AN ABSTRACT OF THE DISSERTATION OF

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Human alteration of natural landscapes leads to biodiversity loss, often from a combination of area effects and fragmentation effects. Smaller habitat patches support fewer species than large ones and incur additional consequences from isolation. Efforts to preempt biodiversity loss from insular habitat fragments are complicated by individualistic species responses and time-delayed extinctions. Understanding how human activity affects bird communities in species rich, disturbance sensitive tropical forests is a conservation priority. Nevertheless, tropical ecosystems remain under-studied; long-term species inventory data from tropical forests are rare.

This dissertation combines a unique set of spatially extensive avian inventories from lowland forests in central Panama with a long history of bird surveys from Barro Colorado Island (BCI), a well-studied land-bridge island isolated within the Panama Canal, to better inform our understanding of how human-altered environments drive long-term changes in tropical forest bird communities. First, I evaluated trait predictors of species extinctions from BCI. I assessed to what degree changes in BCI's bird community can be explained by loss of species sensitive to fragmentation-associated environmental drying. In my second data chapter, I examined the pattern of delayed extinctions on BCI among different species groups. I used species-area models and extinction trends to predict how many species BCI might still lose and how long these remaining species losses could take. Lastly, I focused on lowland forest patches within the Canal zone to evaluate how increasing urbanization influences the use of forest patches by tropical birds, with a focus on species composition, traits, and phylogenetic diversity.

Birds are likely to have disappeared from BCI if they had small populations in the 1920s, specialize on terrestrial arthropods, and are sensitive to forest moisture conditions. As a consequence of

extreme, persistent declines among understory insectivores associated with wet forests, the bird community on BCI has significantly shifted to resemble forest bird communities on the drier portion of the rainfall gradient. Extinctions accelerated 40-60 years following isolation and the island no longer supports the number of species expected for its size and amount of annual precipitation. From six to 92 additional species may be lost from BCI over the next one to nine centuries. Enduring species losses on BCI appear to be a product of habitat loss, edge effects, and negative consequences of isolation for dispersal-limited birds. In lowland forests of the Canal zone, urbanization is associated with community simplification and decreased compositional similarity without subsequent loss of functional diversity. Urban forests broadly favor good dispersers with short development periods, and recent evolutionary histories.

My results reveal the important roles of connectivity, dispersal ability, and sensitivity to local habitat conditions structuring avian community composition in tropical forests of central Panama. Limited human activity and access to large, protected forest tracts appear to be key drivers of avian community composition for both BCI and urban forest fragments. Dispersal-limited tropical birds with small populations, especially habitat specialists sensitive to moisture conditions and human disturbance, may be at greatest risk of extinction in insular rainforest fragments.

Human Alteration of a Neotropical Landscape Drives Long-term Changes in its Forest Bird Communities

by
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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Jenna R. Curtis, Author

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CONTRIBUTION OF AUTHORS

Dr. W. Douglas Robinson contributed to all aspects of this dissertation. Drs. Ghislain Rompré and Randall P. Moore collected and contributed bird survey data. Dr. Suzanne Austin contributed avian life history data and assisted in interpreting results for Chapter 4. Dr. Bruce McCune contributed to statistical analyses for Chapter 2. All authors reviewed results, commented on writing, and assisted with manuscript preparation for their respective chapters.

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DEDICATION

This dissertation is dedicated to ornithologists from underrepresented populations. May an increasingly diverse community of ecologists receive the opportunity to study and protect our one, shared planet.

CHAPTER 1. GENERAL INTRODUCTION

Neotropical rainforests are among the most biodiverse systems on the planet, yet they face an "extinction crisis", losing species at an estimated rate between 14,000 and 40,000 per year (Hughes et al. 1997). Tropical rainforests incur the largest net annual forest losses (Keenan et al. 2015) and as much as 85% of all global forest loss (Whitmore 1997). Lowland tropical rainforests are particularly at-risk to habitat disturbance, loss, and fragmentation given their relative accessibility to anthropogenic activity (Robinson et al. 2004, Rompré et al. 2007, Laurance et al. 2012, Sodhi et al. 2013). Yet tropical communities remain relatively understudied compared to temperate environments (Turner 1996). The limited spatial and temporal scope of most studies in the neotropics leave the long-term effects of tropical forest fragmentation and disturbance unclear (Lindenmayer and Fischer 2013).

Habitat fragmentation alters elements of tropical ecosystems in several major ways. Perhaps the most well-studied consequences of habitat loss are area effects (Arrhenius 1921, Gleason 1925, MacArthur and Wilson 1963). Area effects occur when large, non-insular habitats are separated into smaller patches, and some populations residing within those patches decline. Area is a strong predictor of species richness and diversity; small habitat patches have long been observed to support smaller populations and fewer species than large ones (Bierregaard et al. 1992, Rosenzweig 1995, Harrison and Bruna 1999). Yet loss of area *per se* is not the only driver of biodiversity loss from habitat fragments. Forest fragments have proportionally more edge habitat than non-insular forests and are therefore prone to deleterious "edge effects". Edge effects include changes in abiotic conditions and vegetation characteristics, and increased incidence of invasive species (see reviews in Laurance 2004, Lindenmayer and Fischer 2013). Breaking of habitat into disjunct fragments also alters how ecosystems are regulated, affecting connectivity, gene flow, dispersal, movement and behavior, and other mechanisms by which communities are structured (Stouffer and Bierregaard 1995, Moore et al. 2008, Ibarra-Macias et al. 2011a, Lindenmayer and Fischer 2013).

Urbanization is another major driver of global ecosystem modification and biodiversity loss (Marzluff et al. 2001). Urban environments represent a profound and irreversible form of land conversion unique among types of anthropogenic disturbance (Faeth et al. 2001, Chace and Walsh 2006, Chamberlain et al. 2009). Increasing intensity and frequency of human disturbance within fragmented landscapes is associated with altered abiotic processes (McDonnell et al. 1997, Lambin et al. 2003, Grimm et al. 2008), reduced ecosystem services (Alberti 2010, Wang et al. 2019), as well as biodiversity loss and community homogenization (Cam et al. 2000, Blair 2001, McKinney 2006). Despite abundant research on the ecological consequences of urbanization in temperate regions (see reviews in Marzluff 2001, Chace and Walsh 2006) tropical urbanization studies are lacking (Ortega-Álvarez and MacGregor-

Fors 2011a, Escobar-Ibáñez and MacGregor-Fors 2017). Results from urban studies at northern latitudes may not be transferrable to biodiverse tropical ecosystems where species have had less time to adapt to human activity (Sol et al. 2013, Jokimäki et al. 2016).

Reduction in available habitat by fragmentation and urbanization results in species losses over an extended period of time (Bierregaard et al. 1992, Terborgh 1992, Stouffer and Bierregaard 1995). Given only half of all predicted extinctions resulting from habitat loss or fragmentation may occur in the first 50 years (Brooks et al. 1999) centuries may be necessary to fully document species extinctions following isolation (Ewers and Didham 2006). This time-delayed process of species loss from insular habitat patches is known as faunal relaxation (Diamond 1972). Faunal relaxation results in species depauperate communities with dissimilar ecosystem characteristics compared to intact habitats (Harrison and Bruna 1999, Ewers and Didham 2006). Estimating the magnitude and duration of faunal relaxation are important steps in establishing long-term conservation priorities for isolated forest fragments (Kuussaari et al. 2009).

Birds are frequently used to study the effects of human disturbance and habitat fragmentation (Turner 1996, Escobar-Ibáñez and MacGregor-Fors 2017). Birds are responsive to environmental pressures and good indicators of ecological change (Temple and Wiens 1989, Crick 2004). Avian surveys are relatively inexpensive and easy to conduct. Visual and vocal characteristics for most neotropical bird species have become better known in recent decades, making complete species inventories possible in species-rich tropical environments (Robinson et al. 2004). Neotropical forests hold an important proportion of global avifauna (BirdLife International 2013) and the densest concentration of forest birds on the planet (Stotz et al. 1996). Tropical birds provide valuable ecological services, and changes in avian communities can have measurable consequences for tropical ecosystems (Sekercioglu et al. 2004, Sekercioglu 2006).

The considerable species richness and high sensitivity of tropical ecosystems to habitat degradation suggests even greater consequences of anthropogenic activity for avifauna at low latitudes (Laurance and Bierregaard 1997, Gaston et al. 2003, Stratford and Robinson 2005, Leveau et al. 2017). Lack of extreme seasonal fluctuations in temperature and resources in tropical forests may produce idiosyncratic responses to human disturbance (Ortega-Álvarez and MacGregor-Fors 2011a, Filloy et al. 2015). Tropical bird populations are generally less dense and have a greater proportion of rare or low-abundance species (Karr 1982a, Terborgh et al. 1990). Many tropical bird species possess poor dispersal abilities (Stratford and Robinson 2005, Moore et al. 2008, Robinson and Sherry 2012), in theory leading to greater danger of extinction for isolated populations.

Latin America is the second most rapidly developing region in the world (Cincotta et al. 2000, Maria et al. 2017), with over 81% of the population currently living in urban areas (United Nations 2018). In central Panama, a steep natural precipitation gradient and broad range of habitat types from primary forest to dense metropolis within a small area presents a unique opportunity to evaluate how dynamic environmental conditions influence local bird community composition. 55% of Panama's 972 bird species occur within the vicinity of the Panama Canal (Rompré et al. 2007). Maintaining ecosystem integrity within tracts of highly diverse but unprotected forest near the boundaries of urban areas is a conservation priority (Condit et al. 2001, Robinson et al. 2004).

To-date, very few studies have evaluated forest bird community composition in lowland forests of central Panama (Petit et al. 1999, Robinson et al. 2004, Rompré et al. 2007, 2009). This contrasts with a uniquely extensive long-term avian dataset collected on a single land-bridge island within the Panama Canal. Barro Colorado Island (BCI) is a 1562 ha former hilltop isolated from the mainland from 1910-1914 during construction of the Panama Canal. BCI represents "the most thoroughly studied of all tropical forest fragments" (Robinson 1999). Starting in 1923 and continuing for 86 of the last 94 years, visiting biologists kept records of bird observations on the island. The most active periods of ornithological research on BCI were: 1924-1939 (Chapman 1929, 1938)*;* 1944-1971 (Eisenmann 1952, Willis 1974, Willis and Eisenmann 1979); and 1976-1999 (Karr 1982a, Robinson 2001, G. Angehr *unpublished data*). Regular surveys of the avian community continue on BCI to this day. Although the loss of species from BCI is well-studied (Willis 1974, Karr 1982b, Robinson 1999, 2001), the extinction process and its effects on avian community composition have not been assessed. The unique century-long history of ornithological surveys on BCI, in combination with recent avian inventories from surrounding lowland forests in a complex Central American landscape, provides a valuable opportunity to evaluate factors associated with avian community change on multiple spatial and temporal extents.

Objectives: My dissertation examines how forest fragmentation, long-term isolation, and urbanization drive pervasive but idiosyncratic differences in tropical forest bird communities of Central Panama over time and space. The first two data chapters relate the temporally extensive dataset from BCI with spatially extensive avian inventories from forest patches in central Panama to quantify and describe long-term species losses on BCI. Chapter 2 characterizes changes in avian community composition over time and identifies species attributes associated with ongoing avian extinctions from BCI. I consider to what extent changes in BCI's avian assemblage can be explained by fragmentation-associated climatic drying and a loss of moisture-sensitive species. My third chapter calculates the number of additional species losses on BCI expected in the future, as well as the time remaining until extinctions on BCI are fully realized. I also build multimodel species-area relationships (SARs) to estimate the current species richness capacity of BCI based on its size relative to other lowland forests. Expanding the scope of investigation beyond BCI, Chapter 4 looks at terrestrial lowland forests along the Panama Canal to evaluate how increasing intensity of urbanization influences the use of forest patches by tropical birds, with a focus on species composition, attributes, and phylogenetic diversity. Combining old data and new techniques, my dissertation provides a more comprehensive understanding of how human alteration of the landscape drives long-term changes in tropical forest bird communities.

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CHAPTER 2. CLIMATIC DRYING, ABUNDANCE, AND TERRESTRIAL INSECTIVORY ELEVATE EXTINCTION RISK FOR BIRDS IN A PROTECTED TROPICAL FOREST FRAGMENT

Jenna R. Curtis, W. Douglas Robinson, Ghislain Rompré, Randall P. Moore, and Bruce McCune

Abstract

Alteration of Earth's landscapes by human activities leads to the attrition of biodiversity, often as a consequence of human disturbance and because small remnants preserve fewer species than large ones. Recommendations for maximizing species richness in altered landscapes typically focus on preservation of large habitat patches protected from human activities. Despite a century of protection from human disturbance, 27% of the 228 bird species initially detected on Barro Colorado Island (BCI), a large forest fragment isolated by waters of the Panama Canal, are now absent. We used the uniquely long history of avian surveys from BCI, as well as bird surveys in the surrounding lowland forests, to characterize changes in community composition over time and associate species attributes with extinction risk. The species assemblage on BCI has significantly shifted from one typical of forests along the wetter portions of a strong rainfall gradient to one resembling bird communities in forests on the drier portion of the rainfall gradient. Even with no consistent trend in annual rainfall over the century, bird species associated with interior of wet forests were more likely to now be absent. In addition to sensitivity to forest moisture conditions, species are more likely to have disappeared if they had low abundances in the 1920-30s, and if they are dietary specialists on terrestrial arthropods. Isolated populations of drought-intolerant birds appear to be critically stressed by a combination of local drying effects of isolation and more frequent intense drought. Even with its large size and protection from human disturbance, subtle climatic change has contributed to species loss on BCI.

Introduction

Deforestation and habitat fragmentation are among the greatest threats to global biodiversity, particularly in species-rich lowland neotropical rainforests (Turner 1996, Harrison and Bruna 1999, Pimm and Raven 2000, Robinson et al. 2004, Laurance 2007, Vié et al. 2009, Bradshaw et al. 2009). Certain functional and ecological traits predispose some species to greater risk of extinction in isolated fragments. Among birds, species at highest risk are hypothesized to be dietary specialists with small populations (Şekercioğlu et al. 2002, Henle et al. 2004, Stratford and Robinson 2005, Robinson and Sherry 2012) as well as large-bodied birds (Terborgh 1974, Karr 1982a) and/or species that experience greater nest depredation within fragments (Loiselle and Hoppes 1983, Sieving 1992, Laurance et al. 1993). An additional mechanism that has received less attention is microclimatic change owing to greater light penetration, increased ambient temperatures, wind disturbance, and desiccation in forest fragments (Bierregaard et al. 1992, Camargo 1993, Camargo and Kapos 1995, Laurance 2004, Laurance and Curran 2008, Ingwell et al. 2010). Tropical forest birds sensitive to changes in light regimes, temperatures, or moisture conditions may no longer find suitable conditions in fragments (Karr and Freemark 1983, Turner 1996, Patten and Smith-Patten 2012, Stratford and Stouffer 2015).

Despite multiple attempts to elucidate the drivers of species loss from tropical forest fragments (Kattan et al. 1994, Christiansen and Pitter 1997, Sieving and Karr 1997, Ford et al. 2001, Laurance et al. 2002, Sigel et al. 2006, Patten and Smith-Patten 2012, Robinson and Sherry 2012), very few studies have simultaneously evaluated multiple mechanisms. In addition, consequences of fragmentation may take decades to manifest. Just half of the total predicted extinctions in large fragments occur within the first 25-50 years (Brooks et al. 1999, Ferraz et al. 2003, Ewers and Didham 2006). Yet most of the longest-running forest fragmentation studies span 35 years or less (Bierregaard et al. 1992, Laurance et al. 2002, Stouffer et al. 2006, Sigel et al. 2006, Sodhi et al. 2013, King et al. 2018). Lack of multi-decadal studies leave the quantification of species losses in fragments and evaluation of the responsible mechanisms incomplete (Lindenmayer and Fischer 2013).

A century-long history of ornithological surveys in humid forests of southern Central America provides an opportunity to evaluate hypotheses for species extirpation. Barro Colorado Island (BCI) in Gatun Lake, Panama, is a former rainforest hilltop isolated since 1914 from nearby lowland forests. Uniquely, the BCI bird community has been inventoried by highly skilled ornithologists for 90 years. BCI also sits amidst one of the most thoroughly surveyed regions for birds in all the tropics (Robinson et al. 2004, Rompré et al. 2007). Species distributions across the region are typically associated with annual rainfall amounts (Robinson et al. 2004, Rompré et al. 2007). Forests along the narrow isthmus experience a steep rainfall gradient with northern sites receiving 3500 mm and the most southern sites, only 50 km away receiving 1400 mm ((ACP 2016). The long history of bird study in the region provides an unprecedented level of detail on species' distributions, habitat associations, natural and life history traits and abundances. Thus, BCI presents a unique opportunity to evaluate predictors of biotic community change after habitat isolation.

We identified species attributes associated with avian extinctions and characterized shifts in community composition in order to test associations between species losses and common predictors of fragmentation sensitivity including habitat association, body mass, historical abundance, nest height and type, diet, and foraging height. We also developed a novel variable to assess a species' sensitivity to environmental drying in central Panama, a previously untested driver of species losses on BCI (Karr

1982b). To further evaluate the degree to which community change is influenced by environmental drying, we compared BCI species inventories over the last century relative to regional bird communities that vary across the strong precipitation gradient. Our goal was to evaluate whether changes in the avifaunal assemblage on BCI are characterized by loss of moisture-sensitive species which no longer find adequate environmental conditions on the island, thus recognizing the contribution of subtle climatic change to ongoing species losses in an otherwise undisturbed forest fragment.

Methods

Barro Colorado Island (BCI) is a 1562 ha land-bridge island in Gatun Lake formed in 1914 by construction of the Panama Canal. Average annual precipitation is approximately 2600 mm, with the most rainfall occurring May through December (ACP 2016). The vegetation on BCI is primarily mature semi-deciduous lowland tropical forest from 100 to >500 years old (Foster and Brokaw 1982, Leigh 1999). Younger secondary forest regenerating from previous human disturbance covers approximately half of the island (Terborgh 1974). BCI is also the largest island in Gatun Lake and the most protected from human disturbance. At 1562-ha, it is large enough to support top predators such as large raptors and pumas. Protection from human activities is effective enough for BCI to support sizable populations of gamebirds, such as Crested Guan (*Penelope purpurascens*).

We obtained data from our own annual surveys (1996 to 2018) and from published lists of birds observed on BCI by highly skilled ornithologists from 1925-1994 (Chapman 1929, 1938, Eisenmann 1952, Willis 1974, Willis and Eisenmann 1979, Robinson 1999, 2001, G. Angehr *unpublished data*). Birds were inventoried using a variety of methods, from species lists collected during short visits to abundance estimates derived from comprehensive stationary point and transect counts. All surveys incorporated ad lib observations to some degree. We used detection/non-detection data because not all survey periods collected abundance information and the accuracy of such count data is difficult to quantify (Robinson 2001). We compiled these published observation records into lists of species present in seven non-overlapping time-periods: 1925-29, 1930-37, 1938-51, 1953-69, 1970-78, 1990-2000, and 2001-today. Because bird inventory effort varied across years, these "binned" years represent the most comparable periods of effort. We generated an additional species list from BCI representing predicted, future species composition 20 years from now based on current population trends and author experience. Species not reported as present during a given period were assumed absent. Several common species known to be difficult to identify or detect were missing from earlier datasets, likely due to incomplete knowledge of bird species at the time. We evaluated how those missing species affected our statistical results (Appendix B1).

To provide regional context for BCI, we incorporated bird inventory data from Panama Canal-adjacent “subregions” defined by political administration as well as topographic complexity, geology, and elevation (Rompré et al. 2007; Figure 2.1). We limited our scope of investigation to only those subregions adjacent to the Panama Canal, as these areas contain the assemblage of birds from which the avian community on BCI is most likely derived. Subregions span the entirety of physiographic and environmental variation along the Canal zone in central Panama and represent a strong natural precipitation gradient. Multiple avian inventory methods were implemented within each subregion from 1998 to 2005, including point counts, spot mapping, and standardized area searches (Rompré et al. 2007).

BCI has <0.02% urban land cover surrounding a scientific research station, and is otherwise forest, disturbed only by natural wind events. Mainland subregions along the Panama Canal range from <1% to over 97% urban land cover. Urbanized areas in this region have outsized effects on habitat and avian community composition (Rompré et al. 2007). Sampling units with one or more large cities within their boundaries, despite having as little as 5% total urban cover, generally contained depauperate bird communities in small, remnant patches of degraded forest amidst large zones of species-poor anthropogenically altered habitat. Our objective was to evaluate changes in the BCI bird community relative to comparable mainland habitats and bird communities. Because even lightly urbanized areas in central Panama appear to experience different structuring mechanisms than wholly forested areas, we removed subregions containing major cities with >5% urban cover from our analyses.

Species Traits

To focus our study on tropical forest-associated resident birds, we removed aquatic species as well as vagrants and non-breeding migrants from the dataset. For remaining species, we assigned habitat preference and residency status in the canal region based on published species accounts and extensive author experience (Robinson 1999, 2001, Robinson et al. 2000, 2004). Species were assigned preference for one of four habitat categories: open areas with little to no woody vegetative cover; edge habitat at the boundary of low, woody vegetation; the outer margins of forest of any age (forest edge); and interior of forest of any age. Residency status was classified as permanent resident or breeding migrant (*i.e.,* seasonally occurring nesting species).

For species detected on BCI during any inventory period, we considered an additional six categorical and two continuous attributes previously associated with extinction risk in tropical birds (Henle et al. 2004, Sodhi et al. 2004). We categorized abundance on BCI based on estimated total island-wide population at the time of isolation: common (> 100 individuals); occasional (10-100 individuals); or rare (<10 individuals). Regional abundance was considered but ultimately omitted due to strong correlations with several other variables. We applied one of four possible categories for a species' typical nesting height: ground (<1m); understory (1-5m); mid-story (>5m but below the canopy); or canopy (the top level of vegetation regardless of height). We used three categories for nest type: open cup (bowl, platform, or scrape); enclosed, roofed nests with a single entrance (*e.g.,* pendulum, pyriform, or pouch); or cavity nests in trees, burrows, or termite mounds. We assigned obligate brood parasites the nest attributes of their most common hosts.

We established six dietary guilds according to a species' primary food source: carnivores (vertebrates, snails, carrion, and occasional large arthropods); frugivores (fruits of any size); granivores (seeds and nuts); insectivores (insects and arthropods); nectarivores (flower nectar); and omnivores (generalists which consume food from more than one category). We used four categories for the typical height at which a species searches for food: terrestrial (<1m); understory (greater than >1m but below canopy); arboreal (uppermost canopy vegetation regardless of height); and raptorial hunters that pursue prey across all forest strata. Aerially foraging birds, such as vultures, swifts, swallows, and nighthawks, were omitted because their daily foraging ranges extend well away from BCI.

Our two continuous species attributes were body mass and an index of climatic tolerance. Body mass was the log-transformed mean across sexes from Dunning Jr. (2007). We used the integer linear distance between a species southernmost Canal zone occurrence and the southern entrance to the Panama Canal as a metric of climatic tolerance (henceforth "southern limit"). Geographic ranges of most bird species in central Panama begin in the wettest forests near the Caribbean Sea and extend some distance southward along the rainfall gradient until they either no longer occur in drier forests, or the south coast of the isthmus is reached. Species with low southern limits are distributed across the entire isthmus, reaching their southern distribution boundary somewhere near the Pacific Ocean. Those species tolerate warmer, drier environments than species with higher southern limits, which are restricted to northern, wetter portions of the rainfall gradient.

We further classified all forest birds detected on BCI as exclusively wet forest – those species occurring in forests receiving over 2000 mm of precipitation annually, or transisthmian – birds occurring in forests across the entire precipitation gradient from wet to dry forests. To test whether the proportion of wet forest-associated species now absent from BCI is significantly different from the proportion of absent transisthmian forest birds, we performed two-proportion z-tests, applying a Yates continuity correction where necessary to account for small sample sizes.

Environmental Data

To help characterize the nature of avian community structure across the Canal zone, we included environmental variables potentially associated with avian species distributions in the tropics (Rompré et al. 2007). These included altitude, area, degree of forest fragmentation, percent forest cover, percent urban land cover, plant species richness, and total annual precipitation (see Table B.2 for definitions and sources). We also considered forest age, which was previously found to be informative (Rompré et al. 2007). Forest age was treated as a continuous variable because categories in Rompré et al. (2007) represented a consistent, incremental series of time bins: (1) young secondary forest disturbed <100 years ago; (2) mature secondary forest disturbed 100-500 years ago; and (3) mature primary forest not logged or cultivated for at least 500 years. Only a single set of environmental values were used for BCI regardless of year because we assume changes in the selected environmental factors on BCI over time are very small relative to the overall spatial variation in environmental factors. Temperature was not considered in analyses because daily and annual temperatures did not vary considerably across subregions.

Statistical Analyses

Analyses were performed in R 3.5.2 (R Core Team 2018) and PC-ORD 7.1 (McCune and Mefford 2011). We identified important traits associated with extirpation from BCI using a combination of feature selection, logistic regression, and multiple metrics of predictor importance. Our response was whether or not a bird species is now absent from BCI. We defined "absent" birds as any species once considered a permanent resident that has gone undetected on BCI for at least a decade and has not demonstrated the capacity to re-establish breeding populations post-isolation.

Feature Selection and Regression: We used feature selection to eliminate explanatory variables not relevant to species persistence on BCI to prevent model overfitting. Feature selection was performed with the Boruta package (Kursa and Rudnicki 2010) using default settings and 1000 runs. Boruta is an iterative, wrapper-based method built around the Random Forest classification algorithm that compares the importance score (typically mean accuracy loss) of attributes against re-shuffled copies of the data. Attributes that perform worse than the re-shuffled data are dropped. This process is repeated for a specified number of runs, or until all features are confirmed important or rejected. Unlike stepwise selection procedures, Boruta identifies all relevant features instead of the minimal optimal set. This selection approach is best when the objective is to explore relationships between variables and the response, rather than produce a generalizable or predictive model (Kursa and Rudnicki 2010).

To investigate the relationships between important variables and persistence on BCI, we fitted a generalized linear model (GLM) using the stats package in R (R Core Team 2018). We found no evidence of multicollinearity or overdispersion in our data, so we performed regression with binomial distribution and logit link function. A logistic regression model incorporating granivores and/or arboreal foragers was not possible due to quasi-complete separation of the data (*i.e.,* certain combinations of predictor variables provided strong or perfect separation between extinct and remaining species) that was not resolved by a penalized maximum-likelihood method. Models with quasi-separation lack convergence for parameter estimation. To address this, we combined arboreal and raptorial foragers into a single category and omitted granivores from our final model. Interaction terms between diet and foraging height as well as local abundance and southern limit were considered but omitted due to lack of statistical significance.

We provide several measures of model performance. We used a likelihood ratio F-test to evaluate the significance of the reduction in residual deviance in the fitted model relative to a null model with no parameters. We tested model calibration using the le Cessie-van Houwelingen test in the rms package (Harrell Jr 2019). This test is an improved form of the Hosmer-Lemeshow goodness-of-fit test where well-fitting models show no significant differences between observed responses and predicted probabilities (Le Cessie and Van Houwelingen 1991). McFadden's pseudo-R^2 is a measure of model effectiveness conceptually and mathematically similar to R^2 for ordinary least squares regression (McFadden 1973, Menard 2000). Pseudo-R^2 scores of 0.2-0.4 should be interpreted as good model fit (McFadden 1977, Clark and Hosking 1986). We also used adjusted D^2 to measure the percentage of deviance explained by the fitted model accounting for the number of predictors and observations used (Guisan and Zimmermann 2000). Both D^2 and pseudo-R^2 values were calculated using the modEvA package (Barbosa et al. 2016).

We measured the contribution of individual species attributes to overall model fit using dominance analysis and hierarchical variance partitioning. Dominance analysis compares the contributions of individual predictors to changes in a chosen measure of model fit across all possible model subsets for a given set of predictors (Azen and Traxel 2009). "Dominant" predictors are those that consistently make larger contributions to model fit than other predictors across most (general dominance) or all (complete dominance) subsets of the full model. The resulting dominance score is the average contribution of a single predictor to model fit across combinations of predictors. Using the dominanceanalysis package (Navarrete and Soares 2019), we ranked predictor importance based on general dominance using McFadden's pseudo-R^2 as a measure of fit and estimated error using a bootstrapping procedure with 1000 runs. Hierarchical variance partitioning provides a relative measure of variable contribution as a percentage of overall model performance (Chevan and Sutherland 1991). After confirming monotonicity and normality in the residual structure, we used the hier.part package (Walsh and MacNally 2013) to perform variance partitioning with binomial distribution and log-likelihood as the performance metric. We performed a randomization procedure with 1000 runs to determine statistical significance of variable effects.

Non-parametric Ordination and Cluster Analysis: We used non-parametric analytical techniques to holistically evaluate temporal changes in avian community composition on BCI relative to spatial community variation along the Canal zone. Our response variable was the presence (response value of 1) or absence (response value of 0) of each bird species per sampling area. The initial dataset contained detection/non-detection values for 317 bird species detected at 14 non-urbanized mainland subregions, plus seven distinct BCI avian inventories and one hypothetical future BCI species list. Summary statistics of the initial dataset indicated a coefficient of variation (CV) of species totals of 55.8%, and CV of 22.8% for sampling unit totals. These values show low variability in marginal totals of the species matrix, such that relativizations would have little effect on the final ordination. We removed 18 bird species occurring in less than 5% of sampling units. Our secondary matrix of eight environmental variables was relativized by adjusting to standard deviates.

Outlier analysis using Sørensen distance identified one sampling area, Nueva Providencia (PRO), with a distance value more than 2 standard deviations greater than the mean distance between sites (SD = 3.5). PRO is isolated on the northeastern edge of Gatun Lake and not adjacent to any other evaluated subregion (Figure 2.1). This subregion contained low avian species richness relative to the average for non-urban mainland areas (120 species vs. mean richness of 198) and exhibited peripheral placement with repulsion on at least one axis in preliminary ordinations. PRO did not possess extreme or unusual values for any environmental variables. We believe this subregion was identified as an outlier because it was the only sampling unit on the northeastern side of the Canal zone and, without nearby avian communities of similar species composition, was not as easily ordinated in the context of the other subregions. Additional data from this general region would likely reduce the significance of PRO as an outlier. This sampling unit represents an area for which we have no other avian inventory data from predominantly forested habitat. Because we considered PRO to be within our target population, its bird inventory was as complete as other subregion inventories (Rompré et al. 2007), and we have no reason to doubt the accuracy of its data, we retained this subregion for analysis.

We performed cluster analysis to define groups of subregions with similar species composition. Our data consist of 8 current or historical inventories from BCI, but only one inventory from each mainland subregion. In cluster analysis, close grouping of repeated samples from the same location may mask important differences between those samples over time, especially if successive inventories are more similar to each other than they are to other years or locations. To demonstrate the greatest magnitude of transition between historical and current avian communities on BCI, we only used the earliest (1925-29) and most recent (2000-2018) species inventories in cluster analysis. Cluster analysis of sampling units (subregions) by species composition involved a hierarchical agglomerative clustering strategy with Sørensen distance and the average linkage method. We used the pvclust package (Suzuki et al. 2015), to perform multiscale bootstrap resampling for 10,000 cluster permutations and calculate the Approximately Unbiased (AU) probability value for each cluster. AU values of 95% or greater indicate strong statistical support for the existence of independent groups within the data (Suzuki and Shimodaira 2006).

To measure the strength of differences between groups of subregions in species space identified by hierarchical cluster analysis, we used the pseudo F-statistic generated by permutational, nonparametric multiple analysis of variance (PerMANOVA; Anderson 2001). This procedure generates a statistic analogous to Fisher's F-ratio by comparing the average distance within and between groups. F values close to 1 indicate variation between and within groups are similar, whereas values >1 suggest differences between clusters are greater than chance alone. A hypothesis test of the F-ratio was not possible because testing the observed ratio in the same space that the clusters were generated will always yield a significant result. We conducted analyses using Sørensen distance with cluster assignment as a fixed group (one-way design). Because PerMANOVA is sensitive to differences in group dispersion, we tested homogeneity of cluster variance using a permutational dispersion test (PERMDISP; Anderson 2006) that accommodates non-Euclidean distance measures. Both PerMANOVA and PERMDISP were conducted using the 'vegan' R package (Oksanen et al. 2013).

We ordinated sampling units and bird species in species space using nonmetric multidimensional scaling (NMDS) using Sorensen distances on random starting configurations for 250 runs on both real and randomized data. Ties in the distance matrix were not penalized. Statistical significance of the final stress was evaluated by randomization test comparing the observed final stress against that of data randomized by permuting the values within columns (species).

Results

The historical community of resident, non-aquatic, non-aerial birds on BCI before 1950 consisted of 228 species (Table B.3). Sixty-two bird species are now considered extinct on BCI, representing a 27.2% reduction in species richness. Six additional species may also be extinct but are difficult to detect, largely because of their nocturnal or wide-ranging habits. Those species are omitted from further analysis. Species associated with forest, edge, and open habitats experienced parallel declines, such that the proportion of species within habitat groups did not appear to change overall (Figure B.1). Species losses occurred without replacement; only one species (Great Kiskadee) colonized BCI after its isolation.

Nineteen additional species were detected on BCI after 1951 (Table B.4). Nearly half of these were vagrants unlikely to ever sustain resident breeding populations on BCI. Eight species are "ephemeral", transitory birds that only intermittently or periodically breed on the island. Four additional urban-associated species are experiencing range expansions in central Panama but have yet to establish stable, resident populations on BCI.

Extinction timing was significantly correlated with southern range limit and historical abundance and differed among habitat associations (Appendix B2). Missing species have an average southern limit 8.1km higher than remaining species (Appendix B3). Wet forest species exhibited higher average southern limits than transisthmian species or species associated with open habitats. A significantly greater proportion of wet forest birds disappeared from BCI (51.6% wet vs. 15.7 % transisthmian forest species absent; $z_{df=1} = 16.7$, $p < 0.001$; Figure B.3). This was also true when considering forest interior and edge species separately (forest interior $z_{df=1} = 7.9$, $p = 0.002$; forest edge $z_{df=1} = 7.21$ $p = 0.004$). We found no evidence that forest interior birds lost a greater proportion of species than forest edge-associated species in either wet or transisthmian forests (wet forests $z_{df=1} = 0.04$, $p = 0.58$; transisthmian forests $z_{df=1} = 0.05$, $p = 0.59$).

Feature Selection and Regression

Three important species attributes were significantly associated with species extinction from BCI: historical local abundance, diet, and climatic tolerance based on southern range limit. Foraging height was identified as a tentatively important variable. The model built using only important variables including foraging height significantly reduced residual deviance from the null model (null deviance = 269.35, deviance reduction = 87.7, $p < 0.001$). We found no evidence for lack of fit using the le Cessie-van Houwelingen test ($z = -0.78$, $p = 0.43$). Good model performance was confirmed with a satisfactory McFadden's pseudo-R^2 value (0.35). The amount of deviance accounted for by our model after adjusting for number of predictors and observations was 30%.

Our logistic regression model for species absences from BCI indicated that persistence significantly declined with decreasing local abundance and more northerly (wetter) range limit (Table 2.1). Probability of extinction on BCI was significantly related to terrestrial foraging and insectivorous diets. Dominance analysis suggests local historical abundance was the most important predictor explaining species extinctions on BCI (average increase in $R^2_M = 0.17$, SE = 0.18) followed by southern limit (average increase in $R^2_M = 0.077$, SE = 0.08), diet (average increase in $R^2_M = 0.063$, SE = 0.08), and foraging height (average increase in $R^2_M = 0.021$, SE = 0.027). Hierarchical variance partitioning indicated local historical abundance independently contributed 51.0% of total model fit, followed by southern range limit (23.5%), then diet (19.2%) and foraging height (6.3%).

Cluster Analysis

After a century of species loss, the BCI bird community has shifted from being most similar to nearby wet forest bird communities to now being most similar to communities in drier and more disturbed forests. Hierarchical cluster analyses of 14 mainland sites and two BCI inventories (first and most recent) by 299 species revealed strong support for one cluster of mainland sites ("Cluster 1", p = 0.03) on the southern end of the canal and moderate support for a second cluster ("Cluster 2", p = 0.1; Figure 2.2) containing sites on the northeast side of the canal and west edge of Gatun Lake. Table B.6 summarizes the environmental characteristics of each cluster. There was additional strong support (p = 0.04-0.05) for two smaller "sub-groups" within Cluster 2, differentiating northern subregions with high precipitation (> 2400mm/yr) from drier subregions near the center of the Panama Canal (< 2250 mm/yr precipitation). Nueva Providencia (PRO) was not clustered with any other subregions and there was convincing evidence (p = 0.01) this site represented a distinct forest bird community. Because PRO was not a member of any cluster, we omitted this subregion from tests of heterogenous distance and dispersion among groups.

The earliest inventoried BCI community was grouped with mainland Cluster 2, which includes nearby mainland subregions in north Soberania National Park. The modern BCI bird community occurs within mainland Cluster 1, particularly associated with the Barro Colorado National Monument peninsula (PENIN) and Gigante (GIG). These two subregions adjacent to BCI are comparatively drier and more recently disturbed by anthropogenic and environmental events than Soberania National Park. We found convincing evidence that all bird communities associated with Cluster 1, including the current BCI species assemblage, are independent and distinct from Cluster 2. One-way PerMANOVA between clusters yielded a pseudo-*F* statistic of 8.16, suggesting differences between groups was greater than chance alone. 50.6% of the variance in the data was accounted for by differences between groups. There was no evidence that differences between groups were driven by variation in dispersion (between mainland groups F = 2.58, p = 0.14; including BCI communities F = 1.53, p = 0.27).

