ABSTRACT

BATTLE, KATHRYN EMILY. The Use of Occupancy Modeling to Uncover Species-Habitat Relationships and the Biodiversity Drivers of a Focal Avian Community in the Forests and Coffee Agroecosystems of Puerto Rico. (Under the direction of Drs. Krishna Pacifici and Jaime Collazo).

Conservation practitioners must exercise judicious means to prudently manage ecological risk and uncertainty while advancing conservation objectives. Therefore, many have embraced Structured Decision-Making to clarify such thorny dilemmas and have elected to safeguard biological diversity as the ultimate insurance policy against unknown ecological degradation. While protecting biodiversity is arguably the most important conservation objective worldwide, little consensus exists regarding how best to define, categorize, and measure biodiversity. This ambiguity means that the manner in which we capture biodiversity may ultimately bias habitat management for biodiversity’s sake. Not only does our choice of biodiversity metric affect the soundness of scientifically-based conservation, but also our approach to modeling ecological data can alter the statistical surety which we lend to one habitat management alternative over another. And, while conservation practitioners espouse the importance of landscape-level and community-wide management, such grand endeavors must not eclipse the finer details of ecological systems. Responsible conservation decision-makers must therefore beware of the inevitable biases associated with conducting ecological research in order to make more informed and more robust habitat management decisions.

Conservation practitioners require greater resolution as to which habitat features truly affect biodiversity and the biases which different biodiversity metrics may introduce. I therefore investigated how two different metrics on species-level avian biodiversity (species richness and taxonomic quadratic entropy index of diversity, QEID) respond to features of the
local habitat and the surrounding landscape in the subtropical forests and coffee agroecosystems of Puerto Rico’s Cordillera Central. I first built a hierarchical community-level occupancy model on 27 bird species across 120 sampling sites, with five habitat features (ground cover, understory density, bird-friendly trees, canopy cover, and forested area in the surrounding landscape) as covariates on species-specific occupancy probabilities. Next, I designated ‘hot’ and ‘cold’ spots of avian biodiversity according to both the metrics we employed. I then compared the habitats of these hot and cold spots. I found that canopy cover, forested area in the surrounding landscape, and richness of bird-friendly trees significantly differed between either metric’s hot and cold spots. My data also suggested that ground cover differed between hot spots across the two biodiversity metric. From my research I distilled three caveats regarding habitat management for avian biodiversity: (1) Fine-scale habitat features, rather than generalized habitat types, distinguish hot from cold spots of biodiversity; (2) Managing the habitat to conserve biodiversity requires not just working at finer scales but also across multiple habitat features at those finer scales; (3) The biodiversity metric chosen to capture biodiversity patterns can determine the specific criteria stipulated for habitat management.

Not only how we measure biodiversity but also how we categorize it may affect conservation actions. Biodiverse communities are often subdivided according to various grouping schemes in order to permit an understanding of how not only entire communities but also individual species interact with their environments. However, the way in which an ecological community is subdivided may influence which habitat features are deemed important for conserving each group delineated. In my second chapter, I present the development and application of a novel grouping method and contrast it against two existing
grouping schemes to a focal avian community inhabiting the forests and coffee agroecosystems of Puerto Rico’s Cordillera Central region. I compare how each grouping scheme suggests different habitat features to determine species occupancy and how these determinations compare to results of community-wide occupancy analyses. I also investigate certain species of particular concern whose management may be especially sensitive to the application of various grouping schemes. I found that subdividing a greater community of birds suggests different habitat features to be important for promoting or restricting avian occupancy than when the entire community is considered as a single entity. My results revealed that data-rich ecological subgroups may be responsible for driving the relationships observed between certain habitat features and occupancy at the community level. I also reveal how the application of various grouping schemes can affect certain species of particular concern in terms of the subsequent management actions that would be derived from using different approaches to group-level occupancy modeling. My research demonstrates how different approaches to grouping an ecological community can lead to more tailored inspections of species-habitat relationships but that the application of grouping schemes, particularly a priori ones, invokes ecological assumptions that carry high risks, especially for certain, unique species.
The Use of Occupancy Modeling to Uncover Species-Habitat Relationships and the Biodiversity Drivers of a Focal Avian Community in the Forests and Coffee Agroecosystems of Puerto Rico

by
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A thesis submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the Degree of Master of Science

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DEDICATION

This thesis is especially dedicated *in memoriam* to my mother, Debra Jean Woodward Battle, who nurtured my innate fascination with the living and natural world, who relentlessly encouraged my pursuit of education—both within and beyond the classroom—and who also taught me that all life is precious and just how precious life truly is.

This thesis is also whole-heartedly dedicated to my family and my dear friends, whose support enabled my academic success and whose love cultivated my personal development, through thick and thin. Among those special people to whom I dedicate this thesis, I would like to specifically mention and honor my father, William Olsen Battle, for all his steadfast support, his unwavering dedication, and his love for me and my journey while I grew from childhood into adulthood. Despite this, Dad, I will always be your Little Bug.

I also wish to recognize my sister, Rebecca Elizabeth Battle, who has helped shoulder my set-backs and celebrate my successes. Finally, I wish to also dedicate this work to my Uncle Mike and Mari, who always have my best interest in their hearts and who readily sacrifice their convenience for my benefit (and who knew I would end up working in a jungle!). I love you all dearly and am forever grateful for your love.
Kathryn Emily Battle was born and raised in Henrico County just outside of Richmond, Virginia. She attended Virginia Polytechnic Institute and State University (Virginia Tech) from August 2010 until May 2014, at which time she graduated summa cum laude with her Bachelor of Science in Wildlife Science with a concentration in forestry. During her time at Virginia Tech, Kathryn expanded her passion for wildlife through intense scientific study and the conduction of both biological and ecological research relevant to wildlife conservation.

In particular, her study abroad to Ecuador under the direction of Drs. Ignacio T. Moore and William K. Hopkins stoked her interest in the challenges and opportunities of tropical conservation. These experiences inspired her to continue her education onto the graduate level, eagerly accepting her position as Graduate Research Assistant in the Department of Applied Ecology and the North Carolina Fish and Wildlife Cooperative Research Unit at North Carolina State University in August 2014. She has greatly appreciated her time spent in both Raleigh and Puerto Rico and will remain eternally grateful for the chance to not only contribute to but immerse herself in tropical ecology and conservation.
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LIST OF ABBREVIATIONS

QEID: Quadratic Entropy Index of Diversity
LFGN: Large Frugivores, Granivores, and Nectarivores
LIC: Large Insectivores and Carnivores
SFGN: Small Frugivores, Granivores, and Nectarivores
SIC: Small Insectivores and Carnivores
C1: Cluster 1 of the clusters delineated according to the \( K \)-means cluster analysis across a suite of five natural history traits on the greater avian community of 27 species
C2: Cluster 2 of the clusters delineated according to the \( K \)-means cluster analysis across a suite of five natural history traits on the greater avian community of 27 species
C3: Cluster 3 of the clusters delineated according to the \( K \)-means cluster analysis across a suite of five natural history traits on the greater avian community of 27 species
C4: Cluster 4 of the clusters delineated according to the \( K \)-means cluster analysis across a suite of five natural history traits on the greater avian community of 27 species
DD1: Data-driven group 1, created by Bayesian clustering techniques
DD2: Data-driven group 2, created by Bayesian clustering techniques
DD3: Data-driven group 3, created by Bayesian clustering techniques
DD4: Data-driven group 4, created by Bayesian clustering techniques
DD5: Data-driven group 5, created by Bayesian clustering techniques
In response to the multitude and complexity of threats against the integrity of the natural world, the field of Conservation Biology arose and has since gained special prominence. Rooted in both the natural and social sciences, Conservation Biology seeks to protect species, their habitats, and their greater ecosystems from the degradation and destruction often enacted by anthropocentric development. Early biological and ecological theories shaped the core of Conservation Biology. In particular, Island Biogeography provided the theoretical framework guiding the early applications of conservation efforts through the designation of reserves and protected areas. However, more recent advances in understanding the interplay between human and natural systems have suggested that protection in isolation is doomed to fail.

As Conservation Biology further developed, other theories and schools of thought continued to mold it. One such important influence was the theory of metapopulation dynamics. The discipline of metapopulation biology brought to light the importance of ensuring the regional persistence of a species despite the instability of local populations (Hanski 1998). One step further, metapopulation ecology, a hybridization of landscape ecology and metapopulation dynamics, professes that suitable or even preferable habitat for the species in question exists as discretized patches interspersed within the inhospitable matrix of a given environment (Hanski 1998). Most importantly, the size and degree of isolation of a given
habitat patch predicted the value of that patch for harboring species. This distinction between a suitable habitat ‘patch’ and an unsuitable ‘matrix’ motivated much of Conservation Biology to not only protect remnant habitat but also ensure connectivity between patches in the face of habitat loss and fragmentation (Fahrig and Merriam 1994, Fahrig 2003). These directions also challenged Conservation Biology to consider the effect of habitat across multiple spatial scales. Ecological considerations beyond the patch then encouraged Conservation Biology to embrace principles of Landscape Ecology to better examine how the composition and structure of the surrounding landscape influenced the quality of the matrix, the ability to migrate between patches, the quality and suitability of within-patch habitat itself, and, ultimately, the local biodiversity (Schindler et al. 2008) and ecological processes (Kupfer 2012) yielded from landscape characteristics. More recently, however, the fundamental principles of habitat patch size and isolation have come under scrutiny with the habitat amount hypothesis (Fahrig 2013) underwriting the need to consider these and other cumbersome variables such as spatial scale or habitat configuration.

Not only has Conservation Biology grown to adopt a landscape-level perspective but also a more holistic, ecosystem-wide approach to conservation. This expansion has elevated concerns over large-scale and long-term concepts--such as ecological integrity and evolutionary potential--and has risen with the establishment of Evolutionary Ecology (Stockwell et al. 2003). While the newest fashions in ecological theory continue to shape the development of Conservation Biology, the field has remained true to its core principles of preventing the loss of biological diversity and the erosion of ecological systems (Soulé 1985). With this bedrock, the pursuits of conservationists resonate clearly with the principles of sustainability in the modern age.
A unique aspect of Conservation Biology distinguishing it from other sciences is its active participation in and response to social and political dynamics (Guerry et al. 2015), a necessary ingredient to sustainability. Because natural resources are intimately connected to economic systems and social norms (Rands et al. 2010), conservation efforts must not only exercise the biological and ecological sciences but also practice them in tandem with human values systems (Kareiva and Marvier 2012, Skandrani 2016, but see Soulé 2013). The efforts of Conservation Biology have many success stories to regale. Nevertheless, the field of Conservation Biology cannot rest on its laurels, especially since biodiversity has continued to decline despite this call-to-arms to protect it (Rands et al. 2010).

Today, Conservation Biology is adapting to new and more complicated challenges related to the sustainable development and management of natural resources in the wake of surmounting anthropogenic pressures. Indeed, the impact of mankind has become so pronounced that many scholars label this geological era the Anthropocene (Steffen et al. 2011). The predicaments inflicted on the natural world are quite staggering. However, the exact consequences of these anthropogenic impacts is known less certainly, obfuscating the desirable course of action to ameliorate such impacts. In order to respond to these immense challenges, conservation practitioners require reliable scientific evidence and a logical process that will allow deliberating among competing values while effectively managing risk. Doing so, however, requires that the science informing conservation decisions be applied in a systematic and structured manner. By disengaging competing interests and by embracing uncertainty which would otherwise stall action, structured decision-making (SDM) offers a robust methodology for crafting sustainable solutions to conservation crises (Moore and Runge 2012).
SDM has become a common and favored tool among natural resource managers and serves as a blueprint for strategizing conservation plans. Some notable applications of this process for the sake of conservation include decisions to perform supplemental feeding to restored populations (Chauvenet et al. 2012), the management of invasive and non-native species (Liu et al. 2011, 2012), and, more generally, the identification of thresholds regarding values that impact decision outcomes (Martin et al. 2011). The process is highly regarded among governmental agencies responsible for conserving and managing natural resources as evidenced by the United States Fish and Wildlife Service (USFWS) applying SDM across a variety of taxa and habitats. But, the use of SDM for bird conservation has been especially popular. Because conservationists operate in a world of constraints, precious resources must be directed where there is either the greatest necessity or the best promise for efficacy. However, an assortment of nuances exist in the prioritization schemes enacted by various conservationists (Brooks et al. 2006). Nevertheless, a unifying theme has emerged in modern Conservation Biology: Ensuring the persistence of biological diversity.

Biodiversity

To appreciate the term biological diversity, one must recognize the breadth and depth which it is meant to capture (Purvis and Hector 2000). The term “biodiversity,” an amalgamation of “biological diversity” was first coined by Thomas Lovejoy in his forward to Michael Soulé’s book Conservation Biology. The broad, holistic term was meant to succinctly refer to the collective diversity of all living things. And so, biodiversity is generally defined as the variety and variability of all life on Earth.
For many reasons, protecting biodiversity is consistently highlighted as a conservation priority (Sarkar 2002). In fact, more recent opinions on conservation resonate previous conjectures that the diversity of the collective community, rather than any one particular species, should be the target of conservation (Noss 1990, Dunstan et al. 2011). In light of the constraints placed on conservation efforts and given the ultimate causes of the most pressing conservation crises, it is no surprise that biodiversity has gained such prominence. Despite its critical role in conservation, little consensus has been achieved regarding how best to quantify biological diversity (Purvis and Hector 2000, Sarkar 2002, Hamilton 2005, Sanjit and Bhatt 2005, Morris et al. 2014).

That biodiversity has remained elusive may be attributable to its patterns being ‘non-concepts’ (Hurlbert 1971). Nevertheless, this has not curtailed the development, adoption, and refinement of many various diversity measures (see Delong 1996). Unfortunately, however, this wealth of indices, models, and other such metrics coupled with a dearth of standardization has compromised the utility of diversity ‘rules-of-thumb’ for conservation planning, prioritization, and decision-making (Hamilton 2005), especially in unique or complex ecosystems (Fariña et al. 2009) such as the Neotropics. Additionally, the proliferation of diversity indices has engendered a suite of conflated jargon among ecologists and conservation practitioners (Hamilton 2005). However, the perspective adopted and the metric used to gauge biodiversity can have a profound effect on assessing the conservation value of a given environment. Therefore, an unfocused approach to defining and interpreting ‘biodiversity’ severely hinders conservation planning and policy-making (Moonen and Barberi 2008, Pereira et al. 2013).
The species-level of biodiversity is a particularly well-studied facet of biodiversity (Noss 1990, Heip et al. 1998). Given the alarming rates of species extinctions, preventing extinction and endangerment of species has become a central theme of conservation in the twenty-first century. Therefore, species-level diversity patterns greatly influence conservation by guiding objectives and by serving as evaluation criteria. But this sort of diversity is just one facet of the greater arc of ‘biodiversity,’ which spans all biotic variation across all levels of biological organization, from the genome to the ecosystem (Mouillot and Leprêtre 1999, Purvis and Hector 2000, Pavoine and Bonsall 2011). Arguably, this level has received disproportion attention in guiding the measurement, interpretation, and conservation of biodiversity.

Canonical metrics of biodiversity also reinforce the emphasis placed on species-level biodiversity (Heip et al. 1998, Hamilton 2005). Most simply, the metric of species richness captures biodiversity at its most favored level by tallying the number of unique species represented. Historically, assessments of species-level diversity (species diversity) interpreted the concept as an emergent property of ecological communities, dependent upon not only the number of unique species in the community (‘species richness’) but also the proportional membership of each species present (‘species evenness’) (Heip et al. 1998). The earliest species diversity measures in ecology borrowed from information theory and ascribed different relative weights to species richness and species evenness, with weightings chosen rather subjectively (Hamilton 2005). Among the most popular of these early diversity indices were the Shanon-Wiener Diversity Index (cite Shanon 1948), $H$, and Simpson’s Index of Diversity (cite Simpson 1949), $1-D$. And, indeed, these indices have remained pervasive in both basic and applied ecology. Originally developed to compute grammatical and terminological diversity of manuscripts, the Shanon-Wiener, or Shanon-Weaver, Diversity Index explores the
degree of order or disorder in a given system—such as an ecological community—by summarizing across the proportional contribution of each component—such as a species—in that system. By the nature of its mathematical construct, Shanon-Wiener Diversity Index has no maximum value and this limitlessness hinders interpretation. Additionally, while $H$ tangentially relates to concepts of species evenness it does not outright incorporate this metric. In contrast, the concept of species evenness or equitability is inextricable from Simpson’s Diversity ($D$) since for any given value of species richness, $D$ will decrease as the proportions of those species become more even or equitable. Though subjectivity of these foundational indices permitted ecological theory to explore different perspectives on species diversity, it also dissolved standardization, ultimately compromising their utility and the utility of subsequent diversity indices.

As the importance of hierarchical structuring of ecosystems and spatial scaling of ecological phenomena gained traction, species diversity indices were partitioned across spatial scales or extents. Species diversity was then interpreted either at the microhabitat- or landscape-level (‘point diversity’ and ‘gamma diversity,’ respectively) with the latter metric determined by the mean species diversity among sites within each homogenous habitat (‘alpha diversity’) and the differentiation between each of those sites’ diversity (‘beta diversity’) (Whittaker 1960, 1972). Finally, scaling up to the regional level, the collection of gamma diversity across expansive biogeographic regions defined the regional or ‘epsilon’ diversity (Whittaker 1972). In some realms, these nested measures of diversity became known as inventory diversity when calculated for each predefined scale (Hamilton 2005). Though Whittaker’s contributions did reflect an important paradigm shift in ecological thought from isolated habitat patches to interconnected and hierarchical ecosystems, the Russian dolls of his
inventory diversity proved too cumbersome in application and, for most practical conservation matters, beta diversity gained particular favor.

