.05). Letters correspond to the development classifications outlined in the Methods and the graphed values represent the average pairwise β scores among the three replicate sites within each region (i.e., A-A, B-B, C-C, etc.). The error bars show the standard deviation. Graphs and lines of best fit (ATL = dashed line, PNW = dotted) were generated with Origin Pro 8.1 (2010). The residuals for both beta diversity and urban development fit a normal distribution.

The non-random disassembly of avian assemblages along urban

development gradients in Costa Rica

INTRODUCTION

The prominent ecologist Eugene Odum (1969) admitted "concrete may be a good thing, but not if half of the world is covered with it." Although the percent of the earth's surface covered with anthropogenic structures is actually closer to 6% (Alberti et al. 2003), over 50% of the global population now lives in urban centers (UNDESA 2009). Yet, the concern expressed by Odum (1969) is more relevant now since rates of urbanization continue to rise, especially in developing countries of the tropics that harbor the majority of the earth's terrestrial species (UNDESA 2009). Knowing that urbanization and other anthropogenic land uses are primary causes to species endangerment (Czech et al. 2001), and that urban areas can harbor a relatively large proportion of native fauna (Alberti and Marzluff 2004); it has become increasingly important to integrate urban systems with ecological theory (McDonnell and Pickett 1990, Collins et al. 2000, Alberti et al. 2003) and to adopt urban areas into the conservation framework (McKinney 2002, Miller and Hobbs 2002).

Whether or not communities are assembled at random or by some deterministic set of rules is one of the fundamental questions in ecology (Morin 1999, Feeley 2003). Similar environments may drive biotic communities to converge upon similar combinations and abundances of species due to deterministic environmental filters, or the

representative communities may differ due to different historical or regional assembly

processes (Chase 2003, Ricklefs 2004). Chase (2003) pointed out that within a given

region both empirical and theoretical support exists for environmental filters leading to

convergence on a single stable equilibrium; or multiple histories driving multiple local

communities. Therefore, emphasis should focus on what are the conditions in which we

expect multiple stable equilibria or convergence upon a single, deterministic community

within a given region (Chase 2003). Knowing to what degree local assemblages (i.e.,

taxonomic subsets of a community, Fauth et al. 1996) within particular regions are

influenced by a deterministic environment or historical processes will have important

consequences for land management decisions and conservation or restoration actions

(Miller and Hobs 2002, Chase 2003). With reference to urban development, will

reforesting green areas in cities increase the number of species that can maintain stable

populations within city limits, or does urban development in cities need to be directed or

regulated to limit the negative effects on populations of native species?

For these reasons, my primary goals for this chapter are to describe the

nonrandom *disassembly* patterns of local avian assemblages along multiple urban

development gradients in two distinct ecoregions of Costa Rica and how they relate to the

characteristics of the urban environment. In Costa Rican urban environments it may be

better to approach these questions from a perspective of disassembly (i.e., the nonrandom

process of progressive species declines and losses, Zavaleta et al. 2009) as opposed to

assembly *per se*. The difference between assembly of the urban avifauna or the

disassembly of forest avifauna may be subtle, one of definition, but in this present study

increasing levels of urban development were strongly and negatively correlated with

levels of forest or tree coverage (Table 5 of Ch.1, Figure 4 of the present chapter).

Furthermore, the landscape in which Costa Rica's avifauna has evolved has been

dominated by forests for the past 3-5 million years (Stiles and Skutch 1989) with most of

the anthropogenic change coming over the past 60-70 years (Joyce 2006). The principal

question is still one of which species are found in which sites and how this changes along

an urban disturbance gradient, but with a focus on which species are filtered out as urban

infrastructure replaces the natural habitat.

Many studies in the growing literature of avian responses to urban development

have come from temperate regions (Marzluff et al. 2001, Chace and Walsh 2006), are

based on incomplete development gradients (Marzluff 2001), follow varied

methodologies (Clergeau et al. 2006, Ortega-Álvarez and MacGregor-Fors 2011), fail to

include measured attributes of the environment (Marzluff et al. 2001) or focus primarily

on diversity and richness measures or simple species lists (Marzluff 2001, Ortega-

Álvarez and MacGregor-Fors 2011). Since relatively few studies have examined the

response of species composition and abundance as urban development progresses (Chace

and Walsh 2006, González-Urrutia 2009), the ultimate goals are to generate greater

knowledge of the influential environmental factors and requirements for maintaining

healthy avian populations in urban environments (Germaine et al. 1998, Marzluff et al.

2001), determine to what degree urban development acts as an environmental filter

(Croci et al. 2008), and whether or not the patterns can be generalized across multiple

development gradients in different ecological regions (Chase 2003). Using a well-studied

group like birds (McDonnell and Hahs 2008), my hope is to respond to the urgent need of

information regarding the impacts of urbanization processes for the species-rich tropics

(Reynaud and Thioulouse 2000, Marzluff et al. 2001, Chace and Walsh 2006) and

establish mechanistic predictions (Shochat et al. 2006) or a hierarchical framework (i.e.,

habitat-landscape-region, Clergeau et al. 2006) for future research.

METHODS

The study area, site selection, avian surveys, and quantification of land cover or

environmental variables are the same as those presented in Chapter 1 (Figs. 1-4). The

only differences here are the questions asked, and how I manipulated the data collected to

answer those questions.

I first ran a Nonmetric Multidimensional Scaling ordination (NMS) to

graphically view the ordination of my 54 survey sites in relation to avian species

composition without grouping or constraining the data. This gave me a view of the

biological reality of the system (McCune and Grace 2002), and allowed me to determine

at what level to conduct further analyses. I started with the full, site-by-species matrix

(i.e., 54 sites by 328 species) which contained the number of times each species was

observed in each site throughout the study. I removed species (n = 60) from this matrix

that were only observed once or twice throughout the entire study period (Soh et al.

2006). With this reduced matrix of 268 species I relativized the number of observations

of all species by the total number of observations of each species across all 54 sites

following the general relativization method in PC-ORD 5.32 (McCune and Mefford

2006). This procedure equalizes the relative importance of each species such that

common species do not have a disproportionate effect on the multivariate analysis and

reduces the effect of total quantities to relative or proportional quantities (McCune and

Grace 2002). Using the relativized matrix I ran the NMS autopilot in PC-ORD 5.32

(McCune and Mefford 2006) on "slow and thorough" mode for 500 iterations (250 runs

with real data, and 250 runs with the data randomized). I used the Sorensen/Bray-Curtis

distance measure for the NMS solution as it allows for proportional abundances of

species instead of just presence-absence, and because it is known to perform well with

ecological data (McCune and Grace 2002).

Nestedness

If species among different sites formed nested subsets, then this would imply a

nonrandom pattern of species distributions (Blake 1991) and support the hypothesis that

the avian assemblages are more strongly influenced by the differential loss (i.e.,

disassembly) or extinction of particular species (Feeley 2003). Therefore, I started this

analysis with the full, site-by-species matrix which contained the number of times each

species was observed in each site throughout the study. In both ecoregions there were

three, complete urbanization gradients with nine sites in each that ran from the mature,

interior forest of a large national park or reserve into the urban core of a nearby city. The

full site-by-species matrix contained 54 sites and a total of 328 species and accounted for

a total of 27,639 observations. Based on the results of the NMS I divided the matrix into

two, one for each ecoregion. Each ecoregion contained 27 sites spread along three

gradients, but varied in the number of species each contained (i.e., 267 sp. ATL and 154

sp. PNW).

I removed species from each regional matrix that were only observed once or

twice throughout the entire study period (Soh et al. 2006). Removing these rarely

observed species (n = 60 ATL, n = 30 PNW) removes the noise from the data set and

reduces its size without losing much of the patterns and relationships contained within (McCune and Grace 2002). I uploaded both matrices separately into PC-ORD 5.32 (McCune and Mefford 2006), transformed both matrices to presence-absence matrices (i.e., 1's and 0's), and ran the NESTEDNESS option within the program with 9999 randomization runs. I also exported the presence-absence matrices as text files and used these in Atmar and Patterson's (1995) Nestedness Temperature Calculator for added graphical information.

Convergence of local, urban avian assemblages within and across distinct ecoregions

Although the NMS, to some degree, can graphically show convergence of avian assemblages by placing those sites with similar species composition and abundances closer together, it provides no test of significant overlap or difference of avian assemblages among *a priori* groups. Therefore, I ran Multi-response Permutation Procedures (MRPP) to determine where significant differences in avian assemblages lie along the development gradients. I used the same generally relativized, site-by-species matrix of 54 sites and 268 species from the previous NMS analysis. For the MRPP I divided the 54 sites into 18 groups with three sites each in a second matrix; nine of the groups corresponding with the nine development levels for the ATL region, and the other nine groups representing the same for PNW. I used the same Sorensen/Bray-Curtis distance measure used in the NMS for the MRPP as suggested by McCune and Grace (2002), and the default weighting suggested by PC-ORD for MRPP to run all pairwise comparisons among the groups. I ran these procedures using PC-ORD 5.32 (McCune and Mefford 2006).

Utilizing the nested design of my sampling procedure I then used PC-ORD 5.32 to run a PerMANOVA analysis on the same site-by-species and grouping matrices used for the MRPP and NMS analysis. PerMANOVA is a nonparametric, permutation based multivariate ANOVA that addresses many of the same questions as MRPP, but allows for more complex designs and partitions the variation among the different levels (McCune and Mefford 2006). I ran multiple tests examining the differences in species combinations and relative abundance between different nested levels like region, gradient, and survey site.

Correlation of avian assemblages with environmental factors

With biotic homogenization known to occur among avian assemblages as urban development increases (Chapter 1: Figs. 6 and 7, McKinney 2002 and 2006, Blair 2004), I questioned if environmental similarity among the sites could explain the similarity among the avian assemblages. For a better indicator of the relationship between the local environmental characteristics and the avian assemblages of each site I ran three different Mantel tests. With the first test I used the same matrix used for the NMS and MRPP analyses containing the 268 species observed three or more times throughout the study and all 54 survey sites. The other two Mantel tests were run with matrices specific to each region, both with 27 survey sites each, but varying in the number of species in each that were observed three or more times within each region (ATL = 207 sp., PNW = 124 sp.). All three species matrices were run against matrices containing the five environmental characteristics (e.g., % cover of urban, forest, grass, savanna, and average NDVI [Normalized Difference Vegetation Index], Appendix I) remotely sensed for each survey site (i.e., 54 sites for the full study and 27 sites for each regional test). For

comparing matrices of avian species and environmental characteristics matrices I used

the Sorensen/Bray-Curtis distance measure to calculate pairwise distances among all

sites. This created a scale of dissimilarity between 0 and 1, with a score of zero

indicating avian assemblages with identical species composition and in the same

proportions, or sites with identical environmental characteristics. I ran the Mantel test on

the Sorensen/Bray-Curtis distance matrices using PC-ORD 5.32 (McCune and Mefford

2006).

I also ran an MRPP test with the full site-by-environment matrix (i.e., 54 sites) to

determine whether or not there are specific differences in the environmental

characteristics across the *a priori* groups and where these divisions lie. Again, I divided

the 54 site into 18 groups with three replicate sites each in a second matrix (i.e., with 9 of

the groups corresponding to the nine development levels for the ATL ecoregion and the

other nine groups representing the same for the PNW). I used the Sorensen/Bray-Curtis

distance measure and the default weighting suggested by McCune and Mefford (2006) to

run all pairwise comparisons among groups. For a graphic representation of the

environmental similarity I generated a NMS ordination using the same site-by-

environment matrix with five variables. As above I used the same Sorensen/Bray-Curtis

distance measure and the slow and thorough autopilot setting of PC-ORD 5.32. In order

to show a composite view of how avian assemblages of the survey sites relate to the

environmental characteristics, I returned to the NMS shown in Figure 5 but added the full

54 site-by-environment matrix as a second matrix in PC-ORD 5.32 and overlaid the

environmental variables on the sites in species space ordination using an R^2 cutoff value

of 0.50.

RESULTS

The initial NMS showing how all 54 survey sites orient to each other in relationship to their avian assemblages is shown in Figure 5. There is no overlap between any of the 27 sites of ATL and the 27 sites of PNW. Axis 2 shows a strong separation of the regional sites with ATL sites positively oriented (i.e., towards the top), whereas PNW sites are negatively oriented (i.e., towards the bottom) of the second axis. The first axis shows a good separation of the sites based on their different levels of anthropogenic or urban development. The most urban or developed sites are negatively oriented towards the left, whereas the forested sites are positively oriented towards the right. The distribution of the sites in species space graphically mimics the biological similarities of the avian assemblages in nature. Therefore the assemblages of the urban cores (A) from the Cañas-Palo Verde (CaPV) and Nicoya-Barra Honda (NiBH) gradients were much more similar in species composition and abundance than any other forested site (F, H, and I) of any PNW or ATL gradient. Although in different ecoregions, the urban core site of the Turrialba-Guayabo gradient (TuGu-A) is graphically closer to NiBH-A and CaPV-A than it is to any of the forested sites across different gradients or ecoregions. Therefore, its urban avian assemblage was more similar to urban sites in the other ecoregion than forested sites of its own ecoregion. Furthermore, sites do not separate or group by gradient within each ecoregion. This mixing among gradients within each ecoregion suggests that individual cities and gradients did not undergo different development processes; or more specifically that the processes of urban development in each ecoregion had similar effects on avian assemblages across different cities or gradients.

Nestedness

In both ATL and PNW ecoregions, species are more significantly nested within sites than expected by chance (Fig. 6, ATL: Nestedness = -4.93; PNW: Nestedness = -3.96). With PC-ORD 5.32 negative nestedness values indicate that the species were more strongly nested than expected by chance from the randomization runs. Based on the presence-absence of species, the most urban sites (A-C), in both ecoregions, were nested within (below) the low density urban and rural sites (D, E, and G), which were nested within (below) most of the forested sites (I, H, and F). The forested sites occupy the top spots of Figure 6 indicating they contained the most species, and that the most urban sites (A-C) are nearest the bottom because they contained the fewest species. Table 1 shows the top 25 species as ranked by the NESTEDNESS output in PC-ORD 5.32 for both ecoregions. Graphically these species represent the first 25 columns of Figure 6. Given their presence among a large proportion of the available 27 sites in each ecoregion, these species are considered to have the broadest niche requirements and are the least likely to become extinct and the most likely to colonize other sites (Atmar and Patterson 1995).

Convergence of local, urban avian assemblages within and across distinct ecoregions

Overall, the MRPP demonstrated that avian assemblages could be divided into distinct groups with respect to the level of urban development. The species composition and abundance *within* the 18 *a priori* groups (i.e., quads A-I for both ecoregions) were significantly more similar than *between* them ($T = -13.49$, $A = 0.24$, $P = 0.0001$). The *T* score is the test statistic that refers to the separation between the groups, and the more negative a score is, the stronger the separation (McCune and Grace 2002). The *A* statistic describes the within-group homogeneity in relation to the random expectation, and scores

where $A > 0.3$ are considered "fairly high" with community data sets (McCune and Grace 2002). There was no significant overlap in species composition and abundance between any of the ATL and PNW assemblages (Fig. 7).

Testing the differences among the three city-to-park gradients nested within ecoregion using PerMANOVA revealed that the avian assemblages did not differ significantly between them ($F = 1.20$, df $= 4$, $R^2 = 0.022$, $P = 0.16$). Although within each ecoregion the individual cities likely had their own development history and each national park or reserve a different characteristic size, or path to creation; they did not lead to significant differences in species composition and relative abundances of their avian assemblages. This result is seen in the ordination (Fig. 5) as the different gradients within each region overlap with each other. Yet, when testing for differences between the assemblages of the urban quads (A-I) nested within each region (i.e., most similar to MRPP), there were significant differences as expected ($F = 2.61$, df $= 16$, $P = 0.0002$). In a two-way nested model, treating region and survey site as random effects, the cumulative variance explained was 49.1% ($R^2 = 0.228$ for region, and $R^2 = 0.273$ for survey site). However, since the regions in this study were not randomly assigned, the mixed-model where region was treated as a fixed effect is preferred ($R^2 = 0.349$ for survey site). Even then, nearly 35% of the variance in the avian assemblages could be explained by the level of urban development.

Correlation of avian assemblages with environmental factors.

The Mantel test comparing the distance matrices for avian assemblages and environmental characteristics across all 54 sites demonstrated there is a strong positive association between the avian assemblages and the environmental characteristics at each

site ($R = 0.57$, $t = 18.73$, $P = 0.0001$). The same pattern also holds separately for both the

ATL ($R = 0.75$, $t = 13.81$, $P = 0.00$) and PNW ($R = 0.77$, $t = 13.29$, $P = 0.00$) ecoregions.

The results of the MRPP test using environmental characteristics indicated that the survey

sites also showed greater similarity within the *a priori* development groups (i.e., level of

urban development) than across the different groups ($T = -8.48$, $A = 0.55$, $P = 0.00$).

However, unlike the MRPP with the avian assemblages, there was significant overlap

among the environmental characteristics between urban development groups across the

ATL and PNW ecoregions (Fig. 8). Only three of the five environmental variables (e.g.,

% urban, % forest, and avg. NDVI) showed R^2 correlations greater than 0.50 with the

strongest gradients of community structure (i.e., Axis 1 and Axis 2) and were included in

the composite NMS (Fig. 9).

DISCUSSION

Nestedness

Fernandez-Juricic (2002) demonstrated that avian species form nested subsets in

urban parks of Madrid. However, this smaller-scale perspective (i.e., habitat approach,

Clergeau et al. 2006) considered the built-up urban environment to be matrix, whereas I

was interested in looking at the anthropogenically built environment as useable avian

habitat (Rebele 1994, Pickett et al. 2001, Alberti et al. 2003). Urban development, even

when considered habitat on a larger scale (i.e., landscape approach, Clergeau et al. 2006)

did create nested subsets of avian assemblages across development gradients in Costa

Rica (Fig. 6). The nestedness of successively more urban sites within less developed

sites may be driven by the dominance of widespread species with high tolerance for

people (Fernandez-Juricic 2002), and further supports the theory that nestedness is more commonly found in systems structured by extinction processes (Feeley 2003). Although habitat heterogeneity (Figure 4) should detract from the pattern of nestedness (Feeley 2003), the loss of suitable forest habitat along the urban gradient is likely the mechanism driving the nestedness pattern, and consistent with the concept that urban development drives community disassembly.

However, there were plenty of "deep," conspicuous, and unexpected presences (i.e., gray squares towards the bottom, more urban sites) and absences (i.e., more white squares towards the top, more forested sites) found in the nestedness pattern (Fig. 6). These "unexpected" (Atmar and Patterson 1995) presences and absences should not be considered atypical events since the rarely observed species (i.e., $n < 3$) were already removed from the data set. The absence of a given species from the more forested sites and its presence in the urban sites makes intuitive sense if the species in question is a known inhabitant of non-forested habitat; and avian species that do well in urban environments are usually edge species or habitat generalists (Johnston 2001, Marzluff 2001). Even though the perspective taken here is the disassembly of forest avian assemblages, Stiles (1983) reminds us that we should be careful with general labels since there are many species adapted to, or associated with, the more open and dynamic habitats within or around forests (e.g., light gaps, edges). Such species are shown on Figure 6 as those whose presence is shown below the boundary of perfect nestedness (i.e., the black line) and more towards the right. For example, there are at least 18 species of resident Emberizids in Costa Rica adapted to more open grassland habitats (Garrigues and Dean 2007). Alternatively, the unexpected absence of a given species in forested

sites (i.e., the white squares above the black lines of perfect nestedness), could simply be that it was present and just not detected.

Species commonly found in forested sites, as well as urban sites, represent species that are not filtered out of the avian assemblage by urban development. Such species are often referred to as *urban adapters* (Blair 1996, McKinney 2002) since their repeated presence is an indicator of their ability to survive in the relatively novel urban environments. Most of these species are listed in Table 1 and represent the first 25 columns of the nestedness diagrams for both the ATL and PNW ecoregions (Fig. 6), and are considered to have the lowest chances of extinction and can have the broadest niche requirements (Atmar and Patterson 1995). Blair (1996) and McKinney (2002) also define *urban avoiders* (i.e., species represented by only a few gray squares near the top of Fig. 6) which were not found outside of forested habitats, and *urban exploiters* which were primarily found in non-forested habitats and whose relative abundance increased towards the more developed urban sites (i.e., species represented only by gray squares near the bottom of Figure 6, or some of those listed towards the top of the Detection lists of Table 1). Although the responses of such general groupings of species provide valuable information, they fail to describe the mechanism by which urban development acts as a filter on individual species in the community disassembly process. Therefore, deeper species-level analyses are needed to determine what are the particular traits or taxonomic relationships among species in each of these groups, or how these traits vary among assemblages along urban gradients.

