Reconstructing community assembly: the impacts of alternate histories on contemporary ecology

Brian Weeks

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ABSTRACT

The complexity of ecological and evolutionary processes that govern species distributions has long presented a challenge to understanding community assembly history. The work presented here develops a conceptual framework for integrating phylogenetics and biogeography to reconstruct the assembly of communities, provides empirical support for the broad applicability of this framework, tests whether morphology can serve as a proxy for behavioral ecology, and develops a novel metric of assemblage vulnerability and shows how vulnerability is related to biogeographic history. This dissertation demonstrates the need to merge evolution and ecology to reconstruct community assembly, and provides a framework for doing so. Further, the findings presented here suggest that such an interdisciplinary approach has the potential to both reveal fundamental processes shaping the assembly of natural systems, and to illuminate the functions and properties of ecosystems based on the evolutionary histories of their constituent species.

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Dedication

I would like to dedicate this dissertation to my mom, Elizabeth Copley. She told me that graduate school would be the most rewarding way I could possibly spend my time, and she was right. I would not have done this without her encouragement.

INTRODUCTION

The assembly of biotic communities is an outcome of the interplay between evolutionary and ecological processes across a dynamic landscape and a range of spatio-temporal scales. The resulting complexity makes reconstructing the assembly of communities, and disentangling the relative contributions of ecological and evolutionary processes, an inherently interdisciplinary and complex problem. Despite the challenges, satisfying generalities have emerged, like the understanding that while species composition may change across areas of endemism, similar ecologies will likely have emerged in similar environments (i.e. Buffon's Law; Nelson 1978). However, many of the attempted syntheses of empirical findings preclude confrontation with data or rely on problematic constructs. For example, the understanding that as spatial and temporal scales increase, there is a shift from intra- and inter-specific ecological interactions to evolutionary and biogeographic processes (Cavendar-Bares et al. 2009) has been an impactful idea in community ecology and the study of community assembly, but to date has largely remained untestable, as the approaches to testing this idea have largely been built on the idea of a regional species pool, a construct that tends to be idiosyncratically applied across systems (Webb 2000). With the increasing availability of molecular data and an improved understanding of Earth history, there is potential to leverage fine scale understanding of phylogenetic and phylogeographic relationships to develop an historical null expectation of community composition based on species relationships and testable hypotheses. These new data provide an unprecedented opportunity to merge biogeography, systematics and ecology to understand the interplay between evolutionary and ecological processes in the assembly of biotic communities.

Efforts to integrate evolution and ecology to understand the processes guiding assembly have a long history, stretching back to the use of taxonomic groupings to infer outcomes of

competitive exclusion (Elton 1946) and the recognition that pairs of closely-related species tend not to co-occur (Diamond 1975; Sanderson et al. 2009). More recently, reliance on taxonomic groups to explore reflections of ecological processes in patterns of evolutionary relatedness have given way to phylogenetic methods (Webb 2000; Webb et al. 2002, 2008). These approaches recognize the potential for ecological mechanisms underlying community assembly to be reflected in evolutionary relationships; however, while phylogenetic information is necessary to understanding community assembly, it is not sufficient.

The first chapter of my dissertation develops a conceptual framework for integrating systematics and biogeography to disentangle the roles of evolution and ecology in the assembly of communities. This framework develops an historical null expectation of species co-occurrence based on allopatry, speciation, and dispersion of biotas across landscapes. The framework is based on the empirical findings that species tend to be endemic at some, typically small, spatial scale and that patterns and timing of diversification tend to be congruent across the landscape. Combined, these attributes of species distributions provide information about expected patterns of co-occurrence, particularly with respect to species that are not expected to co-occur due to evolutionary history alone. This chapter develops a generalizable approach to what we call historical assembly analysis, which can serve as a template for generating a null expectation of co-occurrence for any group amenable to phylogenetic and biogeographic reconstruction. In addition to co-occurrence, in this chapter we demonstrate the importance of understanding the spatial and temporal history of accumulation of diversity in a community as context for attributing causality to ecological consequences of heritable traits. The importance of taking such an historical approach to reconstructing assembly is an empirical question that will require implementation of the framework to reconstruct the assembly of a range of communities across

taxa and systems. However, there is reason to believe that in systems in which diversity was largely generated by vicariant speciation, failure to account for history may be particularly misleading.

While there is general agreement – at least for sexually reproducing organisms – that the vast majority of diversity has been generated via allopatric speciation (Coyne & Orr 2004), there is less consensus as to whether that allopatry was the result of vicariance or long distance dispersal. In particular, in birds, there is evidence for speciation events that coincide with geological events dividing ranges (i.e. vicariance; for example, Ribas et al. 2012) and evidence of speciation that happened as a result of isolation following dispersal across a barrier (i.e. long distance dispersal; for example, Smith et al. 2014). While both of these processes tend to produce similar distributions across groups, and can result in concordant patterns of relatedness across the landscape, vicariant speciation results in more consistent spatio-temporal patterns of relatedness across clades.