Non-parametric Ordination

Ordination of non-urban subregions in species space showed BCI bird communities shifted progressively over time such that historical and modern inventories were positioned alongside different clusters of mainland sites (Figure 2.3). All three ordination axes exhibited correlations with at least one environmental factor (Table 2.2). The first axis characterized a progressive change in avian community composition with increasing forest cover from left to right. Axis 2 was most strongly correlated with forest age and precipitation and best represented the natural rainfall gradient along the Canal zone, with wetter subregions occurring higher on Axis 2. Wet forest birds were particularly associated with subregions having the greatest amounts of forest cover and precipitation. Early BCI bird inventories (1925-51) ordinated closely with wet forest species and Atlantic subregions - particularly those receiving the highest amounts of precipitation. Later BCI communities ordinated progressively down the second axis, with modern and predicted BCI bird inventories alongside dry mid-isthmus and Pacific slope subregions.

Our ordination with rare species removed converged on a stable 3-dimensional ordination (final stress = 7.31, final instability = 0.00) with a cumulative R^2 of 88.7%. Axis 1 accounted for 53.8% of the variation in the data, Axis 2 accounted for 21.1%, and Axis 3 accounted for an additional 13.4% of variation. NMDS extracted stronger axes than expected by chance ($p = 0.004$). Though most environmental factors were strongly correlated with Axis 3 (not shown), the greatest correlations were with mean altitude and total area. Axis 3 generally differentiated large subregions with more topographic and habitat complexity from smaller, environmentally homogenous subregions, but did little to characterize differences between clusters or BCI bird communities over time and captured only a small amount of variation in the data. Furthermore, there was no evidence that birds occupied different areas of the ordination based on habitat association.

Discussion

Despite the existence of several factors thought to minimize loss of biodiversity in habitat remnants, namely large patch size, a surrounding habitat matrix resistant to exotic invasion, and effective protection from human disturbance for nearly a century (Laurance et al. 2018), Barro Colorado Island has lost 27.2% of its forest-dwelling bird community. Community ordination revealed precipitation was a potential driver of patterns of community change through time. The oldest and the most recently recorded BCI bird communities are more closely associated with different sets of mainland subregions than they are with each other. The “unprecedented record of natural extinctions” (Terborgh 1974) from BCI reveals three primary factors driving species loss: low initial abundances, dietary specialization on terrestrial insects, and sensitivity to forest moisture conditions. Extirpated species tend to be associated with the interior of wet forests in the region. All species remain present in comparably-sized nearby forests, indicating the losses from BCI are influenced by its isolation from similar surrounding habitat. Today, permanent resident species richness is nearly a third lower without replacement by newly colonizing species.

Attributes of missing species

Local abundance was the single most important variable explaining species losses; species with lower abundance at the time of isolation were generally the first to go extinct. Small populations within isolated fragments may lack the density necessary to support viable populations over long time periods. Large populations are buffered against stochastic fluctuations which carry small populations below the minimum abundance threshold necessary for persistence (Gilpin and Soulé 1986, Lande 1993). Though almost all birds lost from BCI maintain populations on the adjacent mainland, some less than 250m away, physical and behavioral limitations – especially among terrestrial birds - generally prevent dispersal events across the canal (Willis 1974, Stratford and Robinson 2005, Laurance 2008, Moore et al. 2008, Robinson and Sherry 2012). Without the ability to replenish isolated populations from outside sources, species with small enough initial populations eventually go extinct.

Terrestrial insectivorous species were significantly less likely to persist after fragmentation. 78.3% of disappearances in the first four decades after isolation were insectivores, suggesting insect eating birds are lost more quickly than other groups. Stouffer and Bierregaard (1995) postulated alterations of ground-level vegetation structure in small forest fragments, caused by increased treefall and changes in leaf litter composition, could reduce the ability of terrestrial insectivorous birds to locate prey. Though BCI is considered large enough to buffer against many of these negative effects observed in smaller patches, the wind-exposed edges of BCI's peninsulas still experience a significant exposure effect (Asquith and Mejía-Chang 2005). Tropical forest insectivores also occur at lower densities than other groups (Terborgh et al. 1990, Robinson et al. 2000). Wolda (1992) found insect populations in Panamanian forests fluctuate widely over time. Declines in avian insectivores in another relatively undisturbed tropical forest were attributed to an "alarming" reduction in arthropods (Lister and Garcia 2018). Insectivores with naturally low abundances may be particularly sensitive to periodic loss of food resources. However, data on long-term insect population trends for the tropics remains scarce.

Ant-followers are a specialist insectivorous guild that feeds on terrestrial arthropods flushed by army ant swarms. Obligate ant-following birds are thought to be particularly vulnerable to fragmentation due to low population densities and extreme reluctance to cross open areas between forests (Karr 1982b, Stouffer and Bierregaard 1995, Şekercioğlu et al. 2002). Two of the three obligate ant-followers on BCI are now absent despite consistent, stable numbers of ant swarms over time (Willis 1974, Franks 1982). The two extinct ant-followers were historically less abundant and possess more northernly range limits than the species that remains. It is unlikely these species went extinct on BCI due to insufficient habitat area or lack of ant colonies. Rather, these losses appear consistent with our findings that numerically rare terrestrial insectivores near the limits of their distributions and/or climatic tolerance are among the most sensitive to isolation.

Tropical species are adapted to stable climatic conditions and possess narrower physiological tolerances (Busch et al. 2011, Şekercioğlu et al. 2012, Khaliq et al. 2015). Slower metabolisms and smaller hearts in tropical birds confer less physiological stress resistance compared to temperate birds (Robinson and Sherry 2012). Though climatic stressors were previously hypothesized as a source of bird extinctions from BCI (Karr 1982b, Stratford and Robinson 2005), ours is the first to include this variable as a potential explanation for this suite of species. We found a birds' climatic tolerance, indexed by their southernmost occurrence relative to the driest part of the canal, was significantly associated with extinction risk. The average southern distributional limit of birds on BCI decreased over time as species limited to wetter, northern regions disappeared. Birds that tolerate drier conditions (*i.e.,* those that occur further south along the Panama Canal; Rompré et al. 2009), are more likely to persist. Observational evidence indicates some tropical forest birds make non-random seasonal movements across a regional mosaic of microclimatic conditions (Karr and Freemark 1983). Perhaps certain terrestrial species on BCI with limited dispersal abilities were unable to find suitable moist refugia during extended dry periods, even on this large island, and their populations failed to persist (Brawn et al. 2017).

Some species losses among edge or canopy-associated birds are attributable to maturation of early and secondary growth as a result of vegetation succession (Terborgh 1974, Karr 1982b, 1990). However, our observation that open, edge, and forest birds experienced parallel declines suggests loss of open habitat was not exclusively responsible for the observed extinctions. Though we did not find a relationship between extinction risk and habitat association, there is evidence that forest birds are more sensitive to fragmentation. The majority of extinctions, and all extinctions in the first 30 years, were forest associated birds. Forest birds continue to be lost from BCI despite increasing total forest cover as the younger forests mature into tall forest. Sekercioglu et al. (2001) observed the ability to use deforested habitats was the best determinant of species occurrence in forest fragments. Our findings agree; birds widely found in a variety of habitat types, including more disturbed and less forested subregions, now comprise a greater proportion of the bird community on BCI. Sedentary forest birds possess even narrower physiological tolerances and dispersal limitations compared to other tropical bird species (Canaday 1996, Weathers 1997, McNab 2009, Şekercioğlu et al. 2012), and thus may be more extinction-prone.

Evidence for fragmentation-associated drying

Climatic effects of isolation may constrain populations in forest fragments (Karr and Freemark 1983, Terborgh 1992, Kattan et al. 1994, Stouffer and Bierregaard 1995, Şekercioğlu et al. 2002, Stratford and Robinson 2005, Robinson and Sherry 2012). Our study provides comprehensive evidence that environmental drying contributes to the structure of an isolated tropical bird community. The bird community on BCI clearly shifted over time along an axis best characterized by precipitation. Historical BCI bird communities more closely resembled wet rainforest communities on the north side of the isthmus, while later BCI assemblages showed greater association with dry forest communities to the south. However, the observed shift in avian community composition towards drier habitats did not correspond with a reduction in precipitation. Total annual precipitation on the island has not decreased over time (ANAM 2003) though several extended periods of below average precipitation occurred in the past century (Paton 2018).

This community shift without corresponding change in annual rainfall may be explained in part by local drying effects of isolation. BCI experiences a strong exposure effect from desiccating winds across Gatun Lake (Asquith and Mejía-Chang 2005); the island is less humid and contains little permanent water within the forest compared to nearby forest patches of comparable size. Vegetation changes on BCI, where soil moisture is an important factor determining long-term tree species composition (Legendre and Condit 2019), are consistent with environmental drying. Tree mortality rates, particularly among species associated with moist slopes, appear to be rising recently despite stable temperatures (Condit et al. 2017). Overall declines in forest density on the island are associated with increasing severe liana, or woody vine, infestations (Ingwell et al. 2010, Schnitzer et al. 2012) particularly around treefall gaps where lianas constrain tree growth and recruitment (Schnitzer and Carson 2010). Areas on BCI that accumulate water seasonally are desiccating and becoming less distinct from surrounding vegetation (Legendre and Condit 2019). Dominant vegetation composition along the Panama Canal has also shifted to favor species capable of surviving frequent wind exposure and challenging dry seasons (Asquith and Mejía-Chang 2005). Our study suggests changes in species composition associated with environmental drying extends beyond vegetation to birds as well.

Environmental consequences of fragmentation may interact with a pronounced annual dry season that varies in length and severity. Though total annual rainfall remains near its century-long average, there is evidence of increasing rainfall variability, with more frequent extreme wet and dry periods across the region (Aguilar et al. 2005). Karr (1982a) hypothesized the occasional extreme dry period is important for tropical species losses, where even routine dry seasons may critically stress species that rely on moist refuges, perhaps more so if their population sizes are already small. Drier tropical forests have lower densities of arthropod decomposers (Gonzalez and Loreau 2009) and dry periods limit the above-ground activity of terrestrial insects (Kaspari and Weiser 2000, Wall et al. 2008, Powers et al. 2009). Experimental evidence shows the distribution and density of forest floor arthropods on BCI is strongly associated with leaf litter moisture content during the dry season (Levings and Windsor 1984). Length of

Panamanian dry season is negatively correlated with avian demographic rates (Brawn et al. 2017) and is likely a limiting factor for animal populations on BCI (Lubin 1978). Reductions in terrestrial arthropod activity and subsequent trophic consequences of drier microclimatic conditions could help explain the loss of terrestrial insectivores in particular from BCI.

Additional considerations

Even though the BCI forest has remained undisturbed by human activity for nearly a century, the bird community is now more similar to a set of less species rich communities in drier, disturbed forests in the region. This observed shift in community assemblage on BCI over time is made without consideration to regional changes in Canal zone avifauna. The long history of bird surveys on BCI is unique, with no similar data being available from the nearby mainland forests, nor anywhere else in the tropics. It is possible that mainland Canal zone bird communities have also changed, which would not be depicted by our ordination. Anecdotal evidence from Soberania National Park suggests some minor compositional shifts have occurred since the first species lists were generated in the 1970s. However, species losses are limited to birds even more restricted to the wettest forests in central Panama (*i.e.*, centers of abundance in Chagres National Park). BCI is also probably the only subregion that has gained coverage of tall forest over time. Most common forms of anthropogenic disturbance on the mainland, including logging, agricultural conversion, and urbanization, do not affect Barro Colorado Island. Shifts between historical and modern bird communities in Soberania appear to be along the horizontal axis of the ordination defined by forest cover and fragmentation, not in the same direction of change experienced by BCI. Transition of the BCI bird community along the vertical axis of the ordination represents a significant, unprecedented shift in species composition over time not reflected by mainland Panama bird communities.

Notwithstanding the unprecedented importance of BCI's long-term bird survey data, BCI has unique value in informing us of the long-term effects of habitat isolation. Its matrix of water provides a measure of independence from most confounding influences on species colonization dynamics, which are affected by vegetation succession in most other long-term studies of fragmentation (Leigh et al. 2002, Kupfer et al. 2006). Only land-bridge islands provide continuous isolation where the capacity to re-establish populations, at least of many dispersal-limited species (Moore et al. 2008), within the fragment does not vary dramatically through time. Despite its uniquely stable matrix, the long-term avian community dynamics on BCI are relevant to other tropical forests where matrix composition is as hostile to dispersal for forest birds as water is. Experimental release experiments over pasture showed that the same types of birds unable or unwilling to fly over water are also unlikely to move across grazed pasture

(Ibarra-Macias et al. 2011a, 2011b). Thus, BCI remains comparable to a terrestrial forest fragment for most avifauna because dispersal across the canal still occurs for some, but not all, species (Moore et al. 2008). Our results suggest increasing dry season length and more frequent intense droughts are likely to drive further losses on BCI among extinction-prone birds sensitive to forest moisture conditions. Even in this "best case scenario" of tropical forest fragmentation, a very large remnant protected from human disturbance for over a century, avian species losses from BCI reveal important influences of initial population size, specialization, and subtle forms of climate change on long-term maintenance of biodiversity.

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Tables and Figures

Table 2.1. Results from logistic regression of local bird extinctions from BCI as a function of local historical abundance, diet category, foraging height, and southernmost canal-zone range limit.

Parameter	β	S.E.	z-value	p-value
Intercept	5.55	1.11	5.02	<0.001
Southern Limit	-0.06	0.02	-3.51	0.001
Local Abundance – Occasional	-2.82	1.08	-2.61	0.0091
Local Abundance – Rare	-3.86	1.05	-3.66	<0.001
Diet – Insectivore	-1.48	0.46	-3.24	0.001
Diet – Nectarivore	-0.44	0.85	-0.52	0.61
Diet – Frugivore	0.83	1.21	0.69	0.49
Diet – Raptor	-0.06	0.60	-0.10	0.92
Foraging Height - Understory	-0.04	0.88	-0.04	0.97
Foraging Height - Terrestrial	-1.09	0.54	-2.03	0.042

Table 2.2. All Pearson r2, and Kendall (tau) correlation coefficients between environmental variables and the three-dimensional NMDS configuration of sampling units in species space. For definitions of environmental variables, see Table B.2.

	Axis 1		Axis 2		Axis 3	
Variable	r^2	tau	r^2	tau	r^2	tau
AGE_CAT	0.177	-0.348	0.050	-0.162	0.065	-0.174
ALT	0.027	-0.014	0.001	-0.088	0.357	0.522
AREA	0.001	-0.060	0.029	0.088	0.490	0.494
PCT_FOREST	0.274	-0.374	0.035	-0.152	0.269	-0.448
PCT_UNFRAG	0.361	-0.416	0.007	-0.139	0.117	-0.416
PCT_URBAN	0.077	0.356	0.024	0.106	0.232	0.443
PLANTS	0.008	-0.472	0.017	0.180	0.232	-0.321
PRECIP	0.049	-0.287	0.042	0.176	0.263	-0.435

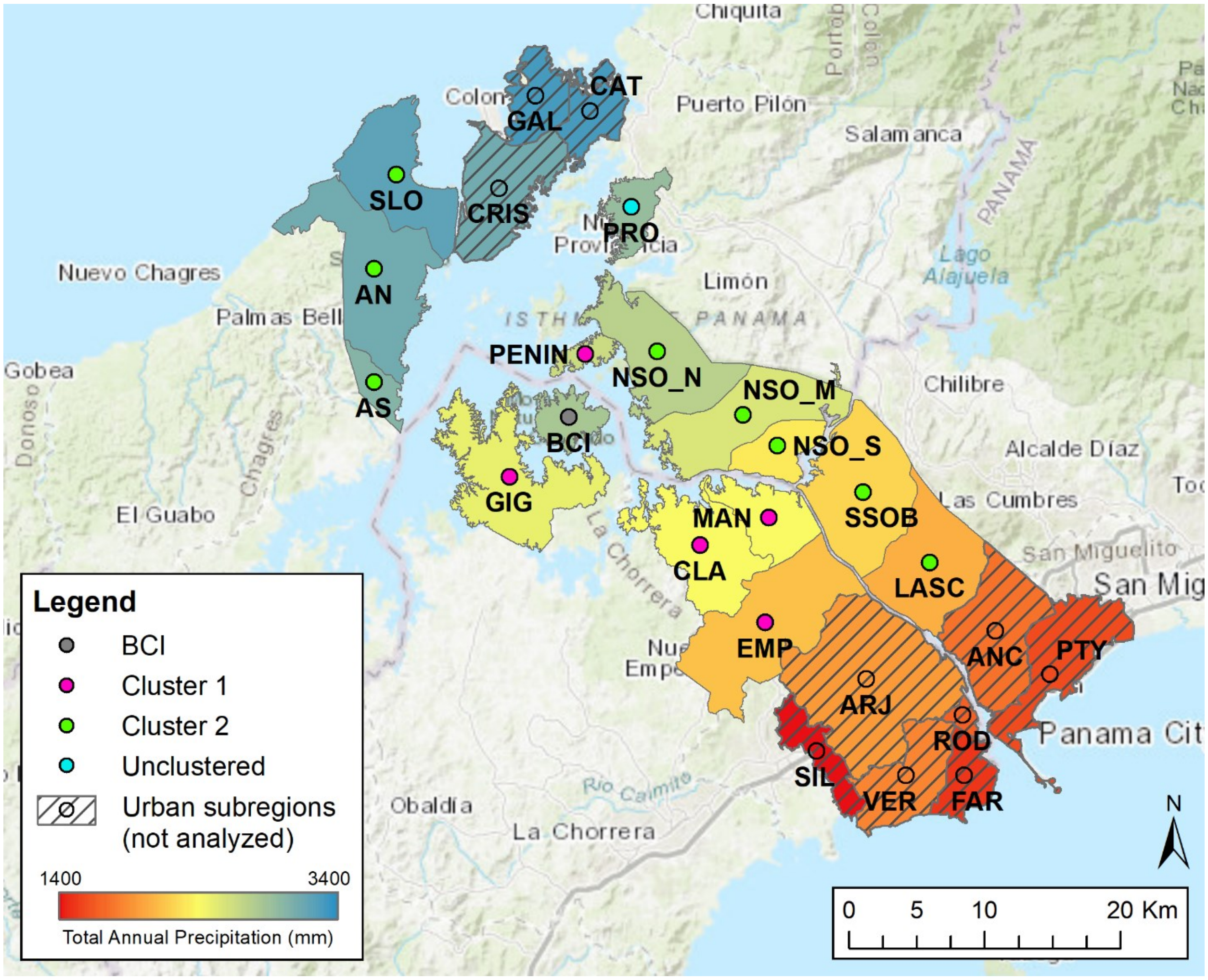

Figure 2.1. Digitized map of physiographic subregions along the Panama Canal (modified from Rompré et al. 2007). Colored dots indicate subregion group membership based on hierarchical cluster analysis (Figure 2.2). Black lines indicate regions used for the study, with fill colors corresponding to mean total annual precipitation for that subregion.

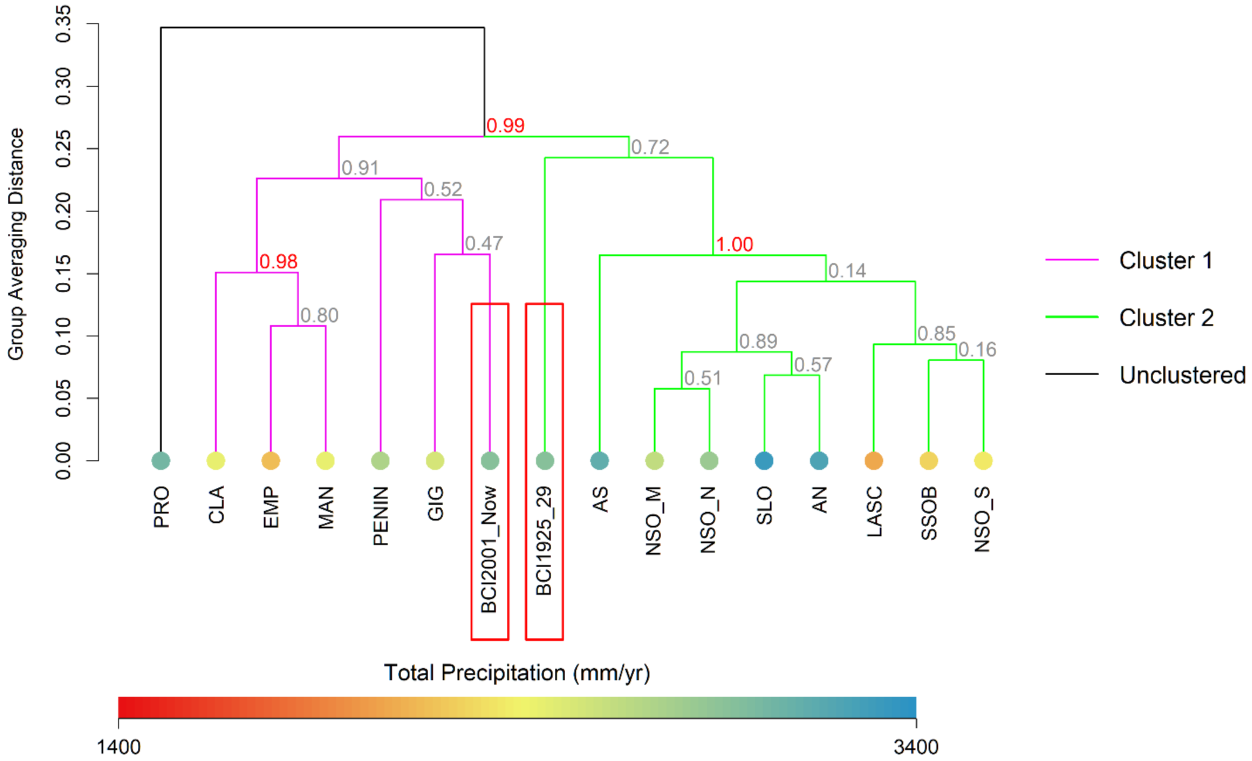

Figure 2.2. Results of hierarchical cluster analysis based on group average Sorensen distance. Values at nodes represent approximately unbiased (AU) probability of that cluster forming based on multiscale bootstrap resampling of the data for 10,000 runs. Red text indicates statistically significant clusters at p > 95%. Colored circles at dendrogram “leaves” correspond to total annual precipitation for that subregion. Colored lines denote independent clusters of subregions. The oldest and most recent bird inventories from BCI are indicated with red rectangles.

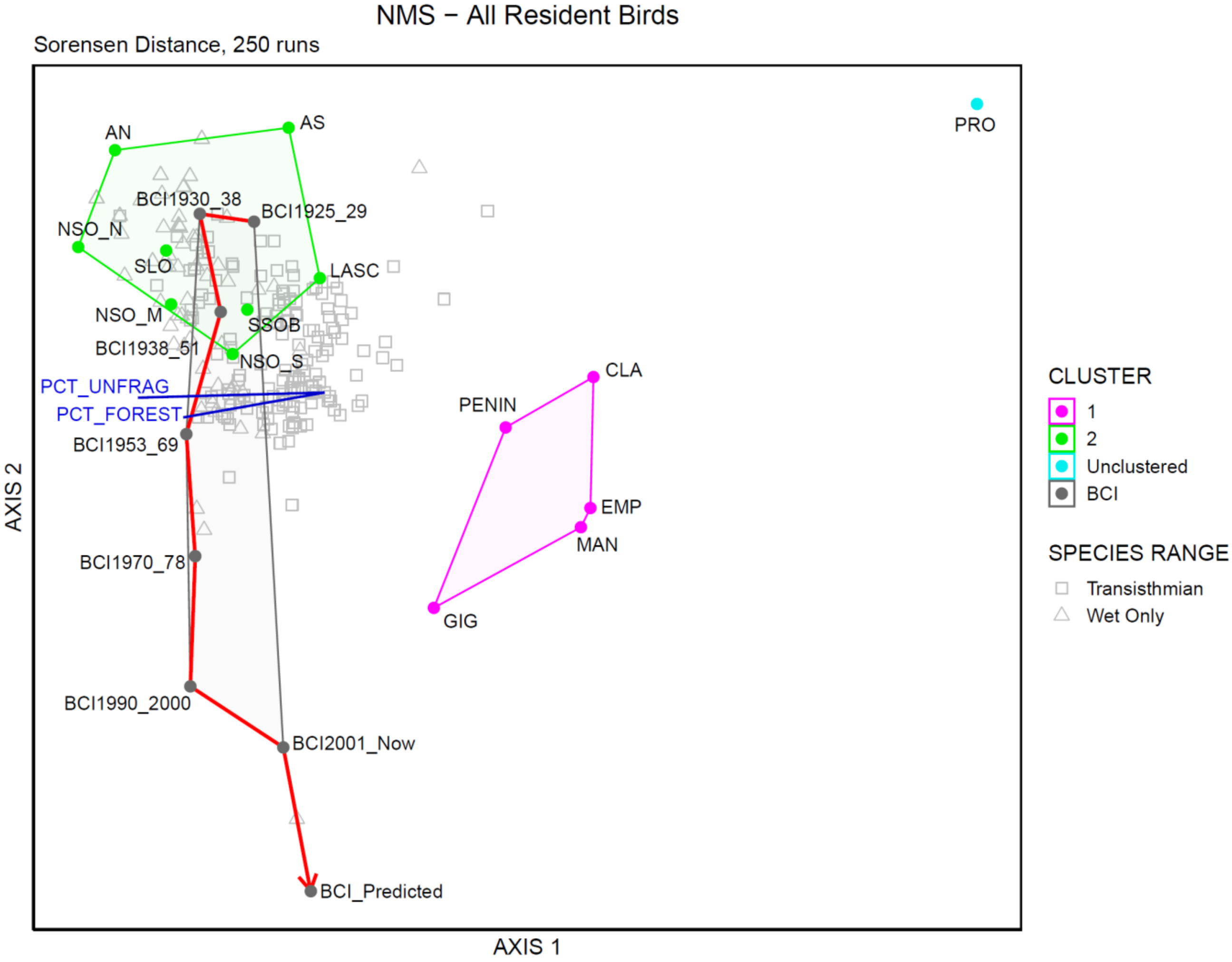

Figure 2.3. NMDS ordination of species and sampling units in species space. Subregions indicated by abbreviations, with colored dots corresponding to group membership based on hierarchical cluster analysis (Figure 2.2). Numbers after BCI indicate census period. Bird species are represented by hollow gray shapes. Squares denote transisthmian birds - those occurring along the entire Canal zone; triangles represent birds that occur in exclusively wet, Atlantic subregions. Red line is a successional vector connecting BCI censuses in chronological order. Dark blue lines and text indicate the strength and direction of significant associations between environmental variables and axes.

CHAPTER 3. EVIDENCE OF LONG-TERM EXTINCTION DEBT AND FAUNAL RELAXATION ON A TROPICAL LAND-BRIDGE ISLAND

Jenna R. Curtis, W. Douglas Robinson, Ghislain Rompré, and Randall P. Moore

Abstract

Efforts to anticipate biodiversity loss within remnant habitat fragments are complicated by faunal relaxation, or the time-delayed disappearance of species long after initial isolation. Lack of long-term data limits our ability to characterize this extended extinction process. The uniquely long history of avian surveys on Barro Colorado Island (BCI), a large forest fragment isolated a century ago by the waters of the Panama Canal, presents a valuable opportunity to enhance our understanding of faunal relaxation for tropical forest birds. We estimated the new species richness capacity of BCI and calculated the time until remaining extinctions are predicted to be fully realized. We examined rates of species losses over time among different taxonomic and ecological groups which vary in their sensitivity to habitat fragmentation. We combined bird surveys from surrounding lowland forests and land-bridge islands to build multimodel averaged species-area relationships (SAR), then used these models to estimate the predicted species richness for BCI given its size. We calculated the time remaining on unresolved extinctions using statistical models of extinction decay fixed on biologically realistic asymptotes. Extinction rates accelerated 40-60 years following isolation. The most extreme and persistent declines occurred among understory insectivorous birds associated with wet forests and sensitive to human disturbance. BCI no longer supports the number of species expected for its area and amount of annual precipitation. Additional factors beyond habitat reduction including edge effects and negative consequences of isolation for dispersal-limited birds likely contribute to the enduring faunal relaxation on BCI. Despite a century of species losses, between 6 and 92 additional species may be lost from BCI over the next one to nine centuries. Our results illustrate the challenges of precisely estimating extinctions within habitat fragments, especially under the constraints of equilibrium theory. Continued regular avian inventories on BCI will further improve our understanding of species-area relationships, faunal relaxation, and extinction debts for forest fragments in dynamic landscapes.

Introduction

The scaling of species richness with habitat area is among the most enduring patterns in ecology (Arrhenius 1921, Gleason 1925, Preston 1960, Schoener 1976, Connor and McCoy 1979, He and Legendre 1996, Lomolino 2000). Remnant forest patches support fewer species compared to large, continuous forests (MacArthur and Wilson 1967, Haddad et al. 2015, Jones et al. 2016). But not all species losses in fragments are immediate; in large habitat patches, it may take decades or even centuries for extinctions to be fully realized (Ewers and Didham 2006, Vellend et al. 2006, Kuussaari et al. 2009, Shaw et al. 2013, Essl et al. 2015, Haddad et al. 2015, Jones et al. 2016). This time-delayed process of species loss towards a new, lower richness is known as faunal relaxation (Diamond 1972). The number of extant species predicted to go extinct as the ecosystem "relaxes" is referred to as the extinction debt (Tilman et al. 1994). When extinction debts are large, the consequences of habitat loss may be underestimated because a number of "doomed" species (*i.e.,* those consigned to future loss) are still encountered within the remnant habitat (Hanski and Ovaskainen 2002). Though evidence for extinction debt exists across many taxa (Brooks et al. 1999, Cowlishaw 1999, Hanski 2000, Vellend et al. 2006, Triantis et al. 2010, Krauss et al. 2010, Cousins and Vanhoenacker 2011, among others), the process by which extinctions are realized within the relaxation period remains poorly known (Cousins 2009, Kuussaari et al. 2009).

Estimating the magnitude of extinction debts and duration of faunal relaxation are important steps in establishing long-term conservation priorities for isolated forest fragments (Kuussaari et al. 2009). Extinction forecasts often rely on statistical models of the species richness-area relationship (SAR), where species number is a function of patch size (Arrhenius 1921, Gleason 1925, McGuinness 1984, Rosenzweig 1995). SARs provide quantitative approaches to predict extinctions associated with area reduction (Hanski et al. 2013). However, even the best fit species-area model provides little insight into the extinction process, the identities of species that will be lost, or the duration of time between initial isolation and the eventual "relaxed" or "equilibrium state" community (MacArthur and Wilson 1963). There is no reason faunal relaxation should necessarily track the species-area curve (Lewis 2005), especially given additional environmental factors that mediate species response to habitat loss including patch size and connectivity (Helm et al. 2006, Cousins and Vanhoenacker 2011, Piqueray et al. 2011, Haddad et al. 2017, Noh et al. 2019), time since isolation (Jones et al. 2016), frequency of disturbance (Hanski and Ovaskainen 2002), and permeability of the newly formed matrix (Stouffer and Bierregaard 1995, Kennedy et al. 2010, Bueno and Peres 2019).

Species also vary in their sensitivity to fragmentation (Ferraz et al. 2003, Stouffer et al. 2009, De Camargo and Currie 2015), such that extinctions are usually non-random (Piqueray et al. 2011). A focus on the species-area relationship ignores differences in extinction risk among species based on their ecological traits, which ultimately influence the magnitude of the extinction debt and length of relaxation time (Hylander and Ehrlén 2013, Matthews et al. 2014). Traits previously correlated with extinction debts include habitat specialization (Kuussaari et al. 2009), vital rates (Vellend et al. 2006, Bommarco et al. 2010, Triantis et al. 2010, Piqueray et al. 2011, Noh et al. 2019), interspecific interactions (MacHunter et al. 2006), dispersal ability (Purschke et al. 2012, Bueno and Peres 2019), and the capacity to persist as small, local populations (Ovaskainen and Hanski 2002). A “deconstruction approach” (Matthews et al. 2014) by which species losses are considered for different functional groups separately may provide further insight into the faunal relaxation process (Haddad et al. 2015). Yet information on which species traits influence extinction rates is scarce, particularly in biodiverse tropical landscapes (Kuussaari et al. 2009, Matthews et al. 2014).

Among the greatest needs in the study of faunal relaxation is long-term data collected at multiple intervals documenting the rate of species losses following habitat reduction (Gonzalez 2000, Kuussaari et al. 2009, Hylander and Ehrlén 2013). Direct observation of faunal relaxation is exceedingly rare (Ferraz et al. 2003, Polus et al. 2007, Halley et al. 2016). One of the key limiting factors in this regard is lack of high quality historical data, unconfounded by factors like variations in matrix permeability or species invasion (Kuussaari et al. 2009). A forest island isolated by the Panama Canal, Barro Colorado Island (BCI) represents an excellent opportunity to improve our understanding of faunal relaxation for tropical birds. No other forest fragment has been as thoroughly and continuously inventoried over time (Robinson 1999). Recent evidence indicates over a quarter of the bird species on BCI have gone missing (*i.e*., locally extirpated; Curtis and Robinson, *in review*). A lack of similar species losses in nearby mainland forest patches of equivalent size provides strong evidence for faunal relaxation on BCI.

Several studies have recognized the opportunity BCI provides for extinction debt analysis (Table 3.1). However, these previous efforts have problematic shortcomings that could produce misleading conclusions. Multiple studies (Terborgh 1974, Halley and Iwasa 2011, Halley et al. 2014, 2016) derive extinction rates from a nearly 50-year old incidental and likely incomplete inventory of birds (Willis 1974, Willis and Eisenmann 1979). Terborgh (1974) estimated only mature forest species losses on BCI using an extinction coefficient from an arbitrary set of five Caribbean land-bridge islands with dissimilar species compositions. Halley and Iwasa (2011) built upon Terborgh’s study by estimating the time necessary for species richness to decline by half, using a model that decays to zero forest-associated species – an ecologically unrealistic asymptote. Halley et al.'s (2014) predicted loss of all but 14 species over the next six millenia incorrectly assumes avian density on BCI is comparable to Amazonian forest bird communities (Terborgh et al. 1990), whereas central Panama bird communities have a strikingly different abundance series (Robinson et al. 2000). Halley et al. (2014) also mistakenly interprets the five previously unrecorded species detected by Robinson (1999) as immigrants when all were temporary, non-breeding vagrants. No study has yet estimated the new expected species richness of BCI, nor has the extinction process been characterized among different taxonomic and ecological groups using the full suite of available time series data. As a result, we still lack a reliable estimate of how many and which birds on BCI might be committed to future extirpation, or the time frame over which these species losses might occur.

In this study, we combine a century of repeated avian inventories with relevant community data from the surrounding landscape to generate data-driven estimates of the new species richness capacity of Barro Colorado Island and calculate the approximate time remaining until these estimates are reached. Extrapolation of observed local extinction trends and modeled species-area relationships demonstrate an ongoing extinction debt for forest birds on BCI. We partition extinction rates over time among different taxonomic and ecological groups to determine which guilds might bear a disproportionate amount of the remaining extinction debt. Our results illustrate the challenge of precisely estimating unpaid extinction debt following habitat isolation, especially under assumptions based on equilibrium theory, which may impose unrealistic constraints on fragments in dynamic landscapes.

Methods

Barro Colorado Island (BCI) is a 15.62 km^2 land-bridge island formed in 1914 by the construction of the Panama Canal. BCI is the largest island in Gatun lake and the most protected from human disturbance. Its large size and protection from human activities are effective enough for BCI to support large raptors, pumas, and sizable populations of gamebirds absent elsewhere along the Canal. The island consists of primarily mature semi-deciduous lowland tropical forest from 100 to >500 years old (Foster and Brokaw 1982, Leigh 1999) with nearly half of its forest cover regenerating from previous human activity (Terborgh 1974). Most forest disturbance on BCI now comes from periodic windstorms and landslides that fell broad patches of trees within the forest interior. BCI receives approximately 2600 mm precipitation annually and is located on the northern end of a strong natural precipitation gradient that ranges from 3500 to 1400 mm average annual rainfall between Atlantic and Pacific coasts (ACP 2016). Though total annual rainfall remains near its century-long average, there is evidence of increasing rainfall variability, with more frequent extreme wet and dry periods across the region (Aguilar et al. 2005)

We obtained data from published lists of birds observed on BCI by highly skilled ornithologists from 1925-1994 (Chapman 1929, 1938, Eisenmann 1952, Willis 1974, Willis and Eisenmann 1979, Robinson 1999, 2001, G. Angehr *unpublished data*) as well as our own annual surveys from 1996 to today. Avian species were inventoried using methods ranging from the pooled species lists of multiple observers to standardized point and transect counts. All surveys incorporated *ad lib* observations to some degree. We compiled these published observation records into species lists from seven non-overlapping time-periods: 1925-29, 1930-37, 1938-51, 1953-69, 1970-78, 1990-2000, and 2001-today. Because survey effort varied across years, these "binned" periods represent the most comparable units of effort.

We focused our study on resident breeding birds affiliated with forest habitats, as these species exhibit the greatest declines following isolation (Gibson et al. 2011), and their habitats are at greatest risk of loss in the Canal zone (Robinson et al. 2004). We excluded aquatic and aerially foraging birds which were poorly detected by most census methods used on BCI. Omitting these species also removed potentially confounding variations in matrix affinity among species. After excluding aquatic species and aerially foraging birds, the Panama Canal represents a similarly hostile habitat to all remaining species in our study. This eliminates the need to account for species persistence within the surrounding matrix, which could bias extinction estimates (Pereira and Daily 2006, De Camargo and Currie 2015, Martins and Pereira 2017).