Correlation of avian assemblages with environmental factors

The strong positive association between the avian and environmental matrices from the MANTEL tests indicated that in addition to the nested arrangement of avian assemblages, that their structure was also strongly correlated with the environmental conditions of the local 16 ha habitat. The amount or percentage of urban cover, or better yet the absence of trees or forest cover, were the best local predictors for the species disassembly along urbanization gradients in Costa Rica (Table 2, Fig. 9). The greater or more positive association of the average local NDVI values with the forested assemblages of ATL (Fig. 9) was not just due to the greater forest cover; but also because the hyperspectral images available to quantify NDVI levels across all study sites were taken in March of 2005, the peak of the dry season in PNW where a large proportion of the trees are deciduous and likely without leaves.

Of the few existing studies that examined the response of avian species composition and abundance to urban development, at least for the tropics most refer to patch size, or the amount of remaining natural vegetation, and the surrounding level of urban development as the principal factors influencing avian assemblages (Chapman and Reich 2007, Ortega-Álvarez and MacGregor-Fors 2009, Reynaud and Thiolouse 2000, Soh et al. 2006, Suarez-Rubio and Thomlinson 2009). These two components usually correlate strongly with the urban gradient studied, and separate the study sites in species space along the first, multivariate axis of ordination analyses, with additional axes describing the strength of the relationship between assemblages and other vegetative characteristics (Chapman and Reich 2007, Reynaud and Thiolouse 2000, Suarez-Rubio and Thomlinson 2009). Both of these patterns were also shown for Costa Rica (Fig. 9).

Although these patterns suggest the order of avian species loss along urban gradients was predictable and that assemblages converged upon a simple, stable equilibrium (Chase 2003), environmental characteristics usually only represent the abiotic background for a disassembly process which undoubtedly is also influenced by the loss of particular species (i.e., competitors or keystone species), habitat types, or geography (Zavaleta et al. 2009). Geographically, the structure of avian assemblages along urban gradients in Costa Rica was greatly influenced by region as there was no overlap of assemblages across regions (Figs. 5 and 9), despite the significant overlap in their environmental similarity (Fig. 8).

Convergence of avian assemblages within and across distinct ecoregions

Such patterns among the avian assemblages along urbanization gradients and across distinct ecoregions support the statement held by Gaston (2000), Chase (2003) and Ricklefs (2004) that both regional and local factors will interact to shape community structure. The results of the MRPP and PerMANOVA tests along with the NMS revealed that the level of urban development and the resulting loss of forest cover strongly shaped the structure of local avian assemblages, which was initially dependent upon the region in which the urban development took place. In fact, the results of the PerMANOVA demonstrated that both region and the level of urban development interacted fairly evenly to explain nearly 50% of the overall variation in the structure of avian assemblages along urban development gradients in Costa Rica.

Furthermore, I should also emphasize that despite the different development histories of individual gradients within a given ecoregion, from mature interior forests through rural and residential areas into urban cores, they all had similar avifaunas. This

discovery was important as this could easily lead to generalized management plans along urban gradients on an ecoregional scale in the Neotropics as opposed to creating many different local ones. However, it's also important to recognize that regional cities were not carbon copies of each other and may contain a couple of biologically unique features (i.e., the deep, unexpected presences and absences of Fig. 6). For example, Green Herons (*Butorides virescens*) were frequently observed in Cañas' urban core, and Black Phoebes (*Sayornis nigricans*) were reliably observed on the electrical wires near Turrialba's downtown gas station. Nonetheless, identifying that the disassembly of avian assemblages along urban gradients for Costa Rica followed general patterns embedded within each ecoregion, and yet harboring local surprises, was a big step towards developing or incorporating the urban realm into national, regional, and local conservation initiatives throughout the Neotropics.

Across regions, where evolutionary histories extend far beyond the anthropogenic development histories of the urban gradients; management and development plans will need to be tailored to each distinct ecoregion given their different species pools. Yet homogenization of urban avian assemblages also occurs across distinct ecoregions (Blair 2001, McKinney 2006), as homologous urban sites (e.g., A-C) were often closer to each other in species composition and relative abundance than they were to most forested assemblages (e.g., F, H, and I) within their own ecoregions (Figs. 5 and 9). These homogenized assemblages were driven by the wide-ranging species that not only tolerated the different climatic conditions of each ecoregion, but also demonstrated a tolerance for local environmental conditions as they became increasingly urban. Urban core assemblages (i.e., sites A) of PNW and ATL shared 13 commonly observed species

(Appendix III), of which seven species were listed among those with a greatest presence across urban gradients of both ecoregions (Table 1).

These results support those of Chapter 1 in that there were important thresholds along urban development gradients, similar across both ecoregions, which can be used as the basis for management and development plans or as testable predictions for other urban areas of the Neotropics. I found that avian species richness declined as levels of urban development increased; and that significant species losses occurred: 1) with fragmentation (i.e., sites F, under 5% urban development); 2) exurban development in rural areas (i.e., sites E and G, 5-25% urban); 3) the rural-urban transition (i.e., sites D, 26-45% urban); and 4) the residential-commercial core of the city (i.e., sites C-A, over 50% urban). Once an approximate value of 50% urban cover was reached, there was little appreciable loss of species. Similar thresholds or divisions along the gradient occur in terms of species composition and relative abundance (Figs. 5 and 7). There is distinct grouping among the forested sites (i.e., sites F, H, and I) with a clear separation between the rural sites (i.e., E and G), which are clearly separated from the residential-commercial sites associated with each city (i.e., C through A). The low density residential areas (i.e., sites D) mark an overlap in the avian assemblages of the city and the surrounding rural areas.

These patterns of species loss and changes in the composition of assemblages thereby allow us to create three distinct management areas along generalized urban gradients. In terms of conservation these three management areas are synonymous with Odum's (1969) management districts, or compartments. According to Odum (1969), the first district would be a "protective" area that includes the natural, forested sites F, H, and

I. This area would consist of the large parks and reserves as well as the forest fragments within the anthropogenic development matrix. The second district would be a "productive" area that includes the rural, undeveloped or agricultural landscape (E) and the small urban settlements (G) contained within it. The third district would represent an area of "urban-industrial" activities that include dense residential and commercial centers (i.e., sites C-A). Given the amount of overlap between the assemblages of the low-density residential areas (i.e, sites D) with both the more urban areas and rural areas, the low-density residential sites could be associated with either the urban-industrial or productive district, or better yet as Odum's (1969) multiple-use-system "compromise environment". The lack of distinct divisions between the assemblages of low-density residential sites (i.e. D) from nearby sites on the gradient (i.e., E and G) may indicate that these areas are of particular concern for management within the urban matrix. Differential management or treatment of low-density residential sites (i.e., D) may drive their assemblages to be more similar to those of more urban sites (i.e., A-C) or more rural sites (i.e., E, G).

As seen here the non-random loss of species from forest avian assemblages with increasing urbanization drives homogenization (Blair 2001, McKinney 2002, McKinney 2006) of bird communities. Whereas understanding how such communities are assembled has always been an important topic for ecology (Morin 1999, Feeley 2003), understanding the *disassembly* of communities is important for conservation and management (Zavaleta et al. 2009). However, in order to fully incorporate the anthropogenically-engineered environment into the conservation framework (Miller and Hobbs 2002), there is a great need to move beyond community level measures of

diversity and composition and take a closer look at taxonomic relationships, functional

traits and guilds to determine how they respond to a rapidly urbanizing environment (Lim

and Sodhi 2004, Croci et al. 2008).

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Table 1. This table shows the ranking of the top 25 species based on their presence and their numbers of detections or observations in both ATL and PNW ecoregions. Species names are abbreviated, with the first four letters of the both the genus and species. Full scientific and English names can be found in Appendix II. Species that are in the top 25 of each list for both ATL and PNW ecoregions are in bold type. Presence was determined by the sorting procedures in the NESTEDNESS calculations, based on which species were present in the greatest number of survey sites. Detection was determined the raw numbers of observations throughout the entire study.

	PRESENCE		DETECTION					
Rank	ATL	PNW	ATL	No.Obs.	%	PNW	No.Obs.	%
1	**MyioSimi**	AmazRuti	**QuisMexi**	666	4.79	**QuisMexi**	1881	15.45
2	**TyraMela**	MelaHoff	MyioSimi	650	4.68	ZenaAsia	1059	8.70
3	**PitaSulp**	CampRufi	**PitaSulp**	646	4.65	ColuInca	581	4.77
4	ThraPalm	ColuInca	**TyraMela**	631	4.54	**TyraMela**	575	4.72
5	AmazTzac	**DendPete**	**TurdGray**	532	3.83	CampRufi	574	4.72
6	TodiCine	**PitaSulp**	TrogAedo	520	3.74	ThryPleu	482	3.96
7	**ThraEpis**	**TurdGray**	ThraEpis	454	3.27	MelaHoff	452	3.71
8	**TurdGray**	ZenaAsia	TodiCine	411	2.96	**PitaSulp**	350	2.88
9	TrogAedo	IcteGalb	PygoCyan	348	2.50	TolmSulp	282	2.32
10	CoerFlav	**TyraMela**	SporAmer	303	2.18	CrotSulc	264	2.17
11	SporAmer	AmazAlbi	PsarMont	295	2.12	DendPete	241	1.98
12	PsarMont	CaloForm	AmazTzac	239	1.72	HyloDecu	241	1.98
13	MelaPuch	PeucRufi	ZonoCape	239	1.72	LeptVerr	237	1.95
14	ElaeFlav	**QuisMexi**	ThraPalm	232	1.67	MyiaTyra	225	1.85
15	SaltMaxi	BrotJugu	**ColuTalp**	227	1.63	CaloForm	198	1.63
16	RampPass	AratCani	HeniLeuc	216	1.55	ChirLine	198	1.63
17	SaltAtri	CrotSulc	PataCaye	214	1.54	TrogMela	177	1.45
18	PygoCyan	MyiaTyra	RampPass	211	1.52	**ColuTalp**	176	1.45
19	ContCine	EuphAffi	CoerFlav	201	1.45	AmazRuti	169	1.39
20	MyioGran	TolmSulp	PassDome	185	1.33	ColuLivi	156	1.28
21	SaltCoer	VirFlavo	ElaeFlav	176	1.27	AmazAlbi	149	1.22
22	**QuisMexi**	**MyioSimi**	VolaJaca	167	1.20	PeucRufi	144	1.18
23	EuphLute	ProgChal	SaltAtri	158	1.14	**TurdGray**	138	1.13
24	**DendPete**	**ThraEpis**	MegaPita	148	1.06	PoliAlbi	137	1.13
25	PsilMori	PiayCaya	MelaPuch	143	1.03	ProgChal	137	1.13
		% of all Observations		*59.08*				*75.77*

Table 2. The environmental variables used to characterize the 54 survey sites and their R^2 correlation scores with the NMS ordination in species space (Figure 9).

Environmental Variables	Axis 1	Axis 2
Urban	0.743	0.001
Forest	0.836	0
Grass	0.019	0.007
Savanna	0.162	0.001
NDVI	0.553	0.36
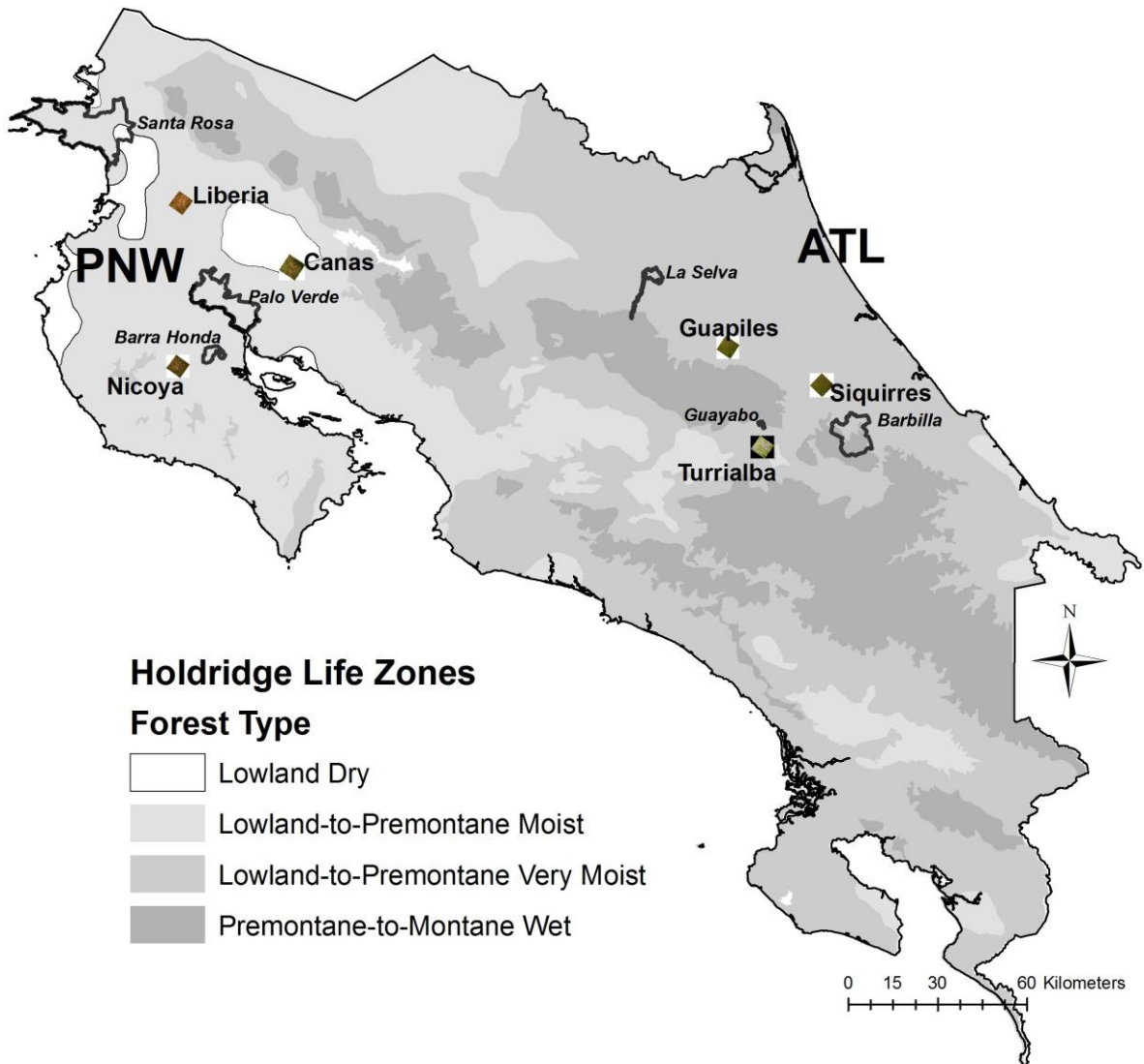
Figure 1. This map shows the two principal ecoregions in Costa Rica where research on birds was conducted. The Atlantic (ATL) sites correspond to the Isthmian Atlantic Moist-Forest ecoregion (National Geographic Society 2010) which is aseasonal and supports flora and fauna characteristic of the lowland and premontane, very moist to wet life zones. The Pacific Northwest (PNW) sites correspond with the Central American Dry-Forest ecoregion (National Geographic Society 2010) which experiences a 4-6 month dry season; thereby supporting a distinct biological community better adapted to the lowland and premontane, dry to moist life zones. In each ecoregion there are three urban development gradients which extend from the core of a city into the interior forest of a nearby national park or reserve. ATL gradients are: Guapiles-La Selva (GuLS), Siquirres-Barbilla (SiBa), and Turrialba-Guayabo (TuGu). PNW gradients are: Liberia-Santa Rosa (LiSR), Canas-Palo Verde (CaPV), Nicoya-Barra Honda (NiBH). The PNW ecoregion covers a geographic extent of approximately 3,050 km^2 whereas the ATL ecoregion covers approximately only 1,800 km^2.
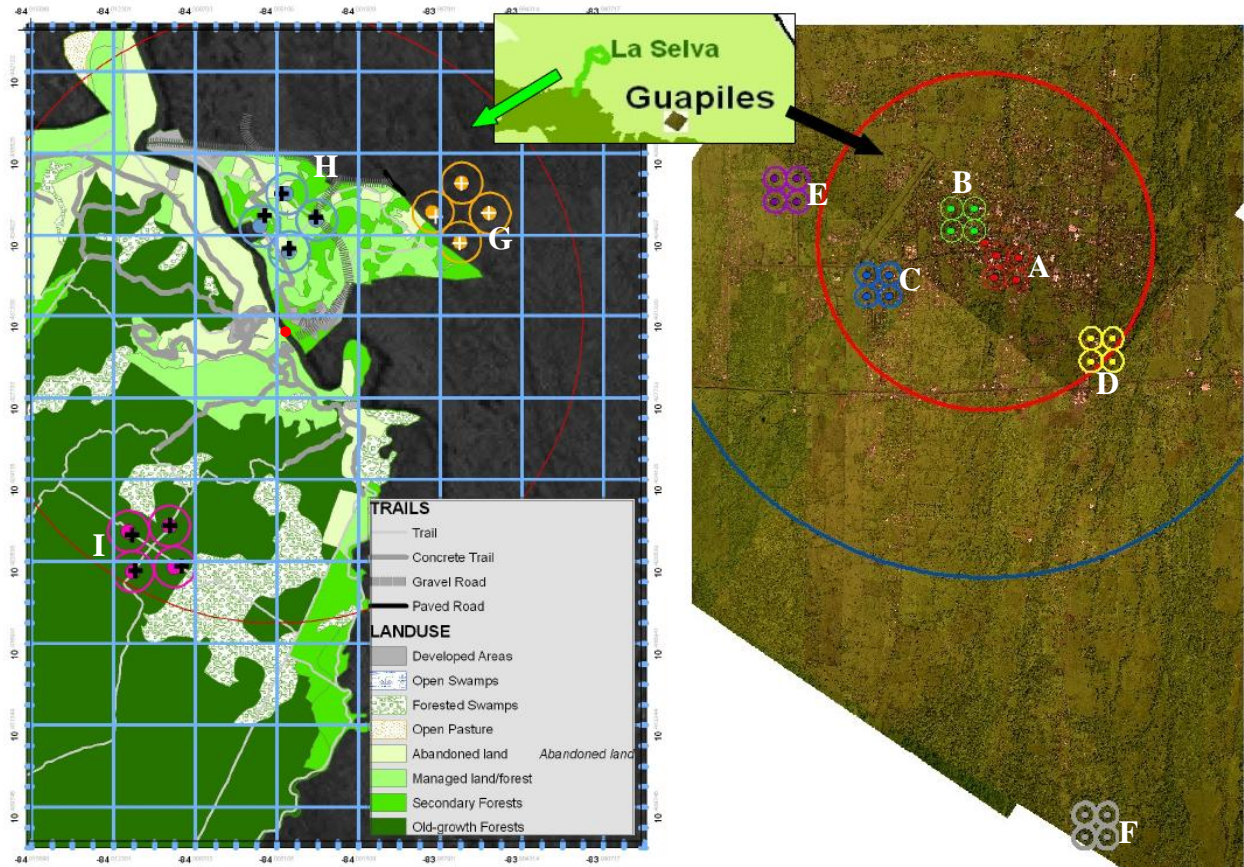
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Figure. 2. This series of images shows the nine sites along the Guapiles-La Selva (GuLS) urban development gradient. Letters correspond to specific sites and different levels of urban development (see Methods-Chapter 1 for details) along the gradient. For scale, the large red circles refer to a 1.5 km buffer extending from the city core and the park station. The blue circle is a 3 km buffer. Light blue grid lines show a 400 m by 400 m grid overlay (i.e., the size of each survey site). Each randomly selected survey site is divided into four, sub-sample sites with 100 m buffers.

