Spring 4-3-2019

Niche Evolution Along a Gradient of Ecological Specialization

Meaghan Conway
University of Maine, meaghan.conway@maine.edu

Recommended Citation

Conway, Meaghan, "Niche Evolution Along a Gradient of Ecological Specialization" (2019). *Electronic Theses and Dissertations*. 3025.
https://digitalcommons.library.umaine.edu/etd/3025

NICHE EVOLUTION ALONG A GRADIENT OF ECOLOGICAL SPECIALIZATION

By

Meaghan Conway

B.A. State University of New York, Binghamton

A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Ecology and Environmental Science)

The Graduate School

The University of Maine

May 2019

Advisory Committee:

Brian J. Olsen, Associate Professor, School of Biology and Ecology, Advisor

Brian J. McGill, Professor, School of Biology and Ecology

Michael T. Kinnison, Professor, School of Biology and Ecology

Adrienne I. Kovach, Assistant Professor, Department of Natural Resources and the Environment, University of New Hampshire

Jacquelyn L. Gill, Associate Professor, School of Biology and Ecology

NICHE EVOLUTION ALONG A GRADIENT OF ECOLOGICAL SPECIALIZATION

By Meaghan Conway

Thesis Advisor: Dr. Brian J. Olsen

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
(in Ecology and Environmental Sciences)
May 2019

The concept of the ecological niche is fundamental to understanding constraints on species distributions in space and time, and in explaining the origin and maintenance of biodiversity. A niche can be broadly defined to include all of the biotic and abiotic conditions that a species requires to persist. Niche breadth, or the degree of specialization, may influence how labile a species niche is, which can have broad implications for species ability to adapt to environmental change, and for explaining patterns of diversification. I investigated mechanism that facilitate or constrain niche evolution at multiple scales. First, I developed an index of specialization in bill morphology using museum specimens across a diverse New World Passerine clade. I used this index of specialization to evaluate the relative influence of geographic and ecological niche partitioning on speciation rates across islands and continents. I then examined evolutionary transition rates among generalist and specialist bill morphotypes to determine if specialization constrains further evolution over long time scales, thus creating an evolutionary dead end. My results suggest that specialization increases speciation rates, and that niche expansion allowing transitions from specialist back to a more generalist bill morphology were common. I further explored mechanisms that drive these broad scale patters by examining patterns of intraspecific niche partitioning in closely related tidal marsh passerines. I found that habitat characteristics that reflected a salinity gradient best explained parallel patterns of bill size divergence among populations of two closely related sparrow species. Lastly, I examined if the definition of specialization varies across niche axes. We found that niche breadth, or the degree of specialization, is correlated among functional, environmental, and competition axes among five species of Passerelid sparrows. By examining the influence of specialization on macroevolutionary patterns of diversification and patterns of niche partitioning within species we gain a more comprehensive understanding of how niches evolve across different temporal and taxonomic scales. I found specialization is associated with increased speciation rates that influence continental-scale patterns of diversification. I also provide evidence that specialists retain the potential for niche expansion at the species and population scale. Patterns of intraspecific niche partitioning along habitat gradient presented here also increase our understanding of how species might adapt to change at scales that are applicable to local conservation. My results suggest strategies to incorporate a diversity of habitat characteristics may be beneficial for conserving intraspecific variation and adaptive capacity of specialist species.

ACKNOWLEDGEMENTS

I received funding from a National Science Foundation RAPID grant (DEB-1340008), the United States Fish and Wildlife Service, The North Atlantic Landscape Conservation Cooperative, The USDA National Institute of Food and Agriculture McIntire-Stennis Project Number ME0-21710, The Maine Agricultural and Forest Experiment Station (MAFES), The University of Maine Graduate Student Government, University of Maine Graduate School, The Garden Club of America, and The Climate Change Institute. I am thankful to Paul Sweet at The American Museum of Natural History, Chris Milensky at The Smithsonian National Museum of Natural History, and Ben Marks at The Field Museum for providing access to specimens. I am thankful for a large number of collaborators who shared their expertise and provided logistical support, including Maine Department of Inland Fisheries and Wildlife, Maine Coastal Islands National Wildlife Refuge (NWR), Moosehorn NWR, Rachel Carson NWR, Parker River NWR, Long Island NWRC, Rhode Island NWRC, Monomoy NWR, Bombay Hook NWR, Edwin B. Forsythe NWR, Blackwater NWR, Moosehorn NWR, and Massachusetts Audubon. I am also thankful to numerous landowners who granted access to their property. I am grateful for our SHARP collaborators, for their wealth of knowledge, constant willingness to help, and their creative and inspiring ideas. I am grateful to a large number of undergraduates, especially Val Watson, Kyle Lima, and Lindsay Ridlon who helped me process and digitize thousands of photos. I was so lucky to have the most wonderful and amazing people share their creativity and insights while putting in long hours in the field to help me collect data, including Kelly Morris, Melody Chimahusky, Angela Hansen, and Laura Gomez-Murillo. I am thankful to the EEE

discussion group and the McOlskin lab group for providing a supportive atmosphere and insightful comments and suggestions, and to Mike Harvey for helpful suggestions on state-dependent speciation analyses. I also thank my committee for insightful discussions, challenging questions, and guidance on analysis. I am thankful to Courtney Conway and my lab mates in Arizona, for making me a better scientist, and inspiring me to pursue a PhD, and to Katy Pope who got me hooked on birds back in the day. I am thankful for friends and lab mates for their support, sharing in the trials and tribulations of graduate work, and providing everything from statistical advice, to baked goods, lending of furred companions, group runs, and just generally not being satchels of Richards, especially Mo Correll, Jennie McCabe, Kate Ruskin, Kate Miller, Jess Haghkerdar, Kaizad Patel, Sonja Birhtisel, Laura Garey, and Kenzie Roeder. I thank the administrative support staff, including Trish Costello, Julie Eubanks, and especially Betty Lee and Becky Addessi for processing mounds of paperwork. I am also grateful for a wonderful and supportive advisor, Brian Olsen, for his enthusiasm, laughter, patience, long winding tangents, whiteboard drawings, sliced bread, and for constantly challenging the capacity of my brain. And lastly, I am thankful for parents who always encouraged and supported my adventures and educational pursuits.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The ecological niche concept plays a central role in understanding constraints on species distributions in space and time, and in explaining the origin and maintenance of biodiversity. Early niche concepts included conditions required for an organism or species to exist (Grinnell 1917) and the functional or ecological role of a species within the environment (Elton 1927). A more quantitative approach defined the niche as an infinite number of specific factors in n-dimensional space that might limit the ability of an organism to exist at a particular location. This n-dimensional concept broadly defined the niche to include all of the biotic and abiotic conditions that a species requires to persist (Hutchinson 1957). Species niches are not static (Holt 2009), yet many questions remain about the ecological and evolutionary processes that describe how a species niche changes over space and time. While there is some evidence that niches can be conserved over long time scales (Martinez-Meyer et al. 2004, Kellermann et al. 2012, Barrow et al. 2018), empirical studies have also documented rapid evolution in response to a variety of selection pressures, suggesting that species niches can also be highly labile (Grant 2002, 2006; Greenberg et al. 2012b, a, 2016; Richardson and Urban 2013, Langin et al. 2015, Noguerales et al. 2016, Friis et al. 2018). How conserved or labile a species niche is can have important consequences for species distributions, their ability to adapt to environmental change (Holt 2003), and for large-scale patterns of diversification (Wiens 2004). Thus, it is important to understand the mechanisms that facilitate or constrain niche evolution within populations and among species. At the macro-evolutionary scale, we need to understand how labile niche breadth is and how those changes relate to diversification. At a smaller taxonomic scale, we need to understand how niches become structured among populations and across environmental dimensions.

At a macroevolutionary scale, how specialized a species niche is may facilitate or inhibit diversification. For instance, niche partitioning is hypothesized to promote rapid radiations of specialized taxa following the colonization of a novel habitat (Schluter 2000, Gavrilets and Losos 2009). However, this process may slow as empty niche space becomes filled (Sepkoski 1998, Rabosky and Lovette 2008, Reddy et al. 2012), and increased specialization is also associated with high extinction risk (Jablonski 2008, Colles et al. 2009), which would cause the reverse effect on diversification. As species become more specialized for a particular ecological niche, they may also become constrained in their ability to adapt to new ecological opportunities due to low genetic variation (Futuyma and Moreno 1988, Futuyma et al. 1995, Kellermann et al. 2009). These patterns have led some to hypothesize that evolution of niche characteristics proceeds from generalized to specialized, and this trend toward ecological specialization is largely irreversible (e.g. the law of the unspecialized: Cope 1896; the generalist-to-specialist hypothesis: Futuyma and Moreno 1988).

While niches are often thought of as a species-level trait, numerous organisms show variation in functional traits across populations (Bolnick et al. 2003), and this intraspecific niche variation can determine a species ability to adapt to changes in environmental conditions (Holt 2009, Laughlin and Messier 2015). The scale at which intraspecific traits vary also has important ecological and evolutionary implications (Bolnick et al. 2003) and can help determine whether taxa are evolutionarily buffered against environmental change (Etterson 2008, Reed et al. 2011, Hoffmann and Sgrò 2011). Ultimately it is this sub-species structure in niches that sets the stage for the macro-evolutionary patterns described above, yet there are many open questions regarding how niche variation is organized within species.

Lastly, a species niche breadth can be defined along multiple dimensions, or niche axes (Hutchinson 1957, Vamosi et al. 2014). Most species are likely generalist on some axes and a specialist on others (Poisot et al. 2011). Correlation of niche breadth among traits can either constrain or facilitate evolution, depending on the context and the direction of selection (Laughlin and Messier 2015). For example, species may lack variation in key physiological traits that may limit their ability to adapt to conditions outside of their current niche (Kellermann et al. 2009), even if they have ample genetic variation to do so in other traits. Therefore, a greater understanding of how niche breadth is related across multiple trait axes will help inform what selective mechanisms are likely to structure niches across populations and open the door to greater macroevolutionary changes.

My dissertation examines how specialization facilitates or constrains niche evolution at multiple scales. My first two chapters use an index of specialization based on bill morphology to examine if specialization facilitates or constrains macroevolutionary patterns across a diverse New World avian clade. My first chapter determines the relative influence of specialization and geographic range size on speciation rates. I also explored whether these processes were similar across island and continental scales. My second chapter estimates character state transitions between generalist and specialist bill morphologies across the same avian clade to test the hypothesis that specialization limits further niche evolution. My last two chapters focus on a suite of passerine birds living in tidal marshes in the northeastern U.S. and compares niches among populations within species. By understanding how niches are structured within species and across niche axes, I will elucidate which evolutionary mechanism may underlie some of the macro-evolutionary patterns I describe in the first two chapters.

Tidal marshes are highly productive ecosystems with low species diversity that exist along an ecological gradient varying in tidal influence and salinity (both of which are novel selection pressures on marsh colonizers from more inland habitats). Phenotypic trait evolution might thus be expected to vary in response to local environmental conditions. Each of five Passerellid sparrow species show differences in how adapted they are to the tidal marsh ecosystem, and this degree of adaptation and dependence on the marsh aligns with the length of their hypothesized evolutionary association with this ecosystem. This suggests that similar environmental factors may play a role in shaping the niches of the species within this clade. As such, they represent a replicated system that can inform our understanding of how niches change following the colonization of a new habitat.

My third chapter focuses on the scale of intraspecific niche partitioning within and among populations of three of these sparrows. A species level niche can change through changes in: 1) population level niche breadth, if the amount of variation within or among individuals within the population changes, or 2) population level niche position, if the mean trait value for a population changes. We examined variation in niches among populations within three species to test predictions of major drivers of intraspecific niche variation. We tested the relative influence of interspecific competition, intraspecific density, and vegetative composition (a proxy for the salinity and tidal gradients) on differences in niche breadth and niche position among populations to determine if similar symptoms of niche evolution occur among taxa that independently colonized the tidal-marsh ecosystem.

My fourth chapter examines variation among multiple niche axes to determine if the definition of specialization changes depending on which niche axis is examined. We tested whether niche breadth is correlated among functional, performance, competitive, and environmental niche axes. We also tested the ability of each niche axis category to predict niche breadth estimated by the remaining niche axes. Understanding how selection along a single environmental axis alters multiple additional niche axes will increase our ability to predict constraints on species response to environmental change.

By examining the influence of specialization on macroevolutionary patterns of diversification and patterns of niche partitioning within species we can gain a more comprehensive understanding of how niches evolve across different temporal and taxonomic scales. We gain an understanding of how species might adapt to change at scales that are applicable to local conservation, and an understanding of drivers of continental-scale patterns of biodiversity.

CHAPTER 2

CONTRASTING DRIVERS OF DIVERSIFICATION RATES ON ISLANDS AND CONTINENTS ACROSS THREE PASSERINE FAMILIES

ABSTRACT

The rates of diversification vary greatly among taxa. Understanding how species-specific traits influence speciation rates will help elucidate mechanisms driving the production and maintenance of biodiversity over broad spatiotemporal scales. Specialization and range size are two characteristics that are thought to predict differences in speciation rates among clades, yet each of these mechanisms can provide predictions for both increases and decreases in speciation. We estimate a continuous index of specialization using avian bill morphology. We determine the relative effect of specialization and range size and shape on speciation rates across 559 species within the Emberizoidea superfamily, a morphologically diverse clade distributed across the Americas and associated islands. We find a significant positive correlation between specialization and speciation rate, and a negative correlation with range size. Only the effect of specialization persisted after removing island endemics, suggesting that ecological specialization is an important driver of diversity across large macroevolutionary scales.

INTRODUCTION

Biodiversity varies widely among clades, and the rates of speciation and extinction that produce these patterns vary widely over geological time, among regions, and across taxa (Sepkoski 1998, Lovette et al. 2002, Weir 2006, Reddy et al. 2012, Jetz et al. 2012, Rabosky et al. 2018). The recent availability of well-resolved phylogenies has heightened interest in identifying factors that drive variation in diversification rates over macroevolutionary scales (e.g., Claramunt et al. 2012, Jetz et al. 2012, Rabosky et al. 2018).

Both geographic and ecological mechanisms have been proposed to drive speciation. Geographic vicariance and long-distance dispersal can divide a species geographical range into genetically insulated units that prime diversification (Gaston 1998). Examples of geographic divergence are found world-wide in diverse taxa, including land snails (Cameron et al. 1996, Cook 2008), salamanders (Kozak et al. 2006), and birds (Price 2008b). Ecology can drive divergence via new ecological opportunities or innovations that allow a species to invade new niches, resulting in diverse clades of specialized species (Schluter 2000). While there is much evidence that specialization following expansion into novel niche space plays a role in adaptive radiations (e.g., Seehausen 2006, Grant and Grant 2008, Reddy et al. 2012), most examples come from islands or lakes, i.e., within a particular geographic context (but see Greenberg and Olsen 2010). It remains unclear if specialization is also associated with rapid diversification over broader geographic scales, and if adaptive radiations on islands and continents are driven by the same factors. In addition, geographic range size and degree of specialization can have both positive and negative effects on speciation rates (Futuyma and Moreno 1988, Rosenzweig 1995, Gaston 2003, Birand et al. 2012). Thus, the relative role of these two potential mechanisms in the speciation process remains unclear across large macroevolutionary scales.

Specialization has been hypothesized to both facilitate and inhibit diversification. While generalists typically show a greater potential to colonize new habitats (Greenberg 1990, Schluter 2000, Sol et al. 2002), novel ecological opportunities can promote rapid diversification by partitioning a single ancestral niche into multiple, smaller niches occupied by genetically insulated units. In this manner a generalist taxon might produce a highly diverse clade of specialized taxa (Simpson 1953, Schluter 2000, Gavrilets and Losos 2009). Such rapid diversification may also arise after the evolution of a "key innovation" allows a lineage to colonize novel niche space (Simpson 1953, Schluter 2000) or to quickly fill the niche of another organism following mass extinctions (Sepkoski 1998, Jablonski 2001). Therefore, lineages that can rapidly evolve novel morphological characteristics may be predisposed to radiate into available niche space (Lovette et al. 2002), and for all three of these scenarios, the radiation produces a clade of taxa with more specialized morphological traits.

If specialization is a process of partitioning the available niche space, rates of diversification may slow as species accumulate and niches are filled (Sepkoski 1998, Weir 2006, Rabosky and Lovette 2008, Reddy et al. 2012, Cooney et al. 2017). Moreover, as species become more specialized for a particular ecological niche, they may become constrained in their ability to adapt to new ecological opportunities due to low genetic variation, representing an evolutionary dead end (Futuyma and Moreno 1988). Niche partitioning may also lead to lower population sizes than their more generalist niche colonizers, which can increase extinction risk and lower the probability for advantageous mutations for further adaptation (Stanley 1986, Gavrilets and Vose 2005). In this manner, specialization could explain dramatic increases in diversification rate early during an adaptive radiation and slower diversification rates later on.

Range size and shape may also influence speciation rates directly through their influence on gene flow and opportunities for geographic isolation, but predictions about the direction of the correlation are contradictory (Rosenzweig 1995, Gaston 1998, 2003; Pigot et al. 2010, Birand et al. 2012). Range area can be positively correlated with speciation rates for several reasons.

Species that are distributed over larger area may have a higher probability of encountering new habitats or ecological niches if the environment is more heterogeneous (Parent and Crespi 2006). In addition, there may be a threshold area necessary for populations at the extreme range edges to experience sufficient genetic isolation to allow speciation, even under high levels of environmental heterogeneity (Losos and Schluter 2000, Parent and Crespi 2006, Seehausen 2006). Large ranges can also allow for larger population sizes, which increases the probability of advantageous mutations for divergent adaptation in different environments (Gavrilets and Vose 2005). In addition to encountering new habitats, large range species may also have a higher probability of encountering dispersal barriers that could isolate populations over short distances (Rosenzweig 1995, Gaston 2003). For instance, regions with high topographic complexity combined with repeated climatic oscillations have the potential to fragment populations and promote allopatric or parapatric speciation if ranges are large enough to fragment during climate change (Kozak et al. 2006, Ashman et al. 2018). However, species with high dispersal ability may be more likely to exhibit large ranges, and this same characteristic may make them more impervious to dispersal barriers, which reduces divergence by maintaining the homogenizing effect of genetic mixing among populations (Mayr 1963, Jablonski and Roy 2003, Coyne and Orr 2004, Claramunt et al. 2012). Individual-based models show that high dispersal can have a negative effect on speciation rates (Birand et al. 2012). Variation in range shape can also affect speciation through similar processes (Pigot et al. 2010). For a given range size, elongated distributions may have a higher propensity to become bisected by barriers (Graves 1988), or give rise to dispersal events at range edges. Elongated or patchy spatial distributions may also result in decreases in gene flow among populations (Gavrilets 2004).

In a similar way to specialization, however, we might not expect diversification rates to remain high in large-ranged species indefinitely. Just as generalists may produce a clade of specialists by partitioning the ecological space, large-ranged species might produce a clade of small-ranged species by partitioning the geographic space. Further, taxa with small ranges, like taxa with specialized niches, experience higher extinction rates than large-ranged species (Jablonski 2008). In this manner, a decrease in range size following speciation events could explain dramatic increases in diversification rate early during a species radiation and slower diversification rates later on. A strong negative correlation between geographic range size and speciation rates could also help explain why there are more species with small ranges, and fewer species with large ranges (Gaston 1998).

Regardless of the ultimate drivers of speciation, island systems often provide biogeographic conditions conducive to rapid diversification. This might be due to geographic isolation from mainland populations, to new ecological opportunities for rapid diversification, or to both causes (Losos and Ricklefs 2009). However, area, geographical isolation, topographic complexity, and ecological diversity all vary greatly among island systems, and may affect the probability of rapid speciation events (Losos and Schluter 2000, Parent and Crespi 2006, Losos and Ricklefs 2009, Rundell and Price 2009). Adaptive radiations on islands have provided many insights into the evolutionary process, but it is unclear how common these drivers are across broader geographic and taxonomic scales.

Our objective is to determine the effect of specialization and range size on speciation rates at a macroevolutionary scale, and determine if the processes are similar on island systems and continental scales. We investigate these questions across three avian families within the superfamily Emberizoidea (*Icteridae, Passerellidae, and Thraupidae*). Members of this clade are not only ecologically diverse, but this clade contains multiple independent origins of specialized bill shapes, from long curved bills of nectivorous species (e.g., *Diglossa, Cyanerpes, Coereba*) to short, stout, seed-crushing bills of granivores (e.g., *Geospiza, Oryzoborous*; (Barker et al. 2013, 2015b). Avian species also have the ability to disperse over large distances and colonize remote islands. Species within this clade occur across the Americas and associated islands, and include isolated, small-range endemics as well as species whose ranges span continents.

While specialization can be defined in a variety of ways (Devictor et al. 2010), avian bill morphology is a well-known functional trait, and the relationship between morphological diversification and ecological specialization is well documented within diverse avian clades (e.g. Schoener 1965, Grant and Grant 2008, Abrahamczyk et al. 2014, Dehling et al. 2016). Moreover, radiations in passerine birds frequently involve bill characters that are functionally related to the utilization of food resources (Lovette et al. 2002, Grant and Grant 2008, Reddy et al. 2012). We developed a continuous metric of bill specialization to more directly reflect the outcome of selection and avoid relying on subjective categorical variables. We also use a quantitative morphometric approach, which has higher statistical power to detect shape differences and captures more information than traditional linear measurements (Rohlf 2000, Foster et al. 2008). By combining our measure of specialization with publicly available data on species geographic distributions, we aim to: 1) determine the relative effect of ecological specialization and geographic distribution on speciation rates, and 2) determine if similar processes occur on islands and continental scales.

METHODS

Taxon sampling

We sampled taxa from three families (*Passerelidea, Icteridea, and Thraupidea*) within the superfamily Emberizoidea, an ecologically and morphologically diverse clade that is distributed across the Americas and associated islands. We only sampled adults, included both males and females, and included specimens from different subspecies and across the breeding range of each species when possible to account for intraspecific variation.

Quantifying Specialization Using Morphometrics

We photographed 2831 specimens (individuals per species: range = 1-10, mean = 5) of 565 species by positioning each study skin with the bill laid laterally against a ruler under a tripod-mounted camera. We digitized each specimen using the program TPSdig2, version 2.30 (Rohlf 2015, 2017). We used the ruler to set the scale in each photo, and outlined the bill shape by placing 5 homologous landmarks and 3 curves, each containing 8 semi-landmarks (Fig. 2.1). We performed all analyses of landmark data in the R package *Geomorph version 3.0.6* (Adams and Otárola-Castillo 2013, Adams et al. 2018). We converted the landmark data to shape information using generalized Procrustes analysis (GPA), using the *gpagen* function. The shape variables produced are the residuals after size, position, and orientation data are removed from each set of shape coordinates. We used the distance minimizing approach for curve sliding, since this method is more conservative and less likely to introduce variance in the data than the bending energy approach (Zelditch et al. 2012). We then obtained the least squares mean Procrustes distance for each species using the *advanced.procD.lm* function to account for any differences in sample size and used the *morphol.disparity* function to calculate an index of morphological uniqueness. Disparity is estimated as the Procrustes variance using residuals of a linear model fit. Procrustes variance is the average Procrustes distance of each species' shape relative to the mean shape of the clade (Zelditch et al. 2003), and essentially represents the position of each species in multidimensional morphological trait space relative to the grand mean consensus shape of all species included in the analysis. We assume that specialization in one morphological direction comes at a cost to specialization in another direction. Thus the grand mean consensus shape is an estimate of the shape of the most generalized bill. Further, morphological disparity, or uniqueness, is thereby a continuous proxy for specialization, where bill shapes that are most dissimilar from the grand consensus mean along any morphological axis are the most specialized. We visualized the major axes of morphological variation, as a general test that we captured ecologically relevant morphological uniqueness, by plotting each species mean in tangent space and examining shape change along PCA axes.

Range Size

We obtained spatial data containing geographic distributions of our focal species from BirdLife International (2017). We obtained geographic ranges for 559 of the 565 species we digitized. These 559 species form the basis of all our trait analyses. We calculated area and perimeter in ArcGIS. We included only breeding and resident ranges for each species to avoid introducing bias between migratory versus non-migratory species. We also calculated a range shape parameter by dividing the total range area by the total perimeter for each species. Species with smaller values have a larger perimeter for a given area, indicating more disjunct ranges with potential for decreased gene flow among isolated populations, or more narrow, elongated ranges with increased potential for isolation by distance, or bisection by barriers. We also determined from range maps if each species is endemic to islands. We denoted island species as those species that only occur on islands, and denoted those occurring on both continents and islands as continental species.

Speciation Rate Estimation

We used time-calibrated trees from a recently published phylogeny of the superfamily Emberizoidea (Barker et al. 2015a, b) to estimate speciation rates. We used two different methods to estimate speciation rate values for each tree tip. First, we calculated species-specific rates using the inverse of the equal splits measure, or DR statistic, which estimates tip-specific rates of diversification without a formal parametric model (Redding and Mooers 2006, Jetz et al. 2012). The equal splits measure is calculated as the sum of the edge lengths from a specific tip to the root of the tree, with each consecutive edge toward the root weighted by a factor of $^1/_2$. The inverse is interpreted as the splitting rate, or species-level lineage diversification rate. We calculated rates across all species using the MCC tree, as well as average rates across 100 trees sampled from the psuedoposterior of the published study (Barker et al. 2015a). The advantage of a lineage specific measure is the ability to capture subtle rate shifts, and simulations show this statistic is still highly correlated with the true rate despite high variance (Title and Rabosky 2018).

The disadvantage of using tip rates, however, is that they will always show rate heterogeneity, even when there is no variation in diversification rates across lineages. Therefore, we also use a tree-wide, model-based approach to obtain speciation rate estimates to assess evidence for speciation rate heterogeneity. Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Rabosky 2014) uses a reversible-jump Markov Chain Monte Carlo approach to estimate the number and location of diversification rate shifts across branches of a phylogenetic tree. BAMM detects shifts automatically, with the number of shifts assumed to follow a Poisson distribution (Rabosky 2014). Recent simulations have shown that BAMM produces accurate rate estimates with low error (Title and Rabosky 2018). We performed four runs of BAMM for 50 million generations, allowing for time-heterogeneous speciation rates. We accounted for incomplete taxon sampling by supplying a global sampling fraction of 95%, as reported in Barker et al. (2015). We estimated values of priors using *setBAMMpriors* in BAMM tools (Rabosky et al. 2014). We discarded the first 10 percent of the sample as burn-in, and checked for convergence by inspecting stability in log-likelihood scores, the number of rate regimes, and the location and number of rate shifts across multiple runs. We also confirmed effective sample sizes for the log-likelihoods and shifts exceeding 1000 using the *CODA* package (Plummer et al. 2006) We extracted mean speciation rates for each study species and summarized the output from the BAMM analysis using BAMMtools v2.1 (Rabosky et al. 2014).

Testing for Trait-dependent Speciation

We treated our measure of specialization (morphological uniqueness), range size, range shape, and island endemism as traits, and used several methods to assess the effect of each trait on speciation rates. We first used quantitative state speciation and extinction (QuaSSE) to investigate the influence of each of our continuous traits on the diversification process (FitzJohn 2010). These models evaluate trait evolution and speciation simultaneously in a phylogenetically explicit likelihood framework, where diversification follows a birth-death process, and speciation rates are allowed to vary as a function of a trait evolving under a Brownian Motion diffusion process. We log transformed our trait values and constructed two likelihood functions for each trait: a model in which speciation rate is constant and independent of the trait value, and a model in which speciation rate is a linear function of the trait value. We kept extinction rates constant in each of our models because we were specifically interested in the speciation process. We included a standard deviation of 0.10 for specialization, estimated from our morphometric data, and a minimum value of 0.001 for range size and and range shape. We accounted for missing taxa for which we lacked trait data within the three families by including a sampling fraction of 0.95. We assessed model support using AIC rankings and Aikaike weights (Burnham and Anderson 2002). We used a similar approach to evaluate the effect of islands vs. continents on speciation rates using Binary State Speciation and Extinction (BiSSE; Maddison et al. 2007). We fit a constrained model where both *mu* (extinction rate) and *lambda* (speciation rate) were equal, and a model that allowed *lambda* to vary between island and continental species. As above, we compared fits using AIC and Aikake weights. We implemented all QuaSSE and BiSSE models in the *diversitree* package in R (FitzJohn 2012).

Since SSE models tend to exhibit a high Type I error rate (Rabosky and Goldberg 2015) we used simulations to evaluate the significance of our results. We simulated trait values on our phylogeny under a Brownian model, using the *fastBM* function in the *phytools* R package (Revell 2012). We used the diffusion parameter estimated from the constant rate QuaSSE model and estimated the root value using the *fastAnc* function in *phytools* (Revell 2012). For each of the 100 simulated trait data sets, we fit both a constant rate QuaSSE model and a model with a linear trait-dependent speciation function, as above. We used the distribution of simulated differences in the log-likelihood values to estimate the proportion of simulated values that are as extreme as that obtained from the observed data.

We also used an independent method to test for a correlation between each of these traits and the DR statistic estimates for each tip using ES-Sim (Harvey and Rabosky 2018). ES-Sim tests for significance of trait-dependent speciation by determining the extent to which the correlation deviates from a simulated null distribution. This method is robust to psuedoreplication and has high power to detect significant correlations across a range of diversification scenarios with a low rate of false positives (Harvey and Rabosky 2018). To construct the null distribution, we simulated trait evolution 1,000 times across the tree using root state and diffusion rate ($\boldsymbol{\sigma^2}$) parameters from the maximum-likelihood fit of an Ornstein-Uhlenbeck (OU) model to the trait data. Model comparison using the *fitContinuous* function in the *Geiger* package (Harmon et al. 2008) showed that OU model fit our trait data better than a Brownian Motion model of trait evolution. We performed these analyses on the entire dataset, and then separately for island endemics and continental species to determine the influence of insularity on the associations between rates of speciation with geographic range and specialization. For our binary trait of island endemism, we also used FiSSE (Fast, intuitive State-dependent Speciation-Extinction analysis) to test for significant differences in speciation rates between islands and continents. FiSSE is a non-parametric test that compares the distribution of branch lengths with and without a binary trait and compares the value of the test statistic to a simulated null distribution of trait history on the phylogeny (Rabosky and Goldberg 2017). We did not test for trait-dependent diversification using the BAMM speciation rate estimates, since existing methods are limited by the number of rate regimes detected (Rabosky and Huang 2016), and we only detected five rate shifts.

