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USING ECOMORPHOLOGY TO UNDERSTAND THE EVOLUTIONARY HISTORY AND SPATIAL BIODIVERSITY OF WADING BIRDS

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BY
ROSSY NATALE

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ABSTRACT

Ecomorphology, the field that looks at the relationship between the morphological features of an organism and its ecology, is a valuable framework that has been applied to answer a wide variety of questions on evolution, ecology, and spatial biodiversity. Here, I focus on the relationship between the skull morphology in a highly diverse order of sea and shorebirds (the Charadriiformes) and its relationship to foraging ecology as a framework to address several questions. After Chapter 1 introduces past research on ecomorphology, Chapter 2 uses 3D morphometric data describing skull shapes of 262 charadriiform species in conjunction with ecological data to understand if foraging ecology, as opposed to allometry (shape changes due to size changes), is the primary predictor of skull shape. This chapter reveals that the predictors of charadriiform skull shape vary depending on the phylogenetic level of analysis, with foraging ecology as the primary predictor at the ordinal level. Chapter 3 focuses on interpreting this relationship between skull shape and foraging ecology and analyzing if the variation seen is the result of the beak evolving semi-independently from the braincase. The analyses in this chapter suggest the charadriiform skull has evolved as two semi-independent sets of bones, or modules, with the module composed of the beak and it's biomechanically associated structures relating more strongly to foraging ecology then the module composed of the braincase. Chapter 4 builds upon this now-established relationship between charadriiform skull shape and foraging ecology to investigate the biodiversity of Charadriiformes across the Midwest and East Coast of the United States with a specific focus on synthesizing morphological data with temporal community assemblage data to understand the relationship between protected areas and charadriiform communities that see pronounced intra-annual changes due to migration. This chapter demonstrated the highly variable spatiotemporal land use patterns of charadriiform birds and provided a preliminary framework for accounting for migration in spatial biodiversity analyses. Chapter 5 reemphasizes how the use of ecomorphology throughout all of these chapters has provided an efficient way to provide broad-scale insights into both macroevolution and present-day spatial biodiversity and suggests future areas of research that expand upon the analyses here. Additional results and data descriptions as described throughout this dissertation are available in the online supplementary file.

CHAPTER 1

INTRODUCTION

Differences in the morphology of species determine how they interact with the environment surrounding them. This relationship between aspects of a species' ecology (how a species eats, moves etc.) and its morphological features is encapsulated by the field of ecomorphology. Ecomorphology is concerned not only with how the functional output of morphological differences relates to differences in ecology, but how this relationship may affect the macroevolution of traits via selective pressures (Bock, 1989). As a broad concept, ecomorphology has existed for centuries (see Bock 1989 for a historical review) but the term itself was not introduced until 1975 by Karr and James. Drawing heavily from the field of comparative anatomy, many of the studies pre-dating the introduction of this term were detailed, highly descriptive monographs focusing on the adaptations species possessed to, for example, efficiently locomote underwater (Storer, 1945), climb trees (Norberg, 1986; Spring, 1965), or consume different dietary items (Lundelius, 1957).

The specific traits focused on in ecomorphological work are those in which there, ideally, are established or tested differences in an ecologically-relevant performance (e.g. bite force, swimming speeds, climbing ability) that is a direct consequence of its morphology (Wainwright, 1991), although work often assumes these relationships or extrapolates from previous work on ecologically similar clades. As outlined by Wainwright (1991), ecomorphological work has two major branches: one which focuses on connecting morphology to ecological characteristics of species and, conversely, one which focuses on providing adaptive explanations for certain morphologies. Work often addresses one or both of these branches. For example, analyses by Norberg and Rayner (1987) have highlighted how wing shape in bat species determines several aspects of flying ability (e.g. speed, maneuverability, ability to carry) and how this, in turn, relates to differences among species that fill different ecological niches (e.g. perching nectarivores, species that feed in flight). In both historical and contemporary work, morphology is characterized in a wide variety of ways ranging from detailed descriptions of both muscles (e.g. Wainwright, 1991) and bones (e.g. Korzun et al., 2009) to collections of linear measurements (e.g. Barbosa and Moreno, 1999) and, more recently, to the use of 3D data (e.g. Vicari et al., 2023) that quantifies the shape or bones or muscles.

Since the term was introduced, ecomorphological work has been conducted on a wide variety of clades and has provided insights into three major areas of interest. First, earlier work often used the comparative anatomy inherent to these studies to contribute to an understanding of taxonomy (Storer, 1945). Later, once phylogenetic hypotheses were more readily available, ecomorphological data was used in conjunction with phylogenies to understand the macroevolution of clades as it relates to adaptive evolution (Wainwright and Reilly, 1994). Sometimes, the insights revealed provide specific evidence that variation in morphology can be explained by specific ecological differences (e.g. trophic level; Acero Murcia et al. 2023) among species. For example, Vicari et al. (2023) found skull shape in toothed whales is explained by several ecological factors (echolocation mode and frequency as well as maximum and minimum prey size) and, similarly, work by Dawideit et al. (2009) has demonstrated how a combination of morphological traits (e.g. wing tip length, bill depth, and tail graduation) explained ≈45% of the variation in the natal dispersal distance of passerine birds.

When these insights are provided, it makes it possible to use morphological data as a proxy for ecology, which is advantageous both for aspects of a species ecology that may be difficult to measure (e.g. natal dispersal distance; Dawideit et al. 2009) and for providing insights into fossil taxa (Wisniewski et al., 2023) or even paleontological sites (Short et al., 2023) for which ecology cannot be directly observed. Additionally, when a relationship between morphology and ecology is established, we become able to use morphological data as a way to paint a picture of the tempo and mode of the evolution of any given clade. Such studies have relied on ecomorphological data to provide insights into how ecological restrictions (Meloro and Tamagnini, 2022), competition (Chira et al., 2020), and sexual dimorphism (Kaliontzopoulou et al., 2015) relate to morphological disparity and rates of trait evolution. This ecomorphological approach to macroevolution allows us to test for patterns of convergent, parallel, and conserved evolution across traits (Davis and Betancur-R, 2017; McLean et al., 2018) and, when combined with biogeographical data, such analyses can also inform our understanding of species colonization and evolution within new biogeographical realms in deep time (Alhajeri et al., 2016).

Secondly, ecomorphology has continued usage in understanding community ecology. These studies have historical roots with early work comparing morphological traits among sympatric bird species within communities (Schoener, 1965; Travis and Ricklefs, 1983). Studying the composition of ecomorphological traits within and between communities can provide insights into abiotic factors in the environment (Drag et al., 2023; Lima et al., 2023; Shi et al., 2018) or biotic factors such as competition between species (Lockwood and Moulton, 1994; Pöysä et al., 1994) that create nonrandom distributions of traits across space, with studies often highlighting how both abiotic and biotic factors interact to determine species composition across space (Poff, 1997; Weiher et al., 1998) or along gradients (e.g. elevation; Ghosh-Harihar 2014). Using ecomorphological data can also inform our knowledge of current and ongoing ecological changes in communities. The term 'ecological fitting' is sometimes used to refer to a phenomenon best exemplified in non-native species colonization where a species may be able to colonize new environments if the available niche space, as determined by both the environment and the species already present, fits the colonizing species phenotype (see Agosta and Klemens 2008 for a review of this concept and both Vizentin-Bugoni et al. 2019 and Gleditsch and Sperry 2020 for applied examples). Often, using trait data in the context of community ecology can provide an efficient and quantitative way to provide a nuanced understanding of community assembly. Work using ecomorphological data along elevation gradients found that, in contrast to hypotheses of environmental filtering where the environment 'filters' traits from occurring in certain habitats, passerine bird lineages exhibited trait diversification *in situ* as species ranges moved to higher elevations (Kennedy et al., 2022). If the trait has strong phylogentic signal, phylogeny can also interact with the environmental filtering of traits and result in a process referred to as clade sorting (Polly et al., 2017).

Lastly, the same types of datasets (either 2D, 3D, or categorical data describing morphology combined with data on species assemblages) that are typically used to analyze community assembly patterns can be applied in a conservation setting by using ecomorphological data as a quantitative way to identify locations with particularly high biodiversity to be protected (González-Maya et al., 2016), where it is changing in response to climate or direct anthropogenic disturbance (Zhao et al., 2022), and to understand best practices for minimizing diversity loss in response to human activity (e.g. agricultural practices; García-Navas et al. 2022). Thus, ecomorphology can be used as a framework to understand how certain clades have evolved over deep time due to selection pressures and adaption, to understand the factors that generated present-day species assemblages in light of ecologically-relevant traits, and to quantify the present-day variation in ecological diversity seen across space.

Bird skull morphology and, in particular, its relationship to foraging ecology has long been viewed as a classic example of ecomorphology and has historically received attention in regard to all three of these aspects. The diversity of skull morphology is extremely abundant and is apparent looking at the beaks of live birds (see figure 1 in Field 2018 for visual examples). While this external beak morphology is readily visible to us and is often studied (Cooney et al., 2017), there is parallel variation in the underlying skeletal morphology of the beak and the remaining portions of the skull that is comprised of the braincase and multiple, connected bony elements (fig 1.1). I will hereafter refer to the sum of these parts as the skull and specifically refer to the isolated components where appropriate. While the relationship between skull morphology and foraging ecology has received the most attention, the avian skull is relevant in many other life history traits. The beak is known to serve as important location for thermoregulation (Friedman et al., 2019; Tattersall et al., 2017); a role that affects species behavior (Ryeland et al., 2017), biogeography, (Fröhlich et al., 2023; Miller et al., 2018; Symonds and Tattersall, 2010), and possibly even responses to changing climates (reviewed in Ryding et al. 2021). Beak morphology, specifically the distal portions of the beak, has also been noted to be critical for effective parasite control (Clayton et al., 2005; Clayton and Walther, 2001; Wagnon et al., 2022) while the relationship between beak morphology and differences in other behaviors such as song production (Derryberry et al., 2012; Huber and Podos, 2006) and burrowing (Cheng et al., 2017a) has also been documented. As demonstrated in a comparative analysis on a group of honeyeaters (family Meliphagidae) by Friedman et al. (2019) and on a taxonomically broad analysis looking across all birds by (Hunt et al., 2023), avian skull evolution has likely been the result of adaptive morphological change for various roles.

It is the relationship between foraging behavior and skull shape that has, however, received the most attention in research on avian skull morphology. The interest in this relationship from an evolutionary perspective is typically noted to extend back to the publication of Charles Darwin's *The Origin of Species* (Darwin, 1845) which drew a parallel between beak shape in the finches of the Galápagos and differences in their foraging ecology, although many had previously drawn relationships between an organism's features and its environment (see Bock 1989 and Motta et al. 1995). Since then, studies have analyzed morphometric (shape) data from the skulls of different avian clades or across birds as a whole to draw connections between skull morphology and foraging behaviors (Steinfield et al., 2023), diet (Grant and Grant, 1996; Guangdi et al., 2015), or both (Felice et al., 2019; Gómez and Lois-Milevicich, 2021). Particularly in recent years, there has been an increase in work using relatively densely collected three-dimensional data from either bird beaks (Olsen, 2017) or whole skulls (Bright et al., 2016; Felice and Goswami, 2018; Felice et al., 2019; Gómez and Lois-Milevicich, 2021; Sun et al., 2018) to, again, understand shape differences in relation of foraging ecology (Ste-

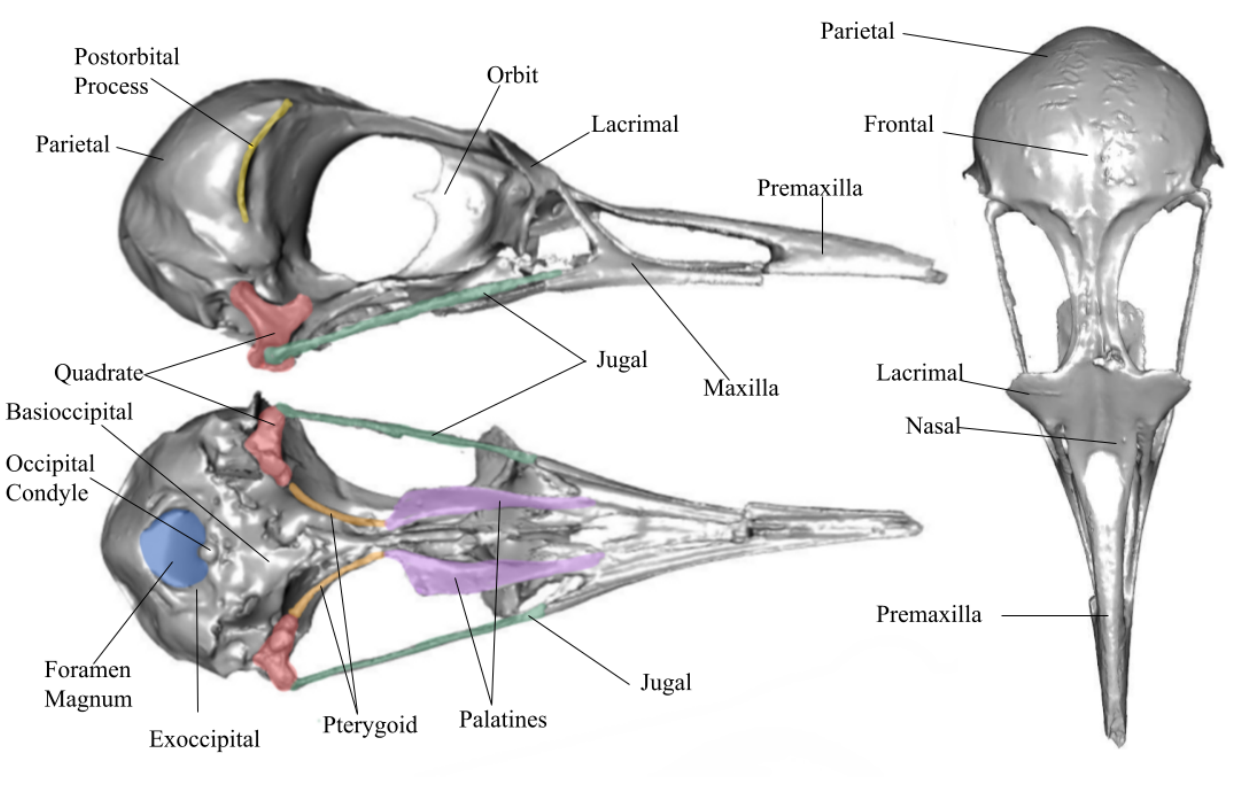

Figure 1.1: A majority of the bones in the avian skull, as depicted on a three dimensional surface scan of a Least Tern *Sterna antillarium* (Specimen Identifier: FMNH 376281). Many portions of the braincase and beak are fused and are thus given approximate labels. The few structures (foramen magnum, postorbital process, quadrates, jugals, pterygoids, and palatines) that can be identified reliably as discrete elements on these surface scans are labeled with different colors. Certain bones (e.g. the, squamaosal) are not labeled as they could not be reliably identified on surface scans. Rather, the portions highlighted are those discussed throughout this dissertation. Nomenclature and anatomy are based on Quayle et al. (2014) and I refer readers to their work for a more comprehensive overview.

infield et al., 2023), diet (Bright et al., 2016; Olsen, 2017), or both (Felice et al., 2019). Some of this work has involved experimental studies explicitly testing the connection between different beak shapes and foraging efficiency in birds such as flowerpiercers (genus Diglossa; Schondube and del Rio 2003) and the African seedcracker (*Pyrenestes ostrinus*; Heckeberg et al. 2021), while other work has used biomechanical metrics based on morphometric data (Navalón et al., 2019) to more explicitly connect form to function.

This dissertation will build upon this ecomorphological foundation using the order Charadriiformes as a case study. The order Charadriiformes contains ≈390 species of birds (see fig 2.2 for overview of families) that vary substantially in size (from ≈20 grams to ≈1850 grams) and are often highly migratory. Charadriiformes is an excellent order to further analyze how skull morphology and foraging ecology relate to one another due to the large amount of ecological and morphological diversity in the group. While the order is typically referred to as 'shorebirds' and does indeed contain species that live in wetland or coastal environments, the order also contains numerous pelagic species (e.g. Auks and skuas; family Alcidae and Stercorariidae respectively), species that live on arid grounds (e.g. seedsnipes, and thick-knees; families Thinocoridae and Burhinidae respectively) or grasslands (e.g. the upland sandpiper *Bartramia longicauda*, mountain plover *Charadrius montanus*, and the monotypic plains wanderer *Pedionomus torquatus*), forest-dwelling species (e.g. the Bukidnon woodcock *Scolopax bukidnonensis*, certain buttonquail species in family Tunicidae), and even Polar species (e.g. sheathbills and some skuas, families Chionidae and Stercorariidae). Paralleling this variation in habitat use is a large amount of variation in foraging ecology and skull shape (fig 1.2). Among pelagic species, the family Alcidae (commonly referred to as Auks) are known to be specialized wing propelled divers (Bédard, 1969; Thaxter et al., 2010). Their relatives, the gulls and terns (family Laridae), include species that are extreme generalists common to anthropogenic environments (Goumas et al., 2020; Lato et al., 2021) and others that are surface or plunge divers (Burger, 1988). Even more unique among these more aquatic species are the three species of skimmers (genus *Rynchops*: family Laridae) which have an elongated, knife-like lower mandible with specialized microstructures (Martin and Bhushan, 2016) that the bird drags through the water to forage as they fly parallel to the waters surface (Zusi, 1962).

More familiar 'shorebirds' or 'wading birds' (as they are commonly called) such as plovers (family Charadriidae), sandpipers (family Scolopacidae), Jacanas (family Jacanidae), and avocets (family Recruvirostridae) forage along shorelines or other wet environments such as flooded fields or wetlands. Some of these species (e.g. avocets, many sandpipers) are known to both wade into the water and forage either in the water column (Dole, 1986) or use combinations of pecking, probing, and skimming in shallow water and soft sediments (MacDonald et al., 2012). Certain Charadriiformes also are more specialized for probing into soft sediments (e.g. mud, sand) such as the American woodcock *Scolopax minor* (Rabe et al., 1983). Other species (e..g plovers) are known to rely on visual cues and sometimes foot-trembling (Osborne, 1982) followed by pecking to obtain food items (Rose and Nol, 2010). Many of these typical shorebirds also have a specialized biomechanical adaptation in their skulls known as rynchokinesis where the distal portions of the beak are able to flex independently from the rest of the skull (Estrella and Masero, 2007; Zusi, 1984), although it is unknown how widespread this is. The order also contains species that feed aerially (family Glareolidae; del Hoyo et al. 1996), predators such as skuas (family Stercoraridae; Bayes et al. 1964; de Almeida Reis et al. 2021), grazing species known to tear off plant material (family Thinocoridae; del Hoyo et al. 1996; Korzun et al. 2009), and scavenging species such as sheathbills (family Chioniidae; Burger 1981; Favero 1996). Charadriiformes are also unique in that they are highly migratory (del Hoyo et al., 1996) and often form mixed-species feeding assemblages where multiple species may forage in specific microhabitats within the same area (Armitage et al., 2007), suggesting that morphologically driven differences in ecology may be important for niche diversification within this group.

In this dissertation, I address two related areas of research using Charadriiformes as an ideal study system for research conducted within an ecomorphological framework due to the ecological and morphological diversity present in the order (fig 1.2). In Chapter 2 (Natale and Slater, 2022), I test the hypothesis that foraging ecology is the primary predictor of charadriiform skull shape using a large 3D geometric morphometric dataset describing skull morphology that is analyzed in a suite of phylogenetic comparative analyses. This chapter demonstrates that foraging ecology is the predominant predictor of differences in skull morphology across the order, but that unique allometric trends within families are more important predictors of skull shape at lower taxonomic levels. Chapter 3 further interprets this relationship between skull morphology and ecology and tests the hypothesis that the charadriiform beak has evolved independently from the rest of the skull. This chapter highlights that the beak and braincase have evolved in a semi-independent (i.e. modular), but still correlated, manner and that this pattern of evolution has manifested in similar relationships between both beak and braincase morphology and foraging ecology when these two components are studied in isolation. Chapter 4 uses the relationship between skull shape and foraging ecology established in Chapters 2 and 3 as the framework through which to analyze the spatial biodiversity of Charadriiformes across the Midwest and East Coast of North America. This section has a particular focus on developing analytical frameworks that use ecomorphological data to understand how we can more explicitly account for the pronounced intra-annual changes in avian communities due to migration in spatial biodiversity analyses. Chapter 4 uses these methods to highlight how the highly migratory nature of these birds complicates our understanding of their use of space and suggests that Charadriiformes are highly flexible in habitat usage, complicating our understanding of area-based conservation for these birds. Chapter 5 highlights my broader conclusions and suggests areas of future research.

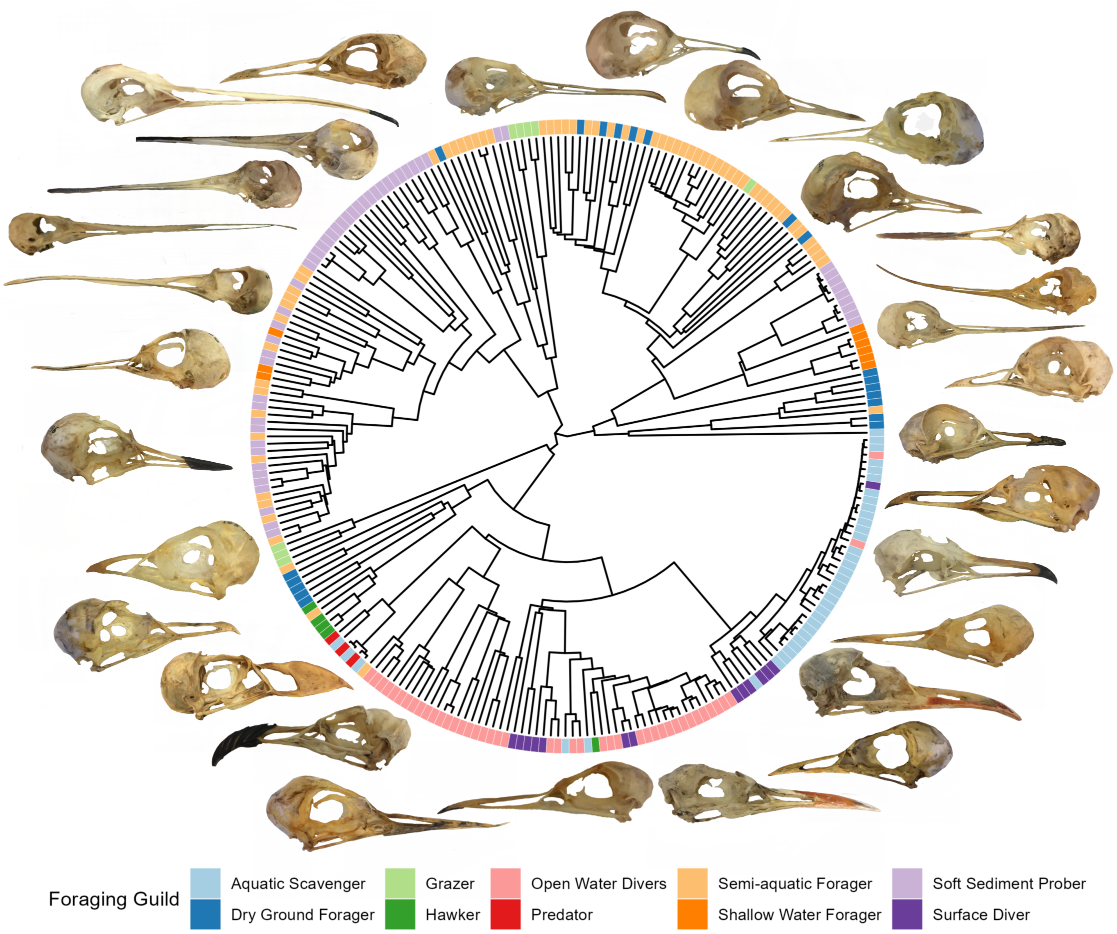

Figure 1.2: Examples of charadriiform skull shape and foraging ecology diversity. A phylogenetic tree (Černý and Natale, 2022) is shown in the center, with one of ten foraging guilds mapped onto the tips (see *Methods* in Chapters 2 and 3 for more details). Representative examples of skull diversity are shown with images of museum specimens surrounding the tree. Species and specimen numbers, starting from the center-right (the most derived tip on the tree) and moving clockwise: *Larus occidentalis* (FMNH 105459), *Larus heermanni* (FMNH 338163), *Chlidonias niger* (FMNH 105798), *Larosterna inca* (FMNH 437527), *Sterna antillarum* (FMNH 376281), *Hydroprogne caspia* (FMNH 360641), *Anous stolidus* (FMNH 346102), *Gygis alba* (314021), *Alca torda* (FMNH 345099), *Fratercula cirrhata* (FMNH 364740), *Stercorarius longicaudus* (FMNH 105259), *Glareola pratincola* (FMNH 105767), *Arenaria interpres* (FMNH 313996), *Actitis hypoleucos* (FMNH 368856), *Limnodromus griseus* (FMNH 376198), *Limosa fedoa* (FMNH 23510), *Gallinago gallinago* (FMNH 342533), *Scolopax minor* (FMNH 438027), *Numenius phaeopus* (FMNH 385840), *Actophilornis africanus* (FMNH 368823), *Rostratula benghalensis* (FMNH 393178), *Charadrius vociferous* (FMNH 390434), *Charadrius tricollaris* (FMNH 368843), *Oreopholus ruficollis* (FMNH 104122), *Pluvialis dominica* (FMNH 105252), *Haematopus ostralegus* (FMNH 363899), *Recurvirostra avosetta* (FMNH 338433), *Himantopus mexicanus* (FMNH 342523), *Burhinus oedicnemus* (FMNH 104449), and *Burhinus bistriatus* (FMNH 289831).

CHAPTER 2

THE EFFECTS OF FORAGING ECOLOGY AND ALLOMETRY ON AVIAN SKULL SHAPE VARY ACROSS LEVELS OF PHYLOGENY

The chapter is also available in:

Rossy Natale and Graham J. Slater (2022). The effects of foraging ecology and allometry on avian skull shape vary across levels of phylogeny. *The American Naturalist*, 200(4):E174–E188.

Minor edits have been made to include updated references and for consistency with the rest of this dissertation.

2.1 Abstract

Avian skull shape diversity is classically thought to result from selection for structures that are well-adapted for distinct ecological functions, but recent work has suggested that allometry is the dominant contributor to avian morphological diversity. If true this hypothesis would overturn much conventional wisdom regarding the importance of form-function relationships in adaptive radiations, but it is possible that these results are biased by the low taxonomic levels of the clades that have been studied. Using 3D morphometric data from the skulls of a relatively old and ecologically diverse order of birds, the Charadriiformes (shorebirds and relatives), we found that foraging ecology explains more than two-thirds of the variation in skull shape across the clade. However, we also found support for the hypothesis that skull allometry evolves, contributing more to shape variation at the level of the family than the order. Allometry may provide an important source of shape variation on which selection can act over short time scales, but its potential to evolve complicates generalizations between clades. Foraging ecology remains a better predictor of avian skull

shape over macroevolutionary time scales.

2.2 Introduction

As discussed, no morphological feature is more commonly associated with the central biological concept that natural selection drives adaptive diversification than the avian skull. This strong relationship could suggest similar patterns to what has been seen in some of the most iconic examples of island adaptive radiation, such as the *Geospiza* finches of the Galápagos Islands (Darwin, 1845; Grant, 1981; Lack, 1947; Schluter and Grant, 1984), Hawaiian honeycreepers (Fringillidae; Freed et al. 1987; Lovette et al. 2002), and Malagasy vangas (Vangidae; Jønsson et al. 2012; Reddy et al. 2012) where adaptive evolution occurred along morphological axes associated with distinct foraging ecologies. Such evolution along diet or foraging mode-related axes of skull shape variation has also been shown to have facilitated adaptive diversification in clades such as waterfowl (Anseriformes; Guillemain et al. 2002; Olsen 2017), Kingfishers (Alcedinidae; Eliason et al. 2020), corvids (Corvidae; Kulemeyer et al. 2009), and warblers (*Phylloscopus*; Price 1991), as well as in guilds of unrelated but ecologically similar taxa, such as carnivorous raptors (Hertel, 1995). Analysis of rates of beak shape evolution across the entire extant avian radiation by Cooney et al. (2017) has revealed pulses of rapid shape change that may suggest expansion in ecomorphospace associated with dietary shifts, and Pigot et al. (2020) have shown that it is possible to predict the foraging guild of extant birds from a few beak measurements. Intra-specific variation in beak morphology has also been associated with spatial variation in diet and foraging ecology (Peterson, 1993) and even with distinct patterns of resource use within populations of the same species (Smith, 1987). This connection has, therefore, been found repeatedly in many disparate avian clades.