Extinction Estimates

Present bird surveys on BCI are the most complete, exhaustive inventories of resident forest and edge-associated species thus far (Robinson 1999). Thus, we have a relatively high degree of confidence in our current estimates of species richness for the island. Similarly thorough survey data from the past is exceedingly rare for temperate avifauna, and generally nonexistent for the tropics. The nearly continuous presence of ornithological activity on BCI over the past century represents a remarkable legacy. Our data contain observations from some of the world's foremost tropical ornithologists during a period of history with no field guides, poor optics, and where the primary means of identifying species often consisted of lethal collection. There have been significant advances in our knowledge of tropical birds since those earliest inventories. Variations in observer identity, experience and effort over time represent a potential source of bias in our species counts. We took steps to use as much of this valuable historical data as possible while also recognizing many of its associated limitations.

Often only a single species inventory was available for an entire survey period. With only one effective "visit" per interval, we could not determine whether unreported species were truly absent from BCI during that time, or simply undetected. We do not know of any method for estimating statistical confidence intervals around richness estimates for single-visit presence/absence data lacking measures of effort. Therefore, we established "logical" intervals within which we have a high degree of confidence the actual species richness for a given survey period lies. The most conservative number of species losses was calculated by assuming any species that went undetected and was then re-detected at a later period could not be considered extirpated during any survey interval in which it was not recorded. For our maximum richness estimate, these irregularly detected species were counted as present even when they were not reported. Our reasoning was species with inconsistent observation histories are characterized by poor detectability and/or an ability to re-colonize the island following temporary extirpation. In either case, failure to detect such species cannot be considered evidence of their loss from BCI.

The minimum species richness estimates consisted of the published, unadjusted species counts for each time interval. In this situation, any species not detected was considered absent from BCI during that period. However, the raw data showed a sharp increase in richness between 1925 and 1953 by as many as 32 species. This is likely due to a combination of incomplete survey effort (observers did not gain trail access to the entire island until the 1950s) and historical unfamiliarity with the vocalizations of several common but difficult to identify species (Willis and Eisenmann 1979). The existing literature does not suggest any new species colonized the island between 1925 and 1953 (Chapman 1938, Eisenmann 1952, Willis 1974), and only Great Kiskadee (*Pitangus sulphuratus*) immigrated after 1950. Thus, any species besides Great Kiskadee observed for the first time on BCI after 1929 represent new detections, rather than colonists establishing new breeding territories. To account for this, we assumed any species other than Great Kiskadee detected during the 1953-1969 survey interval was also present on the island from 1925-1951, and adjusted the minimum richness estimates for our first three species inventories (1925-29, 1930-38, 1938-51) accordingly. We then calculated the average between maximum and minimum richness estimates, because the actual number of species on BCI during any given year was very likely somewhere between these values, with some unreported species being truly absent and others simply undetected or temporarily emigrated.

We next estimated maximum and minimum richness for species grouped by taxonomy and ecological traits. In addition to taxonomic Order, we also considered five categorical traits previously associated with extinction risk in tropical birds (Henle et al. 2004, Sodhi et al. 2005). Based on published species accounts and extensive author experience, birds were assigned preference for one of four habitat categories: open (habitat with little to no woody vegetative cover); edge (habitat at the boundaries of low, woody vegetation); forest-edge (outer margins of forest of any age); and forest-interior (inner core of forest of any age). We obtained primary diet and foraging height from Wilman et al. (2014). We used six dietary guilds according to a species' dominant food source (*i.e.,* food categories with >50% use): carnivores (vertebrates, carrion, and snails); frugivores (fruits of any size); herbivores (plant parts, seeds, and nuts); insectivores (insects and arthropods); and nectarivores (flower nectar). Species with less than 50% use in all prior categories were classified omnivorous. We defined three categories for the typical height at which a species searches for food: ground (<1 m); understory (>1 m but below the canopy); or canopy (top level of vegetation regardless of height). Sensitivity to human disturbance was ranked low, medium, or high based on Stotz et al. (1996). Finally, each species was classified as either dry or wet forest-associated based on whether its range within the Canal zone included dry forests receiving less than

2450 mm precipitation annually or not; and large or small patch-associated depending on whether the species was restricted to forests 15 km^2 or greater, or also occurred in smaller forest patches.

Species-Area Relationship

We modeled the species-area relationship (SAR) for forested habitats along the Panama Canal using existing species inventories from mainland forest patches of different sizes (Figure 3.1) as well as several small forested islands within Gatun lake, excluding BCI. We first apportioned the mainland Canal zone into "subregions" defined by political administration, further dividing regions as necessary to reduce internal topographic and biogeographic variability while ensuring each subregion contained at least one forest fragment (Rompré et al. 2007). We implemented a non-nested sampling design where each surveyed forest patch on the mainland was surrounded by a non-forested matrix, such that patches were independent and akin to actual islands. The largest forest patch in each of our 24 subregions was inventoried during the breeding seasons between 1998 and 2005 using a combination of point counts, spot mapping, targeted surveys of flowering/fruiting trees, and *ad libitum* observations (see Rompré et al. 2007 for a full description of survey methods). We quantified the size of the forest patch surveyed using digitized maps and satellite imagery in ArcGIS (ACP 2016, ESRI 2017). Given considerable size differences in surveyed forests (0.161 to 67.4 km^2) we used results-based stopping rules to ensure all patches were inventoried with equal completeness (Rompré et al. 2007). We additionally surveyed fifteen land-bridge islands in Gatun Lake ranging in size from 0.016 to 7.8 km^2 (Moore 2006). While we did not perform stopping-based rules for the Gatun islands, we are confident, given the high amount of survey time on them for their small size, they were as thoroughly inventoried as the mainland forest patches.

We fit a species-area model to the mainland and Gatun island data, then used the resulting function to predict species richness for an area the size of BCI. The most commonly used form of the SAR is the power model $S = cA^z$ (Arrhenius 1921) where species richness (S) is a function of area (A), the rate of richness increase as area increases (z), and a scaling factor (c) that broadly represents species carrying capacity per unit of area (Rosenzweig 1995, Halley et al. 2013, Matthews et al. 2014). Special consideration must be given to estimate parameters c and z from relevant, data-driven projections rather than arbitrary assignments (Gonzalez 2000, Lomolino 2001, Pereira et al. 2012, Halley et al. 2013). Moreover, it cannot be assumed *a priori* that the power function provides the best fit among potential SAR models (Guilhaumon et al. 2008, Dengler 2009, Triantis et al. 2012, Tjørve 2012). Therefore, we fit a set of 20 candidate species-area models (see Tjørve 2003, 2009, Triantis et al. 2012 for model descriptions) to our species-area data using non-linear regression with unconstrained Nelder-Mead optimization parameter estimation from the sars package (Matthews et al. 2019) in program R (R Core

Team 2019). Regressions were evaluated by examining the residuals for normality and homoscedasticity using Shapiro's normality test and Pearson's product-moment correlation, respectively. Models that failed to converge or had significant ($p > 0.05$) non-normality and/or heteroscedasticity were omitted from subsequent analyses.

For each remaining candidate model, we calculated the Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We constructed a model-averaged (AKA multimodel) SAR curve by summing the predicted richness values from each individual model weighted by its information criterion value. We calculated 95% confidence intervals around the curve using a non-parametric bootstrapping procedure described in Guilhaumon et al. (2010). Briefly, this process involves fitting multimodel SARs to transformed response values from a single candidate model chosen at random with a probability determined by AIC weights. Confidence intervals are calculated around the bootstrapped fitted values resulting from 99 iterations of this procedure.

Estimated Species Richness Capacity

It is not yet clear how the effects of patch size, habitat diversity, and species traits combine to determine the number of species losses within isolated habitat patches (MacArthur and Wilson 1967, Fahrig 2003, Matthews et al. 2014). We therefore estimated the new expected species richness capacity of BCI in several ways. The simplest of these assumes species losses are driven by area reduction alone, and therefore the number of species on BCI would correspond to an area the size of BCI on the fitted mainland and Gatun island SAR curve. Because species traits such as dispersal limitations or sensitivity to disturbance may drive additional extinctions, we calculated a second estimate of expected species richness based on observed response to isolation over time among taxonomic and ecological groups, where we assumed only those groups that have remained stable for the past 40 years or more will continue to persist on BCI. Our third approach was an entirely data-driven method that extended the observed subtle decline in the rate of species losses over time into the future until it eventually leveled out with zero additional species losses.

This final approach estimates both the cumulative total number of species losses expected on BCI as well as the approximate time necessary to fully realize those losses. For each of the other two methods, we assumed species losses follow a first-approximation exponential decay (Diamond 1972, Brooks et al. 1999, Ferraz et al. 2003) where the number of extinctions declines over time to a non-zero horizontal asymptote defined by our estimated new richness capacity. To achieve model convergence, it was necessary to define a "dummy" point on the asymptote at 3000 years in the future, by which time we feel confident all expected extinctions will have occurred, provided no additional habitat disturbance on BCI.

We then calculated the number of years required for species richness on BCI to decline to within one species of that asymptote. To buffer our estimates, we fit extinction decay curves to both the maximum and minimum species richness values from our "logical" confidence intervals, as well as the average between those estimates.

Results

We previously estimated 166 resident non-aquatic, non-aerially foraging birds on Barro Colorado Island currently remain from 228 species occurring in initial surveys (Curtis et al. *in review*). Here, we estimate the historical community of resident, non-aquatic, non-aerial birds on BCI was likely between 221 and 248 species (Figure 3.2). Assuming only those species never re-detected following a period of absence are permanently lost, the present richness could be up to 205 birds. However, if every species no longer detected on BCI is truly extinct, as few as 158 birds may remain.

The mean rate of species losses on BCI was 7 species per decade (Figure 3.2), a rate that has been inconsistent across the 10 decades (Figure 3.3). Initial losses appear to have been slow followed by a period of accelerated loss then a deceleration in losses in the last two decades. Based on the means between our maximum and minimum historical richness estimates, species losses ranged from none between 1925 and 1938, to as many as two per year in the 1960s and 70s. The rate of species losses slowed approximately 19% each decade since 1990.

When considering species richness separately for different taxonomic and ecological groups, we found that - while almost all groups experienced declines following isolation - the degree and timing of these losses varied by species attributes (Figure 3.4). The most extreme and persistent declines occurred among understory birds, Galliformes, insectivores, species associated with wet forests, and species with the highest sensitivity to human disturbance. Birds associated with edge habitat initially exhibited similar precipitous declines, but which have since slowed. Species that showed little to no declines following isolation included canopy foragers and members of the families Trogoniformes (trogons), Coraciiformes (motmots), and Psittaciformes (parrots). Slightly more species associated with open habitats are on BCI today than in the 1920s, despite several species' losses among this group between 1938 and 1978. Several additional groups do not appear to have lost species in the last four decades or more: Tinamiformes (tinamous), Columbiformes (pigeons and doves), Piciformes (woodpeckers), and Falconiformes (falcons), ground foragers, and birds associated with forest patches 15 km^2 or larger.

Species-Area Relationship

We fit a multimodel species-area curve to 24 mainland Panama forests as well as 15 small islands in Gatun lake with avian richnesses from 9 to 271 species. Out of 20 initial candidate models, four were excluded with non-normal residuals (Asymptotic regression, Rational function, Gompertz, and linear). Among the remaining 16 models, a comparison of AIC weights indicated the power function was the best performing model ($AIC_w = 0.25$), with one competitive model (power R), and seven marginally competitive models based on delta AIC values <2.0 (Table C.1; RMSE = 30.74, $R^2 = 0.848$, MAE = 22.58). Both competitive individual functions fit to the overall data were convex-shaped variations of the basic power function without asymptote. A SAR curve fit with only the power function had parameter estimates of z = 0.32 and c = 63.3 (RMSE = 30.83, $R^2 = 0.85$, MAE = 22.6).

Within our data, we observed two distinct species-area relationships differentiated by location along the Panama rainfall gradient. Subregions on the northern half of the Panama Canal that receive 2450 mm or more precipitation per year (Figure 3.1) exhibited considerably higher species richness for a given area than subregions on the dry, southern half of the Panama Canal (Figure 3.5). This difference was such that for all areas >10km^2, a “wet” forest patch would have approximately 50 more species than a “dry” forest patch of equal size. Fitting multimodel species-area curves for “wet” and “dry” subregions separately produced better fits than the combined data (wet subregions RMSE = 24.99, $R^2 = 0.912$, MAE = 17.2; dry subregions RMSE = 29.02, $R^2 = 0.585$, MAE = 20.0). For subregions with at least 2450 mm precipitation, nine models were excluded for failing the Shapiro’s normality test of residuals (power, extended power 2, persistence function 1, Monod, negative exponential, Chapman Richards, asymptotic regression, rational function, and linear). Among the remaining 11 models, the extended power 1 function performed best. However, all other functions except logarithmic were at least marginally competitive (Table C.2). The multimodel SAR built for the remaining “dry” subregions excluded five models which failed the residual normality test (Monod, negative exponential, Chapman Richards, asymptotic regression, and Gompertz). The best remaining model was the power function with two competitive alternatives (Kobayashi and logarithmic; Table C.3).

Estimated Species Richness Capacity

If the new avian species richness capacity of BCI is determined by habitat size alone, our multimodel SAR curve fitted to all mainland and Gatun island data predicts a 15.67 km^2 island would contain approximately 155 species (95% CI 143-173). Our best estimate of the current richness on BCI (166 sp.) falls short but within the confidence intervals of the species richness predicted by the multimodel SAR for a 15.67 km^2 wet subregion (177 sp.; 95% CI 160-197). Yet our best richness estimate still exceeds the prediction for same-size area from the SAR for dry subregions (135 sp.; 95% CI 99-155). Assuming extinctions follow an exponential decay, BCI may not reach the richness predicted by the dry subregion SAR until 2529 CE (Table 3.2). We did not fit decay curves to the estimates from the wet subregion data because these were all larger than the current observed richness on BCI. In view of ongoing species losses of at least 3.5 species per decade, with no recent immigration, there is no reason to assume BCI will ever contain significantly more species than it does today.

Ten taxonomic and ecological groups containing 74 total avian species have not declined on BCI in the last four decades; barring additional environmental disturbance, we can reasonably assume these groups will continue to persist in the future. An additional 79 "transisthmian" or widely distributed species remain on BCI. These species demonstrate the ability to tolerate a broad range of ecological conditions along the Panama Canal and are increasing in proportional representation on BCI (Curtis et al. 2019 *in review*). Assuming these species also persist, up to 153 species may remain on BCI, even if all other species groups go extinct. It could take between 379 and 1008 years for richness to decay to these new values (Table 3.2).

Finally, we observed the rate of extinctions from BCI slowed approximately 19% every decade since 1990 based on changes in the average between maximum and minimum richness estimates. If this trend continues, extinctions will asymptote at approximately 67 cumulative species losses since 1925 (57-79 from "logical" CIs). Given our best estimate of 228 species during initial surveys, this means species richness on BCI would eventually decline to 161 sp. (range 149-171) over the next century (Table 3.2).

Discussion

Despite a century of species loss, the BCI bird community is still relaxing. We predict at least 6 and as many as 92 additional species may be lost from BCI depending on the relative strength of extinction factors including area effects, fragmentation-associated habitat changes, and species sensitivity to isolation. Our maximum estimate of losses so far assumes any species missing is now truly extinct, while our most conservative estimate posits any species that reappeared after a period of non-detection could do so again. This latter estimate is likely overly optimistic, as modern surveys of BCI represent the most thorough and complete inventories to date, and our experience suggests almost no missing species return to establish breeding populations on the island. Even our most conservative estimate of species losses predicts continued extinctions into the next century.

We found the species-area relationship provided an accurate model of avian richness in forest patches along the Panama Canal. However, as an increasing body of literature suggests, the power function alone was insufficient to characterize the shape of this relationship (Guilhaumon et al. 2008, Dengler 2009, Triantis et al. 2012, Tjørve 2012). The performance of our SARs generally improved when we modeled wet and dry forest patches separately. Precipitation is a significant determinant of both plant and avian species richness along the Panama Canal (Rompré et al. 2007). Wet forest tracts have more complex, diverse, and productive vegetation communities (Pyke et al. 2001), and thus have more abundant resources to sustain high species richness than similarly sized dry deciduous forests (Pyke et al. 2001, Rompré et al. 2007).

Based on our SAR curve for high-precipitation forests, BCI should sustain approximately 177 species given its 15 km^2 size and 2600mm average annual rainfall. An equal area of forest within nearby Soberania National Park, which resembles historical forest conditions on BCI, contains 197 resident non-aerially foraging species (Robinson et al. 2000). Islands are expected to have fewer species than equal-sized areas of mainland habitat (Richman et al. 1988, Jones et al. 2016). However, BCI currently hosts fewer birds than predicted by the high-precipitation SAR model and - given the ongoing rate of species losses – may soon fall even below the predicted richness from the general SAR model fit to the entire Canal. BCI appears to be relaxing towards the corresponding dry forest SAR prediction despite no reduction in annual precipitation over time (ANAM 2003). This suggests BCI is undergoing additional isolation-associated drying effects such as increased temperatures, exposure, and soil desiccation in the forest interior (Camargo 1993, Camargo and Kapos 1995, Laurance 2004, Laurance and Curran 2008, Ingwell et al. 2010). BCI still contains more species than Gigante, a slightly larger (19km^2) but more frequently disturbed dry forest as close as 250 m across Gatun Lake to the south. If BCI is truly relaxing towards a dry forest community, we would expect it to eventually contain fewer species than Gigante given its smaller size.

Despite the good fit of our multimodel SARs, it may be misleading to conclude species richness across the Panama Canal can be predicted solely by habitat area. If species-area relationships alone sufficiently explain richness, and fragmentation, disturbance, and isolation do not drive further species losses (Fahrig 2003, Yaacobi et al. 2007), then our modelled SARs provide an accurate estimate of remaining extinctions on BCI. However, this ignores additional factors like precipitation, vegetation, or anthropogenic disturbance that structure species distributions in central Panama (Rompré et al. 2007, 2009, Canale et al. 2012). Predictions from our fitted SAR curves may not be appropriate if mainland habitat patches do not act as discrete units, and/or are subject to different disturbance patterns than BCI (Haddad et al. 2015, Bueno and Peres 2019). Most studies assume habitat patches used to model the SAR curve represent stable community conditions (Kuussaari et al. 2009). Yet fragmented mainland forests in central Panama may have their own extinction debts to pay depending on their current degree of isolation and time since they were last part of contiguous forest (Jones et al. 2016).

SARs assume random processes (Ewers and Didham 2006), which may underestimate species losses when the mechanisms of extinction include additional deterministic processes beyond habitat loss (Seabloom et al. 2002, Fattorini and Borges 2012, Canale et al. 2012, Rybicki and Hanski 2013, Hanski et al. 2013, Matias et al. 2014, Haddad et al. 2015). Deterministic extinction mechanisms within our central Panama landscape could include the adverse effects of isolation on dispersal-limited tropical birds, gradual deterioration of habitat quality due to edge effects, or behavioral constraints on birds that preferentially forage in mixed-species flocks (Stouffer and Bierregaard 1995, Moore et al. 2008, Curtis et al. *in review*). The modeled SAR for dry forests gives us a reasonable baseline estimate of avian losses on BCI due to a combination of area reduction and environmental drying. Continued monitoring on BCI may reveal further extinctions beyond SAR predictions, improving our understanding of the independent roles of area effects and other deterministic ecological or behavioral mechanisms on species losses from forest fragments.

Mechanisms of delayed extinctions

Because the earliest surveys on BCI followed several years after its isolation, historical inventories likely missed the brief pulse of extinctions that occur immediately after habitat loss (Laurance et al. 2002, Kuussaari et al. 2009, Krauss et al. 2010). Our study only considers the delayed species losses that take place in the years, decades, or even centuries following isolation. BCI showed an inconsistent rate of species losses over time, even accelerating 40-60 years after the isolation event. This failure of isolated populations to persist over the long term is a product of both species-specific and landscape qualities (Lande 1993, Ovaskainen and Hanski 2002, Rybicki and Hanski 2013). It likely took several decades before the environmental consequences of isolation began to modify the forest interior on BCI beyond the threshold of tolerance for drought-sensitive birds (Karr and Freemark 1983, Turner 1996, Stratford and Stouffer 2015). Steep avian declines in 1960s and 70s also correspond with an extended period of below average precipitation (Paton 2018) from which multiple populations of dispersal-limited, wet forest-associated species were unable to recover. Edge-associated birds also declined precipitously during this period as the remaining patches of open habitat and young, disturbed woodland on BCI regrew. Loss of edge-associated birds has slowed recently. Any remaining species persist within suitable, regularly disturbed habitat on the outer perimeter of the island, occasionally utilizing temporary habitat created by treefall gaps appearing after large wind storms.

If our predictions are correct, and more local extinctions on BCI will occur, we expect the next extinctions on BCI to occur among nine species known to be declining or in extremely low abundance on the island today. These include steadily diminishing populations of Slate-colored Grosbeak and Spot-crowned Antvireo; species with as few as one or two individuals remaining such as Golden-crowned Spadebill and Black-tailed Trogon; and species that are no longer regularly detected, only rarely maintaining resident breeding populations such as Speckled Mourner, Pheasant Cuckoo, Russet-winged

Schiffornis, Violaceous Quail-Dove, and Barred Forest-Falcon (Table A.1 for species common and scientific names). Declines among all the aforementioned species may be at least partially attributed to changes in available resources and environmental conditions following isolation. We hypothesize the antvireo and spadebill are extremely dispersal-limited and unlikely to experience a "rescue effect" from adjacent mainland populations. For these species, extirpation from BCI would probably be permanent. Others such as the schiffornis, quail-dove, and grosbeak are associated with the core interiors of dense, high-precipitation rainforests. These birds may no longer find sufficient habitat of suitable quality on BCI or occur so rarely that, when they do find habitat, they are unable to find mates and move elsewhere.

Species losses among ecological and taxonomic groups

To our knowledge, very few studies to examine differences in avian extinction rates from a fragment based on characteristics other than habitat specialization (Matthews et al. 2014). We observed the greatest declines among insectivores, Galliformes, understory foragers, and birds associated with wet forests. Tropical insectivores occur at lower densities than most other birds (Terborgh et al. 1990, Robinson et al. 2000) and are particularly sensitive to changes in ground and shrub-layer vegetation structure in forest fragments (Stouffer and Bierregaard 1995). Insect populations in Panamanian forests fluctuate widely over time (Wolda 1992). Therefore, naturally low-abundance insectivores may be the most vulnerable to reductions in microclimatic and food resources on BCI. The continued loss of nectarivores could be indicative of ongoing changes in the floristic community on BCI following isolation (Ingwell et al. 2010, Schnitzer et al. 2012, Condit et al. 2017, Legendre and Condit 2019).

Wet forest birds declined regardless of association with forest patch size. It has been hypothesized these birds possess narrower physiological tolerances than species occurring in dry, southern forests (Karr 1982b, Stratford and Robinson 2005). It may be that drought-intolerant forest birds no longer find suitable moist refugia on BCI given persistent effects and microclimatic drying (Curtis et al. *in review*). A striking 50% decline among dry forest birds associated with large forest patches is due to the small initial size of this group. Only two birds in this category were historically detected on BCI (Rufous-vented Ground-Cuckoo and Great Potoo), of which the Potoo remains. The Ground-Cuckoo belongs to several fragmentation-averse groups including high sensitivity to disturbance, terrestrial foraging and association with core forest interiors.

Extreme dispersal limitations among tropical birds (Moore et al. 2008) constrain which species can maintain population dynamics in habitat fragments (Ovaskainen and Hanski 2002, Ewers and Didham 2006, Lees and Peres 2009, Bommarco et al. 2010). We were unable to estimate dispersal capabilities for all species in this study due to limited morphometric data for our species pool. However, a combination of diet and foraging height may be representative of dispersal ability, as terrestrial insectivorous birds tend to be the most dispersal limited while we hypothesize canopy-foraging carnivores, omnivores, and herbivores are capable of traveling greater distances. Persistence is also correlated with abundance (MacHunter et al. 2006), particularly the number of small populations near the threshold of viability at the time of isolation (Hanski and Ovaskainen 2002). Smaller areas of habitat naturally support fewer individuals. Reduced abundance, coupled with random demographic fluctuations and attrition of genetic variability in isolated populations, increases susceptibility to stochastic extinction events on BCI (Lande 1993).

Of the four Galliformes originally present on BCI, only Crested Guan remains, likely due to the absence of hunting on BCI. Among the three missing species, Great Curassow and Marbled Wood-Quail are nearly extirpated from the region, while the Gray-headed Chachalaca is a bird of young secondary forests uncommon along the northern half of the Panama Canal. We observed very few species losses among trogons, motmots, and pigeons and doves. Almost all birds within these taxonomic orders can inhabit small, dry forest patches. Many are also associated with upper levels of the forest and do not exhibit strong dispersal limitations. Recent observed stability among several additional groups could suggest the remaining habitat on BCI lacks sufficient resources to support its full, original species composition, but can now support those that remain after initial losses.

Conclusions and future directions

Ours is the first work to utilize the full history of avian survey data on BCI to generate evidence-based estimates of extinction debt. Though controlled fragmentation experiments may be more scientifically rigorous (Haddad et al. 2015), the short duration of such studies would fail to capture the temporally extensive faunal relaxation observed in this natural experiment. Repeated avian inventories from BCI give us the unique ability to resolve the timing of extinction events to within a small window. Our prediction of continued but diminishing species losses from BCI assumes the avian community is adjusting towards a new stable state in equilibrium with post-isolation habitat conditions. For equilibrium to occur, the colonization rate must eventually balance the future extinction rate (MacArthur and Wilson 1963). Increasingly prevalent urban generalists in the surrounding Canal zone (namely Great-tailed Grackle, Tropical Mockingbird, and Yellow-headed Caracara) represent species likely to colonize BCI in the future. Nevertheless, the expansion of these urban birds along the Canal raises questions about SAR assumptions of stable reference landscapes (Kuussaari et al. 2009). Continued monitoring of BCI presents a unique opportunity to assess the applicability of equilibrium theory for insular habitat fragments. By regularly inventorying BCI birds, we can track temporal variations in species richness to determine whether the avian community ever reflects equilibrium conditions. Regular inventories on BCI may instead reveal that even large, isolated, and protected systems fail to stabilize over long temporal scales within unstable landscapes.

Perhaps the most striking evidence of enduring faunal relaxation on Barro Colorado Island is its depauperate avian richness relative to similarly-sized patches of comparable mainland habitat. That BCI has already exceeded the number of extinctions predicted by the wet forest species-area relationship suggests habitat reduction alone does not explain the enduring faunal relaxation. Much of the enduring faunal relaxation comes from the gradual atrophy of species whose populations on BCI appear to be unsupported by periodic immigration events from the surrounding landscape. Even when immigration occurs it appears to be rare, establishing small, ephemeral populations that disappear quickly after failing to re-establish breeding populations in habitat that is likely no longer suitable. Because dispersal dynamics appear to be a prominent factor influencing community richness on BCI, the importance of maintaining forests in the surrounding region as sources of immigrants becomes clear. Our current understanding of the BCI bird community indicates several ecological groups, such as canopy species and wide-ranging raptors, persist because of an infrequent flow of individuals from the neighboring parks. If those parks were lost to development, the next nearest sources of forest-dwelling birds are dozens to hundreds of kilometers outside the Canal Area. Thus, our predicted asymptote for richness as faunal relaxation continues would be much lower if regional forests were lost.

A major objective of conservation is to predict the outcomes of human activity for other species. Identifying unpaid extinction debts presents an opportunity to mitigate future biodiversity loss through targeted conservation action (Kuussaari et al. 2009, Wearn et al. 2012, Canale et al. 2012). Unfortunately this is less feasible for manmade land-bridge islands surrounded by an irrevocable, inhospitable barrier to rescue from the wider landscape (Jones et al. 2016). While we may never be able to restore the low-lying tropical rainforests lost to the Panama Canal, understanding extinction dynamics in the habitat that remains can help us better anticipate species losses in other fragmented habitats that lack the same legacy of data as BCI. Though the large size and protected status of BCI may buffer it against the steep trajectory of species losses observed in other fragmented systems (Brooks et al. 1999, Ferraz et al. 2003, Stouffer et al. 2009), unlike those systems, the hostile matrix surrounding BCI is consistent and permanent. Therefore, the full extent of the extinction debt could be much greater on BCI than other fragmented forests where developing vegetation in the surrounding matrix mitigates species losses (Stouffer et al. 2009). While this may limit the long-term regional conservation value of BCI, it also presents a unique opportunity to examine community dynamics in a truly isolated forest fragment.

This study provides a rare, empirical depiction of long-term faunal relaxation. Despite a century of species losses, our results suggest the avian extinction debt on Barro Colorado Island is unlikely to be paid fully in our lifetime. We are at a crucial moment in the study of avian species losses on BCI. Regular surveys on the island must continue to determine whether avian extinctions will continue according to our statistical predictions. If the period of rapid extinctions on BCI has indeed passed, the data collected in the upcoming decades should provide a more representative depiction of the future of species losses on BCI. One key assumption of this and many extinction debt studies is equilibrium – that someday the richness on BCI will stabilize or "bottom out" at some non-zero value. Stability, already rare in nature, appears even less likely in the face of mounting anthropogenic pressures and climate change. Increasingly fragmented mainland forest patches that provide BCI with crucial gene flow and source populations may have their own extinction debts to pay. For faunal relaxation on BCI to end, however long it may take, the preservation of these mainland forests is essential.

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Tables and Figures

Table 3.1. Previous studies of avian extinction debt on Barro Colorado Island and/or species-area relationships along the Panama Canal.

Source	Estimate	Richness Estimate	t_s (years)	t_{50} (years)
Terborgh (1974) *	Approx. 42 mature forest-associated species lost in first 100 years.	NA	NA	605
Halley and Iwasa (2011) †		NA	NA	527
Halley and Iwasa (2011) ‡		NA	NA	339
Halley et al. (2014) §		14 ± 4.5	6500	NA
Rompre et al. (2009) ¶		25	NA	NA

* Per Halley and Iwasa (2011) from the equation $T_{50} = (S_0K)^{-1}$, where $S_0 = 208$ and $K = 10^{-5.1}$. Considering only birds associated with mature forest.

† From power law equation fit to empirical case studies using the formula $T_{50} = 4.35 \times A^{0.652}$.

‡ From Eq.6 (neutral prediction) with $\tau = 5$ and $\rho = 8.29$. Assumes no immigration, stochastic losses, random species distribution

§ Neutral prediction including species immigration, stochastic losses, random distribution

¶ Interpreted from modified SAR curve with b=16

Table 3.2. Estimates of current avian species richness capacity on BCI and the time remaining until the estimate is likely to be reached. Assumes species losses follow a first-order exponential decay (ranges from statistical or logical confidence intervals provided in parentheses where available). Subtract the richness estimate from 166 to obtain the remaining extinction debt.

Source of Estimate	Richness Estimate	Years Remaining
SAR, all data	155 (143-173)	369 (220-625)
SAR, dry subregions	135 (103-163)	424 (241-728)
Stable taxonomic and ecological groups	74	920 (619-1385)
Above, plus transisthmian species	153	386 (232-625)
Extrapolated rate of species losses	160 (149-171)	141*

* estimate from observed trajectory, no confidence intervals available.

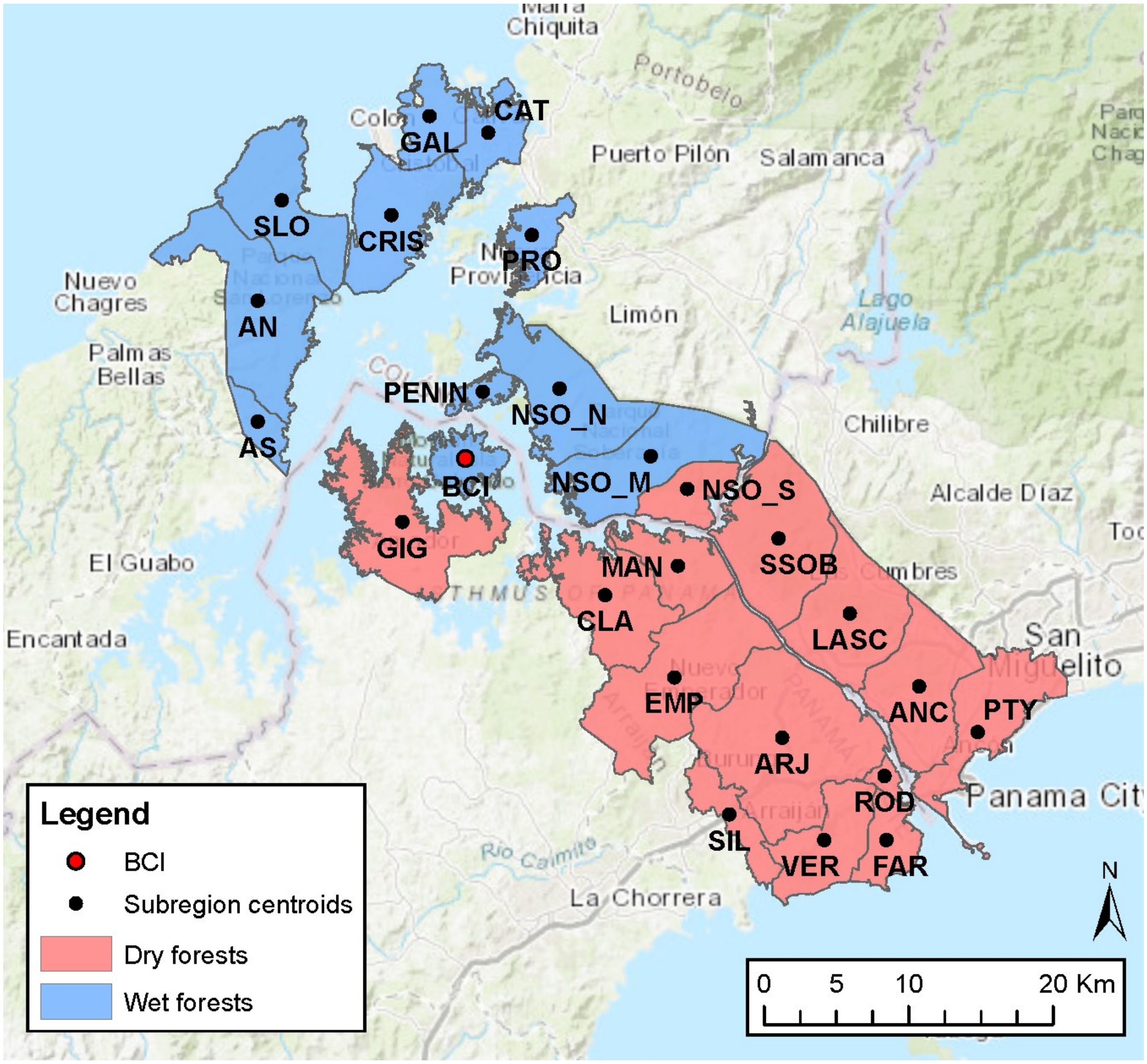

Figure 3.1. Digitized map of physiographic subregions along the Panama Canal (modified from Rompré et al. 2007). Polygons marked with dark outlines indicate regions used for the study. Areas colored red are considered “dry” forests receiving less than 2450 mm average annual precipitation. Areas colored blue are considered “wet” forests receiving an average of 2450 mm or more rainfall each year. Filled dots denote area centroids, with red for BCI and black for all mainland subregions.