Though biodiversity encompasses much more than species-level diversity, this level of biological organization has historically received the greatest attention in both the development of ecological theory and conservation planning. This focus on the species level is not necessarily undesirable, however, since it imparts practicality to an otherwise overwhelming breadth of biodiversity: As Sarkar (2002) explains, defining ‘biodiversity’ is facilitated by understanding which biological entities we can readily and accurately measure. In the case of conservation biology, these entities are most often the species themselves. But while popularized diversity indices provided convenient estimates of the types and relative frequencies of species, these metrics still offered only cursory snapshots of species-level diversity (Hamilton 2005) which either heavily discounted or completely disregarded the evolutionary and ecological variation among species. Recognizing these undesirable consequences of such perfunctory measures, modern ecology has experimented with other diversity indices of varying complexity or elegance. In particular, more modern diversity indices seek to incorporate measures of distinctiveness (Leinster and Cobbold 2012)—be they phylogenetic (Faith and Baker 2006, Morlon et al. 2011), functional (Mouillot et al. 2004, Clough et al. 2009, Conole and Kirkpatrick 2011), or taxonomic (Bertrand et al. 2006, Cassey et al. 2007) —among the species members of a community. Instead of aggregating by ecological traits or evolutionary designations, some researchers aggregate species by their morphological and physiological traits in order to interpret species turn-over in ecological communities caused by intra-specific variation in responses to environmental gradients (Crooks et al. 2001, Lepš et al. 2011). Most notably, the
Quadratic Entropy Index of Diversity (QEID) developed by Izsák and Papp (2000) as an extension of work by (Rao 1982), presents a flexible framework to encapsulate both species richness and differentiation among species in order to holistically evaluate biodiversity at the species level. Most recently, as international diplomacy has targeted the deceleration of biodiversity loss, newer indices have arisen to assess the efficacy of global biodiversity conservation schemes. Two popular indices on this front, the Biodiversity Intactness Index (Scholes and Biggs 2005) and the Biodiversity Representativeness Index (Faith et al. 2008) incorporate known data and expert opinion on species diversity, genetic diversity, and range-abundance curves to equip conservationists with more holistic indices that remain robust across ecologically diverse regions. Despite the myopic, species-centric attention heeded to biodiversity, newer perspectives on understanding and protecting biodiversity adopted from modern evolutionary ecology are finally entering the conservation ethos.

Avian Biodiversity

Among terrestrial vertebrate fauna, birds are the best-studied and their diversification the most prolific. Comprising almost 10,000 species, birds vary greatly in their biology and ecology. Owing to their evolutionary radiation in behaviors, life histories, adaptations, and niches filled, birds have colonized almost every land mass on Earth, with only the most inhospitable places failing to grant birds permanent residency. Despite their being conspicuous and well-studied, new avian species continue to be discovered and their ecology more deeply appreciated. Because of their extensive phylogenetic and taxonomic diversity in addition to the many natural and life history traits of different species, birds are a useful taxa for conservation
planning and prioritization (de Wan et al. 2009), suggesting where terrestrial biodiversity is distributed and concentrated.

Avifauna further serve conservation purposes by acting as biological indicators of environmental change and habitat degradation in managed landscapes (Hansen and Urban 1992, Marzluff and Ewing 2001, Wilson et al. 2010). Being volant and therefore highly mobile, birds can more readily escape unsuitable habitat. This feature makes birds very responsive to landscape heterogeneity (Morelli et al. 2013) and therefore regarded as biological indicators of landscape-level change, too. Finally, the protection of a diverse avian community engenders many other gains for conservation efforts owing to the various ecosystem services which birds perform (Whelan et al. 2008, Philpott et al. 2009). These services prove especially valuable in agricultural settings (Sekercioglu 2012).

The number of bird species and the variety of avian life history traits can vary greatly across the globe. In tropical and subtropical regions of the world, however, avian biodiversity is especially pronounced. Biogeographically, tropical and subtropical regions not only host greater numbers of bird species but their avian inhabitants typically occupy smaller ranges and are more likely to be endemic to those regions. In fact, over 2600 birds are considered Restricted-Range Species, with many of these particular species occupying important Endemic Bird Areas. These Endemic Bird Areas cover only 5% of the Earth’s total land surface and are mostly concentrated in the tropics and subtropics. Additionally, tropical avian ecology has unique characteristics, indicating the existence of unique life history strategies and ecological-evolutionary pressures critical to holistic biodiversity conservation.

To better protect avian biodiversity, we must better conserve the habitats and ecosystem processes on which the birds depend. Because of the dynamics and complexity of tropical and
subtropical ecosystems, the use of proxies as environmental covariates is common. For example, habitats receiving high rainfall tend to support more species-rich communities of avifauna than do xeric habitats. Owing to the high seasonal and annual variation in rainfall, however, other more precise data correlated to rainfall or other climatological aspects of interest can allude to their effects. Data such as latitude and longitude are often correlated to climate and weather patterns and so are two common data proxies in ecological studies. Additionally, species richness patterns can vary with elevation, especially in subtropical and tropical regions. For birds, species numbers tend to maximize at mid-level elevations. Biodiversity further changes in accordance with elevation since high-elevation sites, particularly isolated ones such as individual mountain ranges, are more likely to host endemic or habitat-specializing species.

Understanding species-habitat relationships is a fundamental pursuit of all ecology. But because birds prove so valuable to holistic ecosystem management, understanding which habitat features maximize avian biodiversity is especially critical to conservation planning. However, disentangling these species-habitat relationships proves difficult as different habitat features may only take effect seasonally and may likely have complex dynamics or interactions with other biotic and abiotic features of the environment. Additionally, the spatial extent or scale at which a given habitat feature manifests itself can profoundly affect the ecological phenomena of interest (Levin 1992). Therefore, spatial considerations are omnipresent in ecological studies. Most simply, a given environment can be spatially structured at both its local and landscape scales. While this dichotomy may prove an oversimplification in some regards, it does provide an approachable starting point from which to interpret habitat-species relationships, particularly for highly mobile species like birds.
In general, the local habitat may be defined as the area in which a given species spends the majority of its time or which is readily available to that species (see Northrup et al. 2013). More precisely, this definition of the local habitat may be further delineated by distinguishing between micro- and macrohabitat. Features of the local habitat significant to avian communities, however, are often more directly associated with the macrohabitat since birds are neither especially minute nor very low on the food chain.

Understanding the contribution of the landscape context on ecological phenomena has given rise to an entire field known as Landscape Ecology. While grasping the complexities and nuances of Landscape Ecology are beyond the scope of this review, it is important to note some theories from this field are pertinent not only to Conservation Biology but also avian ecology. In particular, the Fragmentation Hypothesis (Fahrig and Merriam 1994, Fahrig 2003) and the Habitat Patch/Matrix Dichotomies (Ricketts 2001, Watling et al. 2011, Ye et al. 2012, da Silva et al. 2015) are germane to landscape-level conservation.

Because so many bird species of concern in both the tropics and subtropics are forest-dwelling habitat specialists, and because forests in these zones are experiencing rapid degradation, the amount of remaining forest in a landscape can predict the diversity of the bird community within a particular habitat patch (Gascon et al. 1999). This landscape-level influence on intra-patch avian ecology is especially noted in agroecosystems (Sisk et al. 1997, Leyequién et al. 2010). Additionally, the proximity of an agroecosystem to an actual forest can mediate the biodiversity potential realized within that agroecosystem (Anand et al. 2008)
Grouping Species

While ecosystem-wide and landscape-level efforts of modern conservation biology strive to leave no species behind and no ecological process forgotten, the grand scale of this endeavor can inadvertently profess a one-size-fits-all attitude to conservation. Indeed, according to Blaum et al. (2011), “Developing management strategies for biodiversity conservation…is practically impossible using single-species approaches.” Recognizing the fallacy of the single-species approach, the grouping together of species into homogenous clusters offers an enticing avenue for crafting conservation strategies which not only think big-picture but also allow for more fine-tuned control of ecological nuances (Carvajal-Cogollo 2015).

Ultimately, the goal for grouping together species is to create distinct, homogenous assemblages comprised of species who interact with and respond to their environment in a similar manner and so would likewise react similarly to habitat management. The motivations behind grouping species can be varied, with both ecological and practical reasons setting the criteria. Ecologically speaking, species groups may be delineated so as to ensure certain niches or functional roles are fulfilled. This motivation can have direct consequences on ecosystem integrity, community dynamics, and the performance of ecosystem services. Or, an ecologically-based grouping may be delimited in order to draw special attention to protecting unique behaviors or natural and/or life history traits. This approach may again yield the insurance of ecosystem services but can also conserve evolutionary potential by protecting unique lineages, evolutionary histories, or other derived features of interest. Grouping species by life history traits has important consequences for the conservation of biodiversity since these
life histories strongly dictate how individual species and entire communities will likely respond to habitat loss, fragmentation, and other landscape-level changes (Hansen and Urban 1992). Additionally, these life-history traits have evolutionary underpinnings which are important considerations to prudent conservation biology (Stockwell et al. 2003). In general, ecological groupings are constituted either through a resource-centric or functional approach with the former being closely and most commonly associated with the term 'guild' (Verner 1984) and the latter being further subdivided into functional response and functional effect groups (Blondel 2003). While the functional approach to grouping generally examines the species-environment relationships, the functional response approach (see Wilson 1999) emphasizes attributes of how species respond to environmental/habitat conditions whereas the functional effect describes how species influence their environment.

Species groupings may also be specified for practical purposes, with less emphasis on shared biology or ecology. Typically, these practical motivations behind species grouping distinguish between habitat generalists and habitat specialists, natives, non-natives, and endemics, or species of conservation concern (like threatened/endangered statuses) and those not of conservation concern.

In addition to different motivations guiding the distinguishing criteria for assigning species to groups, the act of discriminating such groups can be performed either before or after the collection of system-specific data. Those approaches which determine group categories and assign species in a mutually-exclusive manner to one such category are known as a priori allotments. This strategy employs expert knowledge or other generally-accepted facts on species traits to define and populate ecologically-based groupings within the larger ecological community (see Pacifici et al. 2014). However, a priori, knowledge-based approaches have
the noted drawback of leading to artificial assemblages of syntopic species, which are often taxonomically related. Thus, the grouping together of these syntopic species confounds whether the homogeneity of a given group is due to its common suite of traits or other aspects contingent upon their taxonomic similarity (Blondel 2003, Blaum et al. 2011). In contrast, the sub-setting of a wider community of species into smaller assemblages may be done according to collected data after-the-fact. Such *a posteriori* or data-driven approaches rely on quantitative statistical methods like nearest neighbor statistics, cluster analysis, principle component analysis (PCA), and Monte Carlo techniques.

*A priori* approaches to dividing a broader community of species have predominated much of ecology and conservation. In particular, Guild Theory has strongly influenced the sub-setting of ecological communities into smaller, simpler, and more homogenous groups (Kornan and Kropil 2014). The term 'guild' as originally defined by Root (1967) categorizes species without regard to taxonomic position but instead according to significance of niche overlap, particularly in regards to similar resource usage.

More recently, however, data-driven and other *a posteriori* approaches to grouping ecological communities have gained traction. Most notably, these approaches offer an advantage over their *a priori* counterparts by relying on actual data to offer an even more tailored approach rather than impose group boundaries according to generalized assumptions. One such popular *a posteriori* method uses finite mixture modeling in order to group species according to their relative (dis)similarity in response to various environmental covariates (Dunstan et al. 2011). This novel approach yielded groupings which the researchers referred to as ‘species archetypes’ (Dunstan et al. 2011).
Occupancy Analysis

A fundamental pursuit of all ecological studies is to understand where species occur and the factors which explain their occurrences. Similarly, conservation planning seeks to conserve those habitats or ecosystems which demonstrate features that could or indeed do support those species of interest. Therefore, presence/absence studies offer great insight to answering basic ecological questions and helping guide conservation priorities. An especially useful approach to inferring presence/absence is occupancy analysis (MacKenzie et al. 2002, Efford and Dawson 2012). The mechanics behind occupancy analysis rely on Bayesian statistics and Markov Chain Monte Carlo (MCMC) methods to estimate occupancy probabilities from species detection histories and to determine the likely occupancy state given the occupancy probability.

There are many advantages offered by occupancy analysis over more traditional or classic wildlife survey designs. Most notably, occupancy analyses are extremely convenient and permit the estimation of a detection probability. Therefore, occupancy analyses have proven quite useful to conservation, with many applications for various different research and inference related to conservation planning and decision-making.
Habitat Management and Conservation Planning in Puerto Rico

From a global perspective, the Caribbean consistently ranks as an ecologically important ecoregion (Olson and Dinerstein 1998, Myers et al. 2000, Hoekstra et al. 2005). In particular, the island of Puerto Rico boasts many ecological accolades and is a spot deserving of conservation attention. At a fundamental level, the diversity of habitat types and physiographic regions contained within Puerto Rico provide the canvas upon which all other aspects of the island’s biodiversity appear. Thanks to these environmental dynamics, Puerto Rico is home to diverse communities of native and endemic flora and fauna. In particular, the avian community of Puerto Rico has special merit for conservation efforts on the island (Faaborg et al. 2007, 2013, Latta and Faaborg 2009, Wiley et al. 2014).

Unfortunately, despite all its natural wonders, Puerto Rico has endured a history of environmental destruction and degradation (Brash 1987). Notable land-use changes which altered the ecological dynamics of the island were associated with changes in human demography (César and Bernabe 2007, Curtis and Scarano 2011). These changes in the population size, structure, and geographic distribution of people caused urbanization and urban sprawl to reduce and drastically alter natural, native habitats.

Many major environmental changes to the island’s natural states were also induced by the promotion of agricultural expansion (Bergad 1978, Solá 2011), particularly for coffee culture (Crist 1948). The rise and fall of coffee cultivation in Puerto Rico catalyzed significant social, economic, and ecological changes on the island. However, the revitalization of coffee may allow for more sustainable and eco-friendly practices to take root, in hopes of cultivating ecological and economic rewards from the promotion of coffee agroecosystems.
With increasing anthropogenic pressures on limited amounts of land, modern conservation has adopted a philosophy of promoting multi-purpose lands to sustainably meet the needs and wants of our human population against the wise use and protection of natural resources. One concept of these promising multi-functional lands is that of the agroecosystem, also referred to as agroforests or agro-environmental schemes (Donald and Evans 2006, Moonen and Barberi 2008). In the best of circumstances, agroecosystems offer many potential benefits, such as reduced need for pesticides or other chemical inputs, improved carbon and nitrogen dynamics (Gillis and Price 2016), gains in crop yield and quality (Smith et al. 2008), and increased biological diversity compared to typical agricultural lands. However, much debate surrounds how readily these rewards of agroecosystems can in fact be reaped (Yíridoe and Weersink 1997, Pretty and Bharucha 2014). Nevertheless, agroecosystems are a highly popularized alternative being implemented in tropical and subtropical regions (Mukherji 1983, Miranda-Castro and Padron 2005), which are of interest to global conservation priorities (Brooks et al. 2006)

Puerto Rico contains a great deal of biological and ecological diversity that demands savvier conservation strategies to ensure the existence of such diversity in the face of inevitable yet uncertain land-use changes. Indeed, decades of agricultural development have contributed to the destruction and degradation of habitats in Puerto Rico. (Brash 1987, García-Montiel and Scatena 1994). To ameliorate the ecological consequences of unbridled agricultural and urban expansion, the Puerto Rican Department of Natural and Environmental Resources (PRDRNA) along with the United States Fish and Wildlife Service (USFWS) aim to increase the amount of protected habitat in Puerto Rico from eight to fifteen percent. These natural resource
management agencies are pursuing landscape-level conservation in order to ensure the persistence of key species, functional communities, and biodiversity.

So as to couple ecology and economy, PRDRNA and USFWS are keen to implement conservation action on the island’s remaining agricultural lands. Attempting to reverse the ecological detriments caused by the extensive promotion of sun-grown coffee, USFWS began offering incentivized programs for shade-grown coffee culture in the early 2000s. While much evidence points to the conservation potential of shade-grown coffee and other similar eco-friendly agriculture (Young 2003, Carlo et al. 2004, Miranda-Castro and Padron 2005, Bakermans et al. 2011, Karp et al. 2013), still some evidence refutes those merits, suggesting that the trade-offs of the practice are context-dependent (Clough et al. 2009, Gonthier et al. 2014). If shade-grown coffee proves ecologically valuable, incentivized support for it could revitalize Puerto Rico’s dwindling coffee culture while simultaneously protecting the habitat necessary to conserve biodiversity (Rappole et al. 2003, Young 2003). Thus, the ecological value of shade-grown coffee culture must be more thoroughly assessed to determine how well incentive programs for these and other such agroecosystems might achieve stated conservation goals (Petit and Petit 2003, Komar 2006, Tejeda-Cruz et al. 2010).
My Thesis Research

My thesis research is grounded in avian community ecology, with a focus on better appreciating the inherent biodiversity of native and endemic avifauna in the coffee plantations and forested habitats of central Puerto Rico. My research examines the diversity of these focal avian communities through multiple lenses, using not only different biodiversity metrics but also different approaches to subdividing the greater avian communities. In general, my aim is to understand the environmental features shaping avian species richness and taxonomic diversity while manipulating different ways of applying hierarchical occupancy modeling. More precisely, I explore how alternate biodiversity metrics and different species-grouping approaches influence our interpretation of species-habitat relationships. I pursue this research to understand the nuances of avian biodiversity assessments and monitoring in conservation planning. This work will reveal the relative significance of candidate environmental features at both the localized and landscape-level of the habitat as well as provide both a holistic and tailored perspective on avian community diversity and composition. For this research, I have stipulated two main objectives:

1. **Drivers of Community-wide Biodiversity**

   Describing diversity patterns and inferring the environmental mechanisms responsible for those patterns are central themes in ecology (Levin 1992). However, the manner by which biological diversity is assessed greatly affects our understanding of how the environment shapes communities. For my first research objective, I investigate how environmental features
of both the macrohabitat and the surrounding landscape affect the biological diversity of avian communities. I separately interpret this biological diversity through two perspectives: Taxonomic diversity and species richness.