Recently, a number of studies have presented results that cast substantial doubt on the strength of the form-function relationship between the avian skull and foraging ecology. Miller et al. (2017) noted that morphology and foraging guild exhibit an "imperfect" relationship in Australian honeyeaters (Meliphagidae), with many morphologically similar species foraging in divergent ways. In an analysis of 2D morphometric data from a broad taxonomic sample of extant birds, diet explained only 12% of beak shape variation and birds with different feeding ecologies shared similar morphologies, leading the authors to suggest that selection for broad performance outcomes (e.g., mechanical advantage) combined with limited axes of potential shape variation, might impose constraints on beak diversification (Navalón et al., 2019). Other authors have more specifically implicated allometry as the critical source of avian morphological diversity. Using 3D geometric morphometrics of the entire skull, Bright et al. (2016) found that body size and covariance between the beak and braincase explained nearly 80% of skull shape variation for a polyphyletic assemblage of birds of prey, while birds with distinct diets could not be discriminated from one another on the basis of skull shape. Similar findings have been recovered for Psittaciformes (parrots and relatives: Bright et al., 2019), and evolutionary allometry has even been found to explain a significant proportion of skull shape variation in the two iconic examples of adaptive, diet-driven evolution: Hawaiian honeycreepers and the finches of the Galápagos (Navalón et al., 2020; Tokita et al., 2017). Furthermore, an analysis of 3D landmark data from bird skulls spanning the entire class Aves found that, although relative rates of evolution in some skull components vary between dietary groups, a weak relationship between overall shape and diet is seen in avian skulls (Felice et al., 2019). Allometry-related changes in skull shape have been associated with specific patterns of resource use that have facilitated macroevolutionary radiations in some mammalian clades (Machado, 2020; Marroig and Cheverud, 2005), and may represent a relatively common mode of evolution if size represents the direction of maximum intra-specific genetic and phenotypic variance along which evolution can occur (Schluter, 1996). Collectively, this work has called into question the strength of the relationship both foraging ecology and body size have to avian skull shape.

These highly variable results may be driven by the use of analytical frameworks that assume common allometric trends across clades in which allometry itself may have evolved. Body size and associated allometric shape variation can act as a line of least evolutionary resistance (Marroig and Cheverud, 2005) in young radiations, and might facilitate resource partitioning and optimization of foraging efficiency in ecologically similar assemblages of taxa (Dayan and Simberloff, 1994; Hutchinson, 1959; Kiltie, 1984, 1988; Sherry and McDade, 1982; Werdelin, 1996; Wheelwright, 1985). However, given that genetic co-variances decay rapidly over macroevolutionary timescales (Schluter, 1996), extrapolating results between clades at different taxonomic levels may be flawed. Furthermore, allometric parameters themselves can evolve, generating distinct scaling relationships between shape and size within and between clades (Acero Murcia et al., 2023; Pélabon et al., 2014; Uyeda et al., 2017; Voje et al., 2014). As a result, the processes responsible for generating morphological variation at both the same and different hierarchical levels across a phylogeny are not necessarily the same (Erwin, 2000; Jablonski, 2007; Slater and Friscia, 2019), and the assumption of a common allometric scaling of shape with size in avian clades should be tested against models allowing for variable allometric scaling among clades.

Charadriiformes are an ideal clade within which to evaluate the relative contributions of foraging ecology and evolutionary allometry to skull shape variation due to their exceptional ecological and morphological diversity as well as variation in body size. Among the $\approx$ 390 species, body size ranges from the $\approx$20 gram least sandpiper *Calidris minutilla* to the $\approx$1850 gram great black-backed gull *Larus marinus* (del Hoyo et al., 1996). Previous work has highlighted relationships between foraging ecology and skull shape in taxonomic subsets of the Charadriiform order (Barbosa and Moreno, 1999; Korzun et al., 2009; Sharker et al., 2019; Zusi, 1962; Zweers and Gerritsen, 1996), suggesting that foraging ecology may be the dominant factor determining skull shape. Research on 17 species of Charadriiformes (excluding gulls, terns, and relatives; suborder Lari) found that longer beaks were associated with tactile foraging modes and shorter beaks were associated with visual foraging modes (Barbosa and Moreno, 1999). A detailed, biomechanical study of seedsnipes (Thinocoridae) showed evidence of musculoskeletal adaptations for efficient tearing of vegetation (Korzun et al., 2009), while the skull morphology of skimmers (*Rynchops spp.*) has been proposed to be well-adapted to reduce drag as these birds fly over the water with their lower jaw submerged (Martin and Bhushan, 2016; Withers and Timko, 1977; Zusi, 1962). Other lines of evidence suggest that size might also play an important role in charadriiform foraging ecology and skull shape evolution, although this has yet to be tested explicitly across the order. For example, studies in both terns (Sterninae; Hulsman 1981) and auks (Alcidae; Swennen and Duiven 1977) have demonstrated that gape width is correlated with maximum and preferred prey size.

In this Chapter, we used a phylogenetic comparative framework and 3D geometric morphometric data from 262 species (approximately 70% of recognized species) of Charadriiformes to address three critical questions regarding the relationship between foraging ecology, allometry, and avian skull shape evolution. First, we assessed the relative explanatory power of foraging ecology, body size, and their interaction, for charadriiform skull shape. Second, we explicitly evaluated if a model of common or evolving allometry is supported across the charadriiform order. Finally, we asked if allometric relationships and the relative importance of foraging ecology varied in strength and direction between charadriiform families. Our results highlight how the assumption of common allometry in previous work may have generated variable conclusions about the main factors explaining avian skull shape variation.

2.3 Methods

2.3.1 Morphological and Body Size Data

The morphological data described in this subsection is used in both this chapter as well as Chapter 3 *Interpreting Charadriiform Skull Shape Differences as they Relate to Foraging Ecology and Modular Evolution.*

Three-dimensional surface scans were obtained from non-juvenile museum specimen skulls of 262 species of Charadriiformes (see supplementary file table 1 for specimen information as well as specific scanner settings for each specimen). For 206 species, two individuals were scanned while the remaining 66 were represented by a single specimen. Scans were obtained with either a Comet L3D blue light scanner (Carl Zeiss, Germany) or a Capture Mini desktop structured light scanner (3D Systems, North Carolina). Each surface scan was processed using the software Geomagic DesignX (3D Systems, North Carolina) to remove small holes and scanning artifacts. Models were subsequently decimated to 300,000 triangles and exported as Standard Tessellation Language (STL) files, which are available on the Morphosource data repository (Morphosource project ID: 00000C909). A total of 255 landmarks (42 Type I, normal landmarks placed at discrete points and 213 Type II, semi-landmarks placed along curves; fig 2.1 and see supplementary file table 2 for written descriptions) were digitized on each skull using Stratovan Checkpoint (Stratovan Corporation 2018). We based our landmark configuration on a synthesis of the configurations in Olsen and Westneat (2016) and Olsen (2017), as well as the documentation for the R package `linkr` (Olsen, 2016). Dense sampling along the beak was used to prevent the Pinocchio effect (Walker, 2000; Zelditch et al., 2004), where one distant landmark (e.g. tip of the beak) dominates any signal when analyzing the entire landmark configuration. The landmark set used here aimed to capture differences in overall skull shape as well as features of biomechanical or ecological interest (e.g. points on the quadrate and orbits, respectively).

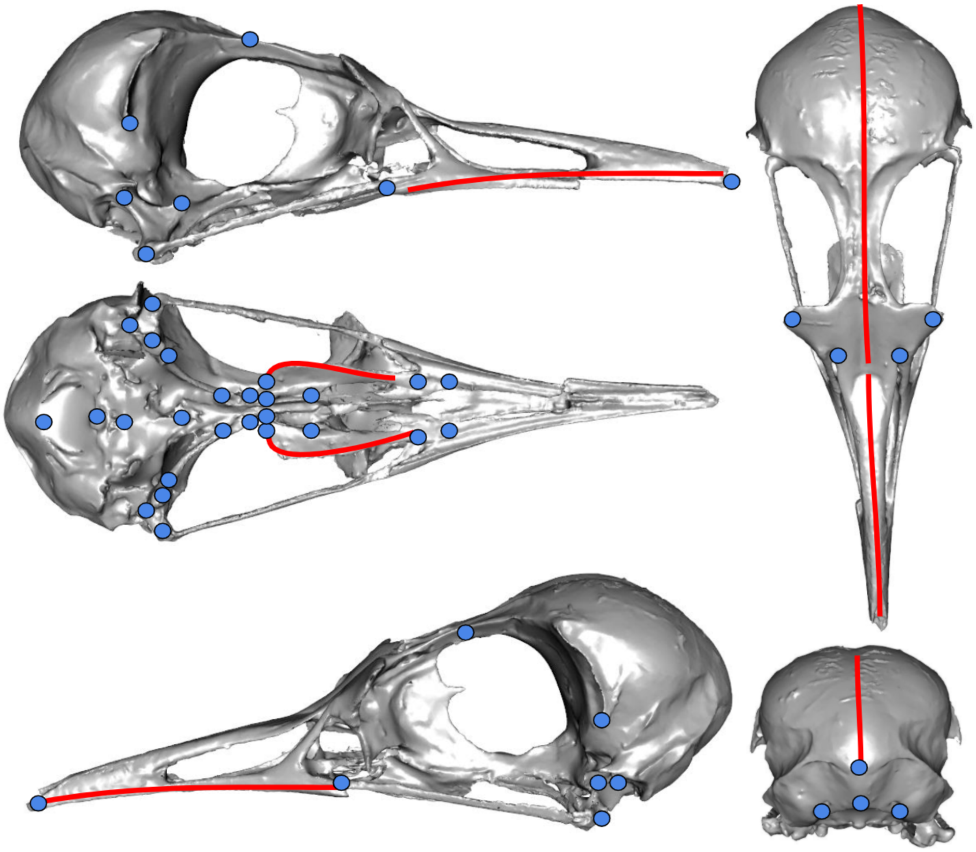

Figure 2.1: The landmark scheme on a surface scan of a Least Tern *Sterna antillarum* (FMNH 376281) skull. Blue dots indicate Type I landmarks, red lines indicate placement of Type II (sliding semi-landmarks). Written description of landmarks are available in supplementary file table 2

All subsequent analyses (unless otherwise noted) in this chapter were run in R (RStudio Team, 2019). 157 specimens had missing landmarks where the skull was either damaged or the scanner did not capture the bone due to shadow, reflectance, variation in coloration, or due to the delicate nature of some components (e.g. the jugals) of the avian skull. These missing landmarks were estimated in one of two ways (details on which landmark sets were completed in which manner are given in supplementary file table 1). For 118 specimens, landmarks from one side of the skull were mirrored across the plane created by the top of the beak, using the `paleomorph` (Lucas and Goswami, 2017) package's mirrorfill function. For 68 other instances where mirroring was not possible, the fixLMtps function in the `Morpho` package (Schlager et al., 2020) was used. This function works by comparing complete landmark sets to those with missing points and uses thin-plate spline interpolation to impute the missing landmarks. To help minimize estimation errors, the function upweights specimens that are closer to the deficient specimen in morphospace. For this study, deficient landmark sets were completed by comparing specimens from the same genus to minimize both potential deviations from the actual shape and the computational intensity of this estimation process.

Once complete landmark sets were obtained for all specimens, Type II semi-landmarks were slid along the curves using the slider3d function in the package `Morpho` (Schlager et al., 2020). Species-average configurations were obtained for species represented by two specimens by first performing a Procrustes superimposition using the procSym function in the `Morpho` package (Schlager et al., 2020) to remove the effects of orientation, size, and translation and then taking the average of each landmark coordinate using the mshape function in the package `geomorph` (Adams et al., 2022; Baken et al., 2021). Once averaged landmark configurations were obtained, the sliding procedure described above was repeated using the same slider3d function on these species-level landmark configurations. The final product of these steps was a set of 255 3D, aligned coordinate points for 262 charadriiform species representing all major families (fig 2.2). I also created two additional data subsets (see supplementary file table 2 for details): one for the braincase and one for the beak and its biomechanically-associated structures (i.e. quadrates, pterygoids, palatines) to analyse these structures in isolation.

To assess how shape relates to body size, an average body mass in grams was obtained for each species from the *Handbook of the Birds of the World* (Billerman et al. 2020; del Hoyo et al. 1996). When a range was given, the midpoint was taken. As body mass is a volumetric measurement, we transformed these values by taking the log of the cube root. We chose to use body mass as opposed to centroid size in subsequent analyses as comparisons of body

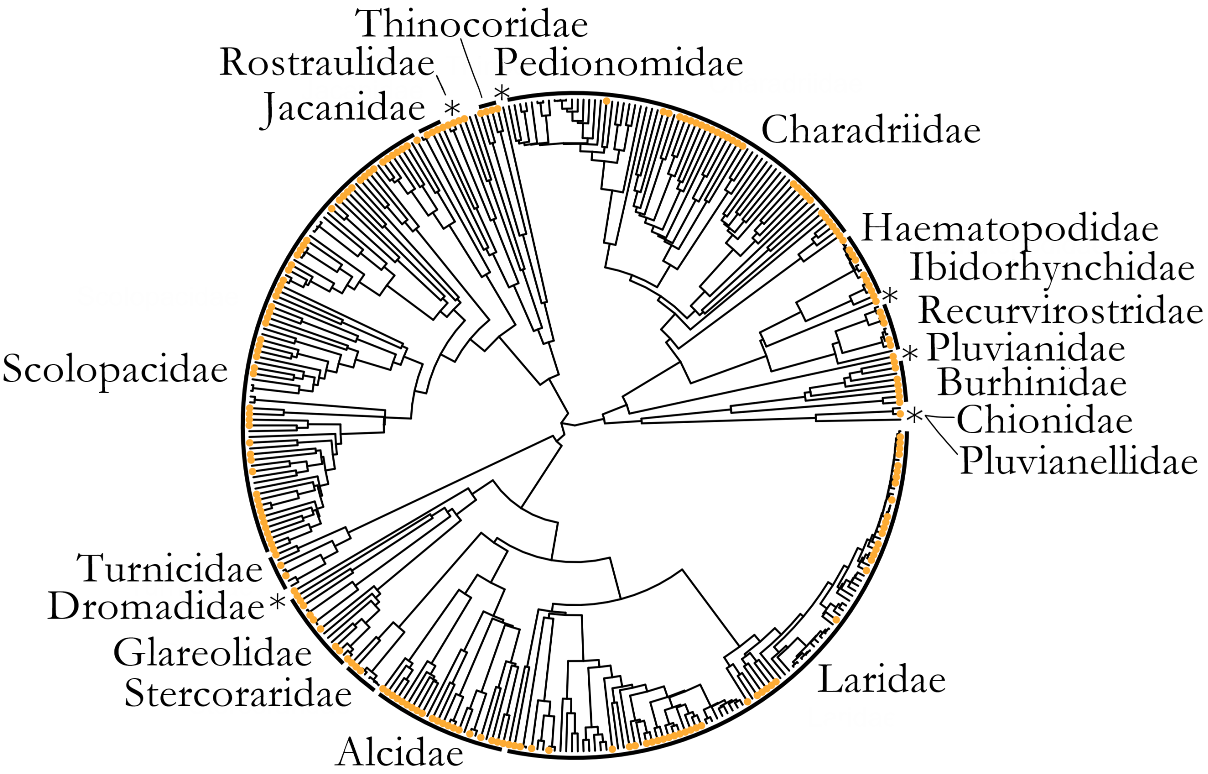

Figure 2.2: Phylogenetic coverage of the species from which 3D data describing skull morphology was obtained. Colored dots at the tips of the tree indicate the species is represented in these analyses and that either one or two specimens were 3D scanned to have 3D geometric morphometric data collected from. The majority of charadriiform families are labeled with black bars and text, while several smaller or monotypic families are labeled with stars.

mass with centroid size calculated from both the whole skull and from a subset of landmarks that excluded points along the beak (a method that has been used to limit potential bias in centroid size estimation from elongated shapes; Kulemeyer et al. 2009) revealed subsets of taxa that follow different scaling patterns (more details available in the supplementary file under the heading *Additional Information on Body Mass and Centroid Size*, including supplementary figures 1, 2 and 3.).

2.3.2 Phylogeny

This tree described here was also used in Chapter 3 *Interpreting Charadriiform Skull Shape Differences as they Relate to Foraging Ecology and Modular Evolution* and Chapter 4 *Charadriiform Spatial Biodiversity across Space and Time in Light of Migration Patterns and Protected Area Coverage.*

The phylogenetic tree used in all analyses here is taken from Černý and Natale (2022). This tree was inferred under a maximum likelihood framework using the program `RaXML` (Stamatakis, 2014) from a supermatrix of 9 nuclear genes, 13 mitochondrial protein-coding genes, 2 mitochondrial ribosomal genes (all downloaded from GenBank; Benson et al. 2013), and 69 morphological characters taken from Chu (1995), representing a total of 336 species. The resulting topology was time-scaled under a relaxed, uncorrelated molecular clock using 18 fossil calibrations in the program `mcmctree` (Yang, 2007). Taxa not present in the morphological dataset used here were pruned from the tree using the drop.tip function in the R package `ape` (Paradis et al., 2020).

2.3.3 Coding of Foraging Guild

The foraging ecology data described in this section is also used in both this chapter as well as in Chapter 3 *Interpreting Charadriiform Skull Shape Differences as they Relate to Foraging Ecology and Modular Evolution.*

Data on species ecology was accumulated to quantify each species foraging niche. We compiled descriptive ecological data for each sampled species from *Handbook of the Birds of the World* (Billerman et al., 2020; del Hoyo et al., 1996). Additional information was recorded from a variety of sources including online videos, scholarly literature, and other online databases (details on additional sources available in supplementary file table 1). As most Charadriiformes are migratory, we recorded information related to foraging for the breeding and non-breeding season separately. We then used the accumulated descriptive data to place each species into a foraging substrate and a foraging technique category adapted from the scheme in DeGraaf et al. (1985). We established fourteen substrate categories (marsh, shoreline, semi-aquatic generalist, water surface, shallow water, lower canopy, pelagic, rocky shore, wet and dry grassland, meadow, arid ground, generalist, ground and air, air, water) and fourteen technique categories (facultative prober, facultative ground forager, ground forager, grazer, pursuit diver, dipper, plunge diver, facultative scyther, facultative terrestrial forager, aquatic scavenger, facultative diver, skimmer, hawker, predator). Written definitions of each category are available in the supplementary file under the heading *Foraging Guild Classification Categories*. A foraging guild was then assigned to each species for both breeding and non-breeding seasons by combining substrate and technique for that season (e.g., pelagic + pursuit diver). Of the 91 possible unique combinations, many were implausible (e.g. arid ground + plunge diver) leaving only 36 occupied foraging guild categories. Each species was therefore assigned to two different categories: one for the breeding season and one for the non-breeding season. Here, we only report results for the non-breeding season and provide the results from the breeding season in the supplementary file under the heading *Chapter 2 Results Using Breeding-Season Specific Foraging Data*.

2.3.4 How Well do Body Mass and Foraging Ecology Predict Charadriiform Skull Shape?

We used Procrustes ANOVAs to assess the proportion of skull shape variation attributable to foraging guild, while still considering variation due to allometry (Table 2.1, row 1). Significance was assessed via residual randomization in a permutation procedure (RRPP) as implemented in the procD.lm function of the `geomorph` package (Adams et al., 2022; Baken et al., 2021). The sum of squares argument was set to type II for each Procrustes ANOVA to ensure we evaluated the effect of each variable despite the impacts of the others (Adams and Collyer, 2018). The pgls implementation of Procrustes ANOVA assumes that residual error in the model is perfectly explained by the phylogenetic covariances among species (Adams and Collyer, 2018). Revell (2010) has shown that this assumption can lead to increased variance in parameter estimates, reduced power, and, in some cases, elevated type I error rates. Instead, we performed a series of analyses as part of each ANOVA to estimate the amount of phylogenetic signal in the residual error of our model and thus appropriately account for it (M. Zelditch, pers. comm., Navalón et al., 2019). We first fitted a non-phylogenetic Procrustes ANOVA using the procD.lm function and extracted the matrix of residuals from this model. We then estimated phylogenetic signal in the residual error term by fitting a multivariate Pagel's lambda (λ) model to the residuals using the transformPhylo.ML function from the `motmot` package (Puttick et al., 2019). The maximum likelihood estimate of λ was then used to transform the phylogenetic covariance matrix derived from our charadriiform phylogeny, which was, in turn, used to define the correlation structure in a second Procrustes ANOVA using the original data and model notation in the procD.lm function.

Table 2.1: Summary of the Procrustes ANOVA models run at various phylogenetic levels and on various sets of the morphological data to address three different research questions. Full details of the pipeline used to conduct these is available in the *Methods* portion of Chapter 2. 'Mass' refers to the transformed body mass variable and 'Whole skull, beak, braincase' indicates that the analyses were repeated on these three different sets of morphological data. Each analysis listed in this table that required foraging guild data was repeated twice, once using the foraging guild for the breeding season and once using the foraging guild for the non-breeding season.

Phylogenetic Level	Morphometric Data	ANOVA Syntax	Question addressed
Order	Whole skull, beak, braincase	Shape∼foraging guild*Mass	How well do body mass, foraging guild, and their interaction predict charadriiform skull shape?
Order	Whole skull	Shape∼Mass+Family Shape∼Mass*Family	Has allometry evolved in Charadriiformes?
Families	Whole skull	Shape∼foraging guild*Mass	Is allometry of variable importance in charadriiform families?

In each ANOVA, we assessed how much of the variation in skull shape could be attributed to foraging ecology, body mass, and the interaction between the two. We repeated the ANOVAs using foraging guild classifications for both the breeding and non-breeding seasons; results were similar for both (see the supplementary file for breeding season results under the heading *Chapter 2 Results Using Breeding-Season Specific Foraging Data*) and so for the rest of this chapter we focus on guild classifications for the non- breeding range and make note of one instance when results differed substantially. To understand whether any relationships between shape, size, and ecology are driven by different parts of the avian skull, we repeated Procrustes ANOVA on subsets of the aligned landmarks corresponding to the beak and braincase separately.

2.3.5 Has Allometry Evolved in Charadriiformes?

It is possible that the strong support for allometry-driven skull shape variation, relative to ecology-driven shape variation, in some avian clades is an artifact of the phylogenetic level studied. Evaluating whether allometric parameters have evolved in geometric morphometric data is challenging, but significantly different slopes between clades in regressions of shape on size may be taken as evidence for shifts in size-shape scaling over macroevolutionary time-scales. To assess this possibility, we fit a set of Procrustes ANOVAs (Table 2.1, row 2) with body mass and family as predictors. We fit two forms of this model; one in which the two predictors were treated as additive effects and one in which an interaction between the two (indicative of evolution of allometry) was included. Model selection was performed using the anova function in R to assess if including the interaction term significantly reduced the residual error in the model. We tested for significant differences in the orientation of allometric slopes between families based on vector correlations using the pairwise function in the `RRPP` package (Collyer and Adams, 2018, 2019). The arccosine of the vector correlation between unit-normed vectors gives the angle between them, which can be evaluated against the null model based on the RRPP fit.

Is Allometry of Variable Importance in Charadriiform Families?

To further evaluate how allometric trends vary across different taxonomic levels, Procrustes ANOVAs assessing how much of the variation in skull shape could be attributed to foraging guild, body mass, and the interaction between the two (Table 2.1, row 3) were also run on families that contain over 20 species as defined by Boyd (2019). This included four families: the Alcidae (auks and relatives), Charadriidae (plovers, lapwings, and relatives), Scolopacidae (sandpipers and relatives), and Laridae (gulls, terns, and relatives). To visualize how shape changes with size, both in Charadriiformes as a whole and in each of these families, the plotRefToTarget and shape.predictor functions from the `geomorph` package (Adams et al., 2022; Baken et al., 2021) were used to warp the mean landmark configuration of the clade to the predicted shape at high and low body masses for that clade.

2.4 Results

2.4.1 How Well do Body Mass and Foraging Ecology Predict Charadriiform Skull Shape?

We found that body mass, foraging guild, and the interaction between body mass and foraging guild were all significant predictors ($p < 0.05$) of whole skull, beak, and braincase shape (Table 2.2). Foraging guild explained ∼71% of whole skull shape variation, body mass explained ∼2%, and the interaction between them explained ∼7%. The strong relationship between whole skull shape and foraging ecology appears to be driven predominantly by the beak, given that foraging guild explained ∼73% of beak shape variation but only ∼44% of the variation in braincase shape. A larger amount of shape variation could be explained by both body mass (∼7%), and the interaction term (∼11%) for the braincase relative to the beak (where body mass explained ∼0.5% and the interaction ∼7%). Effect sizes (Z) for foraging guild were uniformly high ($Z > 10$) in the whole skull, beak, and braincase analysis

Table 2.2: Results of Procrustes ANOVAs. This series of ANOVAs assess the impact of body mass, foraging ecology, and the interaction between the two on whole skull, beak, and braincase shape across the charadriiform order.

Morphological structure	Percent variation explained by foraging guild	Percent variation explained by body mass	Percent variation explained by interaction
Whole skull	R^2 = 0.70583, F $_{31,187}$ = 23.4181, Z = 16.2542, P = 0.001	R^2= 0.01584, $F_{1,187}$ = 17.3472, Z = 3.4643, P =0.001	R^2 = 0.06986, $F_{31,187}$ =2.3177, Z = 5.5991, P = 0.001
Beak/Associated Structures	R^2 = 0.73219, F $_{31,187}$ = 24.3698, Z = 16.8077, P = 0.001	R^2 = 0.00574, $F_{1,187}$ = 6.3021, Z = 2.7261, P = 0.002	R^2 = 0.06816, $F_{31,187}$ = 2.2686, Z = 5.4276, P = 0.001
Braincase	R^2 = 0.43543, F $_{31,187}$ = 7.9998, Z = 11.8971, P = 0.001	R^2 = 0.06694, $F_{1,187}$ = 40.5862, Z = 4.6251, P = 0.001	R^2 = 0.10773 $F_{31,187}$ = 1.9793, Z = 4.3505, P = 0.001

2.4.2 Has Allometry Evolved in Charadriiformes?

A model including an interaction term between family and body mass is strongly preferred over an additive model ($F_{12,257}$ = 4.0105, Z = 5.96, P<0.001), indicating that there are variable allometric relationships among families and that a common allometric model is not appropriate for charadriiform skull evolution. Family explained ∼ 66% of skull shape variation in this interaction model (R^2 = 0.6591,$F_{12,232}$ = 53.8425, Z = 12.5951, P = 0.001). Body mass explained ∼ 2% (R^2 = 0.02457, F $_{1,232}$ = 24.0877, Z = 3.9253, P = 0.001), while the interaction term explained ∼5% of skull shape variation (R^2 = 0.04909, $F_{12,232}$ = 3.9901, Z = 5.9498, P = 0.001).

Pairwise vector correlations revealed significant differences in allometric slopes between several families (fig 2.3 and table 2.3). These tend to be restricted to comparisons in which one or both of the families is relatively species-rich (n >20; e.g., Laridae, Scolopacidae, Alcidae, Charadriidae), although significant differences were recovered for comparisons involving some smaller families (e.g., Glareolidae, Thinocoridae, Haematopodidae).