One way to test whether isolation-limited (e.g. vicariant) modes of speciation or dispersal-limited (e.g. long distance dispersal) modes of speciation have predominated in generating diversity is to explore the relationship between dispersal ability and diversification rates (Claramunt et al. 2012). Positive, negative, and unimodal relationships between dispersal ability and diversification rates have been found in birds. Globally, dispersal has been positively related to diversification rates in birds (Phillimore et al. 2006), while for a major radiation of birds in South America, dispersal has inhibited diversification (Claramunt et al. 2012). Within Northern Melanesia, an intermediate pattern has been documented, with a unimodal relationship between dispersal ability and diversification rate (Diamond et al. 1976; Mayr & Diamond 2001). A unifying hypothesis was proposed in which habitat discontinuity explained these different

relationships (Claramunt et al. 2012). This hypothesis suggested that in more continuous habitats (e.g. South America), even poor dispersers have ample opportunity for dispersion, reducing the inhibition of diversification by dispersal limitation, and producing a negative relationship between dispersal and diversification rate. Conversely in global studies, which included both continuous and discontinuous habitats, dispersal could still stimulate diversification, as dispersal through discontinuous habitats would be limiting for poor dispersers.

The second chapter of my dissertation tests whether dispersal ability is related to diversification rates for birds across Australasian archipelagoes. A positive relationship would imply that dispersal-limited modes of speciation had been the dominant process generating diversity (e.g. long distance dispersal), while a negative relationship would imply a predominant role of isolation-limited modes of speciation (e.g. vicariance). Further, should a vicariant model of diversification be the dominant mode of speciation in this – highly discontinuous – island system, it would imply that habitat discontinuity likely had not resulted in a negative relationship between dispersal ability and diversification rate in other systems, which could not be more discontinuous than islands.

Using hand-wing index, a morphological index of wing shape that is related to flight efficiency (Kipp 1958) and dispersal ability in birds (Lockwood et al. 1998; Moore et al. 2008; Claramunt et al. 2012), and molecular data to estimate diversification rates, we demonstrated that dispersal has inhibited avian diversification in Australasian Archipelagoes. Further, we show that our finding differs from past discovery of a unimodal relationship between dispersal and diversification (Diamond et al. 1976; Mayr & Diamond 2001) due to our ability to estimate clade age using molecular data, rather than our method for approximating dispersal ability. This finding suggests that isolation-limited modes of speciation (e.g. vicariance) have been the

dominant mechanism of diversification in this system. Because this system is comprised of islands, with a focus on oceanic islands, we argue that habitat discontinuity is not likely to shift the relative contributions of dispersal-limited and isolation-limited mechanisms of speciation in other systems. This finding, supports the broad applicability of the conceptual framework developed in Chapter 1, as isolation-limited modes of speciation are expected to result in extreme spatio-temporal congruence of diversification of multiple groups across the landscape.

Historical assembly analysis has the capacity to disentangle the evolutionary and ecological processes influencing community assembly, and in doing so, also reveals aspects of the assembly process that might influence the ecologies of the resulting systems. At ecological timescales, it is clear that historical processes associated with community assembly (e.g. the relative order and timing of arrival into a community) can alter the ecologies of communities (Fukami & Morin 2003; Fukami et al. 2010). While historical contingency has altered community composition and ecosystem functioning at ecological timescales, it is unclear to what extent historical contingency can produce long-lasting ecological impacts that persist across evolutionary timescale (i.e. evolutionary priority effects; Fukami 2015). Initial efforts to answer this question have found limited support for the presence of evolutionary priority effects, however these efforts have been limited by the study system, which to date has been a single island with a single assembly history that is poorly understood (Leopold et al. 2015). An ideal system to test for effects of alternate assembly histories would be a series of natural communities that are ecological replicates but differ in their biogeographic histories.

Because they are comprised of discrete island communities with varied biogeographic histories but similar environments, the Solomon Archipelago are an ideal system to evaluate the ability of historical contingency in assembly to have persistent ecological impacts. Within the

Archpielago, birds are an ideal taxon because their distributions are extremely well known, and they are nearly comprehensively represented in natural history collections. An additional challenge to studies of the ecological outcomes of alternate assembly histories is bridging the scale at which behavioral ecology can be characterized through fieldwork and the scale at which assembly history questions must be asked. Morphology is frequently associated with a range of behaviors in birds (Ricklefs & Travis 1980; Miles & Ricklefs 1984; Fitzpatrick 1985a), and is often used as a proxy for bird behavior; the ability to collect morphological data across scales makes it a powerful tool for characterizing behavioral ecology at a scale necessary to ask questions about alternate community assembly histories.

While morphology has been correlated with behavior in some birds, these studies have largely been restricted to continental species, which may have had more tightly coupled morphological and behavioral evolutionary trajectories than birds in island systems. Islands are known to stimulate rapid evolutionary change as colonists adapt to significantly different environmental and biological contexts in their novel environments, and behavioral traits tend to be more evolutionarily labile than morphological traits (Blomberg et al. 2003). In the Solomon Archipelago, rapid behavioral evolution has decoupled some behaviors from morphology (e.g. behavioral flightlessness; Diamond 1981).