Through this research, I determine whether the perspective adopted on community-level biodiversity (e.g. taxonomic diversity or species richness) influences which local and which landscape-level environmental features prove germane to biodiversity conservation (Rodewald and Yahner 2001, Steiner and Köhler 2003, Defries et al. 2010). I conduct this research so that the natural resource managers and conservation planning partners on the Puerto Rico project may temper their conservation strategies in light of the consequences of relying on different interpretations of biodiversity. Ultimately, I hope to address the applications and caveats associated with these two metrics so as to better promote more informed conservation goals of biologically diverse avian communities.

2. **Drivers of Group-specific Biodiversity**

For my second thesis objective, I explore how environmental features of interest evident at both the local and landscape levels influence the species richness of particular subsets within our focal avian community. Because species within each subset will automatically be less diverse from one another--either taxonomically, functionally, or otherwise depending on the subset criterion—I will not use any sort of species distinctiveness or diversity metric and will rely on species richness alone to summarize the biodiversity of each subset. To distill these subsets, I impose two *a priori* groupings: The first delineates guilds assigned by both primary diet and relative body mass while the second defines clusters
according to five natural history traits using $K$-means cluster analysis. I also impose a data-driven grouping scheme which delineates groups according to species’ modelled responses in occupancy probability to the local and landscape-level environmental features of interest.
LITERATURE CITED


Abstract

Although protecting biodiversity—the variety and variability of all life—is arguably the most important conservation objective worldwide, little consensus exists regarding how best to define and measure biodiversity. The manner in which we capture biodiversity may ultimately bias habitat management for biodiversity conservation. As such, conservation practitioners require greater resolution as to which habitat features truly affect biodiversity and the biases which different biodiversity metrics may introduce. I therefore investigated how two different metrics on species-level avian biodiversity (species richness and taxonomic quadratic entropy index of diversity, QEID) respond to features of the local habitat and the surrounding landscape in the subtropical forests and coffee agroecosystems of Puerto Rico’s Cordillera Central. I built a hierarchical community-level occupancy model on 27 bird species across 120 sampling sites, with five habitat features (ground cover, understory density, bird-friendly trees, canopy cover, and forested area in the surrounding landscape) as covariates on species-specific occupancy probabilities. I then designated ‘hot’ and ‘cold’ spots of avian biodiversity according to both the metrics we employed. Next, I compared the habitats of these hot and cold spots. I found that canopy cover, forested area in the surrounding landscape, and richness of bird-friendly trees significantly differed between either metric’s hot and cold spots. These data also suggested that ground cover differed between hot spots across the two biodiversity metric. From this research I distilled three caveats regarding habitat management for avian biodiversity: (1) Fine-scale habitat features, rather than generalized habitat types, distinguish
hot from cold spots of biodiversity; (2) Managing the habitat to conserve biodiversity requires not just working at finer scales but also across multiple habitat features at those finer scales; (3) The biodiversity metric chosen to capture biodiversity patterns can determine the specific criteria stipulated for habitat management.

Introduction

Humans have become increasingly more populous across the global and our effects on the environment are more prominent than ever before. Because humans have become the dominant force on landscapes worldwide, some experts have proposed that we operate in a new, human-driven geologic era termed the “Anthropocene” (Crutzen 2002, Zalasiewicz et al. 2011). But while the multitude of these anthropogenic effects presently being exerted on natural systems is palpable, their exact consequences are known less certainly (Steffen et al. 2007). Nevertheless, uncertainty in regards to these and other conservation crises does not dismiss our need for rapid response to mitigate if not reverse their undesirable aftermath.

To serve as insurance against these profound but uncertain repercussions, modern conservation movements have emphasized the protection not just of single species but of an array of biological diversity (Soule 1985, Scholes and Biggs 2005). Biodiversity has many economic and environmental benefits (Pimentel et al. 1997) such as enhanced ecosystem services (Beyanas et al. 2009) and maintenance of genetic diversity on which natural selection may act (Mergeay and Santamaria 2012). Therefore, the importance of ‘biodiversity’ indices to evaluate ecological status and to prioritize conservation objectives has gained significance (Sarkar 2002). However, because of the dynamism and complexity of natural systems,
biodiversity has remained an elusive concept (Mouillot and Leprêtre 1999, Pavoine and Bonsall 2011, Pereira et al. 2013).

Despite its irrefutable importance to conservation, little consensus exists regarding how best to define, measure, and interpret “biodiversity” (Purvis and Hector 2000, Hamilton 2005, Sanjit and Bhatt 2005, Faith et al. 2008, Morris et al. 2014). The term “biodiversity,” an amalgamation of “biological diversity” was first coined by Thomas Lovejoy in his forward to Michael Soulé’s book Conservation Biology (Soulé 1980). The broad, holistic term was meant to succinctly refer to the collective diversity of all living things. And so, biodiversity is generally defined as the variety and variability of all life on Earth. Although this broad concept encompasses all levels of biological organization, for conservation purposes, the species level of biological organization has received disproportionate attention (Noss 1990), and perhaps for good reason (Sarkar 2002), especially given the political practicality of this level. But, even within this single facet of the greater biodiversity concept, there exist many metrics and indices to assess species-level biodiversity (see Delong 1996). While canonical metrics like species richness and species diversity still predominate (Heip et al. 1998), these metrics have been critiqued for offering only cursory snapshots of species-level biodiversity (Hamilton 2005) and for a limited capacity to capture all the elements necessary to conserve the beneficial outcomes of biodiversity (Hector and Bagchi 2007). One such lacking element is the recognition that not all species are created equal (see Schmidtz 1998) but that interspecific differentiation reflects valuable ecological traits and evolutionary lineages (Ashley et al. 2003) associated with the benefits of biodiversity. Subsequently, more modern indices have begun to account for such interspecific differentiation (Leinster and Cobbold 2012), whether that differentiation be functional (Mouillot et al. 2004, Clough et al. 2009, Conole and Kirkpatrick 2011),
phylogenetic (Faith and Baker 2006, Morlon et al. 2011), taxonomic (Cassey et al. 2007), or otherwise. Most notably, the Quadratic Entropy Index of Diversity (QEID) developed by Izsák and Papp (2000) and inspired by Rao (1982) presents a flexible framework to encapsulate both species richness and interspecific differentiation in order to more holistically evaluate species-level biodiversity.

Nevertheless, canonical species richness metrics have remained popular and underpin nine of the most iconic global conservation planning and prioritization schemes of the previous two decades (Brooks et al. 2006). This multitude of schemes as well as the different regions which each of these schemes earmark as conservation priorities demonstrates how an unfocused approach to understanding biodiversity does little more than complicate and compromise the utility of biodiversity metrics (Margules and Pressey 2000, Moonen and Barberi 2008).

While global assessments of biodiversity can be insightful, conservation action is executed at much finer scales, either locally or regionally. Despite our not knowing how best to define and assess biodiversity (Pereira et al. 2013), the Caribbean is often recognized as harboring significant biodiversity (Mittermeir et al. 1997, Olson and Dinerstein 1998, Stattersfield et al. 1998, Myers et al. 2000, Hoekstra et al. 2005). Therefore, conservation anywhere within the Caribbean ecoregion would advance a multitude of global conservation frameworks. However, conservation on the island of Puerto Rico would be especially useful given that its area of protected land is third lowest among its peers and less than half of the average for Latin America and the Caribbean (The World Bank Group 2014). Furthermore, Puerto Rico has many unique ecological accolades, especially endemic avifauna, which, if better protected, would promote biodiversity conservation within this significant ecoregion.
For these reasons, many conservation practitioners from both the public and private sectors in Puerto Rico are cooperating to enhance habitat conservation on the island by means of promoting wise habitat management of forests and coffee agroecosystems.

To better protect species-level avian biodiversity, conservation practitioners require more highly resolved evidence on which features of the habitat affect biodiversity patterns. However, the way in which we define and measure ‘biodiversity’ can color which habitat features we identify to be drivers of these patterns (Heino et al. 2005). This may then bias the conservation actions taken to protect biodiversity, especially in terms of habitat management.

In our study presented here, we investigate how two different metrics of species-level biodiversity (species richness and taxonomic QEID) among a focal suite of avifauna respond to features of the local habitat and the surrounding landscape in the subtropical forests and coffee agroecosystems of Puerto Rico. Broadly, this research presented here investigates how the choice of biodiversity metric may influence habitat management decisions. More specifically, I stipulate four main objectives motivating our research: (1) More rigorously inventory avian biodiversity by accounting for imperfect detection of birds, (2) Identify ‘hot’ and ‘cold’ spots of avian biodiversity according to two distinct metrics (species richness and taxonomic QEID), (3) Identify drivers of avian biodiversity by examining its relationships with generalized habitat type and with more detailed habitat features, and (4) Compare and contrast the drivers of avian biodiversity across metrics’ hot and cold spots.
Methods

The study region was located in the western central portion of the main island of Puerto Rico, covering much of the Cordillera Central. Within this region, I stratified by landuse/landcover to randomly generate sampling sites located within forests and coffee plantations. For coffee plantations, I further delimited between sun- and shade-grown cultivation practices. Although a variety of criteria stipulate the designation of ‘shade-grown’ coffee, our interpretations of the coffee culture practice were based primarily upon the percentage of shade provided to the coffee plants by other non-coffee plants, with the threshold set at 30% to distinguish sun- from shade-grown coffee plantations. At each site, I established a center point of a 50-meter radius circular plot at which to conduct point count surveys of the avian community.

My team and I conducted 2-4 visits to each of our sampling plots. During each visit, we visually and aurally sampled for the presence/absence (detection/nondetection) of all species in the avian community following a standard point count protocol for two independent observers. We began sampling on 24 March 2015 and finished sampling on 02 June 2015 to satisfy assumptions about population closure for later analysis (MacKenzie et al. 2002). All point counts were conducted no earlier than sunrise and no later than 4 hours after sunrise. Point counts lasted for a duration of 10 minutes following a 2-minute acclimation period after both observers arrived at the center point. We focused our analysis to only those species which are native, endemic, or are otherwise of conservation concern. These criteria consolidated our focal community to 27 birds (Appendix 1).
To investigate the relationship between habitat construct and biodiversity patterns, my team and I performed a vegetative survey at each sampling site to collect data on the following habitat features: Percentage ground cover, percentage understory density, percentage canopy cover, and species richness of fruiting, flowering, shade-providing, or other such resource-provisioning trees useful to avifauna (henceforth, bird-friendly tree species richness). For all these features except bird-friendly tree species richness, we collected measurements at four 1-m² quadrats within the greater 50-m radius sampling plot. The first quadrat was centered over the sampling plot’s center point, exactly where we had conducted the point count. We randomly sampled the three remaining quadrats using randomly generated bearings and distances (≤49.5m) from the sampling plot’s center point. Within each of the four 1-m² subplots, we estimated percentage ground cover on a continuous scale (0-100%). Both live vegetation and litter (e.g. dead vegetation, sticks, etc.) were considered as ground cover. Exposed soil and rock or gravel were considered bare ground and so were not included in ground cover estimates. We estimated percentage understory density similarly to the Visual Obstruction or Robel Pole Method (Robel et al. 1970 and see Harmoney et al. 1997) using two opposite perspectives but recording quadrat-specific measures using a grid and on a continuous scale rather than using a demarcated pole and assigning height cover classes. We measured percentage canopy cover using a concave spherical densiometer. Afterwards, I averaged the percentages for ground cover, understory density, and canopy cover measurements across all four quadrats to obtain a single measure for each sampling site.

We estimated bird-friendly tree species richness by counting the number of unique tree species of interest (Appendix 2) encountered throughout the entire 50-m radius circular sampling plot. We selected tree species of interest based upon the following guidelines and...
with the help of a local plant expert (A. Morales): We stipulated that tree species of interest (1) Be native, endemic, or long-since naturalized to Puerto Rico, (2) Occur not uncommonly throughout our study region in the Cordillera Central, and (3) Provide some utility to at least one of the 27 focal avian species, either by providing food or shelter resources. For further details on our selection process and surveying of bird-friendly trees, please see Appendix 3.

Additionally, to investigate how the landscape context may shape biodiversity of bird communities, I collected data on the percent of forest cover in the immediate vicinity of the landscape. I defined this ‘immediate vicinity’ according to evidence from the literature linking daily dispersal distance with birds’ body weights (Sutherland et al. 2000) but balanced this against our study design stipulation that points be no closer than 500m. From this, I defined the immediate vicinity landscape to be 250 meters beyond the extent of the sampling plot. I then used GIS via ArcMap (ESRI 2011) to calculate the forested area within this immediate vicinity landscape. For further details on my calculating the percent forested area in the immediate vicinity landscape, please see Appendix 4.

To estimate birds’ occurrence states in forests and coffee plantations of Puerto Rico, I fit a hierarchical community-level occupancy model (Dorazio et al. 2006) to our survey-specific detection/non-detection (‘presence/absence’) data on each of the 27 species of interest collected across our 120 sampling sites. With these occupancy models, I am ultimately interested in the latent, or unknown and unobservable, occurrence state of each species \((i = 1, 2, \ldots, N)\) at site \(j\), represented by the random variable \(Z_{ij}\). For our model, we assumed the true occupancy state of species \(i\) at site \(j\), \(Z_{ij}\), to be a latent (imperfectly observed) variable such that \(Z_{ij} = 1\) when species \(i\) is present at site \(j\) and \(Z_{ij} = 0\) otherwise. Our modeling framework assumed no false positive detections in our data such that if a species was ever detected at a
site, then it was in fact present at that site. However, our repeated surveying protocol allowed our modeling process to differentiate between non-detection and true absence to account for the possibility of false negative detections.

I modeled both an observation and state process. I modeled the observation process on the detection/non-detection data, $X_{ijk}$, as a Bernoulli random variable where $X_{ijk} = 1$ if the $i^{th}$ species was detected at the $j^{th}$ site during the $k^{th}$ survey to that site. I used this observation process to explore possible survey-level covariates (date of survey and the team conducting the survey) which could influence detection. Since detection probabilities did not vary significantly with date-of-survey, I excluded this from subsequent modeling. However, I retained team-conducting-survey since it improved fit for the observation process. I then modeled the state process using species- and site-specific occurrence models assuming occurrence to be a Bernoulli random variable such that $Z_{ij} \sim Bern(\psi_{ij})$ where $\psi_{ij}$ is the occupancy probability of species $i$ at site $j$.

My occupancy model had a hierarchical structure since the species-level parameters are assumed to be random effects drawn from community-level hyperparameters. The distribution on these hyperparameters is assumed to be Normal and is defined by a mean that represents the community-wide response to a particular covariate and by a standard deviation that represents the variation in species’ responses across the entire community. Because I had no strong evidence from previous data or expert opinion, I used vague priors on the hyperparameters. I ran my model in program OpenBUGS version 3.2.3 rev 1012 through program R (R Core Team 2015). I ran the model for three chains each of 10,000 iterations with the first two thousand of those being discarded as burn-in. On the remaining 8,000 iterations, I thinned by 25.
With that occupancy model fit to our team’s detection/nondetection data, I then calculated biodiversity scores according to the metrics of species richness and taxonomic QEID. To calculate species richness of the avian community at each sampling site, I used the ‘known N’ rather than the ‘unknown N’ (Royle et al. 2007) approach as the summation of the latent occurrence states across all known 27 species. I did not account for any potential correlation between a given species’ detection probability and its occurrence probability. To calculate taxonomic diversity of each of these avian communities sampled within the 120 sites, we borrowed the QEID framework proposed by Izsák and Papp (2000). Generally, QEID is modeled as:

\[ QEI\!D = d_{ii'}p_ip_{i'} \]  
Eqn. 1

Where \( d_{ii'} \) is the ‘distance’ between the \( i^{th} \) and the \( i'^{th} \) species and where both \( p_i \) and \( p_{i'} \) are the probabilities of encountering the \( i^{th} \) and \( i'^{th} \) species, respectively. I stipulated taxonomic differences as the interspecific distance required by the QEID formula. I used site- and species-specific occupancy probabilities (\( \hat{\psi} \)) estimated by the occupancy model instead of traditional probabilities of encounter which fail to adjust for false negative detections. Therefore, my calculation of QEID was:

\[ QEI\!D = d_{ii'}\hat{\psi}_{ij}\hat{\psi}_{i'j} \]  
Eqn. 2

To determine the taxonomic distances among the 27 species in our focal avian community, I assigned taxonomic affiliations at the ranks of Order, Family, Subfamily, Genus, and Species since all higher rank designations are common among all birds. Assignments were made according to Sibley and Monroe (1990) to ensure consistency. Taxonomic distance was
then the sum of the number of unshared taxonomic rank assignments between two unique species (Appendix 5).

For purposes of conservation prioritization, I was not just interested in broad species-habitat relationships, but rather whether certain habitat types or habitat features might indicate that sites would support especially high or especially low biodiversity. Therefore, I delimited those sites scoring in the upper 90th percentile as ‘hot’ spots and those sites scoring in the bottom 10th percentile as ‘cold’ spots. These thresholds were determined \textit{a priori}. I did this for both species richness and taxonomic QEID. I also explored other thresholds delimiting hot and cold spots to determine if results are robust to different designations. I also examined 85th/15th and 80th/20th percentiles defining hot/cold spots.

Results

In total, my team and I surveyed 120 sites throughout our study region in Puerto Rico’s Cordillera Central. Table 1.1 presents summary statistics on the five habitat features of interest for these sites. Of these sites, 79 were located on coffee plantations with 46 being in shade-grown coffee culture and 33 being in sun-grown coffee culture. The remaining 41 sites were located in a forested habitat of some type, predominantly secondary-growth or regenerated forest. We detected a total of 54 unique avian species but narrowed the scope of our analysis and inference to 27 avian species that were year-round residents, native or endemic, and of concern to conservation.