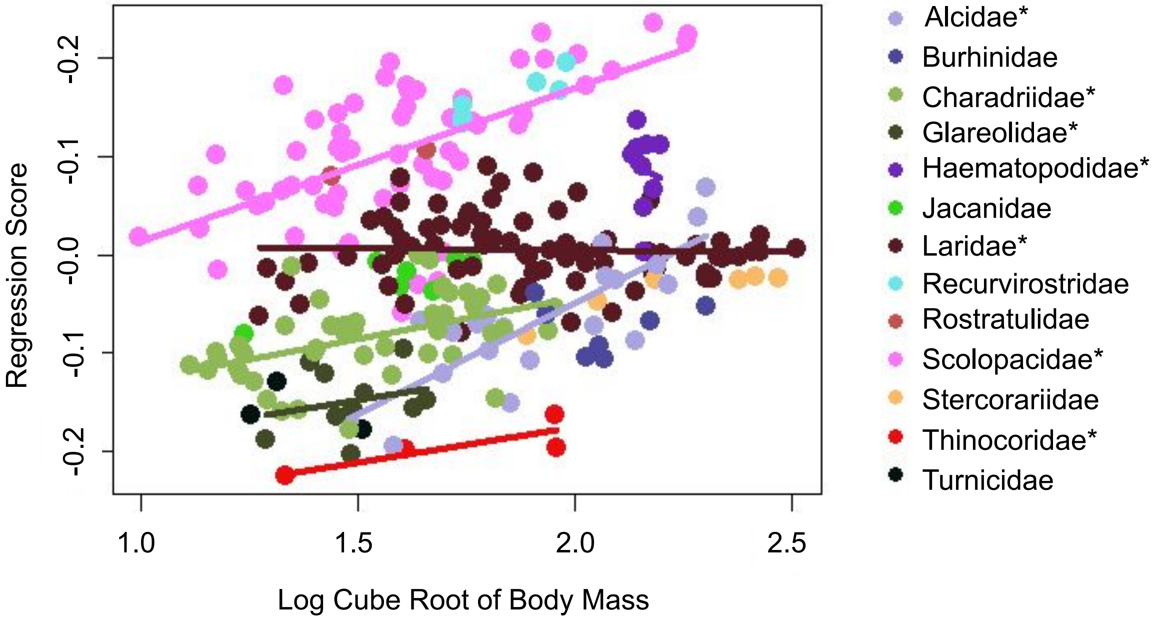

Figure 2.3: Variable allometric relationships among different charadriiform families. Each of the thirteen non-monotypic families from the charadriiform order is encoded by a different color. The regression scores summarize how skull shape changes with body mass. Slopes are shown with a solid line for families, denoted with an asterisk, where significant differences in allometric slopes were recovered between that family and at least one other (see table 2.3.)

Is Allometry of Variable Importance in Charadriiform Families?

We performed family-level Procrustes ANOVAs on four charadriiform families with over 20 species to assess how much skull shape variation could be explained by body mass, foraging guild, and the interaction between the two (fig 2.4). The explanatory power of foraging ecology was substantially lower relative to the ordinal-level analysis in three of the families: ∼23% in the Laridae, ∼ 19% in the Charadriidae, and ∼ 32% in the Scolopacidae. We excluded foraging ecology as a predictor in the Alcidae after it was found that all species shared one foraging guild.

Across these four families, the amount of skull shape variation attributable to body mass

Table 2.3: Pairwise comparisons of allometric slopes between clades. These pairwise comparisons are in the form of vector correlations (r) for allometric slopes between clades that are significantly different at $P<0.1$. 'Angle' refers to the angle between allometric slopes expressed in radians, 95% UCI is the upper confidence limit for the difference between slopes based on randomized residuals in a permutation procedure, Z is the effect size, and P is the probability that the observed angle came from the same distribution as the full randomized sample.

Comparison	r	Angle	95% UCI	Z	P
Alcidae:Laridae	-0.0390	1.610	1.170	2.383	0.006
Charadriidae:Laridae	0.008	1.562	0.879	2.833	0.002
Charadriidae:Scolopacidae	0.674	0.831	0.964	1.333	0.089
Glareolidae:Laridae	-0.426	2.011	1.951	1.700	0.037
Haematopodidae:Scolopacidae	-0.620	2.240	2.225	1.613	0.044
Jacanidae:Laridae	-0.066	1.637	1.823	1.408	0.095
Laridae:Scolopacidae	-0.246	1.820	0.672	3.845	0.001
Laridae:Thinocoridae	-0.071	1.642	1.704	1.579	0.067

was variable, but was consistently higher than the <2% of skull shape variation that could be attributed to body mass at the ordinal level (fig 2.4). The proportion of shape variation attributable to body mass ranged from ∼8% in the Laridae to ∼24% in the Alcidae. We found no consistent trends in how shape changes with size (fig 2.4). For Scolopacidae and Charadriidae, larger species have longer, narrower skulls and smaller species tend to have shorter, wider skulls, although elongation is less extreme in the Charadriidae. In the Laridae and Alcidae, larger species tended to have beaks that curved downwards but varied in how the length of the skull changed with body size. Results using the breeding-season specific foraging data (available in the supplementary file under the heading *Chapter 2 Results Using Breeding-Season Specific Foraging Data*) were broadly consistent with those presented here, but in our analysis of the Charadridae, breeding-season-specific foraging guild did not significantly relate to skull shape.

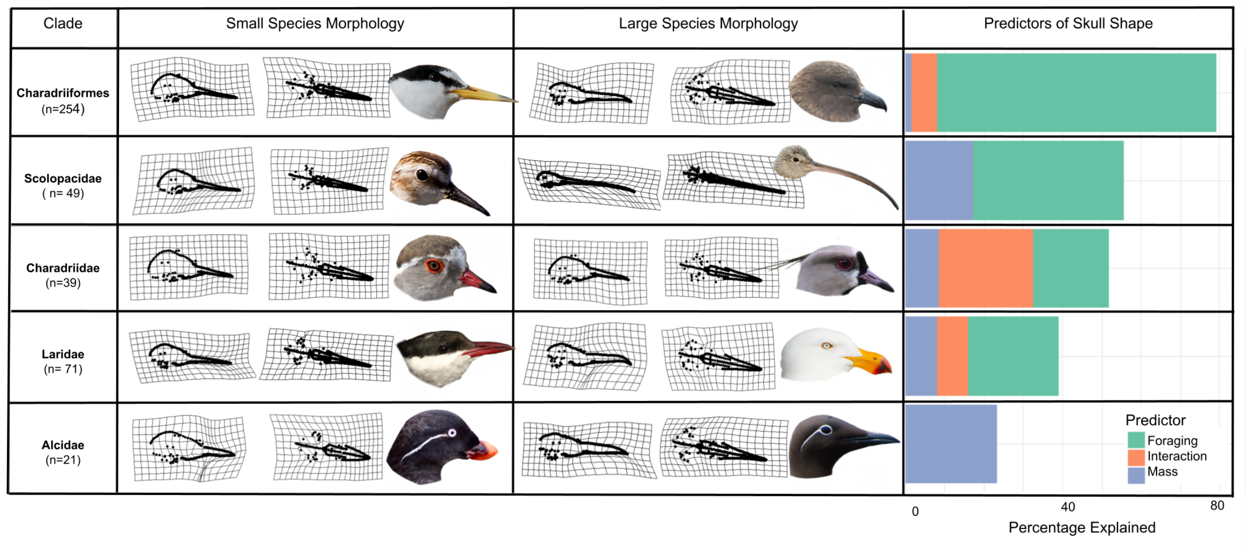

Figure 2.4: Variable relationships between skull shape, foraging ecology, and body mass in several charadriiform clades. All results are based on phylogenetically corrected Procrustes ANOVAs. The n given denotes the number used in our final analysis after species occupying their own unique foraging guild were removed. These results are shown for the charadriiform order as a whole as well as four families with sufficient sample sizes: the Scolopacidae (sandpipers and relatives), Charadriidae (plovers and relatives), Laridae (gulls, terns, and relatives) and Alcidae (auks). The thin-plate splines illustrate the morphology 1.5 standard deviations above and below the mean body size, warped relative to the mean. The bar chart on the right shows the amount of skull shape variation attributable to foraging guild, body mass, and the interaction between these two factors in each clade.The images are representative examples of small and large species from that clade. From left to right, row by row: Little tern (*Sternula albifrons* by Agustín Povedano), Brown skua (*Catharacta antarctica* by Zakhar V. Akulov), Least Sandpiper (*Calidris minutilla* by Fernando Flores), Far Eastern Curlew (*Numenius madagascariensis* by John Harrison), Three-banded plover (*Charadrius tricollaris* by Charles J. Sharp), Southern lapwing (*Vanellus chilensis* by Mdf), Whiskered Tern (*Chlidonias hybrida* by Derek Keats), Pacific Gull (*Larus pacificus* by JJ Harrison), Parakeet Auklet (*Aethia psittacula* by Dave Govoni), Common Murre (*Uria aalge* by thelastweasel). Full image licensing is available in the supplementary file in both supplementary figure 5 and table 5

2.5 Discussion

Recently, support has emerged among comparative biologists for the idea that foraging ecology explains a relatively small proportion of avian skull shape variation (Felice et al., 2019) and that a significant amount of skull shape variation is, instead, attributable to variation in body size (Bright et al., 2016, 2019; Navalón et al., 2019; Tokita et al., 2017; Young et al., 2017). If true, this hypothesis would overturn much conventional wisdom regarding the importance of form-function relationships in adaptive radiations (Lack, 1947; Schluter and Grant, 1984). Using three-dimensional landmark data from the skulls of 262 species from the ecologically diverse order Charadriiformes, we evaluated this hypothesis and recovered evidence that allometric trajectories have evolved over charadriiform evolution. While the relative importance of allometry increases in younger clades, the specific relationship between skull shape, foraging ecology, and body mass is highly clade specific. These results both point to fruitful directions for future research and help explain why past research on the predictors of avian skull shape variation has appeared so contradictory.

The Influence of Foraging Ecology on Skull Shape

The substantial relationship between foraging ecology and skull shape found here for Charadriiformes contrasts strongly with results for other clades. Charadriiformes is an ecologically disparate clade, with diets ranging from herbivory (Korzun et al., 2009) to predation on other birds (de Almeida Reis et al., 2021). It is possible that this ecomorphological diversity, which is greater than many other avian clades that have been comprehensively examined to date, is necessary to recover significant relationships between skull shape and foraging ecology. It is also worth noting that in clades such as parrots (Psittaciformes; Bright et al. 2019) and guilds such as birds of prey (Bright et al., 2016; Guangdi et al., 2015; Sun et al., 2018), where weak or nonexistent relationships between foraging or dietary ecology and skull morphology have been found, both the beak and feet are used to acquire and manipulate food items (Brown and Magat, 2011; Felice et al., 2019; Tsang et al., 2019), while Charadriiforms tend to rely solely on the beak to obtain food items. These results hint that ecomorphological diversity in the skull may be reduced when feeding involves multiple, independent musculo-skeletal systems.

Some studies conducted at higher levels of phylogeny and encompassing a broader range of ecological variation than that found in parrots or birds of prey have also recovered weak relationships between foraging ecology and skull shape (Felice et al., 2019; Navalón et al., 2019). These findings suggest that clade choice is not the only explanation for the differences between our results and those of previous work. We suspect that the intensity of sampling within and between clades may also exert a substantial influence on results. Felice et al. (2019) found a significant but weak relationship between diet and skull shape variation based on a sample of 352 extant species, a 35% increase in size on our dataset. However, their sample spanned the entirety of the class Aves, with the result that individual orders and families were only sparsely represented. In finding that diet explained only 12% of variation in beak shape across a sample of 175 species spanning 94 families of birds, Navalón et al. (2019) suggested that one-to-many mapping of morphology to ecology may cloud form-function relationships at higher phylogenetic levels (see also Friedman et al., 2019). Alternatively, these results may suggest that broad but sparse sampling fails to capture sufficient instances of convergence on similar morphological solutions in response to similar foraging ecologies. Indeed, Pigot et al. (2020) found that foraging ecology could be reliably predicted from 9 trait measurements, many taken from the beak, in a sample that comprised ∼99% of extant bird species. Notably, Pigot et al. (2020) also found that beak morphology is predictive of both diet (the food types consumed) and foraging mode (the way in which it is obtained). It is therefore possible that the low proportion of skull shape variation recovered in some higher level studies (e.g., Felice et al., 2019; Navalón et al., 2019) is also due to the use of relatively coarse dietary categorizations. Indeed, repeating our analyses after collapsing the 36 foraging guilds used into the 10 more coarse guilds used in Chapter 2 that cluster species that forage in generally similar ways (e.g., birds that dive) irrespective of specific foraging technique reduced the amount of skull shape variation that could be attributed to foraging ecology by ∼46% (See supplementary file for full results under the heading *The Use of Coarsely-Defined Foraging Guild Classifications*).

Approaching allometry as an evolving factor shaping avian skull evolution

Although allometry is known to evolve (Voje et al., 2014), most morphometric studies assume common scaling of shape with size across a clade. On the one hand, failure to account for these evolving relationships might contribute to the low amount of skull shape variation attributable to body size in analyses that have looked across broad taxonomic scales. On the other hand, this assumption has the potential to obscure the detection of unique allometric trajectories in sub-clades and, therefore, de-emphasize the importance of allometry as a source of ecomorphological variation on which selection can act over relatively short timescales. Support for a Procrustes ANOVA that included an interaction between family and size, significant differences between allometric trajectories for families in pairwise tests, and the distinct allometric trends seen in individual family-level analyses all support the idea that size-shape relationships for the avian skull have evolved over time. The variability seen in the size-shape relationships for charadriiform families, combined with the relatively low proportion of shape variation explained by size at the level of the order helps explain the discrepancy between studies that have found strong contributions of allometry to skull shape at lower taxonomic levels (Bright et al., 2016, 2019; Tokita et al., 2017) and those that have found relatively modest or insignificant contributions at higher levels (Felice et al., 2019). Our findings indicate that extrapolating results between different taxonomic levels is not advisable. More research is needed to understand at what scale these evolving size-shape relationships differ enough to impact the recovered patterns in taxonomically broad studies.

At the family level, we found substantial variation in the amount of skull shape variation attributable to body mass, foraging ecology, and the interaction between these two factors. Body size-related change may function as an evolutionary line of least resistance, particularly in young clades (Schluter, 1996), and can facilitate rapid ecological divergence, such as the rapid changes we often see in young, island radiations (Cooney et al., 2017), in spite of otherwise strong phenotypic covariance (Felice et al., 2018). Here, we found that allometry explained more of the variation in skull shape in individual charadriiform families than in the order as a whole, supporting the role of allometry as an important source of variation in younger, relatively ecologically conservative clades. It is notable that previous work on a relatively similar scale (Tokita et al., 2017) found that evolutionary allometry accounted for ∼11% and ∼28% of total shape variation in the skulls of Hawaiian honeycreepers and Galápagos finches respectively, suggesting that the age of the clade studied may indeed affect the strength of the allometric relationship recovered.

Our results additionally highlight how, even if allometry is of relatively greater importance at lower taxonomic levels, the importance of size-related shape variation may differ among clades of a similar age. Body size is known to serve a particularly important role in species sorting when prey type is relatively uniform but prey size serves as the primary axis of niche divergence or resource partitioning (Dayan and Simberloff, 1994; Hutchinson, 1959; Kiltie, 1984, 1988; Werdelin, 1996). We did not quantify relative prey size for charadriiform species here, but it is notable that one of the clades to exhibit a strong and substantial allometric component of variation, the Alcidae, consume a wide range of prey sizes (del Hoyo et al., 1996), often feed sympatrically (Linnebjerg et al., 2015), and exhibit a correlation between preferred prey size and gape width (Swennen and Duiven, 1977), leaving open the possibility that size-based resource partitioning may be an important driver of morphological evolution at lower taxonomic levels when foraging modes are relatively more conserved. Similarly, both body size and foraging ecology explained relatively large portions of skull shape variation in the Scolopacidae. Allometric variation in this family appears to relate to changes in specific foraging niche: most large scolopacid species possess elongated skulls that tend to be associated with probing behaviors, while most smaller species possess less elongated skulls that tend to be associated with pecking behaviors (Barbosa and Moreno, 1999). The distinct patterns recovered for Scolopacidae and Alcidae further emphasize that, while allometry may generally be an important source of shape variation in younger clades, extrapolating results across clades at the same taxonomic level may also generate conflicting results. Given the substantial differences between families in the same order recovered here, future work aiming to understand the magnitude of size-shape relationship differences across all birds is warranted.

2.6 Conclusions

Through the use of comprehensive taxonomic sampling, 3D landmark data from the entire skull, and the application of phylogenetically informed statistical analyses, we recovered two important conclusions regarding the roles of allometry and foraging ecology in explaining morphological diversity in the avian skull. First, our support for evolving allometric relationships in Charadriiformes highlights the need to use an analytical framework that accounts for these evolving relationships when studying allometry at a relatively broad taxonomic scale. Secondly, the relatively higher importance of allometry at the familial, relative to the ordinal level, coupled with the highly variable relationship between skull shape, foraging ecology, and body mass seen in these families, provides strong reasoning not to extrapolate results across different taxonomic scales and suggests that the importance of allometry and foraging ecology may be clade-specific. Collectively, our results suggest that foraging ecology is likely a critical predictor of avian skull shape at macroevolutionary scales, as has been classically thought, and that the recent shift toward an allometry-dominated perspective is likely the result of methodological choices and the taxonomic scale of study. Future work is needed to both better understand the relationship between allometry and foraging ecology at lower levels of avian phylogeny, and how allometry itself evolves at higher levels. The subsequent Chapter 3 will begin to address interpreting the relationship between foraging ecology and skull shape in Charadriiformes to build upon the work done in this chapter.

CHAPTER 3

INTERPRETING CHARADRIIFORM SKULL SHAPE DIFFERENCES AS THEY RELATE TO FORAGING ECOLOGY AND MODULAR EVOLUTION

Portions in this chapter under the subheading *Modular Evolution of the Charadriiform Skull* were conducted as part of a collaborative project with Xiaoni Xu.

3.1 Abstract

While connections have been demonstrated between avian skull morphology and foraging ecology, it is unclear if certain portions (e.g. the beak) of the anatomically complex avian skull may evolve semi-independently from others. Previous research has reached differing conclusions on the number of semi-independent units, or modules, that exist in avian skull evolution and on the strength of the covariation, or integration, between these hypothesized modules. Here, we applied comparative methods to 3D geometric morphometric data collected from the skulls of a diverse order of birds (the Charadriiformes) to interpret the relationship between foraging ecology and the morphology of the whole skull, the beak and it's biomechnically associated structures, and the braincase. Building upon this, we also tested support for 11 distinct hypotheses of modular skull evolution. Significant differences in not only whole skull morphology, but the morphology of the beak as well as the braincase, depending on foraging guild were recovered. These patterns appear to be the result of the semi-independent, but still correlated, evolution of the beak and associated structures from the braincase, as these hypothesis of modular evolution were found to be the most supported. However, our results varied when we analyzed subgroups within the order suggesting that, while differences in methodology may contribute to the conclusions of any particular research study, clade-specific dynamics may be the major reason past studies have reached varying

conclusions. These results suggest that, for Charadriiformes, the beak and braincase have evolved in a correlated manner, resulting in the beak being more strongly related to foraging ecology and the braincase relating to a lesser degree.

3.2 Introduction

While Natale and Slater (2022) established that foraging ecology is a strong predictor of charadriiform skull shape at the ordinal level, there is still a lack of understanding of how the breadth of morphological differences in the order directly relates to adaptations for specific ecologies. Exploring and interpreting shape differences in light of ecology can provide direct insights into the form-function relationship of structures from a biomechanical viewpoint (Navalón et al., 2019; Olsen, 2017) and, by providing more causal evidence for the relationship between shape and ecology, can be used as the basis for other macroevolutionary (e.g. analyzing differences in the tempo or evolution; McEntee et al. 2017) or spatial biodiversity analyses (e.g. Funk et al. 2017; Chapter 4). In complex morphological structures, certain subsets (e.g. the beak) of that structure may also be more or less related to ecological factors relative to other subsets. This may be due to a concept known as integration which, in the context of evolutionary morphology, describes the correlated evolution of traits within clades (Zelditch and Goswami, 2021). Differences in the degree of integration within and between different morphological features generates evolutionary modularity: the semi-independent evolution of sets of traits (Klingenberg 2008). Interpreting shape differences in light of ecology and modular evolution can, taken together, provide insights into both the specific form-function relationship of a clade and into broader macroevolutionary patterns that inform our understanding of the evolution of other diverse structures.

Ecological differentiation through differences in morphological structures is particularly interesting in Charadriiformes, which are not only ecologically diverse (e.g. diving species vs. wading species, see *Introduction*) but are also known to co-exit in areas where multiple species in the order co-occur, leading some species to diverge in aspects of diet (Bocher et al., 2014; Davis and Smith, 2001) and foraging behaviors (Baker and Baker, 1973; Davis and Smith, 2001; Isola et al., 2000). There has indeed been previous evidence demonstrating and interpreting the relationship between skull morphology in Charadriiformes and interspecific differences in foraging ecology based on both 2D (Barbosa and Moreno, 1999) and 3D (Lin, 2022) morphometric data. Increasing length of the beak (Barbosa and Moreno, 1999) or whole skull (Lin, 2022) have been noted to be the most prominent (Lin, 2022) or second most prominent (Barbosa and Moreno, 1999) axes of shape variation in principal components analyses on data describing skull morphology, a pattern that has been explicitly connected to variation in foraging ecology (correlating with differences in visual, tactile, sweeping, and routing foraging methods; Barbosa and Moreno 1999). In one study by Baker (1979), the length of the beak (as measured by the top ridge of the external beak; the culmen) related to differences in certain aspects of microhabitat use (vegetation height) in six co-occurring Charadriiform species, highlighting how these morphological differences may confer an adaptive advantage in letting species utilize a unique niche.

While much of the attention focuses on the ways in which divergent beak shapes relate to differences in a species' ecology, the results of the Procrustes ANOVAs in Chapter 2 that focused on the beak and braincase highlight a significant relationship between these structures and foraging ecology when they are analyzed in isolation. Additionally there have been noted adaptations in the remaining portions of the skull of Charadriiformes. Charadriiformes are unique in that species vary in whether visual (e.g. pecking) or tactile (e.g. probing) methods are used to detect food items and in that many charadriiform species foraging nocturnally (Mcneil et al., 1992). Because of these aspects, eye size of charadriiformes has been studied. Phylogenetic comparative analyses by Thomas et al. (2006) found increasing eye size in a set of ≈ 45 Scolopacii and Charadrii was associated with changes in the timing of foraging but not to changes to visual foraging methods, even after controlling for differences in body mass. That differences in eye size do not relate to visual feeding has also been suggested in geometric morphometric analyses by (Lin, 2022). Similar relationships between increased eye size and nocturnality have also been found in more taxonomically broad studies that included, but did not foucs on, Charadriiformes (Garamszegi et al., 2002). Further suggesting there are adaptations in other portions of these skull for distinct foraging ecologies, the endocranial anatomy (e.g. inner ear and brain) of Lari species (gulls, auks, terns, skuas) has been found to be highly variable. Certain clades exhibit morphologies that appear to be related to unique ecological niches such as compressed semicircular canals in wing-propelled diving Alcids and a whole suite of endocranial adaptations in the ecologically distinct black skimmer (*Rynchops niger*; Smith and Clarke 2012). While these adaptations are in internal structures and not the skeletal elements, it is plausible that some of the adaptations noted (e.g. differently sized optic lobes) would be reflected by differences in the braincase morphology.

Other studies have looked at more limited taxonomic subsets. An in-depth comparative anatomical study by Zusi (1962) highlighted morphological adaptations in the skull and mandible of the Black Skimmer (*Rynchops niger*) relative to several closely related species of gulls and terns (family Laridae) such as a strengthened frontonasal hinge, an increased distance between the quadrates, enlarged distal surfaces on the quadrates to strengthen the skull in light of extreme tension and force put on the skull during skimming, and enlarged palatines to allow for greater attachment of musculature. Comparative analyses of the osteo-muscular structures in the skulls of 3 different species of other ecologically anomalous Charadriiformes, the seedsnipes (Thinocoridae), by Korzun et al. (2009) have highlighted how the general proportions (e.g. a short jaw that is high at the base) as well as the specific musculature of these species is well adapted for the removal of plant fragments during foraging. The width of the beak in fourteen species of terns has also been demonstrated to correlate with the length of prey taken by each species (Hulsman, 1981), and differences in beak shape (specifically the roundness of the beak tip) have been noted in a study on diving birds that included three charadriiform species (Sharker et al., 2019). Taken together, there are multiple lines of evidence connecting skull shape and foraging ecology in Charadriiformes but we lack a comprehensive analysis of these patterns across the whole order. Particularly, we lack analyses that consider both the suborder Lari (gulls, terns, auks, and relatives) along with more typical shorebirds (plovers, sandpipers, and relatives) that were often studied in isolation from one another due to either the phylogenetic hypotheses at the time or due to the ecological differences between the Lari suborder and other charadriiform species.

In addition to our lack of a larger-scale understanding of the relationship between charadriiform skull diversity and foraging ecology, it is also unclear if the beak is the primary site of such adaptive macroevolutionary shape change or if the beak and the rest of the skull evolve in a correlated manner. As mentioned, correlated evolution between morphological components on a macroevolutionary scale is encapsulated by the related studies of modularity and integration. A greater degree of modularity represents stronger evolutionary covariation between individual components within a module relative to the associations, or degree of integration, between modules (Adams and Collyer, 2019). The pronounced variation in avian beak shape (Cooney et al., 2017) may have been facilitated by its semi-independent evolution from the rest of the avian skull. Studies analyzing modularity in bird skulls have reached variable conclusions on how correlated the evolution of different skull components have been during avian evolution, but have also differed substantially in the framework and methodology used to assess patterns of modularity. Application of partial least squares (PLS) analysis, as well as calculations of RV coefficients on 2-dimensional landmark points from the skulls (excluding the distal portion of the beak) from 160 species of birds, suggests that the avian skull has evolved as an integrated unit (Klingenberg and Marugán-Lobón, 2013). Similar findings have been suggested using PLS on smaller taxonomic subsets with support recovered for integrated evolution between two subsets of landmarks delimiting the beak from the rest of the skull in analyses on six corvid species (Kulemeyer et al., 2009), on 147 species of birds of prey (Bright et al., 2016), and on 170 species of parrots and cockatoos (Bright et al., 2019).

The methods used in the aforementioned studies tend to rely on directly asking whether a pre-defined hypothesis is supported or not. More recently developed methods (e.g. Adams and Collyer 2019; Goswami and Finarelli 2016) allow us to quantify the strength of covariation between modules under any number of hypotheses while allowing for direct comparisons of the support between each hypothesis. The ability to compare multiple, sometimes similar hypotheses is particularly useful given that, depending on where landmarks are placed, the delineations of what landmarks should be ascribed to a hypothesized module (particularly for landmarks that are placed along borders) is not necessarily clear. It is important to note that finding support for integrated evolution does not necessarily rule out semi-independent evolution between modules. In other words, it is possible for morphological components to evolve in an integrated manner but with certain regions still evolving semi-independently from one another (Drake and Klingenberg, 2010). Many of these newer methods allow us to investigate such patterns in-depth.

To date, studies of bird clades using these relatively new methods have yielded distinct results from past studies. Using a high-resolution geometric morphometric dataset with a likelihood-based approach (Evaluating Modularity with Maximum Likelihood: EMMLi, Goswami and Finarelli, 2016), Felice and Goswami (2018) found that, of the 16 different modularity hypotheses assessed, a seven-module hypothesis was best supported across a broad phylogenetic sample of 352 bird species. However, it has recently been noted that EMMLi appears to have high type I error rates, and a tendency to overfit modular hypotheses compared to a newer method for evaluating modularity hypotheses based on an effect size measure (Adams and Collyer, 2019). Given this disagreement on whether avian skull evolution has been characterized by modular evolution of the beak or not, it is imperative to reevaluate modular patterns in a nuanced framework to provide broader insights into the evolution of complex structures while simultaneously highlighting charadriiform-specific insights.

In this chapter, I use the detailed, 3D geometric morphometric dataset describing charadriiform skull morphology described in Natale and Slater (2022) to both understand how morphology relates to ecology and to understand how this relates to the potential modular evolution of the anatomically complex charadriiform skull. First, to provide a more direct interpretation of the relationship between form and ecology across the whole order and to understand how this relationship differs between morphological subsets of the skull, morphologies of the whole skull (i.e. the beak and braincase) are compared between different ecological groups and analyzed in light of previously published literature. Building upon the differences recovered between subsets, evidence for different patterns of modular evolution in charadriiform skulls was analyzed to further understand the macroevolutionary patterns that have generated these differences. Taken together, the results from this chapter both highlight a strong relationship between charadriiform foraging ecology and skull shape that forms the basis of Chapter 4, and suggest that the strong relationship between foraging ecology and skull shape recovered in Chapter 2 is the result of correlated, adaptive evolution in both the beak and braincase of Charadriiformes over time.

3.3 Methods

3.3.1 Morphological Data Collection

The morphological data used in this section was the same as that used in Natale and Slater (2022): see *Methods* of Chapter 2. In brief, the dataset contains 255 3D geometric landmark points (fig 2.1) collected from the skulls of 262 different charadriiform species. Landmarks were chosen to describe the overall skull shape, including curvature along the braincase, palatines, and beak. The landmarks were aligned to remove the effects of size, rotation, and translation and therefore describe interspecific differences in morphology.