In order to test whether morphological traits can serve as an appropriate proxy for behavior in the Solomon Islands, the third chapter of this dissertation tests whether behavior is correlated with morphology across taxonomic scales. This chapter uses direct behavioral observations of mixed-species foraging flocks across a suite of islands in the Solomon Archipelago to characterize the position in the canopy and foraging maneuvers used by each taxon on each island. The behaviors are then correlated with morphology to establish whether

differences in behavior between very closely related groups despite a history of colonization of islands. Our results suggest that morphology is correlated with foraging behavior both between groups (i.e. at deeper phylogenetic levels) and within taxa (i.e. between different populations of taxa within a single genus). Importantly, because morphology is correlated with behavioral ecology, it can be used to scale up characterization of behavioral ecology so that the effects of alternate assembly histories on contemporary ecologies, or ecosystem properties can be tested.

We use morphology to develop the concept of assemblage fragility, an ecosystem property, and explore the relationships between diversity and assemblage fragility. Biodiversity is related to ecosystem properties and functions in predictable ways (e.g., higher ecosystem function, greater stability of function, and increased resistance to invasion; Naeem et al. 2000; Levine et al. 2004; Fargione & Tilman 2005; Haddad et al. 2011; Byun et al. 2013; Tilman et al. 2014; Hautier et al. 2015). Some of the relationships between biodiversity and ecosystem functioning and properties (e.g., reduced susceptibility to invasion) may influence evolutionary processes, like rates of extinction. As such, there may be a link between the effects of biodiversity on ecosystem function and the assembly of communities across evolutionary time. To date, exploration of this link has been limited by constraints to evaluating biodiversity and ecosystem functioning in natural systems with different levels of diversity and assembly histories.

The fourth chapter of this dissertation develops an ecosystem property: *assemblage vulnerability*, which is a metric of the collective vulnerability of constituent species in a community. We relate assemblage vulnerability to three different metrics of biodiversity, two types of functional diversity and species richness, across the Solomon Archipelago. We demonstrate that, paradoxically, more diverse islands are characterized by more vulnerable

assemblages. We interpret this as evidence that more biodiverse systems have served as "safe harbors" for vulnerable species across evolutionary time. Further, we demonstrate that island connectivity through the Pleistocene has a significant impact on the relationship between biodiversity and assemblage fragility. Biogeographic processes, like island connectivity and isolation as a result of sea level fluctuation, are often overlooked in studies examining the relationship between biodiversity and ecosystem function. These findings have implications for the application of principles derived from biodiversity and ecosystem function studies to natural systems, and also suggest that alternate community assembly histories can have persistent effects on contemporary ecological relationships in communities.

When taken together, the findings presented here demonstrate the necessity of integrating systematics, biogeography, and ecology in reconstructing community assembly. Additionally, this work outlines an exciting avenue of future research: taking advantage of the conceptual framework presented here, and applied to the birds of the Solomon Archipelago to further explore the potential for evolutionary priority effects to shape natural systems. I view this future work as both having the potential to reveal the relative importance of evolutionary and ecological processes in guiding biotic assembly, reconciling conflicting findings in the ecological literature that may be the result of alternate assembly histories, and potentially leading to the ability to make predictive statements about the ecologies of systems based on the evolutionary histories of the constituent species.

CHAPTER 1. INTEGRATING SYSTEMATICS AND BIOGEOGRAPHY TO DISENTANGLE THE ROLES OF HISTORY AND ECOLOGY IN BIOTIC ASSEMBLY

B.C. Weeks, S. Claramunt, and J. Cracraft.

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Abstract:

Aim: We develop a conceptual framework for integrating evolutionary history and ecological processes into studies of biotic assembly.

Location: Global.

Methods: We use theoretical and empirical examples to demonstrate that species distributions are non-random outcomes of first-order processes of biotic evolution: allopatry (isolation of populations), speciation, and dispersion of biotas across landscapes. We then outline generalizable steps for integrating methods of phylogenetic and historical biogeographic analyses into studies of biotic assembly.

Results: We present a framework that can be applied to any biotic assemblage amenable to phylogenetic and historical biogeographic analyses, can accommodate changes in spatial extent and temporal scale, and will facilitate comparison of assembly processes across biotas. Additionally, we demonstrate the utility of an historical approach for providing context to ecological influences on evolutionary processes, such as trait evolution.

Main conclusions: By focusing on reconstructing the histories of individual lineages, an historical approach to assembly analysis can reveal the timing and underlying processes guiding biotic assembly, making it possible to disentangle the roles of history and ecology in the assembly process.