RESULTS

Quantitative traits

Our index of specialization ranged from 0.0007 to 0.1220. Species with high values included those with large stout bills that specialize on large seeds, such as *Melopyrrha nigra, Sicalis taczanowskii, Geospiza magnirostris*, and members of the genus *Oryzoborous*, as well as the long curved bills of nectar specialists in the genus *Cyanerpes* and *Diglossa*. Smaller finch-like and sparrow-like bills that eat a variety of seeds and invertebrates, such as members of *Poospiza, Aimophila,* and *Atlapetes,* had lower values. Figure 2.2 shows locations of representative species along the first four PC axes, which account for 91% of the variation in bill shape. Geographic range size varied from 2.5 km^2 to 1.5 x 10^7 km^2. Many of the smallest range species are island endemics (e.g. *Nesospiza wilkinsi*), while the largest range species, *Volatina jacarina*, is distributed across much of Central and South America and the Caribbean Islands.

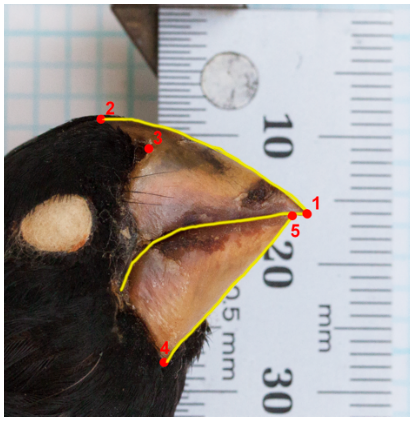

Figure 2.1. Example of digitized specimen. We show five homologous landmarks in red, and semi-landmark curves in yellow.

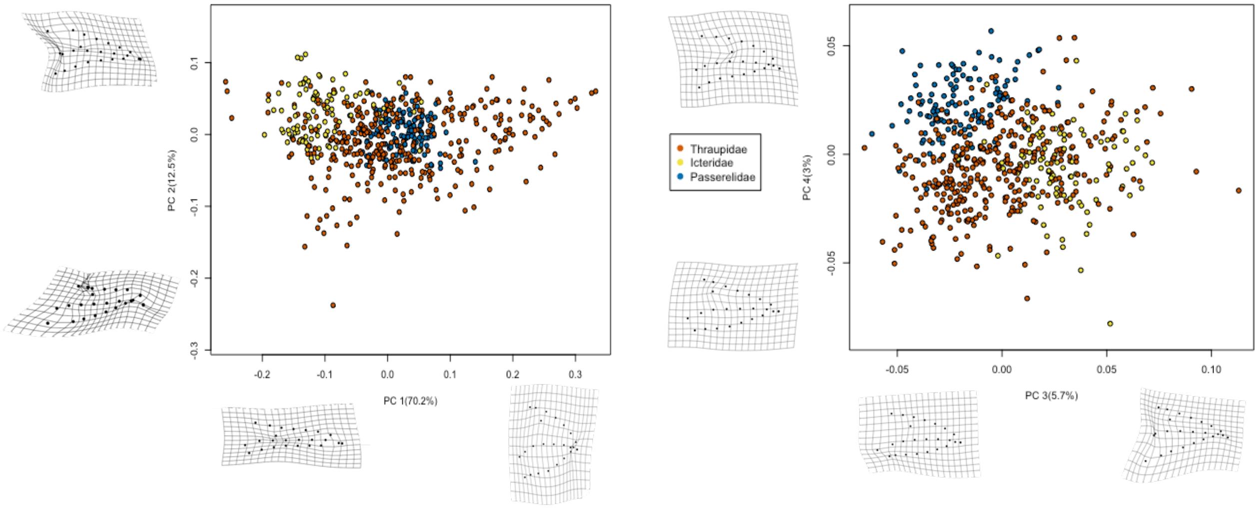

Figure 2.2. Scatterplots of species locations in morphospace. Principal Component (PC) axes 1 and 2 (left) and PC 3 and 4 (right), show major morphological axes of shape variation among species along each axis.

Speciation Rate

We found support for heterogeneity in speciation rates across the MCC tree and among 559 study species in three families within the superfamily Emberizoidea. Speciation rates across the full MCC tree based on the DR statistic ranged from 0.05 to 6.26 species/My, with a median of 0.26 and mean of 0.42 species/My. Results were similar when averaged across 100 trees sampled from the posterior distribution (range 0.05 to 7.04, median = 0.26, mean = 0.42).

Speciation rates from the model-based BAMM analysis and the lineage-specific DR statistic estimated across all 795 species in the tree were correlated (r = 0.66, P <0.001).

Comparative Analysis

QuaSSE model comparisons provide support for faster speciation rates among species that are more specialized and species with smaller or more disparate geographic range sizes (Table 2.1). The best supported BiSSE model indicated faster speciation rates occur on islands (Table 2.1). Simulated trait data showed a fairly low proportion of false positives, with 17%, 21%, and 11% of model comparisons for specialization, range size, and range shape, respectively, resulting in a log-likelihood difference as high or higher than the value from the observed data.

Table 2.1 QuaSSE and BiSSE model selection statistics. Model selection statistics for the relationship between trait values and speciation rates from QuaSSE and BiSSE analysis. Log-Lik is the log of the maximized likelihood, ΔAIC is the difference in AIC values between the model and the best model, w is the model probability, or Aikake weight. Parameter estimates are provided for the best fit model.

	Model	**Log-Lik**	**Δ AIC**	***w***	λ	λm	μ	**diffusion**
Specialization	Linear	-1428.9	0	0.71	0.37	0.06	0	0.01
	Constant	-1430.8	1.74	0.29				
Range Size	Linear	-3340.3	0	0.99	0.54	-0.05	0	0.62
	Constant	-3345.6	8.66	0.01				
Range Shape	Linear	-34490.0	0	0.84	0.25	-0.07	0	0.12
	Constant	-34493.0	3.33	0.16				
					λ_0	λ_1	μ	
Island vs. Continents	Rates vary	-1425.5	0	0.93	0.24	0.39	0	
	Rates equal	-1429.1	5.17	0.07				

ES-sim results further support the results obtained from the QuaSSE analysis, suggesting that both specialization and geographic distributions are important drivers of speciation rates across broad spatial scales (Table 2). We found a significant positive correlation between our index of specialization and the DR statistic (r = 0.17, *P* = 0.03), and a significant negative correlation with range size (r = -0.19, *P* = 0.001) and shape (r = -0.13, *P* = 0.03). These results suggest faster speciation rates are associated with higher degree of specialization, smaller range size, and more narrow or disjunct spatial distributions. Our index of specialization was not correlated with range size (r = 0.01, *P* = 0.79) or range shape (r = 0.03, *P* = 0.54). We also found that speciation rates are higher on islands than continents (r = 0.27, *P* < 0.001). FiSSE results confirmed the difference in rates between island and mainland species (*P* = 0.01). After removing island endemics, specialization was still positively correlated with speciation rates among continental species (r = 0.15, *P* = 0.05), but the effect of range size and shape were no longer significant. We did not detect a significant correlation with any of the three variables among island endemic species, but sample our size was small (*N* = 43 species).

Table 2.2. ES-sim results. We present results from the MCC tree, but were similar when averaged over 100 trees sampled from the psuedoposterior. We log-transformed values for bill uniqueness (specialization), range area, and range shape prior to analysis. The value for the trait-rate correlation is Pearson's r, and the P-value is the 1-tailed test for a significant deviation from the simulated null distribution of trait-rate correlations.

		Pearson's r	**P-value**
All Species	**Specialization**	**0.17**	**0.03**
	Area	**-0.19**	**0.001**
	Shape	**-0.13**	**0.03**
	Island	**0.27**	**<0.001**
Continental Species	**Specialization**	**0.15**	**0.05**
	Area	-0.05	0.20
	Shape	0.01	0.44
Island Endemics	Specialization	-0.01	0.47
	Area	-0.16	0.23
	Shape	-0.24	0.13

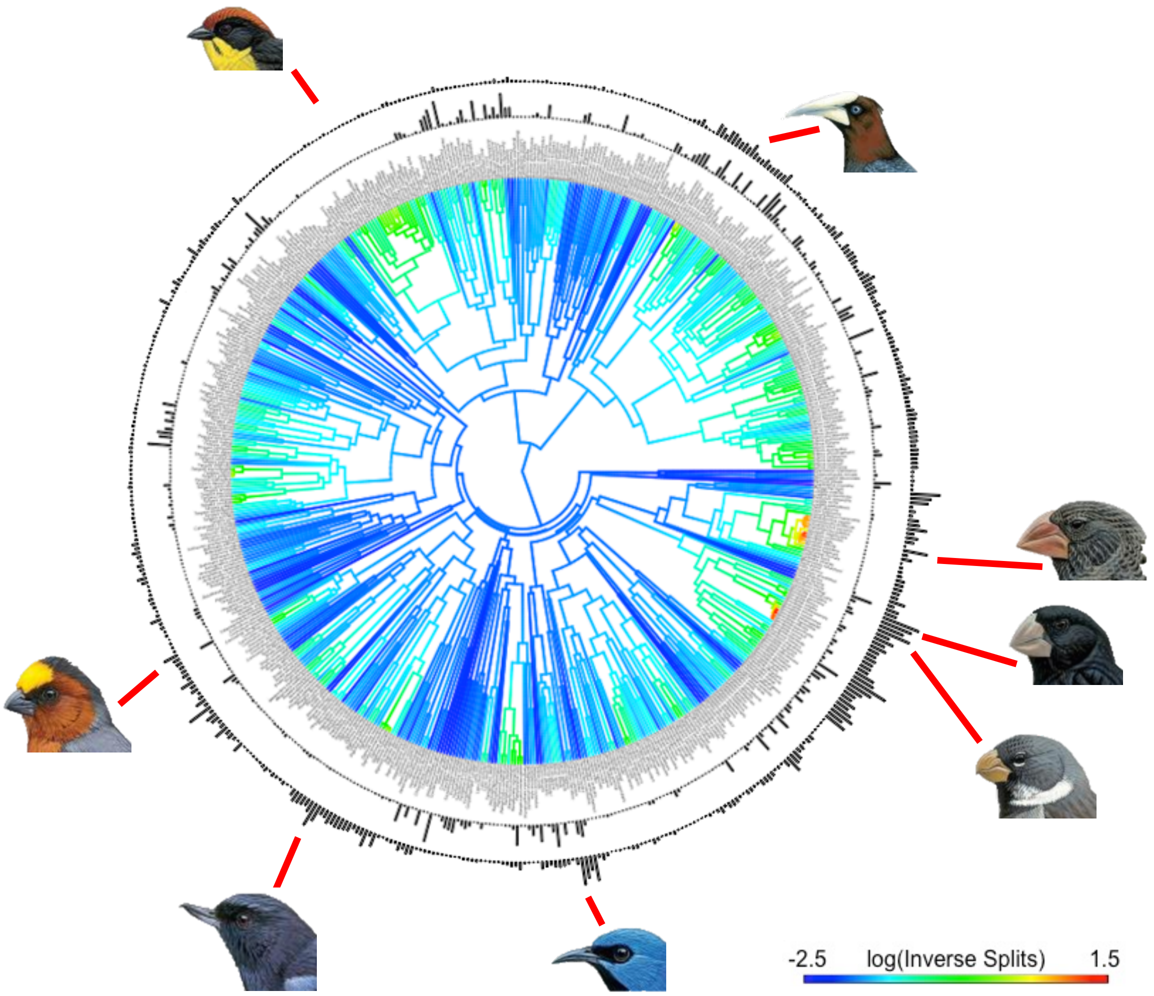

Figure 2.3. Phylogenetic tree of 559 study species. Branches show a gradient representing the log of the Inverse Splits, or DR statistic. Surrounding bars represent range size (inner ring) and morphological uniqueness (outer ring). Images from Birdlife International (2017).

DISCUSSION

By examining the effect of specialization, and range size and shape on speciation rates across a morphologically diverse and broadly distributed clade, we were able to determine the relative importance of ecological and geographic processes across macroevolutionary scales. We found higher speciation rates among species with a higher degree of specialization, with ranges that were smaller, and with ranges with higher ratios of edge to area. This aligns with our prediction that specialist species (as defined by bill morphological uniqueness) are more likely to have experienced a period of rapid diversification in their evolutionary history, perhaps during a period of partitioning of the ecological niche space. Likewise, small-range species are more likely to have experienced a period of rapid diversification in their evolutionary history, perhaps during a period of partitioning of the geographic space.

We found that the effect of specialization on speciation rate persisted after removing island endemics, which includes the radiation of Darwin's finches, suggesting that ecological speciation may be an important driver of global diversity across diverse clades and large geographic scales. Moreover, our morphological uniquness measure captures just a single axis of specialization, and explained as much variation in speciation rates as range size. Including indices of specialization along additional morphological, physiological, or behavioral dimensions would undoubtedly represent incidences of ecological innovation that we did not captured with our metric and may likely explain more variation in diversification. The negative correlation between speciation rates and range size, however, did not persist after removing island endemics. This suggests that the ability of geographic range to predict diversification may largely be captured by differences in the diversification rate between islands and continents. Indeed, our two parameters for geography had greater (albeit non-significant) effect than our morphological uniqueness measure in our island-only model, although our sample size of island taxa was limited (N= 43 island species and 516 continental species). This pattern could be produced by speciation events resulting from the population fragmentation following colonization of a group of islands by a continental taxon (Lerner et al. 2011). In such a scenario, high diversification rates may become correlated with small ranges simply because islands have smaller areas than continents. Any mechanistic difference between speciation on islands and continents might explain the lack of an effect of range size and shape once islands are removed from our combined model. Using a larger sample of island species would provide a more robust test of whether geography plays a larger role on islands than it does on continents. Geographical processes may still play a role on continents, but it does not appear that they explain as much variation in speciation rates as a single narrowly defined metric of ecological specialization within this clade.

The positive correlation between specialization and speciation rates only explained a small amount of the variation, and was not ubiquitous across lineages. For instance, we detected high levels of speciation in some lineages that showed neither strongly specialized bills or small range sizes. Other factors are certainly expected to increase speciation rates that we do not account for, such as climate and sexual selection (Seddon et al. 2008, Nyári and Reddy 2013, Title and Burns 2015, Seeholzer et al. 2017). For example, capuchino seedeaters, which exhibit high rates of diversification (Fig. 3), show little morphological differentiation and average range sizes. Their recent radiation has been attributed to strong selection on pigmentation genes affecting plumage coloration (Campagna et al. 2017). We did not attempt to build a model here that explains the relative importance of all mechanisms of diversification, but simply to compare the relative importance of two oft cited mechanisms in birds (bill specialization and range characteristics) on islands versus continents.

Clades may also differ in their inherent ability to diversify. For example, there is evidence suggesting that finch-like birds may be more prone to diversify than birds with more curved bill shapes such as warblers or thrushes (Lovette et al. 2002, Rundell and Price 2009). Both Hawaiian honeycreepers and Galapagos finches radiated from a finch-like ancestors (Lovette et al. 2002, Burns et al. 2002) who can readily adapt to changes in seed size availability (Benkman 2003, Grant and Grant 2008). We detected the fastest speciation rates among the Galapagos finches and large-billed seed finches within the Sporophilinae sub-family, which are consistent with this hypothesis.

We also found highly specialized species that have long branch lengths and low speciation rates. For example, species within the genus *Cyanerpes* show a high degree of specialization in our morphological uniqueness index, and similar to the *Diglossa* flowerpiercers, they specialize mostly on nectar. Their radiation occurred much longer ago than many other clades, however, and the inverse splits metric we used here would thus result in a lower estimate of divergence rate. It is possible that a clade which specialized closer to the root of the tree would erode its ability to diversify further due to low genetic variation, tradeoffs with other lifestyles, or increases in extinction rate. High degrees of specialization might thereby represent an evolutionary dead end (Futuyma and Moreno 1988). Given that extinction rates are higher in specialists (Jablonski 2008), early radiations would have more time to erode through time and would be expected to possess more extinct species than recent radiations. If this is true, we would expect specialist taxa that do not show increased diversification rates to have disproportionately old splits with their sister taxon relative to specialist taxa that do show high diversification rates. This hypothesis might be more robustly tested across the entire superfamily. Importantly, however, this mechanism would represent another pathway for increased diversification via specialization that would not be captured by our metrics. Our estimates of the importance of bill specialization on diversification rate are thus likely biased low.

The relative strength of geographic and ecological mechanisms may also depend on the landscape scale and biogeographic context over which these processes occur. Our modeling approach failed to find a strong role for geography on continental diversification rates that was independent of bill specialization. Such a pattern might be expected if larger, ecologically homogenous ranges are more likely to speciate than smaller ranges. It's unclear how common such landscapes actually are in the areas we examined. Importantly, however, we did not test for interactions between geographical and ecological specialization. If larger ranges only promote speciation when ecological divergence is also involved, we would not have detected that effect here. Interestingly, however, we might expect a false signal of geography if larger ranges were more likely to diverge ecologically in phenotypic characters other than bill shape. Regions characterized by more topographic complexity and climate fluctuations can cause repeated population fragmentation and promote increase speciation rates (Weir and Schluter 2004). We did not detect this geographic signal. Secondary range expansions following niche divergence in allopatry or parapatry might eliminate the signal of range size on diversification, however, while maintaining the signal of specialization's effect. Our results support some effect of geographic isolating mechanisms following island colonization, but at the large geographic scale of this study, we don't find strong support for geographic range splitting as a major driver of diversification on continents.

Though our results show that higher speciation rates are associated with species on islands, with small range size, and greater degrees of specialization, available methods hamper our ability to determine causation or to separate out the effects of each of our variables. It is possible that ecological specialization occurs following speciation via vicariance or parapatry where resulting species experience differences in habitat, interspecific interactions, or other environmental variables. It is also possible that islands facilitate specialization, leading to lower variation in the degree of specialization among island endemics. Such a pattern would preclude our ability to detect an effect of ecological specialization on islands.

We confirmed heterogeneity in speciation rates within the Emberizoidea super-family, consistent with other studies within this clade (e.g., Barker et al. 2013, Burns et al. 2014, Mason et al. 2017). We further explored the role of ecological and geographic drivers of variation in speciation rates among species. We found support for a single metric of ecological specialization as an important driver of speciation rates across a diverse clade at continental scales. We also found support for differences in speciation rates between islands and continents, suggesting that different mechanisms may be at play across different geographic contexts. Further investigation into variation in diversification processes across different biogeographic regions will help elucidate which mechanisms might be important at different scales. Additional work that includes intra-specific variation across a species range may also provide insights into the diversification process (e.g. Harvey et al. 2017) and determine mechanisms driving higher intrinsic evolutionary lability in certain clades. This additional sentence complies with University of Maine thesis formatting guidelines.

CHAPTER 3

SPECIALISM IS NOT AN EVOLUTIONARY DEAD-END: ESTIMATING TRANSITION RATES BETWEEN GENERALIST AND SPECIALIST MORPHOLOGIES ACROSS A NEW WORLD AVIAN CLADE.

ABSTRACT

Evolutionary theory suggests that diversification proceeds from generalist ancestors to specialist descendants. However, exceptions to this rule have led to alternate hypotheses that predict the evolution of specialized populations from generalist ancestor is interrupted by periods of niche-breadth expansions. We tested predictions of the directionality of the evolution of specialization by estimating character state transition rates between generalists and specialists using a novel index of specialization in bill morphology in a diverse clade of passerine birds. We found higher transition rates from specialist to generalist, suggesting that niche expansion to more generalist morphologies is an important driver of diversity in this clade.

INTRODUCTION

Understanding how species traits influence diversification is essential to determining how biodiversity is created and maintained. Specialization is widely recognized as a major factor driving diversification (Futuyma and Moreno 1988), yet specialization is also associated with high extinction risk (Jablonski 2008, Colles et al. 2009). This pattern has led some to suggest that specialization may be an evolutionary dead end. For example, several hypotheses propose that the direction of change in niche characteristics proceed from generalized to specialized, and this trend toward ecological specialization is largely irreversible (e.g. the law of the unspecialized: Cope 1896; the generalist-to-specialist hypothesis: Futuyma and Moreno 1988). Several mechanisms support the potential for the irreversibility of specialized traits. Specialization is predicted to incur trade-offs where individuals gain a competitive advantage in the short term but compromise their ability to adapt to changing conditions over the long term (Macarthur and Levins 1967). If such a trade-off exists, a lineage that adapts to a narrow set of resources may become increasingly committed to that state through reduced genetic or phenotypic variation and accumulation of mutations that may be disadvantageous outside of its current niche (Futuyma and Moreno 1988, Futuyma et al. 1995, Kellermann et al. 2009).

Therefore, specialist lineages may have limited capacity to exploit or adapt to other niches. Phylogenetic niche conservatism of physiological traits suggests that climatic specialization, for instance, may limit niche expansion by setting limits on the evolution of physiological tolerance (Kellermann et al. 2012). In addition, increasing complexity and covariation among complex traits may lower the propensity for reversal (Gould 1970, Goldberg and Igić 2012). In this manner, specialization in certain physiological or morphological traits may place additional constraints on any traits with which they covary, further limiting a species ability to expand their niche. For example, concealment from predators may limit breadth in host plant usage in some insects (Ehrlich and Raven 1964, Crespi and Sandoval 2000), and egg characteristics may place constraints on plant host quality and phenology of oviposition, selecting for further neurophysiological and behavioral adaptations that limit niche breadth (Price 2008a).

Metapopulation dynamics can add further constraints that prevent niche innovations from spreading or being fixed in a population. If specialism has led to a higher competitive advantage within a narrow niche space, that advantage may cause certain environmental conditions to covary with abundance. With more individuals within a narrow range of environmental conditions, mutations that increase fitness within, rather than outside of these conditions, may be more strongly selected for. This can favor a tendency to stabilize or even increase specialization (Holt and Gaines 1992, Losos et al. 1994). Directional evolution consistent with the generalist to specialist hypothesis is supported in a number of taxa, including dendroctonus wood beetles (Kelley and Farrell 1998), walking sticks (Crespi and Sandoval 2000), Anolis Lizards (Losos et al. 1994), and turtles (Stephens and Wiens 2003).

However, many extant clades are composed of diverse and highly specialized taxa, and a number of exceptions to the generalist to specialist trend have been documented (e.g. Janz, Nyblom, and Nylin 2001; Nosil 2002; Stireman 2005). This suggests that expansion to new resources and environments, rather than niche subdivision, could emerge as a predominant ecological trend driving diversification (Futuyma and Moreno 1988, Schluter 2000). The Oscillation Hypothesis suggests that the evolution of specialized populations from a more generalist ancestor is interrupted by periods of niche-breadth expansions (Janz and Nylin 2008). Such oscillations can result from periodic colonization of novel habitat, or “key innovations” (Jablonski 1993, Schluter 2000), and are thought to replenish variation for future speciation via specialization. Examples of reversals, or niche expansion occur in butterflies (Janz et al. 2001), parasitoid flies (Stireman 2005), and phytophagous insects (Nosil 2002, Nosil and Mooers 2005).

Our objective is to determine whether the frequency of transitions from generalist to specialist are more common than the reverse. We investigate these questions across three avian families within the superfamily Emberizoidea (*Icteridae, Passerellidae, and Thraupidae*). Members of this clade are ecologically diverse and contain multiple independent origins of specialization, from the long, curved bills of nectivorous species (e.g., *Diglossa, Cyanerpes, Coereba*) to the short, stout, seed-crushing bills of granivores (e.g., *Geospiza, Oryzoborous*; (Barker et al. 2013, 2015b).

We developed an index of specialization using avian bill morphology, which reflects the outcome of selection and avoids relying on subjective categorical variables (Conway and Olsen *In Revision*). We used a quantitative morphometric approach, which has higher statistical power to detect shape differences and captures more information than traditional linear measurements (Rohlf 2000, Foster et al. 2008). While specialization can be defined in a variety of ways (Devictor et al. 2010), avian bill morphology is a well-known functional trait, and the relationship between morphological diversification and ecological specialization is well documented (Schoener 1965) (e.g. (Schoener 1965, Grant and Grant 2008, Dehling et al. 2014, Abrahamczyk et al. 2014). Bill morphology is also a highly labile trait, and has shown rapid response to a variety of selection pressures in variable environments (e.g., Grant 2006, 2002; Greenberg, Cadena, et al. 2012; Greenberg, Danner, et al. 2012). We used State-dependent Speciation models to explicitly test transition rates between specialists and generalists across the evolutionary history of the clade.

METHODS

Taxon Sampling

We sampled taxa from three families (*Passerelidae, Icteridae, and Thraupidae*) from a recently published and well-supported phylogeny of the superfamily Emberizoidea, an ecologically and morphologically diverse clade that is distributed across the Americas and associated islands (Barker et al. 2015b). We only sampled adults, included both males and females, and included specimens from different subspecies and across the breeding range of each species when possible to account for intraspecific variation.

Quantifying Specialization Using Morphometrics

We photographed 2831 specimens (individuals per species: range = 1-10, mean = 5) of 565 species by mounting a camera on a tripod and positioning each study skin with the bill laid laterally against a ruler. We digitized specimens using the program TPSdig2 (Rolf 2004). We set the scale using the ruler to standardize each photo, and outlined the shape of each bill by placing 5 homologous landmarks and 3 curves, each containing 8 semi-landmarks (Fig. 1). We performed all analyses of landmark data in the R package *Geomorph* (Adams and Otárola-Castillo 2013, Adams et al. 2018). We converted the landmark data to shape information using generalized Procrustes analysis (GPA), using the *gpagen* function. This function produces shape variables as residuals after size, position, and orientation data are removed from each set of shape coordinates. We used the distance minimizing approach for curve sliding, since this method is more conservative and less likely to introduce variance in the data than the bending energy approach (Zelditch et al. 2012). We then obtained the least-squares-mean Procrustes distance for each species using the *advanced.procD.lm* function to account for differences in sample size, and used the *morphol.disparity* function to calculate an index of morphological uniqueness. Disparity is estimated as the Procrustes variance using residuals of a linear model fit. Procrustes variance is the average Procrustes distance of each species' shape relative to the mean shape of the clade (Miriam Leah Zelditch, Sheets, and Fink 2003), and it represents the position of each species in multidimensional morphological trait space relative to the grand mean consensus shape of all species included in the analysis. This index therefore reflects the outcome of selection towards unique morphological space, and it avoids relying on subjective categorical variables. We visualized the major axes of morphological variation as a general test that we captured ecologically relevant morphological uniqueness by plotting each species mean in tangent space and examining shape change along PCA axes (Fig 3.1).

Estimating Transition Rates with Hidden State Models

We implemented state-dependent speciation and extinction (SSE) models to assess whether transitions from specialist to generalist or generalist to specialist were more frequent. The BiSSE version of SSE models (Maddison et al. 2007) estimate differences in speciation (λ), extinction (μ), and transition (q) rates for clades as a function of a discrete character states, but have been criticized for high rates of "false positive" results (Rabosky and Goldberg 2015), because the null model under this framework is no change across the tree, which is rarely true (Caetano et al. 2018). Hidden State Speciation and Extinction (HiSSE; Beaulieu and O'Meara 2016) is an extension of the BiSSE framework that adds an unobserved trait, or "hidden" character state, to account for variation in diversification rates that is independent of the observed trait of interest, while identifying differences in transition rates among character states (Beaulieu and O'Meara 2016). The hidden state provides a null model with variable rates and an equal number of parameters (i.e., similar complexity). The inclusion of this type of state-independent model (CID) allows for estimation of rate variation and state transitions independent of the observed trait of interest, and thereby accounts for potential correlations between the measured and unmeasured characters that can vary among clades (Beaulieu and O'Meara 2016). This allows evolution of binary characters (i.e., transition rates) to be independent of the diversification process while also allowing for heterogeneity in rates across the tree.

Since HiSSE is only available for discrete binary characters, we defined specialists using two different cutoffs: the 60th and 70th percentiles of our bill morphological uniqueness metric. Thus we defined birds as specialists (coded as a "1") when bill shapes were above the 60th or 70th percentile of distances from the mean bill morphology in multidimensional space, and we considered the remaining species with bills closer to the mean shape as generalists (coded as "0"). We estimated transition rates (q) among each combination of the measured and hidden character states: 1A (specialists with hidden state absent), 1B (specialists where hidden state was present), 0A (generalist with hidden state absent), and 0B (generalist where the hidden state is present). We estimated parameters for six variations of hidden-state models, each of which tested a particular hypothesis regarding transitions from generalist to specialist or vice versa. Since we are interested specifically in character state reversals in this trait, we allowed speciation and extinction rates to freely vary among observed and hidden states for all of these models. Our six models included 1) an "irreversible" model where transitions from specialist to generalists were set to 0 ($q_{1,0}=0$) but all other transition rates were free to vary, 2) an "equal probability" model where transition rates were independent of character states (all transition rates constrained to be equal: $q_{1,0} = q_{0,1} = q_{A,B} = q_{B,A}$), 3) a "variable, but not irreversible" model where all transition rates were allowed to vary freely ($q_{1,0} \neq q_{0,1} \neq q_{A,B} \neq q_{B,A}$), and 4-6) three models which allowed differences in transitions only between hidden states ($q_{1,0} = q_{0,1} \neq q_{A,B} = q_{B,A}$), only from generalist to specialist ($q_{0,1} \neq q_{1,0} = q_{A,B} = q_{B,A}$), or only from specialist to generalist ($q_{1,0} \neq q_{0,1} = q_{A,B} = q_{B,A}$), while all other transition rates were held equal (Table 1, Table 2). To determine if models that allow rates to vary had more support than models where rates were equal across character states, we compared these six models in a Maximum Likelihood framework, and assessed model support using AIC rankings and Akaike weights (Burnham and Anderson 2002).