3.3.2 Foraging Ecology Data Collection

Full details on how foraging data was aggregated and described are available in Natale and Slater (2022): see *Methods* of Chapter 2. As described in that portion, fine-scale foraging data was accumulated for each species by combining information on the foraging method and foraging substrate (e.g. skimmer + water surface) based on previously published literature. To ensure the analyses in this section were computationally feasible and interpretable, I examined differences in skull morphology between foraging guilds at a slightly broader scale. From these 36 foraging guild categories, I placed species into one of ten different foraging broader foraging guilds (table 3.1) meant to encapsulate broader differences in Charadriiform foraging ecology. These broader guilds did not consider differences between the breeding and non-breeding seasons which, as noted in Chapter 2, did not have a larger impact on the results in that portion.

Table 3.1: Foraging guilds of charadriiform birds used in this study based on information in del Hoyo et al. (1996) as well as a survey of literature and other written and video sources (see *Methods* for more details). The guild name and abbreviation are given as well as a description of the guild, representative genera or families, and the number of species in this study assigned to that guild are given.

Guild	Description	Example	N
Dry Ground Forager (DGF)	Species feed by pecking on a variety of dry substrates ranging from grassy meadows to deserts	plovers and lapwings (Charadriidae)	20
Aquatic Scavenger (AQS)	Species feed via two or more mechanisms, one of which was scavenging	many gulls (Laridae)	40
Grazer (GRZ)	Species feed on vegetation or seeds taken from ground or lower canopy	seedsnipes (Thinocoridae) and buttonquails (Turnicidae)	9
Hawker (HWK)	Species feed by catching prey in flight	pratincoles (Glareolidae)	5
Open Water Diver (OWD)	Species feeds in open water (whole body submerged) by either pursuit diving (using wings to pursue prey underwater) or plunge diving (diving from the air to capture prey, can include pursuit)	some gulls, terns (Laridae), alcids (Alcidae)	46
Predator (PRD)	Species feeds on other vertebrates (e.g. small rodents) taken outside of the water	some skuas (Stercoraridae)	3
Semi-aquatic Forager (SAF)	Species feeds in mixture of aquatic habitats and their adjacent areas (e.g. species feeding at shorelines, marshes, or in mixtures of wet and dry meadows). Mixtures of pecking and probing performed	some sandpipers (Scolopacidae)	65
Shallow Water Forager (SWF)	Species that feed by wading and feeding in upper layers of water column via pecking, probing, and moving the beak back and forth in water ('scything')	avocets and stilts (Recurvirostridae)	11
Soft Sediment Prober (SSP)	Species feeds by probing into soft sediments such as sand or wet mud and pulling out buried prey items	snipes, some sandpipers (Scolopacidae), oystercatchers (Haematopodidae)	56
Surface Diver (SFD)	Species feed via diving from the air and capturing prey in upper portions of water column without submerging entire body while diving	many terns (Laridae)	6

3.3.3 Major Axes of Shape Variation and the Distinctiveness of Guilds in Morphospace

To quantify the major axes of shape variation in charadriiform skulls, a principal components analysis was performed on the Procrustes aligned landmark data for the whole skull, the beak and associated bones, and the braincase using the procSym function in the `Morpho` package (Schlager et al., 2020). The same delineations of the beak and braincase (see supplementary file table 2) that were used in Chapter 2 were used in this portion. To qualitatively interpret how these shape differences relate to ecology, the general foraging guilds were mapped onto the morphospace defined by the first two principal components. To quantify the distinctiveness of each guild in morphospace, we used the hypervolume_gaussian function from the R package `hypervolume` (Blonder and Harris, 2019) to calculate a hypervolume for each foraging guild which quantifies the area each guild occupies in morphospace. Hypervolumes were computed based on the principal components that capture a majority ($\sim$90%) of the variation in shape which corresponds to the first five principal components scores for the whole skull and beak subset and to the first ten components for the braincase. Then, the amount of overlap between hypervolumes of each pair of the ten more broadly defined guilds was assessed by computing the Sørensen's similarity index (Sørenson, 1948), using the function hypervolume_overlap_statistics from the same package.

3.3.4 Phylogenetic Signal in Skull Shape and Foraging Ecology

To better understand the relationship between foraging ecology and phylogeny, phylogenetic signal in the shape data was assessed by calculating the multivariate K score (K_{mult}; Adams 2014) for the aligned landmarks from the whole skull, beak, and braincase using the physig function from the `geomorph` package (Adams et al., 2022; Baken et al., 2021). K_{mult} is a multivariate generalization of Blomberg's K (Blomberg et al., 2003) that quantifies deviations from the expected variance obtained under a constant rates Brownian motion process.

To determine whether K_{mult} differed from random expectation, the empirical value was compared to K_{mult} computed for 999 permuted datasets.

3.3.5 Modular Evolution of the Charadriiform Skull

We assessed support for a total of 11 distinct modularity hypotheses (fig 3.1; written definitions are available in supplementary file table 6). These hypotheses can be broadly divided into two groups. This first group was two variations of a relatively simpler 'beak and braincase model' (hereafter referred to as the BKBR1 and BKBR2 hypotheses) that have been suggested in previous work (e.g., Bright et al. 2016) and implicated in the aforementioned analyses understanding shape variation in the beak and braincase. One of these hypotheses (BKBR2; image k in fig 3.1) is a more straightforward separation of the beak from the rest of the skull, while the other (BKBR1; image j in fig 3.1) retains the portions of the skull involved in the linkage system (e.g. the quadrates, ptyergoids, jugals and palatines) in the same module as the beak. We compared support for these hypotheses to a second, more complex group of variations on the seven-module hypotheses of Felice and Goswami (2018). The nasal module that was part of this original seven-module hypothesis was not included as its structure cannot be reliably found across the surface scans we used here due to the elongated, thin, and small nature of many charadriiform beaks. Therefore, we instead adopted a similar version to their original Felice and Goswami (2018) model, adjusting for our differing landmark placement and other methodological choice (i.e. keeping the quadrate and pterygoid as seperate modules), and tested 9 variations based on this relatively complex, seven-module version. Hereafter, we refer to the first version of this hypothesis as the FeliceGoswami (FG) hypothesis with the variations on this hypothesis labeled sequentially $\{FG1, FG2, \ldots, FG8\}$. Variations on both of these hypotheses were generated by altering groupings of landmarks based on either the knowledge of the functional interactions (e.g. the quadrate does not touch the palatine bones, but the two are functionally linked during mouth opening and closing; Olsen and Westneat 2016) or proximity between different parts of the skull (e.g. the basioccipital bone is separated from the neighboring parietal bone in some hypotheses). In addition, we compared support for these 11 hypotheses to a null hypothesis, where all landmarks are considered part of one single module (i.e. no modularity).

We used the Covariance Ratio (CR), as computed in the phylo.modularity function from the R package `geomorph` (Adams et al., 2022; Baken et al., 2021), to quantify the degree of modular signal under each of the 11 different hypotheses. CR quantifies modular signal by determining and comparing the covariances within and between pre-defined modules (Adams and Collyer, 2019). Typically, CR varies between 0 (no covariation between modules but high covariation within modules; high modularity) and 1 (strong covariation between modules relative to between modules; low modularity), though it may theoretically exceed 1 if covariances between modules are greater than covariances within them (Adams and Collyer, 2019). When there are more than two modules in a given hypothesis, the CR value is averaged across pairwise comparisons of modules. A permutation procedure is then used to determine if modular signal in the data under each distinct hypothesis is stronger than expected by chance (Adams, 2016). For each analysis, we used 999 permutations to evaluate significance.

The phylo.modularity function also returns the standardized effect sizes Z_{CR} (Adams and Collyer, 2019) for each hypothesis which we used to compare support for the 11 modularity hypotheses. Z_{CR} evaluates the magnitude of the observed effect relative to the random outcomes of the permutation procedure used to evaluate significance of the CR. Paired effect sizes, $\hat{Z}_{12}$, were also computed using the compare.CR function in the `geomorph` package (Adams et al., 2022; Baken et al., 2021) to allow direct comparisons of support between pairs of modularity hypotheses, including the null hypothesis of no modularity (Adams and Collyer, 2019). The compare.CR function assesses support for each hypothesis relative to one another by performing two sample Z tests on the standard error from the results of the CR

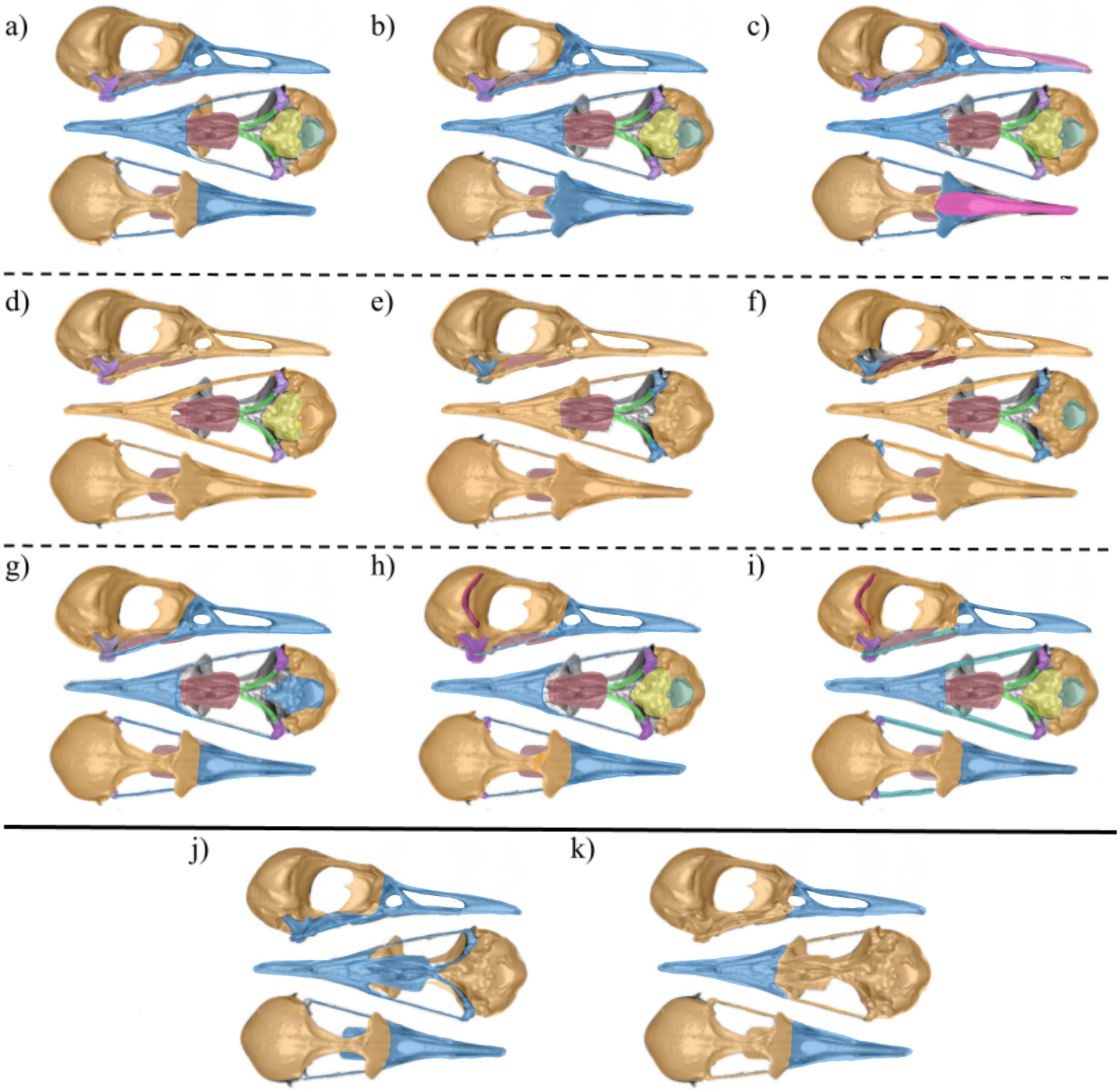

Figure 3.1: The 11 distinct modularity hypotheses tested across the charadriiform order in this chapter. Hypotheses are depicted on a surface scan of a Least Tern *Sterna antillarum* (FMNH 376281) skull. A through i (all above the solid line) correspond to the 'FG' hypothesis proposed in Felice and Goswami (2018) and it's variations. A depicts the original FG hypothesis, b the FG1 hypothesis, c the FG2 hypothesis, d the FG3 hypothesis, e the FG4 hypothesis, and f the FG5 hypothesis. J and k correspond to the two beak and braincase hypotheses with j corresponding to BKBR1 and k corresponding to BKBR2. See the supplementary file table 6 for written definitions of these hypotheses.

permutations and will return two sample Z scores and a p-value for each pairwise comparison, indicating whether there is significantly distinct support for any given hypothesis relative to another. To summarize, these steps return a CR value indicating the degree of integration between the hypothesized modules, standardized effect sizes (Z_{CR}) indicating the strength of modular signal under that hypothesis, and both p and z values (the former are reported here) associated with pairwise comparisons indicating whether or not the support for one hypothesis is significantly greater than support for the other in the pair.

To further understand how modularity may relate to ecology, we repeated these analyses on two subgroups: 1) the Lari (n=114); and, 2) a combined subgroup of the Charadrii and Scolopaci (hereafter referred to as 'Charadrii+Scolopaci'; n=143). We refer readers to supplementary file, table 7 for a detailed list of species in each subgroup. The Lari includes species-rich families such as the Laridae (gulls, terns, and skimmers, n =79) and Alcidae (auks and relatives, n=21), as well as several small families such as the Turnicidae (buttonquails, n=3) and the monotypic Crab Plover (family Dromadidae), while the Charadii+Scolopaci subgroup similarly includes two large families (Charadriidae; plovers and lapwings, n=45 and Scolopacidae; sandpipers and relatives, n =65), as well as several smaller (e.g. Burhinidae; thick-knees, n=7) and monotypic families (e.g. the Ibisbill; Ibidorhynchidae). The separation of the three charadriiform subclades (the Lari, the Charadrii, and the Scolopaci) was done in this way given the ecological similarity of the Charadrii and Scolopaci (the clades that contain the most typical shore and wading birds) relative to the Lari (the clade containing predominantly pelagic and diving birds), so that these results may be interpreted in light of the other analysis in this chapter. We chose to examine modularity only at this level as opposed to, for example, the family level, to ensure that the number of specimens exceeded the number of landmarks in each analysis. For this reason, both the subgroup and ordinal level analyses were run using a reduced density set of landmarks where four Type 1, normal landmarks were excluded and the resolution of the semilandmarks was reduced to

75 semilandmarks in total placed along curves (see supplementary file information under the heading *Details on the Reduced Density Landmarking Scheme Used in Portions of Chapter 3* and supplementary figure 6 for more details on this reduced-density landmark scheme).

3.4 Results

Three major results were found. First, as indicated by the low Sørensen's index value for pairwise comparisons, we found significant shape differences between most foraging guilds in the whole skull, beak and associated structures, and braincase morphologies. Second, A moderate degree of phylogenetic signal was found in charadriiform skull morphology. Lastly, the highest degree of support of was found for hypotheses in which the skull evolved as two semi-independent modules that correspond roughly to the beak and braincase, although this result was not replicated when one suborder, the Lari, was analyzed in isolation.

3.4.1 Major Axes of Shape Variation in the Charadriiform Skull and the Distinctiveness of Guilds in Morphospace

For analysis of the complete landmark set, the first principal component (PC1) explained $\sim$70% of the variation in shape. Negative PC1 scores correspond to elongated, narrow skulls, while positive PC1 scores correspond to skulls that are shorter and wider (fig. 3.2a). The second principal component (PC2) explained $\sim$13% of the variance. Negative PC2 scores correspond to skulls with a large angle between the beak and braincase, a more rounded braincase with large orbits, and more rostrally placed quadrates and foramen magnum. As PC2 scores increase, the skulls become flattened, such that the angle between the beak and braincase decreases, the braincase becomes flatter, and the quadrates and foramen magnum shift caudally. When the braincase is analyzed in isolation, the first principal component (PC1, fig. 3.2b) explained $\sim$38% of the variation in shape. Negative PC1 scores are associated with rounded braincases with dominant orbits and rostrally placed articulation points for the quadrates, while positive scores are associated with more elongated braincases where the quadrate articulation points are positioned caudally. For the analysis of the beak and associated structures only, the first principal component (fig. 3.2c) explained ∼75 % of the variation in shape and related to beak elongation.

The Sørensen's index for each pair of foraging guilds was low (closer to 0 than to 1), demonstrating that species belonging to the same foraging guild cluster together in skull shape morphospace, with little overlap between the hypervolumes of different foraging guilds (table 3.2). This result is largely consistent with convex hulls in the bivariate morphospace plots (fig. 3.2) and held when the beak was analyzed in isolation (table 3.3, upper triangle). The indices were slightly higher for the braincase (table 3.3, lower triangle), but remained lower than 0.42, with most being substantially lower. Shallow water foragers and soft sediment probers were, in general, recovered as very distinctive, with Sørenson's indices of 0, or very close to 0 when compared to most other guilds for the whole skull, beak, and braincase analyses. The exception to their distinctiveness is when they are compared to one another, consistent with their overlap in morphospace in an area of low PC1 scores corresponding to their shared elongated skulls. The various diving classes (surface divers, open water divers, and aquatic scavengers) exhibited a moderate amount of hypervolume overlap, with most pairs having a Sørensen's index below 0.30 with this relatively high value seen in the comparison of surface divers and aquatic scavenger in the braincase analysis. Grazers tended to be distinct from other groups in the whole skull and beak, but not the braincase, analysis while predators and hawkers both overlapped substantially with the various diving classes, but not with the wading classes (e.g. soft sediment probers, semi-aquatic foragers, shallow water foragers).

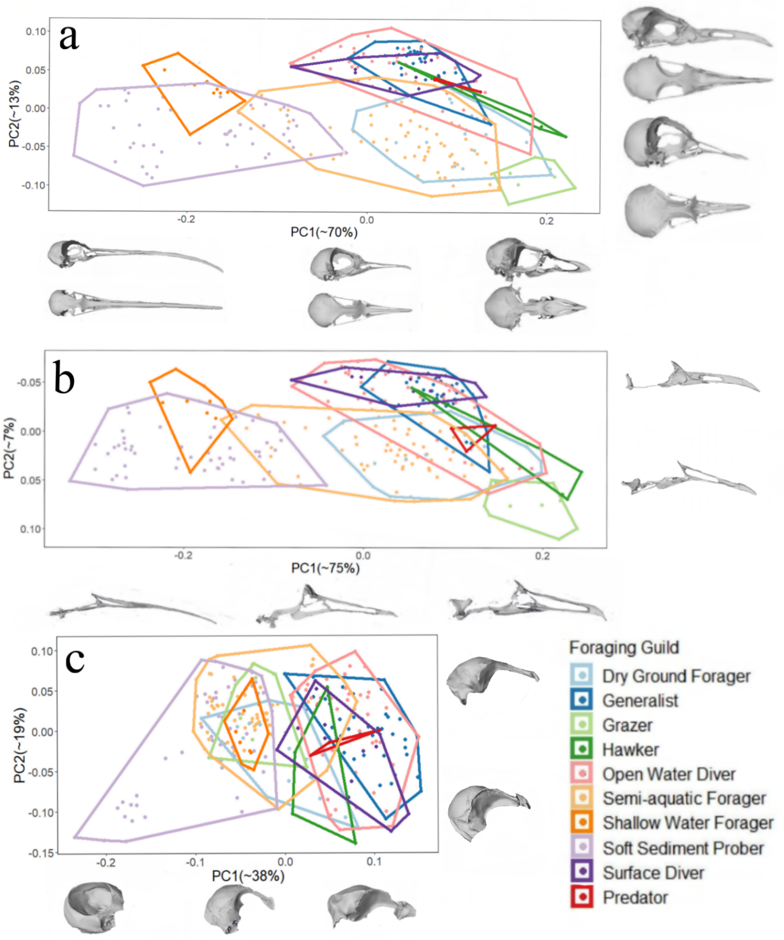

Figure 3.2: The results of a principal components analysis on landmarks from (a) the whole skull, (b) the beak and its associated structures, and (c) the braincase. Each point represents a species morphology digitized from three-dimensional surface scans from 1-2 museum specimens. Foraging ecology is encoded by color. Representative examples of changes along each principal component are shown on the X and Y axis. X axis, listed left to right for each plot. For (a): Eurasian curlew (*Numenius arquata*; FMNH 363888), upland sandpiper (*Bartramia longicauda*; FMNH 376174), crested auklet (*Aethia cristatella*; LACM 117834). For (b) Eurasian curlew (*Numenius americanus*; FMNH 106289), white-tailed lapwing (*Vanellus leucurus*; USNM 645956), parasitic jaeger (*Stercorarius parasiticus*; LACM 87186). For (c) American woodcock (*Scolopax Minor*; FMNH 438027), Andean avocet (*Recurvirostra andina*; ROM 159573), western gull (*Larus occidentalis*; FMNH 105459). Y axis, listed top then bottom for each plot. For (a) Inca tern(*Larosterna inca*, FMNH 437577), three-banded plover (*Charadrius tricollaris*; FMNH 368844). For (b) Inca tern (*Larosterna inca*; FMNH 437577), blacksmith lapwing (*Vanellus armatus*; FMNH 503731). For (c): crab plover (*Dromas ardeola*; USNM 488404), black oystercatcher (*Haematopus bachmanni*; USNM 500644).

Table 3.2: Hypervolume overlap, as measured by Sørensen's index (Sørenson, 1948) from the first 5 principal components from the principal components analysis on the three dimensional landmark data from skulls of 262 charadriiform species. Each cell represents a comparison of the hypervolume for each foraging guild, denoted in the row and column. Values closer to 0 suggest distinctiveness whereas values closer to 1 represent a higher degree of overlap.

	AQS	GRZ	HWK	OWD	PRD	SAF	SWF	SSP	SFD
Dry Ground Forgers (DGF; n=20)	0.05	0.10	0.17	0.08	0.05	0.43	0	0.05	0.07
Aquatic Scavengers (GEN; n=40)		0	0.09	0.13	0.19	0.04	0	0	0.24
Grazers (GRZ; n=9)			0.09	0.03	0	0.09	0	0	0
Hawkers (HWK, n=5)				0.37	0.04	0.09	0	0.01	0.11
Open Water Divers (OWD; n=46)					0.04	0.08	0	0.01	0.18
Predators (PRD; n=3)						0.04	0	0	0.06
Semi-aquatic Foragers (SAF; n=65)							0.06	0.14	0.03
Shallow Water Foragers (SWF, n=11)								0.20	0
Soft Sediment Probers (SSP; n=56)									0
Surface Divers (SFD, n=6)									

Table 3.3: Hypervolume overlap, as measured by Sørensen's index (Sørenson, 1948) from the first 5 principal components resulting from a principal components analysis of three-dimensional landmark data from the beaks (upper triangle) and the first 10 principal components for the braincases (lower triangle) of 262 charadriiform species. Each cell represents a comparison of the hypervolume for each foraging guild, denoted in the row and column. Values closer to 0 suggest distinctiveness whereas values closer to 1 represent a higher degree of overlap.

	DGF	AQS	GRZ	HWK	OWD	PRD	SAF	SWF	SSP	SFD
Dry Ground Forgers (DGF; n=20)	-	0.03	0.12	0.12	0.16	0.06	0.50	0	0.05	0.03
Aquatic Scavengers (AQS; n=40)	0.05	-	0	0.06	0.11	0.21	0.02	0	0	0.30
Grazers (GRZ; n=9)	0.09	0.01	-	0.20	0.06	0	0.07	0	0	0
Hawkers (HWK, n=5)	0.15	0.15	0	-	0.33	0.04	0.07	0	0.01	0.07
Open Water Divers (OWD; n=46)	0.04	0.24	0.01	0.11	-	0.05	0.08	0	0	0.15
Predators (PRD; n=3)	0.02	0.04	0	0	0	-	0.03	0	0	0.02
Semi-aquatic Foragers (SAF; n=65)	0.35	0.09	0.28	0.07	0.07	0.01	-	0.04	0.17	0.01
Shallow Water Foragers (SWF, n=11)	0.10	0.01	0.18	0.06	0	0	0.14	-	0.20	0
Soft Sediment Probers (SSP; n=56)	0.04	0.01	0.10	0.02	0.04	0	0.21	0.09	-	0
Surface Divers (SFD, n=6)	0.21	0.42	0.02	0.30	0.24	0.02	0.14	0.03	0.03	-

3.4.2 Phylogenetic Signal in Skull Shape

Charadriiformes exhibit moderate phylogenetic signal in skull shape ($K_{\text{mult}} = 0.6215$, P = 0.001). Analysis of the two skull partitions showed similar results in the beak ($K_{\text{mult}} = 0.6327$, $P = 0.001$) and in braincase ($K_{\text{mult}} = 0.5949$, $P = 0.001$). The visualizations of phylogenetic signal in skull shape and foraging ecology, as demonstrated by the first two principal components mapped onto a phylogenetic tree (fig. 3.3) highlight this pattern. Species within most families tend to share similar skull shapes and tended to share similar skull shapes with closely related families. For example, similar PC1 and PC2 scores are seen throughout the closely related Lariade (gulls) and the Alcidae (Auks) suggesting these families share similar skull morphologies, as would be predicted by phylogeny. However, some distantly related lineages shared morphologies. For example, PC1 scores of the oystercatchers (Haematopodidae) and the stilt and avocet family (Recurvirostridae) are similar to distantly related sandpipers and relatives (Scolopacidae), signifying both groups share elongated skulls. Additionally, some of the highest PC1 values (shorter skulls) were seen in the coursers and pratincoles (Glareolidae), the buttonquails (Turnicidae) to which they are closely related, and in the seedsnipes (Thinocoridae) to which neither group is closely related.

3.4.3 Modular Evolution of the Charadriiform Skull

We found that all eleven hypotheses tested received significant support ($p<0.05$) relative to a null model, although the CR values for all hypotheses were relatively high (all >0.76), indicating that there was a relatively high degree of covariation between modules. The strength of the modular signal under each hypothesis, as indicated by the Z_{cr} value varied substantially across hypotheses. These Z_{cr} scores (table 3.4) indicate that the strongest signal of modular evolution was under the BKBR2 hypothesis. This two-module hypothesis separates the beak from the remaining portions of the skull and differs from the BKBR1 hypothesis in that cranial elements that are biomechanically linked to the beak (quadrates and jugals) are retained in the braincase module under the BKBR2 hypothesis. The Z_{cr} score for the BKBR1 hypothesis received the second most negative score. Among other hypotheses, the FG5 hypothesis was recovered as having the weakest modular signal (as indicated by the least negative Z_{cr} scores).

When support for each of these hypotheses relative to one another was compared via

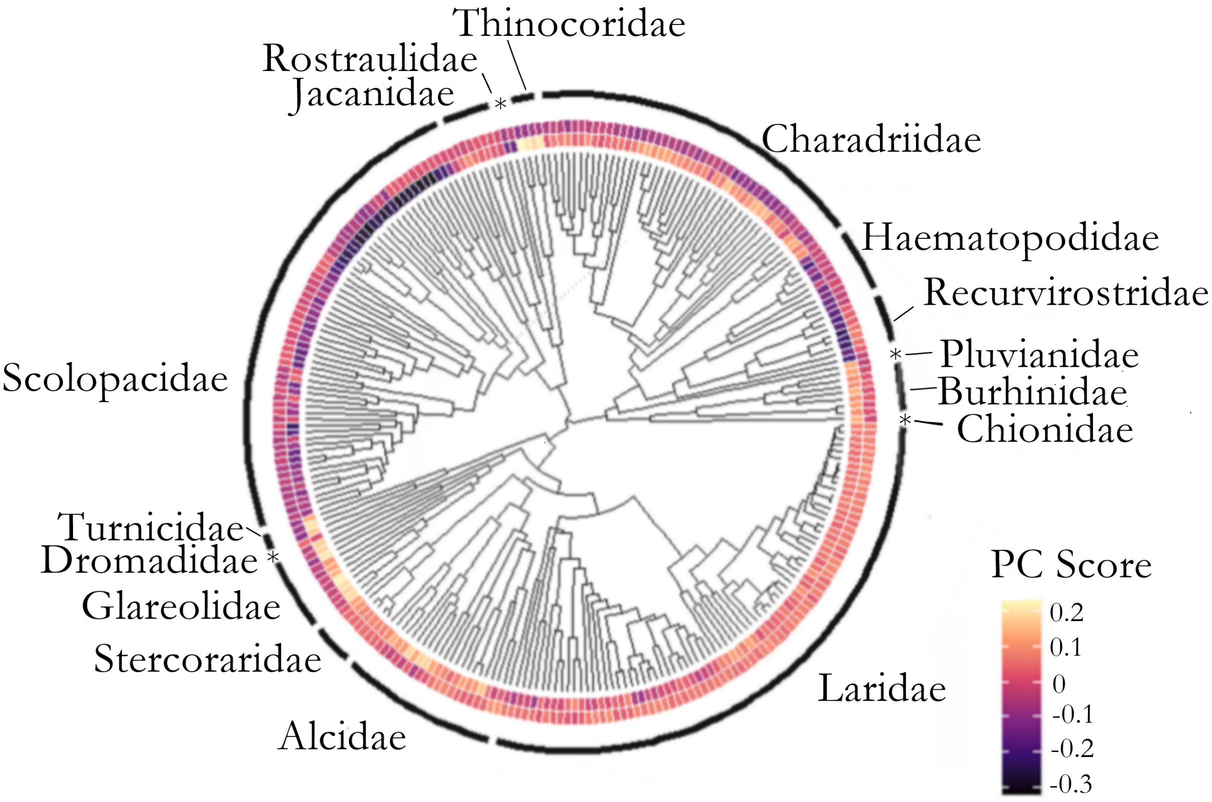

Figure 3.3: A visualization of phylogenetic signal in skull shape for Charadriiformes, as demonstrated by the first two principal components (the inner circle corresponds to the first and the outer circle corresponds to the second) from a principal components analysis on 3D geometric morphometric data from the skulls of 262 different species of Charadriiformes. The majority of charadriiform families are labeled with black bars and text, while several smaller or monotypic families are labeled with stars.

paired effect sizes, we recovered variable results (table 3.5). All hypotheses are strongly preferred ($p<0.05$) over the null model of no modularity. When the various versions of the FG hypothesis were compared to one another, no significant differences were found. Significant support for the two beak and braincase hypotheses, particularly for BKBR2, relative to the FG hypotheses was more common, with significantly greater support for both BKBR hypotheses over the FG4, FG7, and FG8 hypotheses being recovered. Distinct support for one beak and braincase hypothesis over the other could not be discriminated ($p>0.05$) on the basis of pairwise effect sizes.