Introduction

The information contained in the evolutionary relationships of co-occurring species has the potential to illuminate the processes underlying biotic assembly (Elton 1946; Diamond 1975; Webb et al. 2002; Vamosi et al. 2009). In recent years, there have been advances in methods that search for patterns in the phylogenetic relationships among co-occurring species. Interpretations of these patterns have led to the development of the field of community phylogenetics (Webb et al. 2002; Johnson & Stinchcombe 2007; Cavendar-Bares et al. 2009; Vamosi et al. 2009; Vellend 2010). Community phylogenetic studies have focused primarily on the roles of biotic interactions (e.g. competition and predation) and abiotic filters as the causal bases for structuring taxonomic composition (Gleason, 1926; Diamond, 1975; Weiher & Keddy, 1999; Hubbell, 2001; Gotzenberger *et al.*, 2012, and references therein).

Multiple approaches exist for integrating phylogenetic data and species distributions to examine patterns of co-occurrence (Webb et al. 2002; Johnson & Stinchcombe 2007; Kraft et al. 2007; Emerson & Gillespie 2008; Cavendar-Bares et al. 2009; Kembel 2009; Vamosi et al. 2009; Vellend 2010; Swenson 2013; Borregaard et al. 2014; Pigot & Etienne 2015). Increasingly, these approaches are being viewed in the context of two broad categories: site-based approaches and clade-based approaches (Borregaard *et al.*, 2014). Site-based approaches use null-model sampling of a regional species pool to develop an expected pattern of phylogenetic relatedness, assuming a group of species is drawn from the regional pool irrespective of their ecologies. If the observed pattern of phylogenetic relatedness of the species in an assemblage (i.e. groups of co-occurring species that may or may not be interacting ecologically) deviates from the null expectation, this pattern is then interpreted as the outcome of underlying ecological processes (e.g. competition or abiotic filtering; Lovette & Hochachka, 2006; Slingsby & Verboom, 2006;

Helmus *et al.*, 2007). Clade-based metrics examine relationships between sister clades, and have traditionally focused more on questions related to evolutionary history, like inferring the relative importance of different modes of speciation based on degree of range overlap (Barraclough & Vogler 2000). Recently, arguments have been made for the necessity of integrating these two alternative approaches in order to disentangle the influences of evolutionary history and ecological processes on biotic assembly (Wiens 2012; Warren et al. 2014).

Efforts to combine site-based and clade-based approaches have examined shifts in patterns of relatedness at different phylogenetic scales (Borregaard et al. 2014) and incorporated general patterns expected to result from speciation into null expectations (Pigot & Etienne 2015). These advances, while significant, focus on developing regional species-pools instead of reconstructing evolutionary histories. However, evolutionary history is complex and processes like allopatric speciation can result in both general and lineage-specific patterns of phylogenetic relatedness, even at small spatial scales.

The extent to which evolutionary history has resulted in non-random phylogenetic structure in contemporary assemblages is an empirical question. To assess the degree to which current research may be erroneously interpreting historical influence as an outcome of ecological processes, the effects of historical contingency must be distinguished from the effects of ecological processes on the species composition of assemblages (Wiens 2012; Warren et al. 2014). Attempts to apply an historical perspective to understanding assembly have relied on integrating phylogenetic data into studies of biotic assembly. Understanding phylogenetic relationships is necessary when developing expectations of co-occurrence as a result of evolutionary history, but it is not sufficient. To date, what has been missing is the development of historically-driven expectations of co-occurrence, especially those derived from the

mechanistic link between speciation and Earth history, and then the testing of those expectations using phylogenetic and biogeographic analyses.

By considering phylogenetic relationships in conjunction with historical biogeography (i.e. the relationship between Earth history, evolutionary processes, and species distributions; Lomolino *et al.*, 2010), one can reconstruct the accumulation of diversity in an area through space and time. A theoretical framework for incorporating evolutionary processes into studies of assembly is a prerequisite for examining the extent to which evolutionary history is driving the patterns being revealed by community phylogenetic research.

We propose a conceptual framework for the explicit incorporation of first-order processes of biotic diversification (allopatry, speciation, and dispersion of biotas following the breakdown of barriers) into studies of assembly. This new approach, historical assembly analysis (HAA), develops an "historical null expectation" for a local assemblage: the species composition that would be expected based solely on the evolutionary history of the lineages of species in the assemblage. HAA is based on historical biogeography of individual clades at the species level, and aims to reconstruct the assembly process across a dynamic spatial and biological landscape. This approach does not rely on generating "null" expectations of occurrence based on resampling from a single species pool for all species in a local assemblage. Instead, HAA uses congruence and discontinuity in individual lineage histories within an assemblage, in conjunction with Earth history, to develop historical expectations for the presence or absence of individual species in an area. Below, we discuss how community phylogenetic approaches can be integrated with methods of historical biogeography and diversification analysis so that patterns resulting from evolutionary history can be distinguished from those produced by ecological processes.

The role of evolution and biogeography in biotic assembly

Two empirical observations about organismal distributions provide insight into biotic assembly. First, the large majority of species are not widespread but are restricted in distribution; they are endemic to an area of some spatial extent. This results in differences in taxonomic composition across areas (Buffon's law; Nelson, 1978). Second, biotas have historical structure: groups of species sharing a recent common ancestor (clades) are non-randomly distributed (Lynch 1989). Congruent patterns of phylogenetic relatedness across space and time have been repeatedly identified in independent phylogenetic lineages (Nelson & Platnick 1981; Morrone 2014). Moreover, we have increasingly understood the influence of geologic and climatic history on the distribution of taxa at all taxonomic levels as well as across broad temporal and spatial ranges (Rosen 1978; Riddle et al. 2008).