<u>Estimating Transition Rates with Multiple State Models</u>

We were also interested in determining the direction of evolution across morphological space. Assuming that most changes in bill shape are due to Quantitative Trait Loci, lineages that change from one type of specialist to another specialist form on the far side of morphological space likely occupied intermediate forms within the generalist space during the transition. In the models described above, these types of transitions appear as though no trait change has occurred (i.e., specialist to specialist transition), but they hide both a specialist to generalist and a generalist to specialist transition. We run the risk of underestimating the evolutionary lability of specialists without accounting for these transitions across morphological space. To detect them we divided our specialists into four categories based on bill shape. We did this using the first two Principal Component axes, which accounted for 82.7% of the variation in bill shapes, as shown in Figure 3.1. After removing the species coded as generalists (coded as 1) using the 60th percentile cutoff as above, we coded each quadrant of the morphospace as specialist types using the midpoint of each PC axis (coded as 2, 3, 4, and 5; Figure 3.1). We analyzed transition rates among all five categories (generalists and the four categories of specialists, Figure 3.1, 3.2) using

Multi-state Speciation and Extinction (MuSSE) models in the *diversitree* package (FitzJohn 2012). MuSSE is another generalization of the BiSSE method that allows for multiple character states. We set up 6 models (Table 3.3) to test if transition rates were independent of bill morphology, or constrained to a certain direction across the morphospace (i.e, only from generalist to specialist, only specialist to generalist, only specialist to specialist). The most complex (full) model contained separate rate estimates for speciation and extinction, and unconstrained rates of transition among each of the niche categories, and the null model constrained all transition rates as equal. We also included a model that constrained transitions to be equal within each of the 4 transitions above. We calculated fit for each model using maximum likelihood and assessed model fit using AIC and Akaike weights (Burnham and Anderson 2002). We also estimated parameter values using Bayesian MCMC methods. We estimated starting point parameters from the best-fit model. We set the tuning parameter for the MCMC slice sampler (**w**) as the distance between the 5% and 95% quantiles of the marginal distribution for each parameter. We estimated the posterior probability distribution of each parameter using an exponential prior and 1000 MCMC steps.

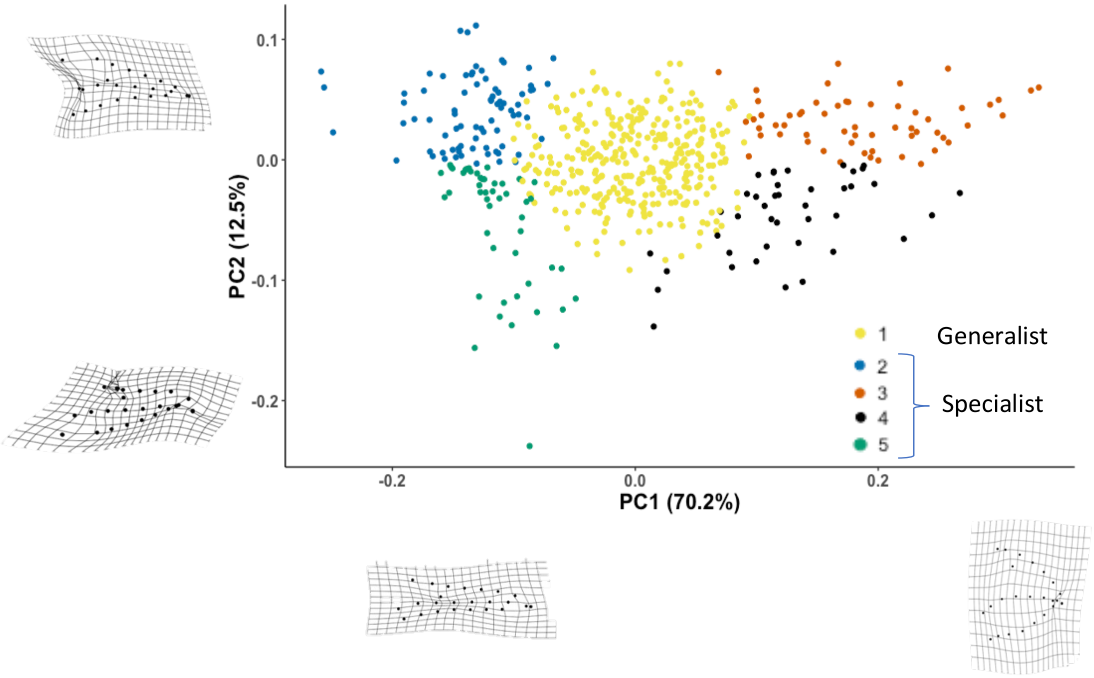

Figure 3.1. Scatterplots of species locations in morphospace. Warps along Principal Component (PC) axes 1 and 2 show major morphological axes of shape variation along each axis. Generalists, coded as 1 (yellow), are those species that scored lower than the 60th percentile in our morphological uniqueness metric. The four specialist groups were determined by using the midpoint of each of the two PC axes after removing generalists.

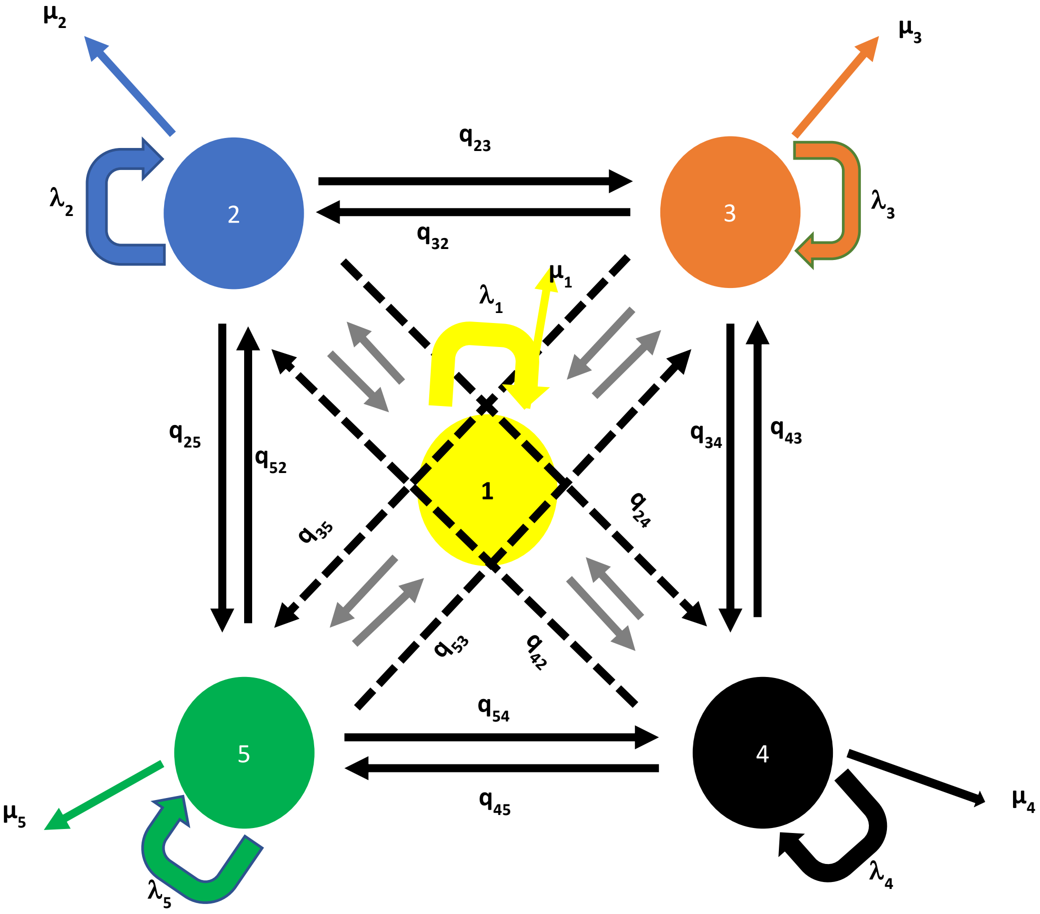

Figure 3.2. Conceptual figure showing parameters estimated is MuSSE models. Numbered circles match positions in morphospace shown in Figure 3.1. λ specifies speciation rates, μ indicates extinction rates. Evolutionary transition rates (q) among character states defined by bill morphology are indicated by gray lines (transitions between generalists and specialists), black lines (transitions to different specialist states), and dotted lines (transitions to specialist states that likely pass through generalist states).

RESULTS

Hidden State Models

The HiSSE model with the highest support showed variable transition rates among all character states (Table 3.1). Transition rates from specialist to generalist were higher than from generalist to specialist, and this directionality was consistent in all models that allowed asymmetric transition rates between observed states (Table 3.2). Transitions between specialist and generalist were slightly higher when a hidden state was present in the full all rates vary model, and the highest transition rates occurred from the hidden to our observed state (Table 3.2). The irreversible model, with transitions from specialist to generalist set to 0 performed poorly, and ranked lower than a model with all transition rates constrained to be equal. Model selection results did not depend on the cutoff we used to define specialist versus generalist (Table 3.2).

Table 3.1. Model selection results from the HiSSE analysis. Log-Lik is the log of the maximized likelihood, ΔAIC is the difference in AIC values between the model and the best model, *w* is the model probability, or Akaike weight. Observed character states are represented by 1 (specialist) and 0 (generalist). Hidden character states are denoted as A (absent) and B (present). All models include unconstrained diversification rates. Thus transition rates (q) are denoted as directional from specialist to generalist ($q_{1,0}$), from generalist to specialist ($q_{0,1}$) and among hidden states ($q_{A,B,}$ $q_{B,A}$).

	Model	**Log-Lik**	**ΔAIC[1]**	***w***
Specialist = 60th percentile	HiSSE - all q differ	-1551.10	0.00	>0.999
	HiSSE - $q_{0,1}$ differs	-1578.21	42.22	<0.001
	HiSSE - $q_{A,B}$ $q_{B,A}$ differ	-1587.10	59.99	<0.001
	HiSSE - $q_{1,0}$ differs	-1590.74	67.28	<0.001
	HiSSE - all q equal	-1599.77	83.34	<0.001
	HiSSE – irreversible ($q_{1,0} = 0$)	-1648.74	181.28	<0.001
Specialist = 70th percentile	HiSSE - all q differ	-1550.91	0.00	>0.999
	HiSSE - $q_{0,1}$ differs	-1562.97	12.13	<0.001
	HiSSE - $q_{A,B,}$ $q_{B,A}$ differs	-1578.43	43.04	<0.001
	HiSSE - $q_{1,0}$ differs	-1580.84	47.86	<0.001
	HiSSE - all qs equal	-1592.22	68.63	<0.001
	HiSSE – irreversible ($q_{1,0} = 0$)	-1625.81	135.81	<0.001

[1] The lowest AIC score was 3134.20 for models using the 60th percentile, and 3133.81 for models using the 70th percentile

Table 3.2. Parameter estimates for transition rates (q) among character states. Models shown define specialist (1) as greater than the 60th percentile of our bill uniqueness metric (top) and greater than the 70th percentile (bottom). Observed character states are represented by 1 (specialist) and 0 (generalist). Hidden character states are denoted as A (absent) and B (present). All models include unconstrained diversification rates.

	Generalist → Specialist		Specialist → Generalist		Hidden States			
Model	0A → 1A	0B→1B	1A → 0A	1B→0B	1A→1B	0A→0B	0B→0A	1B→1A
HiSSE - all qs differ	0.010	0.014	0.023	0.131	0.005	0.000	0.254	0.163
HiSSE - $q_{0,1}$ differs	0.010	0.010	0.099	0.099	0.099	0.099	0.099	0.099
HiSSE - $q_{A,B}$ differs	0.040	0.040	0.040	0.040	0.162	0.162	0.162	0.162
HiSSE - $q_{1,0}$ differs	0.025	0.025	0.084	0.084	0.025	0.025	0.025	0.025
HiSSE - all qs equal	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047
HiSSE - irreversible	0.066	0.066	0	0	0.066	0.066	0.066	0.066
HiSSE - all qs differ	0.004	0.012	0.028	0.141	0.000	0.000	0.203	0.067
HiSSE - $q_{0,1}$ differs	0.009	0.009	0.137	0.137	0.137	0.137	0.137	0.137
HiSSE - $q_{A,B}$ differs	0.037	0.037	0.037	0.037	0.192	0.192	0.192	0.192
HiSSE - $q_{1,0}$ differs	0.023	0.023	0.130	0.130	0.023	0.023	0.023	0.023
HiSSE - all qs equal	0.046	0.046	0.046	0.046	0.046	0.046	0.046	0.046
HiSSE - irreversible	0.053	0.053	0	0	0.053	0.053	0.053	0.053

Multistate Models

Maximum Likelihood model rankings from our MuSSE analysis also supported a model where all transition rates were allowed to vary (Table 3.3). A model allowing transitions from specialist to generalist performed better than one allowing transitions from generalist to specialist to vary. The highest transition rates were from specialist to generalist (range 0.016 – 0.103, mean = 0.073, Figure 3.3, Table A1), consistent with the results from HiSSE. The second highest transition rate was between the two adjacent specialist types that scored high on PC1 (shorter and more stout bills, $q_{3,4}$ = 0.059, Table A3.1), followed by transitions between those two adjacent specialists that scored low on PC1 (long curved bills, $q_{5,2}$ = 0.039, Table A3.1). Transitions between non-adjacent specialist (which presumably hide a generalist to specialist transition) were less common (0.004), and similar in frequency to transitions from generalist to any of the four specialist types (0.004). Figure 3.4 shows reconstructed ancestral states based on the MuSSE model to illustrate character transitions across the phylogeny.

Table 3.3. Model selection results from the MuSSE analysis. Log-Lik is the log of the maximized likelihood, k is the number of parameters, ΔAIC is the difference in AIC values between the model and the best model, *w* is the model probability, or Aikake weight. All models include unconstrained diversification rates. Grouped model constrains rates to be equal within each of 4 groupings, specialist to generalist, generalist to specialist, specialist to specialist in adjacent morphospace, and specialist to non-adjacent-specialist morphospace, but allows transition rates to vary among these 4 groupings.

Unconstrained Parameters	**k**	**lnLik**	**AIC**	**ΔAIC**	***w***
All qs differ	30	-1735.90	3531.86	0.00	0.97
All qs differ by group	14	-1755.40	3538.90	7.00	0.03
Specialist → Generalist differ	15	-1766.90	3563.76	31.90	0.00
Generalist → Specialist differ	15	-1770.40	3570.71	38.86	0.00
Specialist → Specialist differ	19	-1791.70	3621.36	89.50	0.00
All qs equal	11	-1802.60	3627.14	95.28	0.00

Table 3.4. Parameter estimates from transition rates (q) from the MuSSE analysis.

State Transition	Mean (MCMC)	SD (MCMC)	Mean (ML)
Generalist → Specialist	0.004	0.001	0.003
Specialist → Generalist	0.069	0.010	0.069
Specialist → Specialist (non-Adjacent)	0.004	0.003	0.003
Specialist → Specialist (Adjacent)	0.021	0.004	0.020

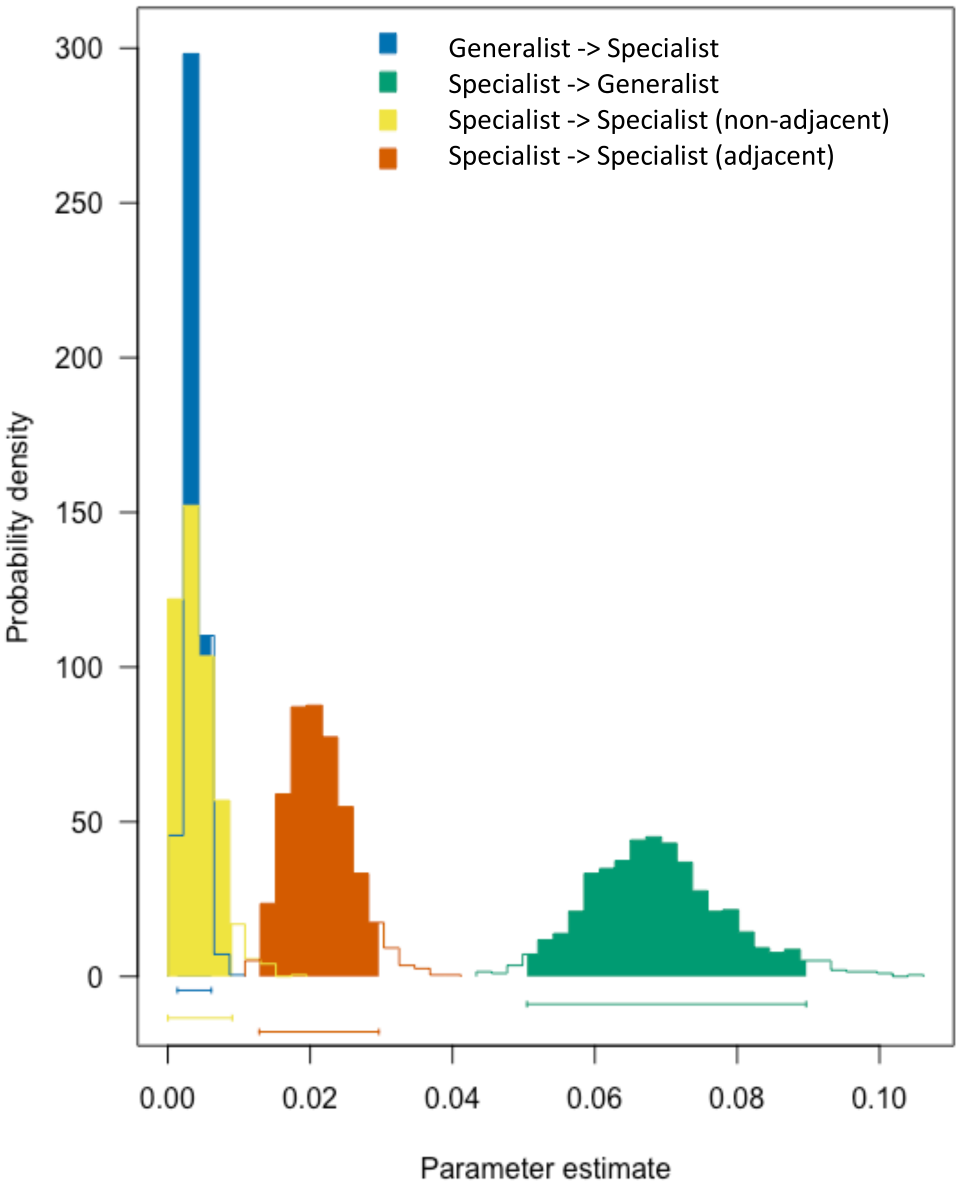

Figure 3.3. Posterior distribution of MuSSE parameter estimates.

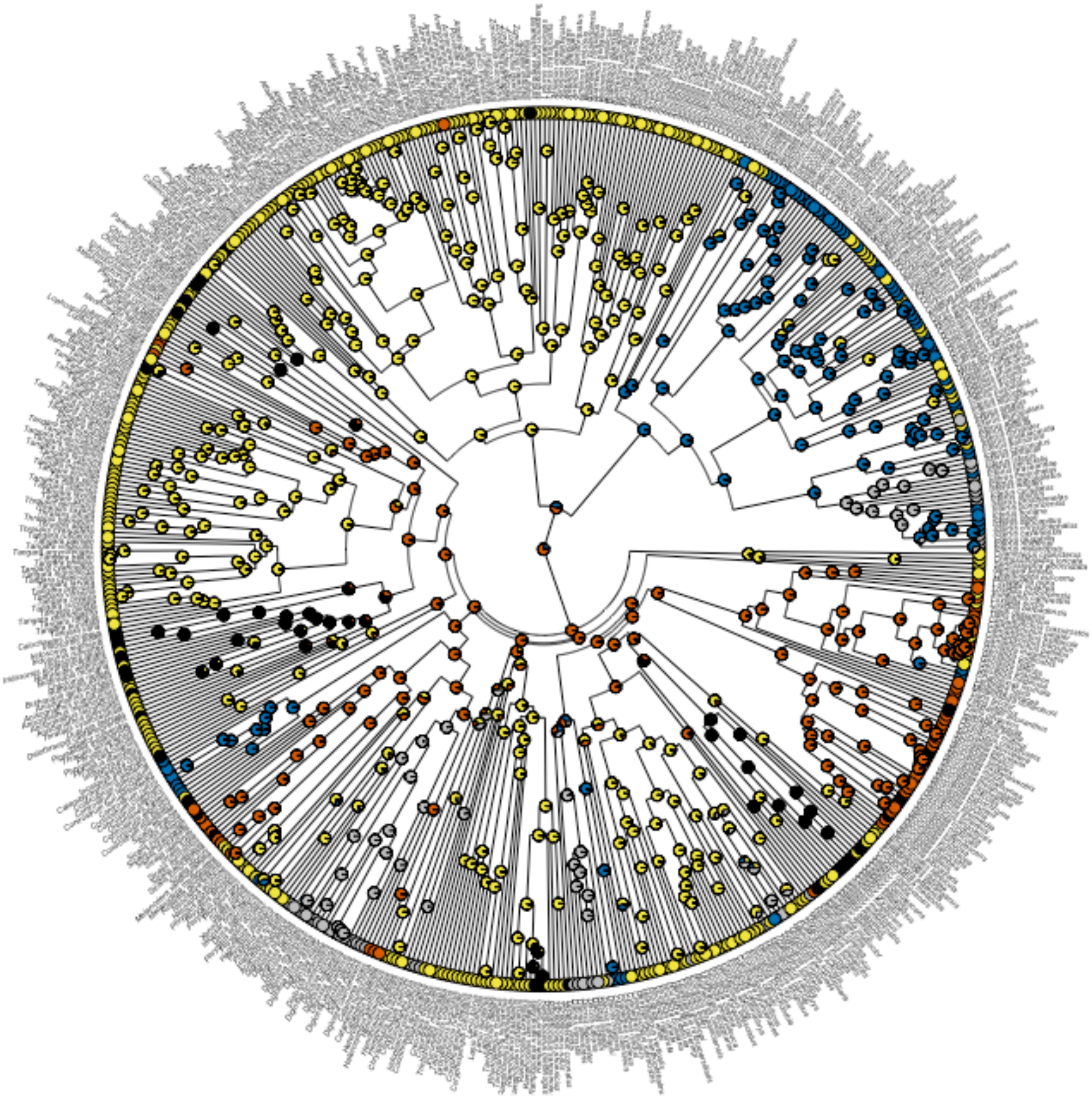

Figure 3.4. Marginal ancestral state reconstruction based on grouped MuSSE model showing transitions among character states.

DISCUSSION

Specialization is assumed to incur tradeoffs that may limit further evolution (Futuyma and Moreno 1988). We developed an index of specialization based on bill morphology to examine transition rates between generalist and specialist bill shapes in three diverse families of Emberizoidea. We estimated transition rates between character states while accounting for variation in diversification rates and potential correlations with unmeasured traits that may vary among clades (Beaulieu and O'Meara 2016). Our results show higher transition rates from specialist to generalist bill morphologies, suggesting that niche expansion is an important part of the evolutionary history of this diverse clade. We did not find support for irreversibility of specialization in avian bill morphology. It is clear, therefore, that specialization in a feeding apparatus does not always limit further niche evolution.

Variable environments often favor more generalist strategies (Kellermann et al. 2009, Quintero and Wiens 2013, Murren et al. 2015), and increases in niche width can occur in response to annual or seasonal fluctuations in resource availability (Boag and Grant 1984). Lineage shifts to more generalist strategies during periods of rapid environmental change may provide one explanation for the higher transition rates from specialist to generalist. A similar pattern of transitions into more generalist feeding strategies has been found in mammals (Price et al. 2012), contradicting the hypothesis that ecological specialization leads to an evolutionary dead-end. Dispersal into new habitats may also induce expansions in niche breadth. For example, repeated dispersal of hummingbird-pollinated angiosperm specialists into areas lacking hummingbirds may lift selection pressures and allow evolution of other modes of pollination (Tripp and Manos 2008). The evolution of "key innovations" can also spur periods of expansion into novel niche space (Jablonski 1993, Schluter 2000), and examples of adaptation to new conditions within relatively few generations are widespread (Hendry and Kinnison 1999, Reznick and Ghalambor 2001, Bell and Gonzalez 2011).

Other studies, however, have found constraints in niche shifts to more generalist strategies. The differences between the findings of these studies and the results we present here may be related to the developmental or physiological complexity of the trait in question (Bull and Charnov 1985, Barrett 2013). For example, some insects have shown constraints in their ability to shift between unrelated or highly dissimilar host plants (Futuyma and Moreno 1988, Futuyma et al. 1995, Crespi and Sandoval 2000, Janz et al. 2001), and the low incidence of transition between carnivory and herbivory in mammals has been attributed to the complexity of differences in physiological and morphological adaptations involved in each dietary strategy (Price et al. 2012). Such transitions would likely require long evolutionary time, during which new lineages with intermediate traits might arise (Price et al. 2012). More distantly related species thus likely show greater variation in their degree of ecological dissimilarity (Davis 2005), and the high rate of transitions to more generalist strategies we report here may differ from the results of single lineage studies or those that examine transitions across a larger taxonomic scale than we examined. While transitions to specialism certainly occur, within the three taxonomic families we examined, more taxonomic diversity was explained by transitions in the opposite direction. Further, transition probabilities between disparate specialist states were likewise very low. As these transitions reasonably occur across generalist morphospace, the low rate of transition from generalist to specialist may be the rate-limiting step for multiple state changes.

This may also suggest that this initial transition into specialist morphospace is limiting factor for producing radiations.

The low rate of transitions from generalist to specialist may be a result of a lower probability of speciation among generalist taxa (Conway and Olsen, *In Revision*). Generalists are often associated with large ranges, high dispersal, and high rates of gene flow, which also decrease rates of speciation (Brown 1995, Gaston 1998, 2003; Williams et al. 2009, Birand et al. 2012, Claramunt et al. 2012). Generalists also have a higher propensity to colonize novel habitats (Greenberg 1990, Schluter 2000, Sol et al. 2002), and the low transition rates from generalist to specialist may suggest that vicariance among generalist populations in novel niche space may be rare. Specialist species also have higher rates of extinction (Jablonski 2008), which may inflate the transition differences if generalists that become specialist are more likely to go extinct. However, this would not explain why transition rates among specialists were higher than that from generalist to specialist (Fig. 4). If specialists in general have higher extinction rates, transitions from generalist to specialist should be hidden by extinction more than the reverse transition, all else being equal. Under this scenario, however. transitions between specialists should be lost at an even greater rate, as extinction probability should be higher for both the initial and final character states. This is not what we observed within the Emberizoidea.

Transition rates between specialists and generalists could also be indirect and involve other important biological or ecological traits. Our HiSSE results suggest there may be another related character state driving transition rates. Both dispersal ability and range size are important characteristics that are often associated with specialization (Brown 1995, Conway and Olsen *in revision*), and make similar macroevolutionary predictions (Gaston 2003, Birand et al. 2015).

Moreover, specialization can occur across multiple niche axes and can be defined in a number of ways (DeVictor et al. 2010). Our index captures a single morphological axis of specialization in a highly labile trait.

Our results provide evidence contradicting a long-held theory that specialization necessarily erodes adaptive capacity leading to an evolutionary dead-end (Futuyma and Moreno 1988). While niche conservatism can constrain evolution of some traits (Kellermann et al. 2012), the degree of conservatism can vary depending on the niche axis and taxonomic scale (Losos 2008, Pearman et al. 2014). The high transition rates from specialist to generalist we report here suggest that niche conservatism does not constraint niche evolution for bill morphology in this clade. While adaptation in any direction may certainly still be limited in small populations (Wiens 2004, Wiens and Graham 2005), a larger proportion of extant diversity among three New World Emberizoidea families was produced from transitions from specialist to generalist than the reverse.

CHAPTER 4

PARALLEL PATTERNS OF NICHE DIVERGENCE IN TWO TIDAL MARSH SPECIALISTS

ABSTRACT

The degree of an organism's specialization, or niche breadth, can determine its geographic distribution. Specialization is also recognized as a major factor influencing both diversification and extinction risk. Understanding factors that influence these two processes is critical for conservation. A species niche varies over space and time, but how these changes mediate extinction and diversification remains unclear. Niches may change both their breadth and position, and we tested several mechanisms proposed to explain these changes. The Ecological Opportunity Hypothesis (EOH) predicts niche breadth expansion following colonization of novel habitats. The Niche Variation Hypothesis (NVH) suggests intraspecific competition increases niche breadth, while interspecific competition can act as a constraint on niche evolution. Finally, ecological variation among populations can increase variation in niche position, increasing niche breadth at the species level. We test these hypotheses by examining patterns of variation in bill size (a functional trait related to diet and thermoregulation) among populations of three species of Passerellid sparrows that colonized tidal marshes at different time scales, and thus differ in their degree of specialization. We quantified the effect of inter- and intraspecific competition and habitat characteristics on niche breadth and position. In support of the EOH, we found that among population divergence increased with time since colonization. We also found support for the effect of habitat characteristics on variation in niche position among populations. Contrary to the NVH, competition was not associated with niche breadth.

Our results suggest that ecological adaptation plays a larger role than interspecific competition in explaining evolution in tidal-marsh specialists, and understanding these processes provides insight into how to conserve diversity in these North American tidal marsh endemics.

INTRODUCTION

Elucidating factors that shape species' niches is essential to understanding constraints on geographic range limits and how ranges might shift in response to environmental change. Species that are more specialized, or use a narrower range of resources, often occupy smaller ranges (Brown 1984, Dapporto and Dennis 2013, Slatyer et al. 2013, but see Gregory and Gaston 2000) and are more prone to population declines and increased extinction risk (Julliard et al. 2004, Jablonski 2008, Colles et al. 2009, Correll et al. 2016, 2017, 2019).

Niches are often characterized as a species-level trait, yet numerous organisms show variation in functional traits across populations (Bolnick et al. 2003), and niches can evolve over time due to individual variation (Holt 2009). Thus, understanding factors that influence trait variation within and among populations will help us better predict how species respond to environmental change. Niches defined at the population scale (hereafter "population niche") can change their: 1) niche breadth if the amount of variation within or among individuals within the population changes, or 2) niche position if the mean trait value for a population changes. Understanding these population-level processes will also help determine factors that create and maintain ecological specialization. Here we examined variation in population niches within three species to identify the major drivers of niche variation at this scale.