Out of a possible 27 focal species that could be detected at any given site, the minimum species richness estimate according to our occupancy model was 18 (mean = 18.21 ± 2.16)
while the maximum species richness estimate was 27 (mean = 26.59 ± 1.03). Species richness estimates showed extremely little variation among sites (Figure 1.1a) with more than two-thirds of all our sampled sites (84/120, 70%) estimated to contain either 24 or 25 species of interest. Only 6 sites contained the maximum whole-number species richness estimate. According to our *a priori* designation of the upper and lower 10th percentiles defining ‘hot’ and ‘cold’ spots, respectively, we delimited those sites having at least 25 species as species richness hot spots and those sites having no more than 21 species as species richness cold spots.

Among all sites sampled, I estimated taxonomic QEID scores to range from 728 (mean = 728.4 ± 136.8) to 1420 (mean = 1420 ± 176.4) (Figure 1.1b). I found the distribution of taxonomic diversity scores across all 120 sampled sites to be defined by the following quartile boundaries: 1209 (Q1), 1349.5 (median), and 1366.75 (Q3). The distribution of sites’ taxonomic QEID scores is not evenly distributed: Ninety-eight (82%) sites had QEID scores estimated within the range of 1054 – 1404. According to my *a priori* percentile-based designation of ‘hot’ and ‘cold’ spots, cold spots of taxonomic QEID scored between 728.4 and 984.9 while hot spots of taxonomic QEID had scored ranging from 1393 to 1420.

Regardless of whether biodiversity is measured according to either species richness (Figure 1.2a) or taxonomic diversity (Figure 1.2b), trends in estimated biodiversity scores for a given habitat type are similar. I observed sites of forested habitat type to have the greatest range in biodiversity scores, from the very minimum biodiversity score estimated to just shy of the maximum value. And, the interquartile range (IQR) of both species richness and taxonomic QEID scores for forested sites is much broader than the IQRs of either coffee culture. Additionally, for sites of either coffee culture, biodiversity scores according to either
species richness or taxonomic diversity are not only relatively higher than those of forested sites but also are concentrated towards the maximum values observed (Figures 1.2a and 1.2b).

I then examined habitat types associated with the hot and cold spots of biodiversity according to either a species richness or taxonomic diversity perspective on species-level avian biodiversity (Table 1.2). The cold spots of species richness are in fact the same cold spots of taxonomic diversity, except that the exact order of sites by ascending biodiversity score is slightly different across the two metrics. Also, between hot spots according to either species richness or taxonomic diversity, six sites are common across the two biodiversity metrics. The twelve common biodiversity cold spots are all located in forested habitats. Of the twelve species richness hot spots, two are in forested habitat, four are in sun-grown coffee plantations, and six are in shade-grown coffee plantations. Of those twelve hotspots of taxonomic diversity, none are in forested habitats. Instead, all taxonomic diversity hotspots are found in coffee plantations, with eight in shade-grown and 4 in sun-grown coffee plantations.

I found three of the five habitat features to vary significantly between hot and cold spots within a given biodiversity metric. Those habitat features were percent canopy cover (Figure 1.3), bird-friendly tree species (Figure 1.4), and percent forested area in the surrounding landscape (Figure 1.5). Regardless of the biodiversity metric, canopy cover is significantly greater at the common cold spots (mean = 92.04 ± 3.60%) than at the hot spots of either species richness (mean = 26.73 ± 9.60%) or taxonomic QEID (mean = 23.31 ± 4.11%). Similarly, cold spots had significantly more forested area in their immediate landscapes (mean = 57.71 ± 14.08%) than did their hot spot counterparts for either species richness (mean = 24.98 ± 14.34%) or taxonomic QEID (mean = 18.03 ± 11.27%). However, the opposite relationship between hot and cold spots within either biodiversity metric is found in regards to the richness
of bird-friendly trees present at the site: Cold spots of avian biodiversity contain significantly fewer trees species (mean = 5.25 ± 0.84%) than do their respective hot spots for either species richness (mean = 8.17 ± 1.18%) or taxonomic QEID (mean = 8.50 ± 1.01%).

Because the exact same sampling sites constituted the cold spots of either species-level biodiversity metric, I then compared values of habitat features just within hot spots across the two metrics. Of the five habitat features explored, I found only percentage ground cover to differ significantly between hot spots according to the two different perspectives on biodiversity. On average, ground cover at the most species rich sites was 76%, while ground cover at the most taxonomically diverse sites was 54%.

Discussion

Preserving biodiversity is an important goal of conservation planning and prioritization. However, biodiversity’s inherent complexity renders metrics on its components as incomplete snapshots of biodiversity patterns at best and, therefore, less amenable to informed conservation decision-making. In this paper, I applied an occupancy modeling framework to achieve a more rigorous estimation of two distinct species-level biodiversity metrics: Species richness and taxonomic QEID. I did so in order to explore more precisely the drivers of biodiversity in subtropical avian communities and to examine whether the metric used to capture such biodiversity patterns biases the determination of its supposed drivers. More specifically, my research was motivated by the following objectives: (1) Identify ‘hot’ and ‘cold’ spots of species-level biodiversity from both a species richness and taxonomic diversity perspective, (2) Identify habitat associations and habitat features driving species-level
biodiversity, and (3) Compare and contrast drivers across ‘hot’ and ‘cold’ spots and between biodiversity metrics.

From this research, I distilled three important caveats regarding the application of species-level biodiversity metrics for conservation purposes: First, although a global priority, biodiversity conservation must act at much finer and more localized spatial scales. I found that regardless of the perspective taken to measure biodiversity, generalized habitat types failed to provide the necessary resolution to guide habitat management and conservation policy for the benefit of biodiversity. Instead, it is the finer-detailed habitat features driving biodiversity patterns, particularly the distinction of ‘hot’ from ‘cold’ spots.

My second caveat is that biodiversity conservation requires holistic habitat management that targets multiple site-level habitat features. I found values of many site-level habitat features to significantly differ between the cold and hot spots of either biodiversity metric. Therefore, managing the habitat to conserve or, better yet, to enhance biodiversity requires not just working at finer scales but also across multiple habitat features at those finer scales.

Finally, the biodiversity metric chosen to capture biodiversity patterns may still determine the specific criteria stipulated for habitat management and conservation decision-making. Despite equivalencies in comparing habitat features between hot and cold spots across the two metrics, the average habitat feature values found at species richness hotspots did differ from those found at taxonomic diversity hotspots. While not statistically significant, these differences could begin to bias conservation efforts towards favoring species-rich communities at the expense of more taxonomically uniform communities, or vice versa.
These data demonstrate that generalized habitat types (forest, sun- and shade-grown coffee) provide little predictive power for estimating biodiversity potential at a site. Besides coffee plantations of either culture having higher and less variable biodiversity scores than forests, I observed no conclusive evidence or clear pattern of how biodiversity changes according to generalized habitat type. Furthermore, I observed similar relative biodiversity scores between habitat types, regardless of biodiversity metric.

Surprisingly, I did observe forested sites tend to have the lowest biodiversity scores from both a species richness and taxonomic diversity perspective on biodiversity. This result contradicts a large body of literature touting forests in landscape matrices as critical refugia for many native and endemic species in the face of agricultural development (Antongiovanni and Metzger 2005, Donald and Evans 2006, Tejeda-Cruz et al. 2010), as well as other research demonstrating the significance of protecting remnant forests for species persistence (Beier et al. 2002, Ruiz-Gutiérrez et al. 2010), especially in agricultural landscapes (Sekercioglu 2012, Karp et al. 2013, Muhamad et al. 2013). However, it is important to consider that the forests in which my team and I sampled were secondary-growth, many of which had only recently regenerated within the past few decades (Ruiz and Lugo 2012). This regeneration process can have a profound and lasting effect on species assemblage in tropical and subtropical forests: Catterall et al. (2012) estimated that no sooner than 150 years following reforestation would tropical rainforests achieve avian species richness comparable to pre-deforestation levels and that endemic birds would still be half as likely to occupy these reforested sites as would their non-endemic forest-dependent counterparts. Future work should examine a more long-term data set on these communities in order to more accurately estimate site-level colonization and
extinction rates. Still, my results suggest that some forests are more biodiverse than others and that simply being a forest does not guarantee high biodiversity.

Additionally, forested sites not only tended to harbor less biodiverse bird communities but also were much more variable in biodiversity scores. This great degree of variability in expected biodiversity of bird communities in forests further compromises the assumption that forests can serve as biodiversity safekeeping. More generally, this variation may suggest that biodiversity within forested sites is more context-dependent (Gascon et al. 1999) than biodiversity in other habitats like coffee agroecosystems. Future work should examine how the landscape context mediates biodiversity in regenerated and regenerating forests, especially in extremely heterogeneous landscapes like those found in Puerto Rico.

On the other hand, sites within coffee plantations of either cultivation technique (sun- or shade-grown) had significantly higher and less variable biodiversity scores. Superficially, this result seems to suggest that both sun- and shade-grown coffee plantations in Puerto Rico’s Cordillera Central serve as viable agroecosystems, at least in terms of bird conservation. However, considering the variation in site-level habitat features within and between the two coffee cultures, we interpret these results as strong evidence refuting the validity of using a general cultivation technique as a reliable proxy for vertebrate biodiversity (Tejeda-Cruz et al. 2010), especially for ecological communities comprised of habitat generalists. Similarly, bird communities within sun-grown coffee plantations may have comparable biodiversity to those within shade-grown coffee plantations given that not only were they equivalent in species richness of natives, endemics, and other birds of conservation concern but were also comparable in taxonomic diversity.
Habitat heterogeneity is the ultimate source of vertebrate biodiversity. Using highly summarized classifications of habitat types, although convenient, does not provide the resolution necessary to distill the more intricate species-habitat relationships fundamental to biodiversity. Instead, the finer-detailed, site-level habitat features better elucidate drivers of biodiversity patterns. In particular, my findings demonstrate percent canopy cover, number of bird-friendly tree species, and the percent forested area of the immediate landscape to each significantly differ between hot and cold spots of either biodiversity metric.

Percent ground cover at a site may serve as a supplementary, if not primary, factor for specifically affecting taxonomic diversity but not species richness. While the differences in percent ground cover between cold and hot spots of taxonomic diversity were trending towards statistical significance (p=0.066), ground covers were not at all statistically significant among hot and cold spots of species richness (p=0.957). In fact, average percent ground cover in the cold spots was practically equivalent to that in species richness hotspots (73.13 +/-9.08% vs. 72.73 +/-10.77%, respectively). Biodiversity through the perspective of taxonomic diversity may have been more responsive to percent ground cover than was species richness because insectivores and carnivores tend to be most responsive to ground cover, likely because insects and small herpetofauna or small mammals are associated with ground cover. Therefore, variation in ground cover—or deviation in ground cover from a certain, desired coverage—may cause species exchange across foraging groups within a community. In our study system, those species belonging to insectivorous and carnivorous foraging guilds represented a huge portion of observable taxonomic diversity, particular at the higher, more taxonomically distinct levels of Order (n=5, 83%) and Family (n= 7, 58%). Therefore, sites with desirable ground cover may attract some of the more taxonomically distinct species of our focal bird community.
and so could support greater taxonomic diversity. Sites without desirable ground cover may still be species-rich if other aspects of the habitat are favorable to species other than insectivorous or carnivorous ones. However, these species are likely to be less taxonomically diverse and so the resultant community may or may not be as species rich but will likely be less taxonomically diverse.

I observed no statistically significant differences among values of any habitat features between hot spots unique to one biodiversity metric or the other. Low sample size is likely a culprit for these differences in habitat values between unique hotspots being statistically insignificant. With such a limited sample size, detecting significant differences requires a very clear signal, with large differences in effect and limited variation in that effect. However, differences in observed percent ground cover between unique hot spots of the biodiversity metrics were trending towards statistical significance \( p=0.083 \), with species richness hotspots having higher ground coverage \( 75.75 \pm 8.59\% \) than taxonomic diversity hotspots \( 54.29 \pm 7.03\% \). I interpret this difference to have ecological meaning, despite statistical insignificance, and I propose that less ground cover may allow better hunting and foraging for the taxonomically distinct carnivorous and insectivorous species of our focal community. Had sample size of unique hot spots between the two metrics been larger, perhaps percent ground cover would have significantly differed. Nevertheless, ground cover may still be an important feature to consider for habitat management as a leverage on taxonomic diversity within an avian community.

In conclusion, my results demonstrate that the complex concept of biodiversity cannot be simply managed according to generalized habitat types alone. Instead, a more detailed assessment of habitat features is needed in order to predict biodiversity potential for
conservation planning purposes. Similarly, avian biodiversity conservation must adopt a more holistic approach to habitat management since a variety of site-level habitat features differ significantly between cold and hot spots of species-level biodiversity. I therefore suggest that conservation policies for Puerto Rico’s coffee agroecosystems stipulate more specific criteria in regards to canopy cover as well as incorporate new criteria regarding bird-friendly trees. I support further policy development on these fronts since private landowners could more readily manipulate these two features and because management of either feature may spell the difference between realizing or restricting avian biodiversity potential. Lastly, while I found no statistically significant differences between unique hot spots of the two metrics, I did find evidence that the perspective on species-level biodiversity may still bias the habitat features selected as drivers of such biodiversity. The metrics used to evaluate biodiversity may also influence the setting of more specific criteria for certain habitat features, such as the range of suggested canopy coverage to support a given (measured) aspect of avian biodiversity. In doing so, such specifications may influence the consequences of habitat management for biodiversity conservation. Although not explored by my research presented here, a variety of other biodiversity metrics, even just within the species level of biological organization, exist. I suggest other metrics which capture functional or phylogenetic (Faith and Baker 2006, Allen et al. 2009) diversity among species be explored, particularly within ecological communities that are relatively depauperate (Tucker and Cadotte 2013), like island habitats. Because of the breadth of the biodiversity concept and the plethora of relevant biodiversity metrics, we encourage conservation decision-makers to assess biodiversity broadly through the comparison of multiple metrics (Gallardo et al. 2011, Morris et al. 2014) and the evaluation of multiple traits (Lefcheck et al. 2014). Such a multifaceted approach to interpreting biodiversity
would yield a more explicit understanding of these potential biases. Additionally, it would elucidate links between different types of diversity (Sahney et al. 2010, Tucker and Cadotte 2013). If adopting a multi-metric approach is not feasible, I urge conservation decision-makers to put serious thought into which aspect of biodiversity they most value and to strongly justify the use of a single biodiversity metric which best captures that valuation.
### TABLES AND FIGURES

**Table 1.1**: Summary statistics on all five habitat features summarized first across all 120 sites sampled and then by common, generalized habitat types.

<table>
<thead>
<tr>
<th></th>
<th>Minimum</th>
<th>Q1</th>
<th>Median</th>
<th>Q3</th>
<th>Maximum</th>
<th>Average (SE)</th>
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<tr>
<td><strong>All Sites (n=120)</strong></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Ground Cover (%)</td>
<td>7.00</td>
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<td>80.13</td>
<td>96.56</td>
<td>100.00</td>
<td>74.65 (2.14)</td>
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<td>78.81</td>
<td>100.00</td>
<td>49.08 (2.81)</td>
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<td>18.50</td>
<td>33.13</td>
<td>47.69</td>
<td>100.00</td>
<td>36.25 (1.93)</td>
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<td>Bird-friendly Trees (n)</td>
<td>2.00</td>
<td>5.00</td>
<td>6.00</td>
<td>7.00</td>
<td>13.00</td>
<td>6.11 (0.19)</td>
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<td>Forest in Landscape (%)</td>
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<td>2.52</td>
<td>11.17</td>
<td>36.88</td>
<td>97.74</td>
<td>25.01 (2.77)</td>
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<td>Ground Cover (%)</td>
<td>38.75</td>
<td>79.75</td>
<td>94.50</td>
<td>98.75</td>
<td>100.00</td>
<td>87.37 (2.30)</td>
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<td>76.50</td>
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<td>92.75</td>
<td>100.00</td>
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<td>100.00</td>
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<tr>
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<td>5.00</td>
<td>6.00</td>
<td>7.00</td>
<td>12.00</td>
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<td>Forest in Landscape (%)</td>
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<td>20.80</td>
<td>52.47</td>
<td>86.61</td>
<td>97.74</td>
<td>52.77 (5.35)</td>
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<td><strong>Sun-grown Coffee Sites (n=33)</strong></td>
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<tr>
<td>Ground Cover (%)</td>
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<td>75.44</td>
<td>98.25</td>
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<td>32.94</td>
<td>79.75</td>
<td>22.34 (3.74)</td>
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<td>Understory Density (%)</td>
<td>5.75</td>
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<td>18.38</td>
<td>33.75</td>
<td>79.00</td>
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<td>Bird-friendly Trees (n)</td>
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<td>Ground Cover (%)</td>
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<td>95.50</td>
<td>100.00</td>
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<td>13.00</td>
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<td>5.48</td>
<td>11.46</td>
<td>70.06</td>
<td>10.11 (2.13)</td>
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</table>
Table 1.2: 95% confidence intervals around the mean estimates for all five habitat features at sites determined to be 'hot' or 'cold' spots according to either species richness or taxonomic QEID.

<table>
<thead>
<tr>
<th></th>
<th>Ground Cover (%)</th>
<th>Canopy Cover (%)</th>
<th>Understory Density (%)</th>
<th>Bird-friendly Trees (n)</th>
<th>Forest in Landscape (%)</th>
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<tr>
<td>Species Richness</td>
<td>72.73 (10.77)</td>
<td>26.73 (9.60)</td>
<td>33.04 (11.56)</td>
<td>8.17 (1.18)</td>
<td>24.98 (14.34)</td>
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<tr>
<td>Taxonomic QEID</td>
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<td>23.31 (4.11)</td>
<td>28.38 (9.68)</td>
<td>8.50 (1.01)</td>
<td>18.03 (11.27)</td>
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<tr>
<td>Cold Spots</td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Species Richness</td>
<td>73.13 (9.08)</td>
<td>92.04 (3.60)</td>
<td>21.31 (7.63)</td>
<td>5.25 (0.84)</td>
<td>57.71 (14.08)</td>
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<td>73.13 (9.08)</td>
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<td>21.31 (7.63)</td>
<td>5.25 (0.84)</td>
<td>57.71 (14.08)</td>
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</table>
**Figure 1.1a:** Distribution of species richness estimates across all 120 sampling sites.