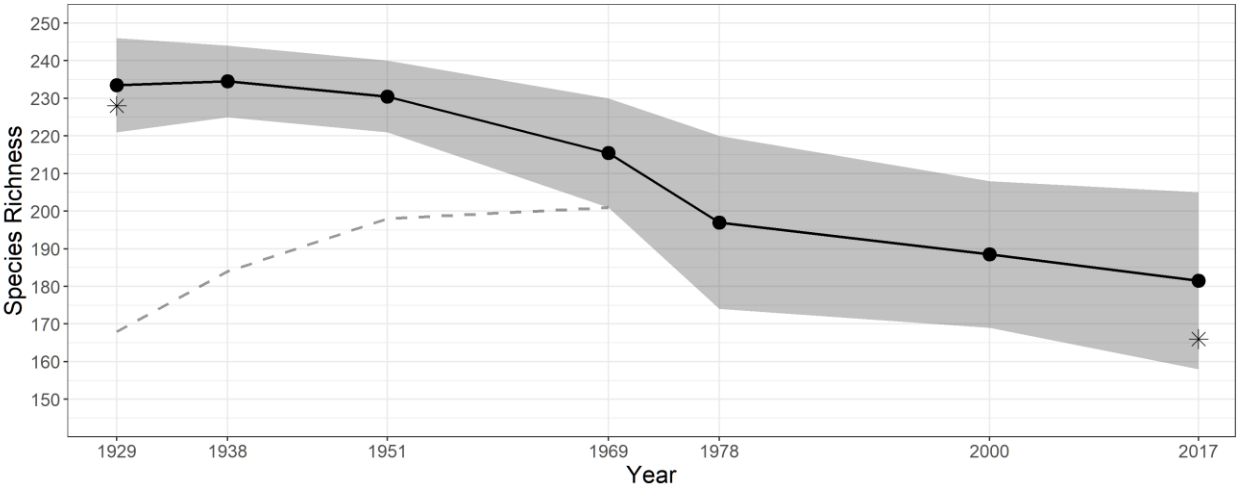

Figure 3.2. Estimated number of resident, non-aquatic, non-aerial birds on BCI over time. Gray area represents the “logical confidence interval”. The upper limit assumes any species redetected after a period of non-detection is never extinct during any absent period. The lower bounds are defined by the raw data (species are considered extinct any time they are not detected), with the first three survey periods adjusted by additional species detected through 1969 to account for incomplete effort/observer skill during earlier surveys. Dashed line represents the unadjusted species richness counts for 1925-51. Circles indicate the average between maximum and minimum richness estimates for each time interval. Asterisks denote our “best estimates” of original and current richness based on (Curtis et al. *in review*)

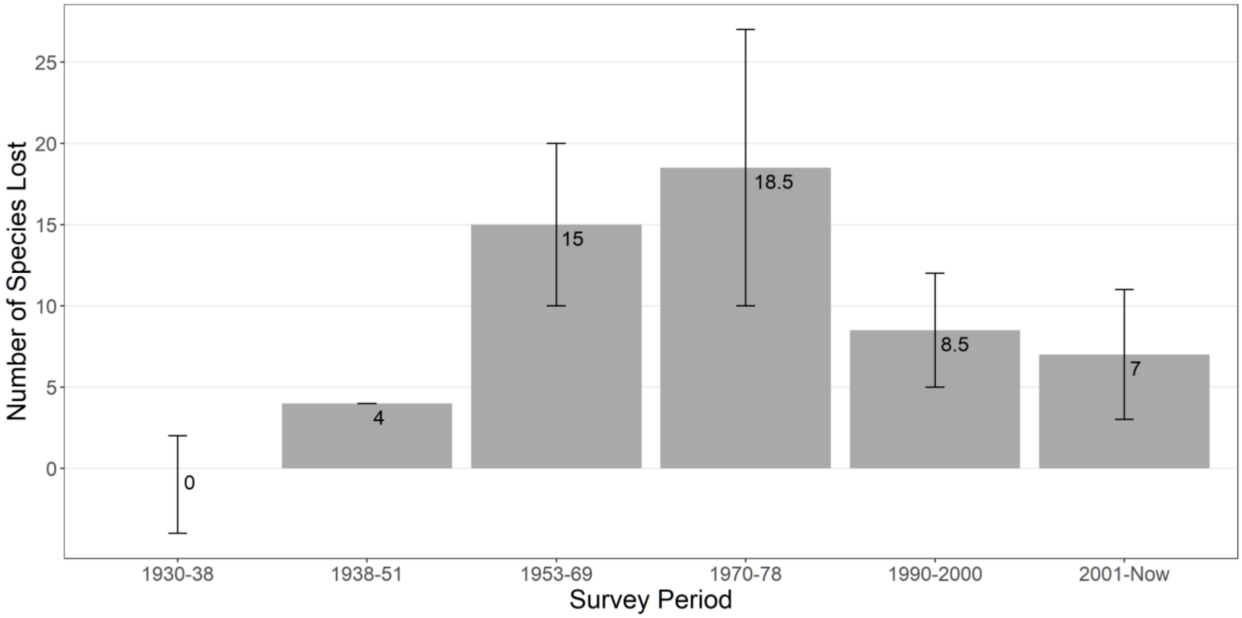

Figure 3.3. Estimated number of bird species lost on BCI during each survey interval after the initial period (1925-29). Grey bars mark the average between upper and lower "logical confidence intervals" (black lines). As in Figure 3.2, the upper limit of species losses for each period is defined by the raw data, where species are considered extinct any time they are not detected, with the first three survey periods adjusted by additional species detected through 1969 to account for incomplete effort/observer skill during earlier surveys. The lower limit of species losses for each period assume any species redetected after a period of non-detection is never extinct during any absent period. The negative lower limit of estimated species losses during the 1930-38 period is the result of species present but missed by observers in the 1920s and first detected in the 1930s. There is no documented evidence that BCI gained new breeding populations of any birds except during 1953-69 (and then only one species).

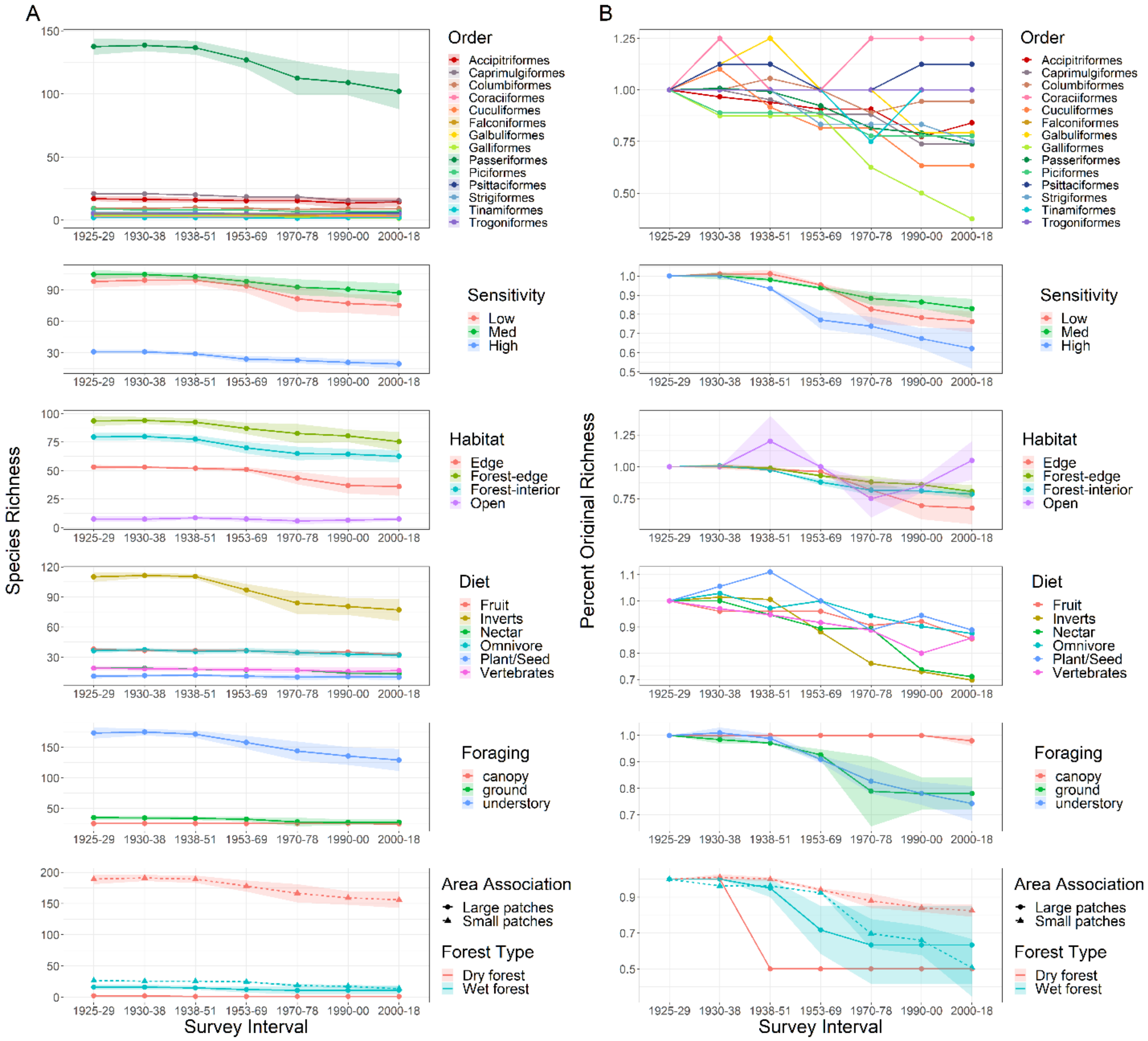

Figure 3.4. Estimated number (A) and percent of initial richness remaining (B) of resident, non-aquatic, non-aerial birds on BCI over time separated by species attributes. See Table 4.1 for category definitions. As before, colored regions represent “logical” confidence intervals with colored circles indicating the average between maximum and adjusted minimum estimates. For ease of interpretation, logical confidence intervals not provided for attributes with for or more categories. See Figure C.1 for species richness over time among taxonomic orders with Passerines removed.

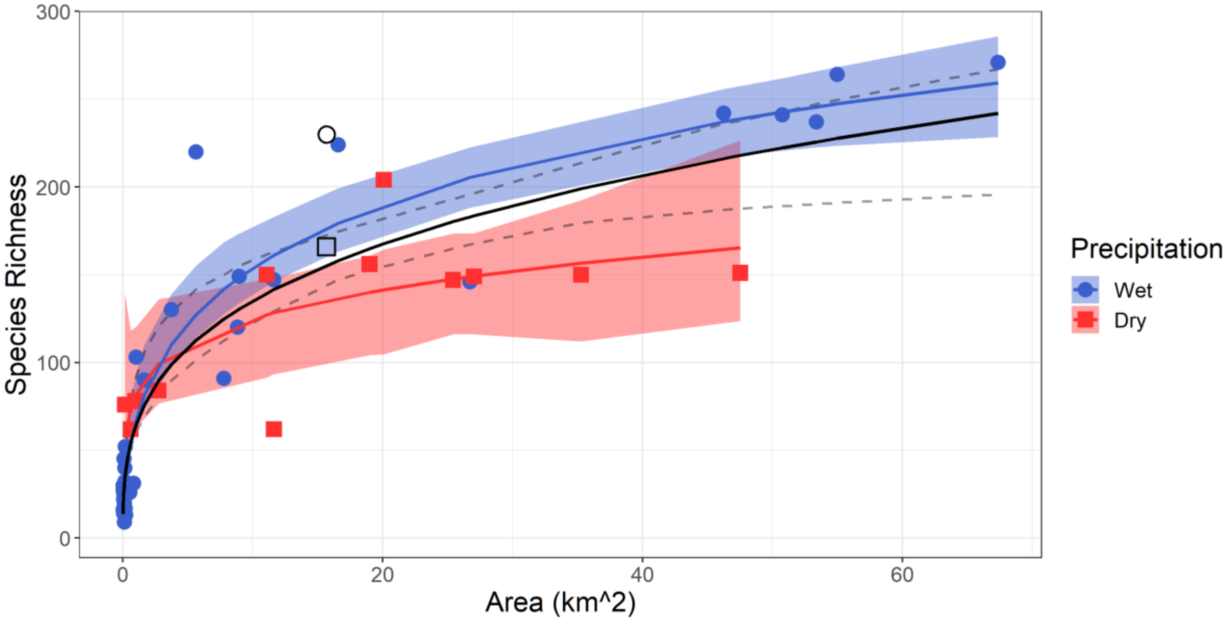

Figure 3.5. Model-averaged species-area curves fit to mainland and Gatun Island forest patches, colored by groups defined by average annual total precipitation. Solid black line represents SAR curve fit to entire species-area dataset, with 95% CIs marked by dashed gray lines. Blue circles indicate “wet” forests receiving greater than 2450 mm average annual precipitation, red squares denote “dry” forests receiving less than 2450 mm precipitation annually. Shaded regions indicate non-parametric bootstrapped 95% confidence intervals. Our best estimates of historical and modern avian species richness on BCI are indicated by an open black circle and square, respectively.

CHAPTER 4. URBANIZATION IS ASSOCIATED WITH UNIQUE COMMUNITY SIMPLIFICATION AMONG TROPICAL BIRDS.

Jenna R. Curtis, W. Douglas Robinson, Ghislain Rompré, and Suzanne H. Austin

Abstract

Given our expanding human footprint, it is important to understand how well remnant habitat patches in urban environments support natural bird communities. Urban forests are often unjustly perceived as statistical outliers with low conservation value. Despite a long history of urban bird research in temperate climates, studies across the full urban gradient in biodiverse and disturbance-sensitive tropical ecosystems remain rare. A unique set of spatially extensive avian survey data from 24 forest patches along the Panama Canal presents a valuable opportunity to assess the consequences of intensifying urbanization on the attributes and occurrence of tropical birds within remnant forests. We surveyed birds in forest fragments ranging from large rainforest preserves to small, isolated patches within a heavily-populated metropolis. Less than half of the 303 resident, non-aquatic bird species occurring in the forests of central Panama were detected in areas with more than 30% urban cover. Regional characteristics of percent urbanization and degree of forest fragmentation best explained differences in avian community composition between forest patches. Wing loading and length, phylogenetic distinctness, and developmental duration best explained a species' degree of urban association. Instead of homogenization, forest patches decreased in compositional similarity as they increased in surrounding urban cover. Our results are best characterized by community "simplification" – a loss of species exclusive of loss of functional or phylogenetic representation. Urbanization was negatively correlated with all metrics of diversity but without associated shifts or reductions in trait space except at the most extreme levels of human disturbance. One urban woodlot is not like another; each urban forest appears to contain a different subset of bird species found within large, intact rainforest communities, generally favoring strong dispersal abilities, short development periods, and recent evolutionary histories among our examined attributes. Even small patches of mature, undisturbed forest maintain phylogenetically and functionally diverse avian communities that resemble larger rainforest tracts. Forest patch-specific attributes such as history and intensity of human disturbance, vegetation structure, and access to nearby large forests likely determine the conservation value of urban forest patches for tropical birds.

Introduction

Urban environments are some of the fastest growing habitats in terms of both spatial coverage and ecological impact (Grimm et al. 2008). Among types of anthropogenic disturbance, the nature of urbanization is unique (Clergeau et al. 1998, Faeth et al. 2001, Chace and Walsh 2006, Chamberlain et al. 2009, 2017, Filloy et al. 2015, Santiago-Alarcon and Delgado-V 2017). Logging, grazing, and agriculture are episodic disturbances that retain the potential for natural regeneration (Blair 1996, Lambin et al. 2003). Urbanization represents a profound and irreversible form of land conversion. Even a small amount of urban cover can have a large ecological footprint (Alberti et al. 2001, Lambin et al. 2001, Grimm et al. 2008, Alberti 2010), affecting environmental subsidies, process rates, hydrologic cycles, and regional climate (McDonnell et al. 1997, Lambin et al. 2003, Grimm et al. 2008, Alberti 2010, Wang et al. 2019). Calls for more attention to urban ecosystems are longstanding (McDonnell and Pickett 1990, Heilig 1994). Yet ornithologists have historically been reluctant to study urban environments, possibly because they are perceived as “unnatural” (McDonnell et al. 1997, Crooks et al. 2004) or because urbanization is gradual and the spatial extent of most cities is small (McDonnell and Pickett 1990, Heilig 1994, Lambin et al. 2001).

Remnant habitat patches within cities are generally characterized by reduced bird species richness (Batten 1972, Cincotta et al. 2000, Cam et al. 2000, O’Connell et al. 2000, Gaston et al. 2003, McKee et al. 2004, Glennon and Porter 2005, McKinney 2008, Aronson et al. 2014, Batáry et al. 2018); homogenization, or increased compositional similarity (Lancaster and Rees 1979, Beissinger and Osborne 1982, Blair 2001, Clergeau et al. 2001, Crooks et al. 2004, McKinney 2006, Ortega-Álvarez and MacGregor-Fors 2009, Filloy et al. 2015); and proportional dominance by a specific subset of synanthropic urban “exploiters” (Blair 1996, McKinney 2002, Sol et al. 2013, Fischer et al. 2015, Leveau and Zuria 2017). Forest fragments isolated within urban habitats have been regarded as poor or low-quality refuges for native birds (Turner and Corlett 1996, Mörtberg 2001, Suarez-Rubio and Thomlinson 2009). But how different are urban forest fragments from their non-urbanized counterparts? This question is commonly investigated in temperate zones (see reviews in Marzluff 2001, Chace and Walsh 2006) but remains under-investigated in the tropics (Ortega-Álvarez and MacGregor-Fors 2011a, Escobar-Ibáñez and MacGregor-Fors 2017).

Neotropical forests hold an important proportion of global avifauna (BirdLife International 2013) and the densest concentration of forest birds on the planet (Stotz et al. 1996). Lack of extreme seasonal fluctuations in temperature and resources in tropical forests may produce idiosyncratic responses to urbanization (Ortega-Álvarez and MacGregor-Fors 2011a, 2011b, Sol et al. 2013, Filloy et al. 2015, MacGregor-Fors and García-Arroyo 2017). Studies from northern latitudes with long histories of human settlement could underestimate the impact of urbanization in developing regions where species have had less time to adapt to human activity (Sol et al. 2013, Jokimäki et al. 2016). The considerable species richness and high sensitivity of tropical birds to habitat degradation suggests even greater urban-associated biodiversity losses at low latitudes (Laurance and Bierregaard 1997, Gaston et al. 2003, Stratford and Robinson 2005, Leveau et al. 2017).

Latin America is the second most rapidly developing region in the world (Cincotta et al. 2000, Maria et al. 2017), with over 81% of the population currently living in urban areas (United Nations 2018) and high rates of land conversion relative to population growth (Heilig 1994). In central Panama, a broad range of habitat types from primary forest to dense metropolis within a small area presents a unique opportunity to evaluate differences between bird communities of urban and non-urban forest patches. 55% of Panama's 972 bird species occur within the vicinity of the Panama Canal, forming a steep gradient of species richness that varies in association with precipitation, forest age, and landscape configuration (Rompré et al. 2007). Urbanization is among the most influential factors of habitat change in the region (Rompré et al. 2008). The Canal watershed is experiencing rapid anthropogenic expansion which outpaces nationwide growth (Cho 2001, Maria et al. 2017). Percent urban cover ranges from < 1% to over 97%, with most of the region's nearly 2 million inhabitants residing in major cities on either end of the Canal zone. Maintaining ecosystem integrity within tracts of highly diverse but unprotected forest near the boundaries of urban areas is a conservation priority (Condit et al. 2001, Robinson et al. 2004). Nevertheless, only three studies previously evaluated forest bird communities within the Canal zone (Petit et al. 1999, Robinson et al. 2004, Rompré et al. 2007), and none incorporated forests in urban areas. Panama's heavily urbanized coastal regions are routinely omitted as outliers rather than being the subject of investigation (Rompré et al. 2007, Curtis et al. 2019 *in review*). The degree and nature of dissimilarity between urban and non-urban forest bird communities along the Panama Canal remains unknown.

In this study, we evaluated how urbanization influences the use of forest patches by birds in a complex Central American landscape. Previous studies assessed changes in forest bird species richness along the urban gradient in the Canal zone (Rompré et al. 2007). However, number of species alone is not a good indicator of the ability of a bird community to maintain ecological services (*e.g.,* pollination, pest control, seed dispersal) in the face of environmental change (Peterson et al. 1998). Functional and phylogenetic diversity are also important determinants of a system's resilience to urbanization. Therefore, our primary focus was on changes in species composition and characteristics between urban and non-urban forest patches. Our objectives were: 1) identify landscape-level correlates of species occurrence patterns within forest patches across a full gradient of urbanization; 2) identify attributes of species that do and do not occupy forests within urban areas; 3) assess evidence for urban homogenization based on the number of shared species and traits among urban environments; and 4) evaluate whether functional and phylogenetic diversity within forest patches decline as urban cover increases.

Methods

Study Area

We studied avian communities in a 65 x 30 km corridor of lowland along the Panama Canal (Figure 4.1). The average altitude is approximately 60 m above sea level and varies between 0 and 400 m. The natural vegetation in this area ranges from dry, seasonal Pacific-slope forests that receive less than 1,650mm precipitation annually to evergreen, premontane Caribbean rainforests with over 3,400mm precipitation annually (ACP 2016). Human impacts are concentrated around two urban centers on either end of the canal: Colon, a city of approximately 400,000 residents along the Caribbean, and Panama City, a metropolitan area that exceeds 1.5 million residents on the Pacific coast (General Comptroller of the Panama Republic 2003). The rest of the region is mostly mature secondary forest with scattered patches of undisturbed old growth (Pyke et al. 2001, ANAM 2003). All forests occur in fragments ranging from <15 ha to over 15,000 ha (Rompré et al. 2009) and almost half of Panama's forest cover is protected in national parks and monuments. The remaining unprotected forest is characterized by small fragments within a mosaic of regenerating second growth, pasture, and urban developments. Panama is unique in that the urban gradient is steep over a small spatial extent; a high percentage of the region's forests occur close to major cities. The broad environmental variation along the Canal provides a valuable opportunity to evaluate the effects of urbanization on forest bird communities over various biophysical, climatic, and geographic conditions.

Subregion Characteristics

We separated the study area into "subregions" primarily defined by political administration. Some subregions were further divided to reduce internal topographic and biogeographical variability (Rompré et al. 2007). Our selected 24 subregions ranged between 4.4 and 106.7 km^2 and spanned the entirety of physiographic and environmental variation along the Panama Canal. Each subregion contained at least one forest fragment as well as other habitat types.

We first characterized subregions by the percent cover of three principal land use categories that represent the majority of habitat in the Canal zone: (1) secondary or primary tropical broadleaf forest, (2) pastures and agriculture, and (3) urbanized. We calculated percent cover using digitized Landsat ETM+ satellite maps, provided by the Panama Canal Authority (ACP), showing the normalized difference vegetation index (NDVI) for the Canal zone from 1999 and 2003; consult Rompré et al. (2008) for additional details (see Table D.1 for full environmental attributes and definitions). We hence refer to subregions with >30% built cover as "urbanized", 3-29.9% built cover as "rural", and <3% built cover as "wildlands" per a modified version of Marzluff (2001). We also calculated the linear distance from the centroid of each subregion to the nearest metropolitan area - either Panama City or Colon. We did not consider additional metrics of urbanization including population size and density and road density because they were highly correlated with percent urban cover (Pearson's r > 0.9).

Forest age was previously found to be an informative explanatory variable for avian species richness in the Canal zone (Rompré et al. 2007). We defined subregion forest age based on the dominant age of all forest patches in a given subregion using a consistent, incremental series of time bins: (1) young secondary forest disturbed <100 years ago; (2) mature secondary forest disturbed 100-500 years ago; and (3) mature primary forest not logged or cultivated for at least 500 years. Finally, we used the proportion of total forest area contained within a subregion's 1-2 largest forest patches as an index of overall degree of subregion forest fragmentation.

Bird Surveys

The focus of our study was on resident birds that utilize forest habitats, as these species are among the most sensitive to human disturbance (Gibson et al. 2011), and remnant forest patches are at greatest risk from development in the Canal zone (Robinson et al. 2004). We inventoried birds in the largest continuous forest patch in each subregion during breeding months (March-July) between 1998 and 2005. Bird surveys consisted of a combination of point counts, spot mapping, and *ad libitum* observations. Additional target surveys were performed on flowering and fruiting trees to observe canopy-dwelling nectarivores and frugivores that are otherwise difficult to detect (Karr 1981, Robinson 1999).

We implemented a results-based stopping rule to ensure all forest patches were surveyed with equal thoroughness despite differences in patch size (Watson 2003). A forest was considered completely surveyed when 20% of the cumulative time spent surveying elapsed without any new species detections, and constructed accumulation curves of species detections over time reached asymptote. Bird species not detected within the largest forest patch were assumed absent from all forests in that subregion.

Functional and Phylogenetic Attributes

Aquatic birds that utilize streams, lakes, or wetlands for foraging, and nocturnal members of the families *Strigidae, Caprimulgidae, Steatornithidae,* and *Nyctibiidae,* were poorly sampled by our diurnal terrestrial surveys and were omitted, along with migratory non-residents and vagrant species, from our analyses. We considered 15 morphometric, life history, habitat, and niche-based traits (Table 4.1) that broadly cover the means through which birds interact with and influence their environment. There is existing precedent for considering these traits when evaluating bird sensitivity to urbanization (Kark et al. 2007, Evans et al. 2011, Callaghan et al. 2019). We obtained species information from published accounts and field guides (Table D.2) as well as extensive author experience with local birds. We considered but did not include IUCN threat level due to lack of variation in the dataset; 96.5% of species in our analyses were of Least Concern (IUCN 2019)

Phylogenetic diversity, or variation in evolutionary history among species, is also an important component of species responses to human disturbance. Ecological attributes are often phylogenetically conserved, meaning species with closely shared evolutionary history share similar characteristics (Derrickson and Ricklefs 1988, Losos 2008). Patterns in phylogenetic diversity may also capture variations in species responses that physical or behavioral attributes do not (Devictor et al. 2010, Flynn et al. 2011, Sol et al. 2014, Monnet et al. 2014). The effect of evolutionary relationships should therefore be considered in evaluations of species responses. We examined relationships between phylogenetic diversity and urbanization, and also incorporated evolutionary effects into our statistical models. Phylogenetic metrics were calculated using a single maximum clade credibility tree based on the pseudoposterior distribution of 1000 dated phylogenies derived with the Hackett backbone from http://birdtree.org (Jetz et al. 2012), generated in program R (R Core Team 2019) with package phangorn (Schliep 2011).

Statistical Analysis

Community ordination was conducted in PC-ORD (McCune and Mefford 2011). All other analyses were performed with Program R. The initial dataset contained presence/absence values for 313 resident bird species detected in the largest forest patches of 24 mainland Canal zone subregions. Summary statistics indicated an initial coefficient of variation (CV) for species totals of 57% and CV of 39% for sampling unit totals. These values suggest low variability in the marginal totals of the community matrix, such that relativizations would have little effect on the final ordination. We removed 10 bird species occurring in fewer than 2 sampling units. Our matrix of seven environmental variables was relativized by adjusting to standard deviates.

Outlier analysis using Sorensen distance identified the Panama City subregion (PTY) as an outlier with an average distance value more than 2 standard deviations greater than the grand mean distance between sites (SD = 2.7). We believe this subregion is an outlier due to its high degree of urbanization (over 97% built cover) and comparatively low species richness relative to the mean (S= 66 vs 163). However, other subregions with similarly low richness and environmental values were not identified as outliers. There was no reason to suspect PTY belonged to a different population than other Canal-adjacent subregions or doubt the accuracy of its bird inventory data. Because evaluating patterns of community composition across a full urban gradient - including the most heavily urbanized subregions - was our primary objective, we retained the PTY subregion for analysis.

We used non-metric multidimensional scaling techniques (NMDS) to evaluate patterns and landscape-level correlates of species occurrence across subregions. NMDS is an iterative ordination procedure that maximizes the correlation between dissimilarity values and distances in Euclidean space (Kruskal 1964). The result is a reduced-dimension depiction of differences in community composition and structure between subregions. We performed NMDS using Sorensen distance on random starting configurations for 250 runs on both real and randomized data. Ties in the distance matrix were not penalized (Kruskal's strategy 1). Statistical significance of the final stress was evaluated by randomization test comparing the observed final stress against that of data randomized by permuting the values within columns (species).

We then used biotic-environmental matching (BIOENV; Clarke and Ainsworth 1993) to identify the suite of environmental variables that best described species occurrence patterns among subregions. BIOENV maximizes the rank correlation between scaled environmental and site by species distance matrices, using Spearman's rho to determine which combination of environmental variables is most strongly associated with differences in bird communities. We used permutation tests with 999 runs to confirm whether the correlation value between landscape variables and community composition was greater than by chance alone. We performed BIOENV using the vegan package (Oksanen et al. 2019) with Euclidean and Sorensen distance measures for landscape characteristics and community data, respectively.

Axis 1 of the NMDS ordination represented a strong urban gradient from predominantly built subregions with small, highly fragmented forest patches to entirely vegetated subregions with large, contiguous forests. Species scores were calculated as weighted average site scores; because the community matrix contained detection/non-detection data, a species score simplifies to the average site score for the sites at which that species occurred. We generated an index of urban association by multiplying all Axis 1 scores for species and subregions by -1 and used this as a response variable in subsequent analyses. Species with high urban index values were associated with forest fragments in urbanized subregions whereas species with low urbanization index values were considered sensitive to human disturbance.

To evaluate whether avian communities increased in compositional similarity among urbanized areas, we compared multivariate homogeneity of dispersions (Anderson et al. 2011) between subregions grouped into three land use categories: wildland (0-2% built cover), rural (3-30% built cover), and urban (>30% built cover) using the 'betadisper' function in package vegan. Group dispersion represents the average distances of individual subregions from their group centroid in species space. More homogenous groups exhibit smaller dispersion due to a greater number of shared species. Thus, this method is also considered a measure of beta diversity or homogenization between sampling areas. Pairwise significance between group means was assessed with permutation tests (9,999 runs in ‘permutest’, vegan package).

To assess whether species responses to urbanization are associated with particular biological traits we implemented stochastic gradient boosted regression trees (BRTs; Friedman et al. 2000). This procedure iteratively develops a large ensemble of simple decision trees constructed from random subsets of the data while progressively minimizing residual errors (De’ath 2007, Elith et al. 2008). BRTs have the advantage of implicitly incorporating interactions and non-linear responses into predictions. They do not require data relativization, and are capable of handling missing predictor values (Breiman et al. 1984, Friedman and Meulman 2003, Elith et al. 2008).

Our response, an index of urban association based on Axis 1 scores from NMDS ordination, was modelled as a continuous variable with a Gaussian error distribution. Our explanatory variables were 15 morphometric, life history, and niche-based species traits (Table 4.1). To account for phylogenetic effects, we also included phylogenetic distinctness as an explanatory variable. Phylogenetic distinctness is a measure of a species’ evolutionary uniqueness based on the number of close relatives in the phylogenetic tree and their cumulative branch distances. We calculated phylogenetic distinctness with the package picante (Kembel et al. 2010) using our maximum clade credibility tree and a fair-proportion index. We weighted species by the inverse number of subregions in which they occurred, reducing the influence of widely distributed species which are less likely to distinguish urban and non-urban communities.

We trained our BRT model on a random selection of 75% of species data, with the remaining 25% set aside for model testing. We implemented BRTs using the ‘gbm.step’ function in package dismo (Hijmans et al. 2017). Per the recommendations of Elith et al. (2008) and Elith and Leathwick (2017) we tuned the following parameters to produce a model with >1000 constituent trees, using 10-fold cross-validation to select the optimal number of trees. We used a bag fraction of 0.5, learning rate of 0.001, and tree complexity of 3. With small datasets, redundant predictors may degrade model performance (Elith et al. 2008). We removed predictor variables that did not improve model performance with an iterative dropping process described in (Elith et al. 2008, Supplement 2). This procedure evaluates the effect of removing individual variables on predictive deviance compared to the full model using 10-fold cross validation, drops the lowest contributing predictor, and repeats this process until all variables that would not increase predictive deviance if omitted are removed.

We evaluated predictor variable influence using a combination of partial dependence plots and the relative contribution of individual predictors. Partial dependence plots show the relationship between a single predictor and the response after accounting for the average effects of all other variables in the model. The relative importance of predictor variables is based on the number of times a variable is used to split a decision tree, weighted by the squared reduction in model deviance as a result of each split, averaged over all trees and scaled so that the sum of all variable influences is 100 (Friedman and Meulman 2003, Elith et al. 2008). Higher values indicate a stronger influence on the response. We identified variables with greater influence than expected due to chance (100 divided by the number of variables in the final model; Müller et al. 2013). We evaluated the fit of our model using the 10-fold cross-validated (CV) correlation coefficient and total percent deviance explained (calculated as null deviance minus residual deviance, divided by null deviance, multiplied by 100) from the training data. Model performance was evaluated using R-squared indicators for predictions on both training and withheld testing data.

Finally, we evaluated the association between subregion urban index values and phylogenetic and functional diversity. All diversity indices were subject to simple linear regression and correlation against subregion urban index to determine the direction, strength, and significance of their association. We used our maximum clade credibility tree to calculate three phylogenetic diversity metrics: Faith's phylogenetic diversity (PD; Faith 1992), the sum of phylogenetic branch lengths among all species in a community; mean pairwise distance (MPD; Clarke and Warwick 1998, Webb et al. 2002, Tucker et al. 2017), the average of all phylogenetic distances among final nodes (species) in a community; and mean nearest taxon distance (MNTD), the average of the shortest phylogenetic distance of each species to its closest relative in the community. Together, these three diversity metrics represent the phylogenetic breadth, complexity, and distinctiveness of a given subregion. However, these metrics are also sensitive to species richness, which was correlated with the amount of forest surveyed in each subregion; larger subregions generally contained more species because they had bigger forest patches. To estimate the effect of urbanization on phylogenetic diversity independent of forest patch size, it was necessary to standardize richness across subregions through rarefaction. We randomly sampled species from each subregion equal to the minimum subregion species richness (N = 66). Phylogenetic diversity metrics were then calculated for these rarefied equal-richness assemblages. We repeated this process for 999 iterations and computed the mean values for our three phylogenetic diversity metrics across all runs.

We measured trait diversity using two indices: functional dispersion (FD; Laliberté and Legendre 2010) and a richness-adjusted form of functional trait distinctiveness derived from (FTD; Scheiner et al. 2017). Functional dispersion (FDisp) quantifies the average distance of individual species to the centroid, or mean, of all species trait values for a community (Laliberté and Legendre 2010). Subregions with more diverse species attributes occupy a larger portion of the trait space and have higher FDisp values. This metric is by nature insensitive to differences in species richness among subregions. Our second measure of trait diversity was derived from Scheiner et al.'s (2017) functional trait distinctiveness. FTD combines species richness, trait evenness, and mean pairwise trait dispersion among species to quantify the effective number of functionally distinct species within a community. By dividing this metric by the total number of species in a subregion, we obtained the proportion of functional richness per species independent of species richness. Large corrected FTD values indicate high per-species trait richness, or a greater number of functionally unique species within the community.

To determine whether high urban index values were associated with reduced dispersion and/or shifts in trait space, we performed significance tests of subregion bird community trait dispersion and variance. We generated distance matrices from species trait data for each individual subregion as well as each primary land use group using the Gower distance measure, which is compatible with mixed data types (Gower 1971). To test if the trait dispersions of one or more subregions were different, we performed an analysis of variance (ANOVA) on the average distances of individual species to subregion centroids based on their attributes in multivariate trait space, using Tukey’s HSD to compare pairwise differences in mean trait dispersion between subregions. We then implemented a permutational multivariate analysis of variance (PERMANOVA; Anderson 2014) using the ‘adonis’ function in the vegan package to determine whether subregion centroid locations differed in multivariate trait space both within and between primary land use groups (urban, rural, or wildland). Where results were significant, we performed post-hoc comparisons between paired subregions with a Bonferroni correction to adjust for multiple comparisons.

Results

We detected 303 resident, non-aquatic bird species associated with forest habitats along the Panama Canal (Table D.3). 129 (42.6%) of these were detected in urbanized subregions with more than 30% urban land cover. All birds found in urban forest patches were also detected in non-urbanized subregions. The average species richness across subregions was 163 species. Individual subregion species richness ranged from 66 in Panama City (PTY) and the adjacent subregion Ancon (ANC), to 274 in Achiote North (AN).

Patterns of Species Occurrence

Percent urban cover and degree of forest fragmentation best explained differences in avian community composition between subregions (BIOENV: Spearman’s rho = 0.742, $p < 0.001$). Ordination of subregions in species space converged on a stable 2-dimensional solution (final stress = 8.06, final instability = 0.00) with a cumulative R^2 of 93.7% (Figure 4.2). Axis 1 captured 85.5% of the variation in the data and Axis 2 accounted for an additional 8.2% of variation in the data. Axis 1 was strongly associated with percent urban cover, degree of forest fragmentation, percent forest cover, and forest age Table 4.2). Non-urbanized subregions were closely clustered on the positive end of this axis while urbanized subregions exhibited broad peripheral placement on the opposite extreme (Figure 4.2). This arrangement of subregions was independent of differences in species richness between sites (Appendix D1). None of our selected environmental variables were strongly associated with the second axis of the ordination (all R^2 values < 2.0; Table 4.2), which primarily served to further differentiate urbanized subregions. Because some effects of urbanization were captured by the second axis, the relationship between urban cover and Axis 1 was not perfectly linear. Using Axis 1 scores as a response variable disregards the full extent of community differences between PTY and the other urban subregions. On the other hand, this assists our treatment of these subregions as a single "urban group".

The first ordination axis effectively captured the urban gradient, so we took the negative values of Axis 1 scores as an index of urban association. Subregion urban index values centered on zero and ranged from 1.93 for Panama City (PTY, 97.9% urban cover) to -0.967 for the northernmost subregion in Soberania National Park (NSO-N, 0% urban cover; Table D.4 for site axes scores). The mean species urban index value was 0.418 (Table D.3). The highest values were 0.798 and 0.762 for Pale-eyed Pygmy Tyrant and Bronzed Cowbird, respectively – species for which nearly half of all detections were in urbanized subregions. The lowest species urbanization index was -0.958, shared by five species (Black-crowned Antpitta, Bicolored Hawk, Dull-mantled Antbird, White-tipped Sicklebill, and Yellow-eared Toucanet) only detected in the two least-urbanized subregions (AN and NSO-N).

Assessment of Urban Homogenization

The wide spread of urbanized subregions on the left periphery of first ordination axis suggests a higher degree of urban bird community heterogeneity relative to non-urbanized subregions. 'Betadisper' found strong support for differences in community dispersion between primary land use groups (df=2,21; F = 5.97; permutational p-value = 0.008). This significance was driven by differences in dispersion between urban and wildland subregions (pairwise permutational p-value = 0.004). By contrast, pairwise differences in dispersion between rural and the other land use groups were not significant (permutational p-values: rural-urban = 0.217; rural-wildland = 0.06). Group dispersion, considered a measure of beta diversity, increased among urban subregions by 18% and 29% compared to rural and wildland sites, respectively. These results indicate forest patches decrease in compositional similarity as their subregions increase in urbanization, with the forests in the most urbanized subregions sharing significantly fewer species than forest patches in areas with little to no urbanization.