Figure 3. This figure shows photos of the nine quadrats, or survey sites, from the Cañas–Palo Verde

(CaPV) urban development gradient. Moving left-to-right, then top-to-bottom the sites decrease in their

respective levels of urban development, or anthropogenic disturbance. Letters correspond to the following

development classifications and are the same for all six gradients: **A** – urban core; **B** –

commercial/residential transition; **C** – high-density residential; **D** – low-density residential; **E** – rural; **F** –

forest fragment; **G** – rural settlement; **H** – secondary/edge forest; **I** – mature/interior forest. Sites A-F of

each gradient are associated with the city and sites G-I are associated with the nearest national park or

reserve. Rural settlement sites (G) are actually a break in the gradient, but allow for landscape

comparisons between similarly developed sites near cities (D-E). See Chapter 1 Methods for more details.
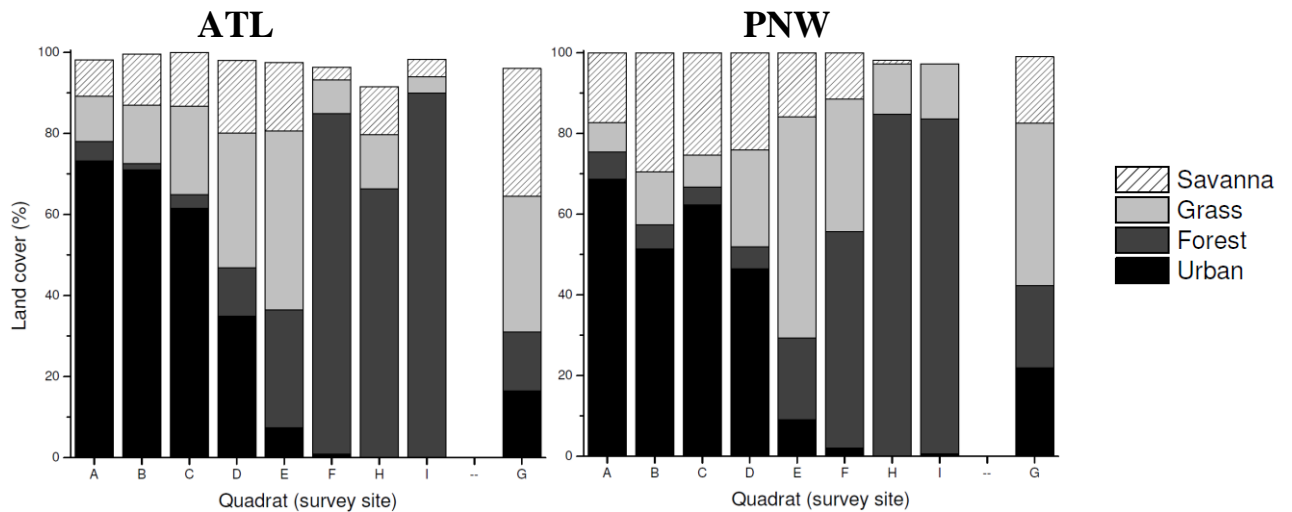
Figure 4. Bar charts showing the average percent of the four main land cover types for each level of urban development in the ATL and PNW ecoregions. The letters along the x axis refer to nine sites or different development levels along each gradient (see Figure 3). The more urban sites are towards the left of each graph and the more forested sites are towards the right. The rural settlement sites (G) are set apart in each graph as they represent a break in the development gradient. These rural settlement sites are more similar in land cover characteristics to sites associated with the city (intermediate between sites D and E), than they are to the geographically closer sites of the national park or reserve (H and I).
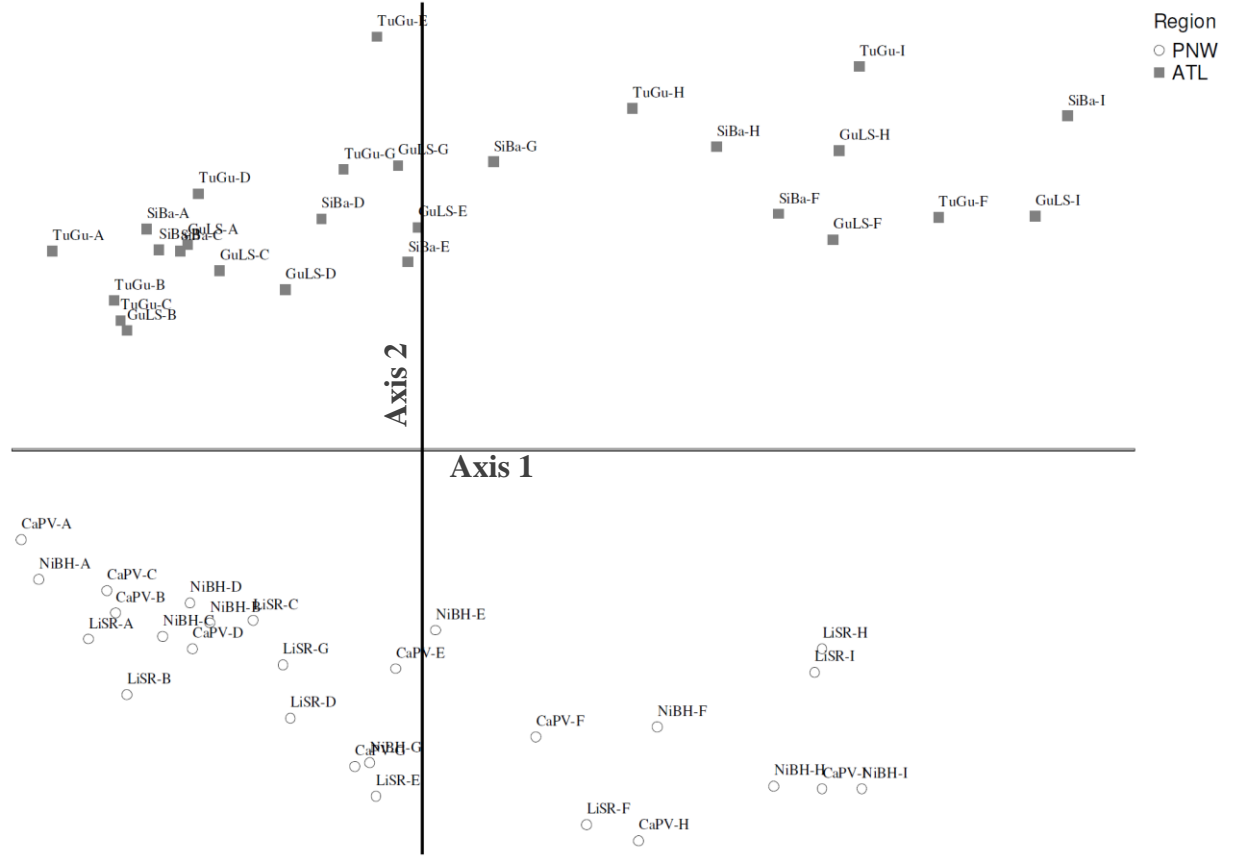
Figure 5. This NMS ordination shows how the 54 survey sites are oriented in species space. Each point in the graphical space represents a particular combination of avian species and their relative abundances. Sites close together have similar avian assemblages and the greater the distance between two sites indicates a greater difference in their assemblages. Sites are labeled by their gradients (first four letters) and their level of development (last letter). For example SiBa-I represents the mature/interior forest of the Siquirres-Barbilla gradient. This 2-dimension solution represents a good ordination, significantly different than expected by chance (Final stress = 11.13, P = 0.004) and explains a high proportion of the cumulative variance in the distribution of 268 species across 54 sites (R^2 = 0.77; Axis 1 R^2 = 0.40, Axis 2 R^2 = 0.37). This ordination was rotated -15° to facilitate interpretation and comparison with other ordinations.
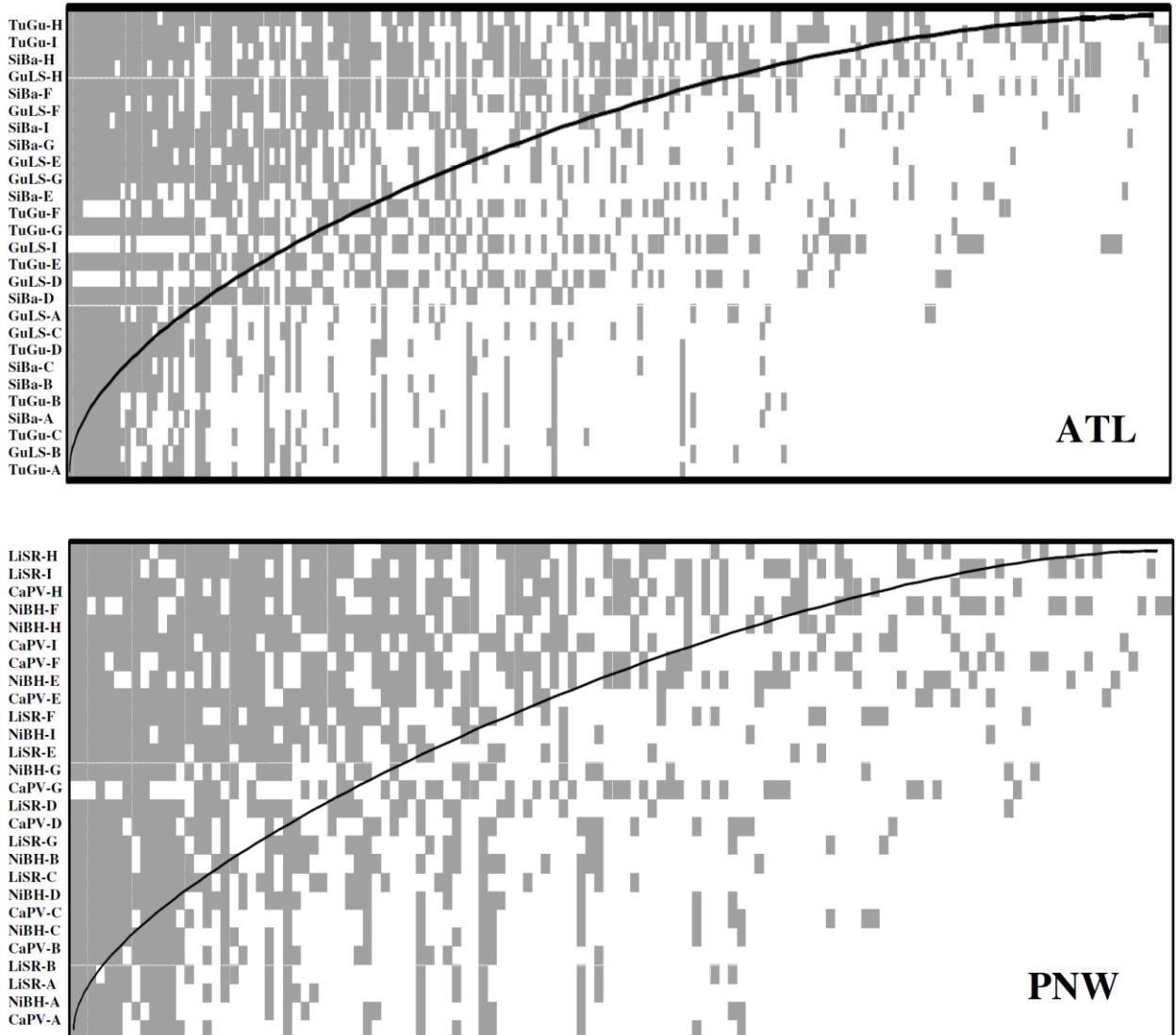
Figure 6. These two figures show the degree of nestedness among the 27 sites along the urban development gradients in the Atlantic (ATL, upper display) and Pacific Northwest (PNW, lower display) ecoregions. The graphs are composed of rows (sites) and columns (species) which have been re-shuffled to place the sites with the most species near the top, and the species found in most sites towards the left (not labeled to lack of space, but see Presence columns of Table 1). Squares that are gray indicate the presence of a particular species in a particular site and white squares mark its absence. The lines in each graph represent the boundary for perfect nestedness. The absences above the line and the presences below the line represent unexpected occurrences. Graphs were generated using Atmar and Patterson's (1995) Nestedness Temperature Calculator and also indicate that sites and species are more significantly nested than expected by chance (ATL: T (temperature) = 30.10°, $P < T = 4.13^{-75}$; PNW: $T = 31.29°$, $P < T = 8.89^{-58}$).

a. PNW   b. ATL

$$\overline{A \quad B \quad C} \quad \overline{\overline{D \quad E}} \quad \overline{G} \quad \overline{F} \quad \overline{\overline{H} \quad I}$$ $$\overline{A \quad B \quad C} \quad \overline{\overline{D \quad E}} \quad \overline{G} \quad \overline{F \quad H \quad I}$$
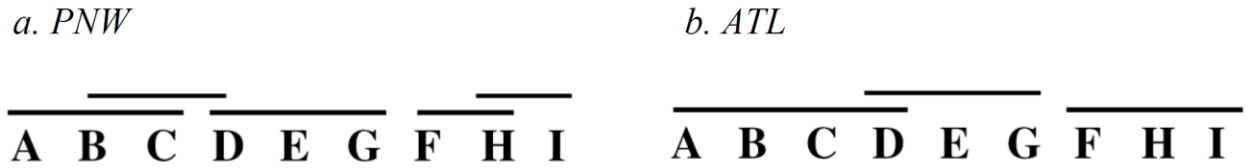
Figure 7. The letters and lines above are a graphic representation of the results of the

MRPP pairwise comparisons between each of the 18 groups. The letters represent the

different levels of urban development within each ecoregion. Solid lines over the letters

indicate which groups had avian assemblages that were similar in species composition

and relative abundance. Breaks between the solid lines, or where letters are not joined by

a single line, show where significant differences in the avian assemblages existed. There

was no significant overlap in the similarity of avian assemblages between any ATL site

and PNW site. Significance in the similarity or difference between avian assemblages

was determined using the pairwise *P*-values generated with PC-ORD 5.32 (McCune and

Mefford 2006). These values were not adjusted or corrected for multiple comparisons.

All significant differences between the assemblages of the PNW region had *P* values

between 0.021 - 0.025. All significant differences between the assemblages of the ATL

region had *P* values between 0.020 – 0.037.
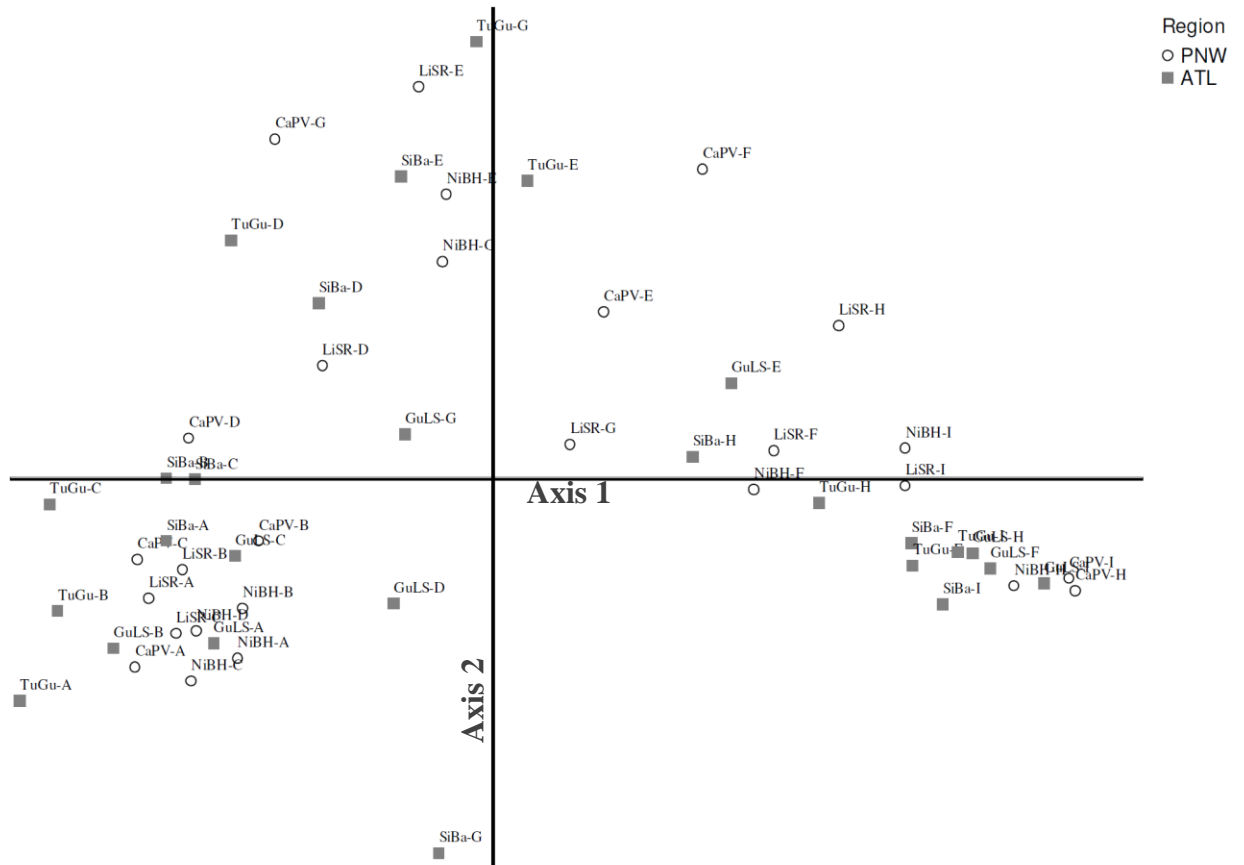
Figure 8. This NMS ordination shows each of the 54 survey sites and how they orient in environmental space. Each point on the graph represents a unique combination of the five environmental variables remotely measured with hyperspectral images (Appendix I). The most urban sites orient negatively (to the left) of Axis 1, and the most forested sites of the fragments and parks orient positively to Axis 1. There is no significant separation of the sites by region in environmental space. The final stress of the two-dimensional solution = 8.21, P = 0.004, and the cumulative variance explained R^2 = 0.96 (Axis 1 R^2 = 0.82, Axis 2 R^2 = 0.14). This ordination was rotated 90° to facilitate interpretation and comparison with other ordinations.
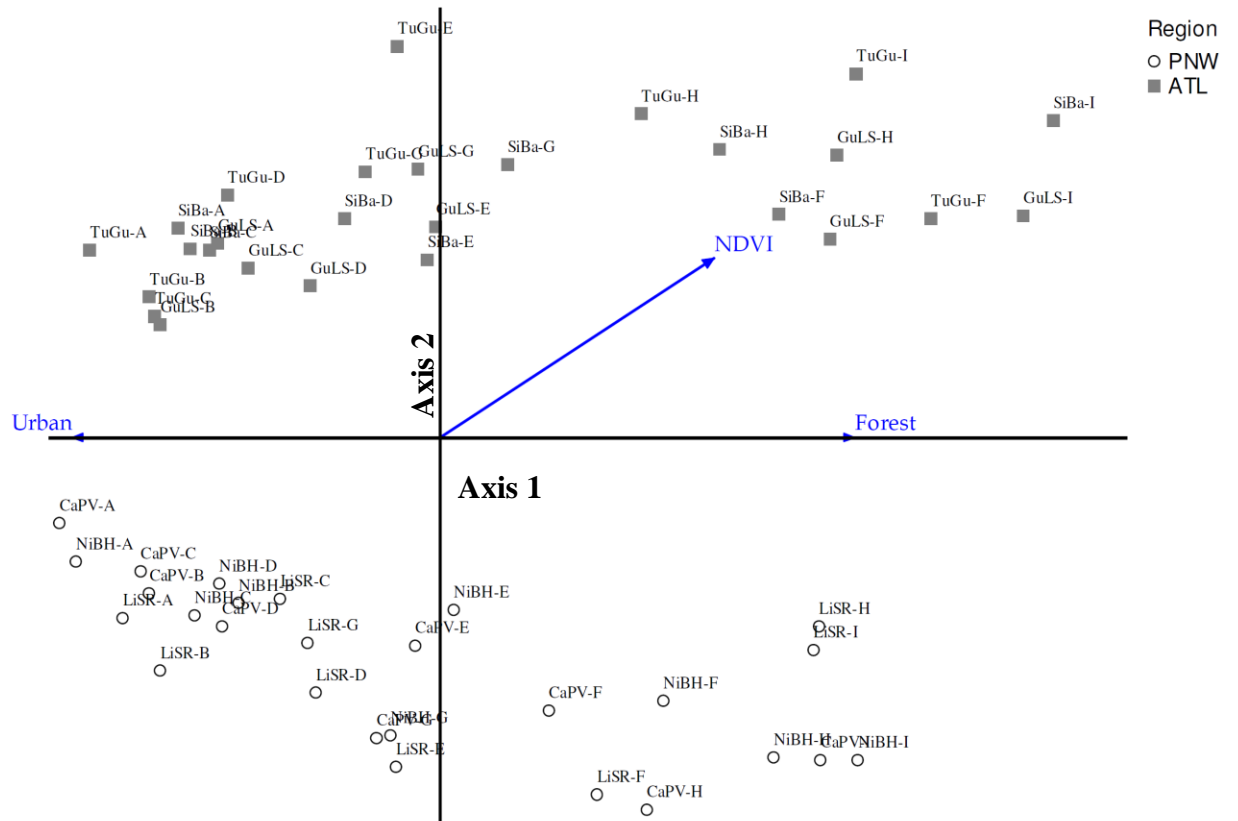
Figure 9. This NMS ordination shows the same two-dimensional solution as Figure 5; however, the environmental characteristics for all 54 sites were loaded into PC-ORD 5.32 as a second matrix and shown as vector overlays. Only those characteristics that had correlations with either axis greater than $R^2 = 0.20$ are shown here (Table 2).

CHAPTER 3

**Penguins and urbanization: challenges promoting local conservation
and environmental awareness in Costa Rica**

INTRODUCTION

Anthropogenic development has had drastic direct effects on native ecosystems (Vitousek et al. 1997), the services they provide (Costanza et al. 1997), and the species they harbor (Czech el al. 2000, McKinney 2002). Urbanization, the pinnacle of anthropogenic development (McKinney 2006), has been one of the principal drivers of environmental decline (Grimm et al. 2008). With the continued increase in the proportion of people moving to urban centers (UNDESA 2010), we can expect further decline in overall environmental health as a direct result. These problems are part of the current global discourse on sustainability, conservation, and the quality of human life for coming decades (Millennium Ecosystem Assessment 2005, Emerson 2010). Much is being discussed on how to address these problems on local and global scales and by governments, NGO's, and communities alike. However, lacking from this discourse is an explicit acknowledgement of the *indirect* effect anthropogenic development, or its ultimate manifestation (i.e. urbanization), has on nature conservation.