**Figure 1.1b:** Distribution of taxonomic quadratic entropy index of diversity (QEID) estimates across all 120 sampling sites.
**Figure 1.2a:** Species richness of the focal bird community by habitat type (forest, sun-grown and shade-grown coffee plantations)

**Figure 1.2b:** Taxonomic quadratic entropy index of diversity (QEID)
Figure 1.3: Percentage canopy cover at hot and cold spots of both species richness and taxonomic quadratic entropy index of diversity (QEID). Species richness scores are shown with circles. Taxonomic QEID are shown with triangles. Cold spots are presented using no fill color and as the first marker in either series of biodiversity metrics. Hot spots are presented using a solid fill color and as the second marker in either series of biodiversity metrics.
Figure 1.4: Number of bird-friendly tree species at sites of hot and cold spots of both species richness and taxonomic quadratic entropy index of diversity (QEID). Species richness scores are shown with circles. Taxonomic QEID scores are shown with triangles. Cold spots are presented using no fill color and as the first marker in either series of biodiversity metrics. Hot spots are presented using a solid fill color and as the second marker in either series of biodiversity metrics.
Figure 1.5: Percent forested area in the surrounding landscape at hot and cold spots of both species richness and taxonomic quadratic entropy index of diversity (QEID). Species richness scores are shown with circles. Taxonomic QEID are shown with triangles. Cold spots are presented using no fill color and as the first marker in either series of biodiversity metrics. Hot spots are presented using a solid fill color and as the second marker in either series of biodiversity metrics.


CHAPTER 2: A NOVEL, DATA-DRIVEN APPROACH TO GROUP-SPECIFIC OCCUPANCY MODELLING AND THE CONSEQUENCES OF IMPOSING DIFFERENT GROUPING TECHNIQUES ON AN ECOLOGICAL COMMUNITY

Abstract

Biodiverse communities are often subdivided according to various classification or grouping schemes in order to understand how not only entire communities but also individual species interact with their environments. However, the way in which an ecological community is subdivided may influence which habitat features are deemed important for conserving each group delineated. Here, I present a novel method, using Bayesian clustering techniques, to group an ecological community. I apply this new method to a focal community of 27 birds occupying the forests and coffee plantations of Puerto Rico’s Cordillera Central. I also apply two existing approaches to group this community. I do so to compare how different grouping schemes can affect the modelled relationships between species occupancy and habitat features. I also perform this group-level occupancy modelling to compare it against community-level approaches. I then examine those species whose management may be especially sensitive to the application of various grouping schemes. My findings demonstrate that subdividing a greater community of birds suggests different habitat features to be important for promoting or restricting avian occupancy than if the entire bird community were considered as a single entity. I also found data-rich ecological subgroups may be responsible for driving the relationships observed between certain habitat features and occupancy at the community level. Finally, the application of various grouping schemes can affect individual species differently in terms of the management actions suggested by the species-habitat relations derived from
those various approaches to group-level occupancy modeling. This may lead to contradictory management outcomes for such species whose occupancy responses to habitat features are highly dependent on the ecological subgroup in which they are assigned. This research demonstrates how different approaches to grouping an ecological community can lead to more tailored inspections of species-habitat relationships but that the application of grouping schemes, particularly *a priori* ones, invokes ecological assumptions which carry high risks, especially for certain, unique species.

Introduction

Conserving species-rich ecological communities is a priority among conservation biologists (Soulé 1985). Doing so requires a precise understanding of how not only entire communities but also individual species interact with their environment. However, achieving this understanding is challenged by the inherent diversity of complex ecological communities. To combat this challenge, ecologists seek ways to structure biological diversity. One such solution is to use classification or grouping schemes (Gourlet-Fleury et al. 2005, Pacifici et al. 2014). A variety of criteria may stipulate the grouping of species, such as similarity in functional roles (Kohler and Huth 1998, Blaum et al. 2011), shared phylogenies or taxonomies (Lockwood et al. 2000, Heino et al. 2005, Cassey et al. 2007), similar responses to environmental covariates (Dunstan et al. 2011), or similarities in species-specific natural history traits. Additionally, groupings may be made *a priori* (whereby species’ group assignments are made according to previous knowledge or intuition), be data-driven (whereby species’ group assignments are might in light of a dataset), or may be dynamically modeled.
(see Wilson 1999 and Leso and Kropil 2007). These myriad grouping schemes may then influence which habitat features are deemed important for conserving each group delineated. In turn, the apparently preferable course of action to meet conservation objectives can be swayed by the manner in which different species are grouped within the greater ecological community.

In addition to grouping species, hierarchical analyses also lend structure in order to better understand complex ecological communities. Hierarchical community-level occupancy modeling (MacKenzie et al. 2002) is one analytical tool particularly useful to ecologists. In general, occupancy modeling relies on a hierarchical structure to statistically infer species’ unobservable or latent occupancy states from observed presence/absence (detection/nondetection) data on those species. More specifically, community-level occupancy modeling pools data among a group, or community, of species and improves inference by allowing the statistical modeling process to ‘borrow’ information from data-rich species to inform estimates on data-poor species. However, this borrowing of information is only useful if species within the same group or community are indeed similar in their responses to characteristics of the habitat or perturbations to it. For this reason, further reducing a single, large and diverse ecological community to smaller but more homogeneous groups can permit even greater accuracy in the estimates yielded from occupancy modeling.

With over 10,000 species worldwide, birds are the most biodiverse class of terrestrial vertebrates. Because of their broad speciation and because of their widely differentiated life histories, birds are a useful taxon for studying more precisely the relationships between habitat and biodiversity as they may be grouped according to a variety of schemes. One such very popular grouping scheme for birds is based on functional roles and utilizes the concept of
foraging guilds (Hawkins 1989, Simberloff and Dayan 1991), which are groupings of organisms from the same taxa and which share similar diets. Despite its utility and ubiquity, grouping birds solely on foraging guilds may prove misleading (see Jaksic 1981 and see Verner 1984): First, the assignment of any species to a particular foraging guild can be subjective and is often complicated by both plasticity in dietary preferences and food resource availability. These complications compromise the crucial assumption underpinning the guild concept: That interspecific competition is the driving force behind community structuring (Kornan and Kropil 2014). Secondly, this approach ignores many other natural and life history traits significant to conservation. To ameliorate these shortcomings, cluster analyses to delineate species groupings based on multiple traits offers a more holistic and objective approach to grouping bird species within the greater bird community than do foraging guild assignments (see Conole and Kirkpatrick 2011). Nevertheless, the assignment of an avian species into a certain foraging guild or cluster based on static natural history traits prohibits uniquely interpreting species’--and, consequently, entire community’s--responses to their ecosystem. Fortunately, data-driven and other a posteriori approaches offer an advantage over those and other common a priori grouping schemes. However, because any such a posteriori approach first requires the collection of field data, it is inherently more resource-demanding. Therefore, to justify the additional expense, such approaches must offer greater resolution to ecological phenomena by providing predictive and prescriptive solutions (Hampton et al. 2013).

In this paper, I present the development and application of a novel, data-driven method which uses Bayesian clustering techniques to group avifauna. I then explore the consequences of using this novel, data-driven approach and two other a priori grouping schemes on conservation efforts in Puerto Rico. Broadly, I do so to determine whether the manner in which
an ecological community is subdivided affects which habitat features will be found as drivers of each subgroup’s species richness. Specifically, I pursue the following research objectives: (1) Compare and contrast the species assignments made according to three different grouping schemes; (2) Determine whether the delineation of ecological subgroups suggests different habitat features to significantly affect group-level occupancy probabilities than if the community had not been subdivided; and, (3) Investigate how management of certain species may be especially affected by whether or not the greater community is subdivided, and, if so, by the grouping scheme applied.

Methods

My study region was located in the western central portion of the main island of Puerto Rico, covering much of the Cordillera Central. Within this region, I stratified by landuse/landcover to randomly generate sampling sites located within forests and coffee plantations. For coffee plantations, I further delimited between sun- and shade-grown cultivation practices. Although a variety of criteria stipulate the designation of ‘shade-grown’ coffee, my interpretations of the coffee culture practice were based primarily upon the percentage of shade provided to the coffee plants themselves by other non-coffee plants, with the threshold set at 30% to distinguish sun- from shade-grown coffee plantations. At each site, I established the center point of a 50-meter radius circular plot which served as the sampling location at which to conduct point count surveys of the avian community.

My team and I conducted 2-4 visits to each of our sampling plots. During each visit, we visually and aurally sampled for the presence/absence (detection/nondetection) of all
species in the avian community following a standard point count protocol for two independent observers. We began sampling on 24 March 2015 and finished sampling on 02 June 2015 to satisfy assumptions about population closure for later analysis (MacKenzie et al. 2002). All point counts were conducted no earlier than sunrise and no later than 4 hours after sunrise. Point counts lasted for a duration of 10 minutes following a 2-minute acclimation period after both observers arrived at the center point. I focused our analysis on only those species that are native, endemic, or are otherwise of conservation concern. I present in Appendix 1 those criteria I stipulated to consolidate our focal community to 27 birds.

Having determined the greater focal community, I then delimited these 27 birds of interest first according to the novel, data-driven approach and then according to two a priori grouping schemes. We developed a novel Bayesian cluster model which amalgamated certain species of the greater community using a Dirichlet process prior and which shared information within the resultant groups. This new, data-driven method to grouping determined likely separations among species in the community given their modelled responses in occupancy probability to each of the five habitat features of interest. We then proceeded with a typical hierarchical occupancy modeling framework, modeling occupancy and its relationship with the habitat features as site-level covariates for each of the resultant groups of our Bayesian clustering process.

My first a priori grouping scheme was according to foraging guilds and mass. I assigned birds to one of four such groups by first considering each species’ primary foraging guild, either carnivorous, frugivorous, granivorous, insectivorous, or nectarivorous (see Table 2.1). Due to functional similarities in pollination or seed dispersal services, I combined frugivores and granivores with nectarivores. Similarly, I combined carnivores with...
insectivores given both their predatory roles in their ecosystems’ food webs. Within each of these two summarized foraging guilds, I sorted species according to average body mass in grams. Any species whose average mass found in the literature was below the 50th percentile of its respective, summarized guild, I designated as “small,” while any species whose average mass according to the literature was greater than or equal to this 50th percentile, I designated as “large.” I imposed these mass-based distinctions in order to achieve foraging guilds reflective of species’ expected value-added toward ecosystem services, with the assumption that larger organisms provide more of the same services than do smaller organisms. These reductions by primary foraging guild and then by mass subdivided the focal community of 27 birds among four foraging-mass guilds: Large Frugivores/Granivores/Nectarivores (LFGN), Small Frugivores/Granivores/Nectarivores (SFGN), Large Carnivores/Insectivores (LIC), and Small Carnivores/Insectivores (SIC).

My second a priori grouping scheme considered a wider array of natural history traits. I imposed natural history trait clusters first by summarizing as much evidence from the literature as I could find on five key natural history traits: Elevation preference, Puerto Rican Endemism, Forest Specializing, Forest Interior Specializing, and Sensitivity to Humans. With these five features capturing important natural history traits of each species, I conducted a K-means cluster analysis to group together those species that are most similar across all five natural history traits considered. This analysis revealed that the community of 27 birds could best be delimited into four clusters according to shared responses across this suite of five traits. I simply designated the resulting clusters as Cluster 1, Cluster 2, Cluster 3, and Cluster 4.

To investigate the relationship between habitat and species richness within avian groups, my team and I performed a vegetative survey at each sampling site to collect data on
the following habitat features: Percentage ground cover, percentage understory density, percentage canopy cover, and species richness of fruiting, flowering, shade-providing, or other such resource-provisioning trees useful to avifauna (henceforth, bird-friendly tree species richness). For all these features except bird-friendly tree species richness, we collected measurements at four 1-m² quadrats within the greater 50-m radius sampling plot. The first quadrat was centered over the sampling plot’s center point, exactly where we had conducted the point count. We randomly sampled the three remaining quadrats using randomly generated bearings and distances (≤49.5m) from the sampling plot’s center point. Within each of the four 1-m² subplots, we estimated percentage ground cover on a continuous scale (0-100%). Both live vegetation and litter (e.g. dead vegetation, sticks, etc.) were considered as ground cover. Exposed soil and rock or gravel were considered bare ground and so were not included in ground cover estimates. We estimated percentage understory density similarly to the Visual Obstruction or Robel Pole Method (Robel et al. 1970 and see Harmoney et al. 1997) using two opposite perspectives but recording quadrat-specific measures using a 1-m² grid and on a continuous scale rather than using a demarcated pole and binning observations into height cover classes. We measured percentage canopy cover using a concave spherical densiometer. I then averaged the percentages for ground cover, understory density, and canopy cover measurements across all four quadrats to obtain a single measure for each sampling site.

My team and I estimated bird-friendly tree species richness by counting the number of unique tree species of interest (Appendix 2) encountered throughout the entire 50-m radius circular sampling plot. For this estimation, I selected tree species of interest based upon the following guidelines and with the help of a local plant expert (A. Morales): I stipulated that tree species of interest (1) Be native, endemic, or long-since naturalized to Puerto Rico, (2)
Occur not uncommonly throughout our study region in the Cordillera Central, and (3) Provide some utility to at least one of the 27 focal avian species, either by providing food or shelter resources. For further details on our selection process and surveying of bird-friendly trees, please see Appendix 3.

Additionally, to investigate how the landscape context may shape species richness of a priori and a posteriori avian groups, I collected data on the percent forested area in the immediate landscape of each site. I defined this ‘immediate landscape’ according to evidence from the literature linking daily dispersal distance with birds’ body weights (Sutherland et al. 2000) but balanced this against our study design stipulation that points be no closer than 500m. From this, I defined the immediate landscape to be 250 meters beyond the extent of the sampling plot. I then used GIS via ArcMap (ESRI 2011) to calculate the forested area within this immediate vicinity landscape. For further details on my calculating the percent forested area in the immediate landscape, please see Appendix 4.

Model Description

To estimate birds’ occurrence states in forests and coffee plantations of Puerto Rico, we developed a Bayesian cluster model. For species $j = 1, \ldots, m$ and sample $i = 1, \ldots, n$ we observe $Y_{ij}$ successes in $N_{ij}$ trials. The likelihood is $Y_{ij} \sim \text{Binomial}(d_j o_{ij})$, where $d_j$ is the detection probability for species $j$ and where $o_{ij}$ is the occupancy indicator. The detection probabilities are modeled as $d_j \sim \text{Beta}(a, b)$. The inclusion indicators are assumed to be a function of the latent Gaussian variables $Z_{ij}$ with $o_{ij} = 1$ if $Z_{ij} > 0$ and $o_{ij} = 0$ if $Z_{ij} < 0$. The covariates affect occupancy via the latent Gaussian variables. The covariate effects are
grouped across species, with $g_j$ being the group label for species $j$ and whereby $g_j \in \{1, ..., G\}$. The occupancy model is then:

$$Z_{ij}|g_j = k \sim Normal(\alpha_j + \sum \{1 = 1\} p^{x_{il} \beta_{lk}}, 1).$$

The intercepts are $a_{ij} \sim Normal(\mu_a, \tau - 2a)$ and the covariated effects are $\beta_k = (\beta_{k1}, ..., \beta_{kp})$ and $T \sim Normal(\mu_b, \Sigma_b)$. The group probabilities are modeled using a stick-breaking construction. Let $Prob(g_j = k) = \pi_k$. Then the stick-breaking representation of $\pi_k$ is: $\pi_k = V_k(1 - \pi_1 - ... - \pi_k - 1)$ where $V_k \sim Beta(1,D)$. The maximum number of groups, $G$, should be large enough that the probability on the final term, $\pi_G$, is small. The priors are $a, b, \tau_a^{-2} \sim Gamma(\epsilon, \epsilon), \mu_a \sim Normal \left(0, \frac{1}{\epsilon}\right), \mu_b \sim Normal \left(0, \frac{1}{\epsilon} I_p\right)$, and $\Sigma_b \sim InvWishart(p + \epsilon, \frac{1}{p + \epsilon} I_p)$. We set $\epsilon = 0.1$ as the default in this code. This default setting gives uninformative priors.

The latent occurrence states are then modelled in the traditional, hierarchical group-level occupancy model (Dorazio et al. 2006) to survey-specific detection/nondetection (‘presence/absence’) data collected across our 120 sampling sites for each of the eight a priori groups (four foraging guilds and four natural history trait clusters) and the five data-driven groups. With these occupancy models, I am ultimately interested in the latent, or unknown and unobservable, occurrence state of each species ($i = 1, 2, \ldots N$) at site $j$, represented by the random variable $Z_{ij}$. For each model, I assumed the true occupancy state of species $i$ at site $j$, $Z_{ij}$, to be a latent (imperfectly observed) variable such that $Z_{ij} = 1$ when species $i$ is present at site $j$ and $Z_{ij} = 0$ otherwise. My modeling framework assumed no false positive detections in our data such that if a species were ever detected at a site, then it was in fact present at that
site. However, my repeated surveying protocol allowed this modeling process to differentiate between non-detection and true absence to account for the possibility of false negative detections.

I modeled both an observation and state process. I modeled the observation process on the detection/non-detection data, $X_{ijk}$, as a Bernoulli random variable where $X_{ijk} = 1$ if the $i^{th}$ species was detected at the $j^{th}$ site during the $k^{th}$ survey to that site. I used this observation process to explore possible survey-level covariates (date of survey and the team conducting the survey) which could influence detection. Since detection probabilities did not vary significantly with date-of-survey, I excluded this from subsequent modeling. However, I retained team-conducting-survey since it improved fit for the observation process. I next modeled the state process using species- and site-specific occurrence models assuming occurrence to be a Bernoulli random variable such that $Z_{ij} \sim Bern(\psi_{ij})$ where $\psi_{ij}$ is the occupancy probability of species $i$ at site $j$.