We recovered distinct CR values and Z_{cr} scores for the two subgroups relative to our

Hypothesis	CR	P	Z_{cr}
FG	0.83	0.001	-3.34
FG1	0.83	0.001	-3.36
FG2	0.82	0.01	-3.74
FG3	0.80	0.01	-4.19
FG4	0.79	0.001	-4.52
FG5	0.86	0.008	-2.58
FG6	0.78	0.001	-4.36
FG7	0.78	0.001	-4.17
FG8	0.79	0.001	-4.47
BKBR1	0.86	0.001	-5.97
BKBR2	0.85	0.001	-7.87

Table 3.4: CR scores, P values, and Z_{cr} scores for each modularity hypothesis tested. The CR scores indicate the degree of correlation during morphological change among the modules in any given hypothesis. CR values closer to 0 indicate high modularity with sets of landmark points evolving more independently from one another, while CR values closer to 1 indicate low modularity where sets of landmarks tend to evolve in a more covaried manner with one another. P values compare the observed CR to permutations to determine if the evidence for modular evolution under that hypothesis is stronger than expected by chance ($p<0.05$). Z_{cr} scores represent a measure of support (see table 3.5 and fig 3.5 for statistical comparisons of these values) for that hypothesis with more negative values representing a stronger modular signal under that hypothesis. See fig 3.1 for descriptions of each hypothesis and 3.4 for visualizations of these values relative to the subgroup-level analyses.

Hypothesis	FG	FG1	FG2	FG3	FG4	FG5	FG6	FG7	FG8	BKBR1	BKBR2
NULL	$\sim$0	$\sim$0	$\sim$0	$\sim$0	$\sim$0	0.01	$\sim$0	$\sim$0	$\sim$0	$\sim$0	$\sim$0
FG		0.99	0.97	0.83	0.35	0.61	0.35	0.61	0.70	0.09	0.09
FG1			96	0.82	0.35	0.60	0.34	0.70	0.71	0.09	0.09
FG2				0.85	0.33	0.62	0.32	0.64	0.66	0.07	0.07
FG3					0.38	0.71	0.38	0.50	0.50	0.06	0.06
FG4						0.78	0.98	0.13	0.12	0.02	0.02
FG5							0.77	0.36	0.35	0.33	0.34
FG6								0.13	0.12	0.25	0.25
FG7									0.98	0.002	0.002
FG8										0.01	0.01
BKBR1											0.09

Table 3.5: P values corresponding to the results of pairwise two sample Z tests across each pair of hypotheses. Each hypothesis is denoted with an abbreviation along the column and row names.. A value of $\sim$0 denotes a value that was <0.0009. See fig 3.1 for descriptions of each hypothesis.

analyses across all Charadriiformes (fig 3.4). In the Lari, CR values skewed lower (all <0.75) while all CR values skewed higher (all > 0.90) in our combined Charadrii+Scolopaci subgroup, suggesting skull modules evolve in a less correlated fashion in the Lari, relative to the Charadrii+Scolopaci. The Z_{cr} scores for each of the modularity hypotheses also varied between the two subgroups but were again universally more negative (indicating stronger support) in both subgroups relative to a null hypothesis of no modularity. The FG4 hypothesis, in which the upper part of the beak and braincase are treated as a single module, received the least negative value (indicating the weakest support) in both subgroups. The most negative Zcr score (indicating the hypothesis with the strongest support) varied between the two families with the BKBR2 hypothesis receiving the most negative scores (similar to our findings at the ordinal level) in the Charadrii+Scolopaci while the FG8 hypothesis, the most finely subdivided of our hypotheses, received the most negative score within the Lari.

Pairwise comparisons of these Z_{cr} scores revealed complex relationships between support for the hypotheses when compared to one another (fig 3.5). In both subgroups, all modularity hypotheses were significantly better ($p < 0.05$) than a null model of no modularity, with the exception of the FG5 hypothesis in the Charadii+Scolopaci suborder. Aside from these significant comparisons to the null hypothesis, significant differences in support were (similar to our order level results) recovered most frequently for comparisons between the FG hypotheses and the two versions of the beak and braincase hypothesis. Although the FG8 hypothesis was the most strongly supported within Lari (fig 3.4, as indicated by the lowest effect size), it is only a significantly more supported hypothesis relative to the FG4 hypothesis for this clade. While the two beak and braincase hypotheses were significantly more supported over a larger number of hypotheses (fig 3.5A), a significant difference in support for one of the beak and braincase hypotheses relative to the other was not recovered in the Lari (fig 3.5A). Both the BKBR1 and 2 hypotheses received significantly stronger ($p<0.05$) support than many of the FG hypotheses in the Charadii+Scolopaci (fig 3.5B), and the two

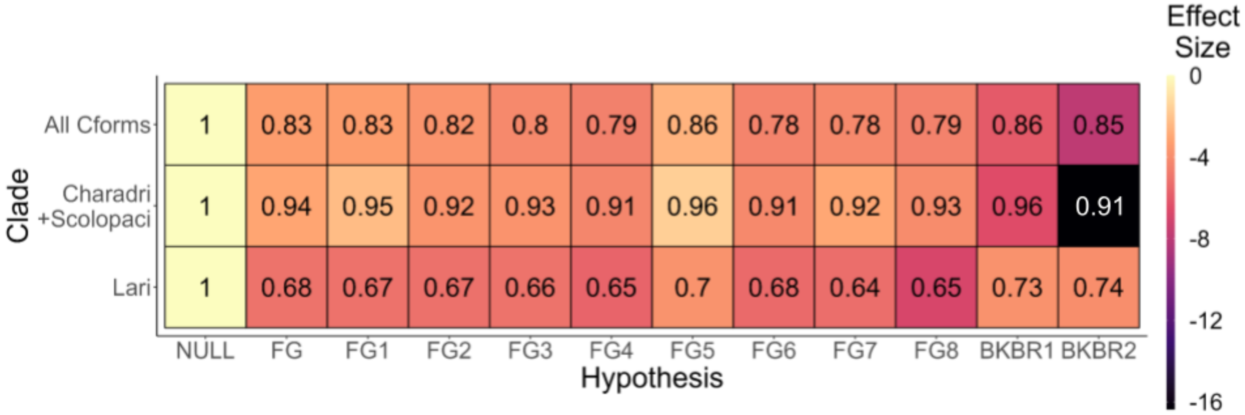

Figure 3.4: The Covariance Ratio (CR) values and effect sizes (Z_{cr} scores) for different modularity hypotheses across the Charadriiform order (‘All Cforms’) as well within two different Charadriiform subgroups: the Lari and a subgroup of the combined suborders Charadrii and Scolopaci (‘Charadrii+ Scolopaci’). The CR value is indicated by the text in each cell, with values closer to 1 indicating a stronger degree of covariation between each pair of modules under that hypothesis. P values for these CR values are not labeled (see tables 3.4 and 3.5, as well as fig 3.5). The effect size (Z_{cr} scores), given by the color of each cell, demonstrates the relative support for that hypothesis, with more negative values indicating a higher modular signal (and therefore higher support) being detected under that hypothesis. NULL indicates the null model of no modularity to which the others were compared. See fig 3.1 for descriptions of each hypothesis.

hypotheses were found to be distinctly supported from one another in this subgroup, with the BKBR2 hypothesis receiving a particularly negative Z_{cr} score of -16.38 (fig 3.4).

3.5 Discussion

The distinct morphospace occupation of foraging guilds, demonstrated by the low amount of overlap between hypervolumes for each foraging guild in a morphospace generated from the 3D landmark data describing the skulls of 262 different charadriiform species, highlighted how whole skull, beak, and braincase shape differed between foraging guilds. A moderate amount of phylogenetic signal was seen in whole skull, break, and braincase shapes with some broad clustering of similar skull shapes among closely related families and several instances of similar morphologies being seen in distinct lineages. The analyses of distinct modular hy-

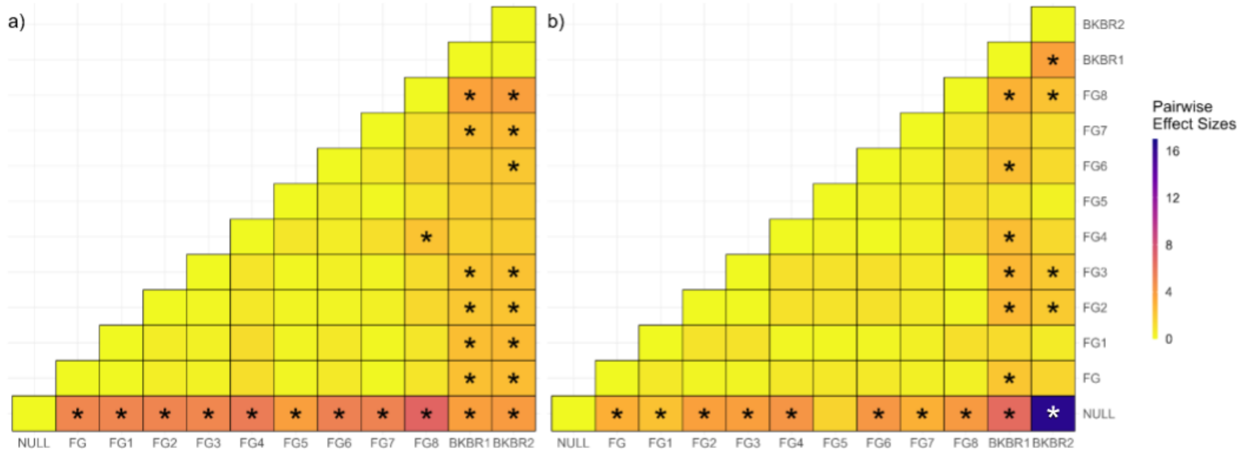

Figure 3.5: Pairwise effect sizes demonstrating variable support for modularity hypotheses for two different subgroups: 1) the Lari and 2) a combined subgroup of the Charadrii+Scolopaci. The pairwise difference is denoted by the color of each cell with a black or white asterisk (distinct colors are used for increased readability) denoting significantly ($p < 0.05$) different support for that given pair of hypotheses. For these pairwise differences, we determined which hypothesis was favored by comparing the effect sizes (fig 3.4) with the more negative value indicating the preferred hypothesis. See fig 3.1 for descriptions of each hypothesis.

potheses most supported an evolutionary hypothesis in which the beak and braincase evolved in a correlated, but semi-independent manner from one another; a finding that informs the hypervolume results by suggesting the existence of a relationship between shape and ecology when the beak and braincase are analyzed in isolation may have resulted from their correlated evolution. These results however, varied between ecologically different subgroups, consistent with the moderate degree of phylogenetic signal seen. Taken together, these results highlight how chardriiform skulls have evolved as a relatively correlated unit to adapt to different foraging modes, but with significantly different patterns seen in subgroups, demonstrating the flexibility of modular and adaptive evolution over macroevolutionary timescales. These adaptations will be discussed below to both highlight the specific relationship between morphology and function in Charadriiformes and to provide insight into questions about the macroevolution of avian skulls more generally.

3.5.1 Ecomorphological Adaptations in the Charadriiform Skull

The results of the principal components and hypervolume analyses showed a significant relationship between charadriiform foraging guilds and the shapes of their skulls that held even when the beak and braincase were analyzed in isolation. This is consistent with the results of Chapter 2 which demonstrated that foraging ecology is the dominant predictor of skull shape differences across the charadriiform order. While that chapter mainly discussed results in light of previous work on a variety of avian clades (Bright et al., 2016; Felice et al., 2019; Guangdi et al., 2015; Pecsics et al., 2019; Sun et al., 2018), this discussion will focus more specifically on interpreting differences in skull shape in light of interspecific differences in charadriiform foraging ecology to provide a comprehensive overview of charadriiform adaptations for foraging. Our results confirm the findings of previous macroevolutionary studies that suggested a relationship between charadriiform skull shape and foraging ecology (Barbosa and Moreno, 1999; Zweers and Gerritsen, 1996) as well as smaller-scale comparative, biomechanical studies (Korzun et al., 2009; Sharker et al., 2019) that have suggested many charadriiform species possess skulls with specific skeletal adaptations that make them well-adapted to differing foraging modes.

The patterns with which each foraging guild mapped onto our morphospace point towards the adaptive significance of shape differences in charadriiform skulls, but also point towards several topics that warrant further investigation. Elongation is commonly found to be the predominant axis of shape variation in principal components analyses on the shapes of bird skulls (Felice et al., 2019; Hunt et al., 2023; Navalón et al., 2020). Our finding that this was also the case for Charadriiformes suggests this may be a common axis of diversification in birds. Our detailed three-dimensional approach confirmed the findings of Barbosa and Moreno (1999) who used linear measurements to demonstrate that probing into sediment (a tactile foraging method used by many sandpipers) is associated with elongation of the bill. Our results suggested that, in addition to elongation, many tactile feeding birds exhibit a rostrally positioned quadrate. The quadrate serves as the hinge point where beak opening begins and its placement in tactile feeding birds may relate to the unique feeding mode known as rhynchokinesis, where distal portions of the beak can flex in addition to (or replacing) the flexion point where the beak meets the braincase (Zusi, 1984). While this behavior is known in Charadriiformes to allow probing shorebirds to capture buried invertebrates (Zweers and Gerritsen, 1996) and several suggestions have been made regarding the potential adaptive significance (Estrella and Masero, 2007; Zusi, 1984), we lack comprehensive knowledge of which species perform rhynchokinesis and the adaptations needed for this behavior. Therefore, while our morphospace also recovered species that feed via tactile probing mechanisms had elongated skulls, further biomechanical analyses using morphometric datasets such as this would build upon this finding to better understand how morphology changes in the positioning of biomechanically important elements (e.g. the quadrates) actually affect the function output. If data on flexion zones could be obtained, it could be used in conjunction with our 3D landmark data to test hypotheses about functional performance or linkage models (e.g. Hoese and Westneat 1996; Olsen 2016; Olsen and Westneat 2016) in a comparative evolutionary framework. The finding that a stronger degree of support relative to most other hypotheses was found for a two-module evolutionary hypothesis (BKBR1; image j in fig 3.1) in which the beak and its biomechanically associated structures evolve semi-independently from the braincase suggests this linkage system may be an important target of adaptive morphological change.

We also found substantial widening of the interquadrate distance and variation in the angle between the beak and braincase as two primary axes of variation. Past comparative anatomical work suggested that the increased distance between the quadrates in diving birds is an adaptation to resist forces acting on the skull when impacting water (Zusi, 1962). However, we found that wide skulls are shared by diving birds, ground foragers, and several other groups such as hawking species mostly confined to the suborder Lari (gulls, auks, pratincoles, buttonquails and relatives). Computer modeling has been used to investigate how factors such as width and depth of beaks affect stress under loading in ground-foraging finches (Soons et al., 2010) or jaw closing speed in aerial feeding birds (Rico-Guevara et al., 2019), but comparative biomechanical work connecting skeletal differences to functional output has yet to be conducted on species in this suborder. Variation in the angle between beak and braincase may be associated with the position of the beak in a bird's visual field (discussed below), but may also represent a change in the relative proportions of the skull that affect the functional output (i.e. mechanical advantage) of the biomechanical system in the avian skull (Olsen and Westneat 2016). Thus, while functional explanations for the major axes of shape variation are again implied, further conclusions cannot be drawn without more comparative modeling work. Because of their diversity, Charadriiformes represent an ideal group to study these outstanding questions, and a particular focus on the presence of rynchokinesis and on the ecomorphology of the Lari may fill in the gaps in our knowledge (see *Conclusions and Future Directions*).

While this relationship between foraging ecology and skull shape is strong, it is notable that it is not perfect. While this could represent a pattern of many-to-one mapping of form to function where one morphology is functionally flexible enough to be simultaneously "optimized" for several different ecological roles (Zelditch et al., 2017), the results here in light of what is known about avian ecology more broadly highlight that considering the multiple life history traits skull shape may be selected for is important, as has been demonstrated in past work (Friedman et al., 2019; Hunt et al., 2023). Specifically in these analyses, the second principal component of skull shape variation in this study was associated with the angle between the beak and braincase, which may be related to interspecific variation in vision (i.e the extent of the binocular visual field) that may be under complex patterns of selection. Vision in birds is known to be adapted for a variety of functions such as provisioning food to young (Martin et al., 2005) and detecting predators (Fernández-Juricic et al., 2008;

Guillemain et al., 2002). Visual fields are even known to vary between species with broadly similar foraging behaviors, but who possess small-scale differences when the breeding and non-breeding habitat variation is considered (Martin and Piersma, 2009). Other factors are also worthy of consideration, such as the role of the avian beak in thermoregulation (reviewed in Tattersall et al. 2017). Indeed, Ryeland et al. (2017) demonstrated for nine charadriiform species that thermoregulatory behaviors (e.g., tucking the beak to minimize heat loss) vary with beak size and temperature, highlighting the potential for selection on beak size as a confounding factor in our study. The skull morphologies of Alcids (auks and relatives; Badikova and Dzerzhynsky 2015), as well as some non-charadriiform birds (e.g., the ground tit, *Parus humilis*; Cheng et al. 2017b), are also thought to be adapted for differing nest-building and burrowing behaviors respectively. Our results suggest that while foraging ecology may at least in certain clades represent a very important axis of niche diversification (and can be used as a way to understand broader macroevolution or spatial biodiversity; see Chapters 2 and 4), if the goal of a research project is to provide a comprehensive overview of the life history drivers of avian skull change, then multiple factors deemed important for that clade should be considered.

It is notable that results were overall quite similar when the whole skull, beak, or braincase shape were analyzed. The avian beak has long been recognized as a critical in foraging ecology and its shape is often quantified in isolation to examine macroevolutionary (Cooney et al., 2017; Pigot et al., 2020) and macroecological (Pigot et al., 2016) patterns. The braincase is often excluded from studies of avian ecomorphology unless the focus has specifically been on the eyes (Lin, 2022; Thomas et al., 2006), but our results support the rare exceptions that demonstrate it is worthy of study. For example, Smith and Clarke (2012) found that the morphology of endocasts differed between various classes of diving birds, likely due to different sensory requirements (e.g. pressure detection, visual requirements) while foraging, emphasizing that the whole skull morphology relates to differences in ecology between species.

That the relationship between foraging ecology and braincase morphology was similar, but weaker, to that seen between beak morphology and foraging ecology also echoes the results of the procrustes ANOVAs in Chapter 2 which recovered that the amount of braincase shape variation attributable to foraging ecology was lower then for beak shape variation. Taken together, this suggests that the braincase may be under more complex evolutionary pressures then the beak, which may be more strongly related to foraging ecology in isolation. The most supported modularity hypotheses (discussed in the following section) suggest that this high, but imperfect, degree of correlation between the the two structures is the results of the modular, but still correlated evolution between the a beak and a braincase module.

3.5.2 Modular Evolution of the Charadriiform Skull in light of Variation in Foraging Ecology

The highest degree of support was found for a two-module hypothesis of Charadriiform skull evolution. Our strong rejection of a null model of no evolutionary modularity stands in apparent contrast to previous findings based on birds of prey (Bright et al., 2016), parrots (Bright et al., 2019), corvids (Kulemeyer et al., 2009), and across a broad sample of all birds (Klingenberg and Marugán-Lobón, 2013) that found evidence for correlated evolution between the beak and braincase. These studies have relied on methods (Partial Least Squares; Bright et al. 2016, 2019; Kulemeyer et al. 2009 and the RV coefficient; Klingenberg and Marugán-Lobón 2013) that assess the evidence for significant correlations between pre-defined modules. Considering the differing approach of these methods and of that used here (Adams and Collyer, 2019), our results are not incongruous with the idea that the skull has evolved in an integrated manner as these previous studies have suggested. In agreement with these previous findings, our analyses all returned relatively high CR values (across all analyses were >0.64) indicating a substantial degree of integration between hypothesized modules. However, these analyses differ from several of these past studies (Bright et al., 2016, 2019; Kulemeyer et al., 2009) in that they include both explicit comparisons of distinct modularity hypotheses relative to one another as well as quantifiable measures of the degree of integration between modules, allowing us a more nuanced understanding of the degree of modular evolution occurring. A similar pattern, a degree of modularity with notable integration between modules, was also recovered in a study on domestic dog skull evolution that relied on calculations of RV coefficients, (Drake and Klingenberg, 2010). Drake and Klingenberg (2010) recovered a degree of integration between the face and remaining portions of the skull, but still found significant support for modular evolution between these two elements. It is notable that a methodologically similar study on a broad sample of bird skulls by (Klingenberg and Marugán-Lobón, 2013), found evidence for integration between the 'face' and braincase and rejected a hypothesis of skull modularity. Given that we found the strongest support for a hypothesis that separated out the beak (including what these authors define as the face) and, under one hypothesis, its biomechanically associated structures from the braincase, the differing results between our study and that of Klingenberg and Marugán-Lobón (2013) may be explained by their exclusion of the distal portions (roughly corresponding to half) of the beak from their analysis.

Little support was found for complex modularity scenarios as evidenced by the pairwise comparisons between the FG hypotheses and the BKBR hypotheses. The discrepancy between this finding and that of Felice and Goswami (2018), who suggested that avian skull is defined by seven evolutionary modules may be explained by the aforementioned tendency of the maximum likelihood method used to favor more complex modularity hypotheses (Adams and Collyer, 2019), a finding that is echoed in research using this method (Bardua et al., 2020; Conith et al., 2022; Goswami and Finarelli, 2016; Marshall et al., 2019; Mitchell et al., 2021). It is, however, notable that some authors (e.g. Mitchell et al., 2021) have found consistent results between this maximum likelihood method and the Covariance Ratio (CR) method, suggesting that in certain species a high number of semi-independent modules may be a genuine pattern. It is also possible that the lack of support for higher degrees of modularity in our work, as compared with Felice and Goswami (2018), may reflect the fact that they placed dense semi-landmarks on regions of the skull that we did not. In general, our results highlight the need for future research to carefully consider methodological choices such as landmark placement and how this relates to the subdivision into hypothesized modules as well as the specific hypothesis testing method used.

Our subgroup level results, however, point to levels of taxonomy as another potential reason for variation in past results and prompt further research into the connection between modularity and factors such as ecology and adaptive change. The extremely low Z_{cr} scores for both the BKBR1 (Z_{cr} score of -8.47) and BKBR2 (Z_{cr} score of -16.38) hypothesis in our Charadii+Scolopaci subgroup suggest that the species in that group may be the primary drivers of support for these two hypotheses at the ordinal level. Charadii+Scolopaci contain species who span the entire range of morphospace in our analyses, but notably contain species with the most extreme negative PC1 values in our whole skull analysis , whereas the Lari tend to be restricted to higher PC1 values. It is unsurprising that if beak lengthening is so profound in the evolution of the Charadrii+ Scolopaci, as noted by Barbosa and Moreno (1999), that our analyses would detect such strong support for the beak evolving as a semi-independent module. It is notable the CR values recovered were universally lower in the Lari relative to the Charadii+Scolopaci, suggesting that under any given hypothesis, hypothesized modules tended to evolve more independently from one another. This is in agreement with the hypervolume analyses which found that many of the diving classes, composed of species from the Lari suborder, tended to have higher amounts of overlap in the hypervolume analyses, suggesting more complex patterns pattern of shape change in light of ecology relative to other clades. A lack of clear modular signal in the Lari may reflect the ecological diversity within the subgroup (containing many diving species but also grazing buttonquails, hawking pratincoles, and predatory skuas) or the presence of many extreme generalist species (e.g. many gull species), but is in generally unclear in light of a lack of comparative work on this subgroup, as was noted in the previous section. Thus, while our results highlight interesting clade-specific dynamics, future work could further investigate how ecological differences between these groups may relate to modularity and potentially how this modularity and integration may relate to adaptive diversification, as has been done in other clades (Navalón et al., 2020).

3.6 Conclusions

Taken together, these analyses highlight that charadriiform skulls vary in shape and that these shape differences relate to differences in foraging ecology. Similar results were seen in hypervolume analyses assessing the distinctiveness of guilds in morphospace when the whole skull and beak only were analyzed and, to a lesser extent, when the braincase only was analyzed. In light of the finding that charadriiform skull evolution has been characterized by semi-independent evolution of the beak and braincase and that this result is driven by the subgroup with the most profound differences in beak shape (the Charadii+Scolopaci), this high degree of correlation between the whole skull morphology, beak morphology, and foraging ecology likely reflects how the whole skull morphology in Charadriiformes has evolved over time to facilitate different foraging modes. Conversely, the lower degree of correlation between the braincase and foraging ecology likely reflects the semi-independent, but still integrated evolution of the braincase from the rest of the skull. In the Lari, the suborder with relatively less extreme morphological differences but greater ecological diversity, no clear patterns of modular evolution were seen and a larger amount of overlap in the morphospace occupied by different foraging guilds was recovered, particularly for the braincase, suggesting that the order has a less clear macroevolutionary trajectory in light of adaptive evolution for different foraging ecologies. This chapter built upon the established relationship between foraging ecology and skull shape in chapter 2 to provide an overview of morphological and ecological differences among all charadriiform families, expanding upon previous work which tended to exclude the subfamily Lari due to phylogenetic hypotheses at the time. The relationship between foraging ecology and skull shape established in Chapters 2 and 3 will be used as the foundation for Chapter 4. Lastly, this chapter highlights areas of charadriiform skull ecomorphology that warrant future research (e.g. the presence of rynchokinesis in light of morphological differences, and diversification in the suborder Lari) that will be discussed in Chapter 5.

CHAPTER 4

CHARADRIIFORM SPATIAL BIODIVERSITY ACROSS SPACE AND TIME IN LIGHT OF MIGRATION PATTERNS AND PROTECTED AREA COVERAGE

4.1 Abstract

Spatial patterns of taxonomic, phylogenetic, and functional biodiversity have long been studied to identify biodiversity hotspots and shortcomings in how protected areas encapsulate those hotspots. The biodiversity of birds has had a particularly unclear relationship to protected areas, potentially due to the migratory nature of these species as this may complicate out understanding of the community composition of any given area. Here, I use morphological data in conjunction with phylogenetic data and detailed temporal abundance data for 85 species of charadriiform birds across the Midwest and the East Coast of North America to quantify spatiotemporal biodiversity of these birds in light of protected areas. To further focus on functional biodiversity, I utilize two different functional biodiversity metrics that account for intra-annual community changes due to migration in different ways. Charadriiform taxonomic, phylogenetic, and functional biodiversity was found to be spread unevenly across space and time. Additionally, regardless of which metric was used to quantify functional biodiversity while accounting for intra-annual changes in community composition, weak to nonexistent relationships between charadriiform function biodiversity and protected area coverage were found, even after accounting for variation in land cover. While future analyses are needed to conduct these analyses at a finer spatial resolution to bolster these results, this provides preliminary evidence that charadriiform land use may not relate to the protected status of lands and that future conservation efforts that explicitly consider the migratory nature of these species will be the most impactful.