As a consequence of the rising proportion of the global population living in urban environments, more people, especially children, are either losing meaningful interaction with nature, or do not know what they are missing. Although these phenomena take different names in the literature, "*extinction of experience* (Pyle 2003, Miller 2005)",

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"*nature deficit disorder* (Louv 2005)", "*shifting baseline syndrome* (Pauly 1995)", and "*environmental generational amnesia* (Kahn 2007)"; in general they all refer to the increasing disconnect between humans and the natural environment. The first two concepts deal primarily with the loss of meaningful outdoor play or exploration among younger generations, whereas the last two concepts focus on different environmental perceptions among different age groups. Despite the minor differences they are conceptually similar and overlap in their negative consequences for human well-being and the conservation of natural resources. Additional studies suggest this lack of interaction and difference in perception lead to younger generations that are less knowledgeable about nature (Balmford et al. 2002, Coyle 2005, Saenz-Arroyo et al. 2005, Weigl 2009), although such claims are often seen as anecdotal or lacking empirical evidence (Kahn 2007, Papworth et al. 2009). However, since conservationists often refer to Baba Dioum's popular mantra "*In the end we will conserve only what we love; we love only what we understand; and we understand only what we are taught.*" as a central tenet of the conservation paradigm, then a decline in the knowledge and understanding of nature should be a principle concern of the conservation and sustainability discussion.

Therefore, as part of my research on urban development in Costa Rica and its impact on avian community structure, I established a survey-based outreach program to determine if 1) there is a lack of knowledge or a difference in perceptions across generations, and 2) outline the relationship of this knowledge with urban development. Costa Rica is a tropical, species-rich country well-known for its environmental awareness (Boza 1993) and, like most countries, has also witnessed a boom in its urban population

(e.g. 33% to 62%) over the past 50 years, with a predicted increase of another 17% by 2050 (UNDESA 2010). Based on the respondents' answers, I present empirical support for the *extinction of experience* and *generational amnesia* concepts, and show they may be accelerated by urban development.

METHODS

Schools

I administered paper based surveys to upper elementary students and their older relatives from six different schools in Costa Rica. The schools included in this study were close to points where I conducted my bird surveys and where administrators and teachers allowed access to their school and classrooms. Four of the schools were located in urban environments whereas the other two were rural. One urban school was in the capital city of San Jose, two were in Liberia the provincial capital of Guanacaste, and the other urban school was in the commercial center of Guapiles, Heredia. One rural school was near Santa Rosa National Park in Guanacaste and the other near La Selva Biological Station in Heredia. The schools were located in different ecological regions: the drier Pacific Northwest (*PNW* - Liberia, Santa Rosa), the wet Atlantic lowlands (*ATL* – Guapiles, La Selva), and the one school from the San Jose greater metropolitan area (*SJO*). The class size and number of sections of 5th grade (i.e. my target level) varied with each school. The urban schools had 2-3 sections of 5th grade alone, with approximately 25 students per section; whereas rural schools usually only had one section with 15 students. Despite the unevenness it created across the survey sample size, I followed the wishes of the teachers and administrators and administered the survey to all the sections

of the 5th grade in urban schools, and included the 6th grade students in the sample in the rural schools.

Surveys

I used multiple copies of the surveys where all respondents could write their answers. Each survey contained 16 questions that addressed their knowledge of local and exotic species of birds; their perceptions of urbanization; perceptions of changes to the state of the environment; and related questions on nature and urban development. All images of birds used in the survey were in full color. Many of the species used in the surveys were widely distributed in Costa Rica across multiple regions and across the urbanization gradient. However, given differences in regional avifauna and the abundance of particular species, the surveys across the different regions differed in a few of the native bird species in each survey. In some cases the regional differences were switched with congeners or with birds of the same family. The students completed the guided survey individually in school during one class period. Each survey was labeled with a unique number and the same number was placed on four additional surveys that students took home (i.e. 2 for parents, and 2 for grandparents). The same instructions the students received in class were given on an instruction sheet that accompanied each survey. I returned within one week to pick up the surveys completed by older family members. I administered the surveys between March 2008 and May 2009. Copies of the survey, in Spanish, are available through the author or are published online in the supplemental materials section.

Analysis. I removed a total of 112 surveys from the analysis because some surveys were answered by siblings, friends, or other family members (n = 68); because the age or

generation could not be determined, or if surveys were identical copies of other family members (n = 44). I only analyzed the responses from a core subset of the 16 survey questions (Box 1) as the other questions did not fit the scope of this paper.   I uncovered few significant differences in the pattern of responses across the different ecological regions (i.e. PNW, ATL, and SJO), therefore, I grouped responses by generation across all regions. For each set of questions I analyzed 1) the difference in responses among the three generations to document if younger generations exhibit a decreased knowledge about nature, and 2) to determine the potential impact of urban development. For this second analysis I only compared students from rural and urban areas as I had not collected data on where parents and grandparents spent their formative years (e.g. rural or urban areas) and in what proportion.   The sample sizes of each generation may vary among the different paired analyses as not all questions were answered by all respondents. I used JMP 8.0 (SAS 2007) for all analyses and statistical tests and OriginPro 8.1 (Origin 2010) to create all graphs.

Naming and identifying the national bird. For both naming the national bird and identifying it from a photo I ran categorical response analyses following the rater agreement protocol. This procedure generated Kappa values and Bowker's/McNemar's test and allowed me to compare results paired by unique test scores (i.e. control for family relationship, Zar 1999, SAS 2007). There were regional differences in each generation's ability to identify the national bird (e.g. Clay-colored Thrush, *Turdus grayi*, or "yigüirro" as its known in Spanish in Costa Rica). This is likely due to the fact that it is anywhere between 1-5 times more abundant in the ATL ecoregion as opposed to the PNW ecoregion (J.Norris unpub. data; no density data for SJO ecoregion). However, the

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yigüirro does have a country-wide distribution (Stiles and Skutch 1989), and in both ATL and PNW ecoregions *yigüirros* reached their highest densities between rural and moderately developed urban areas where I conducted the surveys. The patterns of correctly identifying the *yigüirro* were similar across generations and therefore regional scores were combined for the simplified analysis..

Identifying native and exotic species of birds. I scored the names given for bird species identification rather conservatively, with the exception of the national bird.   The other species were scored correct if respondents could provide the common name usually given to the bird's family (i.e. Troglodytidae = wren, or Tyrannidae = flycatcher), or if they knew the popular local names often quoted by naturalist guides or that appear in field guides like Stiles and Skutch (1989). First, I grouped the species as being either native or exotic, then further divided native species into a charismatic group (e.g. toucan, quetzal, and macaw) and a group of eight species commonly found in urban patios or schoolyards (e.g. "yigüirro", grackle, wren, sparrow, flycatcher, tanager). Pigeons (i.e. Rock Doves) and House Sparrows were dropped from these analyses given their status as naturalized exotic species. Before running the categorical analyses I calculated the average scores for each group of birds across each generation. I used contingency tables and Chi-square tests for a comparison across generations, although the nature of the composite scores prevented me from running matched analyses.

Perceptions: State of the environment.   I used the raw numerical responses for all respondents rating the state of the global environment for all three time periods. I used nonparametric Wilcoxon Signed Rank tests to analyze the numerical scores from the

respondents' perceptions of the state of the environment as the data did not meet the assumption for parametric analyses. Furthermore, I used paired analysis protocols where possible to control for the influence of family relation.

RESULTS

Data collected. All respondents completed different paper copies of the same survey, and I collected surveys from a total of 310 students, 219 parents, and 83 grandparents. The average ages of each generation were as follows: students 11.57 ± 0.91 yrs; parents 38.34 ± 6.64 yrs; and grandparents 61.59 ± 8.49 yrs. With each student survey there were 133 cases where at least one family member responded and 57 cases where 2 or more family members responded. Of the 310 students that completed surveys, 223 students were from schools in urban areas whereas 87 were from rural schools.

Naming and identifying the national bird. Nearly 93% of the students, 100% of the parents, and 99% of grandparents correctly listed the "yigüirro" (Clay-colored Thrush, *Turdus grayi*) as the national bird (Fig. 1). However, from a photo series of 11 native species only 38 % of the students correctly identified the national bird, whereas 80% or more of parents and grandparents correctly identified the same species (Fig. 1). Between students in urban and rural environments there is no difference in their ability to name the "yigüirro" as the national bird, although rural students (46%) outperformed their urban counterparts (35%) when identifying the national bird from photos of native species (Fisher's exact test, n = 310, $X^2 = 3.42$, $P = 0.044$).

Identifying native and exotic species of birds.   Within each generation, respondents

differed significantly in their ability to identify species of birds from different groups

with just two exceptions: grandparents did equally well identifying native species as they

did identifying exotic species (Kappa = 0.82, Bowker's = 2, *P* = 0.16); and students

performed equally as well identifying charismatic species as they did exotic species

(Kappa = 0.99, Bowker's = 1, *P* = 0.32) (Fig. 2). However, across generations students

scored significantly lower than older family members when identifying the same species

of birds across all groups (Table 1, Fig. 2). Like their parents and grandparents, students

did better identifying charismatic species and performed at their worst when identifying

those species common to backyards, patios, and school grounds. Across all

classifications or bird groups, both parents and grandparents correctly identified 56% or

more of the species in the survey. However, for the students their highest score (i.e.

exotic species) barely reached that same level, and their worst score (i.e. patio species)

was 25%. Of the 310 students who completed surveys, 305 identified correctly the

penguin (e.g. the highest score among all species for students).

Overall, students from rural schools did better than their urban counterparts when

identifying native (n = 310, X^2 = 2.62, *P* = 0.07), charismatic (n = 310, X^2 = 7.33, *P* =

0.005), and patio (n = 310, X^2 = 2.86, *P* = 0.063) species of birds. Urban students (57%)

scored higher than rural students (53%) when identifying exotic species of birds, but the

difference was minimal (n = 310, X^2 = 0.33, *P* = 0.32).

Perceptions: State of the environment. There were no significant differences between

parents and grandparents in their perceptions of the state of the global environment today,

50 years ago, or 50 years from now. However, students' perceptions differed

significantly from those of their older relatives across all time periods (Fig. 3). Students

rated the state of the environment 50 years ago significantly lower than both their parents

($Z = -150.50$, d.f. $= 52$, $P = 0.024$) and grandparents ($Z = -140.00$, d.f. $= 52$, $P = 0.016$);

whereas they rated the current state of the environment as being significantly higher than

their parents ($Z = 238.00$, d.f. $= 57$, $P = 0.003$). Additionally, the students also predicted

the state of the environment in 50 years to be significantly higher than what both their

parents ($Z = 461.50$, d.f. $= 52$, $P < 0.0001$) and grandparents ($Z = 371.00$, d.f. $= 52$, $P <$

0.0001) predicted. Both grandparents and parents rated the state of the environment

during this 100 yr time-span as declining rapidly. However, the students only perceived a

decline in the state of the environment over the past 50 yrs, and counter to their older

relatives they predicted the state of the environment will most likely stay the same for the

next 50 years.

Both rural and urban students shared the same perspective for the state of the

environment today and in the past. However, rural and urban students perceive the state

of the global environment in the future differently; urban students are more optimistic

and in fact, believe the state of the global environment will actually improve over the

next 50 yrs (Figure 4).

DISCUSSION

The principal concern is that future generations which are more disconnected

from and less knowledgeable about nature will be less inclined to save it (Balmford et al.

2002, Pyle 2003, Saenz-Arroyo et al. 2005, Kareiva 2008, Papworth et al. 2009). In

Costa Rica there are distinct gaps in the knowledge and perceptions of nature among

Costa Rican students and their older relatives. Grandparents and parents score higher on knowledge based questions than do their children or grandchildren, and maintain perceptions and predictions about the global environment more in-line with what is currently accepted by the scientific community than do the students.

Although these results may only mirror differences in the accumulation of life experiences as one gets older, controlling for such factors is difficult (Papworth et al. 2009) and beyond the scope of this study. However, age and life experiences may have little impact on knowledge or perceptions of nature beyond approximately 38 years of age (e.g. the average age of parents in this study) since there are no significant differences in knowledge or perceptions about nature between the parents and grandparents. This may indicate that the majority of what Costa Ricans learn about nature happens between the ages of 11 and 38, and that this level of knowledge or awareness neither increases nor decreases once this plateau is reached. Yet, to adequately control for the effects of age and life experiences, especially across such a wide range of ages, would require multiple surveys that would span at least 30 to 60 years with the same population of individuals, or surveys across multiple grades and ages. Doing so could help delineate when changes in knowledge and perception about nature occur. Comparing responses between rural and urban populations was an attempt to bypass long-term studies and control for age, with the assumption that rural inhabitants still have greater, or more meaningful interactions with nature since the rural landscape is less developed and where a greater proportion of the population is engaged in agrarian activities.

Although sample sizes among urban and rural parents and grandparents were too low for meaningful comparisons, the differences in knowledge and perceptions between similarly aged students from both rural and urban backgrounds suggest such differences are primarily driven by life experiences. Rural students in this study performed better than urban students when identifying the national bird, native bird species (e.g. both patio and charismatic), and predicted a decline in the state of the global environment in the future (i.e. average scores drop from 5.53 today to 4.88 in the future whereas urban students' average scores actually increase from 5.81 today to 6.07). Greater knowledge about nature could indicate, as assumed, that rural students still have significant interactions with nature. Age could be a factor and these results may be confounded by the fact that rural students (n = 84, avg. = 12.07 yrs) are older than urban students (n = 226, avg. = 11.39 yrs), even though the effect size is less than one year (X^2 = 33.10, p = 0.0001).

The different life experiences between rural and urban students in Costa Rica are more likely influenced by activities outside of the classroom since all Costa Ricans follow a nationalized education curriculum. In fact, most of what people in general learn about nature and science is likely to come from informal sources as opposed to academic training (Coyle 2005, Kohut et al. 2007, Groffman et al. 2010, Nature 2010). Unfortunately, some informal sources such as popular media and the internet often contain information that lack depth or includes misinformation (Holl et al. 1999, Pyle 2003, Nature 2010), which can lead to relatively high levels of awareness but with limited comprehension and frequent misunderstanding (Coyle 2005).

In the present study, Costa Ricans exhibited some skill in being able to identify a wide range of bird species, and all generations did better identifying charismatic species, both exotic and native, than they did common patio species. However, the disparity between the students' ability to identify charismatic and patio species is the most astonishing result. In just 11-12 years they have learned to identify charismatic birds found on other continents, or in distant forested habitats, twice as well as they can identify common species living in and around their homes and school (Fig. 2). Even more worrisome is their inability to identify one of those common patio species as the national bird, despite being able to name it (Fig.1). This occurs even though the nationalized upper elementary science curriculum (i.e. 4th-6th grades, Cycle-II), and the textbooks dedicated to it, include a transversal theme of "*humans as an integral part of nature*" through all three years which focuses heavily on native ecosystems and the processes and species found within (MEP 2011). Although the species chosen for the survey, and the quality of the photos used could be called into question, the lack of all generations, especially students, to identify species common to the residential areas where they live indicates an *extinction of experience* and that they are lacking meaningful interaction with nature in their daily lives.

While I did not evaluate the respondents' use of popular media or technology, or their time spent outside; their increased ability to identify charismatic species not commonly found, if not entirely absent, in the areas where they live and work reinforces the idea of informal learning. This also fits the pattern found in other studies that point out students' increasing interactions with digital screens and popular media (Louv 2005, Coyle 2009).   In Costa Rica over 90% of the households have televisions (INEC 2008)

and children between 10 and 13 years of age spend between 3.2 and 3.8 hours a day watching television (Murillo 2010), a number that increases to 6.7 hours a day in adolescents during vacation (Fournier 2000).

These significant differences in knowledge (Figs. 1 and 2) and perception (Fig. 3) between Costa Rican students and their older family members are also consistent with the phenomenon of *generational amnesia*. According to Papworth et al. (2009) *generational amnesia* only occurs when a difference in perception or knowledge is accompanied by a documented change in the biological system. Students do acknowledge an environmental decline over the past 50 years, although to a significantly lesser degree than their parents and grandparents (Fig. 3). This makes sense as students' practical experiences with nature barely extend through the past decade; a period in which they established the current state of the environment as the norm they will use for future comparisons (Kahn 2007). Yet, the fact students do register a decline in the state of the environment over the past 50 years is noteworthy, indicating some learning about past conditions either from family members, school, or popular media. However, their failure to grasp the continued environmental decline predicted by both their older relatives and the greater scientific community indicates that this message has not been properly delivered or completely understood.

One alternate possibility is that students are just being optimistic that positive changes will occur that lead to sustaining or even improving environmental conditions. Like students elsewhere, this particular generation of Costa Ricans was born into a society that readily recycles and features rapid technological advances. Like earlier generations of Costa Ricans they have grown-up depending upon hydroelectric energy,

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are indoctrinated in the benefits of tropical forests and biodiversity through their academic curriculum, and have witnessed the economic support of millions of ecotourists that annually visit Costa Rica. It is possible that knowledge of these things and the strong, national conservation discourse (Campbell 2002, Schelhas and Pfeffer 2005) overshadow anything they hear to the contrary regarding the state of the environment. Unfortunately, by the time these students reach university age the majority may feel that there will not be enough natural resources for the well-being of their own children (Holl et al. 1999). The importance lies then with being able to determine if this optimism by young people is pervasive beyond the scope of this study, and if it is fueled by genuine beliefs in improvement or by a lack of knowledge or awareness (as indicated here). With our inability to predict the future, conservationists and educators alike may have a difficult task in the future of promoting environmental awareness by striking a delicate balance between environmental reality and environmental optimism, and ironically they may need to do so using the mass media (Holl et al. 1995).

There is a great need to get Costa Ricans, especially students, back outside for meaningful interactions with nature. Although the amount of time students spend outside exploring, or in unstructured play is known to bring social, emotional, physical, and academic benefits to students (Faber-Taylor and Kuo 2006, Vadala et al. 2007, Coyle 2009, Hills et al. 2010), the direct connection between getting people and students outside and the benefits for conservation is less supported in the literature. Even if urban youth did spend significant amounts of time outside exploring their natural world, there is a strong chance the native flora and fauna they encounter represent an impoverished natural community (Turner et al. 2004, Samways 2007). Nonetheless, many natural lessons or

ecological processes can still be appreciated in depauperate, novel urban environments (Pyle 2003, Miller 2005), and such experiences in nature have been important to the formation of the very naturalists and ecologists who today have dedicated their careers to nature research conservation (Putz 1997, Pyle 2003, Stokes 2006, Weigl 2009).

Although the data presented here provide support for the phenomena of *generational amnesia* and the *extinction of experience*, without long-term studies that demonstrate known causal links between nature experience, and changes in conduct or behavior that represent environmentally beneficial actions, then we are only left with a series of questions. If experience or interaction with nature is decreasing in the daily lives of the world's increasingly urban population, then how will this affect knowledge of perceptions about nature in the future? Is a direct causal link between outdoor nature experience and support for conservation initiatives really needed? How could such a link be established? How long can we wait to generate the empirical support? If such trends are occurring in Costa Rica, a biologically rich country with a strong national commitment to nature conservation, then what is happening in other countries? Pyle (2003) is known for asking, "What is the extinction of the condor to the child who has never seen a wren?", but as seen in this study and with today's media savvy youth, a modification of that question should have us asking, "What happens with the wren for the child that only knows the penguin?"

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Box 1. Survey questions used in this analysis*

- What is the national bird of Costa Rica?
- Name the birds in the following photos**.
- On a scale from 1-10, where 1 is poor and 10 is excellent, rate the state of the global environment during the following three periods:
  i. Today
  ii. 50 yrs ago (past)
  iii. 50 yrs from now (future)

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* The full survey contained 16 questions (see supplemental materials) but only those above fall within the scope of this article.

** There were a total of 17 bird photos spread across three questions. The photos included 11 native species and 6 exotic species, although they were not labeled as such.

Table 1. Pairwise comparisons (Chi-square) across generations. A significant P-value indicates significant differences between generations their ability to correctly identify photos of individual bird species from different groups*.