Several mechanisms have been proposed to change population niche breadth. Empty niche space, for example, can provide ecological opportunity for intraspecific niche expansion driven by release from interspecific competition. An increase in ecological opportunity (EO) predicts a negative correlation between species diversity and population niche width, but also depends on factors such as microhabitat diversity (Parent and Crespi 2006). A variety of taxa show an increase in niche breadth (higher degree of intraspecific trait variation) in populations with greater habitat diversity and low species diversity (Cocos finch: Werner and Sherry 1987; marine mammals: Yurkowski et al. 2016; Mexican Jays: McCormack and Smith 2008; alligators: Rosenblatt et al. 2015).

The Niche Variation Hypothesis (NVH) suggests increased intraspecific competition, rather than resource availability, drives niche expansion in species-poor habitats (Van Valen 1965, Roughgarden 1972). This NVH suggests that increases in niche breadth result from increased variation among individuals rather than increases in individual niche breadths. This mechanism predicts wider niche breadth via increased trait variation among individuals in populations with higher intraspecific population density. A number of taxa show patterns of increased intraspecific variation resulting from increased population densities (Svanbäck and Persson 2004, Araújo et al. 2008, Huss et al. 2008, Greenberg and Olsen 2010), although at least one study has found a conflicting pattern (Parent et al. 2014).

While changes in resource availability and intraspecific competition can increase variation within a population, environmental differences among populations can clearly result in local adaptation (LA), producing differences in niche position as shown by shifts in mean trait optima. If this mechanism is the main driver of niche evolution, much of the intraspecific variation would be partitioned among, rather than within populations. An increasing number of examples provide evidence of adaptive divergence related to environmental variables or food resources, even at small geographic spatial scales (i.e., smaller than the organism's dispersal distance; e.g., Richardson and Urban 2013, Langin et al. 2015, Greenberg et al. 2016, Noguerales et al. 2016, Taylor et al. 2018, Friis et al. 2018).

Ecological Character Displacement (ECD) suggests that interspecific competition can influence both niche breadth and niche position (Brown and Wilson 1956, Grant and Grant 2006). This hypothesis predicts either a shift in the population trait mean, a decrease in niche width, or both, in direct response to the presence of interspecific resource competition. For example, a *Geospiza fortis* population showed a shift to smaller seed size coupled with a phenotypic shift to a smaller bill in response to direct competition with a recent colonist with a larger bill, G*eospiza Magnirostris* (Grant and Grant 2006). However, similar inter-population patterns of phenotypic variance can also result from local adaptation along environmental gradients, and few studies of ECD have attempted to correct for geographic clines in phenotypic traits or differences in environmental variables (Meiri et al. 2011, Stuart and Losos 2013).

Importantly, none of these mechanisms are mutually exclusive. For example, variation in within-population niche breadth may result from a balance between intra- (diversifying; NVH) and inter-specific (constraining; EO, ECD) competition. Likewise, variation in niche-mediated trait means among populations can result from differences in both the presence or absence of interspecific competitors (ECD), and differences in environmental conditions (LA; Meiri et al. 2011). Which of these mechanisms are most important, however, drive the scale at which intraspecific traits vary and also has important ecological and evolutionary implications (Bolnick et al. 2003). In particular, the scale at which diversity is created, constrained, and maintained helps determine whether taxa are evolutionarily buffered against environmental change (Etterson 2008, Reed et al. 2011, Hoffmann and Sgrò 2011).

We examined intraspecific trait variation in three tidal-marsh passerines: seaside sparrow (*Ammospiza maritima*), saltmarsh sparrow (*A. caudacuta*), and Nelson's sparrow (*A. nelsoni*). Tidal marshes have several attributes that make them an ideal study system for disentangling many of the hypothesized processes behind niche variation. They exist in discrete habitat patches that are easily delineated, and thus populations can diverge in both niche position and niche breadth. Their relative novelty on a geologic time scale (Malamud-Roam et al. 2006) and the adaptive challenges posed by regular tidal inundation limit colonization have resulted in low species diversity (Greenberg and Maldonado 2006, Greenberg et al. 2006). Thus, sparrow populations with no or just a few interspecific competitors exist across the landscape. North American tidal marsh passerines are good candidates for intraspecific competition as well. Populations vary widely in their intraspecific density (Wiest et al. 2016, 2019) and average higher densities than their nearest non-tidal relatives (Greenberg and Olsen 2010). Tidal marshes also exist along a coastal to brackish river gradient, where tidal influence and salinity (both of which are novel selection pressures on marsh colonizers from more inland habitats) decrease with distance from the coast. Phenotypic trait evolution might thus be expected to vary in response to local environmental conditions.

Together, these unique characteristics of the tidal marsh enable us to test the relative importance of a suite of proposed mechanisms for niche evolution. By sampling populations for each focal species that span the independent environmental, intraspecific density, and interspecific competitor gradients, we test for similar symptoms of niche evolution among three taxa that independently colonized the tidal-marsh ecosystem (Chan et al. 2006). Seaside and saltmarsh sparrows are habitat specialists whose distribution is restricted to coastal tidal marshes, and they exhibit a hypothesized pre-Pleistocene association with tidal salt marshes, with estimated divergence time from their closest non-tidal relative estimated at 1.5 my (Zink and Avise 1990) and 0.6 my (Rising and Avise 1993), respectively (Chan et al. 2006). In contrast, the Nelson's sparrow is thought to have colonized tidal marshes since the last glacial retreat (Chan et al. 2006), and exhibits a broader ecological niche, inhabiting grasslands and hay fields in addition to brackish and coastal tidal marshes (Greenlaw 1993, Nocera et al. 2007, Walsh et al. 2016). This allows us to compare patterns and drivers of niche partitioning among species to determine if the degree of specialization may play a role in how niche variation is partitioned within this ecosystem.

We focused on variation in bill size within and among populations because it is a known functional trait. Bill size has shown rapid short-term changes within species due to differences in resource availability (Boag and Grant 1984, Langin et al. 2015), the addition or subtraction of interspecific competitors (Grant and Grant 2006), and changes in intraspecific competition (Clegg and Owens 2002, Greenberg and Olsen 2010). Bill size also plays a role in thermoregulation by dissipating heat, which could be advantageous in saline or otherwise water-limited environments, and several studies have shown bill size variation related to temperature gradients (Greenberg and Droege 1990, Tattersall et al. 2009, Greenberg et al. 2012a, Luther and Greenberg 2014, Danner et al. 2017, Olsen et al. *In Revision*). We captured sparrows in tidal marshes along the coast of the eastern U.S. between Virginia and Maine to examine patterns of intraspecific niche partitioning within and among populations. We then examined the relative influence of interspecific competition, intraspecific density, and vegetative composition (a proxy for the salinity and tidal gradients) on differences in niche breadth and niche position among populations.

METHODS

Site Selection and Field Data Collection

We selected sites within coastal tidal marshes that spanned the gradient from estuaries to the head of tide in river and back-bay systems from Virginia to Maine, USA (Figure 4.1). At each site we first conducted a point-count survey following standardized methods outlined in the National Marsh Bird Monitoring Protocol (Conway 2011). We recorded all aural and visual detections of unique individuals during a five-minute passive listening period. We did not conduct surveys during periods of rain, high winds (>20 kph), or fog. Following the point count, we captured sparrows in mist nets. We banded each individual with a uniquely numbered U.S. Geological Survey leg band and recorded all standard morphological measurements. To quantify the functional trait values specifically, we measured bill width and depth at the anterior edge of the nares, and length from the anterior edge of the nares to the bill tip. We also conducted vegetation surveys at each site to quantify position along the tidal and salinity gradients. Within 50 m of each netting location, we recorded percent cover of each plant species and water feature (e.g., pannes, pools, creeks).

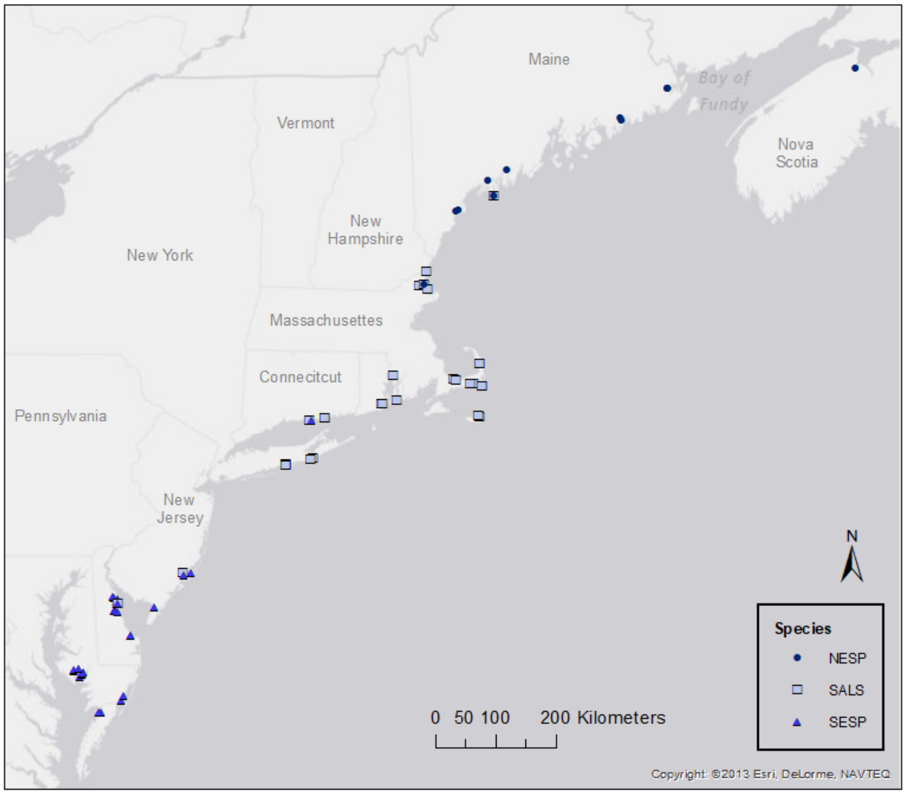

Figure 4.1. Sites located along the eastern coast of the U.S. Location where we captured ≥ 5 seaside sparrows are shown as triangles, ≥ 5 saltmarsh sparrows as squares, and ≥ 5 Nelson's sparrows as circles.

Morphological and Environmental Data

We defined the functional trait (bill size), competitive environment (intra- and inter-specific bird density), and ecological environment (vegetative assemblage) for 70 sites where we captured ≥ 5 individuals at a site (defined as collections of one to three points within a 200m radius). This spatial scale is likely smaller than either a demographically or genetically defined population in most cases, but aligns more closely with the scale at which natural selection via the ecological or competitive environment is expected to act on individuals. The mean distance to the nearest population was 19.5km, with a range between 225m and 223.5km to the nearest population. We calculated the mean and coefficient of variation for bill size within each species and site as an index of the niche position and niche breadth, respectively, for each population. We estimated bill size using a formula that evenly weights the three bill dimensions ((1/3 π) * bill length * bill width * bill depth), following Greenberg and Droege (1990). We used the number of individuals caught per net hour as an index of intraspecific competition at each site. For interspecific competition, we determined presence or absence of each of six Passerellid (*sensu* Chesser et al. 2017) species (saltmarsh, Nelson's, seaside, song, swamp, and savannah sparrow), as well as the number of species present at a site based on point-count data for each site. We also included an index of abundance for each of the six Passerellid species based on the number caught per net hour. We used relative abundance from net captures rather than point counts, because estimates from point counts can be biased low in these habitats compared to banding data (Field et al. 2016). We conducted a Principle Component Analysis on vegetation survey results to reduce the number of cover estimates for 84 cover types.

Statistical Analyses

We first examined how variation in bill size is partitioned among versus within species. We constructed a mixed model using the *lme* function from the *nlme* package (Pinheiro et al. 2018) with bill size as the dependent variable, and species as a random factor. We used the *varcomp* function in the *ape* package (Paradis et al. 2018) to estimate the amount of variance among versus within species.

To test which of the patterns of niche evolution match empirical patterns of intraspecific niche partitioning within and among populations, we first constructed mixed models using the *lme* function from the *nlme* package (Pinheiro et al. 2018) with site as a random effect. Because multiple of these species have sexually dimorphic bills (Greenberg and Olsen 2010), skewed sex ratios (Post and Greenlaw 1982, Hill et al. 2013), and differences in capture probability between males and females, we constructed a sex-corrected bill size for all individuals. We used the residuals of a linear model predicting bill size as a function of sex as our functional trait values. This prevents us from ascribing differences in the sex ratio of our captured individual to differences in niche space at a site. We then modeled sex-corrected bill size as a function of a random effect of population, using AIC_C values and Akaike weights to determine if the model including variance among populations had more support compared to a null model (Burnham and Anderson 2002). We used the *varcomp* function in the *ape* package (Paradis et al. 2018) to estimate the amount of variance within versus among populations for each of the three species.

We used distance-based Redundancy Analysis (dbRDA; Legendre and Anderson 1999) to examine the relative importance of the three categories of predictor variables (inter- and intraspecific competition, and vegetative composition) on variation in niche position and niche breadth among our sites while accounting for isolation by distance. We expect that the independence in histories of genetic drift between any two populations is a function of the degree of genetic isolation between populations. Thus trait divergence should be due to both niche divergence (i.e., changes in the functional characteristics of the trait) and drift (i.e., neutral processes). By using a dbRDA, we explore how divergence in ecological space (the vegetative community and both intra- and inter-specific competition) explains divergence in trait space (using distance matrices for either sex-corrected bill means or variances) while controlling for differences in geographical space. The dbRDA method is a multivariate multiple regression technique that performs principal coordinate analyses on predictor variables and finds linear combinations of the predictor variables (here competition, vegetation, and geographic distance) that explain the greatest amount of variance in the dependent variable (here dissimilarity in bill size population means or variances).

For our dependent variable, we constructed morphological distance matrices using the *dist* function in R to indicate the dissimilarity among sites in 1) niche position (sex-corrected mean bill size) and 2) niche breadth (coefficient of variation in bill size). We retained uncorrected bill size in our calculation of the coefficient of variation for each population because sexual dimorphism can increase inter-individual variation, and thus can be an important component of niche breadth (Bolnick et al. 2003). To account for isolation by distance we computed a geographic distance matrix from individual latitude and longitude coordinates using the *dist* function in R. We converted the geographic distance matrix using the PCNM method (principal coordinates of neighborhood matrices) using the *pcnm* function in the *vegan* package. This method performs a Principal Coordinate Analysis to produce orthogonal variables that represent a range of spatial scales (Borcard and Legendre 2002).

In order to reduce the number of predictor variables in our dbRDA models, we used a two-step process. We first selected the best-performing variables from each of the predictor categories (i.e., plant assemblage, intra-specific competition, inter-specific competition, and geographic distance). Within each of these categories, we constructed models for each single predictor, and combinations of the best-performing single variables (those with positive Adjusted

R^2) in that category (Table A4.2). We used the Adjusted R^2 values to choose the best-fit model within each category of predictor variables that explained the most variation in our dependent variables (dissimilarity in bill-size population means or variances). We then constructed models using all combinations of the best-fit variable or combination of variables from each category (i.e., the vegetation PC axis or combination of axes that produced the highest Adjusted R^2 value, the combination of PCNM axes that produced the highest Adjusted R^2 value, the combination of interspecific competition variables that produced the highest Adjusted R^2, and our single variable for intraspecific competition; Table A2, Table 2). We repeated this process to determine the relative explanatory power of each predictor category on dissimilarity among populations in niche position (sex corrected mean bill size) and niche breadth (coefficient of variation in bill size) for each species. In order to parse out the amount of variation explained by specific categories after accounting for geographic variation, we included an additional set of models with geographic distance as a conditional variable. We also examined the marginal effects for individual variables in our full model to account for any covariation among our predictor variables and determine if a single variable might be driving overall model performance. We performed all dbRDA analyses using the *capscale* function in the R package *vegan* (Oksanen et al. 2016). We used Euclidean distance and scaled all variables in our analyses. We evaluated variable importance using the Adjusted R^2 values corresponding to the estimated amount of variance explained (Oksanen et al. 2013) and evaluated significance of models via permutation testing using the *anova.cca* function in the *vegan* package. We then used linear models to estimate the effect size of the top ranked variables. We log transformed our abundance variables to improve normality of the distributions.

RESULTS

We captured 199 seaside sparrows at 28 sites, 223 saltmarsh sparrows at 30 sites, and 124 Nelson's sparrows at 12 sites (Fig 4.1). Summary statistics of bill size variation for each species is included in supplementary information (Table A4.1). Variance component estimates of a mixed model with bill size as a function of a random effect of species suggests that 83% of the variation in bill size is partitioned between species, while 17% of the variation is within species. We did not correct for sex here, as doing so also corrects for the sex-specific species mean, leaving only intraspecific variation. The amount of sex-corrected bill-size variation among populations varied positively with the time of association in the tidal marsh (Table 4.1). Seaside sparrows showed greater among-population variance (21%) than the other two sparrows (8%), and model support for population partitioning declined with time since colonization (Table 4.1). A mixed model with population as a random factor showed strong support compared to an intercept-only model for both seaside and saltmarsh sparrows. Nelson's sparrows showed a similar amount of variance among populations as saltmarsh sparrows, but the population-partitioning model was equivalent to a null model (Table 4.1). Based on these results, we did not further explore drivers of variation among populations in Nelson's sparrows.

Table 4.1. The estimated percent of variance in bill size partitioned within versus among populations of three Passerellid sparrow species. Variance estimated with the *varcomp* function. ΔAIC_C values and AIC weight (*w*) indicate the amount of support for a mixed effects model with population as a random factor compared to a null model.

	Among Populations	Within Populations	ΔAIC_C	*w*
Seaside sparrow	0.21	0.79	20.46	1.00
Saltmarsh sparrow	0.08	0.92	3.18	0.83
Nelson's sparrow	0.08	0.92	1.26	0.65

The first nine principal components explained 78% of the variation in plant species composition at locations where we caught saltmarsh sparrows (Table A4.3.1). The first seven principal components explained 78% of the variation among seaside sparrow capture locations (Table A4.3.1). The principal component axes described different scales of the habitat gradient (Table A4.3.1, A4.3.2). For example, PC1 for saltmarsh sparrows described an estuarine to upriver salinity gradient, with positive loadings for coastal species such as *Sparitina alterniflora*, wrack, and *Salicornia* spp., and negative loadings for *Typha angustifolia, Schoenoplectus americanus, S. robustus, and Juncus gerardii.* PC4 for seaside sparrows explained a similar salinity gradient, but at a smaller spatial scale. High-marsh species (*Spartina patens*) had positive loadings and low-marsh species (*S. alterniflora, S. pectinata, Salicornia*) had negative loadings, indicating differences in frequency of tidal inundation at the estuarine end of the river gradient.

The first step of our modeling process selected factors that best predicted variation in niche position and breadth for each species within each of our predictor categories (Table A4.2).

For saltmarsh sparrow niche position, independent variables included principal component axes 1, 4, and 5 for vegetation, the number of seaside and swamp sparrows present for interspecific competition, and PCNM axes 1, 4, and 8 for geographic distance. For saltmarsh sparrow niche breadth, independent variables included principal component axis 3 for vegetation, the number of song sparrows present for interspecific competition, and the sixth PCNM axis for geographic distance. For seaside sparrow niche position, independent variables included principal component axes 3 and 4 for vegetation, the number of species present for interspecific competition, and all three PCNM axes for geographic distance. For seaside sparrow niche breadth, independent variables included principal component axes 3, 4, and 5 for vegetation, the number of saltmarsh sparrows present for interspecific competition, and the first PCNM axes for geographic distance.

In the full model set (which included factors listed above for each variable category), a model with geographic distance, vegetation, and intraspecific competition explained the most variation in saltmarsh sparrow niche position (Adjusted $R^2 = 0.27$, Table 2). A model with geographic distance, vegetation, and interspecific competition explained the most variation in seaside sparrow niche position (Adjusted $R^2 = 0.30$, Table 4.2).

The dbRDA results from the conditional models (which included factors listed above for each individual variable category, and geographic distance as a conditional variable) suggested that vegetation (Adjusted $R^2 = 0.11$, $P = 0.01$; Table 4.3), intraspecific competition (Adjusted $R^2 = 0.09$, $P = 0.002$; Table 4.3), and interspecific competition (Adjusted $R^2 = 0.08$, $P = 0.01$; Table 4.3) all explained significant variation in niche position among populations for saltmarsh sparrows, after accounting for the effect of geographic distance. Marginal effects of the full model (that included predictors from each category) suggest only vegetation was a significant predictor in the presence of all top-performing individual variables (Table 4.4). In seaside sparrows, vegetation (Adjusted $R^2 = 0.14$ $P = 0.01$) and interspecific competition (Adjusted $R^2 = 0.06$, $P = 0.047$) each explained a significant amount of variation in niche position after accounting for geographic distance (Table 4.3). Marginal effects of the full model (that included predictors from each category) suggest vegetation was a significant predictor in the presence of all top-performing individual variables for seaside sparrow niche position (Table 4.4).

Because a model with only vegetation and geographic variables explained almost as much (as a model that combined additive effects of vegetation, geographic distance, and a competition variable for both species (Table 4.2), we included an additional set of conditional models. The dbRDA model accounting for the conditional effects of both vegetation and geography for saltmarsh sparrow, intraspecific competition explained 3% and interspecific competition explained 2% of the variation in niche position. Seaside sparrows showed an even weaker pattern, with interspecific competition explaining <1% of the variation in niche position after controlling for the conditional effects of vegetation and geography.

None of the variables we explored in our conditional models explained a significant amount of variation in niche breadth after accounting for geographic distance for either species. None of the variables explained more than 1% of the variation in niche breadth among saltmarsh sparrow or 8% of the variation for seaside sparrow populations (Table 4.3).

Table 4.2. Results of distance-based redundancy analyses (dbRDA). Results show the effects of geography, vegetation, inter- and intraspecific competition on dissimilarity in niche position and niche breadth among populations. The dependent variables are dissimilarity matrices constructed from sex corrected bill size for each population (niche position), and coefficient of variation in bill size for each population (niche breadth). We chose independent variables for each category listed below using the process detailed in Table A4.2a, and included the number of individuals captured per net hour as our measure of intraspecific competition. We scaled all variables prior to analysis. For seaside sparrow niche position, independent variables included principal component axes 1, 4, and 5 for vegetation, the number of seaside and swamp sparrows present for interspecific competition, and pcnm axes 1,4, and 8 for geographic distance. For saltmarsh sparrow niche breadth, independent variables included principal component axes 3 for vegetation, the number of song sparrows present for interspecific competition, and the sixth pcnm axes for geographic distance. For seaside sparrow niche position, independent variables included principal component axes 3 and 4 for vegetation, the number of species present for interspecific competition, and all three pcnm axes for geographic distance. For seaside sparrow niche breadth, independent variables included principal component axes 3, 4, and 5 for vegetation, the number of saltmarsh sparrows present for interspecific competition, and the first pcnm axes for geographic distance.

NICHE POSITION

SALTMARSH SPARROW		**SEASIDE SPARROW**	
Variables	**Adj. R^2**	**Variables**	**Adj. R^2**
vegetation + geography + competition (intra)	0.27	vegetation + geography + competition (inter)	0.30
vegetation + competition (inter) + geography	0.26	vegetation + geography	0.30
vegetation + geography + competition (inter) + competition (intra)	0.25	vegetation + geography + competition (inter) + competition (intra)	0.28

Table 4.2 Continued

vegetation + geography	0.25	vegetation + geography + competition (intra)	0.28
competition (intra) + geography	0.24	vegetation + competition (inter)	0.21
competition (inter) + geography	0.22	vegetation + competition (intra) + competition (inter)	0.21
competition (inter) + competition (intra) + geography	0.21	geography + competition (inter) + competition (intra)	0.20
vegetation + competition (intra)	0.21	competition (intra) + geography	0.18
vegetation + competition (inter)	0.21	competition (inter) + geography	0.18
vegetation	0.21	geography	0.16
competition (inter) + competition (intra) + vegetation	0.20	competition (intra) + competition (inter)	0.15
geography	0.15	vegetation + competition (intra)	0.15
competition (inter)	0.11	competition (inter)	0.14
competition (inter) + competition (intra)	0.10	vegetation	0.13
competition (intra)	0.05	competition (intra)	0.09

NICHE BREADTH			
SALTMARSH SPARROW		**SEASIDE SPARROW**	
Variables	**Adj. R^2**	**Variables**	**Adj. R^2**
vegetation + competition (inter) + geography	0.06	competition (inter) + vegetation	0.17
competition (inter) + geography	0.05	geography + vegetation + competition (inter)	0.15
vegetation + geography	0.05	vegetation + geography + competition (inter) + competition (intra)	0.12
vegetation + geography + competition (inter) + competition (intra)	0.04	vegetation	0.09
vegetation + competition (inter)	0.04	vegetation + geography	0.07
competition (inter) + competition (intra) + geography	0.03	competition (intra) + vegetation	0.06
geography	0.03	competition (intra) + competition (inter) + vegetation	0.05
vegetation + geography + competition (intra)	0.03	geography + competition (intra) + vegetation	0.03
competition (inter)	0.03	competition (inter)	0.02
competition (inter) + competition (intra) + vegetation	0.02	competition (inter) + geography	0.01
vegetation	0.01	competition (intra) + competition (inter)	0.01
competition (intra) + geography	0.01	geography + competition (intra) + competition (inter)	-0.01
competition (inter) + competition (intra)	0.01	geography	-0.01
vegetation + competition (intra)	-0.01	competition (intra)	-0.02
competition (intra)	-0.02	competition (intra) + geography	-0.03

Table 4.3. Conditional dbRDA models. Each model contains variables for the main predictor category and includes geography as a conditional covariate. The proportion of the variation explained after accounting for geographic distance is indicated by the Adj R^2. Predictors with $P < 0.05$ after controlling for geographical influence are highlighted in boldface.

NICHE POSITION

SALTMARSH SPARROW				SEASIDE SPARROW		
Variables	Adj R^2	*P*		Variables	Adj R^2	*P*
vegetation	**0.11**	**0.03**		**vegetation**	**0.14**	**0.01**
interspecific	**0.07**	**0.04**		**interspecific**	**0.06**	**0.047**
intra	**0.09**	**0.003**		intraspecific	0.02	0.17

NICHE BREADTH

SALTMARSH SPARROW				SEASIDE SPARROW		
Variables	Adj R^2	*P*		Variables	Adj R^2	*P*
vegetation	-0.02	0.65		vegetation	0.08	0.1
interspecific	0.01	0.29		interspecific	0.03	0.17
intraspecific	-0.03	0.89		intraspecific	-0.02	0.76

Table 4.4. Marginal effects of each predictor variable from the full dbRDA model.

Saltmarsh Sparrow Niche Position

Variable	Df	Sum of Squares	*P*
vegetation (PC1)	**1**	**1.28**	**0.04**
vegetation (PC5)	1	0.16	0.85
vegetation (PC4)	1	0.41	0.37
Geography (pcnm 1,4,8)	3	1.95	0.15
SESP abundance	1	0.18	0.80
SWSP abundance	1	0.22	0.74
competition (intra)	1	0.27	0.59
Residual	20	8.57	

Seaside Sparrow Niche Position

Variable	Df	Sum of Squares	*P*
vegetation (PC4)	**1**	**1.16**	**0.05**
vegetation (PC3)	1	0.65	0.18
Geography (pcnm 1,2,3)	3	2.23	0.07
competition (intra)	1	0.24	0.65
Species richness	1	0.45	0.35
Residual	20	8.28	

The vegetation PC axes that best explained niche position in saltmarsh sparrows (PC1) was interpreted as the tidal river gradient, with more salt-tolerant coastal cover types, such as *Spartina alterniflora*, *Salicornia* sp., and tidal wrack showing the highest positive loadings, and many brackish species, such as *Typha angustifolia, Schoenoplectus robustus, and Schoenoplectus americanus* receiving the largest negative loadings. Populations had larger bills farther up river ($\beta = -1.6$, SE = 0.04; Figure 4.2). Seaside sparrows occur over a narrower gradient of tidal conditions, and as such the PC axes that best explained their population niche position (PC4) represented a narrower gradient from areas of high tidal marsh that are inundated only a few times a month (e.g. *Disticilis spicata, Spartina patens*) versus lower marsh species that dominate areas flooded as frequently as daily (tall form *Spartina alterniflora, Salicornia, Spartina pectinata*, and wrack). Seaside sparrows showed a decrease in bill size toward more frequently inundated sites (β = -3.6, SE = 1.5; Figure 4.2). Saltmarsh sparrows showed a decrease in bill size as intraspecific density increased (β = -7.09 SE = 4.2; Figure 4.3), and as density of seaside sparrows increased (β = -0.16 SE = 0.1). Although swamp sparrow abundance also appeared in top ranked models, they only occurred at one of our sites, and may not represent a true pattern (β = -1.07, SE = 0.5). Seaside sparrows showed a similar pattern, with a decrease in bill size as the number of species present increased (β = -15.4, SE = 4.9; Figure 4.5).