All occupancy models had a hierarchical structure since the species-level parameters were assumed to be random effects drawn from group-level hyperparameters. The distribution on these hyperparameters was assumed to be Normal and was defined by a mean that represents the group-wide response to a particular covariate and by a standard deviation that represents the variation in species’ responses across the entire group. Because I had no strong evidence from previous data or expert opinion, I used vague priors on the hyperparameters. I ran my models in program OpenBUGS through program R. I ran each model for three chains each of 10,000 iterations with the first two thousand of those being discarded as burn-in. On the remaining 8,000 iterations, I thinned by 25.
Results

The novel, data-driven approach to inferring subdivisions among the greater avian community suggested that there are most likely five distinct groups according to species’ shared responses across the five habitat features of interest (Figure 1). In Table 2.1, for each of the five data-driven groups, I present those species whose posterior probabilities suggest that they most likely be members of that group. I also present summary statistics according to these suggested memberships. It is important to note, however, that in contrast to either a priori grouping scheme, this data-driven approach does not yield fixed group assignments for any species.

I imposed four mutually exclusive guilds according to each species’ primary foraging guild and to its average body mass: Large Frugivores, Granivores, and Nectarivores (LFGN); Small Frugivores, Granivores, and Nectarivores (SFGN); Large Insectivores and Carnivores (LIC); and Small Insectivores and Carnivores (SIC). In Table 2.2, I present summary statistics on the species memberships of each foraging/mass guild. The LFGN guild had the fewest members (n=6) but had the greatest total number of detections (n=902) across all visits to all 120 sampling sites. The other three guilds each had seven members. However, the SIC guild had the fewest total detections (n=526).

In Table 2.3, I present summary statistics for the outcomes of performing a K-means cluster analysis on five natural history traits across the greater avian community. This yielded four distinct natural history trait clusters. The first cluster, C1, consists almost entirely of Puerto Rican endemics that are also forest-specializing but which do not require interior forest and that prefer lowlands. The second cluster, C2, is defined by its members’ shared preferences
for forested habitats, their acute sensitivities to humans, and their occurrences across a wide range of elevations. Besides its largest member (Puerto Rican tanager, \textit{Nesospingus speculiferus}), the third cluster, C3, contains very small and elusive, if not rare, species which display a marked sensitivity to humans and prefer higher elevations. Finally, the fourth cluster, C4, is characterized by its species members' preference for mid-elevations but otherwise rather generalist traits: Non-endemics having no preference for forested habitats and being relative insensitive to human presence.

\textit{Group-level Effects}

My community-level hierarchical occupancy model presented in my first chapter found percentage ground cover, percentage canopy cover, and richness of bird-friendly tree species to each garner much support for exerting a positive effect on the average occupancy probability estimated across all 27 species of our focal avian community. I found support of moderate to high strength for most data-driven groups’ group-level occupancy being affected by localized habitat features (Table 2.4). In response to percentages ground cover and canopy cover, I found strong support for a positive response in group-level occupancy for almost all five data-driven groups. Similarly, I found strong evidence for an effect of percentage understory density on group-level occupancies, but, our models estimated such effects to be negative. My models also demonstrated some support for a positive effect of the richness of bird-friendly tree species on group-level occupancy probabilities. However, this support was relatively weaker than that garnered for the other three within-site habitat features (percentages ground cover, understory density, and canopy cover).
When I delineated this greater avian community according to primary foraging guild and mass (Table 2.5), my models still demonstrated great support for percentage ground cover having a positive effect on group-level occupancy for all four foraging/mass guilds. In particular, I found that occupancy of both the LFGN and SIC guilds demonstrated much greater sensitivity to percentage ground cover at a site than when the community is considered as a whole. Similarly, my models demonstrated much support for a positive effect of percentage canopy cover on group-level occupancy of both the LFGN and LIC guilds. And, I estimate these guilds’ occupancy probabilities to be much more sensitive to the effect of percentage canopy cover than was occupancy of the entire avian community as a whole.

However, for either the SFGN or SIC guild, my models garnered little support for there being any effect of percentage canopy cover on occupancy. Also, I found strong evidence to indicate a positive effect of the richness of bird-friendly tree species on group-level occupancy for both the SFGN and the LIC guilds. And, while occupancy of the LIC guild had a similar sensitivity to bird-friendly trees as did occupancy of the greater avian community, species of the SFGN guild were, on average, much more sensitive to this habitat feature. However, those same estimates for either the LFGN or SIC guild received no support to indicate an effect of bird-friendly trees on those guilds’ occupancy probabilities.

In Table 2.6, I present hyperparameter estimates for the effect of each habitat feature of interest on the cluster-level occupancy probability of each natural history trait cluster. I found very strong support for a positive response in occupancy to percentage ground cover for both clusters 1 and 2 (C1, C2). I also found strong evidence for that same positive effect for cluster 3 (C3). However, on average, those species assigned to cluster 1 (C1) were much more
sensitive to percentage ground cover than would otherwise be predicted from our less tailored community-level occupancy model.

For C1 and C3, my models demonstrated much support that percentage canopy cover would positively affect average occupancy probabilities (Table 2.6). And, I found that C1 was slightly more sensitive to percentage canopy cover than would be expected from the comparable estimate across the greater avian community. I also found some support, though not as strong, for a positive relationship between percentage canopy cover and occupancy for C2. However, support for the effect of percentage canopy cover on C4 occupancy was relatively much weaker.

For almost all natural history trait clusters, I found support evidencing a positive relationship between the richness of bird-friendly trees at a site and cluster-level occupancy (Table 2.6). In particular, this support was greatest for both C2 and C4. However, the hyperparameter estimate for the effect of bird-friendly trees on occupancy of C2 was comparable to that for the greater avian community. And, that hyperparameter estimate for C4 was less than that for the greater avian community. For both clusters C1 and C3, my models demonstrated hardly any support for such an effect of bird-friendly tree species richness on occupancy. Finally, for all but the fourth natural history trait cluster, my models demonstrated little to no evidence for an effect of percentage forested area in the landscape on cluster-level occupancy (Table 2.6). For C4, I found strong support for a negative relationship between occupancy and the percentage forested area in the surrounding landscape.
Species-Level Effects

I selected three species in particular from the greater community of our focal 27 species so that I could compare the effects of imposing different grouping schemes on individual species of interest. For these species-specific comparisons, I chose to examine the Antillean euphonia (*Euphonia musica*, ANEU), the Elfin woods warbler (*Setophaga angelae*, EWWA), and the Puerto Rican tanager (*Nesospingus speculiferus*, PRTA). I selected these species because they are especially important to biodiversity conservation and because they would likely be especially sensitive to certain types of habitat management.

For all species and regardless of the grouping scheme imposed, my models found much support for a positive effect of percentage ground cover on occupancy probabilities (Table 2.7). In contrast, no matter the grouping scheme used, my models never yielded much statistical support for any sort of relationship between the percentage forested area in the surrounding landscape and species' occupancy probabilities. Across these three grouping schemes and among these three particular species, my models most often garnered the strongest statistical support for a proposed relationship between species-specific occupancy probabilities and any one of the five habitat features of interest when species were grouped according to a data-driven approach.

For the Antillean euphonia (Table 2.7), I found some interesting discrepancies for the importance of the richness of bird-friendly trees on occupancy: When considered as either a member of the first data-driven group or as part of the SFGN guild, I found much evidence for a positive relationship between this habitat feature and the Antillean euphonia's occupancy
probability. However, I found no such statistical support for any sort of relationship between the richness of bird-friendly trees and occupancy when the Antillean euphonia is clustered into the first natural history trait cluster. Also, only when grouped into the SFGN guild did my models estimate the effect of trees on the euphonia's occupancy to be greatest and to have garnered the most statistical support. Similarly, I only found strong statistical support for a relationship between bird-friendly trees and occupancy of the Puerto Rican tanager when I grouped according to the foraging/mass guild approach (Table 2.7). Also for the Puerto Rican tanager, neither the guild nor the data-driven grouping schemes supported there being an effect of percentage understory density on occupancy. Instead, only by clustering according to natural history traits did our models reveal strong statistical support for this particular species-habitat relationship.

Across the three grouping schemes applied (i.e. foraging/mass guilds, natural history trait clusters, and data-driven grouping), my models only found strong statistical support for a relationship between occupancy of the Elfin woods warbler and the habitat features ground coverage and canopy coverage (Table 2.7). As previously stated, all three grouping schemes garnered strong or very strong support for there being a positive relationship between percentage ground cover and this warbler's occupancy probability. However, only when clustering according to either natural history traits or when grouping by the data-driven approach did my models garner statistical support for a relationship between Elfin woods warbler’s occupancy and percentage canopy cover. In both instances, my models estimated these relationships to be positive and of comparable magnitudes.
Discussion

In this chapter, I present a novel development and application of Bayesian clustering techniques to group species in a focal avian community. I also compare this new method against two existing methods and I explore the consequences which imposing various grouping schemes have on occupancy modelling and, ultimately, on conservation decisions made in light of it. For this research, I completed three objectives.

My first objective was to compare and contrast the species membership outcomes of the three different grouping assignments. The novel, data-driven grouping approach demonstrated very precise capabilities for subdividing ecological communities. Applying such data-driven approaches not only tailors inference to more homogenous groups of species but also more directly reflects the realized niches of these species by considering the actual dynamics within the given system. Therefore, although a data-driven grouping scheme yielded group-level hyperparameters similar to those for the entire community, this approach does circumvent foibles associated with falsely assuming species’ realized niches. Ultimately, this data-driven approach facilitates more precise occupancy estimation for a community of otherwise unpredictable habitat generalists.

Between the two a priori grouping schemes I imposed, grouping first by primary foraging guild and then by mass yielded greater similarities among resultant guilds, at least in terms of both total species membership and total detections, than did clustering the avian community according to a suite of natural history traits. While such equivalencies are particularly convenient for statistical purposes, they likely compromise biological and ecological realities. This discrepancy between resultant guilds and clusters of either a priori
grouping scheme indicates some of the shortcomings of subdividing an ecological community by few criteria: With fewer traits considered, more of the actual variety in species’ functional niches is curtailed or dismissed. Instead, considering a suite of features better summarizes across the entire breadth of each species’ functional niche. This is particularly important to island ecosystems since these systems tend to be relatively depauperate--at least in comparison to their mainland counterparts--and, therefore, are comprised of more habitat generalists than habitat specialists. Since these habitat generalists may adopt any one of many possible realized niches, research intended to identify species-habitat relationships among an ecological community of generalists must expand its purview to consider the full spectrum of functional niches.

My second objective was to understand how the delineation of various ecological subgroups, rather than the treatment of the entire avian community as a single entity, may cause occupancy models to lend varying levels of statistical support for different species-habitat relationships. I found that subdividing the greater avian community does affect which habitat features will garner the most statistical support as being likely to affect group-level occupancy probabilities. My models found very strong support for almost all data-driven groups’ occupancy probabilities to be either positively or negatively affected by ground coverage, by understory density, and by canopy coverage. I suspect this great deal of statistical support for those hyperparameters can be attributed to two reasons: First, I delineated these data-driven groups according to their species’ modelled responses to habitat features of interest. And, secondly, those three habitat features (ground coverage, understory density, and canopy coverage) are fundamental aspects of habitat construct which strongly determines forage opportunities, evasion from predators, protection from the elements, and suitable nesting sites.
for many of our focal species. In contrast, I believe that the richness of bird-friendly trees at a
given site garnered relatively less support not because these trees are unimportant to predicting
avian occupancy but because many of my focal avifauna tend not to specialize their feeding or
nesting activities to particular tree species. Still, my models did yield moderately strong
evidence that richness of bird-friendly trees does positively affect group-level occupancy of
these data-driven groups. Evidence for a relationship between the percentage forested area in
the surrounding landscape and group-level occupancy was even weaker, suggesting that
landscape context may play a less critical role than one might assume. If so, the hope that
coffee agroecosystems or other protected areas could function as wildlife refugia, despite their
isolation, is viable.

Among the two *a priori* grouping schemes, I observed many deviations in statistical
support for group-level hyperparameters in comparison to statistical support for community-
level hyperparameters. For example, for the most foraging/mass guilds and for most natural
history trait clusters, I found little to no support suggesting that percentage understory density
affects group-level occupancy. My models yielded a similar scenario for the estimated effects
of percentage forested area in the landscape. I propose these inconsistencies in the support
generated for *a priori* group-level hyperparameters versus for community-wide
hyperparameters to suggest that certain key species (or groups of species) may be
disproportionately responsible for the species-habitat trends observed at the community level.
But, given the rather non-specializing behaviors of our island-dwelling avifauna, I caution
against the blind application of *a priori* groupings since such designations impose artificial
distinctions upon species that fail to reflect the breadth of their functional niches. However, I
do recognize the utility and popularity of guild-based and other *a priori* grouping schemes. I
therefore recommend their use be tempered and suggest guild-based ecological research inform conservation such as ecosystem functionality rather than species-specific management.

In comparing these three approaches to subdividing an ecological community, I wish to comment especially on the more novel, data-driven approach. The advantage of modeling occupancy per data-driven groups over community-wide occupancy modeling is that the data-driven approach allows for more tailored, and therefore more precise, estimation of species-habitat relationships. The disadvantage, however, is that the data-driven approach presented here does not conclusively assign species to any particular group. Instead, data-driven group memberships are determined by species’ posterior probabilities.

My third and final objective was to examine more closely certain species of particular interest whose management may be especially affected by whichever grouping scheme is applied to the greater avian community. It is critical that landscape-level and community-wide management efforts, such as those that are currently underway in Puerto Rico, do not accidentally mismanage individual species. My most finely resolved examination of species-habitat relationships compared which of the five habitat features of interest received strong support for affecting species-specific occupancy probabilities when species of the greater community are grouped according to various criteria or grouping schemes.

I chose to concentrate this facet of our analysis on three species that are especially important to biodiversity conservation: Antillean euphonia, Elfin woods warbler, and Puerto Rican tanager. Each of these species is either endemic or native but also tend to be relatively more range-restricted than other the other species which comprise our greater avian community of interest. In particular, the Puerto Rican tanager is of special interest to the conservation of evolutionary lineages because it is not only endemic but also the world's only representative
of the genus *Nesospingus*. Additionally, I selected these three species since they are somewhat unique among their peers as showing particular and somewhat strong preferences for habitat and for foraging whereas many other birds on the island are true generalists. For example, the Antillean euphonia tends to specialize its feeding on mistletoe berries while more than two-thirds of the Puerto Rican tanager's foraging activities are restricted to the understory. And, as its name suggests, the Elfin woods warbler is only found in a particular forest type found only in Puerto Rico that is rapidly disappearing.

That the imposition of different grouping schemes determined whether some habitat features garnered very strong, strong or any statistical support for having an effect on species' occupancy probabilities suggests that my modeling of species-habitat relationships is, in part, an artefact of the modeling process itself. However, my models always clearly demonstrated strong or very strong support for the importance of percentage ground cover at a site and these species' occupancy probabilities, regardless of the grouping approach I imposed. Because this habitat feature garnered strong support at both the community-wide and species-specific levels of our analyses, I confidently propose this aspect of the habitat as a key feature for avian occupancy. And, I recommend that habitat management, particularly, agricultural practices, avoid reducing ground cover and strive to increase ground cover whenever possible. While maintaining ample ground coverage is less a concern in the forested areas of the island, incorporating criteria relevant to protecting ground cover in the coffee plantations to determine a farmer's reception of subsidized or incentivized agricultural packages could benefit avifauna without inflicting undue burdens on coffee farmers.

Finally, I wish to temper any potential misguided conclusions that could stem from the lack of statistical support for an effect of the percentage forested area in the landscape and
avian occupancy. While my models tended to find little support for a relationship between birds' occupancy probabilities in the amount of forest in the surrounding landscape, this result cannot be used to immediately relegate the significance of conserving forested areas or ensuring some degree of landscape connectivity. My work presented here did not examine these nuances of landscape ecology well enough to conclusively dismiss the need for such conservation work which many other studies have supported. Instead, this result of mine should engender confidence that remnant, isolated, and even small forest patches could serve as wildlife refugia and that well-managed coffee plantations could indeed realize the agroecosystem concept despite the extremely diversified matrix that is the reality of Puerto Rico's landscape.

In particular, I wish to emphasize certain discrepancies in the point estimates and the statistical support garnered for those estimates when modeling species-habitat relationships that would lead to conflicting conclusions about the most desirable course of action for habitat management. For the Antillean euphonia, I was not surprised to see that when this species is grouped according to our foraging/mass guild approach, my models report very strong statistical evidence for a very positive relationship between its occupancy and the richness of bird-friendly trees. I also was unsurprised by this result given that the Antillean euphonia prefers to eat mistletoe berries and so its site occupancy is strongly responsive to whether mistletoe occurs which is then determined partly by whether the parasitic plant's preferred host trees are present. This ecological linkage between the Antillean euphonia and common host trees of mistletoe explain our model's output. And, this ecological linkage which is recognized most apparently by considering the Antillean euphonia's dietary habits is further underscored by a modeling process that groups species into foraging guilds. I propose, however, that this
guild-centric perspective was critical to uncovering this species-habitat relationship since our models estimated no effect of bird-friendly tree species richness on euphonia occupancy when I clustered by a suite of natural history traits. This dichotomy suggests that while many Puerto Rican avifauna are relatively hardy generalists, the community-wide approaches to conservation and habitat management should first earmark unusually sensitive species and give these species more specific attention. I recommend that those species earmarked for special treatment be the habitat specialists and should include "picky eaters" such the Antillean euphonia but also the Green mango (*Anthracothorax viridis*), which prefers nectar from flowers of the genus *Heliconia*, among others.