4.2 Introduction

To understand how to protect biodiversity most effectively, we must understand how species are distributed across space. Studying these patterns is done through quantifying spatial biodiversity which has three widely acknowledged facets: taxonomic, phylogenetic, and functional biodiversity. Taxonomic Diversity (TD) is the most straightforward of these and considers the number of taoxnomic units (typically species) present in a given area. Phylogenetic Diversity (PD; reviewed in Winter et al. 2013) and Functional Diversity (FD; reviewed in Cadotte et al. 2011) build upon taxonomic diversity by considering how phylogenetically and ecologically diverse, respectively, a species assemblage is. There is a large body of work quantifying one (MacGregor-Fors et al., 2015; Mönkkönen and Viro, 1997), two (Leclerc et al., 2020; Oliveira et al., 2019), or all (Ke et al., 2018; Morelli et al., 2017) of these three facets across varying spatial scales. Identifying spatial variation in any of these facets is useful to both understand where to prioritize conservation efforts for effective protection (Campos et al., 2017) and to provide a nuanced understanding into how anthropogenic threats may affect biodiversity (Leclerc et al., 2020; Villéger et al., 2010).

It is possible for these three metrics to correlate with one another across space (Zhou et al., 2019) or to show proprtional changes with one another over time (Castro et al., 2023; Petchey et al., 2007). However, there is typically nuance in the relationship between these three facets. Spatial mismatches between TD, PD, and FD have been documented on global (Brum et al., 2017), continental (Zupan et al., 2014), country-wide (Devictor et al., 2010; González-Maya et al., 2016; Sobral et al., 2014; Xu et al., 2019), and hyper-local (Campos et al., 2017; Doxa et al., 2020; Wong et al., 2018) scales as well as along elevational gradients (Schumm et al., 2020; Zhou et al., 2019). Both theoretical (Kelly et al., 2014; Tucker et al., 2018) and applied (González-Maya et al., 2016; Huang et al., 2012; Zhou et al., 2019) work has suggested that mismatches between these facets can stem from both methodological and evolutionary factors, such as how traits are quantified (Huang et al., 2012; Tucker et al., 2018), the complexity of trait evolution (Tucker et al., 2018), and the phylogenetic scale of the analysis (Kelly et al., 2014). The degree of correlation between metrics has also been noted to be spatially dependent in comparisons of TD and FD patterns in mammals across Costa Rica (González-Maya et al., 2016), in comparisons of TD, PD, and FD in global analyses on mammal communities (supplementary information; Huang et al. 2012), and in comparisons of TD, PD, and FD in birds and mammals across Brazil (Sobral et al., 2014). Regardless of the underlying processes driving differences in these facets, understanding how TD, PD, and FD do or do not align provides key insights into community assembly patterns (see Pavoine and Bonsall 2011 for a review) and the appropriateness of using one metric as a proxy for others (most commonly using phylogenetic diversity as a proxy for functional diversity; Lososová et al. 2016 and Tucker et al. 2018). Similarly, mismatched responses in the three facets following long-term changes or disturbances can point to phenomena such as an increase in the presence of generalists (Monnet et al., 2014).

While understanding how the distributions of TD,PD, and FD do or do not align across space provides these various insights, a related line of research focuses more specifically on the relationship between diversity (TD, PD, or FD) and protected areas (hereafter PAs) to assess how well PAs encompass these facets of biodiversity. These concerns fit into research on area-based conservation strategies that focus on creating, improving, or further ensuring the continued protection of PAs as a way to protect species, ecosystems, or ecosystem services (Dudley et al., 2018; Watson et al., 2014). While PAs have been shown to be effective, relative to non-protected areas, in protecting diverse groups of animals (Gillingham et al., 2015; Selig and Bruno, 2010), preventing further habitat degradation (Andam et al., 2008; Gonçalves-Souza et al., 2021; Oliveira et al., 2007), and having positive social implications (Ma et al., 2020), there are concerns over the effectiveness of both marine (e.g. Guilhaumon et al. 2015; Mouillot et al. 2016) and terrestrial (e.g. Araújo et al. 2007) PAs in conserving biodiversity. Many of these concerns are also heightened in an era when climate change and other anthropogenic threats are both altering landscapes within and outside of PAs (Ren et al., 2021) and causing species ranges to shift (Chen et al., 2011; González-Orozco et al., 2023; van Beest et al., 2023).

Meta-analyses by Gray et al. (2016) and Coetzee et al. (2014) compared biodiversity within and outside of PAs and found protected area status to be associated with higher abundances and species richness, but both studies found caveats to these relationships. Gray et al. (2016) found that PAs were not as positively associated with endemic or narrow-range species as they were with overall richness and abundance metrics, nor were they associated with having a higher number of niches (as determined by comparing the number of species to individuals). Coetzee et al. (2014) found the positive relationship between richness and PAs did not hold for certain taxa (i.e. plants) or locations. Other work has found that the relationship between PAs and various facets of biodiversity differs depending on the clade studied. Across Europe, terrestrial PAs perform better then random in encapsulating amphibian phylogenetic (Thuiller et al., 2015; Zupan et al., 2014) and functional diversity (Thuiller et al., 2015), but perform worse than random efforts in encapsulating areas where overall (i.e. not just amphibian) phylogenetic (Thuiller et al., 2015; Zupan et al., 2014) or functional diversity is high (Thuiller et al., 2015). These inconsistencies in the relationship between PAs and specific facets (TD, PD, or FD) or taxa studied complicate our understanding of the efficacy of PAs in encapsulating biodiversity since locations where PAs may be the most ideal for certain taxa may differ substantially from locations where they would be ideal for others (Daru and le Roux, 2016; Zupan et al., 2014).

Birds have a particularly unclear relationship to protected areas, as evidenced by a global study that highlighted mismatches between our current network of PAs and the TD, PD, and FD of non-marine birds (Pollock et al., 2017). Llorente-Culebras et al. (2021) found that although PAs in the Iberian Penninsula often encompass amphibian, reptile, and mammal FD and PD as well as, or better than, expected by chance, the opposite trend was seen in breeding birds. In an analysis by Beresford et al. (2011) on 144 bird species across Africa, 37 did not have suitable habitat within PAs and an additional 85 had less than 25% of suitable habitat within PAs, suggesting that PAs may not be focused on habitats where birds tend to live. Complicating our understanding of this, when breeding birds across France were studied in light of the country's PA network, Devictor et al. (2010) found that the PA network better represented the TD of breeding birds than it did the PD and FD of these same birds, suggesting relationships between bird diversity and protected areas may, again, depend on the geographic range and facet of diversity studied.

Conversely, analyses in other locations have found positive relationships between facets of bird diversity and PAs. Long-term abundance studies of 128 bird species in Finland suggest that PAs successfully buffered species from abundance declines if the species had a larger portion of their regional population within those PAs (Lehikoinen et al., 2019), indicating the positive effects of PAs may be in protecting species that already utilize them. Similarly, a 2020 study on forest birds by Cazalis et al. (2020) found that while PAs do not have greater avian species richness in 8 tropical forest sites across the globe, they do encompass species of greater concern (namely specialists and endangered species) then non-protected tropical forest areas. The authors link this finding to lower rates of forest loss and degradation of quality in protected vs. non-protected areas, again suggesting that while spatial mismatches between avian TD, PD, or FD and PAs may exist, PAs still play an important role in preventing species loss. It is unclear, however, if this is specific to certain habitat types (e.g. whether the PA is in a forest, a wetland etc) or clades as Dornak et al. (2020) found evidence that North American breeding birds used PAs, but still saw population declines. Hence, various factors may affect the relationship between PAs and avian biodiversity. As Dornak et al. (2020) outline, there are several potential reasons PAs may not sufficiently encapsulate avian biodiversity or protect against population declines, two of which will be discussed here as they are particularly relevant for charadriiform birds.

It is, however, unclear how Charadriiformes choose sites for stopping, wintering, or breeding and whether or not PA status may affect the choice of location. Research has suggested that when choosing a nesting site, both the distance to other nesting species (Cunningham et al., 2016) as well as fine-scale habitat variables (e.g. solar radiation or altitude) will influence the specific location charadriiform species will choose to nest in (Keslinka et al., 2019). Studies conducted at more fine spatiotemporal scales have suggested that charadriiform use of PAs may be influenced by a variety of factors including the time of day (bar-tailed godwits, *Limosa lapponica*, in France foraged inside of PAs in the daytime, and outside in the nighttime; Jourdan et al. 2022), human activity (including human and dog recreational use; Murchison et al. 2016, as well as shellfish agriculture; Burger 2018; van Gils et al. 2006), the presence of other species (Burger, 2018), and the width of beaches available (Murchison et al., 2016). A study by Choi et al. (2019) specifically analyzed PAs in coastal areas of China for great knots (*Calidris tenuirostris*) and dunlins (*Calidris alpina*) and found that these species moved in and out of PAs with tidal cycles. Taken together, these studies suggest Charadriiformes may have highly specific habitat requirements, but it is unclear if charadriiform species are tied to locations, specific prey populations, or if they move opportunistically through local environments: the former of which greatly complicates our understanding of charadriiform biodiversity in light of PAs.

Recently, Almeida et al. (2023) examined seasonal changes in the functional diversity of bird assemblages within three habitat types in the Atlantic rain forest to understand community composition changes during annual migration cycles. By analyzing seasonal changes across multiple forest types, the authors were able to provide an in-depth understanding of how niche occupation varied seasonally and how these seasonal relationships varied across habitat types. Similarly, a large-scale analysis by Jarzyna and Stagge (2023) found strong seasonal differences in how both the TD and FD of bird species within the US vary spatially, highlighting how failure to consider such intra-annual changes can affect our understanding of biodiversity across space. Here, I expand upon these ideas and begin to address how to study the relationship between PAs and biodiversity in highly migratory bird species. I utilize detailed weekly modeled abundance datasets for 85 species of Charadriiform seen in the Midwest and East Coast of the United States in conjunction with phylogenetic and functional data to address two related questions. First, I assessed if taxonomic, phylogenetic, and functional diversity correlate with one another across space and time. Secondly, I focus on if PA coverage significantly predicts either the maximum functional diversity seen during annual migration cycles or a metric of annual heterogeneity in any given location. In addressing the latter, I also test if habitat type may be a variable confounding our understanding of how PA coverage relates to charadriiform spatial biodiversity. I find evidence for spatial and temporal mismatches between TD, PD, and FD of charadriiform birds across the study region, highlighting how both choice of biodiversity metric and a failure to consider the marked changes in bird communities due to migration can influence our understanding of avian spatial biodiversity.

4.3 Methods

4.3.1 Spatial Data Formatting and Species Abundance Data Aggregation

All analyses were run in R (version 4.2.1; R Core Team 2021). As the scope of this research was not global, I transformed all aggregated data from its original projection system (which varied) to the Albers Equal Area Conic projection (ESRI 102003): a projection system that respects size and therefore allows me to obtain equal-sized grid cells that represent communities across space. Depending on the original format of the data, I relied on either the st_transform or spTransform functions from the sf (Pebesma, 2018) and sp (Bivand et al., 2013b; Pebesma and Bivand, 2005) packages, respectively, to transform the data from its original projection system.

To determine the species present in each area at each timepoint and in what abundance they were present, I first generated a spatial object delimiting the political bounds of the area of interest (fig 4.1) using the getData and crop functions from the R package `Raster` (Hijmans, 2022). From here, a hexagonal grid of $\approx$ 312 km^2 cells was generated using the st_make_grid function from the `sf` (Pebesma, 2018) package to create a grid covering this area of interest. The ebirdst_download and load_raster functions from the `ebirdst` package (Strimas-Mackey et al., 2022) were used to download weekly, modeled abundance maps for the year 2021 available through the eBird Status and Trends dataset (Fink et al., 2021). I refer readers to `https://ebird.org/science/status-and-trends` for specific details on how these abundance maps were generated. In brief, an abundance map for any given species is generated from citizen science sightings, available through the eBird database (Sullivan et al., 2009), that have been improved, adjusted, or completed through statistical and machine learning methods that consider both human (e.g. differences in search effort or ability) and habitat use variables (e.g. ties between a specific species and a specific suite of environmental characteristics). While there may be downsides to relying on citizen science-based data, analyses by Neate-Clegg et al. (2020) suggest that in temperate regions (such as are focused on here), the trends detected in citizen science data agreed with those detected in a more formal monitoring program compared to other regions (e.g. the tropics).

Weekly abundance maps depicting the estimated number of individuals in each location were downloaded at 26.7 x 26.7 km resolution for all 153 charadriiform species for which abundance maps were available. Once these were accumulated, I used the rasterToPoints function from the R package `raster` (Hijmans, 2022) to generate a SpatialPointsDataFrame of the weekly abundance of each species. Then, each of these points was binned into the previously generated grid cells using the function point.in.poly, available through the `SpatialEco` package (Evans, 2021). A series of processing steps in base R (R Core Team, 2021) were then performed to first remove datapoints outside of the area of interest and to remove species

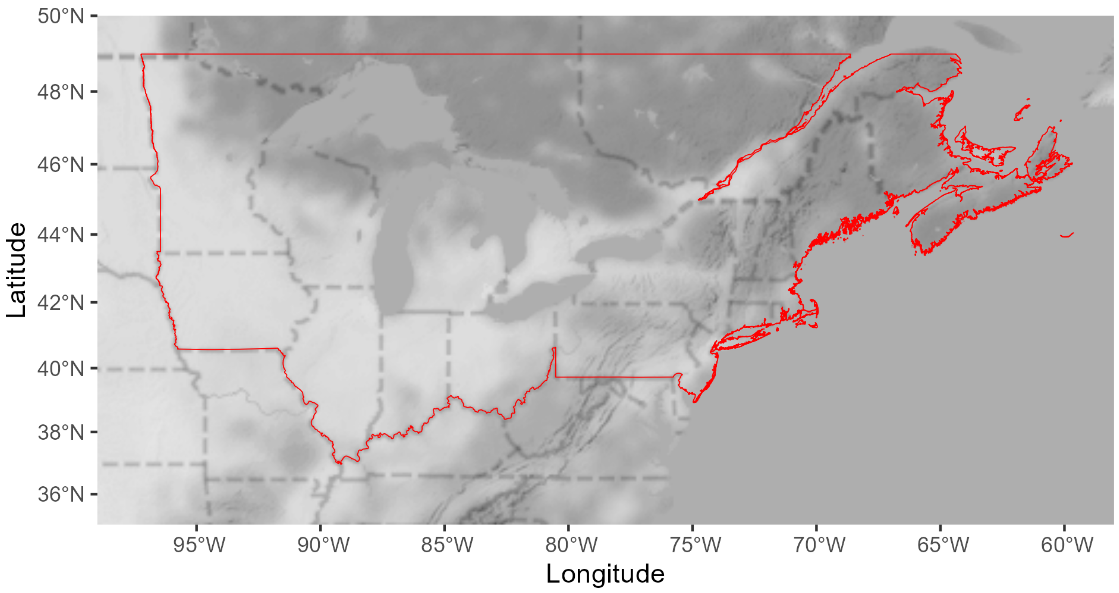

Figure 4.1: Bounds of the area studied in this chapter. The red outline denotes the boundary used to have data included in these analyses. The boundaries encompass the Great Lakes region in the midwestern parts of the United States, the East Coast of the United States, and a small amount of the southernmost portions of Canada.

completely that did not have any datapoints within the area of interest. I opted to download this larger set of data first, then remove the unneeded information, rather than selectively download the data, so I would be able to account for new species being added in the eBird Status and Trends data (Fink et al., 2021). To make the analyses computationally feasible, I slightly reduced the temporal resolution by using the rowwise function from the `dplyr` package (Wickham et al., 2022) to take the mean abundance per species per four-week time period for each grid cell. Lastly, I used the group_by and summarise_at functions also from the `dplyr` package (Wickham et al., 2022) to take mean abundance per species and grid cell. These processing steps left me with the estimated abundance per four-week period in a given grid cell for 85 charadriiform species across the Midwest and East Coast of the United States and into the Southeast portions of Canada. Hereafter, I refer to the species assemblage present in a four-week time point in a given grid cell as a 'spatiotemporal community.' I note that while this is modeled data, I will refer to the modeled species assemblage simply as the species assemblage or the species assemblage present. This is for simplicity and is done because, while the alignment between modeled or citizen science data and other data sources is certainly an area of active research (Walker and Taylor, 2017), this is not the focus here.

4.3.2 Species Phylogenetic and Functional Data Collection

In addition to data on species abundances across space and time, which can be used to calculate TD, information on 1) species phylogenetic relationships and 2) their functional traits were gathered to calculate PD and FD. The time-scaled phylogenetic tree used here originated from Černý and Natale (2022) and I refer readers to the *Methods* of Chapter 2 for a description. This tree was used to generate a cophenetic distance matrix for use in phylogenetic diversity calculations using the cophenetic.phylo function, from the `ape` package (Paradis and Schliep, 2019). The resulting matrix quantifies the pairwise distances between species on the tree based on branch lengths in units of millions of years.

To calculate FD, I gathered data on both foraging ecology and diet. The number of traits (Legras et al., 2020; Zihao et al., 2021), as well as the species pool used to generate functional space (Múrria et al., 2020), are all known to affect the output of functional diversity analyses and I, therefore, was careful to justify the inclusion of specific characteristics. Given that the goal of this analysis was to understand how charadriiform species diversity related to their use of different environments, I included two sets of data related to species-environment interactions and excluded data about other traits such as breeding biology.

The first set was a series of 12 linear measurements from the skulls of Charadriiformes that encapsulate differences in charadriiform foraging ecology. As demonstrated throughout Chapters 2 and 3, while there are broad differences (e.g. diving species compared to pecking species) that are known to relate to differences in charadriiform skull shape (Barbosa and Moreno, 1999; Natale and Slater, 2022), many charadriiform species tend to differ in slight, but significant ways in the use of microhabitats within the same area (e.g. Armitage et al. 2007; Baker 1979; Davis and Smith 2001; VanDusen et al. 2012). The 12 linear measurements (fig 4.2) were collected to quantify this specificity. Measurements were collected using digital calipers from the skulls of 195 skeletal charadriiform specimens from museum collections. Measurements were not standardized but were log-transformed prior to all other analyses after initial data exploration using the hist and shapiro.test functions from base R (R Core Team, 2021) revealed that multiple measurements were not normally distributed. Between 1 and 3 three individuals per species were measured, depending on their availability and, when applicable, the average of the measurements between the specimens was taken. I refer readers to supplementary table 8 for information on each of the specimens used.

Secondly, I included fuzzy encoded dietary characters meant to describe the overall (e.g. not season specific) diets of each species. Charadriiform species are known to differ in diet, again, both on a broad spectrum (e.g. fish vs plant eating species) and in terms of fine detail, with many sympatric species having specific differences in prey items taken (Joseph G. Strauch and Abele, 1979; Linnebjerg et al., 2013; Morera-Pujol et al., 2018; Washburn et al., 2013). Supplementary file table 9 contains specific information for each species on how dietary information was encoded but in brief: information from the *Handbook of the Birds of the World* (del Hoyo et al., 1996) was used to quantify the relative proportion (a value ranging from 0-1) of 7 distinct types of dietary items: aquatic invertebrates (both fresh and saltwater), plant material (including seeds, leaves, berries), terrestrial vertebrates (e.g. birds, mammals, reptiles), fish, eggs, carrion or offal, and terrestrial invertebrates. This left me with a dataset describing the importance of these 7 different items for each species.

These two sets of data were then used to generate a Gower distance matrix (Gower, 1971) using the gawdis function from the R package `gawdis` (de Bello et al., 2021). The

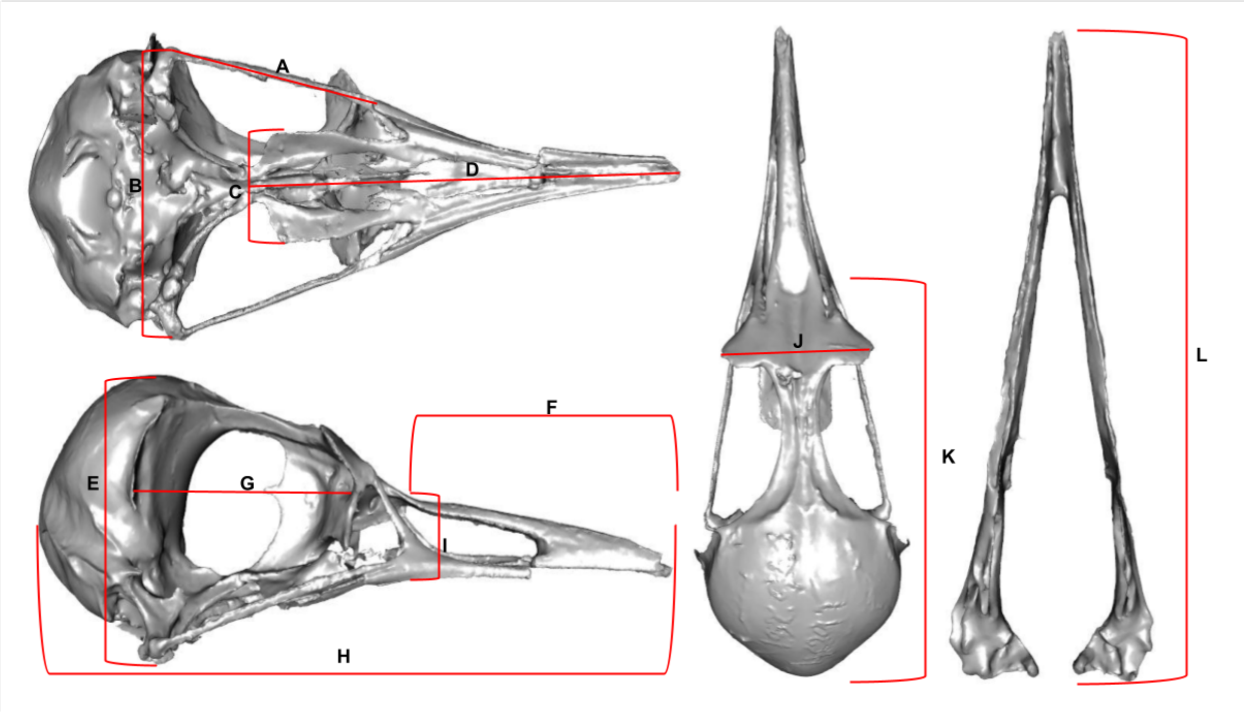

Figure 4.2: The set of 12 linear measurements collected from the skulls of . This includes A) the jugal length, B) the interquadrate width, C) the palatine width, D) the length from the back of the palatines to the tip of the beak. E) the cranial height, F) the beak length, G) the eye width, H) the total length, I) the beak height, J) the frontal width, K) cranial length, and L) the total mandible length. Measurements are shown on a surface scan of a Least Tern *Sterna antillarum* (FMNH 376281) skull.

gawdis function allows for sets of traits to have optimally weighted contributions to the overall Gower matrix. I input one grouped trait (the 12 linear measurements) and one fuzzy encoded trait (dietary composition). For the grouped trait, the function first computes a distance matrix from these measurements in isolation and then optimizes the weight of that matrix to the overall Gower matrix, rather than maximizing the contribution of the individual measurements to the overall Gower matrix. The Gower matrix generated here was made using the 'optimized' setting from the gawdis function, with the number of iterations to determine the optimal weight of each trait or group or traits set at 300. The result of this step was a pairwise distance matrix describing how ecologically similar or distinct each species pair is, with values closer to 0 representing more ecologically similar species and values closer to 1 representing more ecologically distinct species. Of the 85 species analyzed here, the pairwise values ranged from ≈ 0.005 (between the glaucous gull, *Larus hyperboreus*, and the great black-backed gull, *Larus marinus*) to ≈ 0.69 (between the little gull, *Hydrocoloeus minutus*, and the pomarine skua, *Stercorarius pomarinus*).

4.3.3 Calculating Taxonomic, Phylogenetic, and Functional Biodiversity and their Degree of Correlation with one another

To explore these various diversity metrics across space and time, I quantified three different metrics for each spatiotemporal community. First, to quantify TD, I calculated Shannon's diversity index (Shannon, 1948) for the 3551 hexagonal cells for which charadriiform species are present, again keeping each four-week time point separate. Briefly, the index (described in depth in a non-biological setting in Shannon 1948; see Ortiz-Burgos 2016 for a brief overview of its applications in biology) measures the uncertainty with which we would predict the species of any individual pulled from the community at random. Values at or closer to 0 indicate uncertainty is low such that we have a high probability of correctly predicting the species to which next individual pulled from a community belongs, with a value of 0, indicating only one species is present. High values indicate a greater degree of uncertainty and therefore more taxonomically diverse communities. This index was calculated using the `vegan` (Oksanen et al., 2022) package's diversity function.

Secondly, To calculate PD, I calculated the mean pairwise distance (MPD; see Webb 2000 and Webb et al. 2002 for a review of this and similar methods) for each spatiotemporal community. I ran the function ses.mpd from the `picante` package using the 'sample.pool' null model option based on 999 iterations. This function computes the mean pairwise distance, weighted by abundance, using the aforementioned phylogenetic distance matrix for each spatiotemporal community. Low values indicate that species are more phylogenetically clustered, whereas high values indicate phylogenetic dispersion is greater. This function compares the observed values to a null distribution calculated from randomly generated assemblages of the same size (note that this will be based on the 85 species present in the area) as the observed community to give a variety of metrics. Here, I report the quantile of this output which will provide a measure of how phylogenetically clustered or dispersed the observed community is relative to the null models. Values closer to 1 suggest that the community is more phylogenetically dispersed than expected by chance while values closer to 0 suggest the community assemblage is more phylogenetically clustered than expected by chance.

Lastly, I calculated Functional Dispersion (FDis; Laliberté and Legendre 2010) for each spatiotemporal community using the function dbFD from the R package `FD` (Laliberté and Legendre, 2010; Laliberté et al., 2014). FDis is an FD metric that uses the Gower distance matrix to create a functional space via principal coordinates analysis. The metric is then calculated as the average distance to the centroid of this functional space, weighted by each species' abundance. High FDis values indicate that individuals in any spatiotemporal community are dispersed throughout the functional space, whereas low values indicate that individuals are more functionally similar to one another and therefore that the community is less functionally diverse.

To calculate the degree of correlation between these metrics (Shannon's taxonomic diversity metric, the quantile of the phylogenetic diversity metric, the FDis functional diversity metric) across spatiotemporal communities, I performed Spearman's rank correlation tests using the cor function in the R Stats package (R Core Team, 2021). I ran these correlation tests both when all spatiotemporal communities were considered as separate data points (n= 37428 for PD values and 40559 for TD and FD values; TD and FD calculations will work with only one species and PD calculations will not) and using only the maximum annual value for each grid cell (n=3551 for TD,PD, and FD)

4.3.4 Calculating Annual Functional Heterogeneity

To calculate the annual heterogeneity of any given site during yearly cycles, I calculated a multi-unit (typically applied across multiple spatial units, but here applied across different time-points), functional dissimilarity metric using the R package `betapart` (Baselga et al., 2022). The functional dissimilarity metric uses the output of the principal coordinates analyses on the aforementioned Gower distance matrix to generate convex hulls of the species assemblages per time-point. I note that this is not abundance weighted and only considers species as either present or absent. Comparisons of the functional composition of pairs of communities is first computed by calculating the volume shared between these convex hulls (Villéger et al., 2011) through the functional.beta.core function. From here, I calculated a multi-site, functional extension of the Sørensons dissimilarity index (Baselga, 2010). In a two-sample comparison, Sørensons dissimilarity (Sørenson, 1948) quantifies dissimilarity by identifying species unique to each community and species shared between two communities with the formula:

$$B_{\mathrm{sor}} = \frac{b+c}{2a+b+c'}$$

where b is the species unique to the first community, c is the species unique to the second community, and a is the species shared between the two communities. The multi-site extension works with convex hull volumes, not species, and is described in Baselga (2010) as follows:

$$B_{\mathrm{sor}} = \frac{[\sum_{i<j} min(b_{\mathrm{ij}}, b_{\mathrm{ji}})] + [\sum_{i<j} max(b_{\mathrm{ij}}, b_{\mathrm{ji}})]}{2[\sum_{i} S_{\mathrm{i}} - S_{\mathrm{T}}] + [\sum_{i<j} min(b_{\mathrm{ij}}, b_{\mathrm{ji}})] + [\sum_{i<j} max(b_{\mathrm{ij}}, b_{\mathrm{ji}})]'}$$

where each bracketed portion is equivalent to a, b, and c above. The 'min' and 'max'(b_{ij}, b_{ji}) will compare the convex hull of species unique to community i and unique to community j, and use the minimum value and maximum values of the convex hull volumes to give a functional equivalent to b and c. Similarly,'a' in this context is an adjusted version of the convex hull shared by all community compositions with S_i representing the convex hull of all of the species in that time-point and S_T is the volume shared between all time-points. Hereafter, I refer to this multi-time-point version of this functional β_{sor} metric as MTH; Multi-Time-point Hetergeneity. Low values (those closer to 0) of MTH indicate a community has a relatively constant functional composition throughout the year with a great degree of functional overlap between each temporal community. High values (those closer to 1) indicate the location is functionally heterogeneous throughout the year or, in other words, the functional composition changes more substantially from time point to time point (see 4.6 in *Results* of this chapter for visual examples of this). For these calculations, time-points for each cell that had less then 3 species (the minimum number needed to calculate a convex hull) estimated to be present were removed and cells with less then two time-points after that processing step were also removed. This left me with MTH values for 3493 of the 3551 cells across the region.