Generation Comparisons	Species Identification			
Grandparent- Parent (*n* = 260)	**Native**	**Charismatic**	**Patio**	**Exotic**
X^2 =	0.94	0.01	1.69	0.00
Fisher's *P* =	0.21	0.57	0.12	0.57
Parent – Student (*n* = 493)				
X^2 =	48.46	80.91	48.77	19.58
Fisher's *P* =	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Grandparent – Student (n = 387)				
X^2 =	37.07	42.73	42.53	10.26
Fisher's *P* =	< 0.0001	< 0.0001	< 0.0001	< 0.001

* I condensed the scores for all 17 species into average scores for each generation's ability to identify birds from different groups (see Fig. 2). Therefore, I could not run matched analyses to control for the effect of family relationships. This also increased the above sample sizes for each comparison.
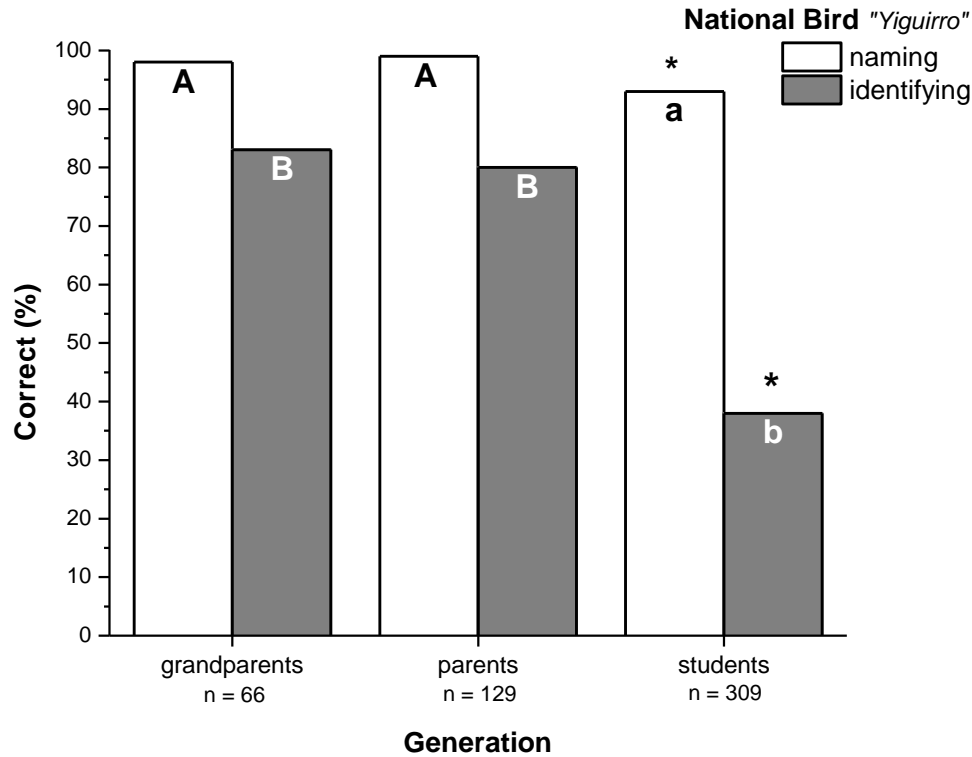
Figure 1. Percentage of respondents in each generation that could correctly name or correctly identify Costa Rica's national bird the "yigüirro" (Clay-colored Thrush, *Turdus grayii*). Different letters represent different comparisons among generations with significant differences denoted with an asterisk and lower case letters. To control for the effect of family relationships, I ran paired categorical response analyses with JMP 8.0 following the rater agreement protocol (*Naming* grandparents-students: Kappa = -0.028 ± 0.025 s.e.m., Bowker's = 4.50, *P* = 0.034; *Naming* parents-students: Kappa = -0.015 ± 0.013 s.e.m., Bowker's = 8.33, *P* = 0.004; *Naming* grandparents-parents: Kappa = -0.017 ± 0.012 s.e.m., Bowker's = 0.0, *P* = 1.00; .*Identifying* grandparents-students: Kappa = 0.161 ± 0.093 s.e.m., Bowker's = 16.33, *P* < 0.0001; *Identifying* parents-students: Kappa = 0.236 ± 0.060 s.e.m, Bowker's = 41.68, *P* < 0.0001; *Identifying* grandparents-parents: Kappa = 0.812 ± 0.105 s.e.m., Bowker's = 0.33, *P* = 0.564).
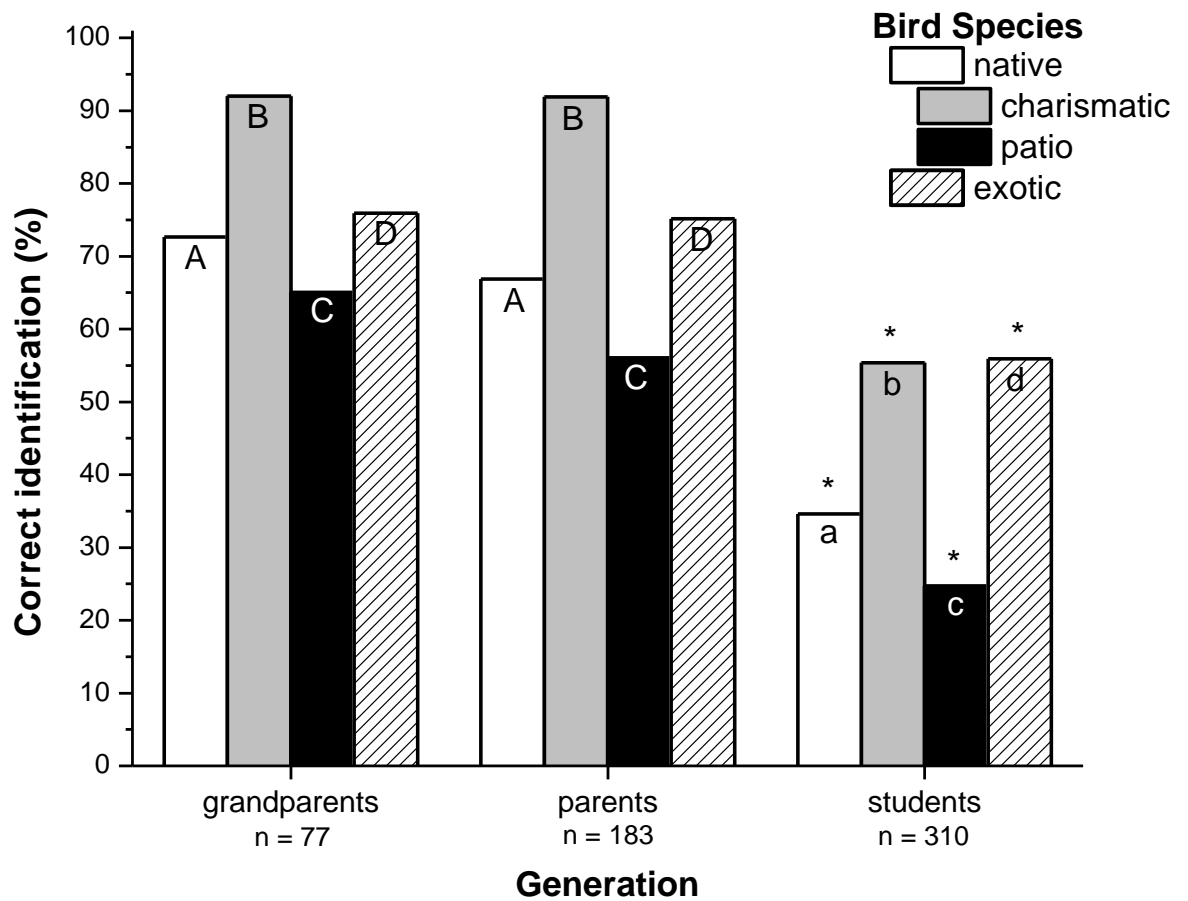
Figure 2. Percentage of respondents in each generation that could correctly identify different species of birds from photos. Of the 17 bird photos respondents identified, 11 were Costa Rican natives and 6 were exotic. The native species were further divided into a group of 3 charismatic species typical to tropical forests, and a group of 8 species common to patios and backyards. The sample sizes shown above refer to the within-generation paired analysis comparing each generation's ability to identify bird species in different groups. Similar letters represent pair-wise comparisons for each bird group across the different generations (see Table 1). Capital letters indicate similar scores and significantly lower scores are shown with lower case letters and asterisks over the bars.
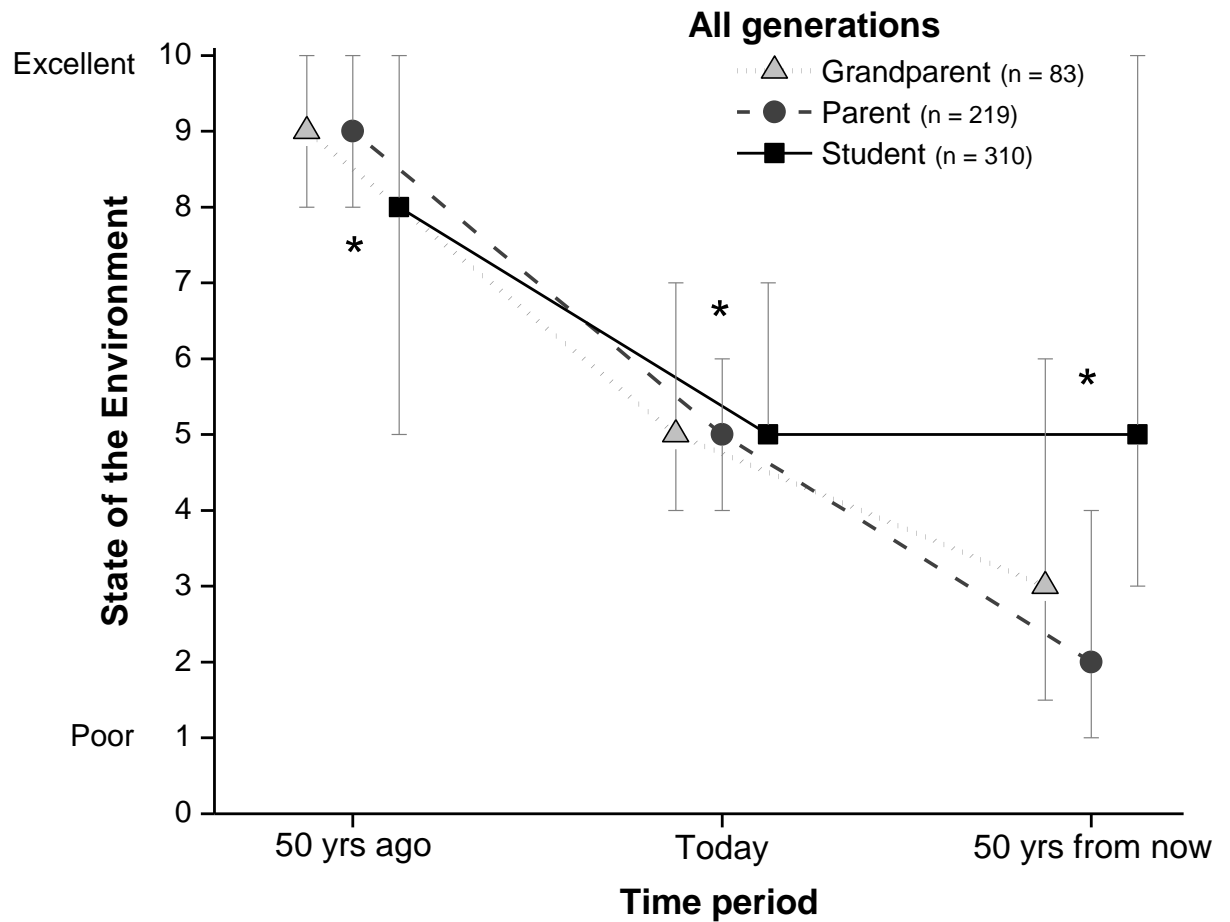
Figure 3. Median scores for the perceptions of the state of the global environment for three generations of respondents during three different periods in time. The error bars around each median span the 25th and 75th percentiles, and asterisks indicate where median student scores significantly differed from those of their older relatives. To control for the effect of family I ran a nonparametric matched pairs analysis using Wilcoxon signed rank tests (see Results for details). Sample sizes above refer to the number of respondents within each generation.
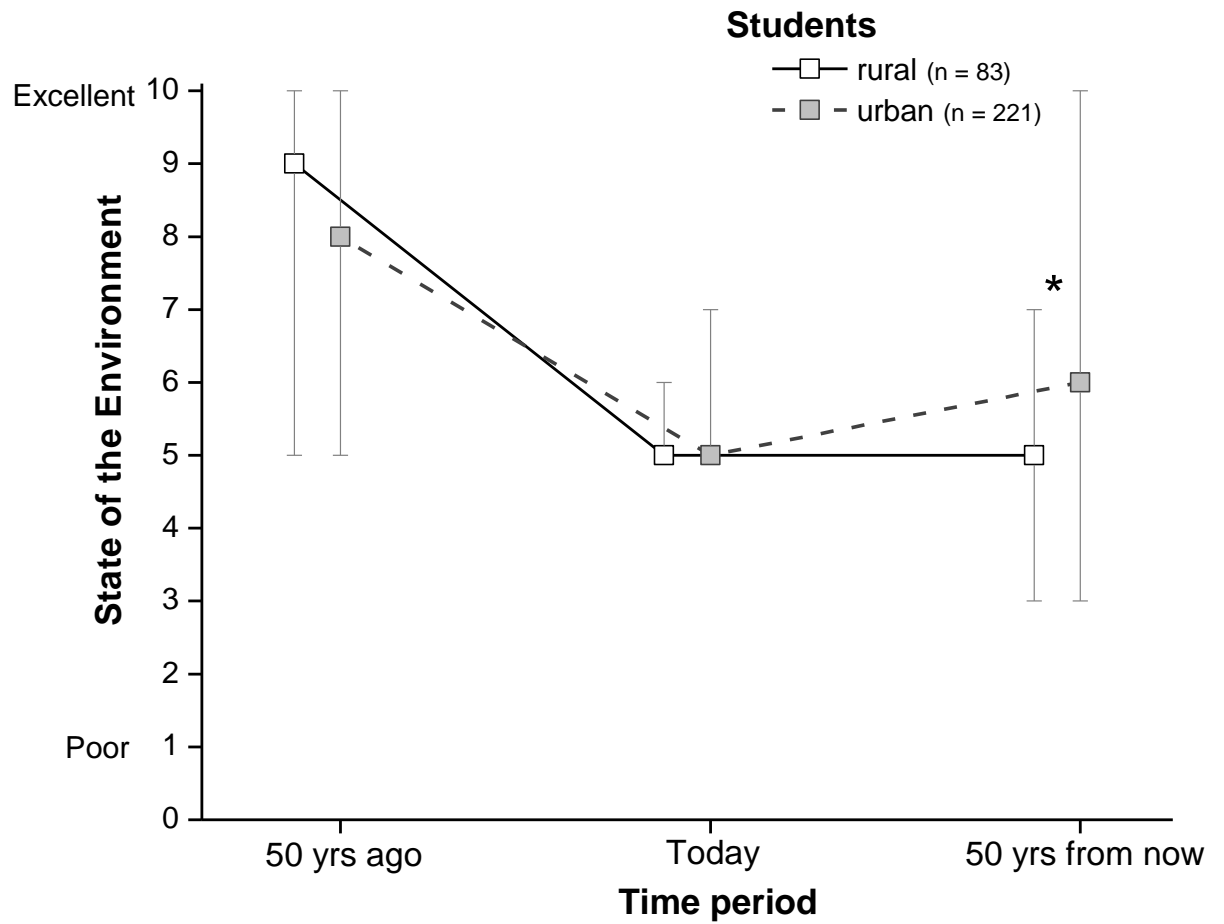
Figure 4. Median scores for the perceptions of the state of the global environment by urban and rural students for three different periods in time. The error bars around each median span the 25th and 75th percentiles, and the asterisks indicate where urban and rural students' perceptions differed significantly. I compared perceptions between rural and urban students using nonparametric Wilcoxon signed ranks test.

APPENDIX I
Image classification for environmental characteristics

The four, sub-sample points and 100m buffers around the urban core (i.e., *A*) and commercial/residential transition (i.e., B) survey sites of the Guapiles – La Selva urban development gradient, overlain on the CARTA (PRIAS 2005) high-resolution (i.e., 1 m) infrared image.
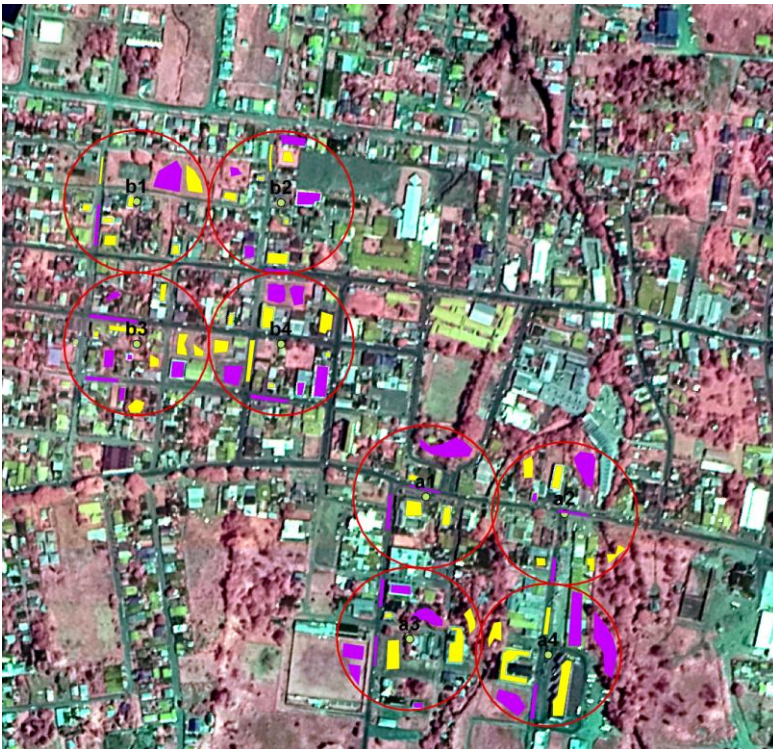
The same image as above, but with the land-use polygons manually drawn over known areas. Half of the polygons were used for training (e.g. purple) and the other half for testing (e.g. yellow) of the land-use classification procedure.
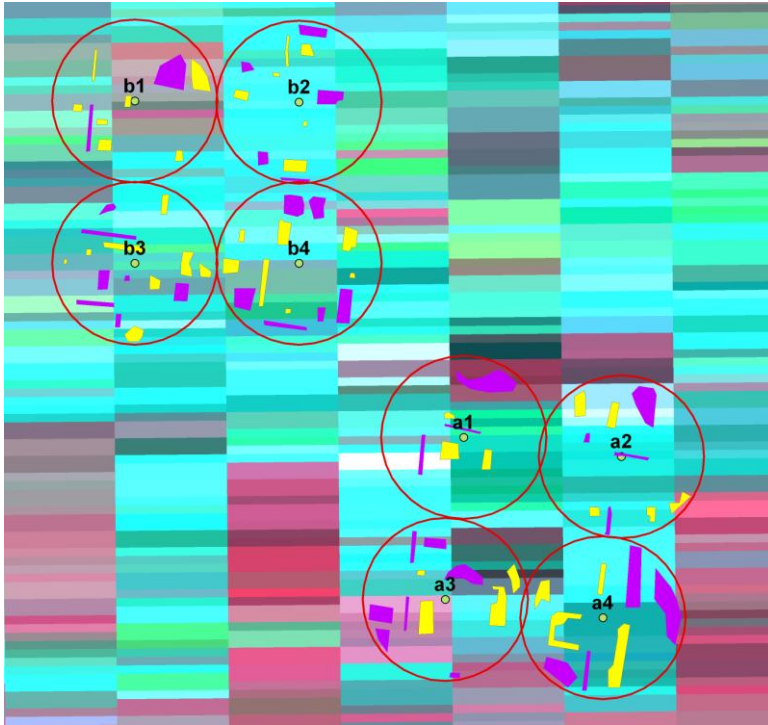
The same four sub-sample points of the survey sites GuapLS-A and GuapLS-B with both the training and testing polygons used in the land-use classification procedure. This time the features are overlaid on the HYMAP hyperspectral image. In the classification procedure pixel values within the polygons of the known land-use areas are used to identify similar land-use areas throughout the 100m buffer zones around each point.
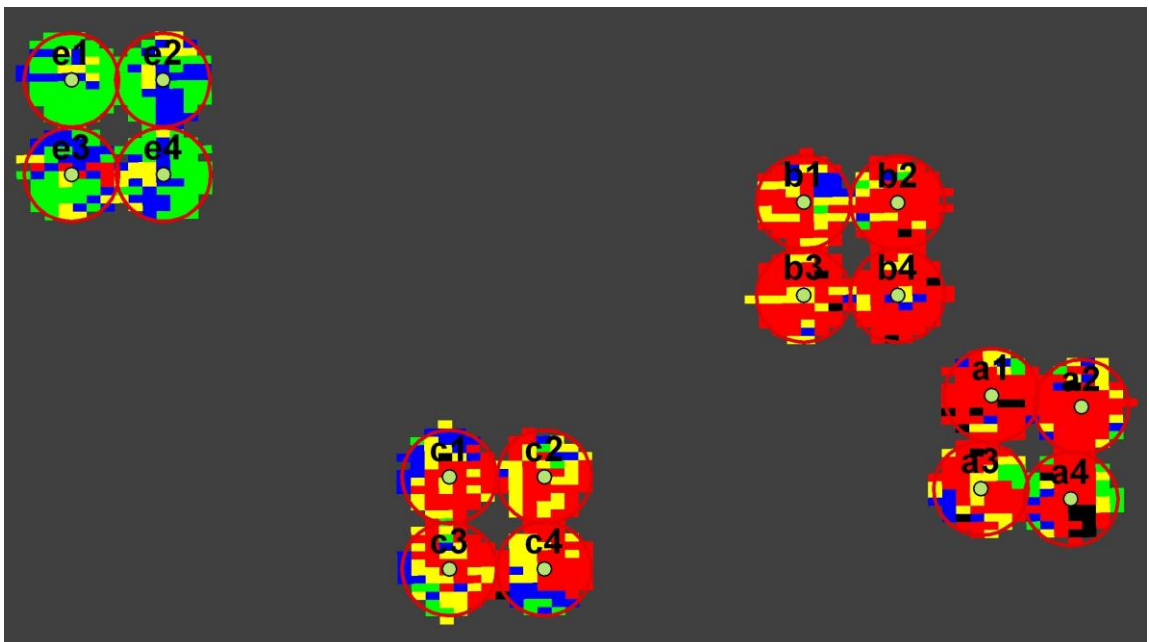
The above image shows the survey sites and sub-sampling points with their 100m buffers for GuapLS-A, GuapLS-B, GuapLS-C, and GuapLS-E, after the classification process. Red pixels are classified as "urban" (i.e., houses, buildings, roads), blue pixels represent "grass" (i.e., fields, lawns, pasture), yellow pixels show areas of "savanna" a multi-strata mix of grass and trees or shrubs (i.e., gardens, or pastures with trees) and green pixels represent "forest" (i.e., stands of trees). Black pixels represent values that went unclassified.