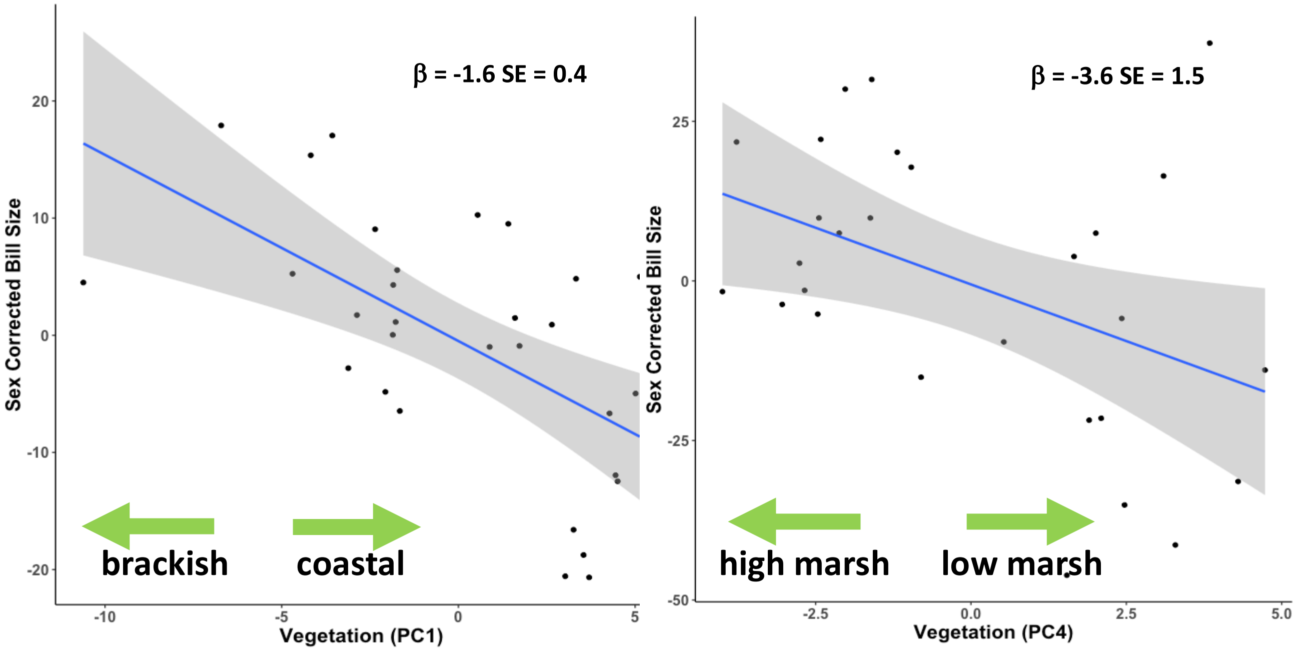

Figure 4.2. Effect sizes from linear models of sex-corrected bill size as a function of vegetation. Variation in vegetation species composition along a principal component axis that captured the tidal gradient from brackish riverine marshes to the estuary (PC1) explained variation in saltmarsh sparrow bill size (left), while variation in vegetation species along a tidal gradient within estuarine marsh (PC4) explained variation in seaside sparrow bill size (right).

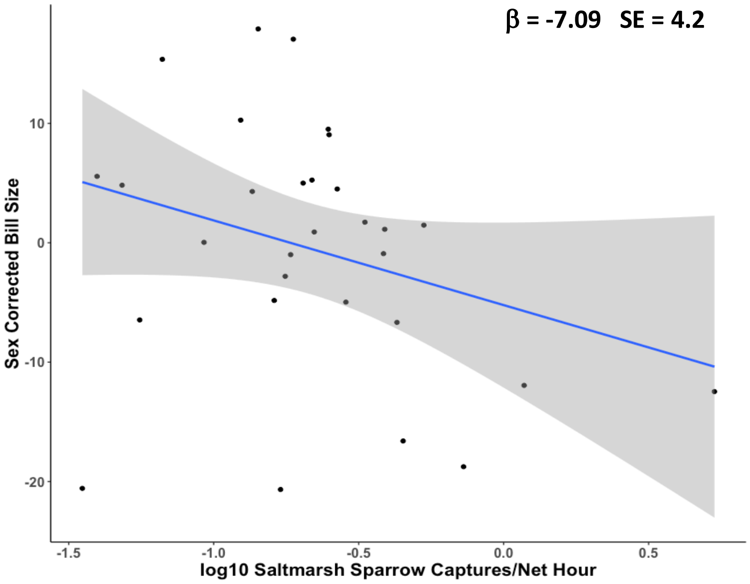

Figure 4.3. Effects of a linear model for saltmarsh sparrow sex-corrected bill size as a function of intraspecific density.

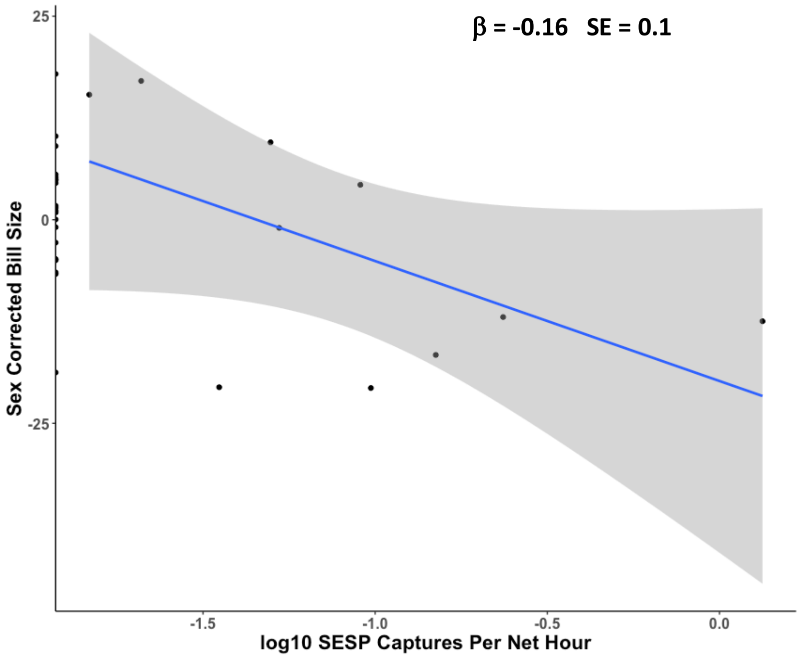

Figure 4.4. Effect size from a linear model with saltmarsh sparrow sex corrected bill size as a function of interspecific density of seaside sparrows.

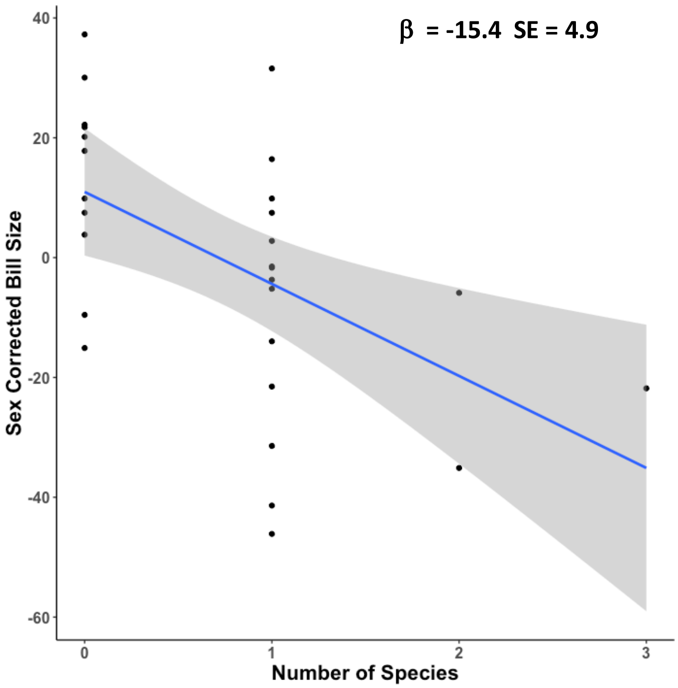

Figure 4.5. Effect size from a linear model with seaside sparrow sex corrected bill size, as a function of interspecific competition.

DISCUSSION

Species range limits are determined by their ecological niche. Thus, understanding factors that facilitate or constrain niche evolution is essential to understanding how species might adapt to environmental change. We examined patterns of intraspecific niche partitioning and drivers of among population variation in niche breadth and position in three tidal-marsh passerines. We found that seaside sparrows, which have the longest ecological association with tidal marshes (Chan et al. 2006), showed the highest amount of niche partitioning among populations. Saltmarsh sparrows, which were intermediate in association time among the three species examined (Chan et al. 2006), also showed significant, albeit less, niche partitioning among populations. Nelson's sparrows, which have only colonized tidal marshes since the last glacial maximum (Walsh et al. 2017), did not show significant among population differentiation. Nelson's sparrows showed the highest variation in bill size overall (CV = 13.35, Table A4.1), while seaside and saltmarsh sparrow showed less variation (CV = 11.5, 10.88 respectively, Table A4.1). For both seaside and saltmarsh sparrows, variation in plant assemblages along a gradient in tidal inundation explained the most among population variation in niche position. This suggests that adaptation to localized environmental conditions has a stronger relative effect on niche position (as shown by the niche functions represented by bill size) than either inter- or intraspecific competition.

We found some support for shifts in niche position with increased interspecific competition for both species, consistent with ECD. However, interspecific competition did not explain as much variation in bill size as the habitat gradient in either species. While bill size has been a central component in studies of ECD (Grant and Grant 2006), interspecific competition for food and nesting sites within tidal marshes is relatively low compared to inland habitats (Post and Greenlaw 1982, 2006; Bayard and Elphick 2010, Greenberg and Olsen 2010, Ruskin et al. 2015). This relaxed interspecific competition compared to inland habitats may allow for increased selection for intraspecific niche divergence (Greenberg and Olsen 2010). We did not find strong support for the NVH or EO at the population scale, as none of the variables we explored (competition or habitat gradient) explained significant variation in niche breadth among populations. The lack of support for NVH within populations may also relate to low levels of competition for food resources in this system (Post and Greenlaw 2006). However, differences in niche position among populations can drive niche expansion at the species scale. Reduced interspecific competition and high productivity may allow for greater morphological variability due to differences in environmental conditions among populations. Such increased variation due to low interspecific competition and increased habitat variation is consistent with EO at the species level scale. The higher degree of niche partitioning among populations in the species with the longest evolutionary history within this system is also consistent with this hypothesis.

Intraspecific variation in niche breadth and position can have important evolutionary implications (Bolnick et al. 2003). Intraspecific niche partitioning presents an important target for divergent natural selection, and environmental gradients are important drivers of adaptive divergence in models of speciation (Doebeli and Dieckmann 2003). Moreover, intraspecific population differentiation is positively correlated with speciation rates, and may be an important factor driving large scale patterns of diversity over space and time (Harvey et al. 2017). We found that seaside sparrows, the species with the longest evolutionary history within tidal marshes, showed the most pronounced pattern of among population divergence, and fine scale habitat variation was the best predictor of differences among populations. Together this suggests that we should see greater partitioning with greater environmental heterogeneity and time of association with a particular ecosystem. Further, if the same process of partitioning is occurring among the three species we examined here, it appears that increased partitioning can continue to evolve for at least hundreds of thousands of years.

Bill size plays a role in heat dissipation (Tattersall et al. 2017), which is important in regulating evaporative water loss in saline environments (Greenberg and Droege 1990, Tattersall et al. 2009, Greenberg et al. 2012b, Greenberg and Danner 2012). We found that saltmarsh sparrow bill size increased upriver, which could reflect a response to higher temperature regimes farther from the coast. We also found that seaside sparrow bill size increased in areas dominated by high marsh vegetation that become drier, hotter, and hypersaline in between the lunar spring tides, and thus could present a greater osmoregulatory challenge than areas flooded by more frequent tides. These findings are consistent with previous studies that show geographic variation in bill size as a function of ambient temperature and moisture gradients both within and among species (Greenberg et al. 2012b, a; Greenberg and Danner 2012, Danner et al. 2017, Olsen et al. *In Revision*). Further, some authors have suggested that selection for thermoregulation can only occur when selection on bill size from competition is released (Greenberg and Olsen 2010). Our results support that hypothesis; in both species we found larger bill sizes in marshes with fewer intraspecific (Figs. 3 and 4) or interspecific (Fig. 5) competitors. Importantly, however, competition for food has not been detected in this system (Post and Greenlaw 2006), so it is unclear how competition would select for smaller bills.

Variation in niche-mediated trait means among populations can result from differences in both the presence or absence of competitors and differences in environmental conditions (Meiri et al. 2011). By examining populations that varied independently along environmental and inter- and intraspecific competitor gradients, we were able to examine the relative influence of each of these factors in driving partitioning of bill morphological space at the population and species scale. While we found some support for interspecific (seaside sparrows) and intraspecific competition (both species), both population density (Wiest et al. 2019) and interspecific competition vary with the plant species assemblages and tidal influence. Seaside and saltmarsh sparrows both breed in coastal tidal marshes (Greenlaw 1993, Walsh et al. 2016, Post and Greenlaw 2018), while Nelson's sparrows breed in both coastal and more brackish areas (Walsh et al. 2016), and swamp sparrows are limited to more brackish and freshwater marshes (Greenberg et al. 1998). Song sparrows use tidal marshes, but are more likely to be found near upland borders since they don't nest extensively within Atlantic tidal marshes (Arcese et al. 2002). Thus, our two focal species overlap with the most potential competitors in marshes with greater heterogeneity in tidal and salinity regimes, and the patterns we found relative to competition may thus be a result of a correlation with these gradients that was not captured by our plant species measurements. Indeed, the direction of the relationships with vegetation and intraspecific competition are consistent. Bill size for both species increased in areas upriver (saltmarsh sparrows) or higher in the marsh (seaside sparrows), which typically have lower intraspecific densities for each species. The does not explain the negative relationship between interspecific species richness and bill size in seaside sparrows, however, as birds in high marsh, not low marsh, are more likely to encounter interspecific competitors. Regardless of whether unmeasured collinearities or independent mechanisms are driving the patterns with intraspecific density and species richness, our competition variables explained less than 5% of the variation in niche position after controlling for vegetation and distance. Clearly, the potential selective role of these variables, or those they represent, is low in this ecosystem.

Patterns of intraspecific niche partitioning have important implications for conservation. One of the criticisms of Species Distribution Models used to predict how species will respond to environmental change is that they do not account for intraspecific niche differentiation and local adaptation (Hällfors et al. 2016). More variable populations often have higher evolutionary potential and may be better able to persist in novel environments and expand their range (Sexton et al. 2009). Therefore, intraspecific variance can affect species ability to persist in the face of environmental change (Durell 2000, Norberg et al. 2012, Forsman and Wennersten 2016). Tidal marsh specialists have shown rapid population declines and are vulnerable to continued sea-level rise (Correll et al. 2016, Field et al. 2017, Ruskin et al. 2017). Furthermore, the species with the greatest niche partitioning among the three we examined shows the slowest rates of decline in our study region (Correll et al. 2016). Designing conservation strategies that conserve among-population variation and evolutionarily unique populations will help retain adaptive capacity in these imperiled species. Our results suggest that habitat diversity can be a good predictor of population differentiation, particularly for species that have a long evolutionary history with the ecosystem. The information presented here increases our understanding of the processes driving the distribution of intraspecific diversity across the landscape, and can help guide conservation that preserves evolutionary potential.

CHAPTER 5

DEGREE OF SPECIALIZATION CORRELATES ACROSS NICHE DIMENSIONS AMONG TIDAL MARSH SPARROWS

ABSTRACT

A species niche is defined across multiple dimensions that include any biotic or abiotic factors that a species requires in order to persist. Ecological specialization is the process of adaptation to a narrow set of available environmental conditions, and can have important consequences for the abundance, distribution, and long-term persistence of species. Yet, specialization is rarely defined across multiple niche axes. Selection for specialization along a single niche axis may lead to positive associations of specialization across other niche axes. Understanding both the origin and long-term persistence of specialization requires a more robust appreciation for how niche breadth changes on one axis may impact that in other dimensions of niche space. We tested if niche breadth is correlated among functional, performance, competitive, and environmental niche axes in a group of five Passerelid species that vary in their degree of habitat specialization within tidal marsh ecosystems. We found that niche size, or specialization, was positively correlated among functional, competitive, and environmental niche axes niche axes suggest that the origin of specialization can result from selection for specialization on a single axis. However, we found a negative correlation between niche size on performance and environmental niche axes, suggesting that the pattern is not ubiquitous.

INTRODUCTION

The ecological niche concept has played an integral role in explaining the origin, maintenance, and distribution of biodiversity. A species niche includes any biotic or abiotic factors that a species requires in order to persist (Hutchinson 1957), and a species range therefore depends on the match between these requirements and available environmental space (Brown 1984, Jackson and Overpeck 2000). Rapid changes in environmental conditions have increased interest in determining how niches respond to change. Species can respond to change by tracking shifts in environmental conditions, or evolution can alter the conditions under which populations can persist (Holt 2003, 2009). When tracking is not possible, niche lability is therefore critical for species persistence. Indeed, several studies have found that specialists, or those species with narrow niches, are more prone to population declines and more sensitive to habitat disturbance than are generalists (Julliard et al. 2004, Devictor et al. 2008, Correll et al. 2017, 2019). However, a species niche can be defined in multiple ways (Ferry-Graham 2002, Chase and Leibold 2003, Devictor et al. 2010), and niche breadth can be defined along multiple dimensions, or niche axes (Hutchinson 1957, Vamosi et al. 2014). Most species are likely generalist on some axes and specialist on others (Poisot et al. 2011). Yet, specialization is rarely quantified across several ecological niche axes (Bonetti and Wiens 2014, Brandl et al. 2015). To understand both the origin and long-term persistence of specialization requires a more robust appreciation for how niche breadth changes on one axis may impact that in other dimensions of niche space.

It is possible that niche breadth could be positively correlated among multiple niche dimensions (Brown 1984). A lack of tradeoffs among niche dimensions would suggest those species that can tolerate large variation in one dimension can tolerate variation in many other niche dimensions, which could explain how generalist species attain large geographic distributions (Brown 1984). However, niche breadth could also be independent across niche axes (Cody 1974, Armbruster et al. 1992, Brändle et al. 2002), or may be correlated among some axes, and not others, yet few studies have compared niche breadth across multiple niche dimensions. Positive correlation of niche breadth among multiple dimensions could result from correlated selection (i.e., selection for specialization on one niche axis is generally accompanied by selection for specialization on another niche axis because of environmental conditions are correlated). For example, a suite of adaptations across multiple niche dimensions may be required to exploit particularly harsh environments (Terborgh 1973, Brown 1984). Such a pattern is consistent with specialization across a suite of functional traits associated with tidal marsh colonization (Grenier and Greenberg 2005, Greenberg et al. 2006, Walsh et al. 2018).

Positive correlations could also result from correlation among traits due to pleiotropy or epistatic effects, where selection for specialized adaptations within one niche domain lead to changes in other traits that decrease the range of environmental conditions exploited by a species in other niche dimensions (Futuyma and Moreno 1988, Hoffmann and Sgrò 2011). For example, tropical species show loss of variation in key traits associated with both cold tolerance and desiccation resistance (Kellermann et al. 2009), and feeding and habitat preferences can be linked through enzymatic constraints in some crustaceans (Borowsky et al. 1985).

Correlations of niche breadth among traits can enhance adaptive specialization if they are subject to similarly correlated selection (i.e. selection favors a specific combination of characteristics; Laughlin and Messier 2015), or they can prevent niche evolution if selection on several correlated traits is antagonistic (Orr 2000). Correlated traits can also limit future adaptive potential, if adaptive specialization along one trait reduces the genetic variance and thus the evolvability for correlated traits (Kellermann et al. 2009, 2012). Thus, a lack of adaptive variation in a single key trait could not only prevent adaptation to conditions outside of the current niche, it might also limit the evolutionary trajectories open to other, correlated traits (Kellermann et al. 2009). While there are examples of how correlation of specialization on multiple axis can facilitate or constrain evolution, we do not understand how widespread these patterns are, nor whether particular categories of niche axis (e.g., abiotic or biotic) are more likely to impact niche breadth across the niche hypervolume (Vamosi et al. 2014).

Our objective is to determine if niche breadth is correlated among functional, environmental, performance, and competitive niche axes. We calculated an index of specialization for each of these niche axis groups for five species in a clade of Passerellid sparrows inhabiting tidal marshes of the northeastern U.S. Tidal marshes provide an ideal system to explore factors that facilitate and constrain niche evolution. They exist in discrete patches within the terrestrial-marine ecotone, allowing for easy delineation of the available niche space. Their latitudinal range provides gradients of climate and tidal amplitude, and they also exist along a coastal to brackish river gradient, where tidal influence and salinity decrease with distance upriver. These ecological gradients allow functional and performance traits to vary in response to local environmental conditions.

Each of our five species have also been reported to show different degrees of “specialization” on tidal marsh ecosystems, although this specialization has never been formally quantified beyond large-scale habitat affinities. Further, the habitat associations within tidal marsh habitats aligns with the hypothesized length of evolutionary association with this ecosystem. Seaside sparrows (*Ammodramus maritimus*) and saltmarsh sparrows (*Ammodramus caudacutus*) breed nearly exclusively in coastal tidal marshes and are hypothesized to have diverged from inland ancestors 1.5 my and 0.6 my, respectively (Greenlaw 1993, Rising and Avise 1993, Chan et al. 2006). The eastern subspecies of the Nelson's sparrow (*Ammodramus nelsoni subvirgatus)* and the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*) diverged from more inland forms following the last glacial maximum (Walsh et al. 2016; Greenberg et al. 1998). They are both found in more brackish areas of tidal marshes than the first two species and to a limited extent in either freshwater marshes or other non-tidal habitats (Beadell et al. 2003, Nocera et al. 2007). The inland subspecies of swamp sparrow (*Melospiza georgiana georgiana*), two subspecies of song sparrows (*Melospiza melodia melodia and M.m. atlantica*) also use tidal marshes of the Atlantic coast to some extent (e.g., for foraging), although they are all more widely distributed, inhabiting an array of terrestrial border habitats, freshwater marshes and bogs, grasslands, and farm fields as well. Together, the seven taxa occupy different positions along the evolutionary pathway to tidal-marsh specialization, and an understanding of how niche breadth covaries among niche axes in these species could help us understand the forces behind the evolution of specialization more broadly.

Colonization of the tidal marsh by multiple bird species has resulted in a suite of parallel evolutionary changes (Grenier and Greenberg 2005, Greenberg et al. 2006). Compared to their closest inland relative, taxa who have colonized tidal marshes have larger and longer bills (due to dietary and thermoregulation differences: (Grenier and Greenberg 2005, Greenberg and Danner 2012, 2013; Olsen et al. 2013), darker plumage (mechanical and bacterial resistance: Greenberg and Droege 1990, Peele et al. 2009, Olsen et al. 2010), and specialized kidney function (salt tolerance: Goldstein 2006). Recent genomic analyses have also shown evidence of selection on genetic regions associated with these traits (Walsh et al. 2018, *In Review*). These patterns further suggest that changes in biotic and abiotic niche axes associated with tidal marsh colonization have repeatedly altered taxa performance (e.g., kidney function, feather wear, thermoregulation) and resulted in the evolution of functional traits (e.g., kidney morphology, feather pigmentation, bill shape). Hence, this system presents a natural laboratory to explore how ecological and evolutionary factors determine niche breadth across multiple axes for taxa with different histories of association with the ecosystem.

We tested if niche breadth is correlated among functional, performance, competitive, and environmental niche axes. We also tested the ability of each niche axis category to predict niche breadth estimated by the remaining niche axes. We examined these patterns in a group of five Passerelid species that vary in their degree of habitat specialization within tidal marsh ecosystems that aligns with their evolutionary history. This variation in habitat specialization among species allowed us to determine if selection for specialization on one dimension aligns with specialization on multiple axes.

METHODS

Site Selection and Field Data Collection

We selected sites within coastal tidal marshes based on their position along river gradients between Virginia and Maine, USA (Figure 5.1). We also selected several sites within grasslands and hayfields bordering marshes to ensure we captured the broader niche breadth inhabited by coastal populations of some of these species. We captured sparrows and measured niche characteristics at 130 locations between 16 May and 24 Aug of 2015 and 2016.

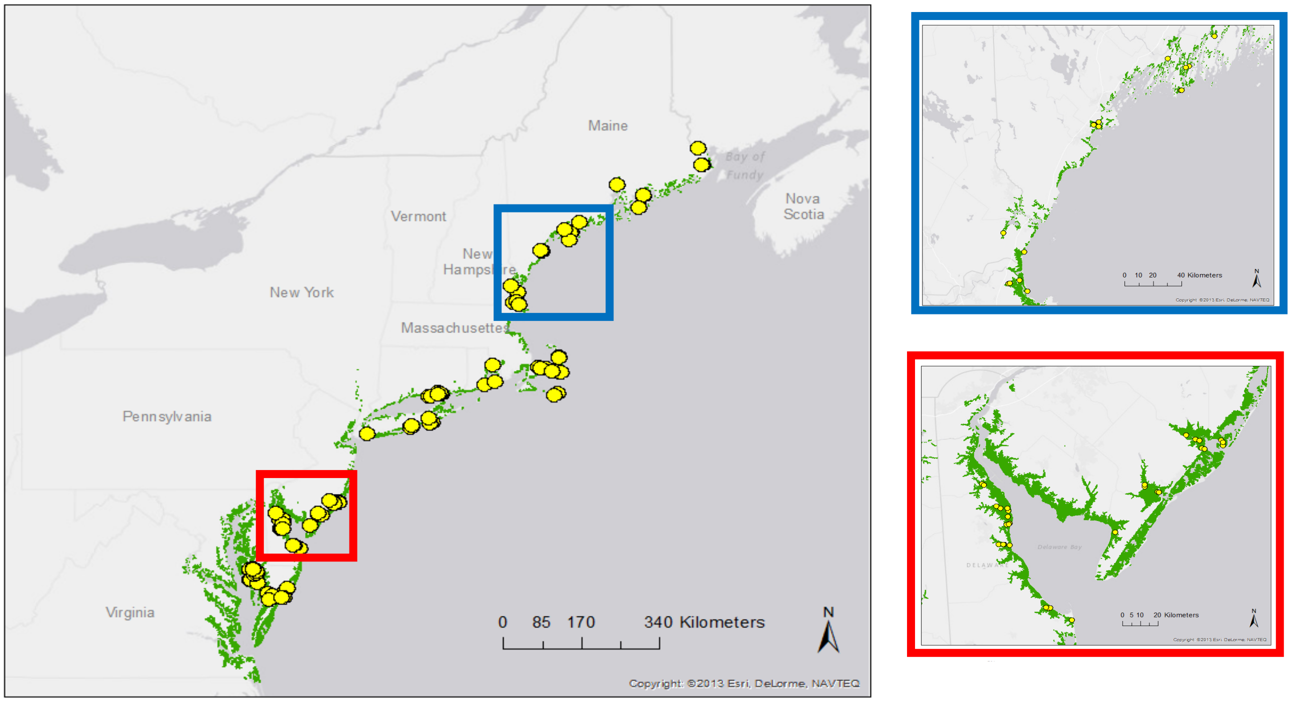

Figure 5.1. Map of sparrow capture locations in tidal marshes across the northeastern and mid-Atlantic coast, USA. Tidal wetlands classified as Estuarine Intertidal Wetland by the National Wetland Inventory (U.S. Fish and Wildlife Service National Wetlands Inventory 2010) are shown in green, and sparrow capture locations are indicated by yellow dots. The map insets to the right outlined in blue and red provide more detail of the extent of the river gradients we captured in our sampling.

Niche Axes – Functional

Functional traits respond evolutionarily to environmental conditions experienced by populations over time, and thus they indicate a longer-term record of niche breadth than can be measured during a single field visit to a population. We measured portions of this longer niche exposure using two well-studied functional traits: bill size and body size. Several studies have shown that temperature and water limitation select for larger bills to maximize the capacity for heat dissipation while minimizing water loss (Greenberg and Droege 1990, Greenberg et al. 2012a, Greenberg and Danner 2012, 2013; Luther and Greenberg 2014, Danner et al. 2017, Olsen et al. In Revision). Body size is also a well-known functional trait associated with temperature (Bergman 1847), and varies in response to summer temperatures across space and time (Gardner et al. 2009, Andrew et al. 2018).

We banded each individual with a uniquely numbered U.S. Geological Survey leg band and recorded a number of standard morphological measurements. Specifically, we measured bill width and depth at the anterior edge of the nares, and bill length from both the anterior edge of the nares to the bill tip and along the length of the skeletal culmen. We also measured both the left and right tarsometatarsus, unflattened wing cord length, and mass to the nearest 0.01 gram. We log-transformed all morphological variables prior to analysis, and conducted two separate Principle Component Analyses (PCAs). We first created an index of body size using the full set of morphological measurements. We then created a second PC axis using just the three bill morphology measures.

Niche Axes – Performance

Performance traits vary with the environmental experiences of individuals over time scales from the immediate to an entire lifetime. They are different from simple phenotypic variation in that their values influence demographic parameters (Nowicki et al. 1998, Byers et al. 2010). Therefore, similar to functional traits, they can capture niche axes over a period of time that is longer than a single site visit, but they are expressions of the niche experienced by individuals and are correlated with the probability of persistence within those conditions. For instance, body temperature could be used as a performance metric in an endotherm, and values that are far outside the thermal neutral zone both reflect the conditions the individual has experienced and might indicate a reduced probability of long-term persistence for the individual in that environment. Performance traits can thus track individual, population-relevant, environmental experiences. We used hematocrit, feather degradation, and skeletal asymmetry as performance traits that track previous environmental experiences within taxa.

Hematocrit values increase with plasma and urine osmolality following dehydration, and can indicate signs of environmental stress (Goldstein and Zahedi 1990). As such, we expect hematocrit to covary with those environmental variables that produce osmotic stress. We expect this trait to be demographically important for our study species, as some tidal-marsh sparrows have increased osmoregulatory capacity (Goldstein et al. 1990, Goldstein 2006). The presence of this adaptation underscores both the appropriateness of osmolality as a performance metric in this ecosystem and the need to expect differences in performance among taxa that experience the same environmental conditions but have different evolutionary histories. To measure the niche axes that control both of these processes, we pierced the ulnar vein of each captured bird and collected a blood sample in a single capillary tube (<70**μ**L). We spun each tube for 10 minutes in a centrifuge (Zipocrit Model LWZIP2) to separate out the blood plasma from the packed cell volume. We measured total blood volume, plasma volume and packed cell volume in the capillary tube with calipers to the nearest 0.01 mm and used the proportion of packed cell volume total blood volume to calculate a hematocrit value.

Feather structure, and its ability to resist breakage and wear, can have important implications for thermoregulation and water repellency (Nilsson and Svensson 1996, Rijke and Jesser 2011). We expected feather wear to covary with an individual's history of abrasion and bacterial degradation. There are multiple reasons to suspect that feather wear has demographic consequences in tidal-marsh birds. The presence of certain bacteria increases degradation of feathers in wild birds and this selection pressure can influence the evolution of feather color (Kent and Burtt 2016). The darker plumage of many tidal-marsh birds relative to their closest inland relatives is thought to have evolved in response to increases in feather degradation by salt-tolerant bacilli in the tidal marshes (Peele et al. 2009). Increased melanism in feathers has also been linked to increased resistance to mechanical abrasions, breakage, and feather wear (Bonser 1995, Mackinven and Briskie 2014), and can serve as an indicator of individual condition (Parejo et al. 2011).