Whenever allopatric speciation generates new diversity, it produces consistent spatial patterns of relatedness (Warren et al. 2014; Pigot & Etienne 2015). For example, as vicariant barriers arise and induce speciation, the resulting sister species do not co-occur; rather, they are isolated from each other by the barrier that caused speciation (Fig. 1). In the absence of this historical knowledge, if a study area were situated on one side of a barrier that resulted in speciation, the apparent pattern —phylogenetic overdispersion, or non-overlapping ranges of closely related species— might be interpreted as evidence of competitive exclusion instead of allopatric speciation (Fig. 1). Because the origin of a barrier can induce speciation across multiple lineages within an assemblage, single vicariant events often result in congruent distributional patterns of phylogenetic relatedness among allopatric sister-species, or across entire biotas (Nelson & Platnick, 1981; Riddle *et al.*, 2008; Morrone, 2014). Consequently, vicariant speciation necessarily results in patterns of phylogenetic overdispersion. Within a

single clade, vicariance produces what we will call *historical areas*: areas that are delineated by barriers that led to isolation and speciation, and the area is the initial range of a species at the time of speciation. When multiple species have congruent historical areas, those areas constituent an area of endemism (Fig. 2).

Emerging patterns in the phylogenetic structure of assemblages, like a shift from phylogenetic overdispersion to clustering as the spatial extent of the analysis increases, have traditionally been attributed to different ecological assembly rules operating at different spatial scales, or extent (Slingsby & Verboom, 2006; Swenson *et al.*, 2006; Cavendar-Bares *et al.*, 2009; Vamosi *et al.*, 2009; Emerson *et al.*, 2011), but those patterns likely reflect a significant influence of history. As the size of the area of analysis changes, the relationship between the study area and historical area(s) can change, potentially changing the expected pattern of phylogenetic relatedness from overdispersion to clustering, especially when the study area spans across multiple speciation barriers. For example, in Amazonian birds, river formation is often invoked as the mechanism by which speciation occurs. In this system, therefore, as the study area increases in size and crosses the boundaries of historical areas (i.e. the study area spans two sides of a river that induced speciation upon its formation), species with different historical areas will be found in the study area, and those species will likely be closely related due to the spatial outcomes of speciation (i.e. sister-species are likely to be present in adjacent areas of endemism).

While the spatial outcomes of evolutionary history may appear simple, they grow increasingly complex as areas are further subdivided by barriers, some species fail to speciate, and barriers break down leading to secondary sympatry. The problem is more acute when the "species pool" includes species with incongruent historical areas (e.g. species from two areas of endemism) or when many, or most, species present in a study area dispersed across a physical or

ecological barrier to reach the area (Cooper et al. 2008; Emerson & Gillespie 2008; Cardillo 2011). The variety of processes that are constantly acting in concert, and the potential for different outcomes for different species with shared spatial histories, challenge the notion that the complexity of the evolutionary patterns in the assembly of a biota can be captured without reconstructing lineage-specific histories. Even if one accepts that a species pool is not static over time (Cavendar-Bares et al. 2009; Pigot & Etienne 2015), the concept itself constrains thinking about how assemblages have been structured by evolutionary processes and raises the question, "How was the pool itself assembled?"

By first considering species in assemblages to be the outcome of *in situ* diversification rather than filtered from an exogenous regional species pool, it becomes possible to incorporate the complexity of biogeographic history into traditional null expectations. Once the influences of allopatry, speciation, and the dispersion of biotas on patterns of co-occurrence are explicitly reconstructed for individual species' lineages, one can to search for deviations from these expected historical patterns (the "historical null") and then identify ecological explanations for them.

Historical assembly analysis

Phylogenies and geographic distributions provide the basic data for reconstructing the landscape features that are likely associated causally with particular speciation events, as well as with the history of connectivity of areas and their biotas (Donoghue & Moore 2003; Riddle et al. 2008; Ree & Sanmartín 2009; Ribas et al. 2012). The fields of systematics and historical biogeography have developed methods for interpreting these data, and can inform the integration of evolutionary processes into ecological studies of biotic assembly. Integration of Earth history,

climate, and historical patterns of diversification provide testable explanations for the variation in assemblage composition that can be attributed to evolutionary history alone.

We propose historical assembly analysis (HAA), a conceptual framework for integrating evolutionary history into biotic assembly, in which phylogenetic and biogeographic tools are used to reconstruct the histories of lineages through time and space (Table 1). HAA focuses on discovering historical areas for each lineage in an assemblage, which is accomplished through an iterative process of testing biogeographical hypotheses. Generalities and mechanistic processes can then be discovered by examining the relationships among the diversification histories of co-occurring lineages, on the one hand, and Earth history on the other (Crisp et al. 2011).