GRAD.QUAD	Urban	Forest	NDVI	Grass	Savanna
CaPV-A	76.37	5.32	0.17	6.81	11.50
CaPV-B	45.28	7.23	0.28	16.11	31.39
CaPV-C	65.73	0.40	0.19	15.73	18.15
CaPV-D	50.10	0.42	0.21	29.31	20.17
CaPV-E	9.13	37.73	0.47	37.93	15.21
CaPV-F	0.00	37.55	0.49	58.65	3.80
CaPV-G	12.56	0.00	0.26	45.37	41.34
CaPV-H	0.00	100.00	0.36	0.00	0.00
CaPV-I	0.00	92.70	0.43	0.00	0.00
GuLS-A	67.08	9.38	0.28	7.71	15.83
GuLS-B	71.52	2.22	0.26	4.85	21.41
GuLS-C	49.50	5.96	0.39	15.11	29.42
GuLS-D	44.01	27.31	0.45	8.06	20.63
GuLS-E	3.29	54.74	0.71	29.01	12.96
GuLS-F	0.00	92.35	0.85	6.67	0.98
GuLS-G	28.69	20.46	0.59	25.74	25.11
GuLS-H	0.00	90.48	0.76	8.07	1.45
GuLS-I	0.00	97.35	0.76	2.65	0.00
LiSR-A	66.12	2.73	0.18	11.11	20.04
LiSR-B	56.00	2.25	0.19	14.00	27.75
LiSR-C	60.16	4.98	0.23	6.37	28.49
LiSR-D	32.14	9.92	0.26	36.11	21.83
LiSR-E	8.89	8.08	0.25	71.72	11.31
LiSR-F	6.05	63.71	0.44	21.37	8.87
LiSR-G	29.63	40.74	0.39	27.25	0.00
LiSR-H	0.00	59.17	0.55	35.14	0.00
LiSR-I	1.80	79.18	0.44	17.99	0.00
NiBH-A	63.46	12.29	0.23	3.88	20.38
NiBH-B	52.78	8.53	0.31	9.33	29.37
NiBH-C	60.88	7.98	0.31	1.60	29.54
NiBH-D	57.17	5.78	0.29	6.77	30.28
NiBH-E	9.25	14.96	0.36	54.53	21.26
NiBH-F	0.00	59.76	0.64	18.31	21.93
NiBH-G	23.67	20.32	0.25	48.33	7.68
NiBH-H	0.00	94.91	0.50	2.61	2.48
NiBH-I	0.00	76.99	0.40	23.01	0.00
SiBa-A	66.73	4.81	0.33	18.04	10.42
SiBa-B	61.45	2.42	0.39	26.82	9.31
SiBa-C	58.61	4.31	0.39	26.59	10.49
SiBa-D	25.00	8.02	0.57	41.23	25.75
SiBa-E	7.39	10.35	0.70	50.65	31.61
SiBa-F	0.37	83.55	0.83	10.97	5.12
SiBa-G	19.03	14.17	0.79	3.69	63.11
SiBa-H	0.00	43.11	0.78	17.91	21.85
SiBa-I	0.00	84.23	0.74	1.30	9.83
TuGu-A	85.76	0.17	0.20	7.97	0.51
TuGu-B	80.17	0.00	0.30	11.45	7.01
TuGu-C	76.44	0.00	0.30	23.56	0.00
TuGu-D	35.56	0.51	0.48	50.60	7.35
TuGu-E	11.28	22.22	0.66	52.99	5.98
TuGu-F	2.38	75.89	0.86	7.47	3.23
TuGu-G	4.52	8.98	0.66	70.98	6.39
TuGu-H	0.12	65.24	0.86	14.31	11.93
TuGu-I	0.00	88.29	0.90	8.32	2.72

This table shows the environmental characteristics used to classify the environment at each of the 54 sites by gradient and quad (GRAD.QUAD). "Urban", "Forest", "Grass", and "Savanna" are percentages based on the total percent cover of each from the sub-sampling areas of each site calculated from the manual classification of pixel values. "NDVI" was calculated from the vegetation indices package included in the image classification software. NDVI scores range from 0 to 1, and are averaged across all pixels within the sub-sampling areas of each site. All image analyses were done using ENVI 4. 0. The values shown here were used in the univariate analyses used in Chapter 1, and the multivariate analyses done in Chapter 2.

APPENDIX II
Full Species List (with abbreviations). Names follow AOU (7th checklist, 51st supplement).

No.	Sci.Name	Scientific Name	Common Name
1	AcciBico	*Accipiter bicolor*	Bicolored Hawk
2	AmauConc	*Amaurospiza concolor*	Blue Seedeater
3	AmaurCon	*Amaurolimnas concolor*	Uniform Crake
4	AmazAlbi	*Amazona albifrons*	White-fronted Parrot
5	AmazAmab	*Amazilia amabilis*	Blue-chested Hummingbird
6	AmazAuro	*Amazona auropalliata*	Yellow-naped Parrot
7	AmazAutu	*Amazona autumnalis*	Red-lored Parrot
8	AmazFari	*Amazona farinosa*	Mealy Parrot
9	AmazRuti	*Amazilia rutila*	Cinnamon Hummingbird
10	AmazSauc	*Amazilia saucerrottei*	Steely-vented Hummingbird
11	AmazTzac	*Amazilia tzacatl*	Rufous-tailed Hummingbird
12	AnthPrev	*Anthracothorax prevostii*	Green-breasted Mango
13	AraAmbi	*Ara ambiguus*	Great Green Macaw
14	AraMaca	*Ara macao*	Scarlet Macaw
15	AramCaja	*Aramides cajanea*	Gray-necked Wood-Rail
16	AratCani	*Aratinga canicularis*	Orange-fronted Parakeet
17	AratFins	*Aratinga finschi*	Crimson-fronted Parakeet
18	AratNana	*Aratinga nana*	Olive-throated Parakeet
19	ArchColu	*Archilochus colubris*	Ruby-throated Hummingbird
20	ArreAura	*Arremon aurantiirostris*	Orange-billed Sparrow
21	ArreConi	*Arremonops conirostris*	Black-striped Sparrow
22	ArreRufi	*Arremonops rufivirgatus*	Olive Sparrow
23	AttiSpad	*Attila spadiceus*	Bright-rumped Attila
24	AulaPras	*Aulacorhynchus prasinus*	Emerald Toucanet
25	BaryMart	*Baryphthengus martii*	Rufous Motmot
26	BasiCuli	*Basileuterus culicivorus*	Golden-crowned Warbler
27	BasiRufi	*Basileuterus rufifrons*	Rufous-capped Warbler
28	BasiTris	*Basileuterus tristriatus*	Three-striped Warbler
29	BrotJugu	*Brotogeris jugularis*	Orange-chinned Parakeet
30	BubuIbis	*Bubulcus ibis*	Cattle Egret
31	BurhBist	*Burhinus bistriatus*	Double-striped Thick-knee
32	ButeMagn	*Buteo magnirostris*	Roadside Hawk
33	ButeNiti	*Buteo nitidus*	Gray Hawk
34	ButePlat	*Buteo platypterus*	Broad-winged Hawk
35	ButoVire	*Butorides virescens*	Green Heron
36	CaciUrop	*Cacicus uropygialis*	Scarlet-rumped Cacique
37	CallBrya	*Calliphlox bryantae*	Magenta-throated Woodstar
38	CaloForm	*Calocitta formosa*	White-throated Magpie-Jay
39	CampGuat	*Campephilus guatemalensis*	Pale-billed Woodpecker

40	**CampHemi**	*Campylopterus hemileucurus*	Violet Sabrewing
41	**CampImbe**	*Camptostoma imberbe*	Northern Beardless-Tyrannulet
42	**CampRufi**	*Campylorhynchus rufinucha*	Rufous-naped Wren
43	**CampZona**	*Campylorhynchus zonatus*	Band-backed Wren
44	**CarpNiti**	*Carpodectes nitidus*	Snowy Cotinga
45	**CaryPoli**	*Caryothraustes poliogaster*	Black-faced Grosbeak
46	**CatAura**	*Cathartes aura*	Turkey Vulture
47	**CathaFus**	*Catharus fuscater*	Slaty-backed Nightingale-Thrush
48	**CathAura**	*Catharus aurantiirostris*	Orange-billed Nightingale-Thrush
49	**CathFusc**	*Catharus fuscescens*	Veery
50	**CathUstu**	*Catharus ustulatus*	Swainson's Thrush
51	**CeleCast**	*Celeus castaneus*	Chestnut-colored Woodpecker
52	**CeleLori**	*Celeus loricatus*	Cinnamon Woodpecker
53	**CercTyra**	*Cercomacra tyrannina*	Dusky Antbird
54	**ChalUroc**	*Chalybura urochrysia*	Bronze-tailed Plumeleteer
55	**ChirLine**	*Chiroxiphia linearis*	Long-tailed Manakin
56	**ChloCani**	*Chlorostilbon canivetii*	Canivet's Emerald
57	**ChloCarm**	*Chlorothraupis carmioli*	Carmiol's Tanager
58	**ChloSpiz**	*Chlorophanes spiza*	Green Honeycreeper
59	**CiccVirg**	*Ciccaba virgata*	Mottled Owl
60	**ClarPret**	*Claravis pretiosa*	Blue Ground-Dove
61	**CoccAmer**	*Coccyzus americanus*	Yellow-billed Cuckoo
62	**CoccMino**	*Coccyzus minor*	Mangrove Cuckoo
63	**CoerFlav**	*Coereba flaveola*	Bananaquit
64	**ColiCris**	*Colinus cristatus*	Crested Bobwhite
65	**ColoColo**	*Colonia colonus*	Long-tailed Tyrant
66	**ColuInca**	*Columbina inca*	Inca Dove
67	**ColuLivi**	*Columba livia*	Rock Pigeon
68	**ColuPass**	*Columbina passerina*	Common Ground-Dove
69	**ColuTalp**	*Columbina talpacoti*	Ruddy Ground-Dove
70	**ConoAlbo**	*Conopias albovittatus*	White-ringed Flycatcher
71	**ContCine**	*Contopus cinereus*	Tropical Pewee
72	**ContSord**	*Contopus sordidulus*	Western Wood-Pewee
73	**ContVire**	*Contopus virens*	Eastern Wood-Pewee
74	**CoraAlte**	*Corapipo altera*	White-ruffed Manakin
75	**CoraAtra**	*Coragyps atratus*	Black Vulture
76	**CraxRubr**	*Crax rubra*	Great Curassow
77	**CrotSulc**	*Crotophaga sulcirostris*	Groove-billed Ani
78	**CrypBouc**	*Crypturellus boucardi*	Slaty-breasted Tinamou
79	**CrypCinn**	*Crypturellus cinnamomeus*	Thicket Tinamou
80	**CrypSoui**	*Crypturellus soui*	Little Tinamou
81	**CyanCyan**	*Cyanocompsa cyanoides*	Blue-black Grosbeak
82	**CyaneCyan**	*Cyanerpes cyaneus*	Red-legged Honeycreeper

83	**CyanLuci**	*Cyanerpes lucidus*	Shining Honeycreeper
84	**CymbLine**	*Cymbilaimus lineatus*	Fasciated Antshrike
85	**CyphPhae**	*Cyphorhinus phaeocephalus*	Song Wren
86	**DacnVenu**	*Dacnis venusta*	Scarlet-thighed Dacnis
87	**DendAutu**	*Dendrocygna autumnalis*	Black-bellied Whistling-Duck
88	**DendFusc**	*Dendroica fusca*	Blackburnian Warbler
89	**DendHomo**	*Dendrocincla homochroa*	Ruddy Woodcreeper
90	**DendMagn**	*Dendroica magnolia*	Magnolia Warbler
91	**DendPens**	*Dendroica pensylvanica*	Chestnut-sided Warbler
92	**DendPete**	*Dendroica petechia*	Yellow Warbler
93	**DendSanc**	*Dendrocolaptes sanctithomae*	Northern Barred-Woodcreeper
94	**DiscConv**	*Discosura conversii*	Green Thorntail
95	**DiveDive**	*Dives dives*	Melodious Blackbird
96	**DryoLine**	*Dryocopus lineatus*	Lineated Woodpecker
97	**DumeCaro**	*Dumetella carolinensis*	Gray Catbird
98	**DysiStri**	*Dysithamnus striaticeps*	Streak-crowned Antvireo
99	**ElaeFlav**	*Elaenia flavogaster*	Yellow-bellied Elaenia
100	**ElanLeuc**	*Elanus leucurus*	White-tailed Kite
101	**ElecPlat**	*Electron platyrhynchum*	Broad-billed Motmot
102	**EmpiAlno**	*Empidonax alnorum*	Alder Flycatcher
103	**EmpiFlav**	*Empidonax flaviventris*	Yellow-bellied Flycatcher
104	**EmpiVire**	*Empidonax virescens*	Acadian Flycatcher
105	**EpinFulv**	*Epinecrophylla fulviventris*	Checker-throated Antwren
106	**EumoSupe**	*Eumomota superciliosa*	Turquoise-browed Motmot
107	**EuphAffi**	*Euphonia affinis*	Scrub Euphonia
108	**EuphAnne**	*Euphonia anneae*	Tawny-capped Euphonia
109	**EuphGoul**	*Euphonia gouldi*	Olive-backed Euphonia
110	**EuphLute**	*Euphonia luteicapilla*	Yellow-crowned Euphonia
111	**FalcPere**	*Falco peregrinus*	Peregrine Falcon
112	**FlorMell**	*Florisuga mellivora*	White-necked Jacobin
113	**FormAnal**	*Formicarius analis*	Black-faced Antthrush
114	**GalbRufi**	*Galbula ruficauda*	Rufous-tailed Jacamar
115	**GeotPoli**	*Geothlypis poliocephala*	Gray-crowned Yellowthroat
116	**GeraCaer**	*Geranospiza caerulescens*	Crane Hawk
117	**GlauAene**	*Glaucis aeneus*	Bronzy Hermit
118	**GlauBras**	*Glaucidium brasilianum*	Ferruginous Pygmy-Owl
119	**GlypSpir**	*Glyphorynchus spirurus*	Wedge-billed Woodcreeper
120	**GymnLeuc**	*Gymnopithys leucaspis*	Bicolored Antbird
121	**GymnNudi**	*Gymnocichla nudiceps*	Bare-crowned Antbird
122	**HabiFusc**	*Habia fuscicauda*	Red-throated Ant-Tanager
123	**HarpBide**	*Harpagus bidentatus*	Double-toothed Kite
124	**HeliBarr**	*Heliothryx barroti*	Purple-crowned Fairy
125	**HeliCons**	*Heliomaster constantii*	Plain-capped Starthroat

126	**HeliLong**	*Heliomaster longirostris*	Long-billed Starthroat
127	**HeniLeuc**	*Henicorhina leucosticta*	White-breasted Wood-Wren
128	**HerpCach**	*Herpetotheres cachinnans*	Laughing Falcon
129	**HeteRubr**	*Heterospingus rubrifrons*	Sulphur-rumped Tanager
130	**HiruRust**	*Hirundo rustica*	Barn Swallow
131	**HyloDecu**	*Hylophilus decurtatus*	Lesser Greenlet
132	**HyloElic**	*Hylocharis eliciae*	Blue-throated Goldentail
133	**HyloMust**	*Hylocichla mustelina*	Wood Thrush
134	**HyloNaev**	*Hylophylax naevioides*	Spotted Antbird
135	**HyloPers**	*Hylopezus perspicillatus*	Streak-chested Antpitta
136	**HyloSubu**	*Hyloctistes subulatus*	Striped Woodhaunter
137	**IcteGalb**	*Icterus galbula*	Baltimore Oriole
138	**IctePect**	*Icterus pectoralis*	Spot-breasted Oriole
139	**IctePros**	*Icterus prosthemelas*	Black-cowled Oriole
140	**IctePust**	*Icterus pustulatus*	Streak-backed Oriole
141	**IcteSpur**	*Icterus spurius*	Orchard Oriole
142	**IcteVire**	*Icteria virens*	Yellow-breasted Chat
143	**JacaSpin**	*Jacana spinosa*	Northern Jacana
144	**KlaiGuim**	*Klais guimeti*	Violet-headed Hummingbird
145	**LateAlbi**	*Laterallus albigularis*	White-throated Crake
146	**LegaLeuc**	*Legatus leucophaius*	Piratic Flycatcher
147	**LepiSoul**	*Lepidocolaptes souleyetii*	Streak-headed Woodcreeper
148	**LeptCass**	*Leptotila cassini*	Gray-chested Dove
149	**LeptCaya**	*Leptodon cayanensis*	Gray-headed Kite
150	**LeptSupe**	*Leptopogon superciliaris*	Slaty-capped Flycatcher
151	**LeptVerr**	*Leptotila verreauxi*	White-tipped Dove
152	**LeucAlbi**	*Leucopternis albicollis*	White Hawk
153	**LeucSemi**	*Leucopternis semiplumbeus*	Semiplumbeous Hawk
154	**LipaUnir**	*Lipaugus unirufus*	Rufous Piha
155	**LophCris**	*Lophostrix cristata*	Crested Owl
156	**LophPile**	*Lophotriccus pileatus*	Scale-crested Pygmy-Tyrant
157	**ManaCand**	*Manacus candei*	White-collared Manakin
158	**MegaCoop**	*Megascops cooperi*	Pacific Screech-Owl
159	**MegaPita**	*Megarynchus pitangua*	Boat-billed Flycatcher
160	**MelaHoff**	*Melanerpes hoffmannii*	Hoffmann's Woodpecker
161	**MelaPuch**	*Melanerpes pucherani*	Black-cheeked Woodpecker
162	**MeloBiar**	*Melozone biarcuata*	Prevost's Ground-Sparrow
163	**MeseCaye**	*Mesembrinibis cayennensis*	Green Ibis
164	**MicrAlbo**	*Microchera albocoronata*	Snowcap
165	**MicrCine**	*Microbates cinereiventris*	Tawny-faced Gnatwren
166	**MicrLanc**	*Micromonacha lanceolata*	Lanceolated Monklet
167	**MicrMarg**	*Microcerculus marginatus*	Scaly-breasted Wren
168	**MicrQuix**	*Microrhopias quixensis*	Dot-winged Antwren