We recorded several measures of feather wear. First, we took photos of each bird with spread retrices against a white background. From the photos, we followed a standardized protocol to score each individual feather for each bird (Borowske 2015). We recorded a qualitative measure of wear according to a standardized scale between 0 (no wear) and 5 (substantial wear). We also counted the number and severity (on a scale of 1 to 3) of fault bars on each feather. We calculated the average wear score for each individual, and summed the number of fault bars per feather. For the second set of measurements, we collected the outermost retrix from each bird, and photographed the collected feather with a Canon T1i and a 60mm macro lens against a white background with a ruler for scale. We digitally measured the overall feather length and the length of the plumulaceous section along the rachis of each feather, excluding the calamus, in Adobe Photoshop CS6 (ver. 13.0.5). We counted the number of fault bars, the number of broken barbs, and after discarding the outer 20% of the length, we counted the total number of barbs. We divided the number of broken barbs by the total barb count and divided the fault bars by the feather length to provide a quantitative measure of feather wear that accounted for differences in tail feather size and structure among species. For both measures of wear (proportion of broken barbs and our qualitative wear score), we accounted for within season variation by calculating the residuals of a linear model fit as a function of Julian date. As such we aimed to estimate the performance of each individual controlling for time of year so that variation in performance was more closely related with variance in spatial environment. We combined these two measures of wear with the three fault bar measurements (counts and severity score) in a PCA and used the first principal component as a composite measure of feather wear in our analysis.

We also included a measure of asymmetry as a performance trait. Fluctuating asymmetry tracks the experiences of individuals during development, covaries with environmental stress (Gest et al. 1986, Møller 1997), and can be associated with overall growth, fecundity, and survival (Møller 1997). We calculated an index of asymmetry as the absolute value of differences in the length of the left and right tarsi of each individual.

Niche Axes - Competition

The presence, absence, and abundance of potential competitors are classic axes that define a realized niche (Hutchinson 1957). Since the abundance and distribution of each of our taxa varies across our study region, this allowed us to define the breadth of potential interspecific competition within populations and across species. To obtain an index of interspecific competition, we conducted a point count survey at each capture site following standardized methods outlined in the National Marsh Bird Monitoring Protocol (Conway 2011). We recorded all aural and visual detections of unique individuals during a five-minute passive listening period. We did not conduct surveys during periods of rain, high winds (>20 km/h), or fog. We created an index of interspecific competition based on the number of Passerellid sparrow species present at each site. We used only Passerellid sparrows since they are close relatives, have similar habitat requirements and diets, and the opportunity for competition exists among all of our study taxa (Mowbray 1997, Arcese et al. 2002, Greenlaw et al. 2018, Post and Greenlaw 2018, Shriver et al. 2018).

Niche Axes – Environmental

We further defined the niche of each taxon using the plant assemblage and local climate. We conducted standardized vegetation surveys at each capture site by recording percent cover of each species present within a 50m radius from the center of the net locations to quantify habitat characteristics that define position along a number of ecological gradients. Plant species composition in these habitats reflect the salinity, elevation, and flooding frequency (Tiner 2013) experienced by those individual birds captured at the site. Vegetation structure is also an important determinant of nest loss due to flooding and predation (Ruskin et al. 2017). We log transformed our plant cover data to improve normality of the distribution, and conducted a PCA to summarize the variation in vegetative composition among sites.

We obtained climatic variables from each capture location during the breeding season (1 May through 31 August of 2015 and 2016) from the Prism Climate Group (2019). We obtained mean, maximum, and minimum daily temperature, and daily precipitation values. We created variables for total precipitation, mean, minimum, and maximum temperature, and variance of the daily mean temperature within the breeding season for each location. We conducted a PCA to reduce the number of variables, and to account for correlation among variables. We included the first principal component axis as an index of position along the climate niche axes.

Estimating Niche Breadth

We obtained data on these nine niche axes for 549 individuals, including 198 seaside sparrows, 259 saltmarsh sparrows, 47 Nelson's sparrows, 36 song sparrows, and 31 swamp sparrows. We used the *hypervolume* package in Program R (Blonder et al. 2018) to create a measure of niche breadth along multiple niche axes. We scaled all variables prior to analysis to ensure that estimates of niche breadth were comparable among axes. We grouped axes into four categories: environmental (the first and second PCs for plant species composition and the PC for climate), morphological (the PCs for bill morphology and body size), performance (hematocrit, fluctuating asymmetry, and the PC for feather wear), and competition (sparrow species richness). For each axis category, we estimated the hypervolume for each species using the *hypervolume_svm* function. We chose this method since the kernel density estimation technique can overestimate the hypervolume in some cases with high dimensional data (Qiao et al. 2017, Blonder et al. 2018). We ran 15 replicates with a random sample of 30 individuals for each species, as hypervolumes increase with number of samples. We also estimated the available space for each species and niche category using a random sample of 150 observations from all of the species (30 samples from each of the 5 species). We used this same rarified, replicate sampling technique to estimate five hypervolumes which each left out a single category of niche axes for each species and the available environmental space.

Predicting Niche Volume Across Axes

We assessed covariation in niche volume across axes by allowing the hypervolume of each single-category niche to predict the hypervolume of the niche with all of the remaining niche categories. We first used the *lm* function in R to run a univariate model for niche category with the species-specific hypervolumes of the niche with a single missing category as the dependent variable, and the niche hypervolume of the missing category as the predictor. We used the Adjusted R^2 value to evaluate the relative performance of each niche category in predicting the size of the hypervolume described by the remaining niche axes. To evaluate the ability of all categories to predict niche size simultaneously, we also evaluated the results of a log-linear model that predicted all twenty five hypervolumes that were missing a single category (five hypervolumes for five species) as a function of the size of the niche described by the missing category nested within the category type. We also conducted a correlation test to determine if niche volume was correlated across any of the single-category niches. We log transformed all hypervolume values for each of these analyses to account for the differences in dimensions among values.

RESULTS

Niche Axes – Functional

The first principal component for morphological measurements explained 52% of the variation in morphology, and indicated differences in body size among species. Song and seaside sparrows had the highest positive scores, while the smaller saltmarsh, Nelson's, and swamp sparrows had negative scores. The first principal component axis for bill morphology explained 71% of the variation in bill size. Bill depth had the highest loading, followed by bill width and skeletal culmen. Song and seaside sparrows had negative scores, while swamp, Nelson's and saltmarsh had positive scores.

The hypervolume for functional traits sampled across all species was 5.79 ± 0.51 SD^2 (Table 1). Swamp sparrows showed the largest variation, with a niche size of 1.95 ± 0.13 SD^2, while seaside sparrows showed the lowest, with a niche size of 0.92 ± 0.14 SD^2 (Table 5.1).

Niche Axes – Performance

The first principal component for feather wear measurements described 33% of the variation among individuals in our analysis. The average number of fault bars among all the feathers had the highest loadings, while our two measures of wear (proportion of broken barbs and our qualitative measure) had the lowest loadings. Hematocrit values ranged from 0.36 to 0.96 (mean = 0.51). Values for fluctuating asymmetry ranged from 0 to 2.2 (mean = 0.30).

The performance niche showed high variation among most of the species sampled. The niche size sampled across all species was 22.79 ± 5.53 SD^3 (Table 1). Swamp sparrows showed the largest variation, with a niche size of 14.08 ± 0.15 SD^3, or 62% of the available space, while Nelson's sparrows showed the lowest size of 1.91 ± 0.49 SD^3, or 8% of the available space (Table 5.1).

Niche Axes – Competition

The number of species present at a site ranged from 1 to 4 (mean = 2.08). Species showed similar variation in the number of species present across the sampled space. The niche size sampled across all species was 1 ± 0.04 SD (Table 1). Swamp sparrows showed the largest variation, with a niche size of 1 ± 0.01 SD, while saltmarsh sparrows showed the lowest, with a volume of 0.81 ± 0.14 SD (Table 5.1).

Niche Axes – Environmental

The first principal component for plant species explained 14% of the variation, and mainly separated out the northern versus more southern sites, representing the latitudinal gradient. The second principal component explained an additional 12% of the variation and represented the upriver salinity gradient, where grasses, *Typha augustifolia, Carex, and Eliocharis* had negative loadings, and coastal species such as *Spartina alterniflora, Spartina patens, Distichilis spicata, Salicornia*, and wrack had the highest positive loadings. The first principal component axis explained 60% of the variation in climate among sites. Mean and maximum temperature had the highest loadings, while variance in mean temperature had the lowest.

The environmental niche space showed large variation among species, and aligned with their time of association with the tidal marsh. The sampled available space had a hypervolume of 20.39 ± 2.43 SD^3 (Table 5.1). Song sparrows showed the largest niche breadth, with a volume of 10.78 ± 1.89 SD^3, while seaside sparrows showed the narrowest, with a volume of 0.69 ± 0.23 (Table 5.1). For estimates of volume with only vegetation, the available space had a niche size of 11.35 ± 1.38 SD^2. Swamp sparrows had the largest niche size of 8.42 ± 0.14 SD^2, and seaside sparrows had the narrowest, with a size of 1.56 ± 0.39 SD^2 (Table 5.1).

Table 5.1. Niche volume. We show the mean and standard deviation estimated from 15 random samples of 150 observations for the available space, and 15 random samples of 30 observations for each species. Environmental niche includes two principal components for plant species composition, and a principal component for climate. The Vegetation niche includes only the two principal components for plant species composition. Functional niche includes a principal component for both body size and for bill size. The Performance niche includes feather wear, hematocrit, and fluctuating asymmetry, and the Competition niche is defined by the species richness of potential sparrow competitors at each site.

	Environmental		Vegetation		Functional		Performance		Competition	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Available	20.39	2.43	11.35	1.38	5.79	0.51	22.75	5.53	1.00	0.04
NESP	7.64	1.87	6.60	1.34	1.06	0.13	1.91	0.49	0.95	0.03
SALS	3.57	1.10	2.82	0.75	1.50	0.32	4.41	2.00	0.81	0.14
SESP	0.69	0.23	1.56	0.39	0.92	0.14	13.31	4.16	0.89	0.14
SOSP	10.78	1.89	5.38	0.75	1.45	0.15	10.31	2.46	0.88	0.05
SWSP	9.81	0.92	8.42	0.14	1.95	0.13	14.08	0.15	1.03	0.01

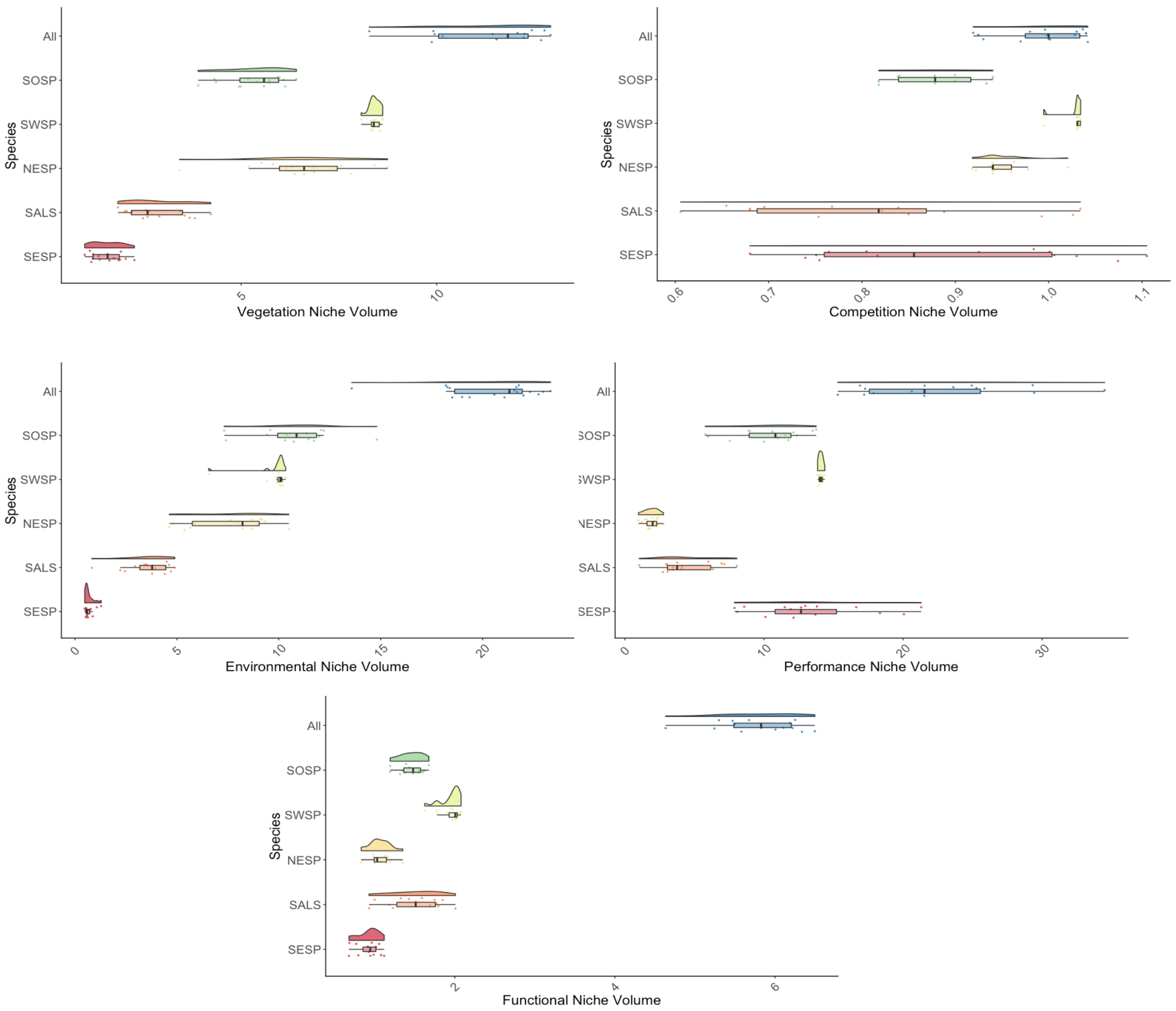

Figure 5.2. Density distribution and box plots showing the mean and standard deviation of niche volume estimates across 15 samples of 30 individuals for each species. We provide estimates across environmental, vegetation, performance, competition and functional trait axes. Niche volume estimated using the *hypervolume_svm* function in the *hypervolume* package in R.

Predicting Niche Volume Across Axes

Results from univariate log-linear regression models suggest that competition and functional traits explain the most variation in niche volume across other niche axes. Competition explained 7% of the variation in volume of the remaining niche axes, while functional traits explained 6% (Table 5.2). The nested linear regression also suggested that functional traits and competition had the highest predictive power ($P = 0.01$; Table 5.3) and that overall, individual category niches explained 10.2% of the variation in the size of the niche delineated by the remaining niche categories.

Competition and vegetation niche axes had the highest correlation coefficient (0.68), followed by functional traits and environmental (0.67; Figure 3, Table 5.4), and functional and environmental (0.61) but none were significant ($P = 0.21$, $P = 0.22$, $P = 0.28$, respectively). The performance niche axis had the lowest correlations overall, and was negatively correlated with both environmental (-0.23) and vegetation niche axes (-0.19, Table 5.4). The vegetation and environmental axes were highly correlated (0.94), but environmental axes included the vegetation axes.

Table 5.2. Effect size and variation explained by log-linear models that predicted the size of a multi-dimensional hypervolume. We defined hypervolumes for niche axes from four categories (Vegetation, Functional, Competition, Environmental, Performance) using the estimated size of a niche defined by axes in the remaining category. The Environmental axes include both vegetation PCs and the single climate PC.

	β	Adj R^2	*P*
Vegetation	0.61	0	0.64
Functional	2.82	0.06	0.35
Competition	15.35	0.07	0.34
Environmental	-0.09	0	0.87
Performance	-0.33	0	0.75

Table 5.3. Parameter estimates, variance, and P values from a single log-linear model that predicted all twenty five hypervolumes. Estimates describe prediction of hypervolumes that were missing a single category (five hypervolumes for five species) as a function of the size of the niche described by the missing category nested within the category type.

	β	SE	*P*
Vegetation	-0.23	0.51	0.66
Functional	2.99	1.90	0.13
Competition	9.99	5.93	0.11
Environmental	0.09	0.42	0.83
Performance	-0.09	0.38	0.81

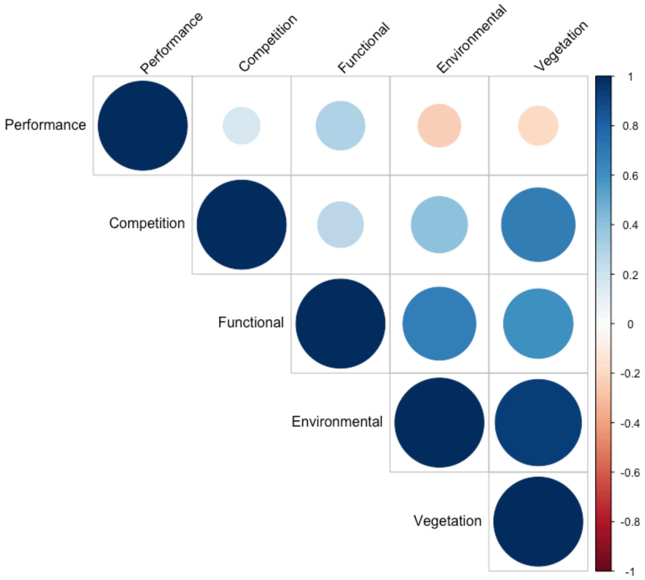

Figure 5.3. Pearson's correlation coefficients for relationships between the size of niches calculated using log transformed hypervolume values for each single niche axis category. The environmental niche included all of the variables defining the vegetation niche in addition to the climate PC.

Table 5.4. Pearson's correlation coefficients. Correlations (as shown in Figure 3 above) show relationships between the size of niches calculated using log transformed hypervolume values for each single niche axis category. The environmental niche included all of the variables defining the vegetation niche in addition to the climate PC.

	Competition	Environmental	Functional	Performance	Vegetation
Competition	1	0.40	0.26	0.17	0.68
Environmental	0.40	1	0.67	-0.23	0.94
Functional	0.26	0.67	1	0.30	0.61
Performance	0.17	-0.23	0.30	1	-0.19
Vegetation	0.68	0.94	0.61	-0.19	1

DISCUSSION

We estimated niche volume across functional, competitive, performance, and environmental niche axes among five closely related sparrow species inhabiting tidal marsh ecosystems of the eastern US. Niche size was positively correlated among most of the individual axes, but performance niche size was negatively correlated with vegetation and environmental axes. This suggests that specialism is correlated among on multiple niche axes. However, the rank order of species changed among several of the niche axes, and the predictive power of the size of any single axis on the remaining niche hypervolume was fairly low.

We found no evidence, however, for tradeoffs in niche breadth in this system along climatic niche axes, plant assemblage axes, an interspecific competitor axes, and the environmental axes behind selection on two functional traits (bill and body size). Taxa that exhibited narrow niche breadth in any of these domains were generally specialized for all of them. Selection for specialization along a single niche axis may lead to positive associations of specialization across other niche axes, at least among the five species we describe. These positive correlations may be a result of correlation among traits (i.e., selection for specialized adaptations within one niche domain lead to changes in other traits – from pleiotropy or epistatic effects, for example – that decrease the range of environmental use by the species in other niche domains) or correlation among selection (i.e., selection for specialization on one niche axis is generally accompanied by selection for specialization on another niche axis because of environmental correlations in conditions). This pattern is consistent with the report of a tidal marsh syndrome of specialization across a suite of functional traits associated with tidal marsh colonization (Grenier and Greenberg 2005, Greenberg et al. 2006, Walsh et al. 2018).

Regardless of the cause, we found no evidence for specialization on one axis being compensated for by a broader niche in another realm among the niche axes we examined. This pattern may not hold over different taxonomic scales or different niche axes. For example, positive correlations between habitat and diet specialization have been reported in European birds (Reif et al. 2016), but not among birds breeding in Germany or in a broad taxonomic group of coral reef fish (Brändle et al. 2002, Brandl et al. 2015).

We found the strongest positive correlations among competition and vegetation axes. Interspecific competition also had the highest predictive power for the remaining niche hypervolume among the five combinations that we tested. We suspect his is because taxa that occupy a broader niche, exist in more diverse environments, and are more likely to overlap the range of a larger number of species. Additionally, our first vegetation PC described the latitudinal cline in plant species. Many of our focal bird species also had range limits across this cline; thus sparrows with a larger latitudinal range extent would be expected to encounter more diverse plant assemblages and more interspecific competitors as well.

We also found a strong positive correlation between the sizes of the functional trait and vegetation axes. The functional niche axes ranked among the top two axes categories in predictive power for the remaining niche hypervolume. In general we suspect this is because taxa that experience more diverse environments are more likely to diverge in functional traits, because they are more likely to experience both different selection pressures and genetic isolation among populations. For the axes we examined there may also be underlying environmental drivers of both functional and environmental diversity. For instance, our first PC for vegetation described the latitudinal cline in plant species which is predicted by a strong temperature gradient. Intraspecific body size is widely known to vary with temperature (Bergmann 1948, Gardner et al. 2009, VanderWerf 2012, Andrew et al. 2018), and latitudinal gradients in bill size have been reported for saltmarsh sparrows over the same range we examined (Olsen et al. *In Revision*) Thus those species with larger latitudinal ranges would likely show larger variation in functional traits associated with the latitudinal temperature gradient. Functional traits in this system are also likely shaped by the gradient of tidal inundation. There is evidence for selection in bill size (Chapter 4) as well as a suite of other functional traits across tidal gradients (Walsh et al. 2018), and the second vegetation PC represented an upriver tidal gradient. In water limited environments such as saline tidal marshes, both temperature and water limitation select for larger bills to maximize the capacity for heat dissipation while minimizing water loss (Greenberg and Droege 1990, Greenberg et al. 2012a, Greenberg and Danner 2012, 2013; Luther and Greenberg 2014, Danner et al. 2017, Olsen et al. In Revision). Thus those species that inhabit a narrow range of temperature and salinity may also show narrow ranges of functional trait variation.

Performance axes showed low correlation with other niche axes, and low predictive power. This niche axis was also the only axis category that showed a negative correlation with the remaining niche hypervolume among our five categories. This could be a result of recent colonizers at the edge of their realized niche showing only low values of performance within tidal marshes, while those that are specialized (low environmental and competitive niches) and adapted to tidal marshes (low functional diversity) are able to show both high and low performance values. Alternatively, our performance metrics may have just shown high interindividual variation across all species. Hematocrit is a highly plastic trait that varies with environmental condition (Potti 2007) and is influenced by a variety of factors aside from osmoregulatory challenges, including energy expenditure and parasite loads (Fair et al. 2007). Further, while differences in melanism can help resist feather wear (Peele et al. 2009, Mackinven and Briskie 2014), differences in feather wear among species and sexes can also result from differences in activity levels and mating systems (Borowske 2015). Thus, individual variation may result in large niche breadth for species with both broad and narrow habitat niche breadth.

Ecological specialization is the process of adaptation to a narrow range of available environmental conditions (Poisot et al. 2011), and can have consequences for the abundance and distribution of species (Brown 1984) and species persistence (Julliard et al. 2004, Devictor et al. 2008, Correll et al. 2017, 2019). Determining how niche breadth changes on one axis may impact that in other dimensions of niche space is integral to understanding the origin and maintenance of specialization. We found that niche size, or specialization, was correlated among niche axes that vary in their temporal scale. For instance, measures of niche size on environmental niche axes that are instantaneous in time, were correlated with variation in functional traits that may evolve over longer multi-generational times scales. These findings suggest that the origin of specialization can result from selection for specialization on a single axis. In this system, species niche breadth within a gradient of tidal inundation were informative about their niche breadth along other niche dimensions in ecological space, and can explain variation in certain functional traits. Tidal regimes in this system are also important predictor of fitness and survival in tidal marsh sparrows (Field et al. 2017, Benvenuti et al. 2018, Maxwell

2018). Focusing on multiple niche axes can further our understanding of how phenotypic variation and environmental conditions might constrain niche evolution (Laughlin and Messier 2015).

LITERATURE CITED

Abrahamczyk, S., D. Souto-Vilaros, and S. S. Renner (2014). Escape from extreme specialization: passionflowers, bats and the sword-billed hummingbird. Proceedings of the Royal Society B: Biological Sciences 281:20140888–20140888.

Adams, D. C., M. Collyer, and A. Kaliontzopoulou (2018). Geomorph: Software for geometric morphometric analyses.

Adams, D. C., and E. Otárola-Castillo (2013). geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution 4:393–399.

Andrew, S. C., M. Awasthy, A. D. Griffith, S. Nakagawa, and S. C. Griffith (2018). Clinal variation in avian body size is better explained by summer maximum temperatures during development than by cold winter temperatures. The Auk 135:206–217.

BirdLife International and Handbook of the Birds of the World (2017). Version 7.0. Available at http://datazone.birdlife.org/species/requestdis.

Araújo, M. S., P. R. Guimarães, R. Svanbäck, A. Pinheiro, P. Guimarães, S. F. dos Reis, and D. I. Bolnick (2008). Netwrok analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology 89:1981–1993.

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten (2002). Song Sparrow (Melospiza melodia). The Birds of North America Online. https://doi.org/10.2173/bna.704

Armbruster, W. S., A. L. Herzig, and T. P. Clausen (1992). Pollination of Two Sympatric Species of Dalechampia (Euphorbiaceae) in Suriname by Male Euglossine Bees. American Journal of Botany 79:1374–1381.

Ashman, L. G., J. G. Bragg, P. Doughty, M. N. Hutchinson, S. Bank, N. J. Matzke, P. Oliver, and C. Moritz (2018). Diversification across biomes in a continental lizard radiation. Evolution 72:1553–1569.

Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette (2013). Going to Extremes: Contrasting Rates of Diversification in a Recent Radiation of New World Passerine Birds. Systematic Biology 62:298–320.

Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette (2015a). Data from: New insights into New World biogeography: an integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. Dryad Digital Repository. https://doi.org/10.5061/dryad.pb787

Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette (2015b). New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. The Auk 132:333–348.

Barrett, S. C. H. (2013). The evolution of plant reproductive systems: how often are transitions irreversible? Proceedings of the Royal Society B: Biological Sciences 280:20130913–20130913.

Barrow, L. N., S. M. McNew, N. Mitchell, S. C. Galen, H. L. Lutz, H. Skeen, T. Valqui, J. D. Weckstein, and C. C. Witt (2018). Deeply conserved susceptibility in a multi-host, multi-parasite system. bioRxiv. https://doi.org/10.1101/424549

Bayard, T. S., and C. S. Elphick (2010). Using Spatial Point-Pattern Assessment to Understand the Social and Environmental Mechanisms that Drive Avian Habitat Selection. The Auk 127:485–494.

Beadell, J., R. Greenberg, S. Droege, and J. A. Royle (2003). Distribution, abundance, and habitat affinities of the coastal plains swamp sparrow. The Wilson Bulletin 115:38–44.

Beaulieu, J. M., and B. C. O'Meara (2016). Detecting Hidden Diversification Shifts in Models of Trait-Dependent Speciation and Extinction. Systematic Biology 65:583–601.

Bell, G., and A. Gonzalez (2011). Adaptation and Evolutionary Rescue in Metapopulations Experiencing Environmental Deterioration. Science 332:1327–1330.

Benkman, C. W. (2003). Divergent selection drives the adaptive radiation of crossbills. Evolution 57:1176–1181.

Benvenuti, B., J. Walsh, K. M. O'Brien, and A. I. Kovach (2018). Plasticity in nesting adaptations of a tidal marsh endemic bird. Ecology and Evolution 8:10780–10793.

Bergmann, C. (1948). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien, Göttingen.

Birand, A., A. Vose, and S. Gavrilets (2012). Patterns of Species Ranges, Speciation, and Extinction. The American Naturalist 179:1–21.

Blonder, B., C. B. Morrow, B. Maitner, D. J. Harris, C. Lamanna, C. Violle, B. J. Enquist, and A. J. Kerkhoff (2018). New approaches for delineating *n* -dimensional hypervolumes. Methods in Ecology and Evolution 9:305–319.

Boag, P. T., and P. R. Grant (1984). Darwin's finches (Geospiza) on isla Daphne Major, Galapagos: Breeding and Feeding Ecology In a Climatically Variable Environment. Ecological Monographs 54:463–489.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister (2003). The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist 161:1–28.

Bonetti, M. F., and J. J. Wiens (2014). Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. Proceedings of the Royal Society B: Biological Sciences 281:20133229–20133229.

Bonser, R. H. C. (1995). Melanin and the Abrasion Resistance of Feathers. The Condor 97:590–591.

Borcard, D., and P. Legendre (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51–68.

Borowske, A. C. (2015). Effects of Life History Strategies on Annual Events and Processes in the Lives of Tidal Marsh Sparrows. PhD Dissertation. University of Connecticut.

Borowsky, R., B. Borowsky, H. Milani, and P. Greenberg (1985). Amylase Variation in the Salt Marsh Amphipod, *Gammarus palustris*. Genetics 111:311–323.

Brandl, S. J., W. D. Robbins, and D. R. Bellwood (2015). Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use. Proceedings of the Royal Society B: Biological Sciences 282:20151147.

Brändle, M., A. Prinzing, R. Pfeifer, and R. Brandl (2002). Dietary niche breadth for Central European birds: correlations with species-specific traits. Evolutionary Ecology Research 4:643–657.

Brown, J. H. (1984). On the Relationship between Abundance and Distribution of Species. The American Naturalist 124:255–279.

Brown, J. H. (1995). Macroecology. University of Chicago Press, Chicago.

Brown, W. L., and E. O. Wilson (1956). Character Displacement. Systematic Zoology 5:49–64.

Bull, J. J., and E. L. Charnov (1985). On irreversible evolution. Evolution 39:1149–1155.

Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.

Burns, K. J., S. J. Hackett, and N. K. Klein (2002). Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. Evolution 56:1240–1252.