Species traits associated with urbanization

Our boosted regression tree model of species urban index association with species traits explained 33.24% of total deviance in the training data and had a mean 10-fold cross-validated correlation coefficient of 0.35 (training data $R^2 = 0.372$). Predictive performance on withheld testing data was low but acceptable ($R^2 = 0.274$). Figure 4.3 summarizes the relative contribution of each predictor after dropping three variables that did not contribute to model performance. Only four traits exhibited a greater predictive power than expected by chance (100 divided by 13 variables, or 7.69%): wing loading, developmental duration (the sum of egg laying, incubation, and nestling periods), phylogenetic distinctness, and relative wing length. Together, these four predictors accounted for 56.1% of model performance (see Figure 4.4 for partial dependence plots). Species from younger phylogenetic lineages and with shorter developmental duration had the strongest associations with urban forest patches. Urban association was lowest at intermediate wing loading values between approximately 0.25 and 0.3. We observed a sharp increase in urban association at relative wing length values greater than 6 mm/g. There was no evidence of 2-way interactions between predictors (all second order interaction sizes <0.03).

Phylogenetic and Functional Diversity

Results of Pearson correlations indicated urbanization was negatively correlated with all phylogenetic and trait diversity metrics (Table 4.3, Figure 4.5). Using simple linear regression, index of urbanization had a marginal but significant effect on four out of five diversity metrics, excluding mean pairwise distance (Figure 4.5A). Subregions with high urban index values exhibited broad variation in diversity response that reduced the explanatory power of linear regression (Figure 4.5). Using urbanization index as a predictor only captured an average 26.2% total variance among diversity metrics (Table 4.3). Residual plots and visual examination of scatterplots confirmed linear models were appropriate. Models fit with a quadratic term for urbanization index did not perform better.

We observed that, while urban subregions differed in their individual species composition, all but one subregion possessed generally similar trait composition. Though we initially found significant difference in trait dispersion between subregions (ANOVA df = 2,3888; F = 2.062; p = 0.002), pairwise comparisons among subregions using Tukey’s HSD showed this significance was driven solely by PTY. When PTY was omitted, the average species distances to subregion centroids in trait space was not significantly different (ANOVA df = 2,3823; F = 1.226; p = 0.213). We also failed to reject the null hypothesis of no difference in multivariate centroid location in trait space based on primary land use cover category (PERMANOVA df = 2,681; F = 1.381; p = 0.223). This result was supported by visual assessment of subregions ordinated in species trait space (Figure D.1); convex hulls drawn around subregions grouped by land use cover category and clustered by the species traits they contained were broadly overlapping.

Within primary land use groups, there was no difference in subregion centroid location in trait space for either wildland or rural subregions (PERMANOVA df = 12,2560; F = 0.82; p = 0.804 and df = 6,1043; F = 1.418; p = 0.076, respectively). However, we found significant differences in trait space centroid location among subregions within the urban land use group (PERMANOVA df = 3,285; F = 2.762; p = 0.004). Post hoc pairwise comparisons revealed these differences were the result of PTY being centered in a different portion of trait space than the remaining urban subregions (ANC, SIL, and ROD; Bonferroni-adjusted p-values = 0.018, 0.03, and 0.006, respectively; all other pairwise corrected p-values = 1.0).

Discussion

We found bird community composition in forests along the Panama Canal can be explained almost entirely by the urban gradient alone. The close association of urban forest bird communities from both sides of the isthmus, despite extreme differences in plant and precipitation conditions, suggests urban disturbance has influence equivalent to the strong precipitation gradient in driving species richness and community composition (Rompré et al. 2007, Curtis et al. 2019 *in review*). Contrary to expectations, urbanization was generally not associated with diversity loss or increased compositional similarity. Each urban forest appears to contain a different subset of the birds found within large, intact rainforest communities, broadly favoring good dispersers with short developmental duration and comparatively recent evolutionary histories.

The attrition of biodiversity is often a consequence of species-area effects, where small remnant habitats preserve fewer species than large ones (MacArthur and Wilson 1967, Haddad et al. 2015). In our study, subregions with the smallest remnant patches were not necessarily those with the lowest species richness, suggesting area effects alone cannot adequately explain the loss of species from urban forests. Inconsistent avifaunal responses to urbanization reveal the importance of local patch characteristics, forest connectivity, and disturbance history. Given the current expanding human influence on habitats, understanding the consequences of urbanization for avifauna in highly biodiverse tropical ecosystems is imperative, yet quantitative ecological data from the tropics remains rare (Ortega-Álvarez and MacGregor-Fors 2011b, Escobar-Ibáñez and MacGregor-Fors 2017, Moreno et al. 2018). The unique set of spatially extensive avian survey data from central Panama provides us with a valuable opportunity to investigate the effects of intensifying anthropogenic activity on the traits, diversity, and occurrence of tropical forest birds.

Lack of homogenization in urban forests

Though many studies associate urbanization with lower overall diversity, leading to increased compositional similarity (Crooks et al. 2004, McKinney 2006, Olden 2006, Devictor et al. 2007, Suarez-Rubio and Thomlinson 2009, Fontana et al. 2011), evidence for community homogenization in the neotropics is mixed (MacGregor-Fors and García-Arroyo 2017). Along the Panama Canal, we found the most urbanized subregions shared the fewest species. The reasons for this level of dissimilarity are likely twofold: an absence of hyperabundant synanthropic birds in large urban woodlots; and strong patch-specific environmental pressures that differ between urban forests.

Previous studies suggest that homogenization is partially driven by the increased prevalence of non-native and anthropophilic species, or “urban exploiters”, across all urban habitats (Blair 1996, McKinney 2006, Olden 2006, Sol et al. 2013). However, our tropical forest ecosystem had a notable absence of such urban exploiters. Globally widespread non-native species often attributed to urban homogenization such as the Rock Pigeon, House Sparrow (*Passer domesticus)*, or European Starling (*Sturnus vulgaris*) either do not occur in Panama or are in such low abundance that they are difficult to detect outside of highly developed metropolitan areas. These birds, as well as the introduced Saffron Finch (*Sicalis flaveola*), are almost never observed in urban woodlots along the Canal. Panama’s additional lack of introduced tropical birds associated with semi-forested habitats such as Red-crested Cardinal (*Paroaria coronata*), estrildid finches (genus *Lonchura*), and non-native Psittaciformes observed elsewhere in the neotropics (*e.g.,* Iriarte et al. 2005, Arendt et al. 2013) merits further research. The underlying reasons for the notable absence of widespread non-native birds in Panama are unclear but may be associated with low propagule pressure (Sodhi et al. 2011) and/or changes in avian pathogen and parasite dynamics across tropical cities (Delgado-V and French 2012, Calegaro-Marques and Amato 2014).

No species increased in prevalence in urban environments. Our most urban-associated species (Pale-eyed Pygmy Tyrant, Bronzed Cowbird, Lance-tailed Manakin, and Yellow-crowned Parrot) still had proportionally more detections in non-urban subregions. Possibly the most abundant city bird in Panama, the Great-tailed Grackle was detected with equal frequency in urban and non-urban forest patches alike. Our lack of a discrete urban species assemblage agrees with previous findings that truly urban tolerant species are uncommon, and even highly urbanized environments still mostly consist of traditionally “urban sensitive” species (Sol et al. 2014). Because all species detected in urban forests also occurred in non-urban forests, urban forests bird communities represented subsets of larger, species-rich forest patches rather than novel communities (Appendix D1). While there was high species turnover among urban forest patches, there was very little turnover across the full urban gradient.

Species traits associated with urbanization

We identified wing loading, relative wing length, phylogenetic distinctness, and developmental duration as significant predictors of avian urban association. Wing loading and relative wing length are morphological traits correlated with different aspects of dispersal ability. Relative wing length is an indicator of movement capacity across the landscape. Birds with longer wings relative to their body size tend to spend more time in the air and can fly greater distances in a single trip (Hamilton 1961, Alexander 2002). In experiments with 10 Panamanian forest bird species, wing length was more correlated with average maximum flight distances than wing load (Moore et al. 2008). We observed a sharp threshold at which birds with longer wings relative to their body size increased association with urban forests. Birds with greater than 6 mm/g relative wing length chiefly consisted of birds from the families Trochilidae, Tyrannidae, and Apodidae – all highly active aerial foragers that spend long periods each day in flight.

Wing load is a measure of both the force necessary to initiate flight (Alexander 2002), as well as the maximum gliding speeds that can be reached (Pennycuick 2008). As wing loading increases, the cost of lift, energy consumed per unit distance of travel, and risk of predation increase (Hedenström 1992, Witter and Cuthill 1993, Pennycuick 2008). We observed a steep initial decline in urban association with increasing wing load, followed by a gradual rise at higher wing loading values. This indicates birds with all but the lowest and highest wing loading values are at a disadvantage in urban patches. The lowest wing loaded birds, mostly small-bodied Passerines, possess the greatest propensity for flight. The highest wing loaded birds include vultures and hawk-eagles - birds for whom high wing loading confers the ability to soar for extended periods in search of patchily distributed resources. However, our observed association between urbanization and wing load may be biased by missing data. Wing loading data was not available for several large-bodied, short-winged, presumably dispersal-limited species such as Crested Guan, Great Curassow, and Black-crowned and Streak-chested Antpittas. Because these species do not occur in any urban subregions, it is likely the inclusion of their wing loading values in our dataset would reduce the strength of urban association among heavily wing loaded birds.

Dispersal of tropical birds varies widely, with some species lacking the physical ability or behavioral inclination to reach isolated forest fragments through hostile/unfamiliar matrices (Willis 1974, Laurance 2008, Moore et al. 2008, Lees and Peres 2009, Ibarra-Macias et al. 2011a). The inclusion of both wing loading and relative wing size as significant predictors of urban association implies birds that can fly for extended periods, longer distances, and/or higher speeds are most likely to occur in urban forest patches. Their greater dispersal ability means they can establish and maintain population connectivity among heavily fragmented urban forests; more easily locate resources outside of small, isolated urban habitat patches; and evade novel urban predators (Chace and Walsh 2006). For these reasons, birds with short wings and high wing loading are likely more susceptible to stochastic population fluctuations due to predation or resource loss and generally less capable of traveling the necessary distances to recolonize urban forest patches following local extinction.

Reduced phylogenetic distinctness and shorter developmental duration were also significantly associated with occurrence in urban forests. Phylogenetically distinct species, those with comparatively unique evolutionary lineages and/or longer evolutionary histories, are usually more specialized, sensitive to disturbance (Sekercioglu et al. 2004, Frishkoff et al. 2014, Edwards et al. 2015) and therefore less successful in novel urban conditions. Likewise, species that need more time to lay eggs and raise young do poorly in cities, possibly due to fewer breeding opportunities and lower overall productivity among slow breeding species (Chamberlain et al. 2009, Sol et al. 2012).

Our final set of trait predictors did not capture more than 33% of the variance in bird urban association. Additional, unexamined traits such as relative brain size (Maklakov et al. 2011, Møller and Erritzøe 2015), immune response (Bradley and Altizer 2007, Audet et al. 2015, Møller et al. 2015), colonial behavior (Coleman and Mellgren 1997, Kark et al. 2007, Callaghan et al. 2019), environmental tolerance (Leveau and Leveau 2005, Sol et al. 2014), or annual total reproductive effort (Chamberlain et al. 2009, Sol et al. 2014) might better predict species occurrence or avoidance of urban forest patches. However, the data necessary to account for these attributes is widely lacking among any avifauna, particularly tropical birds. Future investigations would benefit from further study of the life histories of tropical birds, especially their reproduction, and individual variation in morphology.

Urbanization and diversity

One of the greatest conservation concerns regarding human disturbance is biodiversity loss. Yet we found limited evidence for urbanization-associated diversity declines except in the most extreme metropolitan areas. There was a significant but small negative effect of urbanization on phylogenetic and trait diversity. Increasing MNTD at lower levels of urbanization suggests phylogenetic "packing" – increasing density among existing phylogenetic groups, rather than expansion of the overall phylogenetic tree. Urbanization did not significantly decrease mean pairwise distance (MPD), thus phylogenetic trees did not "shrink" or get smaller as urban use intensified, which would reduce overall branch lengths between species. Instead, urbanization appears to "thin" trees by selectively pruning close relatives that are behaviorally and morphologically redundant.

We found no evidence that urbanization selectively targets specialist species with extreme trait values located at the periphery of trait space. Our results are more consistent with niche packing, the tendency for species-rich communities to be functionally redundant because multiple species fulfill similar ecological roles (MacArthur 1965). The addition of species further "packs" or increases density within the existing trait space rather than expanding it. Niche packing was previously identified as a dominant assembly pattern in high productivity environments including tropical broadleaf forests (Pigot et al. 2016, Pellissier et al. 2018). In our study, species-rich communities did not extend beyond the trait space of species-poor communities, suggesting richer communities had denser, rather than larger, trait spaces. Additionally, species-poor communities largely maintained trait and phylogenetic diversity, in one case (ANC) maintaining equivalent phylogenetic and trait diversity with only a third the species richness. This suggests species-rich bird communities along the Panama Canal contain more functionally complementary species. Whether this was due to the narrowing of individual niches or greater trait diversity among birds in species-rich communities could not be elucidated by our study.

Individual urbanized subregions exhibited very inconsistent diversity responses. This disparity is best observed between PTY and ANC which, despite sharing the highest urban index values and lowest species richness, had significantly different diversity metrics. Diversity within ANC resembled subregions with much lower urban index scores. Conversely, PTY was the only subregion to exhibit significant changes in trait space, along with much lower phylogenetic diversity scores. Yet these two sites had similar levels of urbanization. Therefore, while urban land use is broadly associated with diversity declines along the Panama Canal, position along the urban gradient alone cannot sufficiently predict whether a forest will lose phylogenetic or trait diversity.

Most urban subregions did not shift or shrink in trait space, suggesting urban forest patches may be able to maintain their original ecosystem services, trophic functions, and evolutionary histories. However, species with similar ecological attributes may still vary in their delivery of ecosystem services (Moran et al. 2004, García et al. 2013). It cannot necessarily be assumed that differences in species identity won't have meaningful consequences for overall ecosystem function, even with comparable trait representation among urban forest patches. Furthermore, the cumulative species richness of all forests in urban subregions combined was less than most individual rural or wildland subregions by themselves, indicating even a network of several urban forests may not support the same population-level diversity or resilience of a single large forest in a non-urbanized landscape (Rompré et al. 2007).

Nevertheless, there does appear to be a threshold at which extent of subregion urbanization becomes meaningful to forest bird community trait and phylogenetic diversity. PTY significantly decreased in trait dispersal and shifted location in trait space, suggesting the threshold of urban effects lies somewhere between 60 and 90% urban cover. Reductions in trait and phylogenetic diversity in PTY can be attributed to the reduction or total loss of raptors, nectarivores, terrestrial leaf-litter searchers, and members of the families *Momotidae* (motmots), *Trogonidae* (trogons), and *Thamnophilidae* (antbirds).

Antbirds and puffbirds (family *Bucconidae*) were the only families to notably decline across all urban subregions relative to non-urban forests.

Patch dynamics and landscape connectivity

There was a notable lack of community homogenization with increasing urbanization in our study. In temperate regions, deterministic habitat processes select for similar urban-tolerant species across habitats (McKinney 2006, Devictor et al. 2007). However, local factors including vegetation complexity and vertical heterogeneity may be more relevant than landscape context to endemic tropical birds (Suarez-Rubio and Thomlinson 2009). Bird community composition in urban forests along the Panama Canal is more likely influenced by patch-specific selection pressures such as history of disturbance, local resource availability, or permeability of the surrounding matrix. Patchy resources that may influence urban forest bird community composition include microclimatic refugia and forest structure. ROD has the greatest topographic complexity among surveyed urban forest patches. Its retention of drought-sensitive forest birds like Golden-crowned Spadebill and Russet-winged Schiffornis that other urban forests lack could be attributed to the greater availability of wet microclimatic refugia within its more varied terrain. The occurrence of the very large Lineated Woodpecker in only ANC is likely due to the abundance of large, mature trees in this area, unique among urban subregions.

Another important aspect of patch quality is history and intensity of human disturbance. PTY, the most bird depauperate urban forest, also has the longest history of human disturbance and most intensive current anthropogenic use. PTY is the only urban forest patch in our study with permanent built structures and regular use within the forest interior (including a popular tourist viewpoint at the center of the patch). While all urban forest patches are surrounded by some degree of human use, only PTY is adjacent to the most heavily developed zone of human occupancy on the entire isthmus. This extensive degree of anthropogenic disturbance, singular among our forest patches, explains PTY's significant loss of all but the least sensitive, most urban-adapted forest bird species including Yellow-headed Caracara, Bronzed Cowbird, Tropical Pewee, and Tropical Mockingbird. Frequency of human disturbance within the forest may account for PTY's total lack of large raptors whereas, SIL – the farthest patch from metropolitan areas – retains the most large-bodied raptors among urban subregions.

Though considered a rural subregion based on percent urban cover, the bird community of FAR resembles an urban forest in all avian diversity metrics. FAR contains heavily degraded second-growth forest surrounded by comparatively little urban cover, but adjacent to the largest highway in central America and therefore frequently subject to human disturbance. Many low-lying, easily accessible forests along the Canal like FAR have been completely harvested and subsequently regrown. Young secondary forests appear to possess only those birds with sufficient dispersal abilities to recolonize the patch. Mature urban forest patches with limited history of deforestation are likely to retain disturbance-intolerant species groups that would permanently disappear after total forest loss. The importance of dispersal ability for re-colonizing urban forest patches such as FAR following extirpation explains the significance of wing loading and relative wing length as predictors of avian occurrence in urban forests.

Perhaps the most important factor for diversity retention in urban forest fragments is habitat connectivity (Martensen et al. 2008, Losos and Ricklefs 2009). PTY is separated from the nearest large forest tract by over 2km of dense urban cover that represents a highly impermeable matrix to all but a small subset of the regional bird community. Forest patches with consistently higher than expected diversity for their degree of urbanization (ANC and ROD) are also the closest in proximity to extensive, undisturbed tracts of rainforest. Until the early 1990s, ANC was connected by a small spur of forest to Camino de Cruces National Park, and from there to the more expansive Soberania National Park. Likewise, ROD borders the Arraijan protected forest, separated in some places by a single two-lane roadway. Access to source populations from high quality rainforest habitat is key to the continued presence of dispersal-limited, disturbance-sensitive birds like Plain Xenops, Black-capped Pygmy-Tyrant, and Blue-crowned Manakin unable to maintain or re-establish populations in more isolated urban forest patches. Likewise antbirds and puffbirds, families which declined across all urban subregions, contain proportionally more species averse to crossing non-forested gaps and with low observed persistence in more isolated forest fragments (Lees and Peres 2009).

It is generally recognized that a combination of stochastic and deterministic processes drive population dynamics in fragmented habitats (MacArthur and Wilson 1967, Hanski et al. 1997, 2013). However, if turnover in community composition between small urban forest patches were the result of stochastic species losses from each individual fragment, we should expect more urban communities than PTY to exhibit reduced phylogenetic diversity and trait dispersion simply by chance alone. Instead, we found all forest patches except PTY occupied the same region of multidimensional trait space, regardless of differences in species composition and richness. Because smaller urban forests supported fewer taxonomically and functionally similar species, stochasticity may play some role in determining which among several potentially redundant birds occupies any given urban forest patch - whereas larger non-urban forests appear to have sufficient resources to support multiple similar species. Deterministic factors selecting for very subtly different resource utilization in each urban forest could also explain why we did not find niche-based factors such as diet, foraging, or nesting behavior to be reliable predictors of species response to urbanization across the entire landscape.

Conclusions and conservation implications

Across the urban gradient of the Panama Canal, tropical bird communities exhibited complex, disparate responses to increasing levels of landscape urbanization. Instead of the homogenization of bird community characteristics in woodlands surrounded by urbanization, we observed community simplification: a reduction in species richness without subsequent loss of ecological function or diversity. While urban forests possess fewer total species, most functional and phylogenetic groups can be found at all levels of urbanization, and only begin to disappear at the greatest extents of landscape urbanization. It appears that a combination of patch-level factors such as intensity or duration of human disturbance and connectivity with the surrounding landscape determine the conservation value of habitat patches for tropical forest birds.

The majority of the world's human population experiences nature through remnant habitats within urban centers (Dunn et al. 2006). Conserving urban biodiversity is as essential for furthering conservation awareness as it is to maintaining genetic diversity or ecosystem function. Our results show that forest fragments in all but the most heavily urbanized areas are suitable for the persistence of phylogenetically and functionally diverse avifauna. Structurally heterogenous woodland habitats incorporating mature, undisturbed forest in connectivity with other like patches are most likely to retain natural avian community characteristics, even if they are reduced in size and richness. The retention of large tracts of continuous, undisturbed forest close to cities is a unique feature of the Panamanian isthmus and is probably key to maintaining urban forest diversity in our system. Future conservation efforts should prioritize the connectivity and protection of these complex habitats, as they likely provide the greatest variety of ecological resources for birds.

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Tables and Figures

Table 4.1. Description of the 15 species attributes evaluated by our analyses, grouped by general categories. See Table D.2 for full descriptions and sources of each trait.

Category	Trait	Description
Life history	clutch size	average number of eggs per complete clutch
	developmental duration	total length of time from clutch initiation to fledging (in days)
	development mode	degree of precociality or altriciality; categorical
Morphometrics	body mass	mean adult weight (g)
	relative wing length	single wing chord length adjusted for body mass (mm/g)
	wing loading	amount of mass supported per unit wing area (g/cm²)
Ecological/Niche	nest type	nest construction open cup, enclosed, or cavity/burrow; categorical
	nest height	nest located on the ground, understory, midstory, or canopy; categorical
	diet preference	primarily eats fruits, invertebrates, nectar, plants/seeds, live vertebrates, dead vertebrates (scavenges), or is omnivorous; categorical
	diet breadth	number of major diet types consumed
	foraging height	searches for food on the ground, understory, midstory, canopy, aerially, or at multiple heights; categorical
	foraging behavior	attacks prey by gleaning, sallying, scratching/prying, chasing/screening, or sub-surface extraction; categorical
	foraging breadth	number of foraging strata (heights) utilized
Habitat preferences	habitat - forest interior	associated with inner core of forested habitat; binary yes/no
	habitat - edge/open	associated with shrub, grass, agriculture, or other non-forested habitats; binary yes/no

Table 4.2. All R^2, and Kendall (tau) correlation coefficients between environmental variables and the two-dimensional NMDS configuration of sampling units in species space. For definitions of environmental variables, see Table D.1.

	Axis 1		Axis 2	
Variable	**R^2**	**tau**	**R^2**	**tau**
AGE	0.57	0.651	0.015	0.084
AREA	0.093	0.304	0.001	0.072
DEG_FRAG	0.606	0.618	0.019	-0.137
DIST_TOWN	0.257	0.387	0.105	0.27
PCT_AG	0.093	-0.349	0.132	0.189
PCT_FOREST	0.635	0.674	0.001	-0.123
PCT_URBAN	0.642	-0.734	0.132	-0.046

Table 4.3. Phylogenetic and trait diversity measures modeled as simple linear functions of subregion urbanization score.

Diversity aspect	Metric	Estimate	S.E.	t-value	p-value	Adjusted R^2	Pearson's r
Phylogenetic	PD	-35.42	16.43	-2.155	0.04	0.1368	-0.4176
	MPD	-0.9625	0.5845	-1.647	0.114	0.0693	-0.3313
	MNTD	-1.4374	0.4384	-3.279	0.003	0.2977	-0.5729
Trait	FDisp	-0.0074	0.0014	-5.173	<0.001	0.5283	-0.7408
	FTD	-0.0058	0.0018	-3.146	0.005	0.2789	-0.557

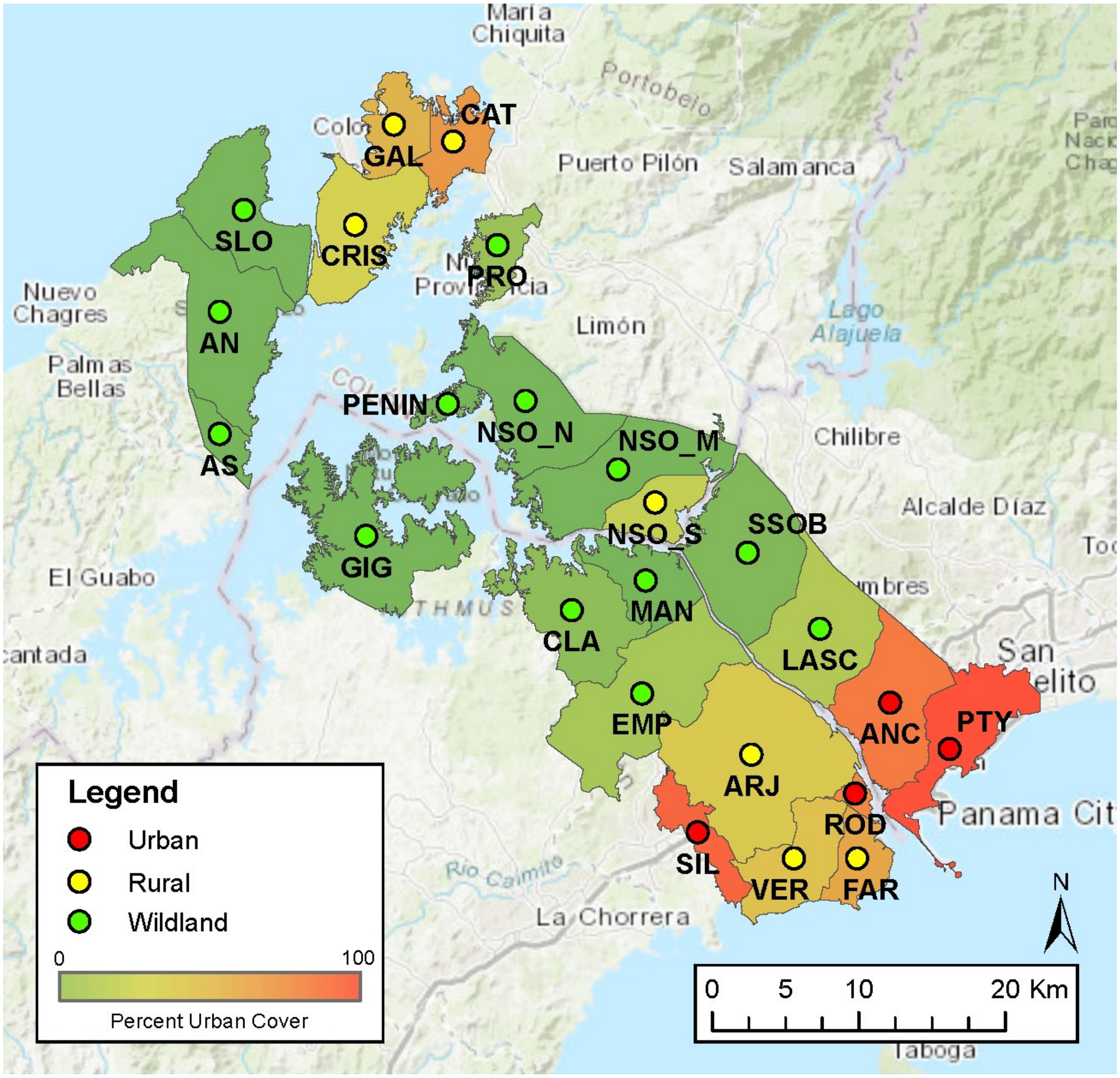

Figure 4.1 Digitized map of physiographic subregions along the Panama Canal modified from Rompré et al. (2007). Dark gray outlines indicate regions used for the study, with fill colors corresponding to total percent urban cover for that subregion. Circles located on polygon centroids are colored by primary land use group (see "Subregion Characteristics" in Methods).

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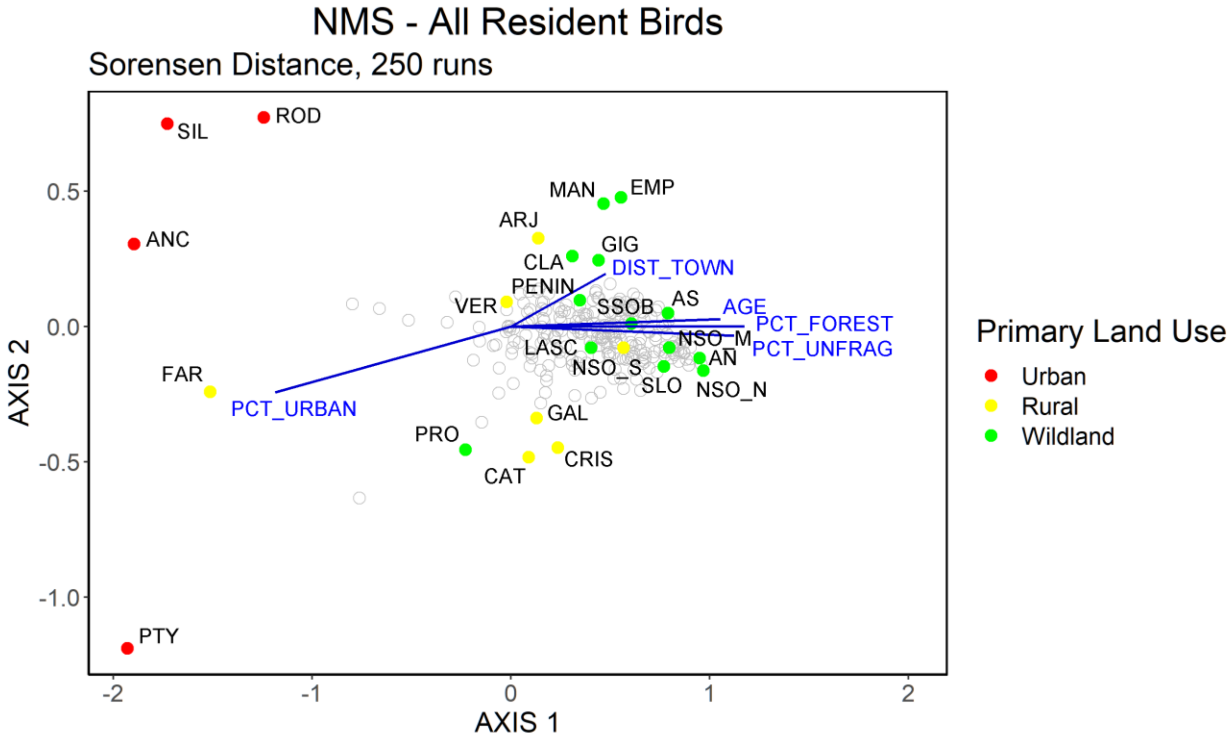

Figure 4.2. NMDS ordination of resident, non-aquatic forest-associated species and forest patch sampling units in species space. Subregions indicated by abbreviations, with colored dots corresponding to group membership based on percent urban cover. Bird species are represented by gray circles. Blue lines and text indicate the strength and direction of significant associations between environmental variables and each axis

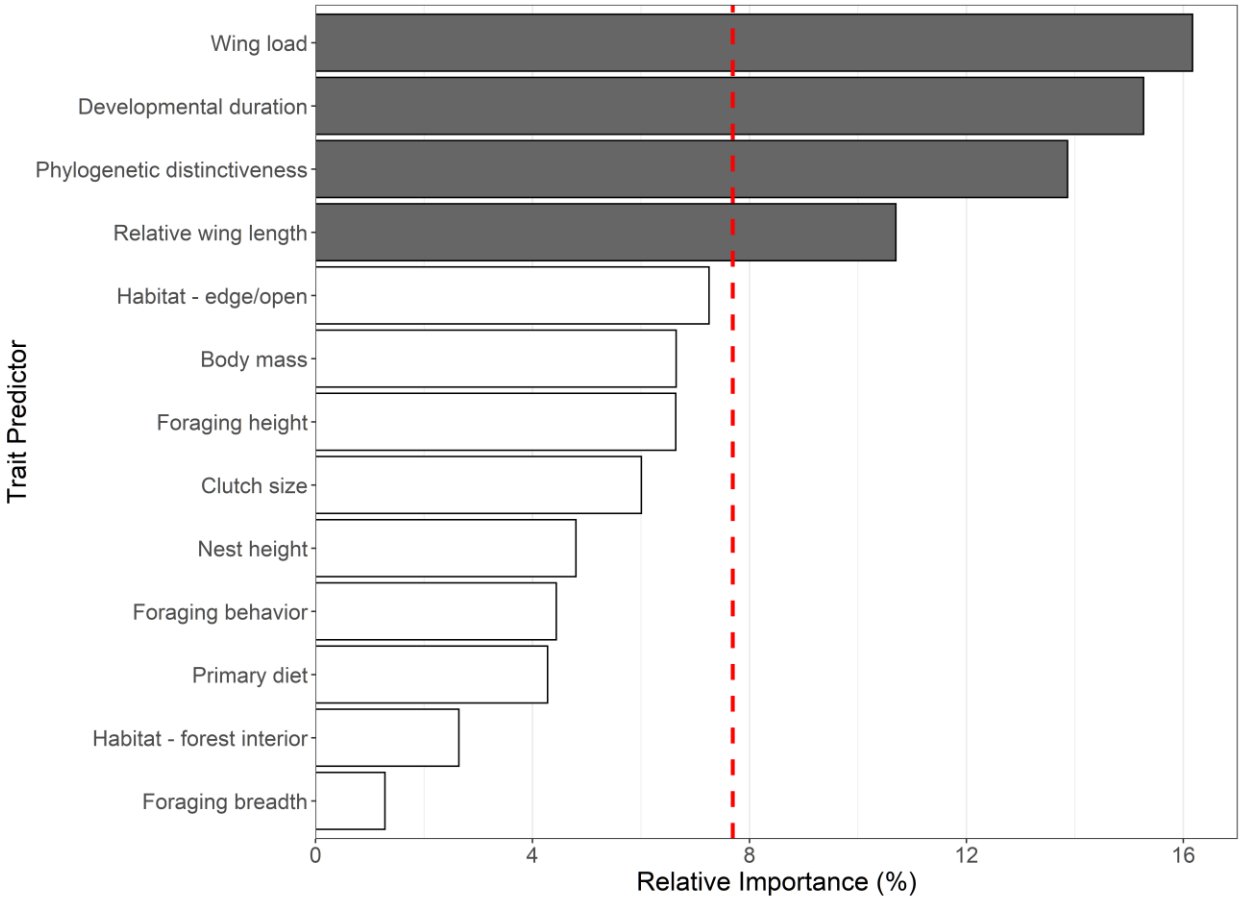

Figure 4.3. Relative percent contributions of predictor variables for a boosted regression tree model. Developed with cross-validation on the training data using tree complexity of 3, learning rate of 0.001, and bag fraction of 0.5 Dashed red line marks the threshold of statistical significance at 7.69% relative importance. Dark grey predictors extending past this line perform significantly better than chance.

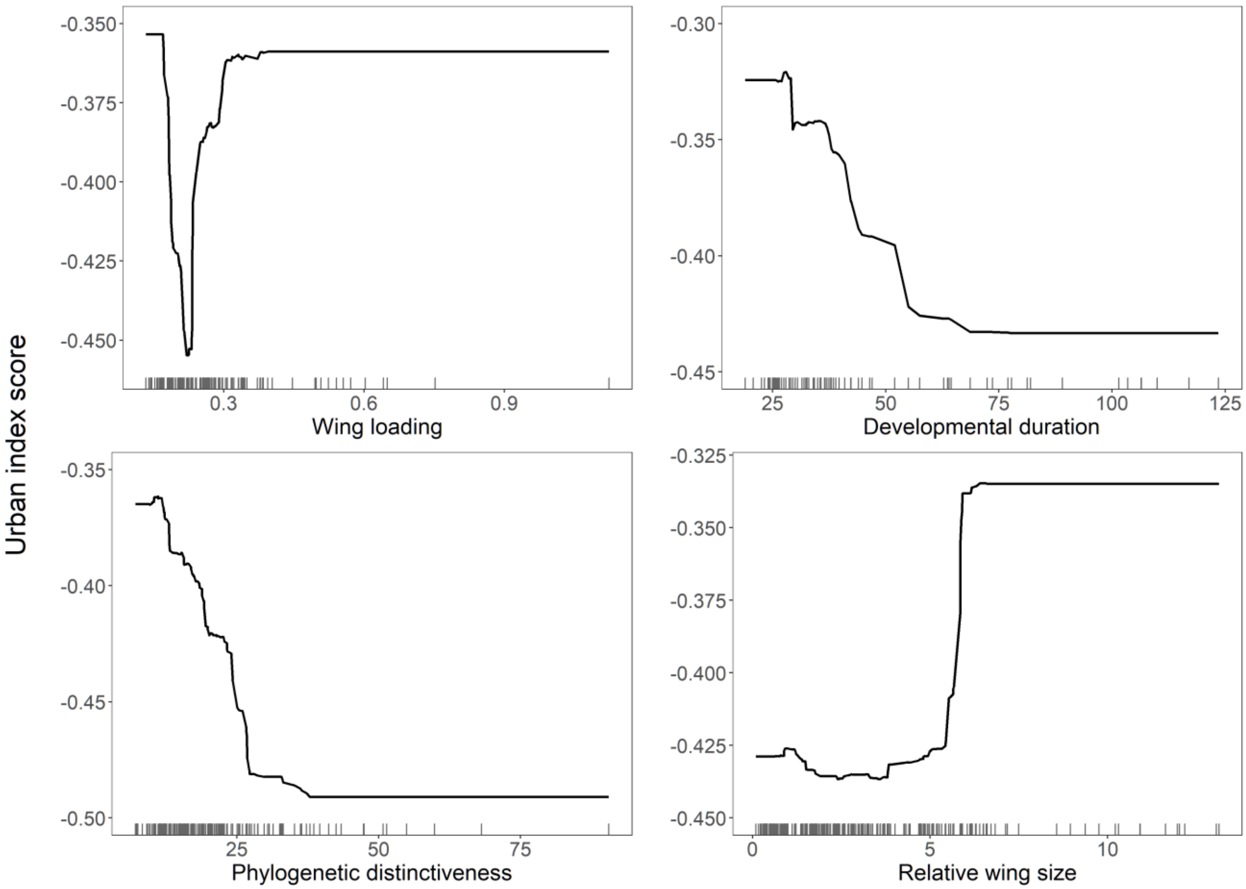

Figure 4.4. Partial dependence plots for the four most influential predictors in the model of species association with urban forests. Rug plots at the inside bottom show the distribution of species across that variable, in deciles. Vertical axes are centered to have a mean of zero on the logit scale.