4.3.5 Protected Area and Land Cover Data Aggregation

Data on the boundaries of PAs within the US was gathered from the UGSG Protected Area Database of the U.S. ('PAD-US'; USGS, 2022) and from the Canadian Protected and Conserved Areas Database (CPCAD; Environment and Climate Change Canada 2022). From PAD-US I gathered all available information on lands owned explicitly by agencies, designations (land protected by legislation), easements (land where development is restricted), and marine PAs. Data on land proclamations that denote planning boundaries was removed. Within these analyses, it is not feasible for me to filter this data further and therefore the term PA throughout these analyses is used to encompass formally protected lands and other effective area-based conservation measures (OECM), not only areas that fit more specific criteria (e.g. being federally protected). This data was accumulated from these two sources and the function intersect from the R package `raster` (Hijmans, 2022) was used to find overlap between each grid cell and the locations of PAs. Overlap between PAs was accounted for and the total area covered by PAs within each cell was calculated using the function st_area from the `sf` package (Pebesma, 2018). Lastly, this was converted into a percentage of the total grid cell covered by PAs.

While Charadriiformes are diverse in their habitat preferences, it is likely their spatial biodiversity is, at least somewhat, affected by stronger affinities for some habitats (e.g. wetlands) relative to others (e.g. forests). To account for this, I also collected data on land coverage per grid cell and accounted for this as a factor. Data on land coverage was taken from the Commission for Environmental Cooperation's land over database (Commission for Environmental Cooperation , CEC). This raster dataset describes land cover across North America at a 30 x 30m resolution and places each pixel into one of 18 different land cover categories. 14 of these were present in the area of interest. I removed five of these 14 (sub-polar taiga needleleaf forest, sub-polar or polar shrubland-lichen-moss, sub-polar or polar grassland-lichen-moss, sub-polar or polar barren-lichen-moss, and barren land) from any future analyses because they were present in relatively small quantities in the area with a maximum of ≈ 1.2, ≈ 0.015, ≈ 0.055, ≈ 0.045, and $\approx 15\%$ coverage in a given cell, respectively. This left me with nine different habitat types that were analyzed: water (both fresh and saltwater were combined), temperate or sub-polar needleleaf forest, temperate or sub-polar broadleaf deciduous forest, mixed forest, temperate or sub-polar shrubland, temperate or sup-polar grassland, wetland, cropland, and urban or built up areas. This dataset was imported into R using the R package `raster`. Following this, the function exact_extract from the R package `exactextractr` (Daniel Baston, 2022) was used to determine the pixel composition of each grid cell. The pixel count was then multiplied by 900 (the area in square meters of each pixel) to get the area of each grid cell covered by each land class. This was finally converted into a percentage of the total land cover in each area covered by each given land class. The result of these steps was data on the percentage of each cell covered by PAs and covered by the nine different habitat types.

4.3.6 Assessing the Relationship between Functional Diversity and Protected Area Coverage

I ran both global and localized regression models (summarized in table 4.1) assessing the degree to which protected area coverage can predict max FDis for any cell and the MTH of each cell. Globally, preliminary Moran's I tests run with the function moran.test as well as a Lagrange multiplier test (Anselin, 1988) ran using the lm.LMtests function (both functions from the `spdep` package; Bivand and Wong 2018; Bivand et al. 2013b) revealed significant evidence for spatial autocorrelation (Morans I for maximum FDis = 0.3948, $p< 2.2e\text{-}16$, Morans I for MTH = 0.3114997111, $p< 2.2e\text{-}16$). Because of this, I ran the `spdep` package functions poly2nb and nbrlistw to generate a queen's case contiguity-based neighbor and weights list, respectively, for the communities (note that rook's case contiguity would give equivalent results due the hexagonal grid cell pattern). This weights list was used in a spatial regression model that accounted for spatial error to test the relationship between the percentage of each grid cell covered by protected area and both the maximum FDis seen at any time point as well as the MTH of each cell. These tests were run with the function errorsarlm from the `spatialreg` R package (Bivand et al., 2013a; Bivand and Piras, 2015). Each model included the percentage of each habitat type and protected area coverage as predictor variables (e.g. maximum FDis ∼ percentage PA+ percentage wetland + percentage cropland etc...; see 4.1 for full syntax).

To gather preliminary evidence for region-specific relationships between PA coverage and both maximum FDis and MTH, I tested for spatial variation in this relationship using two Geographically Weighted Regressions (GWRs; Brunsdon et al. 1996). This exploratory spatial method is an extension of Ordinary Least Squares (OLS) regression that will run a local regression for each grid cell, only incorporating data from a certain nearby bandwidth. This allows us to assess if the relationship between PA coverage and our FD metrics varies through space or, in other words, if PA coverage may be more or less predictive of FD in certain areas. To run these two GWRs (one where the response variable is maximum FDis and one where it is MTH), I first estimated the optimal bandwidth for the model using the bw.gwr function from the R package `GWmodel` (Gollini et al., 2015; Lu et al., 2014) and then ran the same linear model syntax as above (maximum FDis ∼percentage PA+ percentage wetland + percentage cropland etc...) in a geographically weighted regression using the `GWmodel` package's gwr.basic function. The results of these global and local regressions, as well as for TD, PD, and FD across spatiotemporal communities, were plotted using the R package `ggmap` (Kahle and Wickham, 2013).

Table 4.1: Summary of Spatial Models used to assess the relationship between protected area (PA) coverage, land type variables, and both maximum functional dispersion (FDis) and Multi-timepoint heterogeneity(MTH). Two 'global' models run across the whole region of interest to test for the relationship broadly and two 'local' models with a set bandwidth within which the relationship was assessed were run to understand how this relationship varies across space. Under 'Syntax' some of the land cover variables are abbreviated to TempSP (Temperate or Sup-Polar needleleaf forest), TSPdeciduous (Temperate or Sub-polar broadleaf Deciduous forest), TSPshrubland (Temperate or Sub-polar Shrubland), TSPgrassland (Temperate or Sup-polar Grassland), and UrbanBU (Urban Built-Up).

Scale	Model Type	Dependent Variable	Syntax
Global	Spatial Regression with Spatial Error	Maximum Functional Dispersion	maxFDis∼PA +TempSP +TSPdeciduous +MixedForest+ TSPshrubland+ TSPgrassland+ Wetland+ Cropland+ UrbanBU+ Water
Global	Spatial Regression with Spatial Error	MTH(β_{sor})	MTH∼PA +TempSP +TSPdeciduous +MixedForest+ TSPshrubland+ TSPgrassland+ Wetland+ Cropland+ UrbanBU+ Water
Local (bandwidth of ≈ 94 km)	Geographically Weighted Regression	Maximum Functional Dispersion	maxFDis∼PA +TempSP +TSPdeciduous +MixedForest+ TSPshrubland+ TSPgrassland+ Wetland+ Cropland+ UrbanBU+ Water
Local (bandwidth of ≈ 114 km)	Geographically Weighted Regression	MTH(β_{sor})	MTH∼PA +TempSP +TSPdeciduous +MixedForest+ TSPshrubland+ TSPgrassland+ Wetland+ Cropland+ UrbanBU+ Water

4.4 Results

Four major results are outlined here. First, the 85 charadriiform species present in this area tended to be broadly dispersed across space, with only a select number of locations seeing high numbers of species or of individual birds. Second, taxonomic, phylogenetic, and functional diversity varied across time and space and correlated with one another to varying degrees. Third, MTH values were high throughout the region overall but did vary across space. Fourth, regardless of the metric used to quantify functional diversity while accounting for intra-annual changes due to migration, no significant relationships were seen between PAs, most land cover variables, and functional diversity.

4.4.1 General Points about Charadriiform Diversity across the Midwest and East Coast

Based on the aggregation procedure used here, 85 species have modeled data available in the region of study. While I did not explicitly quantify how this aligns with other data sources describing the ranges of birds, I note that this undoubtedly does exclude species (e.g. the Atlantic Puffin; *Fratercula arctica*) or specific seasons for certain species (e.g. every season except the breeding season for the Arctic Tern *Sterna paradisaea*) for which data have not been modeled, but that the availability of species-level data is not the focus here. Of the 8377 grid cells across the area of interest, 4826 ($\approx$58%) of these had no charadriiform species present at any time point and these grid cells were excluded from further analyses. In the remaining 3551 cells that did have charadriiform species present, the number of distinct species estimated within any four week time point was as high as 43, and the number of estimated individuals as high as $\approx$687. Most time point and location combinations had lower numbers of species present, with a few exhibiting exceptionally high numbers of distinct species and/or individuals (fig 4.3). A full summary of the species seen across the area, the number of cells each species was present in, their mean abundance, and maximum abundance are available in supplementary file table 10. There are 40,559 spatiotemporal communities for which there are 1 or more charadriiform species present in that cell and timepoint combination.

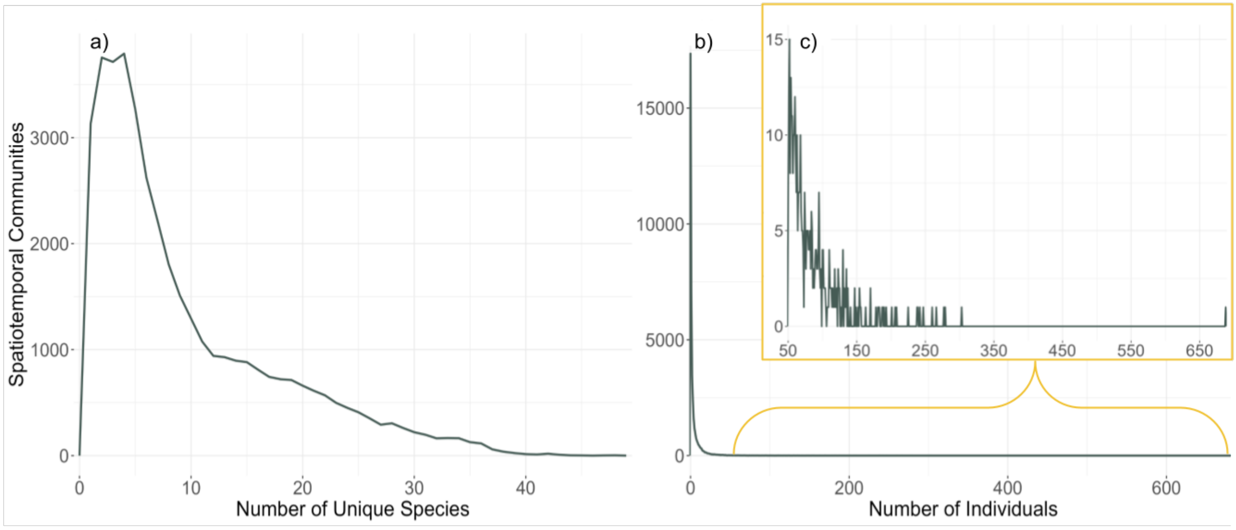

Figure 4.3: Summary of the charadriiform species and individuals estimated to be present within the ≈40,500 grid cell and timepoint combinations; referred to as "spatiotemporal communities". A) summarizes the number of spatiotemporal communities which have certain numbers of species seen and b) summarizes the number of cells which have certain numbers of individuals estimated. C) is a zoomed-in version of a portion of b) to highlight certain cells with a large number of individuals estimated. As seen in both a) and b), across the Midwest and East Coast, most locations have a small number of both estimated unique species and individual birds, with a small number of locations hosting exceptionally high numbers of either species or individuals.

4.4.2 Taxonomic, Phylogenetic, and Functional Diversity Across Annual Migration Cycles

When all spatiotemporal communities were compared to one another, the three merics correlated significantly with one another across space, but in varying ways. There was a weak,

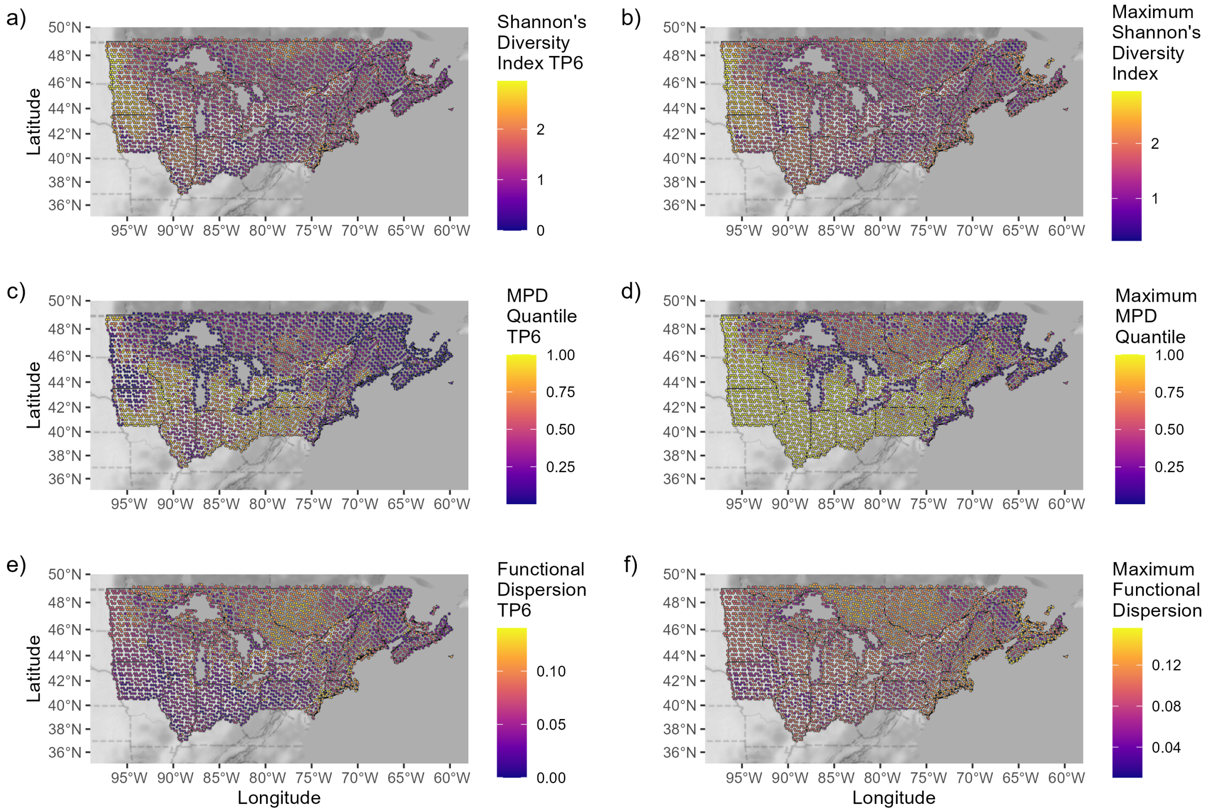

Figure 4.4: Maps of taxonomic, phylogenetic, and function biodiversity across the Midwest and East Coast for 85 different charadriiform species. The first row (a and b) show Shannon's diversity index (a metric of taxonomic diversity that considers the abundances of different species), the second row (c and d) shows the Mean Phylogenetic Distance (MPD) quantile (a measure of phylogenetic diversity), and the third row (e and f) shows functional dispersion (a measure of how functionally/ecologically diverse each community is). The first column (a, c, and e) show one, arbitrarily chosen static timepoint (TP; TP6 corresponds to May 24th-June 14th) to highlight spatial mismatches between these three facets of biodiversity within any given timepoint. The second column (b, d and e) show the maximum value for these different metrics within any given four week timepoint. In all plots, higher values indicate high diversity in that given metric.

but significant negative correlation between TD as measured by Shannon's index and PD as measured by the quantile of the MPD value relative to null models (Spearman's rank correlation $\rho =$ -0.11, $p < 0.001$). Similarly, the MPD quantile showed a weak positive, but again significant correlation with FDis ($\rho =0.04$, $p < 0.001$). Conversely, TD and FDis were much more highly positively correlated ($\rho = 0.77$, $p < 0.001$).

These results changed when only the maximum values of TD, PD, and FD for any four-week time-point were analyzed. The maximum value of Shannon's TD showed significant, moderate correlations with both the MPD quantile (ρ = 0.28, p $<$ 0.001) and with FDis (ρ = 0.29, p $<$ 0.001). The maximum MPD quantile and FDis showed a very weak negative correlation with one another (ρ = -0.05, p $<$ 0.005). These varying degrees of mismatch are apparent visually (fig 4.4). While there is some degree of alignment between the example timepoint shown (fig 4.4, the first column shows estimated values from May 24th-June 14th) such as relatively high FDis and Shannon's Diversity index in the Northern portions of Minnesota during this timepoint, there are also broad swatches of disagreement, such as high FDis values in the upper portions of the Great Lakes region at a time point where the MPD quantile is low. Similarly, there is an even lower degree of agreement between the maximum values for Shannon's TD, the MPD quantile, and FDis with the highest values for each being seen in different portions of the region of interest.

4.4.3 Calculating Multi-Time-point Heterogeneity

Values of MTH (β_{sor}) were generally high (>0.5) across the region of interest (fig 4.5). There were no clear spatial patterns in MTH across the region of interest, although lower values tended to be seen exclusively on the East Coast, particularly in New Brunswick, Nova Scotia, and the Easternmost portions of Quebec. However, β_{sor} values varied from 0 to ≈ 0.99. Figure 4.6 shows the community composition of two example communities; one with a low MTH (β_{sor} of ≈ 0.28) and one with a high MTH (β_{sor} of ≈ 0.89).

4.4.4 Assessing the Relationship between Functional Diversity, Annual Heterogeneity, and Protected Area Coverage

The global spatial regression indicated weak relationships between protected area coverage and both maximum FDis and MTH. Full results are summarized in table 4.2. None of the

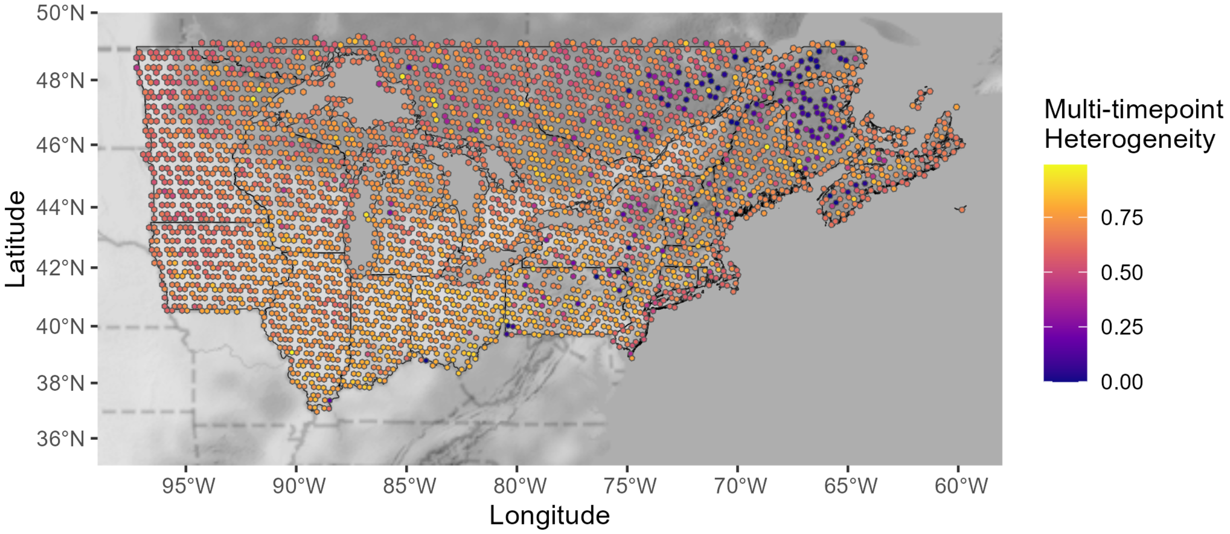

Figure 4.5: Multi-Timepoint Heterogeneity (MTH; as measured by a functional, multi-timepoint version of the β_{sor} metric) of charadriiform species across the Midwest and East Coast. Values closer to 1 indicate the functional composition is more heterogeneous throughout the year, whereas low values indicate the functional composition in that location stays more constant throughout the year. Note that three or more species need to be present at two or more time points in each grid cell for MTH to be calculated and therefore certain cells may be based on different numbers of spatiotemporal communities being compared to give the overall heterogeneity metric.

land cover variables nor the PA percentage were significant predictors of maximum FDis as determined by the P and Z values, except for the intercept ($Z = 2.1$ and $p = 0.04$). Contrasting this, several land cover variables (temperate or sup-polar needleleaf forest, temperate or sub-polar broadleaf deciduous forest, cropland, and urban built-up) were significant predictors ($p < 0.05$ and Z scores>2 or <-2) of MTH. However, it is important to note that the coefficients were very small (all <0.003 with the exception of the intercept) indicating the relationship is significant but very weak.

Locally, however, geographically weighted regressions highlighted how PA coverage and habitat type related more closely to both maximum FDis and MTH in certain areas (high R^2 indicating model is able to explain variation in that given area better; fig 4.7). Local R^2 values varied from 0.2 - 0.93 for maximum FDis and from 0.07 - 0.71 for MTH. Higher R^2 for the FDis model were seen along portions of the East Coast, portions of Iowa, and in

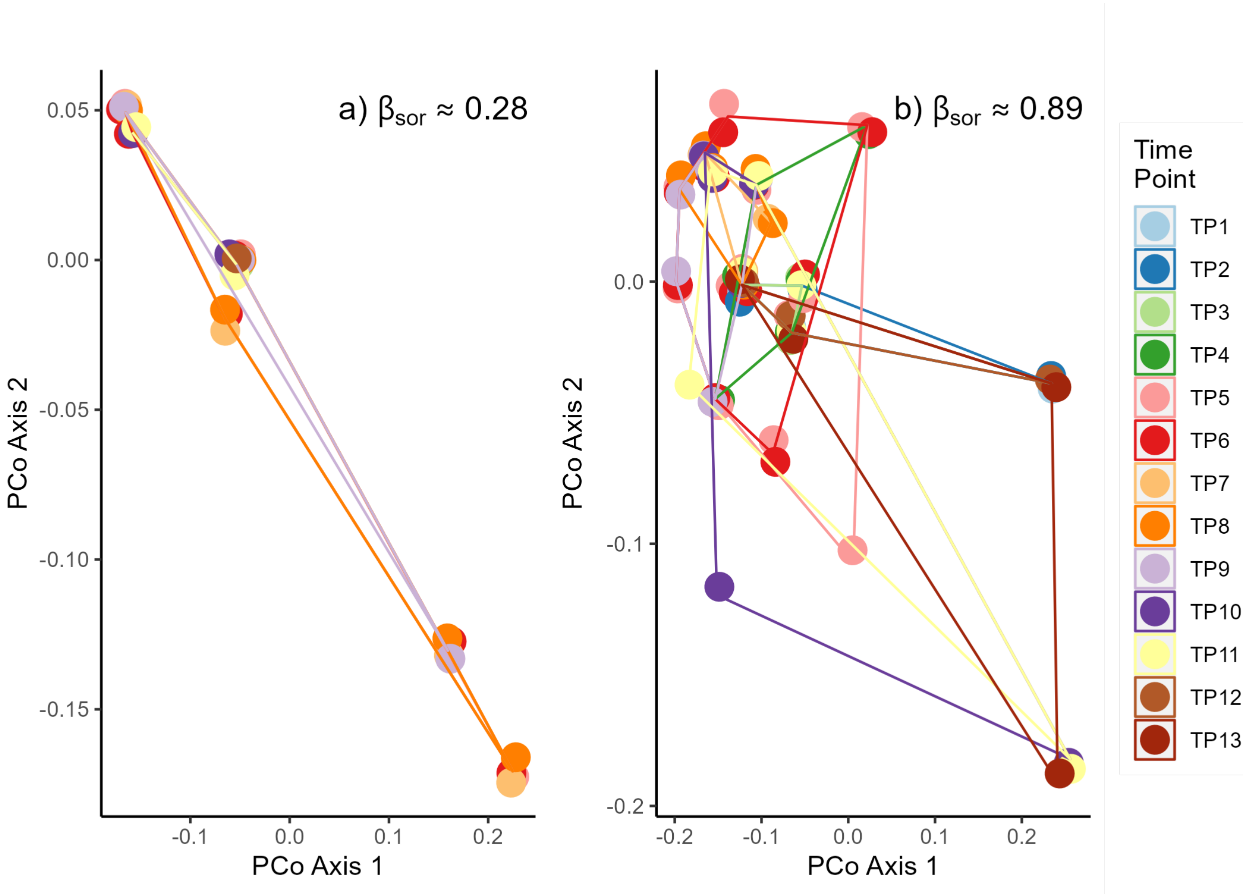

Figure 4.6: Examples of two locations with differing multi-timepoint heterogeneities throughout the year, as measured by β_{sor}. The points on each graph represent species in a trait space, generated from principal coordinates analysis on a Gower distance matrix based on ecological data for 85 different charadriiform species. Different colors show different four week timepoints per annual migration cycles. A) shows a community with a relatively low β_{sor} value and demonstrates how the communities overlap in functional space between the timepoints. B) shows a community with a relatively high β_{sor} value and demonstrates how these communities overlap much less in trait space between the timepoints. The points have been jittered to reduce overlap caused by certain species being present in multiple timepoints.

the Southernmost portions of Ontario and Quebec. The R^2 for the MTH model were more homogeneous across the region of interest, but were higher in Illinois, Indiana, portions of Minnesota, and New Brunswick. The coefficients describing the strength of the relationship between PA coverage and both FDis and MTH also varied but were universally low (ranging from -0.0012 to 0.0015 for FDis and ranging from -0.004 to 0.008 for MTH).

Table 4.2: Results of Global Regression Models on both Functional Dispersion (Maximum FDis) and Muti-Timepoint Heterogeneity (MTH). These results are from two spatial error regression models testing how well the variation in Maximum FDis and MTH of charadriiform communities across the Midwest and East Coast can be explained by both the amount of Protected Areas (PAs) and the amount of different land types in that area. Some of the land cover variables are abbreviated to TempSP (Temperate or Sup-polar needleleaf forest), TSPdeciduous (Temperate or Sub-polar broadleaf Deciduous forest), TSPshrubland (Temperate or Sub-polar shrubland), TSPgrassland (Temperate or Sup-polar grassland), and UrbanBU (Urban Built-Up). The estimated coefficient (Esimate), standard error (Std. Error), Z value, and P value (p) are given for each variable as well as for the intercept.