I found further evidence that the type of grouping scheme used to subdivide a greater avian community has management implications for certain bird species upon examining modelled estimates of species-habitat relationships for the Puerto Rican tanager. When grouping according to foraging guild and body mass, our model estimated no effect of and found no statistical support for a relationship between percent understory density and the tanager's occupancy. I found this result surprising given that the Puerto Rican tanager is known to spend the vast majority of its foraging efforts in the understory (Cruz 1980 and Cruz 1988). However, this feature was then estimated to have a strong, positive effect on the tanager's occupancy when we clustered the bird community according to a suite of five distinct natural history. This apparent contradiction as to whether the percentage understory density is evidenced to have an effect on the occupancy probability of the Puerto Rican tanager suggests that this species' utilization of the understory may extend beyond its foraging habits. More directly, however, this discrepancy demonstrates that our grouping according to foraging guild
hinged more so upon shared similarities in what foods are consumed rather than where foods are consumed.
**Table 2.1**--Summary statistics and outcomes of grouping the avian community by a data-driven approach which grouped species based on similarities in relationships between habitat features and their modeled occupancy probabilities. Species members' codes presented are standardized to the American Ornithologists' Union, AOU.

<table>
<thead>
<tr>
<th></th>
<th>DD1</th>
<th>DD2</th>
<th>DD3</th>
<th>DD4</th>
<th>DD5</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total Membership</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(n)</td>
<td>9</td>
<td>6</td>
<td>5</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td><strong>Species Members'</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AOU Codes</td>
<td>ANEU, BANA, CAEL, GRKI, PRFL, PRSO, PRWO, PUEB, RLTH</td>
<td>ADWA, ANMA, EWWA, LAPE, PREM, PRTA</td>
<td>BFGR, GAGR, LOKI, PRLC, YFGR</td>
<td>BWVI, PRSP, PRTO</td>
<td>BAWW, GRMA, PROR, PRVI</td>
</tr>
<tr>
<td><strong>Total Detections</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(n)</td>
<td>1520</td>
<td>155</td>
<td>488</td>
<td>714</td>
<td>168</td>
</tr>
</tbody>
</table>
Table 2.2--Summary statistics and outcomes of grouping the avian community \textit{a priori} by foraging/mass guilds. Species members' codes presented are standardized to the American Ornithologists' Union, AOU.

<table>
<thead>
<tr>
<th></th>
<th>Large Frugivore, Granivore, Nectarivore (LFGN)</th>
<th>Small Frugivore, Granivore, Nectarivore (SFGN)</th>
<th>Large Insectivore, Carnivore (LIC)</th>
<th>Small Insectivore, Carnivore (SIC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Membership (n)</td>
<td>6</td>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Species Members' AOU Codes</td>
<td>BWVI, CAEL, PROR, PRSP, PUEB, RLTH</td>
<td>ANEU, ANMA, BANA, BFGR, GRMA, PREM, YFGR</td>
<td>GAGR, GRKI, LOKI, PRLC, PRSO, PRTA, PRWO</td>
<td>ADWA, BAWW, EWWA, LAPE, PRFL, PRTO, PRVI</td>
</tr>
<tr>
<td>Total Detections (n)</td>
<td>902</td>
<td>782</td>
<td>835</td>
<td>526</td>
</tr>
</tbody>
</table>


Table 2.3—Summary statistics and outcomes of clustering the avian community *a priori* by five natural history traits through *K*-means cluster analysis. Species members' codes presented are standardized to the American Ornithologists' Union, AOU.

<table>
<thead>
<tr>
<th></th>
<th>Natural History Trait Cluster 1 (C1)</th>
<th>Natural History Trait Cluster 2 (C2)</th>
<th>Natural History Trait Cluster 3 (C3)</th>
<th>Natural History Trait Cluster 4 (C4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Species Membership (n)</td>
<td>10</td>
<td>6</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Species Members' AOU Codes</td>
<td>ADWA, BANA, CAEL, LAPE, PRFL, PRLC, PROR, PRSO, PRTO, PUEB</td>
<td>ANEU, ANMA, GAGR, PRSP, PRVI, PRWO</td>
<td>EWWA, GRMA, PREM, PRTA</td>
<td>BAWW, BFG, BWVI, GRKI, LOKI, RLTH, YFGR</td>
</tr>
<tr>
<td>Total Detections (n)</td>
<td>1184</td>
<td>722</td>
<td>129</td>
<td>1010</td>
</tr>
</tbody>
</table>
Table 2.4—Estimates (and standard deviations) for the group-level hyperparameters of each habitat feature of interest on average group-level occupancy for all five data-driven groups delineated. The first column presents these same hyperparameters but estimated across the entire community of 27 focal avian species from our previous chapter's work. Estimates which garnered strong support (e.g. at least 75% of the Bayesian credible interval does not overlap zero) are indicated with an asterisk (*).

<table>
<thead>
<tr>
<th>Habitat Feature</th>
<th>Entire Community</th>
<th>Data-driven Group 1 (DD1)</th>
<th>Data-driven Group 2 (DD2)</th>
<th>Data-driven Group 3 (DD3)</th>
<th>Data-driven Group 4 (DD4)</th>
<th>Data-driven Group 5 (DD5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground Cover (%)</td>
<td>1.57* (1.28)</td>
<td>3.41* (2.17)</td>
<td>3.55* (2.21)</td>
<td>3.93* (2.27)</td>
<td>3.74* (2.14)</td>
<td>3.81* (2.08)</td>
</tr>
<tr>
<td>Understory Density (%)</td>
<td>-0.84* (0.81)</td>
<td>-3.19* (1.68)</td>
<td>-2.06 (2.51)</td>
<td>-2.12* (2.39)</td>
<td>-2.05* (2.60)</td>
<td>-1.90 (2.51)</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>1.70* (1.69)</td>
<td>3.00* (2.23)</td>
<td>2.25* (2.74)</td>
<td>2.55* (3.34)</td>
<td>2.42* (2.66)</td>
<td>2.05* (2.79)</td>
</tr>
<tr>
<td>Bird-friendly Trees (n)</td>
<td>4.81* (3.53)</td>
<td>3.51* (4.13)</td>
<td>2.25* (3.17)</td>
<td>2.57* (3.34)</td>
<td>2.40* (3.39)</td>
<td>2.53* (3.31)</td>
</tr>
<tr>
<td>Forest in Landscape (%)</td>
<td>-1.13 (2.58)</td>
<td>-2.27 (4.23)</td>
<td>-1.57 (3.59)</td>
<td>-1.79 (3.84)</td>
<td>-1.61 (3.74)</td>
<td>-1.52 (3.69)</td>
</tr>
</tbody>
</table>
Table 2.5—Estimates for the group-level hyperparameters of each habitat feature of interest on average group-level occupancy for all four foraging/mass guilds delineated. The first column presents these same hyperparameters but estimated across the entire community of 27 focal avian species from our previous chapter's work. Estimates which garnered strong support for being either positive or negative are indicated with an asterisk.

<table>
<thead>
<tr>
<th>Habitat Feature</th>
<th>Entire Community</th>
<th>Large Frugivore, Granivore, Nectarivore (LFGN)</th>
<th>Small Frugivore, Granivore, Nectarivore (SFGN)</th>
<th>Large Insectivore, Carnivore (LIC)</th>
<th>Small Insectivore, Carnivore (SIC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground Cover (%)</td>
<td>1.57* (1.28)</td>
<td>4.6* (2.13)</td>
<td>1.24* (1.14)</td>
<td>2.25* (1.55)</td>
<td>4.62* (1.88)</td>
</tr>
<tr>
<td>Understory Density (%)</td>
<td>-0.84* (0.81)</td>
<td>0.23 (2.47)</td>
<td>-0.43 (1.30)</td>
<td>-1.06 (1.75)</td>
<td>-0.73 (2.63)</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>1.70* (1.69)</td>
<td>2.70* (2.10)</td>
<td>0.51 (1.02)</td>
<td>5.38* (2.25)</td>
<td>1.93* (2.20)</td>
</tr>
<tr>
<td>Bird-friendly Trees (n)</td>
<td>4.81* (3.53)</td>
<td>0.46 (2.87)</td>
<td>7.18* (5.03)</td>
<td>4.22* (2.37)</td>
<td>-0.16 (2.80)</td>
</tr>
<tr>
<td>Forested Area in Landscape (%)</td>
<td>-1.13 (2.58)</td>
<td>0.11 (3.17)</td>
<td>-2.28 (2.73)</td>
<td>-0.34 (3.11)</td>
<td>0.36 (3.16)</td>
</tr>
</tbody>
</table>
Table 2.6—Estimates for the cluster-level hyperparameters of each habitat feature of interest on average cluster-level occupancy for all four natural history trait clusters delineated. The first column presents these same hyperparameters but estimated across the entire community of 27 focal avian species from our previous chapter’s work. Estimates which garnered much support for being either positive or negative are indicated with an asterisk.

<table>
<thead>
<tr>
<th>Habitat Feature</th>
<th>Entire Community</th>
<th>Natural History Trait Cluster 1 (C1)</th>
<th>Natural History Trait Cluster 2 (C2)</th>
<th>Natural History Trait Cluster 3 (C3)</th>
<th>Natural History Trait Cluster 4 (C4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground Cover (%)</td>
<td>1.57* (1.28)</td>
<td>4.73* (2.20)</td>
<td>2.22* (1.60)</td>
<td>2.17* (2.32)</td>
<td>0.41 (0.73)</td>
</tr>
<tr>
<td>Understory Density (%)</td>
<td>-0.84* (0.81)</td>
<td>1.39 (2.49)</td>
<td>1.03 (2.30)</td>
<td>1.98 (2.88)</td>
<td>-0.42 (0.80)</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>1.70* (1.69)</td>
<td>3.05* (2.52)</td>
<td>1.41* (1.81)</td>
<td>2.51* (2.57)</td>
<td>0.66 (1.11)</td>
</tr>
<tr>
<td>Bird-friendly Trees (n)</td>
<td>4.81* (3.53)</td>
<td>0.45 (2.94)</td>
<td>4.92* (2.63)</td>
<td>1.30 (2.72)</td>
<td>2.07* (2.46)</td>
</tr>
<tr>
<td>Forested Area in Landscape (%)</td>
<td>-1.13 (2.58)</td>
<td>0.21 (3.13)</td>
<td>0.88 (3.17)</td>
<td>0.01 (3.17)</td>
<td>-4.12* (2.21)</td>
</tr>
</tbody>
</table>
Table 2.7—Species-specific mean estimates (and standard deviations) for the effect of each habitat feature on three focal species’ occupancy probabilities. Estimates reported from data-driven groups are in fact the group-level hyperparameters rather than species-specific estimates since those estimates are unavailable using that approach. Those estimates which garnered very strong support (e.g. more than 95% of the Bayesian credible interval does not overlap zero) between the foraging/mass guild and the natural history trait cluster are presented with double asterisks, **. Those estimates which garnered strong support (e.g. at least 75% of the Bayesian credible interval did not cross zero) are presented with a single asterisk, *. The absence of an asterisk indicates no such statistical support for the estimate.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ground Cover (%)</th>
<th>Understory Density (%)</th>
<th>Canopy Cover (%)</th>
<th>Bird-friendly Trees (n)</th>
<th>Forested Area in Landscape (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Antillean Euphonia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ANEU</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SFGN guild</td>
<td>1.67* (1.93)</td>
<td>0.44 (2.07)</td>
<td>0.80 (1.93)</td>
<td>7.59** (6.18)</td>
<td>-2.23 (4.07)</td>
</tr>
<tr>
<td>C1 cluster</td>
<td>5.03** (2.81)</td>
<td>0.87 (3.99)</td>
<td>2.54 (3.86)</td>
<td>0.43 (4.00)</td>
<td>0.23 (4.19)</td>
</tr>
<tr>
<td>DD1</td>
<td>3.41** (2.17)</td>
<td>-3.19** (1.68)</td>
<td>3.00** (2.23)</td>
<td>3.51* (4.13)</td>
<td>-2.27 (4.23)</td>
</tr>
<tr>
<td><strong>Elfin Woods Warbler</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EWWA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SIC guild</td>
<td>4.66** (2.51)</td>
<td>-1.33 (3.90)</td>
<td>2.37 (3.70)</td>
<td>-0.04 (3.91)</td>
<td>0.41 (4.32)</td>
</tr>
<tr>
<td>C3 cluster</td>
<td>2.71* (3.13)</td>
<td>2.39 (3.58)</td>
<td>2.95* (3.58)</td>
<td>1.25 (3.84)</td>
<td>0.02 (4.30)</td>
</tr>
<tr>
<td>DD2</td>
<td>3.55** (2.21)</td>
<td>-2.06 (2.51)</td>
<td>2.25** (2.74)</td>
<td>2.25 (3.17)</td>
<td>-1.57 (3.59)</td>
</tr>
<tr>
<td><strong>Puerto Rican Tanager</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PRTA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LIC guild</td>
<td>3.18** (3.20)</td>
<td>0.67 (3.09)</td>
<td>5.55** (3.50)</td>
<td>4.39* (3.90)</td>
<td>-0.31 (4.24)</td>
</tr>
<tr>
<td>C3 cluster</td>
<td>2.88* (3.17)</td>
<td>2.71* (3.48)</td>
<td>2.97* (3.57)</td>
<td>1.80 (3.53)</td>
<td>0.07 (4.31)</td>
</tr>
<tr>
<td>DD2</td>
<td>3.55** (2.21)</td>
<td>-2.06* (2.51)</td>
<td>2.25** (2.74)</td>
<td>2.25 (3.17)</td>
<td>-1.57 (3.59)</td>
</tr>
</tbody>
</table>
Figure 2.1—Data-driven approach to testing for the likely number of homogeneous groups among the greater community of 27 bird species. Results suggest that five distinct groups exist according to species’ common responses in occupancy probability to the five habitat features of interest.
Figure 2.2—Dendrogram of the grouping results from the data-driven approach. Likely break points separating the five data-driven groups are indicated by a bold, dashed horizontal line. These break points lie between 0.6 and 0.7 in accordance with the estimated posterior probability for five groups shown above in Figure 1. Number references refer to species ordered alphabetically according to their four-letter code standardized by American Ornithologists’ Union (AOU).
LITERATURE CITED


Introduction

The protection of biodiversity is arguably the greatest priority of conservation in the twenty-first century. However, the immense biological reality which the term “biodiversity” encompasses can hinder efficient conservation management. In particular, the breadth and depth of living things which vary across microscopic genes to vast ecoregions present a particular challenge not only in defining certain aspects of interest but also in measuring those aspects precisely. Additionally, habitat management for purposes of biodiversity conservation is complicated by the fact that efforts enacted today will exact future repercussions that cannot be predicted certainly. Nevertheless, this uncertainty does not erase the need for swift and efficacious conservation action. Therefore, *Structured Decision-Making* has been readily adopted among conservationists since its processes allow for selecting the best alternative among a suite of alternatives proposed to satisfy a specific objective while accounting for the different consequences and trade-offs of choosing among those alternatives.

In Puerto Rico, a concerted effort among governmental and nongovernmental bodies--including the United States Fish and Wildlife Service (USFWS), the Puerto Rican Department of Natural Resources and Environment (Spanish: PRDRNA), and a conservation nonprofit known as “Casa Pueblo”-- is underway. These entities have partnered with the intent of increasing total protected area on the island from its current eight to a hopeful fifteen percent. So that environmental protection can be coupled with a rejuvenation of the agricultural
economics sector, there is sincere interest to support agroecosystems, or, lands which provide sustainable agricultural output while also serving as valuable wildlife habitat or performing much-needed ecosystem services. For Puerto Rico, these would be coffee agroecosystems given the extent to which that crop has already been cultivated on the island and the market potential for coffee as a cash crop. However, achieving this harmony between agricultural and ecological priorities proves no easy feat. In order to do so, conservationists working in Puerto Rico require more highly resolved information regarding those habitat characteristics which encourage or impede occupancy by native or endemic species of conservation concern.

With over 10,000 species described, birds are the most diverse taxa of vertebrate fauna. Because of this diversity and the myriad ecological services which they perform, birds are a focal point for conservation, especially in the Neotropics. Therefore ongoing conservation efforts in Puerto Rico have specified the need to create and conserve suitable habitat for birds on these coffee agroecosystems. However, because biodiversity assessment is equivocal, it is not known certainly where biodiversity is concentrated nor do we understand exactly which habitat features promote the occurrence of particular species of interest. To better address this need, my thesis work stipulated the following research questions: (1) How does the choice of biodiversity metric influence our understanding of the habitat features driving those same biodiversity patterns which we observe? and (2) How does the imposition of different grouping schemes to better tailor community-wide occupancy analyses affect our modelling of species-habitat relationships? I presented these questions which motivated my master’s research in my thesis chapters one and two, respectively.
Synopsis of Methods and Analyses

My team and I sampled the avian community at a total of 120 sites situated across the Cordillera Central region of Puerto Rico. This is a mountainous region located in the southwestern and western central part of the island and is the coffee basket of Puerto Rico. I randomly selected sites to be located in either forested land covers or coffee agricultural land uses according the data from the National Land Cover Database (NLCD) of 2012. Before including any sites in our sampling pool, I ground-truthed the land covers and, for coffee plantations, I interpreted the cultivation to be either sun- or shade-grown. I also obtained access permission from landowners for those sites located on private lands. In order to better distill species-habitat relationships, my team and I performed a vegetative survey at all 120 sampling sites that measured the percentage canopy cover, the percentage understory density, the percentage ground cover.