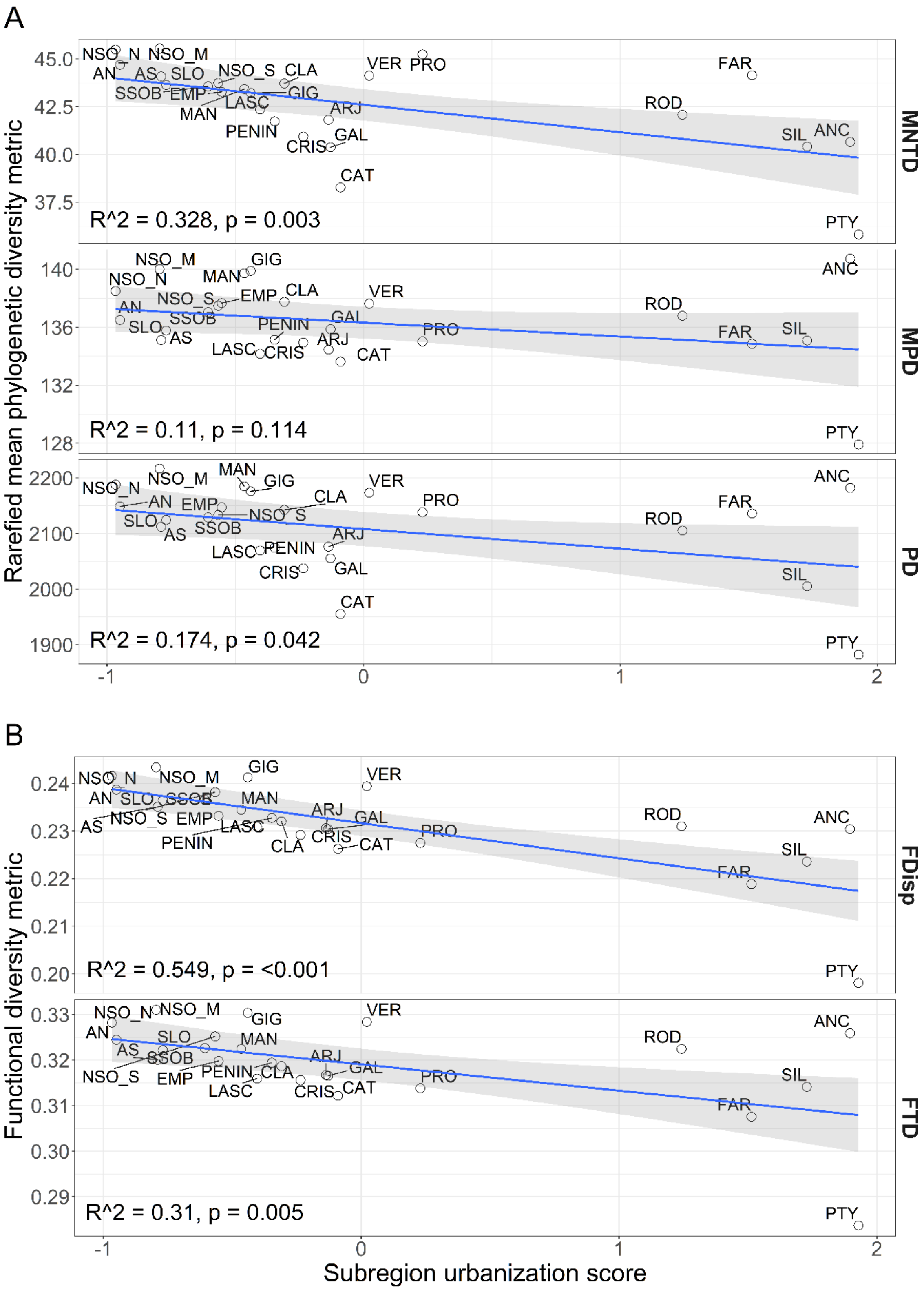

Figure 4.5. Simple bivariate relationships between phylogenetic (A) and functional (B) diversity metrics as and subregion urbanization score. Subregions are represented by hollow circles and abbreviated codes.

Fitted simple linear regressions shown as blue lines with 95% confidence interval shaded gray. See Table 4.3 for additional measures of linear fit and correlation. A: Phylogenetic diversity metrics include mean nearest taxon distance (MNTD), mean pairwise distance (MPD), and Faith's distance (PD). B: Functional diversity metrics include functional dispersion (FDisp) and richness-adjusted functional trait dispersion (FTD).

CHAPTER 5. GENERAL CONCLUSIONS

The combined effects of habitat conversion and deforestation pose the greatest risk to bird populations globally (Vié et al. 2009). Alteration of Earth's landscapes by human activities leads to the attrition of biodiversity through a multifaceted combination of deterministic and stochastic processes, most notably the protracted loss of species from small, insular habitat fragments (MacArthur and Wilson 1963, Harrison and Bruna 1999). The number of avian studies from the neotropics lags behind the rapid intensification of anthropogenic disturbance in that region (Escobar-Ibáñez and MacGregor-Fors 2017). A better understanding of how human-associated habitat degradation such as fragmentation, isolation, and urban conversion affects tropical forest bird communities is a conservation priority. In this dissertation, I used a unique set of spatially and temporally extensive avian surveys from Central Panama to characterize bird community compositional changes in association with various forms of human disturbance, particularly urbanization and isolation. My results highlight the pervasive, but idiosyncratic and often case-specific nature of avian response to human disturbance.

What do BCI and urban forest fragments in central Panama have in common? Across my three chapters, I observed the important roles of dispersal ability, connectivity, and sensitivity to local habitat conditions. Habitat connectivity is considered among the most important predictors of avian diversity in fragmented landscapes (Martensen et al. 2008, Losos and Ricklefs 2009). I found that access to large tracts of undisturbed rainforest is a key driver of species richness and community composition among Canal zone forest fragments. Chapter 4 revealed even limited connectivity to large rainforest preserves allows small urban forest patches to retain unexpectedly high trait diversity for their size and degree of regional urbanization. Likewise, biodiverse national parks surrounding BCI appear to be an important source of species immigration to the island. Even infrequent immigration events are essential for the persistence of isolated populations via mechanisms such as gene flow and maintenance of metapopulation dynamics (Hanski et al. 1997, Ibarra-Macias et al. 2011, Lindenmayer and Fischer 2013). As lowland tropical forests become increasingly fragmented and isolated (Robinson et al. 2004, Keenan et al. 2015), biodiversity across remnant habitat patches is likely to further decline from the benchmarks established in this study.

Connectivity is important for tropical forest fragments due in part to extreme dispersal limitations among tropical birds (Moore et al. 2008). Dispersal dynamics are a prominent factor influencing species assemblages both on BCI and within urban forest fragments. The most isolated forest fragments in central Panama tend to have the fewest species and the lowest diversity. In Chapter 4, I observed birds with short, small wings relative to their mass were less likely to occur in remote urban forests. From Chapters 2 and 3, ability to cross the Panama Canal appears to influence which birds persist on BCI. My results suggest insular bird communities generally contain a limited subset of the regional bird community capable of dispersing well.

Nevertheless, even some birds physically capable of crossing the Panama Canal fail to persist on BCI. Another common theme from my dissertation is species sensitivity to deterministic, patch-specific factors. For BCI, which is protected from human disturbance, this means sensitivity to subtle climatic change within forest fragments, particularly the local drying effects of isolation. In Chapter 2, I found tolerance of dry forest conditions is a key indicator of resilience to fragmentation and edge effects on BCI. In Chapter 3, I observed a period of extended drought was associated with accelerated extinctions from BCI, especially among wet forest birds. An increase in frequency of intense dry seasons (Aguilar et al. 2005) could introduce physiological stresses beyond the tolerances of the remaining drought-sensitive birds on BCI (Stratford and Robinson 2005), and would likely produce another accelerated extinction period.

For unprotected lowland forest fragments, sensitivity to human disturbance is an important determinant of avian community composition. In Chapter 4, forest patches exposed to the most frequent and intense human activity had the lowest taxonomic and functional diversity. High urban sensitivity was associated with longer evolutionary histories and extended developmental duration. Urbanization appears to favor a recent evolution and rapid pace of life comparatively rare among tropical birds (Wiersma et al. 2007, Smith et al. 2017). This chapter was limited by general lack of quantitative morphological and reproductive data for tropical birds. Future research would benefit from continued efforts to fill gaps in our knowledge of tropical avian physiology and life histories.

Further considerations and conservation implications

Though I observed variation in response to fragmentation among taxonomic Orders in Chapters 3 and 4, results generally differed between BCI and urban forest fragments. Steep, steady declines in Galliformes and Cuculiformes on BCI were not reflected in urban forest fragments. Instead, in the absence of protection from human disturbance, urban forests lost comparatively older lineages of large-bodied raptors and gamebirds. Trogoniformes, which showed no species losses on BCI over time, are completely gone from two smaller forests in heavily urbanized regions. These idiosyncratic differences in response to fragmentation among taxonomic groups along a gradient of human activity from completely protected to highly disturbed merit further consideration to see if similar patterns hold true in other regions of the tropics.

Chapter 4 examined landscape characteristics on a regional scale to determine that urbanization is among the most important factors driving avian community composition in central Panama. The coarse resolution of my study could not quantify to what degree patch-level habitat characteristics such as ambient temperatures, canopy density, plant diversity, or vegetation structure within urban forests are associated with loss or retention of avian diversity. Further consideration could also be given to the unique disturbance history of each patch as well as the nature of its surrounding matrix; the latter likely plays an important role in determining frequency of dispersal into insular forest patches (Faeth et al. 2001, Suarez-Rubio and Thomlinson 2009). Nevertheless, landscape characteristics are often the primary predictors of urban species assemblages (Suarez-Rubio and Thomlinson 2009, Filloy et al. 2015) and finer resolution studies could fail to detect relationships between species traits and habitat variables (Kennedy et al. 2010).

I was unable to consider species abundances in my dissertation because no count data were available for either modern Canal zone bird inventories or any BCI bird inventories before the 1990s except one (Willis 1974). Abundance data from the neotropics are rare and there have been recent calls for more high quality benchmarks of tropical bird communities (Ortega-Álvarez and MacGregor-Fors 2011, Robinson and Curtis *in press*). In Chapter 2, I concluded species with small populations in the 1920s and 1930s were more likely to have disappeared. This conclusion would be better supported by empirical data on initial species abundances and trends over time. Measures of avian abundance, especially those obtained from regular, repeated surveys over long intervals, provide a much greater degree of detail regarding species response to isolation or urbanization than the presence/absence responses used in my dissertation.

Recommendations for maximizing species richness in human-altered landscapes typically focus on preservation of large habitat patches and protection of those habitats from anthropogenic activities. Yet BCI, a large fragment protected from human disturbance for over a century, continues to lose species. It may be argued that Barro Colorado Island (BCI), as a large land-bridge island isolated by an unchanging matrix (water) and protected from human disturbance for nearly a century, is dissimilar to circumstances facing most terrestrial tropical forest fragments. Yet the common themes of connectivity, dispersal ability, and sensitivity observed throughout my dissertation suggest BCI can be a useful indicator of the long-term consequences of isolation for any forest fragment within a permanent, inhospitable matrix, be it water or heavily developed urban areas.

My dissertation emphasizes the conservation importance of large, interconnected forest patches protected from human disturbance. Large remnant forests support more species than small ones, and limiting human disturbance appears to preserve functional diversity regardless of fragment size. However, even within protected reserves, special consideration must be given to dispersal-limited, drought-intolerant species which are more sensitive to effects of fragmentation beyond loss of area *per se*. As we enter an unprecedented era of human development, my results highlight how complex, trait-mediated, and occasionally stochastic species responses to disturbance and isolation challenge our ability to predict consequences of human activity for biodiversity.

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APPENDICES

APPENDIX A - Bird Species Common and Scientific Names and Codes

Table A.1. Common names, scientific names, and 4-letter abbreviated codes for all resident, non-aquatic birds detected in forested subregions of central Panama. Taxonomy based on the 59th supplement to the AOS checklist of North American birds (Chesser et al. 2018).

Common Name	Scientific Name	4-letter Code
Great Tinamou	Tinamus major	GRTI
Little Tinamou	Crypturellus soui	LITI
Gray-headed Chachalaca	Ortalis cinereiceps	GHEC
Crested Guan	Penelope purpurascens	CRGU
Great Curassow	Crax rubra	GRCU
Tawny-faced Quail	Rhynchortyx cinctus	TFQU
Marbled Wood-Quail	Odontophorus gujanensis	MAWQ
Rock Pigeon	Columba livia	ROPI
Pale-vented Pigeon	Patagioenas cayennensis	PVPI
Scaled Pigeon	Patagioenas speciosa	SCPI
Short-billed Pigeon	Patagioenas nigrirostris	SBPI
Plain-breasted Ground-Dove	Columbina minuta	PBGD
Ruddy Ground-Dove	Columbina talpacoti	RUGD
Blue Ground-Dove	Claravis pretiosa	BLGD
Ruddy Quail-Dove	Geotrygon montana	RUQD
Violaceous Quail-Dove	Geotrygon violacea	VIQD
Olive-backed Quail-Dove	Leptotrygon veraguensis	OBQD
White-tipped Dove	Leptotila verreauxi	WTDO
Gray-chested Dove	Leptotila cassinii	GCDO
Little Cuckoo	Coccycua minuta	LITC
Squirrel Cuckoo	Piaya cayana	SQCU
Striped Cuckoo	Tapera naevia	STCU
Pheasant Cuckoo	Dromococcyx phasianellus	PHCU
Rufous-vented Ground-Cuckoo	Neomorphus geoffroyi	RVGC
Greater Ani	Crotophaga major	GRTA
Smooth-billed Ani	Crotophaga ani	SBAN
Groove-billed Ani	Crotophaga sulcirostris	GBAN
Common Pauraque	Nyctidromus albicollis	COPA
Great Potoo	Nyctibius grandis	GRPO
Common Potoo	Nyctibius griseus	CPOT
White-necked Jacobin	Florisuga mellivora	WNJA
White-tipped Sicklebill	Eutoxeres aquila	WTSI
Rufous-breasted Hermit	Glaucis hirsutus	RBHE
Band-tailed Barbthroat	Threnetes ruckeri	BTBA
Green Hermit	Phaethornis guy	GREH
Long-billed Hermit	Phaethornis longirostris	LBIH
Stripe-throated Hermit	Phaethornis striigularis	STHR

Purple-crowned Fairy	Heliothryx barroti	PCFA
Black-throated Mango	Anthracothorax nigricollis	BTMA
Rufous-crested Coquette	Lophornis delattrei	RCRC
Long-billed Starthroat	Heliomaster longirostris	LBST
Garden Emerald	Chlorostilbon assimilis	GAEM
Violet-headed Hummingbird	Klais guimeti	VHHU
Scaly-breasted Hummingbird	Phaeochroa cuvierii	SBRH
White-vented Plumeleteer	Chalybura buffonii	WVPL
Bronze-tailed Plumeleteer	Chalybura urochrysia	BTPL
Crowned Woodnymph	Thalurania colombica	CRWO
Blue-chested Hummingbird	Amazilia amabilis	BCHH
Snowy-bellied Hummingbird	Amazilia edward	SBEH
Rufous-tailed Hummingbird	Amazilia tzacatl	RTAH
Sapphire-throated Hummingbird	Lepidopyga coeruleogularis	SHTH
Violet-bellied Hummingbird	Juliamyia julie	VBHU
Uniform Crake	Amaurolimnas concolor	UNIC
Southern Lapwing	Vanellus chilensis	SOLA
Gray-headed Kite	Leptodon cayanensis	GHKI
Hook-billed Kite	Chondrohierax uncinatus	HBKI
Pearl Kite	Gampsonyx swainsonii	PEKI
White-tailed Kite	Elanus leucurus	WTKI
Double-toothed Kite	Harpagus bidentatus	DTKI
Tiny Hawk	Accipiter superciliosus	TIHA
Bicolored Hawk	Accipiter bicolor	BIHA
Crane Hawk	Geranospiza caerulescens	CRHA
Plumbeous Hawk	Cryptoleucopteryx plumbea	PLHA
Common Black Hawk	Buteogallus anthracinus	COBH
Savanna Hawk	Buteogallus meridionalis	SAHA
Great Black Hawk	Buteogallus urubitinga	GBLH
Roadside Hawk	Rupornis magnirostris	ROHA
White Hawk	Pseudastur albicollis	WHHA
Semiplumbeous Hawk	Leucopternis semiplumbeus	SEHA
Gray-lined Hawk	Buteo nitidus	GLHA
Crested Eagle	Morphnus guianensis	CREA
Harpy Eagle	Harpia harpyja	HAEA
Black Hawk-Eagle	Spizaetus tyrannus	BLHE
Ornate Hawk-Eagle	Spizaetus ornatus	ORHE
Black-and-white Hawk-Eagle	Spizaetus melanoleucus	BAWH
Barn Owl	Tyto alba	BANO
Tropical Screech-Owl	Megascops choliba	TRSO
Vermiculated Screech-Owl	Megascops guatemalae	VESO
Crested Owl	Lophostrix cristata	CROW
Spectacled Owl	Pulsatrix perspicillata	SPEO

Central American Pygmy-Owl	Glaucidium griseiceps	CAPO
Mottled Owl	Ciccaba virgata	MOOW
Black-and-white Owl	Ciccaba nigrolineata	BLWO
Striped Owl	Pseudoscops clamator	STRO
Slaty-tailed Trogon	Trogon massena	STTR
Black-tailed Trogon	Trogon melanurus	BTAT
White-tailed Trogon	Trogon chionurus	WTAT
Gartered Trogon	Trogon caligatus	GATR
Black-throated Trogon	Trogon rufus	BTHT
Whooping Motmot	Momotus subrufescens	WHMO
Rufous Motmot	Baryphthengus martii	RMOT
Broad-billed Motmot	Electron platyrhynchum	BBMO
White-necked Puffbird	Notharchus hyperrhynchus	WNPU
Black-breasted Puffbird	Notharchus pectoralis	BBPU
Pied Puffbird	Notharchus tectus	PIPU
White-whiskered Puffbird	Malacoptila panamensis	WWPU
Gray-cheeked Nunlet	Nonnula frontalis	GCNU
White-fronted Nunbird	Monasa morphoeus	WFNU
Great Jacamar	Jacamerops aureus	GJAC
Spot-crowned Barbet	Capito maculicoronatus	SCBA
Collared Aracari	Pteroglossus torquatus	COAR
Yellow-eared Toucanet	Selenidera spectabilis	YETO
Keel-billed Toucan	Ramphastos sulfuratus	KBTO
Yellow-throated Toucan	Ramphastos ambiguus	YTTO
Olivaceous Piculet	Picumnus olivaceus	OLPI
Black-cheeked Woodpecker	Melanerpes pucherani	BCWO
Red-crowned Woodpecker	Melanerpes rubricapillus	RCRW
Cinnamon Woodpecker	Celeus loricatus	CIWO
Lineated Woodpecker	Dryocopus lineatus	LIWO
Crimson-bellied Woodpecker	Campephilus haematogaster	CBWO
Crimson-crested Woodpecker	Campephilus melanoleucos	CCRW
Laughing Falcon	Herpetotheres cachinnans	LAFA
Barred Forest-Falcon	Micrastur ruficollis	BAFF
Slaty-backed Forest-Falcon	Micrastur mirandollei	SBFF
Collared Forest-Falcon	Micrastur semitorquatus	COFF
Red-throated Caracara	Ibycter americanus	RTCA
Crested Caracara	Caracara cheriway	CRCA
Yellow-headed Caracara	Milvago chimachima	YHCA
Bat Falcon	Falco rufigularis	BAFA
Orange-chinned Parakeet	Brotogeris jugularis	OCPA
Blue-fronted Parrotlet	Touit dilectissimus	BFPA
Brown-hooded Parrot	Pyrilia haematotis	BHOP
Blue-headed Parrot	Pionus menstruus	BHEP

Red-lored Parrot	Amazona autumnalis	RLPA
Mealy Parrot	Amazona farinosa	MEAP
Yellow-crowned Parrot	Amazona ochrocephala	YCPA
Sapayoa	Sapayoa aenigma	SAPA
Fasciated Antshrike	Cymbilaimus lineatus	FAAN
Great Antshrike	Taraba major	GANT
Barred Antshrike	Thamnophilus doliatus	BAAN
Black-crowned Antshrike	Thamnophilus atrinucha	BCAS
Russet Antshrike	Thamnistes anabatinus	RUAN
Spot-crowned Antvireo	Dysithamnus puncticeps	SPCA
Moustached Antwren	Myrmotherula ignota	MOAN
Pacific Antwren	Myrmotherula pacifica	PAAN
White-flanked Antwren	Myrmotherula axillaris	WFLA
Checker-throated Antwren	Epinecrophylla fulviventris	CTAN
Dot-winged Antwren	Microrhopias quixensis	DWAN
Dusky Antbird	Cercomacroides tyrannina	DUAN
Jet Antbird	Cercomacra nigricans	JEAN
Bare-crowned Antbird	Gymnocichla nudiceps	BACA
White-bellied Antbird	Myrmeciza longipes	WBEA
Chestnut-backed Antbird	Myrmeciza exsul	CBAN
Dull-mantled Antbird	Myrmeciza laemosticta	DMAN
Zeledon's Antbird	Myrmeciza zeledoni	ZEAN
Spotted Antbird	Hylophylax naevioides	SPAN
Wing-banded Antbird	Myrmornis torquata	WBAA
Bicolored Antbird	Gymnopithys bicolor	BIAN
Ocellated Antbird	Phaenostictus mcleannani	OCAN
Black-crowned Antpitta	Pittasoma michleri	BCAP
Streak-chested Antpitta	Hylopezus perspicillatus	SCHA
Black-faced Antthrush	Formicarius analis	BFAN
Tawny-throated Leaftosser	Sclerurus mexicanus	TTLE
Scaly-throated Leaftosser	Sclerurus guatemalensis	STLE
Olivaceous Woodcreeper	Sittasomus griseicapillus	OLWO
Long-tailed Woodcreeper	Deconychura longicauda	LTWO
Ruddy Woodcreeper	Dendrocincla homochroa	RUWO
Plain-brown Woodcreeper	Dendrocincla fuliginosa	PBRW
Wedge-billed Woodcreeper	Glyphorynchus spirurus	WBWO
Northern Barred-Woodcreeper	Dendrocolaptes sanctithomae	NOBW
Cocoa Woodcreeper	Xiphorhynchus susurrans	COWO
Black-striped Woodcreeper	Xiphorhynchus lachrymosus	BSWO
Straight-billed Woodcreeper	Dendroplex picus	SGBW
Red-billed Scythebill	Campylorhamphus trochilirostris	RBSC
Streak-headed Woodcreeper	Lepidocolaptes souleyetii	SHWO
Plain Xenops	Xenops minutus	PLXE

Slaty-winged Foliage-gleaner	Philydor fuscipenne	SWFG
Buff-throated Foliage-gleaner	Automolus ochrolaemus	BTFG
Brown-capped Tyrannulet	Ornithion brunneicapillus	BCTY
Southern Beardless-Tyrannulet	Camptostoma obsoletum	SOBT
Yellow Tyrannulet	Capsiempis flaveola	YETY
Yellow-crowned Tyrannulet	Tyrannulus elatus	YCTY
Forest Elaenia	Myiopagis gaimardii	FOEL
Gray Elaenia	Myiopagis caniceps	GRAE
Greenish Elaenia	Myiopagis viridicata	GREL
Yellow-bellied Elaenia	Elaenia flavogaster	YBEL
Lesser Elaenia	Elaenia chiriquensis	LEEL
Olive-striped Flycatcher	Mionectes olivaceus	OSTF
Ochre-bellied Flycatcher	Mionectes oleagineus	OBFL
Sepia-capped Flycatcher	Leptopogon amaurocephalus	SECF
Yellow-green Tyrannulet	Phylloscartes flavovirens	YGTY
Paltry Tyrannulet	Zimmerius vilissimus	PATY
Northern Scrub-Flycatcher	Sublegatus arenarum	NOSF
Black-capped Pygmy-Tyrant	Myiornis atricapillus	BPYT
Pale-eyed Pygmy-Tyrant	Lophotriccus pilaris	PEPT
Southern Bentbill	Oncostoma olivaceum	SOBE
Slate-headed Tody-Flycatcher	Poecilotriccus sylvia	SHTF
Common Tody-Flycatcher	Todirostrum cinereum	COTF
Black-headed Tody-Flycatcher	Todirostrum nigriceps	BHTF
Brownish Twistwing	Cnipodectes subbrunneus	BRTW
Olivaceous Flatbill	Rhynchocyclus olivaceus	OLFL
Yellow-olive Flycatcher	Tolmomyias sulphurescens	YOFL
Yellow-margined Flycatcher	Tolmomyias assimilis	YMFL
Golden-crowned Spadebill	Platyrinchus coronatus	GCRS
Royal Flycatcher	Onychorhynchus coronatus	ROFL
Ruddy-tailed Flycatcher	Terenotriccus erythrurus	RDTF
Sulphur-rumped Flycatcher	Myiobius sulphureipygius	SRFL
Black-tailed Flycatcher	Myiobius atricaudus	BTFL
Bran-colored Flycatcher	Myiophobus fasciatus	BCOF
Tropical Pewee	Contopus cinereus	TROP
Long-tailed Tyrant	Colonia colonus	LTTY
Bright-rumped Attila	Attila spadiceus	BRAT
Choco Sirystes	Sirystes albogriseus	CHSI
Rufous Mourner	Rhytipterna holerythra	RMOU
Dusky-capped Flycatcher	Myiarchus tuberculifer	DCFL
Panama Flycatcher	Myiarchus panamensis	PAFL
Great Kiskadee	Pitangus sulphuratus	GKIS
Boat-billed Flycatcher	Megarynchus pitangua	BOBF
Rusty-margined Flycatcher	Myiozetetes cayanensis	RMFL

Social Flycatcher	Myiozetetes similis	SOFL
Gray-capped Flycatcher	Myiozetetes granadensis	GCAF
White-ringed Flycatcher	Conopias albovittatus	WRFL
Streaked Flycatcher	Myiodynastes maculatus	STRF
Piratic Flycatcher	Legatus leucophaius	PIRF
Tropical Kingbird	Tyrannus melancholicus	TRKI
Fork-tailed Flycatcher	Tyrannus savana	FTFL
Russet-winged Schiffornis	Schiffornis stenorhyncha	RWSC
Speckled Mourner	Laniocera rufescens	SPMO
Masked Tityra	Tityra semifasciata	MATI
Black-crowned Tityra	Tityra inquisitor	BCRT
Cinnamon Becard	Pachyramphus cinnamomeus	CIMB
White-winged Becard	Pachyramphus polychopterus	WWBE
Purple-throated Fruitcrow	Querula purpurata	PTFR
Blue Cotinga	Cotinga nattererii	BLCO
Rufous Piha	Lipaugus unirufus	RUFP
Lance-tailed Manakin	Chiroxiphia lanceolata	LATM
White-ruffed Manakin	Corapipo altera	WRMA
Blue-crowned Manakin	Lepidothrix coronata	BCRM
Golden-collared Manakin	Manacus vitellinus	GCMA
Red-capped Manakin	Ceratopipra mentalis	RCMA
Scrub Greenlet	Hylophilus flavipes	SCRG
Green Shrike-Vireo	Vireolanius pulchellus	GRSV
Tawny-crowned Greenlet	Tunchiornis ochraceiceps	TCGR
Lesser Greenlet	Pachysylvia decurtata	LESG
Golden-fronted Greenlet	Pachysylvia aurantiifrons	GFGR
Yellow-green Vireo	Vireo flavoviridis	YGVI
Black-chested Jay	Cyanocorax affinis	BCHJ
Scaly-breasted Wren	Microcerculus marginatus	SCBW
House Wren	Troglodytes aedon	HOWR
White-headed Wren	Campylorhynchus albobrunneus	WHWR
Rufous-breasted Wren	Pheugopedius rutilus	RBSW
Black-bellied Wren	Pheugopedius fasciatoventris	BBEW
Rufous-and-white Wren	Thryophilus rufalbus	RAWW
Stripe-breasted Wren	Cantorchilus thoracicus	SIBW
Isthmian Wren	Cantorchilus elutus	ISWR
Bay Wren	Cantorchilus nigricapillus	BAYW
Buff-breasted Wren	Cantorchilus leucotis	BBRW
White-breasted Wood-Wren	Henicorhina leucosticta	WBWW
Song Wren	Cyphorhinus phaeocephalus	SONW
Tawny-faced Gnatwren	Microbates cinereiventris	TFGN
Long-billed Gnatwren	Ramphocaenus melanurus	LBGN
Tropical Gnatcatcher	Polioptila plumbea	TRGN

Clay-colored Thrush	Turdus grayi	CCTH
White-throated Thrush	Turdus assimilis	WTTH
Tropical Mockingbird	Mimus gilvus	TRMO
Yellowish Pipit	Anthus lutescens	YEPI
Yellow-crowned Euphonia	Euphonia luteicapilla	YCEU
Thick-billed Euphonia	Euphonia laniirostris	TBEU
Fulvous-vented Euphonia	Euphonia fulvicrissa	FVEU
White-vented Euphonia	Euphonia minuta	WVEU
Tawny-capped Euphonia	Euphonia anneae	TCEU
Lesser Goldfinch	Spinus psaltria	LEGO
Rosy Thrush-Tanager	Rhodinocichla rosea	ROTT
Orange-billed Sparrow	Arremon aurantiirostris	OBSP
Black-striped Sparrow	Arremonops conirostris	BSTS
Eastern Meadowlark	Sturnella magna	EAME
Red-breasted Blackbird	Leistes militaris	RBBL
Yellow-billed Cacique	Amblycercus holosericeus	YBIC
Crested Oropendola	Psarocolius decumanus	CROR
Chestnut-headed Oropendola	Psarocolius wagleri	CHOR
Montezuma Oropendola	Psarocolius montezuma	MORO
Scarlet-rumped Cacique	Cacicus uropygialis	SRCA
Yellow-rumped Cacique	Cacicus cela	YRCA
Yellow-backed Oriole	Icterus chrysater	YBOR
Yellow-tailed Oriole	Icterus mesomelas	YTOR
Shiny Cowbird	Molothrus bonariensis	SHCO
Bronzed Cowbird	Molothrus aeneus	BROC
Giant Cowbird	Molothrus oryzivorus	GICO
Great-tailed Grackle	Quiscalus mexicanus	GTGR
Buff-rumped Warbler	Myiothlypis fulvicauda	BURW
Rufous-capped Warbler	Basileuterus rufifrons	RCWA
Dusky-faced Tanager	Mitrospingus cassinii	DFTA
Hepatic Tanager	Piranga flava	HETA
Red-crowned Ant-Tanager	Habia rubica	RCAT
Red-throated Ant-Tanager	Habia fuscicauda	RTAT
Carmiol's Tanager	Chlorothraupis carmioli	CATA
Blue-black Grosbeak	Cyanocompsa cyanoides	BGRO
Blue-gray Tanager	Thraupis episcopus	BGTA
Palm Tanager	Thraupis palmarum	PALT
Golden-hooded Tanager	Tangara larvata	GHOT
Plain-colored Tanager	Tangara inornata	PCTA
Bay-headed Tanager	Tangara gyrola	BHTA
Saffron Finch	Sicalis flaveola	SAFI
Green Honeycreeper	Chlorophanes spiza	GRHO
Sulphur-rumped Tanager	Heterospingus rubrifrons	SRTA

Blue-black Grassquit	Volatinia jacarina	BGRA
Gray-headed Tanager	Eucometis penicillata	GHET
White-shouldered Tanager	Tachyphonus luctuosus	WSTA
Tawny-crested Tanager	Tachyphonus delatrii	TCTA
White-lined Tanager	Tachyphonus rufus	WLTA
Flame-rumped Tanager	Ramphocelus flammigerus	FRTA
Crimson-backed Tanager	Ramphocelus dimidiatus	CBTA
Shining Honeycreeper	Cyanerpes lucidus	SHHO
Red-legged Honeycreeper	Cyanerpes cyaneus	RLHO
Scarlet-thighed Dacnis	Dacnis venusta	STDA
Blue Dacnis	Dacnis cayana	BLDA
Bananaquit	Coereba flaveola	BANA
Yellow-faced Grassquit	Tiaris olivaceus	YFGR
Thick-billed Seed-Finch	Sporophila funerea	TBSF
Variable Seedeater	Sporophila corvina	VASE
Slate-colored Seedeater	Sporophila schistacea	SCSE
Yellow-bellied Seedeater	Sporophila nigricollis	YBSE
Ruddy-breasted Seedeater	Sporophila minuta	RBSE
Black-headed Saltator	Saltator atriceps	BHSA
Buff-throated Saltator	Saltator maximus	BTSA
Slate-colored Grosbeak	Saltator grossus	SCOG
Streaked Saltator	Saltator striatipectus	SSAL

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APPENDIX B - Chapter 2 Supplemental Material

Appendix B1 - Likely Species Analyses

Several difficult to identify or detect species, including nocturnal birds and small upper-canopy passerines, were missing from earlier datasets, likely due to observer inexperience with tropical bird vocalizations (Willis and Eisenmann 1979) or lack of access to all parts of the island. To evaluate the effect of these common but poorly detected species (AKA "likely species"), we repeated ordination procedures on a reduced species matrix where 21 species we deemed were likely present during historical surveys but not reported were removed (Table B.1). To quantify the effect of likely species on the ordination, we compared NMDS ordination scores between the primary and reduced species datasets using Mantel's asymptotic approximation method with a randomization test for 999 runs. This evaluates the null hypothesis of no correlation between distance matrices for the same sampling units. (Mantel 1967). The standardized Mantel statistic (r) ranges from 0 to 1, with larger values representing higher correspondence between two ordinations. We calculated the percentage redundancy of the ordinations as r^2 multiplied by 100. We found strong agreement between ordinations including and omitting these species ($r = 0.991$). We conclude missed detections resulting from historical observer inexperience or unfamiliarity with a few tropical bird sounds did not appreciably influence NMDS results.

Appendix B2 - Timing of Species Extinctions

Our data suggest timing of extinctions differed between habitat associations and local abundance categories. The earliest extinctions were forest-dwelling insectivores historically rare on BCI. We found a moderate and significant positive correlation between extinct species' historical abundance on BCI and decade of last observation (Spearman's Rho = 0.34, p = 0.007). There was also a significant negative association between southern distributional limit and decade of last observation (Spearman's Rho = -0.29, p = 0.02; Figure B.2). Just under half of the total species extinctions (30 sp., 48.4%), but only a quarter of forest-associated extinctions, occurred after 1970. Most forest interior bird extinctions (19 sp., 82.6%) occurred before 1970, whereas most forest edge (17 sp., 68%), edge (9 sp., 69.2%), and all open associated species went extinct after 1970.

Appendix B3 – Southern Limits

We used a species' southern distributional limit, the integer linear distance between a species' southernmost Canal zone occurrence and the Pacific entrance to the Panama Canal as an index of climatic tolerance. Forest species are more restricted to northerly (wetter) portions of the precipitation gradient than edge and open associated birds combined (9.7 ± 10.1 km mean southern range limit vs 2.7 ± 7.1 km, respectively). Wet forest species exhibited a higher southern limit than transisthmian species (23.8 ± 7.1 km mean vs. 6.2 ± 7.4 km). Differences in average southern limit between missing and remaining species are summarized in Table B.5.

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Tables and Figures

Table B.1. Common and scientific names of "likely species". Likely species defined as difficult to detect species missing from species inventories, likely due to observer unfamiliarity with these species, lack of nocturnal surveying, or inability to access all parts of Barro Colorado Island.

Common*	**Scientific**
Short-tailed Nighthawk	Lurocalis semitorquatus
Vermiculated Screech-Owl*	Accipiter superciliosus
Black-and-white Owl*	Megascops guatemalae
Collared Forest-Falcon	Ciccaba nigrolineata
Brown-capped Tyrannulet	Micrastur semitorquatus
Yellow-crowned Tyrannulet	Myrmotherula ignota
Forest Elaenia*	Ornithion brunneicapillus
Paltry Tyrannulet	Tyrannulus elatus
Black-capped Pygmy-Tyrant	Myiopagis gaimardii
Sulphur-rumped Tanager	Zimmerius vilissimus
Scarlet-thighed Dacnis	Myiornis atricapillus
Tiny Hawk*	Contopus cinereus
Long-tailed Tyrant*	Colonia colonus
Scrub Greenlet*	Hylophilus flavipes
White-vented Euphonia*	Campylorhynchus albobrunneus
Dusky-faced Tanager*	Euphonia minuta
Tropical Pewee*	Myiothlypis fulvicauda
White-headed Wren*	Mitrospingus cassinii
Buff-rumped Warbler*	Heterospingus rubrifrons
Black-headed Saltator*	Dacnis venusta
Moustached Antwren	Saltator atriceps

* Denotes species likely present on BCI at the time of isolation but not detected before 1950.

Table B.2. Environmental factors used to characterize avian community structure along the Panama Canal corridor. Full descriptions of these environmental factors can be found in Rompré et al. (2007).