Burns, K. J., A. J. Shultz, P. O. Title, N. A. Mason, F. K. Barker, J. Klicka, S. M. Lanyon, and I. J. Lovette (2014). Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. Molecular Phylogenetics and Evolution 75:41–77.

Byers, J., E. Hebets, and J. Podos (2010). Female mate choice based upon male motor performance. Animal Behaviour 79:771–778.

Caetano, D. S., B. C. O'Meara, and J. M. Beaulieu (2018). Hidden state models improve state-dependent diversification approaches, including biogeographical models. Evolution 72:2308–2324.

Campagna, L., M. Repenning, L. F. Silveira, C. S. Fontana, P. L. Tubaro, and I. J. Lovette (2017). Repeated divergent selection on pigmentation genes in a rapid finch radiation. Science Advances 3:e1602404.

Chan, Y. L., C. E. Hill, J. E. Maldonado, and R. C. Fleischer (2006). Evolution and conservation of tidal-marsh vertebrates: molecular approaches. Studies in Avian Biology 32:54–75.

Chase, J. M., and M. A. Leibold (2003). Ecological Niches. University of Chicago Press, Chicago, IL.

Chesser, R. T., K. J. Burns, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen, J. D. Rising, D. F. Stotz, and K. Winker (2017). Fifty-eighth supplement to the American Ornithological Society's *Check-list of North American Birds*. The Auk 134:751–773.

Claramunt, S., E. P. Derryberry, J. V. Remsen, and R. T. Brumfield (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proceedings of the Royal Society B: Biological Sciences 279:1567–1574.

Clegg, S. M., and P. F. Owens (2002). The 'island rule' in birds: medium body size and its ecological explanation. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:1359–1365.

Cody, M. L. (1974). Competition and the structure of bird communities. Princeton University Press, Princeton, N.J.

Colles, A., L. H. Liow, and A. Prinzing (2009). Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. Ecology Letters 12:849–863.

Conway, C. J. (2011). Standardized North American Marsh Bird Monitoring Protocol. Waterbirds 34:319–346.

Cooney, C. R., J. A. Bright, E. J. R. Capp, A. M. Chira, E. C. Hughes, C. J. A. Moody, L. O. Nouri, Z. K. Varley, and G. H. Thomas (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. Nature 542:344–347.

Cope, E. D. (1896). The primary factors of organic evolution. The Open Court Publishing Company, Chicago, IL.

Correll, M. D., E. H. Strasser, A. W. Green, and A. O. Panjabi (2019). Quantifying specialist avifaunal decline in grassland birds of the Northern Great Plains. Ecosphere 10:e02523.

Correll, M. D., W. A. Wiest, T. P. Hodgman, W. G. Shriver, C. S. Elphick, B. J. McGill, K. M. O'Brien, and B. J. Olsen (2017). Predictors of specialist avifaunal decline in coastal marshes. Conservation Biology 31:172–182.

Correll, M. D., W. A. Wiest, B. J. Olsen, W. G. Shriver, C. S. Elphick, and T. P. Hodgman (2016). Habitat specialization explains avian persistence in tidal marshes. Ecosphere 7:e01506.

Coyne, J. A., and H. A. Orr (2004). Speciation. Sinauer Associates, Sunderland, Mass.

Crespi, and Sandoval (2000). Phylogenetic evidence for the evolution of ecological specialization in Timema walking-sticks. Journal of Evolutionary Biology 13:249–262.

Danner, R. M., E. R. Gulson-Castillo, H. F. James, S. A. Dzielski, D. C. Frank, E. T. Sibbald, and D. W. Winkler (2017). Habitat-specific divergence of air conditioning structures in bird bills. The Auk 134:65–75.

Dapporto, L., and R. L. H. Dennis (2013). The generalist–specialist continuum: Testing predictions for distribution and trends in British butterflies. Biological Conservation 157:229–236.

Davis, E. B. (2005). Comparison of climate space and phylogeny of Marmota (Mammalia: Rodentia) indicates a connection between evolutionary history and climate preference. Proceedings of the Royal Society B: Biological Sciences 272:519–526.

Dehling, D. M., S. A. Fritz, T. Töpfer, M. Päckert, P. Estler, K. Böhning-Gaese, and M. Schleuning (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047–1055.

Dehling, D. M., P. Jordano, H. M. Schaefer, K. Böhning-Gaese, and M. Schleuning (2016). Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. Proceedings of the Royal Society B: Biological Sciences 283:20152444.

Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail, S. Villéger, and N. Mouquet (2010). Defining and measuring ecological specialization. Journal of Applied Ecology 47:15–25.

Devictor, V., R. Julliard, and F. Jiguet (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507–514.

Doebeli, M., and U. Dieckmann (2003). Speciation along environmental gradients. Nature 421:259–264.

Durell, S. E. A. L. V. D. (2000). Individual feeding specialisation in shorebirds: population consequences and conservation implications. Biological Reviews 75:503–518.

Ehrlich, P. R., and P. H. Raven (1964). Butterflies and plants: a study in coevolution. Evolution 18:586–608.

Elton, C. (1927). Animal Ecology. Sidgwick and Johnson, London, UK.

Etterson, J. R. (2008). Evolution in response to Climate Change. In Conservation Biology: Evolution in Action. Oxford University Press, Incorporated, pp. 145–163.

Fair, J., S. Whitaker, and B. Pearson (2007). Sources of variation in haematocrit in birds: Haematocrit variation in birds. Ibis 149:535–552.

Ferry-Graham, L. A. (2002). Using Functional Morphology to Examine the Ecology and Evolution of Specialization. Integrative and Comparative Biology 42:265–277.

Field, C. R., T. S. Bayard, C. Gjerdrum, J. M. Hill, S. Meiman, and C. S. Elphick (2017). High-resolution tide projections reveal extinction threshold in response to sea-level rise. Global Change Biology 23:2058–2070.

Field, C. R., C. Gjerdrum, and C. S. Elphick (2016). How does choice of statistical method to adjust counts for imperfect detection affect inferences about animal abundance? Methods in Ecology and Evolution 7:1282–1290.

FitzJohn, R. G. (2010). Quantitative Traits and Diversification. Systematic Biology 59:619–633.

FitzJohn, R. G. (2012). Diversitree : comparative phylogenetic analyses of diversification in R: *Diversitree*. Methods in Ecology and Evolution 3:1084–1092.

Forsman, A., and L. Wennersten (2016). Inter-individual variation promotes ecological success of populations and species: evidence from experimental and comparative studies. Ecography 39:630–648.

Foster, D. J., J. Podos, and A. P. Hendry (2008). A geometric morphometric appraisal of beak shape in Darwin’s finches: Beak shape of Darwin’s finches. Journal of Evolutionary Biology 21:263–275.

Friis, G., G. Fandos, A. J. Zellmer, J. E. McCormack, B. C. Faircloth, and B. Milá (2018). Genome-wide signals of drift and local adaptation during rapid lineage divergence in a songbird. Molecular Ecology 27:5137–5153.

Futuyma, D. J., M. C. Keese, and D. J. Funk (1995). Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. Evolution 49:797–809.

Futuyma, D. J., and G. Moreno (1988). The evolution of ecological specialization. Annual Reviews in Ecology and Systematics 19:207–233.

Gardner, J. L., R. Heinsohn, and L. Joseph (2009). Shifting Latitudinal Clines in Avian Body Size Correlate with Global Warming in Australian Passerines. Proceedings of the Royal Society B: Biological Sciences 276:3845–3852.

Gaston, K. J. (1998). Species-range size distributions: products of speciation, extinction and transformation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 353:219–230.

Gaston, K. J. (2003). The structure and dynamics of geographic ranges. Oxford University Press, Oxford ; New York.

Gavrilets, S. (2004). Fitness landscapes and the origin of species. 2004 ed. Princeton University Press, Princeton, NJ.

Gavrilets, S., and J. B. Losos (2009). Adaptive Radiation: Contrasting Theory with Data. Science 323:732–737.

Gavrilets, S., and A. Vose (2005). Dynamic patterns of adaptive radiation. Proceedings of the National Academy of Sciences 102:18040–18045.

Gest, T. R., M. I. Siegel, and J. Anistranski (1986). The long bones of neonatal rats stressed by cold, heat, and noise exhibit increased fluctuating asymmetry. Growth 50:385.

Goldberg, E. E., and B. Igić (2012). Tempo and mode in plant breeding system evolution. Evolution 66:3701–3709.

Goldstein, D. L. (2006). Osmoregulatory Biology of Saltmarsh Passerines. Studies in Avian Biology 32:110–118.

Goldstein, D. L., J. B. Willams, and E. J. Braun (1990). Osmoregulation in the field by salt-marsh savannah sparrows *Passerculus sandwichenses belldingi*. Physiological Zoology 63:669–682.

Goldstein, D. L., and A. Zahedi (1990). Variation in osmoregulatory parameters of captive and wild house sparrows (P*asser domesticus*). The Auk 107:533–538.

Gould, S. J. (1970). Dollo on Dollo's law: Irreversibility and the status of evolutionary laws. Journal of the History of Biology 3:189–212.

Grant, P. R. (2002). Unpredictable Evolution in a 30-Year Study of Darwin's Finches. Science 296:707–711.

Grant, P. R., and B. R. Grant (2006). Evolution of Character Displacement in Darwin's Finches. Science 313:224–226.

Grant, P. R., and B. R. Grant (2008). How and why species multiply: the radiation of Darwin's finches. Princeton University Press, Princeton.

Graves, G. R. (1988). Linearity of Geographic Range and Its Possible Effect on the Population Structure of Andean Birds. The Auk 105:47–52.

Greenberg, R. (1990). Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. Animal Behaviour 39:375–379.

Greenberg, R., V. Cadena, R. M. Danner, and G. Tattersall (2012a). Heat Loss May Explain Bill Size Differences between Birds Occupying Different Habitats. PLoS ONE 7:e40933.

Greenberg, R., K. M. Cammen, A. G. Wilson, B. J. Olsen, B. Ballentine, N. C. McInerney, and R. C. Fleischer (2016). Geographic population structure and subspecific boundaries in a tidal marsh sparrow. Conservation Genetics 17:603–613.

Greenberg, R., P. J. Cordero, S. Droege, and R. C. Fleischer (1998). Morphological Adaptation with No Mitochondrial DNA Differentiation in the Coastal Plain Swamp Sparrow. The Auk 115:706–712.

Greenberg, R., and R. M. Danner (2012). The influence of the California marine layer on bill size in a generalist song bird. Evolution 66:3825–3835.

Greenberg, R., and R. M. Danner (2013). Climate, ecological release and bill dimorphism in an island songbird. Biology Letters 9:20130118–20130118.

Greenberg, R., R. Danner, B. Olsen, and D. Luther (2012b). High summer temperature explains bill size variation in salt marsh sparrows. Ecography 35:146–152.

Greenberg, R., and S. Droege (1990). Adaptations to Tidal Marshes in Breeding Populations of the Swamp Sparrow. The Condor 92:393.

Greenberg, R., and J. E. Maldonado (2006). Diversity and Endemism in Tidal-marsh Vertebrates. Studies in Avian Biology 32:32–53.

Greenberg, R., J. E. Maldonado, S. Droege, and M. V. McDonald (2006). Tidal Marshes: A Global Perspective on the Evolution and Conservation of Their Terrestrial Vertebrates. BioScience 56:675.

Greenberg, R., and B. Olsen (2010). Bill size and dimorphism in tidal-marsh sparrows: island-like processes in a continental habitat. Ecology 91:2428–2436.

Greenlaw, J. S. (1993). Behavioral and Morphological Diversification in Sharp-Tailed Sparrows (Ammodramus caudacutus) of the Atlantic Coast. The Auk 110:286–303.

Greenlaw, J. S., C. S. Elphick, W. Post, and J. D. Rising (2018). Saltmarsh Sparrow (Ammospiza caudacuta) version 2.1. In The Birds of North America (P.G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Gregory, R. D., and K. J. Gaston (2000). Explanations of Commonness and Rarity in British Breeding Birds: Separating Resource Use and Resource Availability. Oikos 88:515–526.

Grenier, J. L., and R. Greenberg (2005). A biogeographic pattern in sparrow bill morphology: parallel adaptation to tidal marshes. Evolution 59:1588–1595.

Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. The Auk 34:427–433.

Hällfors, M. H., J. Liao, J. Dzurisin, R. Grundel, M. Hyvärinen, K. Towle, G. C. Wu, and J. J. Hellmann (2016). Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecological Applications 26:1154-1169

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger (2008). GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Harvey, M. G., and D. L. Rabosky (2018). Continuous traits and speciation rates: Alternatives to state-dependent diversification models. Methods in Ecology and Evolution 9:984–993.

Harvey, M. G., G. F. Seeholzer, B. T. Smith, D. L. Rabosky, A. M. Cuervo, and R. T. Brumfield (2017). Positive association between population genetic differentiation and speciation rates in New World birds. Proceedings of the National Academy of Sciences 114:6328–6333.

Hendry, A. P., and M. T. Kinnison (1999). Perspective: The Pace of Modern Life: Measuring Rates of Contemporary Microevolution. Evolution 53:1637.

Hill, J. M., J. Walsh, A. I. Kovach, and C. S. Elphick (2013). Male-Skewed Sex Ratio in Saltmarsh Sparrow Nestlings. The Condor 115:411–420.

Hoffmann, A. A., and C. M. Sgrò (2011). Climate change and evolutionary adaptation. Nature 470:479–485.

Holt, R. D. (2003). On the evolutionary ecology of species' ranges. Evolutionary Ecology Research 5:159–178.

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences 106:19659–19665.

Holt, R. D., and M. S. Gaines (1992). Analysis of adaptation to heterogeneous landscapes: implications for the evolution of fundamental niches. Evolutionary Ecology 6:433–447.

Huss, M., P. Byström, and L. Persson (2008). Resource heterogeneity, diet shifts and intra-cohort competition: effects on size divergence in YOY fish. Oecologia 158:249–257.

Hutchinson, G. E. (1957). Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Jablonski, D. (1993). The tropics as a source of novelty. Nature 364:142–144.

Jablonski, D. (2001). Lessons from the past: Evolutionary impacts of mass extinctions. Proceedings of the National Academy of Sciences 98:5393–5398.

Jablonski, D. (2008). Species Selection: Theory and Data. Annual Review of Ecology, Evolution, and Systematics 39:501–524.

Jablonski, D., and K. Roy (2003). Geographical range and speciation in fossil and living molluscs. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:401–406.

Jackson, S. T., and J. T. Overpeck (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26:194–220.

Janz, N., K. Nyblom, and S. Nylin (2001). Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. Evolution 55:783–796.

Janz, N., and S. Nylin (2008). The Oscillation Hypothesis of Host-Plant Range and Speciation. In Specialization, speciation and radiation: The evolutionary biology of herbivorous insects. University of California Press, pp. 203–215.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers (2012). The global diversity of birds in space and time. Nature 491:444–448.

Julliard, R., F. Jiguet, and D. Couvet (2004). Common birds facing global changes: what makes a species at risk? Global Change Biology 10:148–154.

Kellermann, V., B. van Heerwaarden, C. M. Sgro, and A. A. Hoffmann (2009). Fundamental Evolutionary Limits in Ecological Traits Drive Drosophila Species Distributions. Science:1244–1255.

Kellermann, V., V. Loeschcke, A. A. Hoffmann, T. N. Kristensen, C. Fløjgaard, J. R. David, J.-C. Svenning, and J. Overgaard (2012). Phylogenetic constraints in key functional traits behind species' climate niches: patterns of desiccation and cold resistance across 95 Drosophila species. Evolution 66:3377–3389.

Kelley, S. T., and B. D. Farrell (1998). Is Specialization a Dead End? The Phylogeny of Host Use in Dendroctonus Bark Beetles (*Scolytidae*). Evolution 52:1731.

Kent, C. M., and E. H. Burtt (2016). Feather-degrading bacilli in the plumage of wild birds: Prevalence and relation to feather wear. The Auk 133:583–592.

Kozak, K. H., D. W. Weisrock, and A. Larson (2006). Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: *Plethodon*). Proceedings of the Royal Society B: Biological Sciences 273:539–546.

Langin, K. M., T. S. Sillett, W. C. Funk, S. A. Morrison, M. A. Desrosiers, and C. K. Ghalambor (2015). Islands within an island: Repeated adaptive divergence in a single population. Evolution 69:653–665.

Laughlin, D. C., and J. Messier (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends in Ecology & Evolution 30:487–496.

Legendre, P., and M. J. Anderson (1999). Distance-based redundancy analysis: testing multispecies response in mulitfactorial ecological experiements. Ecological Monographs 69:1–24.

Lerner, H. R. L., M. Meyer, H. F. James, M. Hofreiter, and R. C. Fleischer (2011). Multilocus Resolution of Phylogeny and Timescale in the Extant Adaptive Radiation of Hawaiian Honeycreepers. Current Biology 21:1838–1844.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1003.

Losos, J. B., D. J. Irschick, and T. W. Schoener (1994). Adaptation and Constraint in the Evolution of Specialization of Bahamian Anolis Lizards. Evolution 48:1786.

Losos, J. B., and R. E. Ricklefs (2009). Adaptation and diversification on islands. Nature 457:830–836.

Losos, J. B., and D. Schluter (2000). Analysis of an evolutionary species–area relationship. Nature 408:847–850.

Lovette, I. J., E. Bermingham, and R. E. Ricklefs (2002). Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:37–42.

Luther, D., and R. Greenberg (2014). Habitat type and ambient temperature contribute to bill morphology. Ecology and Evolution 4:699–705.

Macarthur, R., and R. Levins (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. The American Naturalist 101:377–385.

Mackinven, K., and J. V. Briskie (2014). Differential wear of feathers in the polymorphic New Zealand Fantail (Rhipidura fuliginosa) – a selective advantage of melanism? Emu 114:154–159.

Maddison, W. P., P. E. Midford, and S. P. Otto (2007). Estimating a Binary Character's Effect on Speciation and Extinction. Systematic Biology 56:701–710.

Malamud-Roam, K. P., F. P. Malamud-Roam, E. B. Watson, J. N. Collins, and B. L. Ingram (2006). The quaternary geography and biogeography of tidal saltmarshes. Studies in Avian Biology:11–31.

Martinez-Meyer, E., A. Townsend Peterson, and W. W. Hargrove (2004). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13:305–314.

Mason, N. A., K. J. Burns, J. A. Tobias, S. Claramunt, N. Seddon, and E. P. Derryberry (2017). Song evolution, speciation, and vocal learning in passerine birds. Evolution 71:786–796.

Maxwell, L. M. (2018). Drivers of Introgression and Fitness in the Saltmarsh-Nelson's Sparrow Hybrid Zone. MS Thesis, University of New Hampshire [Online.] Available at http://search.proquest.com/docview/2117273456/abstract/D8317B8F94084FAFPQ/1.

Mayr, E. (1963). Animal species and evolution. Belknap Press of Harvard University Press, Cambridge.

McCormack, J. E., and T. B. Smith (2008). Niche expansion leads to small-scale adaptive divergence along an elevation gradient in a medium-sized passerine bird. Proceedings of the Royal Society B: Biological Sciences 275:2155–2164.

Meiri, S., D. Simberloff, and T. Dayan (2011). Community-wide character displacement in the presence of clines: A test of Holarctic weasel guilds: Character displacement and clines. Journal of Animal Ecology 80:824–834.

Møller, A. P. (1997). Developmental Stability and Fitness: A Review. The American Naturalist 149:916–932.

Mowbray, T. B. (1997). Swamp Sparrow (Melospiza georgiana). The Birds of North America Online. https://doi.org/10.2173/bna.279

Murren, C. J., J. R. Auld, H. Callahan, C. K. Ghalambor, C. A. Handelsman, M. A. Heskel, J. G. Kingsolver, H. J. Maclean, J. Masel, H. Maughan, D. W. Pfennig, et al. (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. Heredity 115:293–301.

Nilsson, J.-A., and E. Svensson (1996). The Cost of Reproduction: A New Link between Current Reproductive Effort and Future Reproductive Success. Proceedings of the Royal Society B: Biological Sciences 263:711–714.

Nocera, J. J., T. M. Fitzgerald, A. R. Hanson, and G. Randy Milton (2007). Differential habitat use by Acadian Nelson's sharp-tailed sparrows: implications for regional conservation. Journal of Field Ornithology 78:50–55.

Noguerales, V., V. García-Navas, P. J. Cordero, and J. Ortego (2016). The role of environment and core-margin effects on range-wide phenotypic variation in a montane grasshopper. Journal of Evolutionary Biology 29:2129–2142.

Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille (2012). Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change 2:747–751.

Nosil, P. (2002). Transition rates between specialization and generalization in phytophagous insects. Evolution 56:1701–1706.

Nosil, P., and A. Ø. Mooers (2005). Testing hypotheses about ecological specialization using phylogenetic trees. Evolution 59:2256–2263.

Nowicki, S., S. Peters, and J. Podos (1998). Song Learning, Early Nutrition and Sexual Selection in Songbirds. American Zoologist 38:179–190.

Nyári, Á. S., and S. Reddy (2013). Comparative Phyloclimatic Analysis and Evolution of Ecological Niches in the Scimitar Babblers (Aves: Timaliidae: Pomatorhinus). PLoS ONE 8:e55629.

Olsen, B. J., J. L. Froehly, A. C. Borowske, C. S. Elphick, C. R. Field, A. R. Kocek, A. I. Kovach, R. A. Longenecker, W. G. Shriver, J. Walsh, and K. J. Ruskin (In Revision). A test of a corollary of Allen's rule suggests a role for population density. Journal of Field Ornithology.

Olsen, B. J., R. Greenberg, I. A. Liu, J. M. Felch, and J. R. Walters (2010). Interactions between sexual and natural selection on the evolution of a plumage badge. Evolutionary Ecology 24:731–748.

Olsen, B. J., R. Greenberg, J. R. Walters, and R. C. Fleischer (2013). Sexual dimorphism in a feeding apparatus is driven by mate choice and not niche partitioning. Behavioral Ecology 24:1327–1338.

Orr, H. A. (2000). Adaptation and the Cost of Complexity. Evolution 54:13–20.

Paradis, E., S. P. Blomberg, B. M. Bolker, J. W. Brown, J. Claude, H. S. Cuong, R. Desper, G. Didier, B. Durand, J. Dutheil, and et al. (2018). Analyses of Phylogenetics and Evolution.

Parejo, D., N. Silva, É. Danchin, and J. M. Avilés (2011). Informative content of melanin-based plumage colour in adult Eurasian kestrels. Journal of Avian Biology 42:49–60.

Parent, C. E., D. Agashe, and D. I. Bolnick (2014). Intraspecific competition reduces niche width in experimental populations. Ecology and Evolution 4:3978–3990.

Parent, C. E., and B. J. Crespi (2006). Sequential colonization and diversification of Galapagos endemic land snail genus Bulimulus (Gastropoda, Stylommatophora). Evolution 60:2311.

Pearman, P. B., S. Lavergne, C. Roquet, R. Wüest, N. E. Zimmermann, and W. Thuiller (2014). Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage: Phylogenetic assemblage structure. Global Ecology and Biogeography 23:414–424.

Peele, A. M., E. H. Burtt, M. R. Schroeder, and R. Greenberg (2009). Dark Color of the Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) May Be an Evolutionary Response to Occurrence and Abundance of Salt-tolerant Feather-degrading Bacilli in Its Plumage. The Auk 126:531–535.

Pigot, A. L., A. B. Phillimore, I. P. F. Owens, and C. D. L. Orme (2010). The Shape and Temporal Dynamics of Phylogenetic Trees Arising from Geographic Speciation. Systematic Biology 59:660–673.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, and B. Van Willigen (2018). Linear and nonlinear mixed effects models.

Plummer, M., N. Best, K. Cowles, and K. Vines (2006). CODA: Convergence diagnosis and output analysis for MCMC. R News 6:7–11.

Poisot, T., J. D. Bever, A. Nemri, P. H. Thrall, and M. E. Hochberg (2011). A conceptual framework for the evolution of ecological specialisation: Evolution of ecological specialisation. Ecology Letters 14:841–851.

Post, W., and J. S. Greenlaw (1982). Comparative costs of promiscuity and monogramy: A test of reproductive effort theory. Behavioral Ecology and Sociobiology 10:101–107.

Post, W., and J. S. Greenlaw (2006). Nestling diets of coexisting salt marsh sparrows: Opportunism in a food-rich environment. Estuaries and Coasts 29:765–775.

Post, W., and J. S. Greenlaw (2018). Seaside Sparrow (Ammospiza maritima). The Birds of North America Online. In The Birds of North America (P.G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA https://doi.org/10.2173/bna.seaspa.02.1

Potti, J. (2007). Variation in the hematocrit of a passerine bird across life stages is mainly of environmental origin. Journal of Avian Biology 38:726–730.

Price, P. W. (2008a). Adaptive Radiation: Phylogenetic Constraints and Ecological Consequences. In Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects. University of California Press.

Price, S. A., S. S. B. Hopkins, K. K. Smith, and V. L. Roth (2012). Tempo of trophic evolution and its impact on mammalian diversification. Proceedings of the National Academy of Sciences 109:7008–7012.

Price, T. (2008b). Speciation in birds. Roberts and Co, Greenwood Village, CO

Qiao, H., L. E. Escobar, E. E. Saupe, L. Ji, and J. Soberón (2017). A cautionary note on the use of hypervolume kernel density estimators in ecological niche modelling. Global Ecology and Biogeography 26:1066–1070.

Quintero, I., and J. J. Wiens (2013). What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades: Climatic niche width of species. Global Ecology and Biogeography 22:422–432.

Rabosky, D. L. (2014). Automatic Detection of Key Innovations, Rate Shifts, and Diversity-Dependence on Phylogenetic Trees. PLoS ONE 9:e89543.

Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J. Near, M. Coll, and M. E. Alfaro (2018). An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559:392–395.

Rabosky, D. L., and E. E. Goldberg (2015). Model Inadequacy and Mistaken Inferences of Trait-Dependent Speciation. Systematic Biology 64:340–355.

Rabosky, D. L., and E. E. Goldberg (2017). FiSSE: A simple nonparametric test for the effects of a binary character on lineage diversification rates. Evolution 71:1432–1442.

Rabosky, D. L., M. Grundler, C. Anderson, P. Title, J. J. Shi, J. W. Brown, H. Huang, and J. G. Larson (2014). BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods in Ecology and Evolution 5:701–707.

Rabosky, D. L., and H. Huang (2016). A Robust Semi-Parametric Test for Detecting Trait-Dependent Diversification. Systematic Biology 65:181–193.

Rabosky, D. L., and I. J. Lovette (2008). Density-Dependent Diversification in North American Wood Warblers. Proceedings: Biological Sciences 275:2363–2371.

Redding, D. W., and A. Ø. Mooers (2006). Incorporating Evolutionary Measures into Conservation Prioritization. Conservation Biology 20:1670–1678.

Reddy, S., A. Driskell, D. L. Rabosky, S. J. Hackett, and T. S. Schulenberg (2012). Diversification and the adaptive radiation of the vangas of Madagascar. Proceedings of the Royal Society B: Biological Sciences 279:2062–2071.

Reed, T. E., D. E. Schindler, and R. S. Waples (2011). Interacting Effects of Phenotypic Plasticity and Evolution on Population Persistence in a Changing Climate. Conservation Biology 25:56–63.

Reif, J., D. Hořák, A. Krištín, L. Kopsová, and V. Devictor (2016). Linking habitat specialization with species' traits in European birds. Oikos 125:405–413.

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things): phytools: R package. Methods in Ecology and Evolution 3:217–223.

Reznick, D. N., and C. K. Ghalambor (2001). The population ecology of contemporary adaptations: What empirical studies reveal about the conditions that promote adaptive evolution. In Microevolution Rate, Pattern, Process (A. P. Hendry and M. T. Kinnison, Editors). Springer Netherlands, Dordrecht, pp. 183–198.

Richardson, J. L., and M. C. Urban (2013). Strong selection barriers explain microgeographic adaptation in wild salamander populations: microgeographic adaptive divergence in salamanders. Evolution 67:1729–1740.

Rijke, A. M., and W. A. Jesser (2011). The Water Penetration and Repellency of Feathers Revisited - Revisión de la Penetración y la Repelencia de Agua de las Plumas. The Condor 113:245–254.

Rising, J. D., and J. C. Avise (1993). Application of Genealogical-Concordance Principles to the Taxonomy and Evolutionary History of the Sharp-Tailed Sparrow (Ammodramus caudacutus). The Auk 110:844–856.

Rohlf, F. J. (2000). Statistical power comparisons among alternative morphometric methods. American Journal of Physical Anthropology 111:463–478.

Rosenblatt, A. E., J. C. Nifong, M. R. Heithaus, F. J. Mazzotti, M. S. Cherkiss, B. M. Jeffery, R. M. Elsey, R. A. Decker, B. R. Silliman, L. J. Guillette, R. H. Lowers, and J. C. Larson (2015). Factors affecting individual foraging specialization and temporal diet stability across the range of a large “generalist” apex predator. Oecologia 178:5–16.

Rosenzweig, M. L. (1995). Species diversity in space and time. Cambridge University Press, Cambridge ; New York.

Roughgarden, J. (1972). Evolution of Niche Width. The American Naturalist 106:683–718.

Roulin, A. (2007). Melanin pigmentation negatively correlates with plumage preening effort in barn owls. Functional Ecology 21:264–271.

Rundell, R. J., and T. D. Price (2009). Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends in Ecology & Evolution 24:394–399.

Ruskin, K. J., M. A. Etterson, T. P. Hodgman, A. C. Borowske, J. B. Cohen, C. S. Elphick, C. R. Field, R. A. Longenecker, E. King, A. R. Kocek, A. I. Kovach, et al. (2017). Demographic analysis demonstrates systematic but independent spatial variation in abiotic and biotic stressors across 59 percent of a global species range. The Auk 134:903–916.

Ruskin, K. J., T. P. Hodgman, M. A. Etterson, and B. J. Olsen (2015). Divergent oviposition preferences of sister species are not driven by nest survival: the evidence for neutrality. Behavioral Ecology and Sociobiology 69:1639–1647.

Schluter, D. (2000). The ecology of adaptive radiation. Oxford University Press, Oxford.