When a group is chosen for assembly analysis, its constituent species and their potential biotic interactions can be seen as a consequence of the history of the area as well as species-specific evolutionary dynamics. Area histories are fluid, with changes in landscape and species composition themselves potentially changing ecological interactions. Thus, ecological interactions operate within a dynamic historical context to influence the structure of one or more assemblages within the study area.

The goal of HAA is to partition the causal dynamics of species composition within an assemblage into factors that are a consequence of species evolutionary histories and the factors that are a function of local ecological dynamics. Although the precise methods to develop an historical null expectation will vary across studies, there are conceptual steps that can be followed in undertaking HAA in any system amenable to phylogenetic and historical biogeographic analyses (Table 1). The first step to HAA is to delimit the study area that is relevant for the species of interest. The study area could be as spatially restricted as a single study plot, or as large, for example, as an area of endemism or a biome (such as Amazonia). The

size of the study area will likely be related to the species being studied ("target species"). Whereas Amazonia may be too large and complex to study the assembly of its butterfly fauna—with its high diversity and many small areas of endemism—it might be a reasonable study area for analysis of birds or mammals. If the study area were a local assemblage (i.e. of limited spatial extent), a broader choice of study taxa could be possible. This step in HAA establishes the context for all subsequent steps and entails delimiting the boundaries of an assemblage and quantifying its diversity (Magurran & McGill 2011; Morin 2011).

Once a study area has been delineated, the second step is reconstructing the history of the assemblage in that area, which requires placing the study area into a broader spatial context, defined by the histories of speciation of the species being analyzed (Fig. 2). In order to do this, one identifies the distributions and original ranges of members of the assemblage and their close relatives to identify the barriers potentially responsible for speciation. Understanding the historical context of the study area is an iterative process; general patterns, like areas of endemism, may guide initial taxonomic sampling for more detailed phylogenetic and historical biogeographic analyses that provide lineage-specific histories, allowing the relevant historical areas to be discovered for each target species (Table 1, Steps 2a-2c).

By identifying patterns of congruence in the distributions of target species and their close relatives (e.g. if the distributions of target species and their close relatives largely follow the boundaries of areas of endemism; Cracraft, 1985; Goloboff, 2007; Kreft & Jetz, 2010; Arias *et al.*, 2011), one can understand the hierarchical structure of distributions. For example, a species may be endemic to a single area of endemism, its genus may be endemic to a region, and the family may be endemic to a continent (Table 1, Step 2a). Historical areas can be of variable size depending on the historical barriers that led to isolation and speciation of the target species

within that area. The size of historical areas can be different for different species within the same taxonomic groups (e.g. multiple species of birds within the same genus), or be consistent due to conserved dispersal abilities. Thus, reconstructing patterns of speciation using phylogenetic and biogeographic analysis to understand lineage-specific histories is key to deciphering the causal dynamics of co-occurrences, and to identifying the relevant historical area for each target species. Central to developing a detailed understanding of historical areas is the iterative process of identifying the relevant close relatives of the target species, reconstructing their phylogenetic relationships, and then assessing their spatial history using methods of historical biogeography (Table 1, Steps 2b-2c).

Time-calibrated phylogenies reveal both evolutionary relationships and timing of diversification for the target species and their close relatives (Swofford et al. 1996; Arbogast et al. 2002; Rannala & Yang 2003; Felsenstein 2004; Drummond et al. 2012). Phylogenies also enable the delineation of historical areas and the use of historical biogeography to discover shared historical relationships across lineages and areas (Nelson & Platnick 1981; Hovenkamp 2001; Porzecanski & Cracraft 2005; Ree & Smith 2007; Ronquist & Sanmartín 2011). For example, multiple species in the Inambari area of endemism in south-western Amazonia are sister to species distributed in adjacent areas of endemism in southern or north-western Amazonia (Ron 2000; Ribas et al. 2012); therefore, it is necessary to incorporate those other biogeographic regions into the analysis. If phylogenies are time-calibrated, speciation events can potentially be associated with the events in Earth history that established allopatry and speciation (Crisp et al. 2011; Ribas et al. 2012). This may reveal a persistent role for these barriers in limiting range expansion via dispersion across the landscape, and can potentially explain the absence of certain species from an assemblage. Long-distance dispersal events can also be

inferred using phylogenies and geographic distributions through the discovery of target species that do not share biogeographic or temporally congruent patterns with other members of the assemblage (Crisp et al. 2011; Ronquist & Sanmartín 2011). Through historical biogeographical analysis one can reconstruct area-relationships (i.e. the history of geological connectivity among areas) and potentially identify species that may be absent from an area due to biogeographic history alone.

The third step of HAA is to identify the potential changes in Earth history (e.g., geomorphological changes, climatic changes, etc.) that may have shaped biotic distributions (Table 1, Step 3). Patterns of speciation and biogeography across groups can be used in connection with reconstructions of landscape change to understand how physical factors have shaped those landscapes and their constituent species during assembly (Campbell et al. 2006; Badgley et al. 2008; Picard et al. 2008; Cheng et al. 2013).