Variable	**Description**	**Source**
AGE_CAT	Categorical. Represents dominant relative forest age (1=secondary; 2=mature secondary; 3=primary mature forests) estimated using ANAM (2003) criteria for species composition and disturbance history.	(Pyke et al. 2001)
ALT	Maximum altitude per subregion in meters above sea level.	(Rompré et al. 2007)
AREA	Total area in km² per region	(Rompré et al. 2007)
PCT_FOREST	Proportion forest cover, calculated by dividing forested area by total area in each subregion.	(Rompré et al. 2007)
PCT_UNFRAG	Degree of fragmentation, represented by percent total forest area included in 1 or 2 largest fragments within subregion.	(Rompré et al. 2007)
PCT_URBAN	Proportion urban cover, calculated by dividing urban area by total area in each subregion.	(ANAM 2003; ACP 2016)
PLANTS	Plant and tree species richness within 1 ha plots. Plant data obtained from Pyke et al. (2001). Trees defined as woody plants >10cm dbh. Kriging used to interpolate geographic plant richness for each subregion centroid (see Rompré et al. (2007) for details).	(Condit 1998; Pyke et al. 2001; Perez et al. *unpublished report*)
PRECIP	Mean annual precipitation in mm for subregion, obtained from both ACP and atlases. For subregions without precipitation data, values obtained by interpolation from isohyets available for that period (Rompré et al. 2007).	(ACP 2016; Santiago and Mulkey 2005; Pyke et al. 2001; Condit 1998)

Table B.3. Extinction status and select species attributes for all birds observed on Barro Colorado Island, Panama since 1925. See Table A.1 for scientific names corresponding to species' common names.

Common Name	**Missing ***	**Habitat**	**BCI Historical Abundance**	**Diet**	**Foraging Height**	**Southern Limit (km)**	**Last Decade**
Great Tinamou	No	forest - interior	common	omnivore	terrestrial	2	-
Little Tinamou	No	edge	rare	omnivore	terrestrial	0	-
Gray-headed Chachalaca	Yes	edge	rare	omnivore	arboreal	0	1970
Crested Guan	No	forest - interior	common	omnivore	arboreal	22	-
Great Curassow	Yes	forest - interior	rare	omnivore	terrestrial	22	1920
Marbled Wood-Quail	Yes	forest - interior	rare	omnivore	terrestrial	20	1950
Pale-vented Pigeon	No	forest - edge	common	frugivore	arboreal	25	-
Scaled Pigeon	No	forest - edge	common	frugivore	arboreal	0	-
Short-billed Pigeon	No	forest - edge	common	frugivore	arboreal	22	-
Plain-breasted Ground-Dove	No	open	rare	omnivore	arboreal	0	-
Ruddy Ground-Dove	No	edge	occasional	omnivore	arboreal	0	-
Blue Ground-Dove	No	forest - edge	rare	omnivore	arboreal	0	-
Ruddy Quail-Dove	No	forest - interior	common	frugivore	terrestrial	10	-
Violaceous Quail-Dove	No	forest - interior	rare	frugivore	terrestrial	17	-
White-tipped Dove	No	edge	occasional	frugivore	terrestrial	0	-

Gray-chested Dove	No	forest - interior	common	frugivore	terrestrial	0	-
Squirrel Cuckoo	No	forest - edge	common	insectivore	arboreal	0	-
Striped Cuckoo	No	edge	rare	insectivore	arboreal	30	-
Pheasant Cuckoo	No	forest - interior	rare	insectivore	terrestrial	2	2000
Rufous-vented Ground-Cuckoo	Yes	forest - interior	rare	insectivore	terrestrial	15	1930
Greater Ani	No	forest - edge	common	insectivore	arboreal	0	-
Smooth-billed Ani	Yes	edge	rare	insectivore	arboreal	0	1970
Common Pauraque	No	edge	rare	insectivore	terrestrial	0	-
Great Potoo	Yes*	forest - edge	rare	insectivore	arboreal	5	2010
Common Potoo	Yes*	forest - edge	rare	insectivore	arboreal	0	2010
White-necked Jacobin	No	forest - edge	common	nectarivore	arboreal	0	-
Rufous-breasted Hermit	No	forest - edge	rare	nectarivore	arboreal	25	-
Band-tailed Barbthroat	No	forest - interior	rare	nectarivore	arboreal	5	-
Green Hermit	No	forest - interior	rare	nectarivore	arboreal	29	-
Long-billed Hermit	No	forest - interior	common	nectarivore	arboreal	0	-
Stripe-throated Hermit	No	forest - interior	common	nectarivore	arboreal	0	-
Purple-crowned Fairy	No	forest - edge	rare	nectarivore	arboreal	15	-

Black-throated Mango	Yes*	edge	common	nectarivore	arboreal	0	1970
Rufous-crested Coquette	Yes	forest - edge	rare	nectarivore	arboreal	15	1990
Long-billed Starthroat	Yes	edge	rare	nectarivore	arboreal	0	1970
Garden Emerald	Yes	edge	common	nectarivore	arboreal	0	1970
White-vented Plumeleteer	No	forest - interior	rare	nectarivore	arboreal	0	-
Crowned Woodnymph	No	forest - interior	common	nectarivore	arboreal	0	-
Blue-chested Hummingbird	No	forest - edge	common	nectarivore	arboreal	5	-
Snowy-bellied Hummingbird	No	edge	occasional	nectarivore	arboreal	0	-
Rufous-tailed Hummingbird	No	edge	common	nectarivore	arboreal	0	-
Sapphire-throated Hummingbird	No	edge	occasional	nectarivore	arboreal	0	-
Violet-bellied Hummingbird	No	forest - interior	common	nectarivore	arboreal	0	-
Gray-headed Kite	No	forest - edge	occasional	raptor	raptorial	2	-
Hook-billed Kite	No	forest - edge	rare	raptor	raptorial	15	-
Pearl Kite	No	open	rare	raptor	raptorial	0	-
White-tailed Kite	No	open	rare	raptor	raptorial	0	-
Double-toothed Kite	No	forest - interior	occasional	raptor	raptorial	2	-
Tiny Hawk	Yes	forest - edge	rare	raptor	raptorial	29	1970

Bicolored Hawk	No	forest - interior	rare	raptor	raptorial	29	-
Crane Hawk	No	forest - interior	rare	raptor	raptorial	12	-
Common Black Hawk	No	edge	rare	raptor	raptorial	0	-
Great Black Hawk	No	edge	rare	raptor	raptorial	0	-
Roadside Hawk	Yes	edge	rare	raptor	raptorial	0	1970
White Hawk	No	forest - edge	rare	raptor	raptorial	2	-
Semiplumbeous Hawk	No	forest - interior	occasional	raptor	raptorial	12	-
Gray-lined Hawk	No	forest - edge	rare	raptor	raptorial	0	-
Crested Eagle	Yes	forest - edge	rare	raptor	raptorial	29	1970
Harpy Eagle	Yes	forest - interior	rare	raptor	raptorial	29	1950
Black Hawk-Eagle	No	forest - edge	occasional	raptor	raptorial	10	-
Ornate Hawk-Eagle	Yes	forest - edge	rare	raptor	raptorial	29	1970
Black-and-white Hawk-Eagle	No	forest - edge	rare	raptor	raptorial	25	-
Tropical Screech-Owl	Yes	edge	rare	raptor	raptorial	20	1950
Vermiculated Screech-Owl	No	forest - interior	occasional	raptor	raptorial	15	-
Crested Owl	Yes*	forest - interior	occasional	raptor	raptorial	20	2000
Spectacled Owl	No	forest - interior	occasional	raptor	raptorial	10	-

Mottled Owl	Yes*	forest - edge	occasional	raptor	raptorial	0	2010
Black-and-white Owl	No	forest - edge	occasional	raptor	raptorial	5	-
Slaty-tailed Trogon	No	forest - interior	common	omnivore	arboreal	0	-
Black-tailed Trogon	No	forest - interior	rare	omnivore	arboreal	15	-
White-tailed Trogon	No	forest - interior	occasional	omnivore	arboreal	15	-
Gartered Trogon	No	forest - interior	common	omnivore	arboreal	0	-
Black-throated Trogon	No	forest - interior	common	omnivore	arboreal	5	-
Whooping Motmot	No	forest - edge	occasional	omnivore	arboreal	0	-
Rufous Motmot	No	forest - interior	common	omnivore	arboreal	5	-
Broad-billed Motmot	No	forest - interior	occasional	omnivore	arboreal	5	-
White-necked Puffbird	Yes	forest - edge	rare	insectivore	arboreal	5	1970
Black-breasted Puffbird	No	forest - edge	common	insectivore	arboreal	15	-
Pied Puffbird	Yes	forest - edge	occasional	insectivore	arboreal	20	2000
White-whiskered Puffbird	No	forest - interior	common	insectivore	arboreal	5	-
Gray-cheeked Nunlet	Yes	forest - interior	rare	insectivore	arboreal	30	1950
White-fronted Nunbird	Yes	forest - interior	rare	insectivore	arboreal	25	1950
Spot-crowned Barbet	Yes	forest - edge	rare	insectivore	arboreal	32	1920

Collared Aracari	No	forest - edge	occasional	omnivore	arboreal	0	-
Keel-billed Toucan	No	forest - edge	common	omnivore	arboreal	0	-
Yellow-throated Toucan	No	forest - edge	common	omnivore	arboreal	15	-
Black-cheeked Woodpecker	No	forest - edge	common	insectivore	understory	10	-
Red-crowned Woodpecker	Yes	edge	rare	insectivore	understory	0	1960
Cinnamon Woodpecker	Yes	forest - interior	occasional	insectivore	understory	15	2000
Lineated Woodpecker	No	forest - edge	occasional	insectivore	understory	0	-
Crimson-crested Woodpecker	No	forest - interior	occasional	insectivore	understory	0	-
Barred Forest-Falcon	No	forest - interior	occasional	raptor	raptorial	10	-
Collared Forest-Falcon	No	forest - interior	occasional	raptor	raptorial	3	-
Red-throated Caracara	Yes	forest - edge	rare	raptor	raptorial	18	1990
Yellow-headed Caracara	No	open	rare	raptor	raptorial	0	-
Bat Falcon	No	forest - edge	rare	raptor	raptorial	0	-
Orange-chinned Parakeet	No	edge	common	omnivore	arboreal	0	-
Brown-hooded Parrot	No	forest - edge	rare	granivore	arboreal	15	-
Blue-headed Parrot	No	forest - edge	common	granivore	arboreal	0	-
Red-lored Parrot	No	forest - edge	common	granivore	arboreal	0	-

Mealy Parrot	No	forest - edge	common	granivore	arboreal	10	-
Yellow-crowned Parrot	No	edge	rare	granivore	arboreal	0	-
Fasciated Antshrike	Yes	forest - edge	rare	insectivore	arboreal	20	1970
Barred Antshrike	Yes	edge	rare	insectivore	arboreal	0	1970
Black-crowned Antshrike	No	forest - interior	common	insectivore	arboreal	2	-
Spot-crowned Antvireo	No	forest - interior	occasional	insectivore	arboreal	12	-
Moustached Antwren	Yes	forest - interior	rare	insectivore	arboreal	18	1930
Pacific Antwren	Yes	forest - edge	rare	insectivore	arboreal	20	1950
White-flanked Antwren	No	forest - interior	common	insectivore	arboreal	2	-
Checker-throated Antwren	No	forest - interior	common	insectivore	arboreal	5	-
Dot-winged Antwren	No	forest - interior	common	insectivore	arboreal	3	-
Dusky Antbird	No	forest - edge	occasional	insectivore	arboreal	0	-
White-bellied Antbird	Yes	forest - edge	rare	insectivore	terrestrial	0	1970
Chestnut-backed Antbird	No	forest - interior	common	insectivore	terrestrial	9	-
Spotted Antbird	No	forest - interior	common	insectivore	terrestrial	2	-
Bicolored Antbird	No	forest - interior	common	insectivore	terrestrial	5	-
Ocellated Antbird	Yes	forest - interior	occasional	insectivore	terrestrial	18	1970

Streak-chested Antpitta	Yes	forest - interior	rare	insectivore	terrestrial	18	1970
Black-faced Antthrush	Yes	forest - interior	occasional	insectivore	terrestrial	3	1950
Scaly-throated Leaftosser	No	forest - interior	occasional	insectivore	terrestrial	2	-
Plain-brown Woodcreeper	No	forest - interior	common	insectivore	understory	5	-
Wedge-billed Woodcreeper	No	forest - interior	occasional	insectivore	understory	10	-
Northern Barred-Woodcreeper	No	forest - interior	occasional	insectivore	understory	5	2010
Cocoa Woodcreeper	No	forest - interior	common	insectivore	understory	0	-
Black-striped Woodcreeper	No	forest - interior	common	insectivore	understory	18	-
Red-billed Scythebill	Yes	forest - interior	rare	insectivore	understory	35	1930
Plain Xenops	No	forest - interior	common	insectivore	understory	0	-
Buff-throated Foliage-gleaner	Yes	forest - interior	rare	insectivore	arboreal	19	1960
Brown-capped Tyrannulet	No	forest - edge	common	insectivore	arboreal	0	-
Southern Beardless-Tyrannulet	No	forest - edge	common	insectivore	arboreal	0	-
Yellow Tyrannulet	No	edge	rare	insectivore	arboreal	0	-
Yellow-crowned Tyrannulet	No	forest - edge	common	omnivore	arboreal	0	-
Forest Elaenia	No	forest - edge	common	insectivore	arboreal	3	-
Yellow-bellied Elaenia	Yes	edge	occasional	insectivore	arboreal	0	1970

Lesser Elaenia	No	edge	occasional	insectivore	arboreal	0	-
Ochre-bellied Flycatcher	No	forest - interior	common	omnivore	arboreal	0	-
Paltry Tyrannulet	No	forest - edge	common	omnivore	arboreal	0	-
Northern Scrub-Flycatcher	No	edge	rare	insectivore	arboreal	0	-
Black-capped Pygmy-Tyrant	No	forest - interior	common	insectivore	arboreal	15	-
Southern Bentbill	No	forest - edge	common	insectivore	arboreal	0	-
Slate-headed Tody-Flycatcher	No	edge	rare	insectivore	arboreal	0	-
Common Tody-Flycatcher	No	edge	common	insectivore	arboreal	0	-
Brownish Twistwing	Yes	forest - interior	rare	insectivore	arboreal	18	1950
Olivaceous Flatbill	No	forest - interior	occasional	insectivore	arboreal	5	-
Yellow-olive Flycatcher	No	forest - edge	rare	insectivore	arboreal	0	-
Yellow-margined Flycatcher	No	forest - edge	common	insectivore	arboreal	2	-
Golden-crowned Spadebill	No	forest - interior	occasional	insectivore	arboreal	3	-
Royal Flycatcher	Yes	forest - interior	rare	insectivore	arboreal	10	1930
Ruddy-tailed Flycatcher	No	forest - interior	occasional	insectivore	arboreal	0	-
Sulphur-rumped Flycatcher	Yes	forest - interior	rare	insectivore	arboreal	25	1930
Black-tailed Flycatcher	Yes	forest - edge	rare	insectivore	arboreal	5	1930

Tropical Pewee	No	edge	rare	insectivore	arboreal	0	-
Long-tailed Tyrant	Yes	forest - edge	occasional	insectivore	arboreal	29	1990
Bright-rumped Attila	No	forest - interior	common	insectivore	arboreal	3	-
Rufous Mourner	No	forest - interior	common	omnivore	arboreal	10	-
Dusky-capped Flycatcher	No	forest - edge	common	insectivore	arboreal	0	-
Panama Flycatcher	No	forest - edge	rare	insectivore	arboreal	0	-
Great Kiskadee	No	edge	rare	insectivore	arboreal	0	-
Boat-billed Flycatcher	No	edge	occasional	insectivore	arboreal	0	-
Rusty-margined Flycatcher	No	edge	common	insectivore	arboreal	0	-
Social Flycatcher	No	edge	common	insectivore	arboreal	0	-
Gray-capped Flycatcher	No	forest - edge	rare	insectivore	arboreal	25	-
White-ringed Flycatcher	No	forest - edge	rare	insectivore	arboreal	29	-
Streaked Flycatcher	No	edge	occasional	insectivore	arboreal	0	-
Piratic Flycatcher	No	edge	occasional	omnivore	arboreal	0	-
Tropical Kingbird	No	edge	common	insectivore	arboreal	0	-
Russet-winged Schiffornis	No	forest - interior	rare	omnivore	arboreal	5	-
Speckled Mourner	No	forest - interior	rare	omnivore	arboreal	18	-

Masked Tityra	No	forest - edge	occasional	omnivore	arboreal	0	-
Black-crowned Tityra	Yes*	forest - edge	rare	omnivore	arboreal	25	-
Cinnamon Becard	No	edge	rare	insectivore	arboreal	5	-
White-winged Becard	No	edge	occasional	insectivore	arboreal	5	-
Purple-throated Fruitcrow	No	forest - edge	common	omnivore	arboreal	3	-
Blue Cotinga	No	forest - edge	rare	frugivore	arboreal	15	-
Rufous Piha	Yes	forest - interior	occasional	omnivore	arboreal	20	1990
Lance-tailed Manakin	Yes	forest - edge	rare	omnivore	arboreal	0	1990
White-ruffed Manakin	No	forest - interior	rare	omnivore	arboreal	30	-
Golden-collared Manakin	No	forest - edge	occasional	frugivore	arboreal	0	-
Red-capped Manakin	No	forest - interior	common	frugivore	arboreal	2	-
Scrub Greenlet	Yes	forest - edge	rare	insectivore	arboreal	0	2000
Green Shrike-Vireo	Yes	forest - edge	rare	insectivore	arboreal	2	1990
Lesser Greenlet	No	forest - edge	common	insectivore	arboreal	2	-
Golden-fronted Greenlet	No	forest - edge	rare	insectivore	arboreal	2	-
Yellow-green Vireo	No	edge	rare	insectivore	arboreal	0	-
Black-chested Jay	Yes	forest - edge	rare	omnivore	arboreal	3	1970

Scaly-breasted Wren	Yes	forest - interior	rare	insectivore	terrestrial	15	1930
House Wren	No	edge	rare	insectivore	arboreal	0	-
White-headed Wren	Yes	forest - interior	rare	insectivore	arboreal	35	1950
Black-bellied Wren	Yes	forest - interior	rare	insectivore	arboreal	15	1960
Isthmian Wren	No	open	rare	insectivore	arboreal	0	-
Bay Wren	Yes	forest - edge	rare	insectivore	arboreal	25	1950
Buff-breasted Wren	Yes	forest - edge	rare	insectivore	arboreal	5	1950
White-breasted Wood-Wren	Yes	forest - interior	occasional	insectivore	terrestrial	3	1950
Song Wren	Yes	forest - interior	occasional	insectivore	terrestrial	15	1960
Long-billed Gnatwren	Yes	forest - edge	occasional	insectivore	arboreal	2	1990
Tropical Gnatcatcher	No	forest - edge	common	insectivore	arboreal	0	-
Clay-colored Thrush	No	edge	rare	omnivore	arboreal	0	-
White-throated Thrush	No	forest - edge	rare	omnivore	arboreal	25	-
Tropical Mockingbird	No	edge	rare	omnivore	arboreal	2	-
Yellow-crowned Euphonia	No	edge	rare	frugivore	arboreal	5	-
Thick-billed Euphonia	No	edge	occasional	frugivore	arboreal	5	-
Fulvous-vented Euphonia	No	forest - edge	occasional	omnivore	arboreal	0	-

White-vented Euphonia	Yes	forest - edge	occasional	frugivore	arboreal	29	2010
Rosy Thrush-Tanager	Yes	forest - edge	rare	insectivore	terrestrial	5	1930
Orange-billed Sparrow	No	forest - edge	rare	omnivore	terrestrial	3	-
Black-striped Sparrow	Yes	edge	rare	omnivore	terrestrial	0	1990
Yellow-billed Cacique	No	open	rare	omnivore	arboreal	3	-
Crested Oropendola	No	forest - edge	rare	omnivore	arboreal	20	-
Chestnut-headed Oropendola	No	forest - edge	common	omnivore	arboreal	3	-
Scarlet-rumped Cacique	No	forest - interior	rare	omnivore	arboreal	15	-
Yellow-rumped Cacique	No	forest - edge	common	omnivore	arboreal	3	-
Yellow-backed Oriole	No	forest - edge	occasional	omnivore	arboreal	3	-
Yellow-tailed Oriole	Yes	forest - edge	rare	omnivore	arboreal	15	1940
Giant Cowbird	No	forest - edge	occasional	omnivore	terrestrial	5	-
Great-tailed Grackle	No	open	rare	omnivore	terrestrial	0	-
Buff-rumped Warbler	Yes	forest - interior	rare	insectivore	terrestrial	20	1960
Rufous-capped Warbler	Yes	forest - edge	occasional	insectivore	arboreal	3	1960
Dusky-faced Tanager	Yes	forest - edge	rare	insectivore	arboreal	25	1970
Red-throated Ant-Tanager	No	forest - edge	rare	omnivore	arboreal	3	-

Blue-black Grosbeak	No	forest - edge	occasional	omnivore	arboreal	3	-
Blue-gray Tanager	No	edge	common	omnivore	arboreal	0	-
Palm Tanager	No	edge	common	omnivore	arboreal	0	-
Golden-hooded Tanager	No	forest - edge	common	omnivore	arboreal	0	-
Plain-colored Tanager	No	edge	common	omnivore	arboreal	0	-
Bay-headed Tanager	No	forest - edge	rare	omnivore	arboreal	20	-
Green Honeycreeper	No	forest - edge	common	omnivore	arboreal	0	-
Sulphur-rumped Tanager	No	forest - edge	occasional	omnivore	arboreal	30	-
Blue-black Grassquit	No	open	occasional	omnivore	arboreal	0	-
Gray-headed Tanager	No	forest - interior	occasional	omnivore	arboreal	0	-
White-shouldered Tanager	No	forest - edge	common	omnivore	arboreal	2	-
White-lined Tanager	Yes	open	rare	omnivore	arboreal	3	1960
Flame-rumped Tanager	Yes	edge	rare	omnivore	arboreal	20	1960
Crimson-backed Tanager	No	edge	occasional	omnivore	arboreal	0	-
Shining Honeycreeper	No	forest - edge	common	frugivore	arboreal	15	-
Red-legged Honeycreeper	No	forest - edge	common	frugivore	arboreal	0	-
Scarlet-thighed Dacnis	No	forest - edge	occasional	omnivore	arboreal	29	-

Blue Dacnis	No	forest - edge	common	omnivore	arboreal	0	-
Bananaquit	No	edge	rare	omnivore	arboreal	10	-
Yellow-faced Grassquit	No	edge	rare	omnivore	arboreal	30	-
Thick-billed Seed-Finch	No	edge	rare	granivore	arboreal	0	-
Variable Seedeater	No	edge	common	granivore	arboreal	0	-
Slate-colored Seedeater	No	forest - edge	rare	granivore	arboreal	0	-
Yellow-bellied Seedeater	No	open	occasional	granivore	arboreal	0	-
Black-headed Saltator	No	edge	rare	omnivore	arboreal	29	-
Buff-throated Saltator	Yes	edge	rare	omnivore	arboreal	3	1960
Slate-colored Grosbeak	No	forest - interior	occasional	omnivore	arboreal	18	-
Streaked Saltator	Yes	edge	rare	omnivore	arboreal	3	1970

* The status of missing species marked "Yes" with an asterisk is uncertain. Populations of these species appear functionally extirpated, but poor detection rates may allow them to persist in small, unencountered populations on the island. These birds were omitted from data summaries and logistic regressions.

Table B.4. Residency status of non-aquatic, non-aerial species first detected on BCI after 1950. Sorted by decade of first detection. Residency categories include “vagrant/flyover”: species unlikely to maintain stable, resident breeding populations on BCI; “ephemeral”: transitory breeders that maintain only intermittent breeding populations; “expanding”: birds experiencing range expansions along the canal but not yet permanent residents of BCI - often urban associated; and “colonized”: new species with stable, permanent breeding populations. See Table A.1 for scientific names corresponding to species’ common names.

Common Name	**Status**	**Decade**
Violaceous Quail-Dove	Ephemeral	1950
Gray-lined Hawk	Vagrant	1950
Great Kiskadee	Colonized	1950
White-throated Thrush	Ephemeral	1950
Tropical Mockingbird	Expanding	1950
Great-tailed Grackle	Expanding	1950
Slate-colored Seedeater	Ephemeral	1950
Brown-hooded Parrot	Vagrant	1990
White-tailed Kite	Vagrant	1990
White-ruffed Manakin	Ephemeral	1990
Golden-fronted Greenlet	Ephemeral	1990
Yellow-crowned Euphonia	Ephemeral	1990
Orange-billed Sparrow	Vagrant	1990
Scarlet-rumped Cacique	Vagrant	1990
Yellow-faced Grassquit	Ephemeral	1990
Pearl Kite	Vagrant	2000
Bicolored Hawk	Vagrant	2000
Yellow-headed Caracara	Expanding	2000

Table B.5. Average southern range limit between missing and extant bird species on BCI by habitat association (with SD in parentheses).

Habitat Association	**Average Southern Limit (km)**	
	Missing	**Extant**
All habitats	13.8 (± 11.2)	5.7 (± 8.5)
All forest-associated	16.8 (± 10.3)	7.0 (± 8.7)
Forest interior	19.3 (± 8.2)	7.4 (± 7.9)
Forest edge	14.6 (± 11.6)	6.7 (± 9.4)
Edge	3.5 (± 7.4)	2.9 (± 7.8)
Open	3.0 (± 0.0)	0.33 (± 1.0)

Table B.6. Mean environmental factor values for each mainland subregion cluster identified using hierarchical cluster analysis (with ranges italicized in parentheses). See Table B.2 for definitions of environmental factors.

Cluster	**# Subregions**	**Bird Richness**	**Forest Age**	**Altitude (m)**	**Area (km^2)**	**Percent Forest**	**Percent Unfrag.**	**Percent Urban**	**Plant Richness**	**Precip (mm/yr)**
1	5	150.2 (147-156)	2.4	231.6 (109-349)	47.7 (11.2-78.5)	67.0 (43.0-91.0)	88 (80-99)	0.4 (0-1)	74.0 (67-85)	2338.2 (2100-2550)
2	8	237.9 (220-271)	2.5	204.6 (111-278)	49.6 (20.0-74.0)	78.9 (46.2-94.8)	95 (78-100)	0.7 (0.1-3.1)	81.9 (57-96)	2623.1 (1935-3250)
PRO	1	120	2	137	17.28	63	81	1.1	109	3000

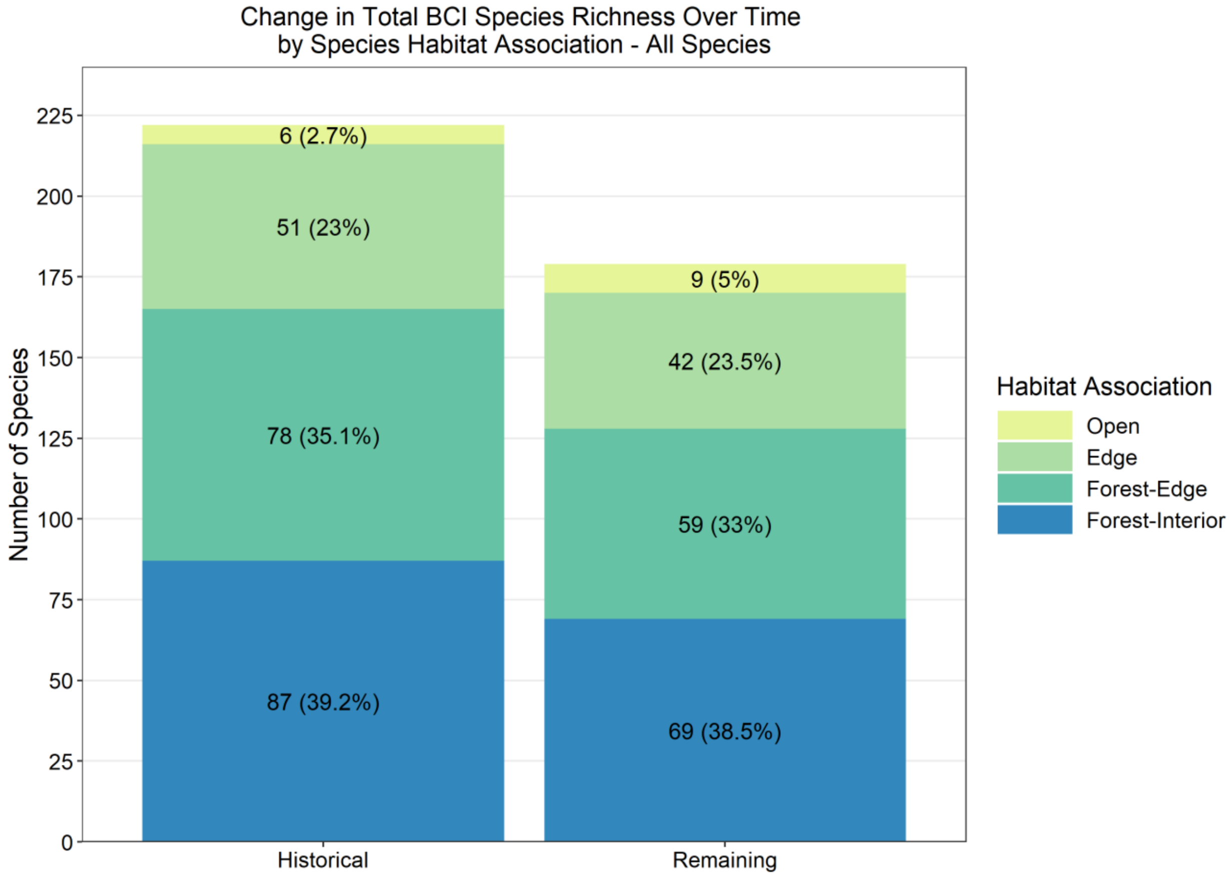

Figure B.1. Change in BCI species richness over time by species habitat association, between the complete historical non-aerial, non-aquatic resident bird community and the remaining bird community today. “Historical refers” to pre-1951bird community, including likely but undetected birds. The remaining bird community includes permanent residents and non-permanent species that intermittently breed on the island. Values in columns denote number of species in that habitat association group (with percentage out of total species richness for that period in parentheses).

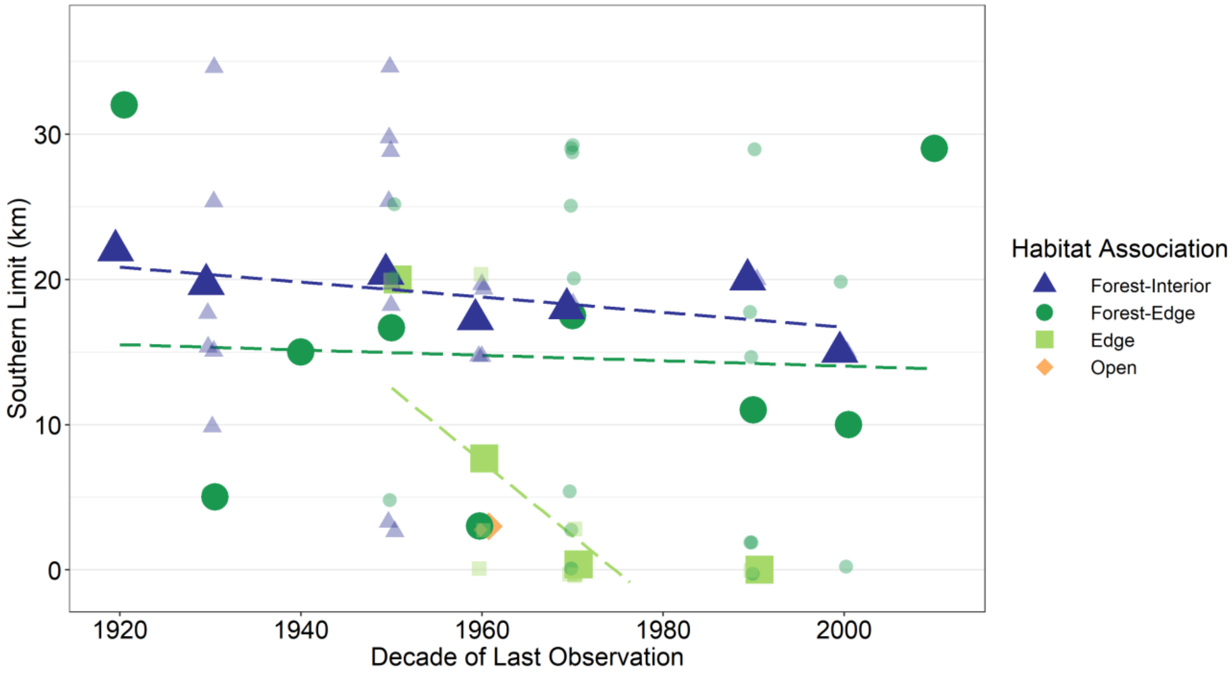

Figure B.2. Southern Panama Canal zone range limits for extinct species on BCI. Grouped by date of last reported observation and habitat association, with best-fit linear regression lines between southern limit and decade of extinction (dashed lines). Small shapes are individual extinctions, large shapes represent individual decade means for each habitat type.

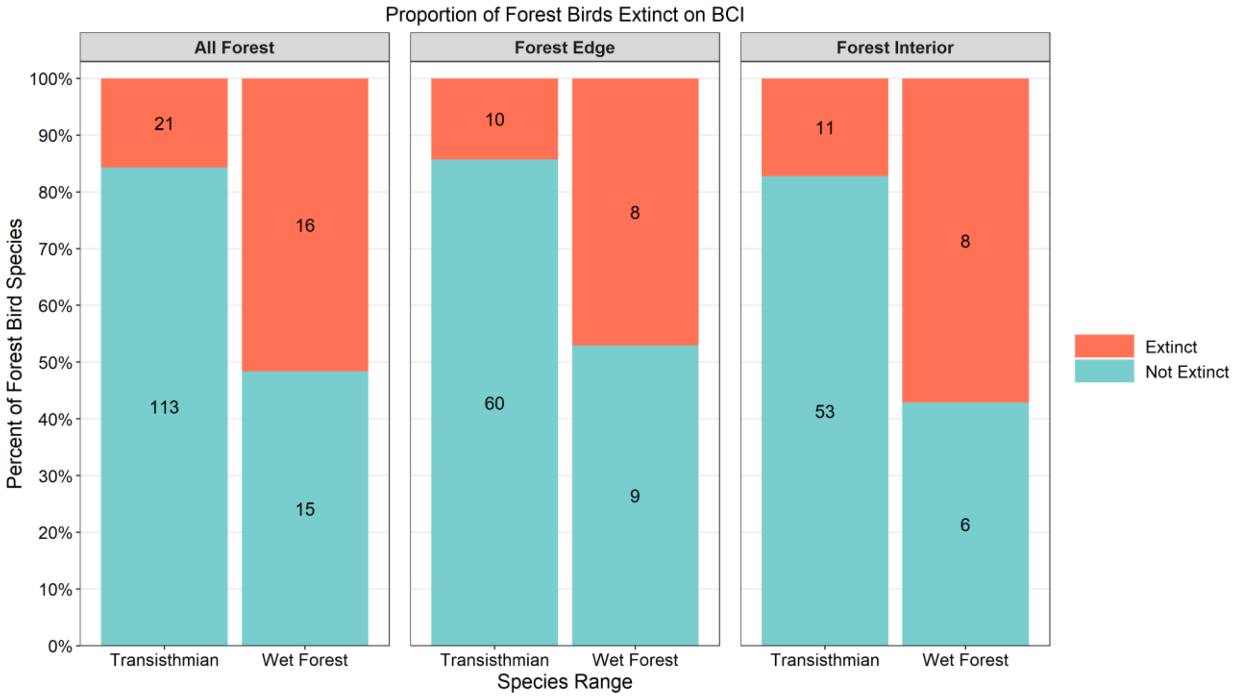

Figure B.3. Proportion of transisthmian and wet forest birds extinct on BCI across all forest-associated species as well as broken down by core forest interior and forest edge association. Transisthmian birds occur in subregions along the entire Canal zone, while wet forest species occur exclusively in forests with >2000mm precipitation annually. Extinct birds are any species considered to have once been a permanent breeding resident that has gone undetected for a least a decade and has not demonstrated the capacity to re-establish breeding populations on the island post-isolation.

APPENDIX C - Chapter 3 Supplemental Material

Table C.1. Information criteria values for species-area functions meeting the assumptions of normality and homoscedasticity, fit to all mainland and Gatun Island species richness and area data.

Function	AICc	AICw	ΔAIC
power	363.077	0.248	0.000
powerR	364.972	0.096	1.895
epm1	365.086	0.091	2.009
p2	365.192	0.086	2.115
mmf	365.315	0.081	2.238
heleg	365.315	0.081	2.238
epm2	365.339	0.080	2.262
weibull3	365.340	0.080	2.263
p1	365.428	0.076	2.351
koba	366.946	0.036	3.869
betap	367.789	0.023	4.712
weibull4	367.881	0.022	4.804
loga	375.909	0.000	12.832
monod	379.359	0.000	16.282
negexpo	388.320	0.000	25.243
chapman	390.671	0.000	27.594

Table C.2. Information criteria values for species-area functions meeting the assumptions of normality and homoscedasticity, fit to “wet” subregions receiving >2450 mm average precipitation annually.

Function	AICc	AICw	ΔAIC
epm1	266.540	0.151	0.000
mmf	266.614	0.146	0.074
heleg	266.614	0.146	0.074
weibull3	266.848	0.130	0.308
koba	267.208	0.108	0.668
powerR	267.398	0.099	0.858
p1	267.828	0.080	1.288
p2	268.538	0.056	1.998
betap	269.025	0.044	2.485
weibull4	269.139	0.041	2.599
loga	284.547	0.000	18.007

Table C.3. Information criteria values for species-area functions meeting the assumptions of normality and homoscedasticity, fit to “dry” subregions receiving <2450 mm average precipitation annually.