Schoener, T. W. (1965). The Evolution of Bill Size Differences Among Sympatric Congeneric Species of Birds. Evolution 19:189–213.

Seddon, N., R. M. Merrill, and J. A. Tobias (2008). Sexually Selected Traits Predict Patterns of Species Richness in a Diverse Clade of Suboscine Birds. The American Naturalist 171:620–631.

Seehausen, O. (2006). African cichlid fish: a model system in adaptive radiation research. Proceedings of the Royal Society B: Biological Sciences 273:1987–1998.

Seeholzer, G. F., S. Claramunt, and R. T. Brumfield (2017). Niche evolution and diversification in a Neotropical radiation of birds (Aves: *Furnariidae*). Evolution 71:702–715.

Sepkoski, J. J. (1998). Rates of speciation in the fossil record. Philosophical Transactions of the Royal Society B: Biological Sciences 353:315–326.

Shriver, W. G., T. P. Hodgman, and A. R. Hanson (2018). Nelson's Sparrow (Ammospiza nelsoni). In The Birds of North America (P.G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA https://doi.org/10.2173/bna.nstspa.01.1

Simpson, G. G. (1953). The major features of evolution. Columbia University Press, New York.

Slatyer, R. A., M. Hirst, and J. P. Sexton (2013). Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16:1104–1114.

Sol, D., S. Timmermans, and L. Lefebvre (2002). Behavioural flexibility and invasion success in birds. Animal Behaviour 63:495–502.

Stanley, S. M. (1986). Population Size, Extinction, and Speciation: The Fission Effect in Neogene Bivalvia. Paleobiology 12:89–110.

Stephens, P. R., and J. J. Wiens (2003). Ecological diversification and phylogeny of emydid turtles. Biological Journal of the Linnean Society 79:577–610.

Stireman, J. O. (2005). The evolution of generalization? Parasitoid flies and the perils of inferring host range evolution from phylogenies: Evolution of generalization? Journal of Evolutionary Biology 18:325–336.

Stuart, Y. E., and J. B. Losos (2013). Ecological character displacement: glass half full or half empty? Trends in Ecology & Evolution 28:402–408.

Svanbäck, R., and L. Persson (2004). Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms: Density-dependent individual specialization. Journal of Animal Ecology 73:973–982.

Tattersall, G. J., D. V. Andrade, and A. S. Abe (2009). Heat Exchange from the Toucan Bill Reveals a Controllable Vascular Thermal Radiator. Science 325:468–470.

Tattersall, G. J., B. Arnaout, and M. R. E. Symonds (2017). The evolution of the avian bill as a thermoregulatory organ. Biological Reviews 92:1630–1656.

Taylor, J. N., W. M. Ternes, and M. S. Lattanzio (2018). Natural selection favors local specialization in a widespread habitat generalist. Evolution 72:2090–2099.

Terborgh, J. (1973). On the Notion of Favorableness in Plant Ecology. The American Naturalist 107:481–501.

Tiner, R. W. (2013). Tidal Wetlands Primer. University of Massachusetts Press.

Title, P. O., and K. J. Burns (2015). Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. Ecology Letters 18:433–440.

Title, P. O., and D. Rabosky (2018). Tip rates, phylogenies, and diversification: what are we estimating, and how good are the estimates? bioRxiv. https://doi.org/10.1101/369124

Tripp, E. A., and P. S. Manos (2008). Is floral specialization an evolutionary dead end? Pollination system transitions in *Ruellia* (Acanthaceae). Evolution 62:1712–1737.

U.S. Fish and Wildlife Service National Wetlands Inventory (2010). Download Seamless Wetlands Data by State. *Download Seamless Wetlands Data by State.* [Online.] Available at http://www.fws. gov/wetlands/Data/State-Downloads.html.

Vamosi, J. C., W. S. Armbruster, and S. S. Renner (2014). Evolutionary ecology of specialization: insights from phylogenetic analysis. Proceedings of the Royal Society B: Biological Sciences 281:20142004–20142004.

Van Valen, L. (1965). Morphological Variation and Width of Ecological Niche. The American Naturalist 99:377–390.

VanderWerf, E. A. (2012). Ecogeographic Patterns of Morphological Variation in Elepaios (*Chasiempis* spp.): Bergmann's, Allen's, and Gloger's Rules in a Microcosm. Ornithological Monographs 73:1–34.

Walsh, J., P. Benham, P. Deane-Coe, P. Arcese, B. G. Butcher, Y. L. Chan, Z. A. Cheviron, C. S. Elphick, A. I. Kovach, B. J. Olsen, W. G. Shriver, et al. (*In Review*). Genomics of rapid ecological divergence and parallel adaptation in songbirds. Evolution Letters.

Walsh, J., G. Clucas, M. MacManes, K. Thomas, and A. Kovach (2018). Divergent selection and drift shape the genomes of two avian sister species spanning a saline-freshwater ecotone. bioRxiv. https://doi.org/10.1101/344614

Walsh, J., I. J. Lovette, V. Winder, C. S. Elphick, B. J. Olsen, G. Shriver, and A. I. Kovach (2017). Subspecies delineation amid phenotypic, geographic and genetic discordance in a songbird. Molecular Ecology 26:1242–1255.

Walsh, J., R. J. Rowe, B. J. Olsen, W. G. Shriver, and A. I. Kovach (2016). Genotype-environment associations support a mosaic hybrid zone between two tidal marsh birds. Ecology and Evolution 6:279–294.

Weir, J. T. (2006). Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. Evolution 60:842–855.

Weir, J. T., and D. Schluter (2004). Ice sheets promote speciation in boreal birds. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:1881–1887.

Werner, T. K., and T. W. Sherry (1987). Behavioral feeding specialization in Pinaroloxias inornata, the "Darwin's Finch" of Cocos Island, Costa Rica. Proceedings of the National Academy of Sciences 84:5506–5510.

Wiens, J. J. (2004). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Wiens, J. J., and C. H. Graham (2005). Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Wiest, W. A., M. D. Correll, B. G. Marcot, B. J. Olsen, C. S. Elphick, T. P. Hodgman, G. R. Guntenspergen, and W. G. Shriver (2019). Estimates of tidal-marsh bird densities using Bayesian networks: Tidal-Marsh Bird Densities. The Journal of Wildlife Management 83:109–120.

Wiest, W. A., M. D. Correll, B. J. Olsen, C. S. Elphick, T. P. Hodgman, D. R. Curson, and W. G. Shriver (2016). Population estimates for tidal marsh birds of high conservation concern in the northeastern USA from a design-based survey. The Condor 118:274–288.

Williams, S. E., Y. M. Williams, J. VanDerWal, J. L. Isaac, L. P. Shoo, and C. N. Johnson (2009). Ecological specialization and population size in a biodiversity hotspot: How rare species avoid extinction. Proceedings of the National Academy of Sciences 106:19737–19741.

Yurkowski, D. J., S. Ferguson, E. S. Choy, L. L. Loseto, T. M. Brown, D. C. G. Muir, C. A. D. Semeniuk, and A. T. Fisk (2016). Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecology and Evolution 6:1666–1678.

Zelditch, M. L., H. D. Sheets, and W. L. Fink (2003). The ontogenetic dynamics of shape disparity. Paleobiology 29:139–156.

Zelditch, M. L., D. L. Swiderski, and H. D. Sheets (2012). Geometric Morphometrics for Biologists. 2nd edition. Academic Press, Waltham, MA.

Zink, R. M., and J. C. Avise (1990). Patterns of Mitochondrial DNA and Allozyme Evolution in the Avian Genus *Ammodramus.* Systematic Zoology 39:148–161.

APPENDIX A: SUPPLEMENTAL TABLES

Table A3.1. Mean and standard deviation of the MCMC analysis and Maximum Likelihood parameter estimates for the full MuSSE model allowing all rates to vary freely. Lambda is the speciation rate for each bill shape category as denoted in Figure 1, mu is the extinction rate, and q is the transition rate, subscripts denote the direction of transitions in morphological space.

Parameter	ML Estimate	MCMC (Mean)	MCMC (SD)
lambda_1	0.211	0.214	0.015
lambda_2	0.338	0.365	0.044
lambda_3	0.349	0.442	0.083
lambda_4	0.166	0.159	0.048
lambda_5	0.241	0.284	0.058
mu_1	0.000	0.007	0.008
mu_2	0.000	0.041	0.039
mu_3	0.000	0.118	0.108
mu_4	0.000	0.044	0.045
mu_5	0.000	0.070	0.065
q_{12}	0.002	0.003	0.003
q_{13}	0.001	0.003	0.003
q_{14}	0.004	0.006	0.004
q_{15}	0.004	0.005	0.003
q_{21}	0.103	0.107	0.025
q_{23}	0.000	0.006	0.006
q_{24}	0.000	0.005	0.005
q_{25}	0.026	0.037	0.018
q_{31}	0.083	0.088	0.026
q_{32}	0.026	0.025	0.013
q_{34}	0.059	0.084	0.042
q_{35}	0.012	0.015	0.010
q_{41}	0.091	0.075	0.039
q_{42}	0.000	0.011	0.011
q_{43}	0.000	0.031	0.047

Table A3.1
Cont.

q_{45}	0.000	0.009	0.009
q_{51}	0.016	0.022	0.017
q_{52}	0.039	0.052	0.025
q_{53}	0.000	0.009	0.009
q_{54}	0.000	0.010	0.011

Table A4.1.1. Summary statistics on bill size for three sparrow species. We calculated bill size as 1/3 π * bill length * bill width * bill depth, following Greenberg and Droege (1990).

	Minimum	Median	Mean	Maximum	SD	CV
SESP	247.00	338.20	342.50	478.60	40.29	11.76
SALS	147.00	208.00	208.50	271.10	22.93	11.00
NESP	131.70	190.60	190.00	250.70	24.67	12.99

Table A4.1.2. Summary statistics on bill size for males and females for three sparrow species. We calculated bill size as 1/3 π * bill length * bill width * bill depth, following Greenberg and Droege (1990).

	Female				Male			
	Mean	Median	SD	CV	Mean	Median	SD	CV
NESP	204.30	209.58	16.07	7.86	187.86	188.05	25.10	13.35
SALS	200.97	203.34	21.39	10.64	210.91	209.54	22.94	10.88
SESP	323.79	324.12	33.52	10.35	350.83	349.28	40.35	11.50

Table A4.2.1. Preliminary dbRDA models to determine best predictors for each category. In order to reduce the number of models, we conducted a two-step approach using dbRDA models to determine the combination of factors that explained the most variation in niche position and niche breadth among populations of saltmarsh and seaside sparrows in tidal marshes of the northeastern U.S. The dependent variables are dissimilarity matrices constructed from sex corrected bill size for each population (niche position), and coefficient of variation in bill size for each population (niche breadth). For each of 3 categories of predictors that had multiple variables (geographic distance, interspecific competition, and vegetation PC axes), we first constructed a model for using single predictors. We also constructed models using combinations of the predictors that had positive Adjusted R^2 values. Following this step, we combined our single variable for intraspecific competition (the number of individuals caught per net hour), with the variables in the top model for each of the three categories. Full model set containing independent variables from each category are listed in table 2b. We scaled all variables prior to analysis.

Saltmarsh Sparrow Niche Position

Geographic Distance (PCNM axes)		**Interspecific Competition**		**Vegetation (PC Axes)**	
Model	**Adj. R^2**	**Model**	**Adj.R^2**	**Model**	**Adj.R^2**
PCNM1 + PCNM4 + PCNM8	0.17	SWSP + SESP (Abundance)	0.11	PC1 + PC4 + PC5	0.21
ALL	0.17	SESP + NESP + STSP + SWSP + SOSP + SAVS (abundance)	0.09	PC1 + PC5	0.19
PCNM1 + PCNM8	0.15	SWSP (abundance)	0.06	PC1 + PC4	0.17
PCNM1 + PCNM4	0.11	SWSP (presence)	0.06	PC1	0.16
PCNM1	0.10	SESP + NESP + STSP + SWSP + SOSP (abundance)	0.05	PC4 + PC5	0.03
PCNM4 + PCNM8	0.06	Total abundance	0.04	PC5	0.03
PCNM6	0.05	SWSP + SOSP (abundance)	0.04	PC4	0.01
PCNM1 + PCNM4 + PCNM6 + PCNM8	0.04	SESP (abundance)	0.03	PC2	0.01

Table A4.2.1 Continued

PCNM8	0.03	SWSP + NESP (Abundance)	0.03	PC3	-0.004
PCNM1 + PCNM6 + PCNM8	0.01	SESP + NESP (abundance)	0.02	PC9	-0.01
PCNM4	0.01	SESP (presence)	0.02	PC6	-0.02
PCNM9	0.00	Number of Species Present	0.01	PC7	-0.02
PCNM1 + PCNM4 + PCNM6	0.00	SESP + SOSP (abundance)	0.01	PC8	-0.03
PCNM2	-0.01	SESP + NESP + STSP + SWSP + SOSP + SAVS (presence)	0.00		
PCNM3	-0.01	SOSP (presence)	-0.01		
PCNM4 + PCNM6	-0.01	NESP (presence)	-0.02		
PCNM5	-0.02	NESP (abundance)	-0.02		
PCNM1 + PCNM6	-0.03	STSP (abundance)	-0.02		
PCNM6 + PCNM8	-0.03	STSP (prsence)	-0.02		
PCNM7	-0.03	SOSP (abundance)	-0.02		
		NESP + SOSP (abundance)	-0.04		

Saltmarsh Sparrow Niche Breadth

Geographic Distance (PCNM axes)		**Interspecific Competition**		**Vegetation (PC Axes)**	
Model	**Adj. R^2**	**Model**	**Adj.R^2**	**Model**	**Adj.R^2**
PCNM6	0.03	SOSP (abundance)	0.03	PC3	0.01
PCNM6 + PCNM8	0.03	SWSP + SOSP (abundance)	0.01	PC8	0.01
PCNM3 + PCNM6	0.02	SESP + SOSP (abundance)	0.00	PC5	0.01
PCNM3 + PCNM6 + PCNM8	0.02	STSP (presence)	0.00	PC2	0.00
PCNM8	-0.01	SWSP (abundance)	-0.01	PC9	0.00
PCNM2	-0.01	SWSP (presence)	-0.01	PC3 + PC8	-0.01
PCNM4	-0.01	SESP + NESP + SOSP (abundnace)	-0.01	PC7	-0.02
PCNM5	-0.01	SESP + SOSP + SWSP (abundance)	-0.01	PC4	-0.02
PCNM3	-0.01	NESP (abundance)	-0.02	PC1	-0.02
PCNM1	-0.02	SAVS (abundance)	-0.02	PC6	-0.03
PCNM3 + PCNM8	-0.02	NESP (presence)	-0.02	PC5 + PC9	-0.05
PCNM7	-0.02	SESP + NESP + STSP + SWSP + SOSP + SAVS (abundance)	-0.02	PC3 + PC5	-0.05
PCNM9	-0.03	NESP (presence)	-0.02	PC3 + PC9	-0.07
PCNM1:9	-0.11	SOSP (presence)	-0.02	PC3 + PC5+ PC9	-0.09
		Total abundance	-0.02		
		SESP (abundance)	-0.03		
		STSP (abundance)	-0.03		
		STSP + NESP (abundance)	-0.03		

Table A4.2.1 Continued

SESP (presence)	-0.03
Number of Species Present	-0.03
SESP + SWSP (abundance)	-0.03
NESP + SESP (abundance)	-0.04

Seaside Sparrow Niche Position

Geographic Distance (PCNM axes)		Interspecific Competition		Vegetation (PC Axes)	
Model	**Adj. R^2**	**Model**	**Adj.R^2**	**Model**	**Adj.R^2**
PCNM1 + PCNM2 + PCNM3	0.16	Number of Species Present	0.14	PC3 + PC4	0.13
PCNM2 + PCNM3	0.13	SALS + SWSP + SOSP (presence)	0.11	PC3 + PC4 + PC7	0.13
PCNM1 + PCNM2	0.13	SALS + SWSP (presence)	0.11	PC4	0.11
PCNM2	0.11	SALS + SOSP (presence)	0.07	PC4 + PC7	0.11
PCNM1 + PCNM3	0.04	SWSP (presence)	0.05	PC1:7	0.09
PCNM3	0.02	SOSP + SWSP (presence)	0.05	PC3	0.01
PCNM1	0.02	SALS (presence)	0.04	PC3 + PC7	0.01
		SOSP (presence)	0.02	PC7	-0.01
		SWSP (abundance)	0.02	PC1	-0.01
		SWSP + SOSP (abundance)	0.01	PC2	-0.01
		SALS + SWSP (abundance)	0.00	PC5	-0.01
		SALS (Abundance)	-0.01	PC6	-0.02
		SALS + SWSP + SOSP (abundance)	-0.01		
		SOSP (abudance)	-0.02		
		SALS + SOSP (abundance)	-0.03		

Seaside Sparrow Niche Breadth

Geographic Distance (PCNM axes)		Interspecific Competition		Vegetation (PC Axes)	
Model	**Adj. R^2**	**Model**	**Adj.R^2**	**Model**	**Adj.R^2**
PCNM1	-0.01	SALS (Abundance)	0.02	PC3 + PC4 + PC5	0.09
PCNM2	-0.02	SALS +SOSP (Abundance)	0.02	PC3 + PC4	0.08
PCNM3	-0.03	SALS +SWSP (Abundance)	0.01	PC3 + PC5	0.05
PCNM1 + PCNM2	-0.03	SALS + SWSP + SOSP (abundance)	0.00	PC4 + PC5	0.04
PCNM1 + PCNM3	-0.05	SOSP (presence)	-0.02	PC3	0.04

Table A4.2.1 Continued

PCNM2 + PCNM3	-0.06	SOSP (abundance)	-0.02	PC4	0.03
PCNM1 + PCNM2 + PCNM3	-0.07	SWSP (abundance)	-0.02	PC5	0.01
		Number of Species Present	-0.02	PC2 + PC5	0.00
		SWSP (presence)	-0.02	PC2	-0.01
		SALS (presence)	-0.03	ALL	-0.01
		SWSP + SOSP (abundance)	-0.03	PC1	-0.02
		SWSP + SOSP (presence)	-0.04	PC6	-0.03
		SALS + SOSP (presence)	-0.04	PC7	-0.03
		SALS + SWSP (presence)	-0.05		
		SALS + SWSP + SOSP (presence)	-0.07		

Table A4.3.1. Loadings for the first 9 principle components for vegetation species cover at sites with saltmarsh sparrows.

Vegetation Species	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Alopecurus_pratensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Amaranthusm_cannabinu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Apiacea_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Argentina_anserina	-0.17	0.11	-0.06	-0.04	0.03	0.17	0.11	0.06	-0.02
Atriplex_patula	-0.11	-0.18	0.12	0.20	0.18	0.02	-0.07	0.05	0.24
Baccharis_halimifolia	0.04	0.00	-0.03	0.16	0.00	-0.10	-0.06	0.16	-0.12
bare_ground	0.04	0.04	0.05	0.03	-0.03	-0.03	0.11	-0.05	-0.02
calystegi_sepium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chamerion_angustifolium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cirsium_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Comarum_palustre	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cuscuta_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dactylis_glomerata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Distichlis_spicata	-0.36	0.00	0.26	-0.04	0.14	-0.44	0.19	-0.29	0.18
Drodera_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eliocharis_spp	-0.09	0.10	0.09	0.03	0.19	0.11	0.02	0.01	-0.05
Elymus_repens	0.02	-0.19	0.04	-0.10	0.05	0.18	-0.17	0.27	-0.06
Glaux_maritima	-0.10	-0.17	-0.11	0.29	-0.07	0.07	-0.01	-0.21	0.06
Heliotropium_curassavicum	0.01	-0.25	0.20	-0.15	-0.11	0.31	-0.28	0.07	-0.04
Hypericum_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
iris_versicolor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iva_frutescens	-0.04	-0.02	0.53	0.32	-0.03	-0.22	0.14	0.49	-0.04
Juncus_balticus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus_gerardii	-0.44	-0.31	-0.07	-0.04	-0.10	-0.28	-0.11	-0.13	-0.32
Juncus_roemerianus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
juniper	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juniperus_Virginiana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lathyrus_japonicus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leymus_molli	-0.03	-0.09	0.07	-0.07	-0.02	0.07	-0.02	0.11	-0.05
Limonium_nashi	-0.02	-0.41	-0.05	0.06	0.13	-0.09	0.07	0.11	-0.35
Nuphar_lutea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A4.3.1 Continued

Nyphaea_odorata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
open_water	0.02	0.03	0.13	-0.07	-0.07	0.00	-0.04	0.02	-0.38
PPC	0.00	0.02	0.25	-0.05	0.12	-0.07	-0.15	0.04	0.02
Peltandra_virginica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phleum_pratense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phragmites_spp	0.15	0.43	0.20	0.00	-0.36	-0.13	-0.33	-0.05	-0.03
Pinus_taeda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago_maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polygonum_hydropiperoides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pontederia_cordata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prunus_virginiana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Puccinellia_maritima	-0.12	0.05	-0.10	-0.07	0.00	0.12	0.08	0.06	0.04
Ranunculus_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Reubus_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhinanthus_minor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhynchospora_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
road	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rosaceae_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saggitaria_lancifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salicornia_spp_	0.13	-0.32	0.22	-0.21	0.28	0.04	-0.28	-0.07	0.41
Schoenoplectus_americanus	-0.24	0.25	0.08	0.06	0.23	0.12	0.00	0.10	-0.28
Schoenoplectu_.pungens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Schoenoplectus_robustus	-0.35	0.24	0.11	-0.06	0.05	-0.04	-0.31	-0.22	0.02
Schoenoplectus_tabernaemontani	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
solidago_graminifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago_sempervirens	-0.35	-0.06	-0.11	0.24	-0.21	0.23	-0.29	0.05	0.09
Spartina_alterniflora_s	0.29	0.12	-0.17	0.47	0.42	-0.05	-0.09	-0.19	-0.05
Spartina_alterniflora_t	0.02	-0.05	-0.09	-0.42	0.10	-0.10	0.17	-0.06	0.00
Spartina_cynosuroides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spartina_patens	-0.07	0.07	0.10	0.00	-0.17	0.15	-0.07	-0.01	0.07
Spartina_pectinata	-0.13	0.05	-0.10	-0.07	0.00	0.12	0.09	0.07	0.05
standing_water	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum_officinale	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thalictrum_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thlaspi_arvense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Toxicodendron_radicans	-0.03	-0.08	0.03	0.13	-0.01	0.05	-0.02	-0.07	0.03

Table 4.3.1 Continued

Trifolium_pratense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin_maritima	-0.15	-0.09	-0.22	0.13	-0.07	0.18	0.08	-0.04	-0.02
Typha_angustifolia	-0.21	0.21	0.02	-0.05	0.25	0.20	0.14	0.15	0.16
unknown_cordgrass	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_fern	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_goldenrod	-0.02	-0.01	0.05	-0.10	-0.06	0.01	-0.07	-0.14	0.03
unknown_grass	-0.21	0.16	0.01	-0.03	0.23	0.24	0.10	0.08	-0.02
unknown_herbaceous	-0.04	-0.09	0.07	0.34	-0.08	0.08	-0.07	-0.13	0.13
unknown_rush	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_shrub	-0.05	-0.04	0.11	-0.06	0.15	0.10	-0.03	0.11	-0.02
unknown_succulent	-0.04	-0.03	0.03	0.07	0.00	-0.02	-0.02	-0.10	0.10
unknown_vine	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_woody	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
upland	0.03	0.08	-0.13	-0.08	0.37	-0.11	-0.49	-0.03	-0.28
Vicia_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
wrack	0.13	-0.07	0.45	0.02	0.02	0.41	0.23	-0.52	-0.33
Carex_all	-0.02	0.04	0.05	0.00	0.16	0.05	-0.01	0.02	0.02

Table A4.3.1. Loadings for the first 9 principle components for vegetation species cover at sites with seaside sparrows.

Vegetation Species Cover	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Alopecurus_pratensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Amaranthusm_cannabinu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Apiacea_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Argentina_anserina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Atriplex_patula	-0.01	-0.03	0.06	-0.01	0.07	-0.10	0.01	-0.21	-0.10
Baccharis_halimifolia	-0.05	-0.13	0.37	0.03	-0.04	-0.28	0.39	-0.10	-0.25
bare_ground	0.03	-0.04	-0.03	-0.02	-0.03	0.17	0.07	-0.05	0.24
Calystegi_sepium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chamerion_angustifolium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cirsium_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Comarum_palustre	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A4.3.2 Continued

Cuscuta_spp	-0.02	-0.10	0.10	0.05	-0.04	-0.04	0.15	0.07	-0.07
Dactylis_glomerata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Distichlis_spicata	0.35	0.03	-0.06	-0.54	0.00	0.15	-0.14	-0.43	-0.28
Drodera_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eliocharis_spp	0.08	-0.03	-0.05	0.08	0.03	-0.03	0.01	-0.02	-0.04
Elymus_repens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glaux_maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Heliotropium_curassavicum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypericum_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iris_versicolor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iva_frutescens	0.39	0.42	-0.01	0.05	-0.31	0.04	0.32	-0.07	0.39
Juncus_balticus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus_gerardii	0.15	-0.03	-0.07	0.12	-0.14	-0.08	-0.15	0.02	-0.18
Juncus_roemerianus	0.19	0.13	-0.01	-0.01	-0.20	-0.28	-0.25	0.06	-0.06
Juncus_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
juniper	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juniperus_Virginiana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lathyrus_japonicus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leymus_molli	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Limonium_nashi	0.02	0.06	0.07	0.10	-0.03	0.23	0.00	-0.08	-0.10
Nuphar_lutea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nyphaea_odorata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
open_water	0.31	0.00	-0.22	0.16	0.08	-0.12	0.11	0.15	-0.18
PPC	-0.14	-0.02	-0.06	-0.08	-0.15	0.15	-0.02	0.07	-0.13
Peltandra_virginica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phleum_pratense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phragmites_spp	0.27	-0.35	0.50	0.11	0.19	0.25	-0.43	-0.04	0.25
Pinus_taeda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plantago_maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polygonum_hydropiperoides	-0.04	-0.15	0.20	0.03	0.04	-0.18	0.19	-0.19	-0.22
Pontederia_cordata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prunus_virginiana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Puccinellia_maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Reubus_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhinanthus_minor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A4.3.2 Continued

Rhynchospora_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
road	0.27	0.02	-0.11	0.12	0.28	0.43	0.26	-0.05	0.03
Rosaceae_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Saggitaria_lancifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salicornia_spp	-0.19	0.23	-0.08	0.26	0.00	0.24	-0.06	-0.08	-0.30
Schoenoplectus_americanus	0.29	0.02	-0.14	0.05	0.45	-0.11	0.11	0.28	-0.15
Schoenoplectu_.pungens	0.06	0.01	-0.03	-0.18	0.32	0.16	0.04	0.36	-0.27
Schoenoplectus_robustus	0.14	-0.12	-0.01	0.23	0.31	-0.31	-0.06	-0.38	0.09
Schoenoplectus_tabernaemontani	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago_graminifolia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago_sempervirens	0.09	0.13	0.21	0.18	0.05	0.08	0.10	-0.02	0.06
Spartina_alterniflora_s	-0.19	0.67	0.25	-0.02	0.35	-0.08	-0.12	-0.26	-0.08
Spartina_alterniflora_t	-0.13	-0.27	-0.38	0.20	0.00	0.19	0.19	-0.47	-0.06
Spartina_cynosuroides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spartina_patens	0.25	-0.06	0.19	-0.40	-0.13	-0.01	0.26	-0.05	-0.10
Spartina_pectinata	0.25	0.04	-0.13	0.24	-0.02	-0.27	-0.07	-0.06	0.06
standing_water	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum_officinale	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thalictrum_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thlaspi_arvense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Toxicodendron_radicans	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trifolium_pratense	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin_maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Typha_augustifolia	0.16	-0.04	-0.07	0.13	-0.14	-0.08	-0.14	0.02	-0.18
unknown_cordgras	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_fern	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_goldenrod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_grass	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_herbaceous	-0.01	-0.02	0.34	0.19	-0.10	0.11	0.27	0.12	-0.12
unknown_rush	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_shrub	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_succulent	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_vine	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unknown_woody	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
upland	0.10	0.07	0.07	0.17	-0.23	0.22	-0.18	-0.06	-0.29
Vicia_spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A4.3.2 Continued

wrack	0.17	0.07	0.15	0.29	-0.17	0.14	-0.04	0.01	-0.22
Carex_all	0.08	-0.01	-0.02	0.04	-0.18	-0.05	-0.17	0.04	-0.15

BIOGRAPHY OF THE AUTHOR

Meaghan was born in the Bronx, the northernmost borough of the big apple, the best city on earth. Her nomadic tendencies were evident at an early age, when she migrated north at the ripe old age of two. Meaghan spent some time in the Hudson Valley, where she learned to read trail maps just as efficiently as subway maps. After a short stint in Connecticut for high school, she became the first in the family to snag a bachelor's degree, from the State University of New York in Binghamton, the literal and figurative armpit of the Empire State. With this new fancy piece of paper in hand, and no longer able to resist the strong influence of her migratory tendencies, Meaghan flew the coop. The first stop was southern Mississippi, an unlikely destination, but one that sealed her fate as a bird nerd. At a small rehabilitation clinic tucked in the woods, those feathered little nuggets captured her heart and her intrigue. San Antonio was next on the list, where she discovered a new found love of breakfast burritos at Rolando's taco house, and made friends with parrots, panthers, and primates. Meaghan quickly felt caged by captive animal husbandry, and gravitated toward a more rewarding career in scientific research that required walking through mosquito infested marshes on the Colorado River, and collecting cow patties that she strategically placed in owl burrows. She spent some time chasing Condors through the mountains of California and snuggling with seabirds on some remote islands before settling in Tucson. Apparently, she apparently contracted a brain parasite during her time in the Peruvian cloud forest or was high on prickly pear syrup. After a quick phone call, she was lured by Brian's boisterous laughter, and decided to trade the joy of basking in the sunshine and mountain views for a place called vacationland. She quickly discovered, however, that she had been scammed into a desolate life of PhDom, on a block of ice in the arctic tundra. She has so far been lucky in avoiding losing limbs to frostbite. She is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences from the University of Maine in May 2019.