The final step of HAA is to synthesize across all previous steps, matching the timing and spatial patterns of biotic diversification with Earth history in order to understand the causal linkages between the two. This step establishes an historical expectation of co-occurrence in a local assemblage. Contemporary barriers such as rivers that led to speciation can be expected to limit co-occurrence of the resulting sister species or sister clades. Past barriers responsible for ancient speciation events (e.g. tectonic processes in the Andes, former connections of Amazonia and the Atlantic Coast Forest, or palaeoriver drainages) may have since disappeared, allowing for secondary sympatry of sister lineages in a local assemblage. This process of allopatry of populations, speciation, and the breakdown of barriers allowing for secondary sympatry has led to the accumulation of diversity in local assemblages. By reconstructing these processes through time for an area and the biota found there, one can view the composition and landscape dynamics

of local assemblages through time and identify persistent barriers of evolutionary significance that continue to shape species composition in an area. Once expectations of assemblage composition based on HAA have been developed, deviations from those expectations can be attributed to ecological processes. For example, if there is evidence that a barrier that induced speciation across a number of lineages has since broken down, but two of the sister species remain allopatric, this may be evidence of ecological interactions limiting co-occurrence. To demonstrate how HAA might be applied to a group to reconstruct biotic assembly, we apply HAA to a group of birds at an iconic biological research station in South America.

The assembly of *Pteroglossus* toucans at Cocha Cashu: An empirical example of HAA

Four species of *Pteroglossus* toucans are found at the 97 ha Cocha Cashu Biological; they will serve as an exemplar assemblage of interest, providing an empirical example of how to conduct HAA. The analysis could be expanded to include more species, for example all fruit-eating birds, but the methodological steps discussed here would not change. Defining the assemblage of interest, the first step of HAA, is question-driven. For example we may want to know why and how the four species of *Pteroglossus* came to co-exist and what role competitive exclusion may have played in limiting the co-occurrence of other *Pteroglossus* at Cocha Cashu (Table 1). To begin, we want to understand the historical and spatial context of the *Pteroglossus* assemblage (Table 1, Step 2a). Their distributions, and those of their close relatives (Fig. 3), reveal a spatial context in which Cocha Cashu is in the Inambari area of endemism, which is nested in Amazonia, and finally nested in South America. This spatial hierarchy is confirmed by a comparison to the congruent distributions of additional bird taxa (Fig. 3b). The assemblage can then be studied in relation to evolutionarily relevant historical areas and barriers (Table 1, Step

2a). Birds at Cocha Cashu usually have their closest relatives in other parts of Amazonia, but species found in the Atlantic Forest, the Choco west of the Andes, or in Central America could conceivably also be sister to the Amazonian species. This prioritizes Amazonian species for sampling in the phylogenetic reconstruction of the group, but also highlights the fact that sampling more broadly to include other South and Central American *Pteroglossus* species could potentially be informative (Table 1, Step 2b). Phylogenetic analysis of *Pteroglossus* identifies the sister-taxa of the four target taxa and provides information about the timing of the diversification of the clade (Fig. 3a).

We can use the phylogenetic relationships and timing of diversification recovered by Patel *et al.* (2011) as a framework for understanding the relevant area-relationships (Table 1, Step 2c) as well as potential historical explanations for the group's diversification (Table 1, Step 3). The divergence and distributions outside of Amazonia of the *P. torquatus* group (found west of the Andes and in Central America) and *P. bailloni* (present in the Atlantic forest) are evidence of deep historical structure within the genus in South America. Within Amazonia all *Pteroglossus* taxa are isolated from their closest relative(s) by a major river. All four *Pteroglossus* taxa at Cocha Cashu have sister-taxa that are allopatric and isolated from their sister-taxon by either the Solimões or Madeira Rivers. This implies that such barriers, once formed, place important constraints on dispersion, which influences the assembly process in terms of its temporal pattern and taxonomic composition. This spatial pattern, taken in conjunction with similar patterns for other Amazonian groups (e.g., *Psophia, Myrmeciza* and *Xiphorhynchus*; Fig. 3b), suggests that these barriers are likely causally associated with the area of endemism (Inambari) that contains Cocha Cashu.

Incorporating the timing of diversification of this group we can synthesize and understand the assembly of the target taxa in relation to landscape change (Table 1, Steps 3 and 4). The assembly of *Pteroglossus* at Cocha Cashu was not a simultaneous process. Although the time-calibrated phylogeny (Patel *et al.*, 2011; Fig. 3a) identifies spatial congruence in three taxa having sister-groups across the Madeira river, they differ temporally. Thus, *P. inscriptus humboldtii* and *P. castanotis castanotis* have sister-taxa resulting from speciation at roughly 400 ka, whereas *P. beauharnaesii* diverged from its sister-species about 1.5 Ma. This suggests that *P. beauharnaesii* was present at Cocha Cashu prior to *P. inscriptus humboldtii* and *P. castanotis castanotis*, both of which originated approximately the same time. These spatio-temporal patterns also characterize other groups. For example, *Psophia leucoptera* is found at Cocha Cashu and diverged from its sister group, which is also distributed east of the Madeira River, ~1.7-1.8 Ma (Ribas et al. 2012). *Pteroglossus azara mariae* shows a different spatial pattern, with its sister-taxon north of the Solimöes River, but it too diverged about 400 ka.