169	**MicrSemi**	*Micrastur semitorquatus*	Collared Forest-Falcon
170	**MionOlea**	*Mionectes oleagineus*	Ochre-bellied Flycatcher
171	**MitrCass**	*Mitrospingus cassinii*	Dusky-faced Tanager
172	**MnioVari**	*Mniotilta varia*	Black-and-white Warbler
173	**MoloAene**	*Molothrus aeneus*	Bronzed Cowbird
174	**MomoMomo**	*Momotus momota*	Blue-crowned Motmot
175	**MonaMorp**	*Monasa morphoeus*	White-fronted Nunbird
176	**MoroEryt**	*Morococcyx erythropygus*	Lesser Ground-Cuckoo
177	**MyadMela**	*Myadestes melanops*	Black-faced Solitaire
178	**MyiaCrin**	*Myiarchus crinitus*	Great Crested Flycatcher
179	**MyiaNutt**	*Myiarchus nuttingi*	Nutting's Flycatcher
180	**MyiaTube**	*Myiarchus tuberculifer*	Dusky-capped Flycatcher
181	**MyiaTyra**	*Myiarchus tyrannulus*	Brown-crested Flycatcher
182	**MyioAtri**	*Myiornis atricapillus*	Black-capped Pygmy-Tyrant
183	**MyioGran**	*Myiozetetes granadensis*	Gray-capped Flycatcher
184	**MyioLute**	*Myiodynastes luteiventris*	Sulphur-bellied Flycatcher
185	**MyioMacu**	*Myiodynastes maculatus*	Streaked Flycatcher
186	**MyioMini**	*Myioborus miniatus*	Slate-throated Redstart
187	**MyioSimi**	*Myiozetetes similis*	Social Flycatcher
188	**MyioViri**	*Myiopagis viridicata*	Greenish Elaenia
189	**MyrmAxil**	*Myrmotherula axillaris*	White-flanked Antwren
190	**MyrmExsu**	*Myrmeciza exsul*	Chestnut-backed Antbird
191	**MyrmImma**	*Myrmeciza immaculata*	Immaculate Antbird
192	**MyrmSchi**	*Myrmotherula schisticolor*	Slaty Antwren
193	**NothHype**	*Notharchus hyperrhynchus*	White-necked Puffbird
194	**NyctAlbi**	*Nyctidromus albicollis*	Common Pauraque
195	**NyctGris**	*Nyctibius griseus*	Common Potoo
196	**OdonLeuc**	*Odontophorus leucolaemus*	Black-breasted Wood-Quail
197	**OncoCine**	*Oncostoma cinereigulare*	Northern Bentbill
198	**OporForm**	*Oporornis formosus*	Kentucky Warbler
199	**OporPhil**	*Oporornis philadelphia*	Mourning Warbler
200	**OreoPere**	*Oreothlypis peregrina*	Tennessee Warbler
201	**OrtaCine**	*Ortalis cinereiceps*	Gray-headed Chachalaca
202	**OrtaVetu**	*Ortalis vetula*	Plain Chachalaca
203	**OryzFune**	*Oryzoborus funereus*	Thick-billed Seed-Finch
204	**PachAgla**	*Pachyramphus aglaiae*	Rose-throated Becard
205	**PachCinn**	*Pachyramphus cinnamomeus*	Cinnamon Becard
206	**ParkNove**	*Parkesia noveboracensis*	Northern Waterthrush
207	**ParuPiti**	*Parula pitiayumi*	Tropical Parula
208	**PassCiri**	*Passerina ciris*	Painted Bunting
209	**PassDome**	*Passer domesticus*	House Sparrow
210	**PataCaye**	*Patagioenas cayennensis*	Pale-vented Pigeon
211	**PataFlav**	*Patagioenas flavirostris*	Red-billed Pigeon

212	**PataNigr**	*Patagioenas nigrirostris*	Short-billed Pigeon
213	**PenePurp**	*Penelope purpurascens*	Crested Guan
214	**PeucRufi**	*Peucaea ruficauda*	Stripe-headed Sparrow
215	**PhaeFulv**	*Phaeothlypis fulvicauda*	Buff-rumped Warbler
216	**PhaeGuy**	*Phaethornis guy*	Green Hermit
217	**PhaeLong**	*Phaethornis longirostris*	Long-billed Hermit
218	**PhaeStri**	*Phaethornis striigularis*	Stripe-throated Hermit
219	**PheuLudo**	*Pheucticus ludovicianus*	Rose-breasted Grosbeak
220	**PiayCaya**	*Piaya cayana*	Squirrel Cuckoo
221	**PicuSimp**	*Piculus simplex*	Rufous-winged Woodpecker
222	**PionSeni**	*Pionus senilis*	White-crowned Parrot
223	**PiprGris**	*Piprites griseiceps*	Gray-headed Piprites
224	**PiprMent**	*Pipra mentalis*	Red-capped Manakin
225	**PiraLudo**	*Piranga ludoviciana*	Western Tanager
226	**PiraRubr**	*Piranga rubra*	Summer Tanager
227	**PitaSulp**	*Pitangus sulphuratus*	Great Kiskadee
228	**PlatCanc**	*Platyrinchus cancrominus*	Stub-tailed Spadebill
229	**PoecSylv**	*Poecilotriccus sylvia*	Slate-headed Tody-Flycatcher
230	**PoliAlbi**	*Polioptila albiloris*	White-lored Gnatcatcher
231	**PoliPlum**	*Polioptila plumbea*	Tropical Gnatcatcher
232	**ProgChal**	*Progne chalybea*	Gray-breasted Martin
233	**ProtCitr**	*Protonotaria citrea*	Prothonotary Warbler
234	**PsarMont**	*Psarocolius montezuma*	Montezuma Oropendola
235	**PsarWagl**	*Psarocolius wagleri*	Chestnut-headed Oropendola
236	**PsilMori**	*Psilorhinus morio*	Brown Jay
237	**PterTorq**	*Pteroglossus torquatus*	Collared Aracari
238	**PulsPers**	*Pulsatrix perspicillata*	Spectacled Owl
239	**PygoCyan**	*Pygochelidon cyanoleuca*	Blue-and-white Swallow
240	**PyriHaem**	*Pyrilia haematotis*	Brown-hooded Parrot
241	**QuerPurp**	*Querula purpurata*	Purple-throated Fruitcrow
242	**QuisMexi**	*Quiscalus mexicanus*	Great-tailed Grackle
243	**RampMela**	*Ramphocaenus melanurus*	Long-billed Gnatwren
244	**RampPass**	*Ramphocelus passerinii*	Passerini's Tanager
245	**RampSang**	*Ramphocelus sanguinolentus*	Crimson-collared Tanager
246	**RampSulf**	*Ramphastos sulfuratus*	Keel-billed Toucan
247	**RampSwai**	*Ramphastos swainsonii*	Chestnut-mandibled Toucan
248	**RhynBrev**	*Rhynchocyclus brevirostris*	Eye-ringed Flatbill
249	**RhytHole**	*Rhytipterna holerythra*	Rufous Mourner
250	**SaltAtri**	*Saltator atriceps*	Black-headed Saltator
251	**SaltCoer**	*Saltator coerulescens*	Grayish Saltator
252	**SaltGros**	*Saltator grossus*	Slate-colored Grosbeak
253	**SaltMaxi**	*Saltator maximus*	Buff-throated Saltator
254	**SarcPapa**	*Sarcoramphus papa*	King Vulture

255	**SayoNigr**	*Sayornis nigricans*	Black Phoebe
256	**SeiuAuro**	*Seiurus aurocapilla*	Ovenbird
257	**SetoRuti**	*Setophaga ruticilla*	American Redstart
258	**SittGris**	*Sittasomus griseicapillus*	Olivaceous Woodcreeper
259	**SpizOrna**	*Spizaetus ornatus*	Ornate Hawk-Eagle
260	**SporAmer**	*Sporophila americana*	Variable Seedeater
261	**SporTorq**	*Sporophila torqueola*	White-collared Seedeater
262	**StelRufi**	*Stelgidopteryx ruficollis*	Southern Rough-winged Swallow
263	**StelSerr**	*Stelgidopteryx serripennis*	Northern Rough-winged Swallow
264	**SturMagn**	*Sturnella magna*	Eastern Meadowlark
265	**SturMili**	*Sturnella militaris*	Red-breasted Blackbird
266	**SynaBrac**	*Synallaxis brachyura*	Slaty Spinetail
267	**TachAlbi**	*Tachycineta albilinea*	Mangrove Swallow
268	**TachDela**	*Tachyphonus delatrii*	Tawny-crested Tanager
269	**TachLuct**	*Tachyphonus luctuosus*	White-shouldered Tanager
270	**TachRufu**	*Tachyphonus rufus*	White-lined Tanager
271	**TangGyro**	*Tangara gyrola*	Bay-headed Tanager
272	**TangIcte**	*Tangara icterocephala*	Silver-throated Tanager
273	**TangInor**	*Tangara inornata*	Plain-colored Tanager
274	**TangLarv**	*Tangara larvata*	Golden-hooded Tanager
275	**TapeNaev**	*Tapera naevia*	Striped Cuckoo
276	**TaraMajo**	*Taraba major*	Great Antshrike
277	**TereEryt**	*Terenotriccus erythrurus*	Ruddy-tailed Flycatcher
278	**ThalColo**	*Thalurania colombica*	Violet-crowned Woodnymph
279	**ThamAnab**	*Thamnistes anabatinus*	Russet Antshrike
280	**ThamAtri**	*Thamnophilus atrinucha*	Western Slaty-Antshrike
281	**ThamDoli**	*Thamnophilus doliatus*	Barred Antshrike
282	**ThraEpis**	*Thraupis episcopus*	Blue-gray Tanager
283	**ThraPalm**	*Thraupis palmarum*	Palm Tanager
284	**ThreRuck**	*Threnetes ruckeri*	Band-tailed Barbthroat
285	**ThryAtro**	*Thryothorus atrogularis*	Black-throated Wren
286	**ThryMode**	*Thryothorus modestus*	Plain Wren
287	**ThryNigr**	*Thryothorus nigricapillus*	Bay Wren
288	**ThryPleu**	*Thryothorus pleurostictus*	Banded Wren
289	**ThryRufa**	*Thryothorus rufalbus*	Rufous-and-white Wren
290	**ThryThor**	*Thryothorus thoracicus*	Stripe-breasted Wren
291	**TiarOliv**	*Tiaris olivaceus*	Yellow-faced Grassquit
292	**TigrMexi**	*Tigrisoma mexicanum*	Bare-throated Tiger-Heron
293	**TinaMajo**	*Tinamus major*	Great Tinamou
294	**TityInqu**	*Tityra inquisitor*	Black-crowned Tityra
295	**TitySemi**	*Tityra semifasciata*	Masked Tityra
296	**TodiCine**	*Todirostrum cinereum*	Common Tody-Flycatcher
297	**TodiNigr**	*Todirostrum nigriceps*	Black-headed Tody-Flycatcher

298	**TolmSulp**	*Tolmomyias sulphurescens*	Yellow-olive Flycatcher
299	**TrogAedo**	*Troglodytes aedon*	House Wren
300	**TrogCali**	*Trogon caligatus*	Gartered Trogon
301	**TrogClat**	*Trogon clathratus*	Lattice-tailed Trogon
302	**TrogColl**	*Trogon collaris*	Collared Trogon
303	**TrogEleg**	*Trogon elegans*	Elegant Trogon
304	**TrogMass**	*Trogon massena*	Slaty-tailed Trogon
305	**TrogMela**	*Trogon melanocephalus*	Black-headed Trogon
306	**TrogRufu**	*Trogon rufus*	Black-throated Trogon
307	**TurdGray**	*Turdus grayi*	Clay-colored Thrush
308	**TyraForf**	*Tyrannus forficatus*	Scissor-tailed Flycatcher
309	**TyraMela**	*Tyrannus melancholicus*	Tropical Kingbird
310	**TyraVert**	*Tyrannus verticalis*	Western Kingbird
311	**VeniFumi**	*Veniliornis fumigatus*	Smoky-brown Woodpecker
312	**VermChry**	*Vermivora chrysoptera*	Golden-winged Warbler
313	**VirFlavi**	*Vireo flavifrons*	Yellow-throated Vireo
314	**VirFlavo**	*Vireo flavoviridis*	Yellow-green Vireo
315	**VirOliva**	*Vireo olivaceus*	Red-eyed Vireo
316	**VirPhila**	*Vireo philadelphicus*	Philadelphia Vireo
317	**VolaJaca**	*Volatinia jacarina*	Blue-black Grassquit
318	**WilsCana**	*Wilsonia canadensis*	Canada Warbler
319	**WilsCitr**	*Wilsonia citrina*	Hooded Warbler
320	**WilsPusi**	*Wilsonia pusilla*	Wilson's Warbler
321	**XenoMinu**	*Xenops minutus*	Plain Xenops
322	**XiphEryt**	*Xiphorhynchus erythropygius*	Spotted Woodcreeper
323	**XiphFlav**	*Xiphorhynchus flavigaster*	Ivory-billed Woodcreeper
324	**XiphLach**	*Xiphorhynchus lachrymosus*	Black-striped Woodcreeper
325	**XiphSusu**	*Xiphorhynchus susurrans*	Cocoa Woodcreeper
326	**ZenaAsia**	*Zenaida asiatica*	White-winged Dove
327	**ZimmVili**	*Zimmerius vilissimus*	Paltry Tyrannulet
328	**ZonoCape**	*Zonotrichia capensis*	Rufous-collared Sparrow

APPENDIX III

Reduced list of 268 sp. for avian assemblage analyses

Scientific Name	ATL-A	ATL-B	ATL-C	ATL-D	ATL-E	ATL-F	ATL-G	ATL-H	ATL-I	PNW-A	PNW-B	PNW-C	PNW-D	PNW-E	PNW-F	PNW-G	PNW-H	PNW-I	Total Obs.
Quiscalus mexicanus	86	164	173	113	52	--	66	12	--	313	344	405	366	216	12	225	--	--	2547
Tyrannus melancholicus	132	88	91	97	79	22	90	30	2	92	87	112	128	78	31	35	11	1	1206
Zenaida asiatica	1	--	3	--	--	--	--	--	--	177	272	272	212	46	6	68	5	1	1063
Pitangus sulphuratus	72	102	101	104	117	37	54	58	1	23	24	20	54	33	28	96	64	8	996
Myiozetetes similis	73	81	81	84	107	20	147	51	6	10	11	15	14	8	2	2	--	1	712
Turdus grayi	60	72	87	57	60	29	79	73	15	8	16	22	26	34	5	20	6	1	670
Columbina inca	4	8	3	6	2	--	--	--	--	27	64	64	80	82	55	166	34	9	604
Campylorhynchus rufinucha	--	--	--	--	--	--	--	--	--	22	56	42	74	59	97	92	103	29	574
Troglodytes aedon	16	63	58	103	98	3	115	62	2	2	3	15	9	2	--	13	--	--	564
Thraupis episcopus	86	83	74	51	38	13	70	33	6	30	14	17	12	7	--	7	--	--	541
Thryothorus pleurostictus	--	--	--	--	--	--	--	--	--	--	--	--	--	5	153	2	114	208	482
Melanerpes hoffmannii	--	--	1	4	18	--	--	2	--	27	44	45	53	52	61	83	69	18	477
Todirostrum cinereum	24	32	53	54	84	21	74	68	1	--	--	--	--	--	--	--	--	--	411
Columbina talpacoti	12	27	41	40	63	3	35	6	--	26	37	40	42	30	--	1	--	--	403
Hylophilus decurtatus	--	--	--	--	1	53	1	35	49	--	--	--	--	2	51	--	77	111	380
Pygochelidon cyanoleuca	53	65	62	61	20	--	71	16	--	--	--	--	--	--	--	--	--	--	348
Crotophaga sulcirostris	--	1	2	12	47	--	4	13	--	6	15	11	31	64	13	122	2	--	343
Tolmomyias sulphurescens	--	--	--	1	1	24	7	13	15	--	3	--	1	12	89	3	76	98	343
Dendroica petechia	7	17	11	18	20	--	9	2	--	26	24	38	40	32	33	40	4	4	325
Leptotila verreauxi	--	--	1	7	22	12	20	9	1	--	--	--	--	--	21	14	124	78	309
Sporophila americana	12	31	43	61	60	3	66	24	3	--	--	--	--	3	--	--	--	--	306
Psarocolius montezuma	4	7	2	11	19	126	22	76	28	--	--	--	--	--	--	--	--	--	295
Passer domesticus	40	74	44	26	1	--	--	--	--	31	--	4	32	--	--	--	--	--	252
Columba livia	68	24	1	--	--	--	--	--	--	81	32	25	13	1	--	4	--	--	249
Thraupis palmarum	46	39	32	27	15	9	28	33	3	7	4	2	1	--	--	--	--	--	246
Volatinia jacarina	2	5	1	43	65	5	23	23	--	--	1	1	13	45	15	--	--	--	242
Amazilia tzacatl	18	19	25	26	16	26	65	41	3	--	--	--	--	--	--	--	1	--	240
Zonotrichia capensis	27	50	37	21	24	--	38	42	--	--	--	--	--	--	--	--	--	--	239
Myiarchus tyrannulus	--	--	--	--	--	--	--	--	--	--	--	1	1	20	77	16	64	46	225
Megarynchus pitangua	--	--	--	3	1	83	17	33	11	--	--	1	3	2	21	11	21	16	223
Henicorhina leucosticta	--	--	--	--	--	87	3	55	71	--	--	--	--	--	--	--	--	--	216
Patagioenas cayennensis	44	63	60	21	9	6	10	1	--	--	--	--	--	--	--	--	--	--	214
Ramphocelus passerinii	9	9	15	22	43	13	40	57	3	--	--	--	--	--	--	--	--	--	211
Coereba flaveola	21	22	30	28	9	3	31	38	19	--	--	--	--	--	--	--	--	--	201
Calocitta formosa	--	--	--	--	--	--	--	--	--	1	3	1	9	38	64	43	31	8	198
Chiroxiphia linearis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	66	1	40	91	198
Progne chalybea	18	22	12	5	1	--	2	--	--	94	15	5	9	5	1	8	--	--	197
Patagioenas flavirostris	10	38	50	13	12	1	3	14	2	--	3	3	4	10	7	--	6	2	178
Trogon melanocephalus	--	--	--	1	--	--	--	--	--	--	--	--	--	10	44	9	78	36	178
Elaenia flavogaster	7	12	10	19	35	3	52	36	2	--	--	--	--	--	--	--	--	--	176
Amazilia rutila	--	--	--	--	--	--	--	--	--	5	12	21	18	14	26	6	48	19	169
Saltator atriceps	5	3	6	20	40	5	42	30	7	--	--	--	--	--	--	--	--	--	158
Amazona albifrons	--	--	--	--	--	--	--	--	--	2	8	8	11	13	35	12	38	22	149
Peucaea ruficauda	--	--	--	--	--	--	--	--	--	3	13	14	58	23	13	15	4	1	144
Melanerpes pucherani	8	4	7	11	13	18	13	61	8	--	--	--	--	--	--	--	--	--	143
Thryothorus thoracicus	--	--	--	--	--	24	1	52	65	--	--	--	--	--	--	--	--	--	142
Euphonia luteicapilla	1	1	7	24	31	19	5	11	5	2	3	2	8	3	3	6	6	--	137
Polioptila albiloris	--	--	--	--	--	--	--	--	--	--	--	--	--	6	55	--	30	46	137
Basileuterus rufifrons	--	--	--	--	--	--	--	1	--	--	--	--	--	--	20	--	47	68	136
Myrmeciza exsul	--	--	--	--	--	91	--	12	27	--	--	--	--	--	--	--	--	--	130
Patagioenas nigrirostris	--	--	--	--	--	22	1	46	58	--	--	--	--	--	--	--	--	--	127
Piaya cayana	--	--	--	2	2	7	1	17	9	--	--	2	1	9	32	5	29	8	124
Psilorhinus morio	--	1	--	5	17	52	8	20	21	--	--	--	--	--	--	--	--	--	124