Function	**AICc**	**AICw**	**ΔAIC**
power	89.68886	0.289171	0
koba	90.39353	0.203299	0.704677
loga	90.46349	0.196311	0.774638
linear	92.81815	0.060484	3.129291
epm2	93.78961	0.037212	4.100753
p2	93.89423	0.035316	4.205378
p1	94.26883	0.029284	4.579973
powerR	94.31151	0.028665	4.622655
epm1	94.36135	0.02796	4.672498
mmf	94.40314	0.027382	4.714286
heleg	94.40314	0.027382	4.714286
weibull3	94.40314	0.027382	4.714286
ratio	96.90701	0.00783	7.218153
weibull4	100.7063	0.001172	11.01747
betap	100.7408	0.001151	11.05196

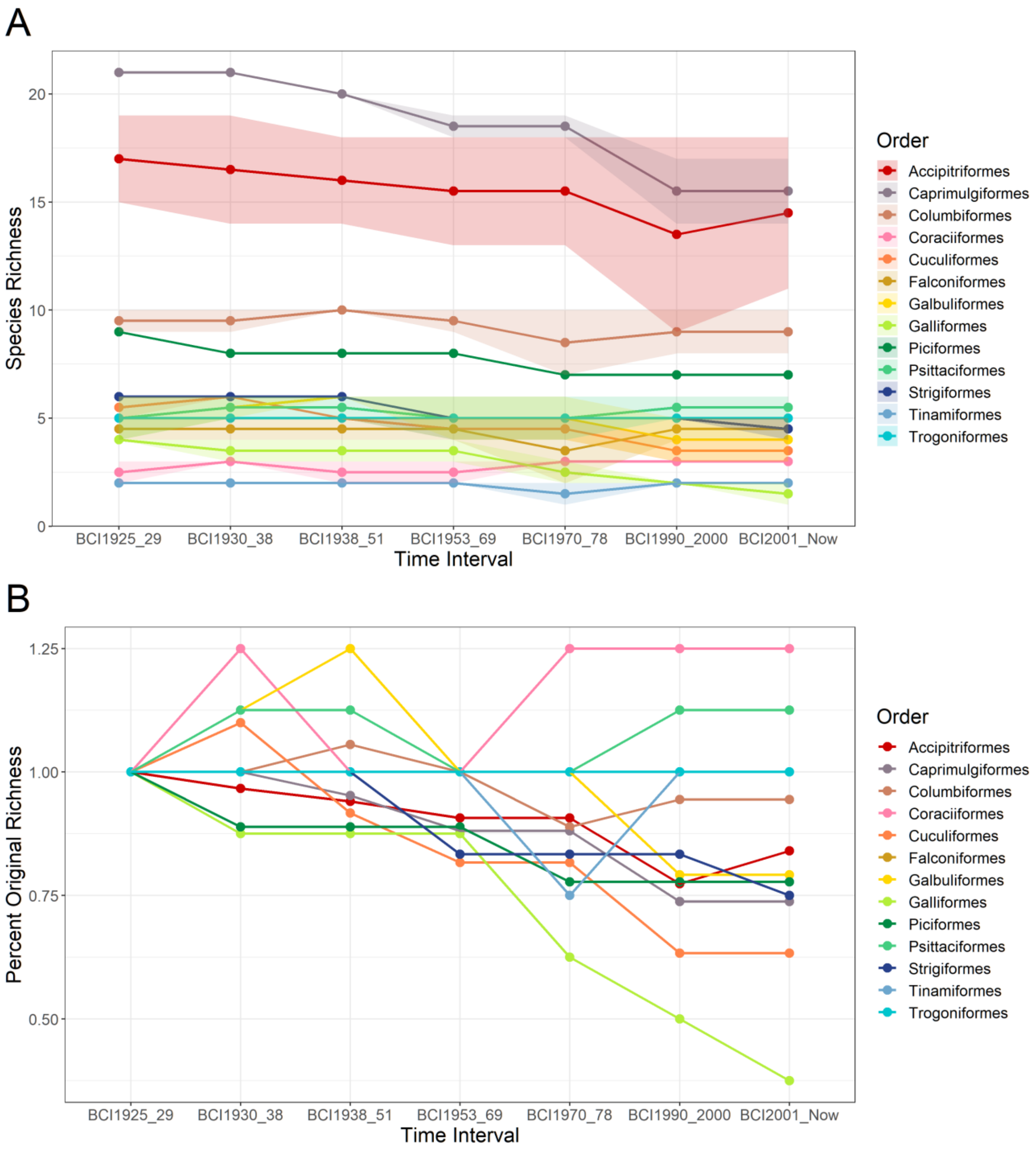

Figure C.1. Estimated species richness (A) and percent of initial richness remaining (B) of resident, non-aquatic, non-aerial birds on BCI over time by taxonomic order with Passeriformes removed. In A, colored regions represent “logical” confidence intervals with colored circles indicating the average between maximum and adjusted minimum estimates.

APPENDIX D - Chapter 4 Supplemental Material

Appendix D1 - NMDS Accounting for Species Richness

Because the underlying structure of our NMDS ordination could be driven by differences in species richness between subregions, we performed a repeated rarefaction procedure to standardize the number of species across sample areas. This consisted of randomly sampling without replacement species from each subregion equal to the smallest subregion richness (N = 66). We performed NMDS ordination on these equal-richness subregions in the same manner as NMDS for the full dataset, coercing a 2-axis solution to ensure greater comparability among ordinations. We used non-symmetric, scaled Procrustes superimposition in package vegan to maximize similarity between our ordination of rarefied communities and the original, full ordination. Procrustes superimposition uniformly scales and rotates observations in one ordination to minimize its sum of squared differences with a second ordination (Oksanen et al. 2019). A Procrustes statistic (Procrustes *r*) calculated as the square root of (1 – Procrustes sum of squared residuals) gives a measure of correlation between ordinations in their optimal symmetric superimposition. We assessed the significance of the Procrustes statistic via the ‘protest’ function in vegan with 999 permutations of Procrustes superimposition. We extracted the subregion and species scores from the ordination of rarefied, equal-richness subregions following Procrustes superimposition and then repeated the entire rarefaction process for 999 total iterations. Finally, we calculated the mean and standard deviation of subregion and species axes scores across all iterations. From these results we could visually assess the potential range of NMDS results if all subregions varied in species composition but not richness.

We found a weak, marginally significant correlation between the average Procrustes statistic from 999 ordinations of rarefied subregions of equal richness and our ordination of the full dataset (Procrustes *r* mean = 0.412, range 0.115-0.642; p-value mean = 0.097, range <0.001-0.915). Procrustes sum of squared residuals (ss) ranged between 0.588 and 0.987 (mean ss = 0.821). High richness subregions with a larger species pool to draw from exhibited broader variation in axis scores than low-richness subregions with fewer potential species combinations (Figure D.2B). Nevertheless, we observed a similar ordination structure (Figure D.2A) with the first axis primarily defined by decreasing urbanization and fragmentation and increasing forest cover and age (Table D.5), and high correlation between original and mean rarified axes scores (Pearson’s R for sites: Axis 1 = 0.835, Axis 2 = 0.643; Pearson’s R for species: Axis 1 = 0.947, Axis 2 = 0.801).

These results emphasize that the urban-forest gradient is the primary driver of avian community structure along the Panama Canal independent of species richness. They also corroborate our observation that depauperate urban forest bird communities are subsets of larger and more species-rich forest patches, rather that novel communities. After accounting for differences in richness, most subregions generally occupied the same region of species space regardless of degree of urbanization, though the most heavily and least urbanized subregions always occupied separate, non-overlapping portions of the first axis (Figure D.1) suggesting a high degree of urbanization eventually limits which species from large, contiguous rainforests occur in urban forest fragments.

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Tables and Figures

Table D.1. Environmental factors used to characterize avian community structure along the Panama Canal corridor. Full descriptions of these environmental factors can be found in (Rompré et al. 2007).

Variable	Description	Source
AGE_CAT	Categorical. Represents dominant relative forest age (1=secondary; 2=mature secondary; 3=primary mature forests) estimated using ANAM (2003) criteria for species composition and disturbance history.	(Pyke et al. 2001)
ALT	Maximum altitude per subregion in meters above sea level.	(Rompré et al. 2007)
AREA	Total area in km^2 per region	(Rompré et al. 2007)
PCT_FOREST	Proportion forest cover, calculated by dividing forested area by total area in each subregion.	(Rompré et al. 2007)
PCT_UNFRAG	Degree of fragmentation, represented by percent total forest area included in 1 or 2 largest fragments within subregion.	(Rompré et al. 2007)
PCT_URBAN	Proportion urban cover, calculated by dividing urban area by total area in each subregion.	(ANAM 2003; ACP 2016)
PLANTS	Plant and tree species richness within 1 ha plots. Plant data obtained from Pyke et al. (2001). Trees defined as woody plants >10cm dbh. Kriging used to interpolate geographic plant richness for each subregion centroid (see Rompré et al. (2007) for details).	(Condit 1998; Pyke et al. 2001; Perez et al. *unpublished report*)
PRECIP	Mean annual precipitation in mm for subregion, obtained from both ACP and atlases. For subregions without precipitation data, values obtained by interpolation from isohyets available for that period (Rompré et al. 2007).	(ACP 2016; Santiago and Mulkey 2005; Pyke et al. 2001; Condit 1998)

Table D.2 Candidate predictor species attributes and their sources, with relevant derivation notes where necessary.

Trait	Type of Data	Source(s)	Notes
Clutch size	continuous	(Skutch 1945, 1947, 1948, 1962, 1976, 1985, Stutchbury et al. 1996, Whittaker 1996, Pereira et al. 2004, Hanson 2006, Jetz et al. 2008, Master 2011, Whitacre and Peregrine Fund (U.S.) 2012, Gilbert and Schulenberg 2013, Dzielski et al. 2016, Snow et al. 2017), Robinson & Robinson *unpublished field notes*	
Developmental duration	continuous	(Skutch 1947, 1962, 1963, 1969, 1973, 1976, 1983, 1985, 1996, Iwaniuk and Nelson 2003, Hanson 2006, Jones and Griffiths 2011, Whitacre and Peregrine Fund (U.S.) 2012, Green and Kannan 2017, Valdez and Ortega-Santos 2019)	The sum of egg laying, incubation, and nestling periods (in days)
Development mode	categorical with six levels: • Precocial 1 • Precocial 2 • Precocial 3 • Semialtricial • Altricial 1 • Altricial 2	(Starck 1993)	See source for category level definitions

Body mass	continuous	(Dunning Jr 2007)	
Relative wing length	continuous	(Wetmore, A. 1965, 1968, 1972, Wetmore, Alexander et al. 1985, Robinson & Robinson *unpublished field notes)*	
Wing loading	continuous	(Hartman 1961, Moermond and Denslow 1985, Graves 2017)	
Nest type	categorical with three levels: • o: open cup, bowl, platform, or scrape (o) • e: enclosed (*e.g.,* pendulum, pyriform, or pouch) • c: cavities in trees, burrows, or termite mounds	(Robinson 1999, 2001, Robinson et al. 2000, 2004)	
Nest height	categorical with four levels: • g: ground, <1m • u: understory, 1-5m • m: mid-story, >5m but below canopy • c: canopy, top level of vegetation regardless of height	(Robinson 1999, 2001, Robinson et al. 2000, 2004)	
Diet preference	categorical with seven levels: • carnivores (vertebrate prey) • frugivores (fruits of any size) • herbivores (plant parts, seeds, and nuts) • insectivores (insects and arthropods) • and nectarivores (flower nectar) • scavengers (carrion) • omnivores (multiple categories)	(Wilman et al. 2014)	based on single food category with >50% total use per Wilman et al. (2014); species with less than 50% use in any single diet category were classified omnivorous

Diet breadth	integer	(Wilman et al. 2014)	number of non-omnivore diet preference categories with non-zero use
Foraging height	categorical with six levels: • ground • understory (<2m) • mid-height (>2m but below canopy) • canopy (top level of vegetation regardless of height) • aerial (above vegetation structures) • mixed	(Wilman et al. 2014)	based on single foraging strata with >50% use per Wilman et al. (2014); species with less than 50% use in any single category were classified "mixed"
Foraging behavior	categorical with six levels: • G: gleaning • S: sallying • GS: gleaning and sallying • GP: gleaning and scratching/prying • C: chasing/screening • E: sub-surface extraction	(Robinson 1999, 2001, Robinson et al. 2000, 2004)	attack behaviors defined in Remsen Jr and Robinson 1990
Foraging breadth	integer	(Wilman et al. 2014)	number of non-mixed foraging strata categories with non-zero use
Habitat association - forest interior	categorical - yes or no	(Robinson 1999, 2001, Robinson et al. 2000, 2004)	
Habitat association - edge/open	categorical - yes or no	(Robinson 1999, 2001, Robinson et al. 2000, 2004)	

Table D.3. NMDS ordination axes scores based on Sorensen distances for 303 resident, non-aquatic forest associated birds detected in two or more subregions along the Panama Canal. Taxonomy based on the 59th supplement to the AOS checklist of North American birds (Chesser et al. 2018). See Table A.1 for scientific names corresponding to species' common names.

Common Name	**Axis 1**	**Axis 2**
Great Tinamou	0.4969	0.00652
Little Tinamou	0.16581	0.09063
Gray-headed Chachalaca	-0.02167	0.06056
Crested Guan	0.81778	-0.09981
Great Curassow	0.77592	-0.09646
Marbled Wood-Quail	0.70669	0.03264
Rock Pigeon	-0.14595	-0.35385
Pale-vented Pigeon	-0.02407	-0.02069
Scaled Pigeon	0.46016	-0.04798
Short-billed Pigeon	0.63008	0.08312
Ruddy Ground-Dove	0.17992	-0.18196
Blue Ground-Dove	0.57814	-0.12185
Ruddy Quail-Dove	0.4131	0.09655
Violaceous Quail-Dove	0.61116	-0.07125
Olive-backed Quail-Dove	0.89559	-0.14349
White-tipped Dove	0	0
Gray-chested Dove	0.07512	-0.03254
Little Cuckoo	0.86968	-0.03478
Squirrel Cuckoo	0	0
Striped Cuckoo	0.35191	-0.02066
Pheasant Cuckoo	0.43471	-0.04358
Rufous-vented Ground-Cuckoo	0.74127	0.07181
Greater Ani	0.40691	-0.022
Smooth-billed Ani	0.35279	-0.00792
White-collared Swift	0.80645	-0.09015
Vaux's Swift	0.14961	-0.28326
Short-tailed Swift	0.21748	-0.04085
Band-rumped Swift	0.10571	-0.11788
Lesser Swallow-tailed Swift	0.59638	0.05568
White-necked Jacobin	0.48169	-0.00197
White-tipped Sicklebill	0.95841	-0.14091
Rufous-breasted Hermit	0.27613	-0.07524
Band-tailed Barbthroat	0.39953	-0.05812
Green Hermit	0.90416	-0.12023
Long-billed Hermit	0.08384	0.05173
Stripe-throated Hermit	0.08384	0.05173
Purple-crowned Fairy	0.60806	-0.12035

Black-throated Mango	0.6298	-0.07099
Rufous-crested Coquette	0.77788	-0.0758
Garden Emerald	0.01639	-0.05245
Scaly-breasted Hummingbird	0.51519	0.08374
White-vented Plumeleteer	0.09157	0.12891
Bronze-tailed Plumeleteer	0.56707	-0.23011
Crowned Woodnymph	0.35457	-0.02673
Blue-chested Hummingbird	0.35323	0.01894
Snowy-bellied Hummingbird	-0.27767	0.10937
Rufous-tailed Hummingbird	0.08203	0.00819
Sapphire-throated Hummingbird	0.5266	-0.06198
Violet-bellied Hummingbird	0.08384	0.05173
Uniform Crake	0.90416	-0.12023
Black Vulture	0	0
Turkey Vulture	0.07512	-0.03254
King Vulture	0.72798	-0.04783
Gray-headed Kite	0.33986	-0.02168
Hook-billed Kite	0.59568	0.01868
Swallow-tailed Kite	0.52443	-0.1585
White-tailed Kite	0.55312	-0.05025
Double-toothed Kite	0.24616	0.03252
Plumbeous Kite	0.66189	-0.13826
Tiny Hawk	0.69242	-0.01969
Bicolored Hawk	0.95841	-0.14091
Crane Hawk	0.66442	0.05113
Plumbeous Hawk	0.72891	0.05965
Common Black Hawk	0.63051	-0.19665
Savanna Hawk	0.29263	0.05024
Great Black Hawk	0.65317	-0.04735
Roadside Hawk	0.15535	0.08824
White Hawk	0.5551	0.07679
Semiplumbeous Hawk	0.57711	0.02054
Gray-lined Hawk	0.2413	0.06727
Short-tailed Hawk	0.17527	0.05998
Zone-tailed Hawk	0.37508	0.04246
Crested Eagle	0.81375	-0.07845
Harpy Eagle	0.84423	-0.13054
Black Hawk-Eagle	0.57871	0.08888
Ornate Hawk-Eagle	0.88137	-0.12148
Slaty-tailed Trogon	0.26993	0.05695
Black-tailed Trogon	0.5455	-0.11858
White-tailed Trogon	0.49309	-0.02521
Gartered Trogon	0.16619	0.02006

Black-throated Trogon	0.43719	-0.0207
Whooping Motmot	0.04661	0.12012
Rufous Motmot	0.25413	0.05369
Broad-billed Motmot	0.53872	0.08897
White-necked Puffbird	0.4368	0.10481
Black-breasted Puffbird	0.56336	0.00465
Pied Puffbird	0.51824	-0.09927
White-whiskered Puffbird	0.46945	0.03171
White-fronted Nunbird	0.87271	-0.09831
Great Jacamar	0.82171	-0.06044
Spot-crowned Barbet	0.90214	-0.07789
Collared Aracari	0.38388	0.04394
Yellow-eared Toucanet	0.95841	-0.14091
Keel-billed Toucan	0	0
Yellow-throated Toucan	0.48853	-0.10299
Olivaceous Piculet	0.69634	-0.15476
Black-cheeked Woodpecker	0.50335	-0.00161
Red-crowned Woodpecker	-0.02407	-0.02069
Cinnamon Woodpecker	0.56415	-0.11909
Lineated Woodpecker	0.31294	-0.02852
Crimson-bellied Woodpecker	0.88137	-0.12148
Crimson-crested Woodpecker	0.25163	0.01784
Laughing Falcon	0.59664	-0.09165
Barred Forest-Falcon	0.54834	0.10098
Slaty-backed Forest-Falcon	0.61602	0.05831
Collared Forest-Falcon	0.08384	0.05173
Red-throated Caracara	0.79452	0.02297
Crested Caracara	0.6298	-0.07099
Yellow-headed Caracara	0.1909	-0.1451
Bat Falcon	0.6468	-0.06384
Orange-chinned Parakeet	-0.01509	-0.00418
Brown-hooded Parrot	0.53873	0.01438
Blue-headed Parrot	0.08384	0.05173
Red-lored Parrot	0.16619	0.02006
Mealy Parrot	0.52625	-0.0221
Yellow-crowned Parrot	-0.51576	0.02195
Sapayoa	0.87834	-0.05796
Fasciated Antshrike	0.46397	-0.04279
Great Antshrike	0.66424	-0.10548
Barred Antshrike	0.17978	-0.2006
Black-crowned Antshrike	0.08384	0.05173
Russet Antshrike	0.87834	-0.05796
Spot-crowned Antvireo	0.54939	0.05732

Moustached Antwren	0.77601	0.00357
Pacific Antwren	0.71535	-0.11291
White-flanked Antwren	0.43719	-0.0207
Checker-throated Antwren	0.43719	-0.0207
Dot-winged Antwren	0.43719	-0.0207
Dusky Antbird	0.27829	0.07917
Jet Antbird	0.52572	-0.04956
Bare-crowned Antbird	0.73549	-0.17041
White-bellied Antbird	0.14208	0.13787
Chestnut-backed Antbird	0.46266	-0.02686
Dull-mantled Antbird	0.95841	-0.14091
Spotted Antbird	0.43719	-0.0207
Wing-banded Antbird	0.85078	-0.06494
Bicolored Antbird	0.46945	0.03171
Ocellated Antbird	0.55467	0.0323
Black-crowned Antpitta	0.95841	-0.14091
Streak-chested Antpitta	0.61812	-0.09893
Black-faced Antthrush	0.49073	0.0549
Tawny-throated Leaftosser	0.81657	-0.0744
Scaly-throated Leaftosser	0.41341	0.04989
Olivaceous Woodcreeper	0.37982	-0.13614
Long-tailed Woodcreeper	0.65974	-0.12543
Ruddy Woodcreeper	0.48035	-0.05982
Plain-brown Woodcreeper	0.43719	-0.0207
Wedge-billed Woodcreeper	0.56336	0.00465
Northern Barred-Woodcreeper	0.53872	0.08897
Cocoa Woodcreeper	0	0
Black-striped Woodcreeper	0.58952	-0.11661
Straight-billed Woodcreeper	0.44945	-0.24406
Streak-headed Woodcreeper	-0.06127	-0.24694
Plain Xenops	0.23325	-0.01575
Buff-throated Foliage-gleaner	0.76344	0.00025
Brown-capped Tyrannulet	0.35323	0.01894
Southern Beardless-Tyrannulet	0	0
Yellow Tyrannulet	0.14878	-0.16233
Yellow-crowned Tyrannulet	0	0
Forest Elaenia	0.4484	0.00304
Gray Elaenia	0.77646	-0.10756
Greenish Elaenia	0.10681	0.02722
Yellow-bellied Elaenia	-0.08844	-0.07159
Lesser Elaenia	0.09472	-0.09533
Olive-striped Flycatcher	0.8691	-0.09558
Ochre-bellied Flycatcher	0.25413	0.05369

Sepia-capped Flycatcher	0.67691	-0.0985
Yellow-green Tyrannulet	0.49904	0.15595
Paltry Tyrannulet	0.15643	0.06507
Black-capped Pygmy-Tyrant	0.44279	0.10539
Pale-eyed Pygmy-Tyrant	-0.79783	0.0823
Southern Bentbill	0.08384	0.05173
Slate-headed Tody-Flycatcher	0.67262	-0.13136
Common Tody-Flycatcher	0.30995	-0.14292
Black-headed Tody-Flycatcher	0.52109	0.00589
Brownish Twistwing	0.65252	0.05254
Olivaceous Flatbill	0.47421	0.00348
Yellow-olive Flycatcher	0.06485	0.08612
Yellow-margined Flycatcher	0.43719	-0.0207
Golden-crowned Spadebill	0.42742	0.13167
Royal Flycatcher	0.55909	0.06043
Ruddy-tailed Flycatcher	0.25413	0.05369
Sulphur-rumped Flycatcher	0.8233	-0.10504
Black-tailed Flycatcher	0.54706	-0.02557
Bran-colored Flycatcher	0.48536	-0.0795
Tropical Pewee	0.32246	-0.25599
Long-tailed Tyrant	0.85441	-0.09224
Bright-rumped Attila	0.43719	-0.0207
Choco Sirystes	0.90214	-0.07789
Rufous Mourner	0.66442	0.05113
Dusky-capped Flycatcher	0.22145	-0.03975
Panama Flycatcher	0.1059	-0.10023
Great Kiskadee	0.0043	-0.10134
Boat-billed Flycatcher	-0.00595	-0.01418
Rusty-margined Flycatcher	0.24431	-0.09574
Social Flycatcher	0.04172	-0.05869
Gray-capped Flycatcher	0.65126	-0.08789
White-ringed Flycatcher	0.8691	-0.09558
Streaked Flycatcher	0.15492	-0.00284
Piratic Flycatcher	0.16468	-0.04784
Tropical Kingbird	0	0
Fork-tailed Flycatcher	0.08896	0.01755
Russet-winged Schiffornis	0.42656	0.12418
Speckled Mourner	0.69661	-0.0227
Masked Tityra	0.09622	0.06284
Black-crowned Tityra	0.81308	-0.07515
Cinnamon Becard	0.72811	-0.03474
White-winged Becard	0.55146	-0.19298
Purple-throated Fruitcrow	0.53872	0.08897

Blue Cotinga	0.60195	-0.05925
Rufous Piha	0.85441	-0.09224
Lance-tailed Manakin	-0.66139	0.0661
Blue-crowned Manakin	0.34145	0.03723
Golden-collared Manakin	0.34737	0.07153
Red-capped Manakin	0.25413	0.05369
Scrub Greenlet	0.3071	-0.12597
Green Shrike-Vireo	0.38452	0.00904
Tawny-crowned Greenlet	0.51936	-0.03856
Lesser Greenlet	0	0
Golden-fronted Greenlet	-0.15637	-0.05393
Yellow-green Vireo	-0.1595	-0.0034
Black-chested Jay	0.16305	0.02933
Gray-breasted Martin	0.09547	-0.14607
White-thighed Swallow	0.89559	-0.14349
Southern Rough-winged Swallow	0.01119	-0.21193
Scaly-breasted Wren	0.62984	0.00239
House Wren	-0.05945	-0.15449
White-headed Wren	0.86968	-0.03478
Rufous-breasted Wren	0.13539	0.12673
Black-bellied Wren	0.37581	0.02807
Rufous-and-white Wren	-0.31941	0.01491
Stripe-breasted Wren	0.83644	-0.07274
Isthmian Wren	0.01366	-0.01029
Bay Wren	0.49467	-0.09569
Buff-breasted Wren	0.24751	-0.12931
White-breasted Wood-Wren	0.36706	0.04543
Song Wren	0.43719	-0.0207
Tawny-faced Gnatwren	0.61674	0.11883
Long-billed Gnatwren	0.08384	0.05173
Tropical Gnatcatcher	0.08384	0.05173
Clay-colored Thrush	-0.07515	-0.06754
White-throated Thrush	0.88137	-0.12148
Tropical Mockingbird	0.17416	-0.24526
Yellowish Pipit	0.86968	-0.03478
Yellow-crowned Euphonia	0.08384	0.05173
Thick-billed Euphonia	0.18343	-0.02841
Fulvous-vented Euphonia	0.45388	-0.03997
White-vented Euphonia	0.63414	-0.00161
Lesser Goldfinch	0.74897	-0.0886
Rosy Thrush-Tanager	0.44143	-0.07084
Orange-billed Sparrow	0.50987	0.05102
Black-striped Sparrow	0.49758	-0.11007

Eastern Meadowlark	0.40489	-0.26547
Red-breasted Blackbird	0.65175	-0.23813
Yellow-billed Cacique	0.67608	-0.11754
Crested Oropendola	0.63439	0.10632
Chestnut-headed Oropendola	-0.01208	0.0006
Montezuma Oropendola	0.86968	-0.03478
Scarlet-rumped Cacique	0.46266	-0.02686
Yellow-rumped Cacique	0.19058	0.12051
Yellow-backed Oriole	0.16822	-0.02706
Yellow-tailed Oriole	0.33301	-0.13431
Shiny Cowbird	0.80982	-0.11782
Bronzed Cowbird	-0.76217	-0.63457
Giant Cowbird	0.4433	-0.11245
Great-tailed Grackle	-0.18883	-0.12453
Buff-rumped Warbler	0.84109	-0.0905
Rufous-capped Warbler	0.51756	-0.19248
Dusky-faced Tanager	0.8691	-0.09558
Red-crowned Ant-Tanager	0.50525	-0.03448
Red-throated Ant-Tanager	0.32894	0.01776
Carmiol's Tanager	0.89559	-0.14349
Blue-black Grosbeak	0	0
Blue-gray Tanager	-0.02407	-0.02069
Palm Tanager	0	0
Golden-hooded Tanager	0.53106	-0.05969
Plain-colored Tanager	0	0
Bay-headed Tanager	0.77592	-0.09646
Saffron Finch	0.61184	-0.11046
Green Honeycreeper	0.47472	-0.02293
Sulphur-rumped Tanager	0.78334	-0.02768
Blue-black Grassquit	0.3509	-0.11235
Gray-headed Tanager	0.32057	-0.00446
White-shouldered Tanager	0.24616	0.03252
Tawny-crested Tanager	0.89559	-0.14349
White-lined Tanager	0.58741	0.0609
Flame-rumped Tanager	0.77788	-0.0758
Crimson-backed Tanager	0.0075	-0.07916
Shining Honeycreeper	0.66981	0.02622
Red-legged Honeycreeper	0.23167	-0.08689
Scarlet-thighed Dacnis	0.61814	-0.16216
Blue Dacnis	0.25429	-0.01576
Bananaquit	0.30813	-0.12598
Yellow-faced Grassquit	0.32153	-0.16238
Thick-billed Seed-Finch	0.4043	-0.07215

Variable Seedeater	0.15156	-0.06174
Slate-colored Seedeater	0.41646	0.01131
Yellow-bellied Seedeater	0.55146	-0.19298
Ruddy-breasted Seedeater	0.7228	-0.09401
Black-headed Saltator	0.86968	-0.03478
Buff-throated Saltator	0.49083	-0.0046
Slate-colored Grosbeak	0.6127	0.07063
Streaked Saltator	0.16468	-0.04784

Table D.4. NMDS ordination axes scores based on Sorensen distances between 24 Canal zone subregions.

Site	**Axis 1**	**Axis 2**
FAR	-1.513	-0.242
SIL	-1.728	0.749
ROD	-1.242	0.772
VER	-0.021	0.090
ARJ	0.137	0.326
EMP	0.554	0.476
CLA	0.309	0.259
MAN	0.466	0.453
PTY	-1.928	-1.190
ANC	-1.895	0.304
LASC	0.404	-0.079
SSOB	0.606	0.010
NSO_S	0.567	-0.080
NSO_M	0.796	-0.079
NSO_N	0.967	-0.164
PENIN	0.347	0.096
GIG	0.440	0.244
SLO	0.770	-0.149
AN	0.950	-0.118
AS	0.790	0.048
GAL	0.129	-0.339
CRIS	0.236	-0.448
CAT	0.091	-0.484
PRO	-0.229	-0.456

Table D.5. All R^2, and Kendall (tau) correlation coefficients between environmental variables and average axis scores from 999 two-dimensional NMDS configurations of rarefied, equal-richness sampling units in species space. For definitions of environmental variables, see Table D.1.

	Axis 1		**Axis 2**	
Variable	**R^2**	**tau**	**R^2**	**tau**
AGE	0.598	0.651	0.045	0.164
AREA	0.097	0.29	0.025	-0.058
DEG_FRAG	0.484	0.61	0.002	-0.129
DIST_TOWN	0.241	0.387	0.253	0.343
PCT_AG	0.224	-0.371	0.106	0.247
PCT_FOREST	0.655	0.645	0.001	-0.08
PCT_URBAN	0.495	-0.688	0.079	-0.115

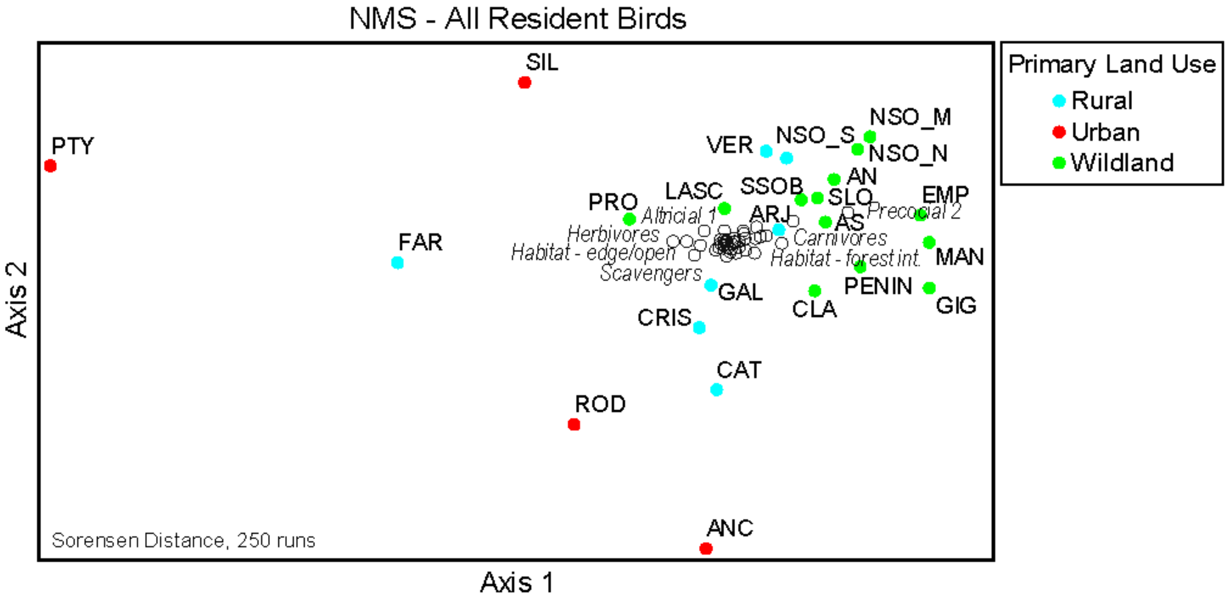

Figure D.1 NMDS ordination of forest patch sampling units in trait space. Subregions indicated by abbreviations, with colored dots corresponding to group membership based on percent urban cover. Avian species traits represented by hollow black circles. Select traits with the highest and lowest Axis 1 scores labeled with italic text, see Table D.2 for full trait definitions.

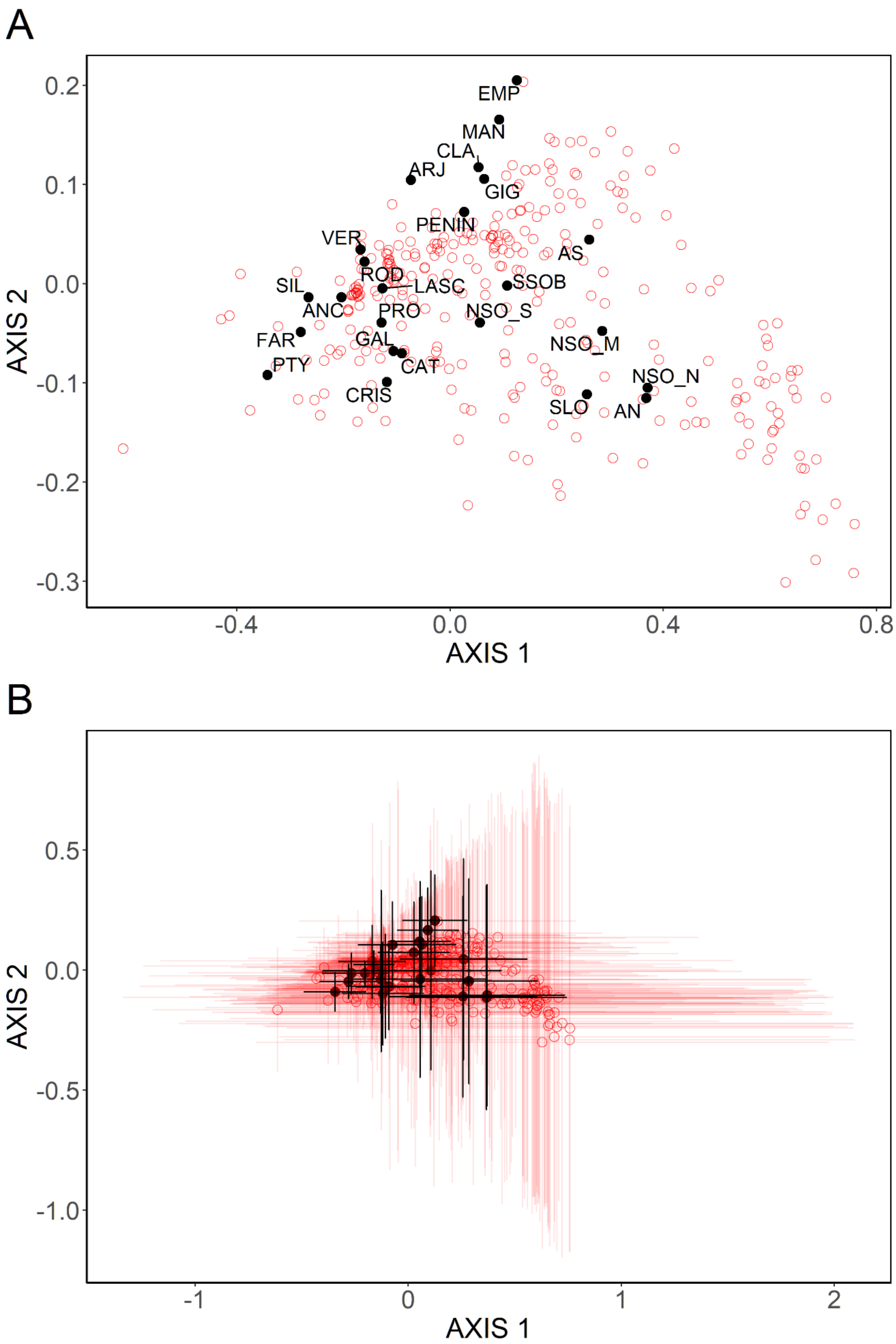

Figure D.2. Results from 999 NMDS ordinations of rarefied, equal-richness subregions in species space with Procrustes superimposition to maximize congruence with the ordination of the full dataset (Figure

4.2). A) mean axes scores across all runs. Subregions are indicated by filled black circles and abbreviated names. Hollow red circles denote individual bird species. B) As before, mean axes scores are denoted by black circles for subregions and hollow red circles for species. Horizontal and vertical lines extending from circles indicate the 95% confidence interval for subregion and species scores on Axis 1 and 2, respectively. Subregion names removed to enhance interpretability. Subregions and species are placed identically to Figure D.2A.