	Maximum FDis				MTH			
Variable	Estimate	Std. Error	z value	p	Estimate	Std. Error	z value	p
Intercept	0.20	9.43e-02	2.10	0.04	0.66	0.01	44.70	< 2.2e-16
PAs	−2.42e-05	2.63e-05	-0.92	0.36	-0.00024	0.00014	-1.68	0.09
TempSP	-1.08e-03	9.42e-04	-1.15	0.25	-0.0021	0.00025	-8.29	2.22e-16
TSP deciduous	-1.25e-03	9.45e-04	-1.32	0.19	0.00088	0.00021	4.34	1.4e-05
MixedForest	-7.84e-04	9.44e-04	-0.83	0.41	0.000201	0.00022	0.92	0.36
TSP shrubland	-1.14e-03	9.53e-04	-1.19	0.23	-0.0014	0.00077	-1.78	0.075
TSP grassland	-9.49e-04	9.83e-04	-0.97	0.33	0.000297	0.00089	0.33	0.74
Wetland	-9.45e-04	9.46e-04	-0.998	0.32	0.00043	0.00026	1.66	0.097
Cropland	-1.23e-03	9.43e-04	-1.31	0.19	0.00042	0.000166	2.52	0.01186
UrbanBU	-8.72e-04	9.52e-04	-0.92	0.36	0.00093	0.00026	3.53	0.00042
Water	-1.02e-03	9.44e-04	-1.078	0.28	0.00031	0.00018	1.7389	0.082

4.5 Discussion

The analyses conducted here quantified charadriiform diversity across the Great Lakes region in light of protected area coverage, land cover variation, and community changes due to

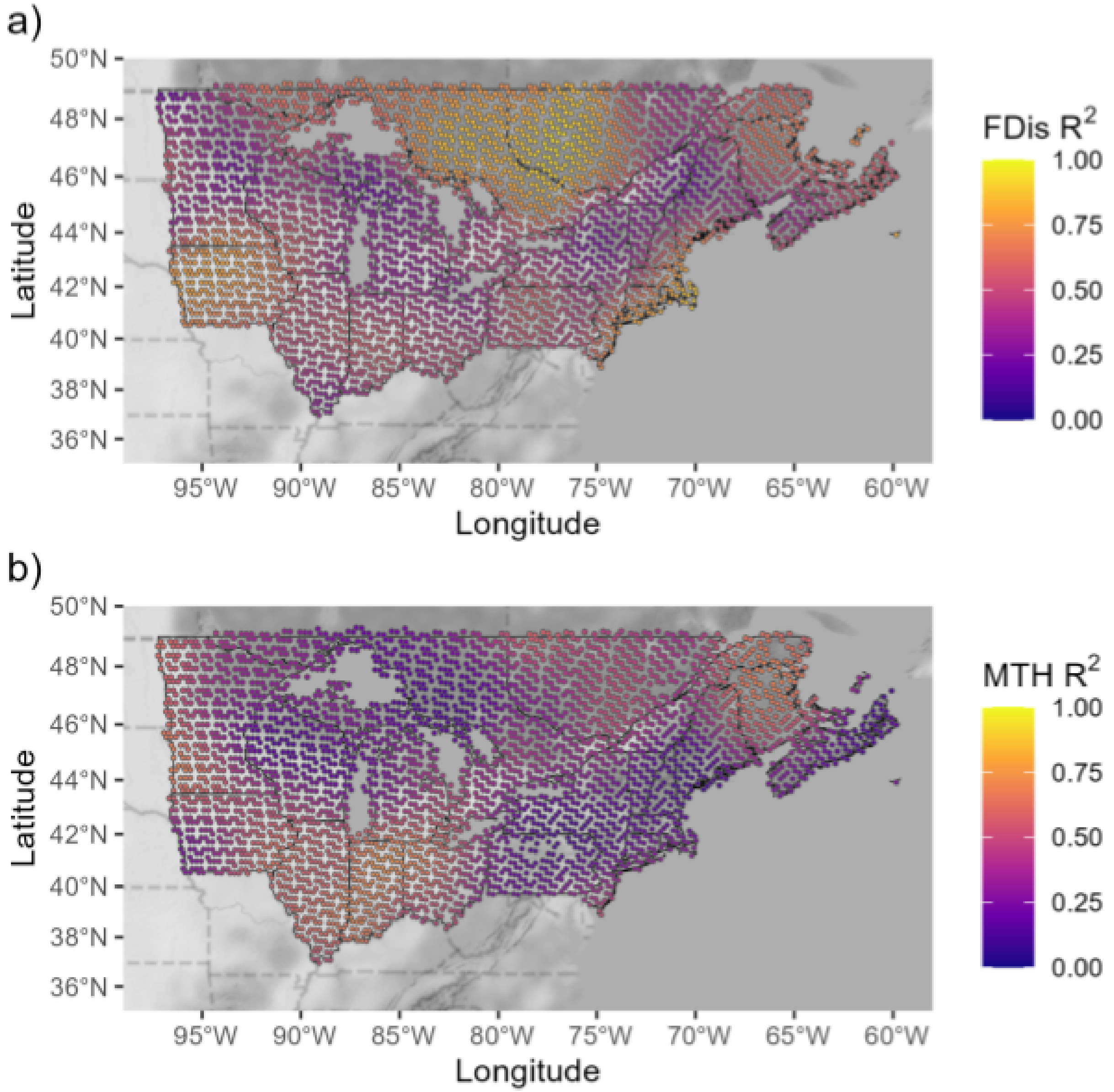

Figure 4.7: Local R^2 values from two geographically weighted regressions (GWRs) explaining the goodness of fit for regression models (summarized in table 4.1 of protected area coverage and different land cover variables (e.g. percentage covered by Croplands) on both a) maximum Functional Dispersion (FDis) and b) Multi-timepoint heterogeneity (MTH). The two GWR models run regressions locally, with a predetermined bandwidth of (of ≈94 and ≈114 km respectively) determining how many datapoints are included in the regression focusing on each cell. R^2 values closer to 1 indicate the regression better explains the variation in FDis or MTH, while values closer to 0 indicate the model poorly explains the variation in that region.

migration. Through these analyses, I revealed species-specific insights as well as broader methodological considerations that can be broadly summed in three main points. First, the entire suite of analyses highlight how differing conclusions may be reached in spatial biodiversity analyses depending on the specific diversity facet quantified and depending on how temporal variation due to migration is or is not accounted for. Secondly, local and global regressions, while possibly affected by data resolution differences, highlight the geographically heterogeneous and nuanced relationship between PAs and charadriiform biodiversity that warrants further investigation. Lastly, the application of a multi-site dissimilarity metric in a functional context to look at changes within communities during annual avian migration cycles demonstrates the utility of ecomorphology in this context and provides a promising future area of research. These three points are each considered here.

4.5.1 The Use of Different Biodiversity Metrics Affects our Conclusions of How Biodiversity Varies Across Space

Broadly speaking, the lack of strong alignment between the three different facets of biodiversity (TD, PD, and FD) across space is in agreement with previously published literature that has found metrics to align in certain areas and not in others (González-Maya et al., 2016; Huang et al., 2012; Sobral et al., 2014). The lack of a clear correlation among all three facets when all spatiotemporal communities were considered is likely due to migratory patterns that make the species composition in any area highly dynamic which is, in turn, known to create regionally-variable spatiotemporal patterns in biodiversity measures (Jarzyna and Stagge, 2023). This finding, coupled with the fact that the magnitude of the correlations changed when the maximum values were used, suggests that (in agreement with the strong spatial and seasonal decoupling seen in the analyses of Jarzyna and Stagge 2023) failing to consider even short-term temporal changes may affect our understanding of the biodiversity in avian communities in regions with highly seasonal climates. Previous research quantifying avian biodiversity has varied in how they handled the temporal uncertainty when quantifying bird community assemblages. Many studies focused on specific regions use survey data taken at specific timepoints (Almeida et al., 2023; Devictor et al., 2010; Dornak et al., 2020; Lehikoinen et al., 2019) but it is also common for studies (particularly large scale studies, e.g. Pollock et al. 2017) to use data outlining the range as a whole, or more commonly, to focus specifically on either the breeding range (Pollock et al., 2017) or (approaching this slightly differently) on the whole range of birds that are known to breed in an area (Beresford et al., 2011). In general, both studies relying on survey data and range maps also often exclude data on non-breeding ranges (Devictor et al., 2010; Dornak et al., 2020; Llorente-Culebras et al., 2021; Pollock et al., 2017).

In Charadriiformes, it is plausible that the peak diversity for any facet is reached not within the breeding range, but at stopover sites during migration and at wintering sites where mixed species flocks are known to be common (Barnard et al., 1982; Capasso et al., 2022; Gerasimov and Gerasimov, 1998). Indeed, peak values for TD, PD, and FD were seen at all possible 13 time-points, depending on the grid cell. That peak values were seen at distinct time points is in agreement with similar analyses looking at a broader taxonomic sample by Jarzyna and Stagge (2023) who found several distinct types of spatiotemporal patterns of TD and FD (e.g. when the two peak relative to the seasons) for birds within the region studied here. For highly migratory birds that use habitats opportunistically (see *Global and Local Regressions Highlight the Importance of Data Resolution as well as Chardriiform Specific Patterns*), the increasing use of telemetry tracking (Beausoleil et al., 2022; Connare and Islam, 2023; Cooper and Marra, 2020) and large scale citizen science initiatives (e.g. eBird; Sullivan et al. 2009) are enabling more nuanced investigations into both species-specific responses to anthropogenic change (e.g. understanding how individuals may adjust migration due to fluctuating environmental conditions; Dossman et al. 2023) and into taxonomically broad but region-specific spatiotemporal patterns of avian biodiveristy(Jarzyna and Stagge, 2023). In Charadriiformes specifically, radio tracking has been used to find species (Anderson et al., 2019) and subspecies (Battley et al., 2012) specific spatiotemporal migration patterns and to identify stopover sites not previously thought to be used by charadriiform species (Chan et al., 2019). The results here provide an analysis conducted on a broad spatial scope that emphasizes the importance of using these data-intensive sources that explicitly consider temporal variation to provide a necessary, comprehensive view into biodiversity across space. Similarly, differing results depending on whether maximum FDis or MTH were used in the global regression analyses further emphasize how this takeaway extends to consider annual changes in community composition.

In addition to highlighting how shorter-term temporal changes affect our ultimate understanding of which regions are important for shorebirds, the specific correlations between the three metrics and the patterns seen across space highlight the importance of metric choice. It is particularly notable that the East Coast, of the US, where we may typically expect shorebirds to be hyperdiverse, tended to have low PD values and that PD itself correlated poorly with both TD and PD in our analyses considering all spatiotemporal points. The relationship between PD and FD has been frequently discussed, as PD has the potential to be an efficient proxy for FD in an area (Lososová et al., 2016; Tucker et al., 2018). Previous work has found stronger degrees of correlation between PD and FD, even when sets of traits encompassing broad ecological differences have been used (González-Maya et al., 2016), although the strength of correlation has often been found to be dependent on which functional traits are used (Zhou et al., 2019) or how FD is characterized (Huang et al., 2012). It is possible that because, particularly in coastal regions where certain species may be hyperabundant, these abundances have a much greater impact on the mean phylogenetic distance, as opposed to FDis since FDis is calculated via a weighted average procedure and is therefore explicitly giving less weight to the hyperabundant species. Charadriiformes represent an ideal group to study how sometimes extreme variations in abundance may affect diversity calculations. Contrasting the low degree of correlation between PD and FD, I saw the highest degree of correlation between Shannon's diversity index and FDis when the spatiotemporal communities were kept as separate data points and this correlation coefficient dropped (from 0.76 to about 0.28) when the maximum value was taken. While further analyses at a finer spatial scale are needed to test this, I suggest that this drop in correlation is likely due to the concentration of Charadriiformes to a small number of locations (4.3) such that most sites, at their peak diversity values, contain a small number of phylogenetically distinct, functionally similar species (TD is low, FD is low, but PD is high) but a small number specific locations and timepoints have a large number of species (TD is high), with more species being represented phylogenetically (low PD), and a wider variety of niches being filled (high FD). These varying results depending on metrics and using either maximum or timepoint data, again, highlights the importance of considering temporal variation and specific metric when looking at biodiversity across space.

4.5.2 Global and Local Regressions Highlight the Importance of Data Resolution as Well as Charadriiform-Specific Patterns

In general, PA coverage as well as different land cover variables were non-significant predictors of the maximum FDis in any given area and weak, but significant predictors of MTH. PAs and land cover variables became much stronger predictors of both FDis and MTH in certain areas when analyzed in local regressions. These results echo those of González-Maya et al. (2016) who also found that the relationship between TD, FD and PAs varied spatially in analyses on terrestrial mammals across Costa Rica. While the results here broadly echo this finding, they also highlight specific methodological concerns as well as interesting aspects of charadriiform ecology that affect our understanding of how these birds use land.

From a methodological perspective, it is possible that mismatches between the resolution of the grid cells, the bird abundance data, the land cover data, and the PA data obscured relationships between these variables. The land cover data was at a very fine-scale resolution (30x30m), while the bird abundance data used was at a coarser resolution (26700 x 26700m; note that finer scale resolution data is available, but was not computationally feasible here), as was the size of the grid cells (each about $3.12 \times 10^7 m^2$). The locations where charadriiform diversity may be particularly high can be highly localized. One of the most well-known examples of this is the variety of charadriiform species (e.g. Red Knots, Sanderlings, Dunlins etc...) arriving at the Delaware Bay in the late spring to feed on abundant horshoecrab eggs (Castro and Myers, 1993; Tsipoura and Burger, 1999). Locations such as Delaware Bay are known to be exceptional for having not only a broad diversity of species but particularly high abundances of species with the average peak daily count between 1986-1992 as high as 216,177 individual charadriiform birds seen in that location (Clark et al., 1993). It is possible in regions such as this that diversity is related to fine-scale differences in habitat, but that averaging both bird abundances and land cover variables across relatively large grid cells that may not appropriately encompass an area (e.g. a coastline may be long and thin) is obscuring finer-scale relationships.

It is also plausible that Charadriiformes do in fact not have any particular affinity for any given habitat type, at least not across a broad scale. It is notable that a small number of landcover variables (two forest types as well as croplands and urban built-up lands) were significant predictors of MTH. While these relationships were weak (low estimated coefficient values), they were significant even across such a large scale suggesting that the landscape heterogeneity in this regions may represent an important starting point for future research. While Charadriiformes do contain typical "shorebirds" (e.g. plovers, sandpipers) associated with shorelines or wetlands, the order also contains common non-wetland-associated species. In fact, two of the top five most commonly seen species (measured by the percentage of cells the species was estimated in) are known to be predominately forest dwelling (*Scolopax minor* estimated in ≈ 99 % of the cells here) or highly opportunistic in habitat type (*Charadrius* *vociferous* estimated in ≈ 83 % of the cells here; del Hoyo et al. 1996). More generally, many 'wetland' species are known to opportunistically use wetlands that are temporarily available relative to, for example, an ocean-side beach that exists year-round (Golet et al., 2018; Skagen et al., 2008; Steen et al., 2018). Multiple studies have found that the use of these more variable habitats by shorebirds varies seasonally due to variable climate conditions from year to year. Steen et al. (2018) found that the use of temporary wetlands, seasonal wetlands, and croplands in the Prarie pothole region of the upper midwest of the US by four charadriiform species varied between a dry and wet year as certain land cover types became more or less available. On a more man-made side, similar within-year variation in the use of flooded rice fields in portions of North America not studied here has also been noted in response to both climate conditions such as changes in rainfall (Golet et al., 2018) and changes in agricultural practices (Sesser et al., 2016; Strum et al., 2013). These studies suggest the lack of relationship found here may reflect high flexibility in sites chosen for wintering, stopover, and breeding in response to annual fluctuations in key climatic factors such as precipitation.

It is also possible there is a lack of relationship between diversity and either PAs or land cover variables due to species preferences for more specific environmental conditions that do not relate to PA status or habitat type. Studies that have found varying use of areas by Charadriiformes depended on natural (Burger, 2018; Choi et al., 2019; Jourdan et al., 2022) and anthropogenic (Burger, 2018; Murchison et al., 2016) factors suggest that the positive relationships seen between avian diversity and PAs in other work (Cazalis et al., 2020; Lehikoinen et al., 2019) may not be seen in Charadriiformes due to both a higher degree of plasticity in use of environments and a sensitivity to disturbances within those PAs. The results discussed in this subsection and the previous both provide preliminary evidence that, while area-based conservation strategies (e.g. focusing on PAs) are undoubtedly critical (e.g. see Lehikoinen et al. 2019), they may not be the most effective conservation technique across broad regions when considered in isolation for highly migratory species. Rather, focusing on the connectivity of these habitats, monitoring individual populations, or more explicit considerations of this habitat use flexibility (e.g. Steen et al. 2018) when considering shorebird conservation may prove more fruitful. That local regressions between explained variation in functional dispersion and MTH suggests that, in more localized areas, area-based conservation practices may be more effective, although these more fine-scale relationships warrant further investigation (see *Future Directions: Charadriiform Biomechanics, Charadriiform Spatial Dynamics, and Integrating Ecomorphological Data into Predictive Models* in Chapter 5).

4.5.3 Multi-timepoint Functional Biodiversity as a Useful Insight into the Biodiversity of a Location

The suite of analyses used here employed a multi-time-point extension of the Sørenson's dissimilarity index: a non-multi-point version of which was used in Chapter 3 to understand differences in skull shape between different charadriiform foraging guilds. It is worth acknowledging that my specific application of this methodology could be built upon, as its current use does not include data on abundances, which are again highly variable in multi-species shorebird assemblages. However, similar to how Almeida et al. (2023) investigated functional differences in avian communities in different forest types in South America, using a multi-time-point dissimilarity metric here provided novel insight into the biodiversity of Charadriiformes across space. Differing results in both global and local regressions between the use of the MTH metric and the max FDis value highlights how useful insights can be provided by looking at heterogeneity metrics.

In temperate areas, it is obvious that the composition of bird species changes throughout the year, although data aggregation in this analysis revealed certain generalists that are present (e.g. ring-billed gull *Larus delawarensis* and killdeer *Charadrius vociferus*) through the year and that, in turn, locations sometimes only had the same suite of species year-round. In other locations, these common species were present but the location would be more heterogeneous throughout the year as less common species migrated in and out of the region during migration. As climate change proceeds and species ranges shift (Hoveka et al., 2022), increasing homogenization of communities has been noted with generalists becoming more common (Devictor et al., 2008) and this phenomenon has been shown to degrade ecosystem stability (as measured by analyzing plant biomass data across years; Wang et al. 2021). The methodology used here provides a way to understand homogenization, not across space as it is typically thought of, but within annual migration cycles and could easily be used to integrate data on specialized species with restricted ranges into large-scale spatial biodiversity studies to understand potential losses to the heterogeneity of a location if their ranges become more restricted such that they may be lost from an assemblage. In this chapter, linear measurements from skulls were critical to provide nuanced insights into how the ecology of spatiotemporal communities varied beyond what could be given through more coarse ecological classifications, such as dietary categories. The continued use of morphological data in such spatiotemporal analyses will be beneficial not only due to the efficiency in collecting these types of data, but also because it lends itself well to collaborative, large-scale work (see Chapter 5).

4.6 Conclusions

In this chapter, I built upon the established relationship between charadriiform foraging ecology and skull shape by using ecomorphological data in conjunction with freely available data on species ranges, PA coverage, and land cover to understand how the diversity of these birds is spread across space and time in light of PAs. Across the region of interest, most locations had a small number of charadriiform species present at any given timepoint, but a few locations and time-points had exceptionally high concentrations of charadriiformes estimated to be present in that area. The three facets of biodiversity (taxonomic, phylogenetic, and functional diversity) correlated to various degrees across space and time, and another metric quantifying the functional heterogeneity of species assemblages per yearly migration cycle showed different spatial patterns. Both of these findings highlight how, in highly migratory species, considering intra-annual changes in community composition due to migration may provide novel insights into a clade's spatial biodiversity. PA coverage was found to be a non-significant predictor of two functional diversity metrics (one a maximum value and one a heterogeneity metric) across the whole region. While the resolution of the data sources needs to be reconciled in future analyses, the finding that PAs were significant predictors of these diversity values in localized areas, as well as the finding that certain land cover types were significant predictors of annual heterogeneity, suggests that future analyses investigating charadriiform spatiotemporal land use patterns at a smaller scale will provide the most useful conservation insights.

CHAPTER 5

FUTURE DIRECTIONS AND CONCLUSIONS

This dissertation used detailed ecomormorphological data from a hyperdiverse order of birds, the Charadriiformes, to first understand how foraging ecology and body mass interact to explain variation in skull shape within the order (Chapter 2). Building upon this established relationship, I further investigated how skull shape differences related to the whole skull, beak, and braincase morphology and, in turn, how these different components of the skull have evolved in a modular, but still correlated manner (Chapter 3). Lastly, I used this relationship between skull morphology and foraging ecology as the basis for understanding the spatial biodiversity of Charadriiforms in light of protected area coverage and migration (Chapter 4). Taken together, these three chapters have used ecomorphology as a framework to point toward future areas of research in the realms of adaptive evolution, biomechanics, and conservation of both Charadriiformes and other taxa. Additionally, these results can be synthesized to provide multi-faceted insights into both macroevolutionary and spatial biodiversity-related questions. These future directions and broader conclusions are discussed in turn below.

5.1 Future Directions: Charadriiform Biomechanics, Charadriiform Spatial Dynamics, and Integrating Ecomorphological Data into Predictive Models

Potential areas of future research are suggested by each chapter here. First, Chapter 2 and Chapter 3 highlight gaps in our knowledge of the form-function relationship in certain charadriiform clades. As mentioned, interspecific differences in the ecology and skull morphology of the Lari (gulls, terns, skimmers, auks, coursers, buttonquails, skuas and the crab plover) are not well understood with the exception of certain ecological aspects (predominantly diet; Lato et al. 2021), select morphological structures within the group (Smith and Clarke, 2012), or a very limited interspecific comparisons (Sharker et al., 2019; Zusi, 1962). Despite the ecological diversity in this group which includes species ranging from grazing buttonquails (family Turnicidae) to pursuit diving auks (family Alcidae) to hawking pratincoles (family Glareolidae), it was difficult throughout this work to provide direct explanations of how variation in skull morphology in this group relates to differences in foraging behavior without studies directly analyzing how differences in, for example, the width of the skull related to variation in the ability to dive. This suborder has undoubtedly been difficult to study due to the unresolved taxonomic position of many of these species (Pereira and Baker, 2010) and likely due to the difficulties studying species that feed in the air or underwater (although see Enstipp et al. 2018). However, the results here suggest that ecomorphological variation in this group is present and that further study may better inform our understanding of how it has evolved, especially considering that the suborder Lari have been found to have accelerated rates of bill shape evolution when compared to a broad sample of all birds (Cooney et al., 2017).

Similarly, the support found in Chapter 3 for biomechanically informed modularity hypotheses and variation seen in components of the linkage system elements (e.g. quadrates, jugals) in the morphospace, suggested that the linkage system may be an important location of adapative change over time. Future work could further investigate the patterns of how the linkage system varies in this order, the rates of evolution of the whole system or it's individual components, or the functional consequences of changes within the morphology of the system. In regards to the latter, the potential relationship between changes in the linkage system of the skull and rynchokinesis warrants future biomechanical study. Rynchokinesis is seen in several bird clades (Zusi, 1984), including many charadriiform species (Estrella and Masero, 2007) but how common it is across Charadriiformes is unknown. While it is unclear if it would be possible to survey for this behavior across all of these species, 3D geometric morphometric data could be used in conjunction with museum specimens (to determine points of flexion) to model this distinct mode of cranial kinesis in these birds to understand how it relates to morphological differences in the skull.

Additionally, the focus on avian ecomorphology could be expanded beyond the skull and it's relationship to foraging ecology. How both skull morphology or foraging ecology relates to other morphological elements could be investigated, as previous research on wing morphology in different species of waterbirds has found it to be significantly associated with differences in foraging behaviors (Baumgart et al., 2021). The relationship between skull morphology (whether it be in Charardriiformes or other birds) and other ecological traits such as migration, thermoregulation, or nest building could be investigated to provide a more comprehensive overview of the factors shaping avian skull evolution beyond foraging ecology, as has been done in previous work on both songbirds (Friedman et al., 2019) and across broad samples of extant birds (Hunt et al., 2023). To further explore how skull diversity has evolved in Charadriiformes, future research could investigate diversification rates in the whole skull morphology, it's individual components (e.g. the linkage system as mentioned previously), or individual bones (e.g. Felice et al. 2019) as it relates to diverse ecological factors.

More broadly, the suite of analyses in Chapter 4, while they need to be further refined, highlight the utility of ecomorphology to efficiently and effectively describe both the macroevolutionary patterns of a clade and, when combined with spatial data, how ecomorphological traits can be used in spatial biodiversity analyses. There has been a relatively recent interest in quantifying what spatial biodiversity may look like in future timepoints in light of range shifts that are predicted to occur as climate change proceeds. As has been suggested elsewhere (Pigot et al., 2020), ecomorphology could provide a useful framework through which niches could be quantified to understand how well functional diversity (which will shift spatially in the future; Escobar-Luján et al. 2022; Gallagher et al. 2013; Thuiller et al. 2006; Wang et al. 2023) will be encapsulated by PAs which will, without human action, remain where they are. Morphological data has an advantage in being less ambiguous then descriptive ecological data and, because measurements can be collected in a repeatable fashion, can be used for broad comparisons if multiple researchers collect data (Ricklefs and Miles, 1994). Predictive research in light of PA coverage is commonly done for taxonomic diversity (Araújo et al., 2011; Markovic et al., 2014), but adding trait data that may be available already through trait databases such as AVONET (Tobias et al., 2022) or morphological databases such as morphosource (morphosource.org; Duke University) may add another dimension to these predictions.

Building more directly upon Chapter 4, future work could use the same or similar methods on an expanded taxonomic (i.e. looking at all birds in a community, not just Charadriiformes) and/or spatial scale of study. In the case of the latter, expanding the spatial scale of analyses may highlight interesting regional patterns in annual community composition changes, as has been done in recent work by Jarzyna and Stagge (2023) who used the same abundance dataset used here to understand spatiotemporal patterns of a large number of avian species across regions of North America. Expanding either the taxonomic scale or the spatial scale of analyses would provide broader insights into avian migration and community composition patterns than could be gained by the more specific focus of the work described in this dissertation.

The fourth chapter also highlights the potential challenges with integrating charadriiform species into these types of predictive spatial biodiversity studies. While the highly migratory nature of many charadriiform species may (through long-term monitoring of abundances, phenotypes, and behaviors) make these species important sentinels of global change, (Piersma and Lindström, 2004), it also complicates our understanding of how their ranges may shift in the future since the temporal dynamics of migration, the abundances and ranges of charadriiform prey items, as well as the climate of the locations these birds use will all be in flux. The findings here echo that of Piersma and Lindström (2004) who argue that it is unlikely, if not impossible, to make precise predictions of how shorebird populations will fare in the future in light of both their highly migratory behavior and the variety of threats the group faces (Sutherland et al., 2012), but that an improved understanding of Charadriiformes and climate change could be gained by better understanding how these birds interact with their habitats throughout the year. Such insights are already being gained for endangered charadriiform species such as the spoon-billed sandpiper (*Calidris pygmaea*; Chowdhury et al. 2022) and may become more feasible with the increased availability of tracking technologies (Flack et al., 2022) and large, detailed datasets such as the one used both here (Fink et al., 2021) and in other recent work (Jarzyna and Stagge, 2023). More specifically, this work suggests several starting points for such future analyses. Adopting a similar ecomorphological approach used here on a more detailed spatial scale may provide an effective, feasible starting point to try to understand broader patterns in charadriiform biodiversity across space. Looking at a more localized spatial scale would allow more nuanced investigations into annual heterogeneity and land use. Beginning these analyses by either looking at the specific habitat types (two types of forests, croplands, and urban areas) that significantly predicted MTH or by focusing on areas where the R^2 value was high in the geographically weighted regressions in Chapter 4 may prove fruitful starting points.

5.2 Broader Conclusions: Insights into Charadriiform Ecology, Evolution, and Ecological Diversity Across Space

This work has highlighted the exceptional ecology and morphological diversity of Charadriiformes that is best predicted by adaptations for different foraging modes with more slight diversification within families driven by allometric change (Chapter 2). This exceptional morphological diversity is the result of modular, but still correlated evolution of the beak and braincase (Chapter 3) and contributes to the exceptional ecological diversity of charadriiform assemblages across the Midwest and East Coast of the United States (Chapter 4). Morphologically, this work, particularly Chapter 3, confirms that Charadriiformes often possess the most extremes of avian skull morphology, as has been found in past work quantifying beak shape diversity across all birds which highlighted how Charadriiformes are often recovered at the most extreme points in the beak morphospaces generated (Cooney et al., 2017; Navalón et al., 2019). As discussed in chapter 2, this morphological diversity relates to both foraging ecology at the ordinal scale and allometry at the family level scale; a finding that also sheds light on why past research has varied so substantially in what analyses have determined to be the primary factors explaining variation in avian skull shape. In light of the results in Chapter 4, these small-scale differences in foraging niche are likely important for the hyper-concentrated, diverse species assemblages seen in certain locations. The relationship between these exceptional charadriiform assemblages and protected areas remains unclear, but the analyses here present a starting point for future analyses to better understand land use patterns of these species. Together, this dissertation has highlighted both the present-day spatial diversity of this ecologically diverse order of sea and shorebirds and the macroevolutionary patterns that have led to their notable skull morphologies.

5.3 Data Use Statements

This material uses data from the eBird Status and Trends Project at the Cornell Lab of Ornithology, eBird.org. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the Cornell Lab of Ornithology.

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