Species																			Total
Eumomota superciliosa	--	--	--	--	--	--	--	--	--	--	--	--	3	13	45	4	38	20	123
Ramphastos sulfuratus	--	--	--	2	--	55	1	16	49	--	--	--	--	--	--	--	--	--	123
Icterus galbula	1	1	5	1	3	6	6	14	5	3	8	10	13	21	13	5	3	1	119
Myiozetetes granadensis	7	1	--	15	29	20	8	37	2	--	--	--	--	--	--	--	--	--	119
Saltator maximus	6	1	8	10	18	7	12	45	12	--	--	--	--	--	--	--	--	--	119
Phaethornis striigularis	--	--	--	--	--	35	1	23	45	--	--	--	--	--	--	--	5	7	116
Contopus cinereus	9	2	6	10	16	--	40	31	--	--	--	--	--	--	--	--	--	--	114
Crypturellus cinnamomeus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	5	--	54	54	113
Myiarchus tuberculifer	--	--	--	--	1	23	6	24	14	--	--	--	--	--	1	--	16	27	112
Dendroica pensylvanica	1	--	--	1	3	32	9	36	18	--	--	--	--	--	--	--	1	--	101
Dives dives	--	--	--	3	6	6	7	3	--	--	7	4	16	13	6	30	--	--	101
Phaethornis longirostris	--	--	--	--	--	67	1	8	25	--	--	--	--	--	--	--	--	--	101
Thryothorus nigricapillus	--	--	--	--	--	12	8	47	34	--	--	--	--	--	--	--	--	--	101
Arremonops conirostris	--	1	--	9	31	11	24	24	--	--	--	--	--	--	--	--	--	--	100
Lepidocolaptes souleyetii	--	--	--	3	6	21	4	25	9	--	--	--	--	--	--	--	15	17	100
Saltator coerulescens	2	14	24	20	21	--	11	2	1	--	--	4	--	--	1	--	--	--	100
Myiarchus crinitus	--	--	1	1	2	4	--	1	--	--	--	--	--	--	8	1	26	47	91
Tangara larvata	4	5	2	--	1	6	16	41	16	--	--	--	--	--	--	--	--	--	91
Aratinga canicularis	--	--	--	--	--	--	--	--	--	2	6	3	20	9	14	24	5	6	89
Euphonia affinis	--	--	--	--	--	--	--	--	--	1	2	2	20	13	16	1	20	13	88
Brotogeris jugularis	--	--	1	3	12	6	2	4	--	1	5	2	1	10	16	11	9	3	86
Buteo magnirostris	2	2	--	5	10	4	--	--	--	--	--	--	2	2	7	7	23	20	84
Ramphastos swainsonii	--	--	--	--	--	27	2	10	45	--	--	--	--	--	--	--	--	--	84
Vireo flavoviridis	--	--	--	1	--	--	--	--	2	3	4	--	2	7	23	--	20	18	80
Euphonia gouldi	--	--	--	--	--	27	2	15	33	--	--	--	--	--	--	--	--	--	77
Cacicus uropygialis	--	--	--	--	--	23	1	14	38	--	--	--	--	--	--	--	--	--	76
Tiaris olivaceus	--	--	--	--	5	--	41	29	--	--	--	--	--	--	--	--	--	--	75
Columbina passerina	--	--	--	--	--	--	--	--	--	--	--	--	1	14	25	9	20	1	70
Vireo flavifrons	1	--	--	--	--	3	--	1	5	--	--	--	--	1	11	2	14	32	70
Polioptila plumbea	--	--	--	--	--	12	3	17	11	--	--	--	--	1	7	--	4	12	67
Manacus candei	--	--	--	--	--	9	1	33	23	--	--	--	--	--	--	--	--	--	66
Ramphocaenus melanurus	--	--	--	--	--	10	--	27	11	--	--	--	--	--	2	--	13	2	65
Arremonops rufivirgatus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	10	--	28	26	64
Icterus pustulatus	--	--	--	--	--	--	--	--	--	--	--	--	3	13	18	11	17	--	62
Pteroglossus torquatus	--	--	--	1	4	16	3	16	20	--	--	--	--	--	--	--	1	1	62
Trogon caligatus	--	--	--	--	4	23	1	19	11	--	--	--	--	--	--	--	1	3	62
Piranga rubra	2	--	--	1	3	7	7	15	5	1	1	--	1	2	6	--	5	3	59
Attila spadiceus	--	--	1	5	1	15	2	18	16	--	--	--	--	--	--	--	--	--	58
Tityra semifasciata	--	--	--	2	8	17	4	13	4	--	--	--	--	5	--	2	--	2	57
Oreothlypis peregrina	--	1	4	--	1	4	2	6	8	--	1	2	--	1	12	1	5	7	55
Momotus momota	--	--	--	--	--	--	2	6	2	--	--	--	--	--	4	--	21	17	52
Nyctidromus albicollis	--	--	--	1	4	3	8	11	--	--	--	--	--	4	4	--	13	4	52
Trogon massena	--	--	--	--	--	20	--	9	23	--	--	--	--	--	--	--	--	--	52
Coragyps atratus	12	1	4	12	7	--	3	1	--	--	1	--	--	5	2	2	1	--	51
Habia fuscicauda	--	--	--	--	--	27	--	24	--	--	--	--	--	--	--	--	--	--	51
Dendrocolaptes sanctithomae	--	--	--	--	--	10	1	18	3	--	--	--	--	--	1	--	4	13	50
Electron platyrhynchum	--	--	--	--	--	1	--	24	25	--	--	--	--	--	--	--	--	--	50
Arremon aurantiirostris	--	--	--	--	--	7	--	15	27	--	--	--	--	--	--	--	--	--	49
Thryothorus atrogularis	--	--	--	--	--	18	2	25	4	--	--	--	--	--	--	--	--	--	49
Archilochus colubris	--	--	--	--	--	--	--	--	--	--	--	--	2	5	12	--	23	6	48
Campylorhynchus zonatus	5	--	2	2	2	7	2	19	7	--	--	--	--	--	--	--	--	--	46
Sturnella magna	--	--	--	1	2	--	4	5	--	--	--	--	1	29	2	2	--	--	46
Campephilus guatemalensis	--	--	--	--	--	3	1	7	18	--	--	--	--	--	--	--	7	9	45
Zimmerius vilissimus	--	--	--	1	1	4	7	17	14	--	--	--	--	--	--	--	1	--	45
Trogon elegans	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	14	30	44
Camptostoma imberbe	--	--	--	--	--	--	--	--	--	--	--	--	--	1	13	--	7	20	41

Species																			Total
Chlorostilbon canivetii	--	--	--	--	--	--	--	--	--	1	1	1	--	2	15	1	14	5	40
Pionus senilis	1	--	--	3	1	20	1	9	5	--	--	--	--	--	--	--	--	--	40
Thamnophilus doliatus	--	--	2	3	11	--	11	2	--	--	--	--	--	--	--	--	11	--	40
Amazona farinosa	--	--	--	--	--	17	1	9	9	--	--	--	--	--	--	1	--	--	37
Crypturellus soui	--	--	--	--	--	4	1	22	9	--	--	--	--	--	--	--	--	--	36
Oryzoborus funereus	--	1	1	3	11	2	5	12	--	--	--	--	--	--	--	--	--	--	35
Pachyramphus aglaiae	--	--	--	--	--	--	--	--	--	--	--	--	--	2	4	24	5	--	35
Thamnophilus atrinucha	--	--	--	--	--	10	1	10	14	--	--	--	--	--	--	--	--	--	35
Xiphorhynchus susurrans	--	--	--	--	2	17	1	15	--	--	--	--	--	--	--	--	--	--	35
Thryothorus rufalbus	--	--	--	--	--	--	--	--	--	--	--	--	--	1	17	--	16	--	34
Amazona auropalliata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	12	10	9	33
Myiarchus nuttingi	--	--	--	--	--	--	--	--	--	--	--	--	--	--	8	--	11	14	33
Tangara icterocephala	--	--	--	--	--	1	--	5	27	--	--	--	--	--	--	--	--	--	33
Aratinga finschi	11	5	2	1	3	--	1	7	--	1	--	1	--	--	--	--	--	--	32
Thryothorus modestus	--	--	--	--	15	--	3	--	1	--	--	--	--	--	--	--	13	--	32
Anthracothorax prevostii	2	7	5	1	1	--	--	1	--	--	1	2	2	1	2	2	4	--	31
Hirundo rustica	--	--	2	3	1	--	1	--	--	--	--	--	2	14	1	7	--	--	31
Parula pitiayumi	--	--	--	--	--	--	--	9	21	--	--	--	--	--	--	--	--	--	30
Todirostrum nigriceps	--	--	--	--	--	20	--	6	4	--	--	--	--	--	--	--	--	--	30
Cercomacra tyrannina	--	--	--	--	--	9	1	17	2	--	--	--	--	--	--	--	--	--	29
Butorides virescens	--	1	3	--	--	--	--	--	--	11	1	1	5	6	--	--	--	--	28
Glaucidium brasilianum	--	--	--	--	--	--	--	--	--	--	1	--	4	1	1	4	13	4	28
Glyphorynchus spirurus	--	--	--	--	--	18	--	1	9	--	--	--	--	--	--	--	--	--	28
Thalurania colombica	--	--	--	--	--	9	--	7	12	--	--	--	--	--	--	--	--	--	28
Tinamus major	--	--	--	--	--	--	--	7	21	--	--	--	--	--	--	--	--	--	28
Mionectes oleagineus	--	--	--	--	--	11	--	4	12	--	--	--	--	--	--	--	--	--	27
Penelope purpurascens	--	--	--	--	--	1	--	3	2	--	--	--	--	--	--	--	8	12	26
Pipra mentalis	--	--	--	--	--	1	--	--	25	--	--	--	--	--	--	--	--	--	26
Baryphthengus martii	--	--	--	--	--	2	3	15	5	--	--	--	--	--	--	--	--	--	25
Psarocolius wagleri	--	--	--	--	--	11	--	3	11	--	--	--	--	--	--	--	--	--	25
Microcerculus marginatus	--	--	--	--	--	9	--	3	12	--	--	--	--	--	--	--	--	--	24
Myiodynastes luteiventris	--	--	--	--	--	--	--	--	--	--	--	1	1	2	4	7	3	6	24
Trogon rufus	--	--	--	--	--	5	--	9	9	--	--	--	--	--	--	--	--	--	23
Xenops minutus	--	--	--	--	--	5	--	3	14	--	--	--	--	--	--	--	1	--	23
Leptotila cassini	--	--	--	--	--	7	--	13	2	--	--	--	--	--	--	--	--	--	22
Icterus prosthemelas	2	--	--	3	4	5	7	--	--	--	--	--	--	--	--	--	--	--	21
Molothrus aeneus	--	1	--	1	12	--	5	1	--	--	--	--	--	1	--	--	--	--	21
Phaeothlypis fulvicauda	--	--	--	--	--	3	--	4	14	--	--	--	--	--	--	--	--	--	21
Amazilia saucerrottei	--	--	--	--	--	--	--	--	--	--	--	2	--	1	1	2	6	8	20
Amazona autumnalis	--	--	--	--	--	4	--	5	6	--	--	--	--	--	--	--	4	1	20
Cathartes aura	--	--	--	11	--	--	--	4	--	--	1	--	--	--	2	--	2	--	20
Hylocichla mustelina	--	--	--	--	--	1	--	15	4	--	--	--	--	--	--	--	--	--	20
Laterallus albigularis	--	--	--	--	12	3	1	4	--	--	--	--	--	--	--	--	--	--	20
Buteo platypterus	--	--	--	--	--	6	--	2	--	--	--	--	--	--	2	--	2	7	19
Cymbilaimus lineatus	--	--	--	--	--	--	--	18	--	--	--	--	--	--	--	--	1	--	19
Pachyramphus cinnamomeus	--	--	--	--	1	4	--	11	3	--	--	--	--	--	--	--	--	--	19
Formicarius analis	--	--	--	--	--	--	--	8	10	--	--	--	--	--	--	--	--	--	18
Geothlypis poliocephala	--	--	--	--	4	--	--	1	--	--	--	--	--	3	10	--	--	--	18
Poecilotriccus sylvia	--	--	--	--	--	1	--	--	2	--	--	--	--	--	--	--	13	1	17
Stelgidopteryx ruficollis	1	1	--	--	4	--	6	4	--	--	--	--	--	--	--	--	--	--	16
Stelgidopteryx serripennis	1	1	1	1	--	--	7	4	--	--	--	--	--	--	--	1	--	--	16
Ortalis cinereiceps	--	--	--	--	2	4	--	6	3	--	--	--	--	--	--	--	--	--	15
Xiphorhynchus lachrymosus	--	--	--	--	--	2	--	1	12	--	--	--	--	--	--	--	--	--	15
Celeus loricatus	--	--	--	--	--	--	--	5	9	--	--	--	--	--	--	--	--	--	14
Lophotriccus pileatus	--	--	--	--	--	--	--	4	10	--	--	--	--	--	--	--	--	--	14
Aratinga nana	--	--	--	--	4	3	1	1	4	--	--	--	--	--	--	--	--	--	13

Appendix III – Reduced species list (observed 3 or more times)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
Colonia colonus	--	--	--	--	--	--	1	12	--	--	--	--	--	--	--	--	--	--	13
Empidonax flaviventris	--	--	--	--	--	4	--	--	2	--	--	--	--	--	1	--	1	5	13
Hylocharis eliciae	--	--	--	--	--	--	--	--	--	--	--	--	--	--	6	1	3	3	13
Morococcyx erythropygus	--	--	--	--	--	--	--	--	--	--	--	--	--	1	2	--	9	1	13
Myiopagis viridicata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	7	6	13
Oncostoma cinereigulare	--	--	--	--	--	1	--	1	--	--	--	--	--	--	--	--	11	--	13
Caryothraustes poliogaster	--	--	--	--	--	--	4	5	3	--	--	--	--	--	--	--	--	--	12
Colinus cristatus	--	--	--	--	--	--	--	--	--	--	--	--	--	8	4	--	--	--	12
Crax rubra	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4	8	12
Heliothryx barroti	--	--	--	--	--	5	--	4	3	--	--	--	--	--	--	--	--	--	12
Legatus leucophaius	--	--	1	1	7	--	--	2	1	--	--	--	--	--	--	--	--	--	12
Pyrilia haematotis	--	--	--	--	--	3	1	2	4	--	--	1	--	--	--	--	1	--	12
Sittasomus griseicapillus	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	3	8	12
Bubulcus ibis	1	--	--	--	3	--	1	4	--	--	--	--	--	1	--	1	--	--	11
Chlorophanes spiza	--	--	--	--	--	2	--	1	8	--	--	--	--	--	--	--	--	--	11
Mniotilta varia	--	--	--	--	--	2	--	2	2	--	--	--	--	--	--	--	1	4	11
Tangara gyrola	--	--	--	--	--	--	--	2	9	--	--	--	--	--	--	--	--	--	11
Dacnis venusta	--	--	--	--	--	1	--	4	5	--	--	--	--	--	--	--	--	--	10
Empidonax virescens	--	--	--	1	--	4	--	--	2	--	--	--	--	--	--	--	--	3	10
Mesembrinibis cayennensis	--	--	--	--	--	8	--	1	1	--	--	--	--	--	--	--	--	--	10
Microchera albocoronata	--	--	--	--	--	--	--	--	10	--	--	--	--	--	--	--	--	--	10
Tachyphonus rufus	--	--	2	3	1	--	4	--	--	--	--	--	--	--	--	--	--	--	10
Xiphorhynchus flavigaster	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	8	10
Crypturellus boucardi	--	--	--	--	--	--	--	5	4	--	--	--	--	--	--	--	--	--	9
Euphonia anneae	--	--	--	--	--	--	--	--	9	--	--	--	--	--	--	--	--	--	9
Heliomaster constantii	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	3	5	9
Jacana spinosa	--	--	--	--	5	--	--	2	--	--	--	--	--	--	2	--	--	--	9
Pheucticus ludovicianus	1	--	--	1	2	--	1	1	--	--	--	1	1	1	--	--	--	--	9
Piranga ludoviciana	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4	5	9
Querula purpurata	--	--	--	--	--	9	--	--	--	--	--	--	--	--	--	--	--	--	9
Tachyphonus delatrii	--	--	--	--	--	--	--	1	8	--	--	--	--	--	--	--	--	--	9
Tyrannus forficatus	--	--	--	--	--	--	--	--	--	--	--	--	--	4	3	1	1	--	9
Galbula ruficauda	--	--	--	--	--	--	--	8	--	--	--	--	--	--	--	--	--	--	8
Synallaxis brachyura	--	--	--	--	7	--	1	--	--	--	--	--	--	--	--	--	--	--	8
Taraba major	--	--	--	--	--	2	--	6	--	--	--	--	--	--	--	--	--	--	8
Basileuterus culicivorus	--	--	--	--	--	--	--	--	7	--	--	--	--	--	--	--	--	--	7
Catharus ustulatus	--	--	--	--	--	3	--	2	1	--	--	--	--	--	--	--	--	1	7
Chlorothraupis carmioli	--	--	--	--	--	--	--	--	7	--	--	--	--	--	--	--	--	--	7
Dendroica fusca	--	--	--	--	--	1	--	1	4	--	--	--	--	--	1	--	--	--	7
Lipaugus unirufus	--	--	--	--	--	--	--	--	7	--	--	--	--	--	--	--	--	--	7
Micrastur semitorquatus	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	5	1	7
Microrhopias quixensis	--	--	--	--	--	1	--	3	3	--	--	--	--	--	--	--	--	--	7
Oporornis philadelphia	--	--	--	--	4	--	--	--	1	--	--	--	--	--	2	--	--	--	7
Rhytipterna holerythra	--	--	--	--	--	--	--	4	3	--	--	--	--	--	--	--	--	--	7
Sturnella militaris	--	--	--	--	--	--	3	4	--	--	--	--	--	--	--	--	--	--	7
Ara ambiguus	--	--	--	--	--	2	--	--	4	--	--	--	--	--	--	--	--	--	6
Basileuterus tristriatus	--	--	--	--	--	--	--	1	5	--	--	--	--	--	--	--	--	--	6
Coccyzus minor	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	5	6
Dendrocygna autumnalis	--	--	--	--	--	--	--	--	--	--	1	--	--	2	2	--	1	--	6
Dryocopus lineatus	--	--	--	--	--	--	--	5	--	--	--	1	--	--	--	--	--	--	6
Herpetotheres cachinnans	--	--	--	--	--	--	1	--	--	--	--	--	--	1	1	--	2	1	6
Myiodynastes maculatus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	4	6
Phaethornis guy	--	--	--	--	--	--	--	1	5	--	--	--	--	--	--	--	--	--	6
Ramphocelus sanguinolentus	--	--	--	--	--	--	--	5	1	--	--	--	--	--	--	--	--	--	6
Tangara inornata	--	--	--	--	--	--	--	6	--	--	--	--	--	--	--	--	--	--	6
Catharus aurantiirostris	--	--	--	--	3	--	--	--	2	--	--	--	--	--	--	--	--	--	5

Contopus virens	--	--	--	--	--	2	--	--	--	--	--	--	--	--	3	--	--	--	5
Cyanerpes lucidus	--	--	--	--	--	--	1	3	1	--	--	--	--	--	--	--	--	--	5
Cyanocompsa cyanoides	--	--	--	--	--	3	--	--	2	--	--	--	--	--	--	--	--	--	5
Mitrospingus cassinii	--	--	--	--	--	--	--	3	2	--	--	--	--	--	--	--	--	--	5
Myiornis atricapillus	--	--	--	--	--	--	--	1	4	--	--	--	--	--	--	--	--	--	5
Sayornis nigricans	3	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	5
Tachycineta albilinea	--	--	--	--	--	--	5	--	--	--	--	--	--	--	--	--	--	--	5
Tigrisoma mexicanum	--	--	--	--	--	--	--	--	--	--	--	--	--	4	--	--	1	--	5
Vermivora chrysoptera	--	--	--	--	1	--	--	3	1	--	--	--	--	--	--	--	--	--	5
Wilsonia canadensis	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--	--	1	5
Ara macao	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	2	4
Aramides cajanea	--	--	--	--	--	1	--	3	--	--	--	--	--	--	--	--	--	--	4
Buteo nitidus	--	--	--	--	--	--	--	--	--	--	--	1	--	1	2	--	--	--	4
Contopus sordidulus	--	--	--	--	--	2	--	--	1	--	--	--	--	1	--	--	--	--	4
Icterus spurius	--	--	--	--	1	--	--	--	--	--	--	1	--	2	--	--	--	--	4
Megascops cooperi	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4	--	4
Odontophorus leucolaemus	--	--	--	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	4
Passerina ciris	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	3	4
Seiurus aurocapilla	--	--	--	--	--	--	--	1	--	--	--	--	--	--	1	--	1	1	4
Tapera naevia	--	--	--	--	3	1	--	--	--	--	--	--	--	--	--	--	--	--	4
Tityra inquisitor	--	--	--	--	1	1	--	2	--	--	--	--	--	--	--	--	--	--	4
Wilsonia citrina	--	--	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--	4
Wilsonia pusilla	--	--	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--	4
Carpodectes nitidus	--	--	--	1	--	1	--	--	1	--	--	--	--	--	--	--	--	--	3
Ciccaba virgata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	3
Coccyzus americanus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	2	--	3
Corapipo altera	--	--	--	--	--	--	--	1	2	--	--	--	--	--	--	--	--	--	3
Dumetella carolinensis	--	--	--	--	--	--	--	1	2	--	--	--	--	--	--	--	--	--	3
Dysithamnus striaticeps	--	--	--	--	--	1	--	--	2	--	--	--	--	--	--	--	--	--	3
Florisuga mellivora	--	--	--	--	--	--	1	2	--	--	--	--	--	--	--	--	--	--	3
Hylopezus perspicillatus	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	3
Icterus pectoralis	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	--	--	3
Klais guimeti	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	--	--	--	3
Leptopogon superciliaris	--	--	--	--	--	--	--	1	2	--	--	--	--	--	--	--	--	--	3
Melozone biarcuata	--	--	--	--	3	--	--	--	--	--	--	--	--	--	--	--	--	--	3
Monasa morphoeus	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	3
Myadestes melanops	--	--	--	--	--	--	--	2	1	--	--	--	--	--	--	--	--	--	3
Myrmeciza immaculata	--	--	--	--	--	--	--	1	2	--	--	--	--	--	--	--	--	--	3
Notharchus hyperrhynchus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	--	3
Pulsatrix perspicillata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	2	3
Saltator grossus	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	3
Setophaga ruticilla	--	--	--	--	--	2	--	1	--	--	--	--	--	--	--	--	--	--	3
Tachyphonus luctuosus	--	--	--	--	--	1	--	--	2	--	--	--	--	--	--	--	--	--	3
Trogon collaris	--	--	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	3
Tyrannus verticalis	--	--	--	--	--	--	--	--	--	--	--	--	1	1	1	--	--	--	3
Vireo olivaceus	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	1	1	3
Vireo philadelphicus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	3
Total No. Observations	1041	1273	1301	1349	1573	1734	1649	2419	1495	1040	1148	1248	1431	1195	1519	1302	1783	1495	25995