It is estimated that a total of fifty-six avian species inhabit Puerto Rico. However, my thesis research to better understand which and how certain habitat features affect birds’ occupancy status was restricted to those birds that are native, endemic, or otherwise of conservation concern. This limited my attention to twenty-seven focal bird species. On these focal birds my team and I collected presence/absence data during three repeat visits to each of our 120 sampling sites. With these data, I first built a hierarchical community-level occupancy model to more rigorously estimate the occupancy probability and determine the occupancy status of each of our twenty-seven focal birds. Then, to better tailor these species-specific estimates by dividing the greater community into more homogenous and more meaningful subgroups, I built hierarchical group-level community occupancy models. These group-level
occupancy models explored three different approaches to subsetting the greater avian community of 27 species: Two *a priori* and one data-driven approaches. The first *a priori* approach yielded four groups according to species’ shared primary foraging guilds and average body mass. The second *a priori* approach created four clusters based off results of a K-means cluster analysis on five natural history traits. Finally, the data-driven approach revealed five groups delineated by species’ similar responses in occupancy probabilities across five habitat features.

To estimate how the habitat affects birds’ occupancy probabilities, my team and I conducted a simple habitat assessment and vegetative data survey at each of the 120 sampling sites. We conducted these surveys following the collection of presence/absence (detection/nondetection) data on our focal bird species. Because Puerto Rico is located in the tropics, the habitat characteristics we surveyed did not change seasonally and we were able to perform habitat inventories prior to any farm management or other agricultural activities. I therefore am confident that the habitat characteristics which we surveyed were very similar to those perceived by the birds during the time at which we sampled the avian community. Our habitat assessment focused on five habitat features that are critical to resource provisioning and the creation of suitable, if not preferable, habitat for our focal birds: Percentage ground cover, percentage understory density, percentage canopy cover, percentage of forested area in the surrounding landscape, and the number of “bird-friendly” trees. These bird-friendly trees were selected with the help of a local tree expert (A. Morales) according to criteria that were relevant to both the ecology of my focal avian community and the spatial sampling of my study.
Major Findings of Chapter 1

For my first chapter, I was broadly interested in comparing and contrasting two different biodiversity metrics for the purposes of clarifying expected outcomes of conservation planning. In this chapter, I stipulated three research objectives. The first was to examine whether two different species-level biodiversity metrics (Species Richness and Taxonomic Diversity) identify similar ‘hot’ and ‘cold’ spots of biodiversity on the island. For the second objective, I investigated the drivers of species-level biodiversity, first at the coarser, more summarized level of habitat type and then by the finer, more detailed level of the habitat features themselves. And, finally, I compared the relationship of each biodiversity metric to various habitat features of interest to determine whether the two metrics are driven by different habitat features.

My results indicated that finer-scale habitat features, not generalized habitat types, must be considered to more accurately predict whether a parcel of land will be a hot or cold spot of avian biodiversity. Regardless of whether biodiversity is assessed using a species richness or a taxonomic diversity metric, trends in estimated biodiversity scores for a particular habitat type are similar. I found all cold spots of biodiversity to be situated in forested habitats. But, I also found forested sites to have the greatest range in biodiversity scores for both biodiversity metrics that I employed. And, although hotspots of either metric were almost exclusively located in coffee plantations, plantations under both sun- and shade-grown management were equally represented. My examination of five finer-scale habitat features revealed three of those habitat features to significantly differ between the hot and cold spots of biodiversity designated by either metric: I found hot spots of both species richness and taxonomic diversity to have
significantly less canopy coverage and surrounding forested area than did either of those metrics’ respective cold spots. However, my findings also suggested the opposite relationship between a given biodiversity metric’s hot and cold spots in regards to the number of bird-friendly trees at the site in question, with hot spots containing significantly more bird-friendly tree species than their respective cold spots. When I compared just within hot spots but across our two biodiversity metrics, I found only one habitat features to significantly differ: Hot spots according to species richness had greater percentage ground cover than did those according to taxonomic diversity.

Implications of Major Findings of Chapter 1

In light of the findings detailed in Chapter 1, I propose three recommendations to conservation practitioners: First, biodiversity conservation requires action at finer and more localized spatial scales since generalized habitat types failed to prove reliable indicators of biodiversity estimates, particularly the distinction of hot from cold spots. Secondly, biodiversity conservation must adopt a holistic approach such that multiple, finer-scale habitat features are targeted since no single feature predominantly drives the ecological dynamics responsible for creating biodiverse communities. And, finally, conservation planning must carefully consider which facets of biodiversity it most values. My research suggested that the metric chosen to assess biodiversity patterns can have furtive consequences on conservation outcomes since habitat management schemes developed in light of one metric may compromise other aspects of biodiversity better captured by another metric.
Major Findings of Chapter 2

Ecological communities are diverse and dynamic entities of biological organization comprised of both individual units (species) but also the sum of those units. Therefore, research for the purposes of conserving species-rich ecological communities ought to clarify not only how entire communities but also how individual species interact with their environments. Subdividing, subsetting, or otherwise grouping together species of a greater, biodiverse ecological community facilitates research that is both community-wide but also more species-specific. However, enforcing different grouping schemes or criteria may bias which habitat features are deemed important for conserving those groups delineated. Therefore, the second chapter of my thesis investigated how the imposition of three different grouping schemes (two a priori and one data-driven) on the focal community of 27 birds might suggest different habitat features to drive occupancy probabilities.

The first of my two a priori grouping schemes invoked the very popular guild concept to demarcate four mutually exclusive guilds amongst the 27 focal birds: Large Frugivores/Granivores/Nectarivores (LFGNs), Small Frugivores/Granivores/Nectarivores (SFGNs), Large Insectivores/Carnivores (LICs), and Small Insectivores/Carnivores (SICs). Results from guild-specific occupancy models demonstrated that some but not all guilds were responsive to those habitat features which were found to be significant according to our previous community-wide occupancy modeling. For example, both the LFGN and LIC guilds were much more sensitive to the significant effect of percentage canopy cover on occupancy than was the entire avian community as a whole. However, the effect of percentage canopy cover on occupancy was no longer significant for either SFGN or SIC. Also, occupancy of the
LIC guild had a similar sensitivity to bird-friendly trees as did occupancy of the greater avian community. But, bird-friendly trees did not significantly affect occupancy estimates for either LFGN or SIC guilds. Occupancy of the SFGN guild, however, was more sensitive to the effect of bird-friendly trees than occupancy of the greater avian community. By subsetting the avian community according to primary guild first and then by body mass of birds, this analysis discovered differences between guild-level occupancy estimates in response to the habitat features percentage canopy cover and richness of bird-friendly trees, with occupancy of large-bodied birds responding differently, on average, than that of small-bodied birds of the same primary foraging behaviors.

The second *a priori* grouping scheme employed *K*-means clustering on five natural history traits. Initial cluster assignments were cleaned in order to yield clusters which were statistically more similar in terms of number of species members and total number of detections. In comparison to my previous community-level occupancy modeling across all 27 species of interest, I found even more discrepancies in the support garnered and estimated effects of habitat features on average occupancy probabilities for each natural history trait cluster. Surprisingly, I found percentage canopy cover to have no significant effect on average occupancy of any cluster except for cluster 1. Similarly, the number of bird-friendly trees had a significant effect on average occupancy only for cluster 2. Finally, occupancies for all but the fourth natural history trait cluster were not significantly impacted by the percentage forested area in the landscape surrounding any given site. However, whereas the community-wide response to surrounding forested area was significant and positive, the average response in cluster 4 occupancy to this habitat feature was significant and very negative. When comparing just between natural history trait-based clusters, the responses of each cluster’s
average occupancy estimates were found to respond uniquely in terms of the significance of and sensitivity to different habitat features.

Finally, the data-driven approach to subsetting the greater community of 27 birds revealed five groups according to similarities in species’ responses to environmental covariates (the habitat features examined in our habitat assessment and vegetative survey) on their estimated occupancy probabilities.

I also explored whether management of certain species would be especially affected by the grouping scheme imposed upon the greater avian community. For three particular species—the Antillean euphonia (*Euphonia musica*, ANEU), the Elfin woods warbler (*Setophaga angelae*, EWWA), and the Puerto Rican Tanager (*Nesospingus speculiferus*, PRTA)—I found remarkable differences in the estimated sensitivity to and the amount of statistical support garnered for percentage understory density, percentage canopy cover, and the richness of bird-friendly tree species according to the delineations imposed to group these and other species of the greater avian community. However, I also found that for these three species, regardless of the grouping scheme imposed, my models always revealed strong evidence for a very positive relationship between percentage ground cover and species-specific occupancy probabilities. In contrast, none of my models under any grouping scheme ever demonstrated much support for any sort of relationship between species-specific occupancy and the percentage forested area in the surrounding landscape.
Implications of Major Findings of Chapter 2

My investigating the consequences of subdividing ecological groups in occupancy modeling provided greater resolution of species-habitat relationships that would otherwise have remained confounded or masked had the avian community been treated as a single, homogeneous entity. My dissecting the greater community of 27 bird species into various groups allowed focusing on those species most likely responsible for the community-wide habitat relationships that were modeled in Chapter 1. This also facilitated more precise evaluations of species-habitat relationships in order to tailor conservation action and habitat management to target particular types of species. Doing so affords a precision that is often not enjoyed by landscape-level conservation planning.

My comparing the species-habitat relationships modeled on ecological subgroups made according to different grouping schemes also clarified the biases or tendencies associated with various grouping schemes. Most practically, I found that for certain sensitive species of interest—the Antillean Euphonia, the Elfin woods warbler, and the Puerto Rican tanager—my models garnered more or less support for their being a strong relationship between certain habitat features and species-specific occupancy rates. This was especially true for the modeled relationships between occupancy and both the richness of bird-friendly trees and the percentage understory density. My examination of the species-specific implications of community-wide occupancy modeling demonstrated the need to justify the application of any grouping scheme, especially \textit{a priori} ones. This fine-scale analysis also presented a novel method for grouping species using a data-driven approach. While this novel approach does permit more tailored modeling over both the less advantageous one-size-fits-all community-
level modeling and the presumptive group assignments imposed by *a priori* approaches, I do recommend that this data-driven approach be used as a means to further refine community-level to group-level (rather than species-specific) management. This is because the group-level estimates derived from the data-driven approach are amalgamated across a dynamic, rather than fixed, species membership. However, I recognize and promote this approach for its utility to examine more precisely whether occupancy by certain species assemblages is or is not responsive to particular habitat features of interest than would otherwise be possible via community-level hierarchical occupancy modelling alone. Additionally, we find this data-driven approach especially suitable for our Puerto Rican ecosystem given that many avifauna of our focal community exhibit surprisingly broad functional niches and so can assume a wide diversity of realized niches. This diversity is not accommodated by restrictive *a priori* grouping approaches.

However, our applying a data-driven approach to grouping also demonstrated the greater expense required of this or any other data-driven approach, a luxury often not enjoyed freely by conservation efforts. So, our investigating species-habitat relationships according to occupancy models fit to data-driven ecological groups confers two benefits: First, it proximately offers our current conservation partners more confident assessments of how certain habitat management actions are likely to affect certain birds’ occupancy states by removing the ecological assumptions inherent to *a priori* analyses. This benefit is conferred by comparing and contrasting results of occupancy models performed at the community level with those analyzed at the data-driven group-level, essentially allowing conservation practitioners to focus in on finer details rather than just the “big picture.” Secondly, the data-driven facet of our research ultimately provides a standard for comparing how well any *a priori* grouping
schemes would capture the ecological reality of those species and systems under conservation concern. Such comparisons could permit future conservation work to judiciously allocate resources towards those species whose management is best served by data-driven analyses and away from those species whose habitat needs can be captured well by more convenient a priori knowledge.

Significance of This Work

My thesis research offers significant insight to the ecological dynamics of a tropical avian community whose management is critical to ensuring long-term, landscape-level conservation goals in Puerto Rico. My thesis research also provides science-based, practical management suggestions that will clarify uncertainties which would otherwise compromise informed conservation decision-making. Both chapters of my research utilized hierarchical occupancy modeling to more rigorously estimate the occurrence of avian species on the island. My first chapter also explored the consequences of using different biodiversity metrics on conservation planning, particularly in terms of identifying ‘hot’ and ‘cold’ spots of avian biodiversity to guide habitat prioritization and suggest habitat management intended to augment biodiversity of avifauna. My second chapter then examined occupancy modeling on more homogeneous subsets of the greater avian community at greater resolution and investigated the consequences of three different approaches to subdividing the avian community.
Suggestions for Future Studies

While my thesis research provides greater resolution to the complexities of tropical ecology and conservation, still there remains much to be done that could further advance this line of research. I highlight two specific recommendations for future studies. The first recommendation I advocate is to employ dynamic occupancy modeling across the current detection/nondetection data set, and, to continue to develop this data set into the future. This would permit occupancy analyses to model across a more long-term data set, thereby reducing the risk that results are based on atypical ecological circumstances and increasing the chance that occurrence trends and the species-habitat relationships inferred from them do indeed reflect ecological truth. The second recommendation I propose is to explore the legitimacy of different categorizations of coffee plantation management for the purpose of creating and assessing plantations as agroecosystems. I suggest this in light of my finding that generalized habitat types alone are too highly summarized to provide a meaningful indication of an agroecosystem’s avian biodiversity potential. Instead, one must consider the finer-scale habitat features. Therefore, designating more detailed categories of coffee plantations across a suite of their habitat features and vegetative structure would tailor the popular but overly simplistic “sun-” and “shade-grown” classifications.
## Appendix 1: Focal Birds’ Taxonomic Assignments

<table>
<thead>
<tr>
<th>Common Name</th>
<th>AOU Code</th>
<th>Order</th>
<th>Family</th>
<th>Subfamily</th>
<th>Genus</th>
<th>Specific epithet</th>
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Appendix 2: “Bird-friendly” Tree Species of Interest. I detail the Linnean nomenclature from Family downward for “bird-friendly” tree species of interest. Because many trees demonstrate much morphological diversity that can complicate accurate identification in the field or have wide evolutionary radiation but similar functional roles, some trees are only identified down to Genus. I did not specify palm trees past the family level given their disputed taxonomy and their existence as (functional) ornamentals.

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Specific Epithet</th>
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</table>
Appendix 3: Selecting and Surveying Bird-friendly Trees

To select the list of “bird-friendly” trees that I presented in Appendix 2, I first compiled all information from the literature on endemic, native, or fully naturalized trees described to be in Puerto Rico. At this time, I also stipulated that those trees be known to provide some sort of resource or service to at least one of the twenty-seven focal bird species during any stage of its lifetime. I consulted with a local silvics and botany expert (A. Morales) who helped cull my preliminary list to contain only those tree species that would be common to the specific regions and habitats (coffee plantations and montane forests) in which we sampled. This list of trees was then field-tested for a period of one week during which time A. Morales, a field technician, and I visited a random sample of 12 sun-grown coffee plantations, 12 shade-grown coffee plantations, and 16 forested sites to ensure our list captured trees that were indeed common to the region and habitats. At my discretion and with the counsel of A. Morales, we also added those tree species which we encountered multiple time and which directly provide a resource or service to our focal birds but which had previously been excluded from the tree list.

To familiarize ourselves with the tree species, we also spent our time field-testing the preliminary tree list to learn the identification and basic natural history of each tree on the finalized list. We relied heavily on the books Common Trees of Puerto Rico and the Virgin Islands\(^1\) and Rare and Endemic Trees of Puerto Rico\(^2\). Both books we used each in the field. For any trees whose identification we were uncertain we took numerous pictures and called once again on the expertise of A. Morales for confirmation.


Appendix 4: Calculating Percentage Forested Area in the Landscape

In order to calculate the percentage forested area in the landscape, we constrained our “landscape” perspective to 250 meters beyond the outer extent of our 50-meter radius sampling plot on which we conducted our avian point counts. We chose this distance of 250 meters given allometric data on estimated daily dispersal distances for some of our focal birds. We obtained the landcover/landuse data for all of Puerto Rico from the National Landcover Database (NLCD) from 2012. In ArcMap (ESRI) we condensed the following forest land covers into a single land cover type (forest). The seventeen land cover types listed below include all such land covers identified by the NLCD in Puerto Rico to be some sort of forest, shrubland, or woodland. Our consolidation therefore summarized mostly across seral stages (primary or secondary), dominant leaf phenology (deciduous or evergreen)

1. Dry and moist serpentine woodland and shrubland
2. Lowland moist noncalcareous shrubland and woodland
3. Mature primary and secondary montane wet noncalcareous evergreen elfin woodland cloud forest
4. Mature primary and secondary montane wet noncalcareous evergreen Sierra Palm forest
5. Mature secondary dry and moist serpentine semideciduous forest
6. Mature secondary lowland moist evergreen noncalcareous forest
7. Mature secondary montane wet noncalcareous evergreen forest
8. Mature secondary montane wet serpentine evergreen forest
9. Montane wet alluvial shrubland and woodland
10. Montane wet evergreen noncalcareous shrubland and woodland
11. Wet serpentine shrubland and woodland
12. Young secondary dry and moist serpentine semideciduous forest
13. Young secondary lowland moist evergreen noncalcareous forest
14. Young secondary montane wet alluvial evergreen forest
15. Young secondary montane wet noncalcareous evergreen forest
16. Young secondary montane wet serpentine evergreen forest

We next buffered a circular zone of 300-meter radius around the center point of every sampling plot. We then calculated the area in square meters that belonged to our consolidated “forest” landcover type. For those sampling plots that were located in a forested habitat, we subtracted an area of 7,853.98 square meters from the previous estimate. This subtraction removed the amount of forested area confined inside the sampling plot itself and so ensured that our estimate of forest cover was pertinent to the landscape beyond our sampling plots. Finally, we converted these forested area estimates in square meters to percentages of the total landscape area
### Appendix 5: Interspecific Taxonomic Distances

This appendix reports the number of unique taxonomic rankings from Order to Specific epithet between each of my twenty-seven focal bird species.

<table>
<thead>
<tr>
<th></th>
<th>ADWA</th>
<th>ANEU</th>
<th>ANMA</th>
<th>BANA</th>
<th>BAWW</th>
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