Two hypotheses can explain temporal disparity in the assembly of *Pteroglossus* at Cocha Cachu. One is dispersal across the Madeira around 1.0-1.5 Ma and then later ~400 ka. However, a more likely hypothesis that accounts for congruent biogeographic patterns is that of river history. River barriers can wax and wane, but they also meander and are involved in river capture events. We hypothesize there were one or more instances of "mega-river capture" involving the Madeira that transferred some of the biota from one side to the other. Importantly, there is evidence within Amazonia of major river-capture as well as rapid shifts in directionality (Almeida-Filho & Miranda 2007; Rossetti & Valeriano 2007), including for the Madeira (Hayakawa & Rossetti 2015).

Conclusions about the assembly of *Pteroglossus* at Cocha Cashu based on HAA are different from those based on a traditional community phylogenetic approach. For this analysis, we again considered the four *Pteroglossus* species found at Cocha Cashu to be the local assemblage. We compared the mean nearest-taxon distance (MNTD) of the species in the local assemblage to the expected MNTD based on null sampling from a regional species-pool. We implemented this traditional community phylogenetic approach using the *Phylocom* software (Fig. 4; Webb *et al.*, 2008). When applying either of two conceptions of a regional species pool, the entire genus or only those *Pteroglossus* found east of the Andes, Cocha Cashu appears to show phylogenetic overdispersion (Fig. 4). While not significant –likely due to the small number of taxa included for simplicity– this example demonstrates three key points. First, allopatry of close relatives is expected and can result in signals of phylogenetic overdispersion; this is in agreement with Pigot and Etienne (2015). Second, as larger regional species pools are used, the phylogenetic signal can be expected to shift toward phylogenetic clustering, as more distantly distributed species are typically more distantly related, reflecting the hierarchical nature of area-relationships. Third, as the size of the assemblage is increased, encompassing multiple historical areas, there is a clear shift from phylogenetic overdispersion to phylogenetic clustering. All of these outcomes are consistent with predictions that can be made if evolutionary history is producing spatially nested patterns of phylogenetic relatedness.

HAA provides an expectation of co-occurrence that can serve as an historical "null" hypothesis in community phylogenetic analyses. For example, because all four *Pteroglossus* species found within Inambari are also found at Cocha Cashu, the species composition of our assemblage seems to have been dictated entirely by evolutionary history. Neither biotic interactions nor abiotic filtering prevented the *Pteroglossus* species not found at Cocha Cashu

from coexisting with the target taxa; rather, the other *Pteroglossus* are absent from the assemblage because of historical reasons. If other sites within Inambari were surveyed, and one or more of the target taxa were missing, those absences might be attributable to ecological processes operating at a local level, although neutral processes such as demographic stochasticity should be ruled out first (Hubbell 2001). While these exemplar taxa had congruent historical areas, this may not always be the case, even for close relatives (e.g. *Tangara* at Cocha Cashu; Fig. 3c), highlighting the necessity of HAA's lineage-based approach to reconstructing assembly. Thus, only after historical expectations have been formulated through HAA can methods for identifying the influence of ecological processes (e.g., Maurer *et al.*, 2013; Price *et al.* 2014) be applied. By providing insights into the timing and order of the accumulation of diversity, HAA may facilitate the expansion of existing studies of the importance of these aspects of assembly on contemporary ecology (e.g. Leopold *et al.*, 2015).

Historical assembly analysis of trait evolution

In addition to understanding the species composition of assemblages, HAA provides a powerful historical context within which ecological processes relevant to biotic assembly can be examined. For example, the role of traits in biotic assembly is a longstanding area of interest for many ecologists. Most ecological characteristics that can influence the assembly process, such as trophic guild membership and functional traits, typically reflect heritable components of the phenotype; hence, they can be influenced by evolutionary history. As such, they are amenable to historical analysis, including ancestral-state reconstructions and modeling of trait evolutionary dynamics using methods in comparative phylogenetics to model trait evolution and to characterize niche conservatism (Schluter et al. 1997; Losos et al. 1998; Pagel 1999; O'Meara et

al. 2006; Moen et al. 2009; Mayfield & Levine 2010).

Reconstructing the evolution of a trait along a phylogeny makes it possible to estimate the points at which that trait changed states. Based on the historical biogeographic and environmental reconstructions used in HAA to understand co-occurrence, one can determine the biological context within which those trait-state changes occurred. For example, if two species that co-occur have different trait states (e.g., large and small bodies), HAA can provide the information necessary to determine whether that trait diverged before or after sympatry of the two species (Fig. 5). If either or both of the co-occurring species possesses a derived trait-state (i.e., if an individual species' trait diverged after secondary contact), it would then be appropriate to examine the potential eco-evolutionary drivers of that trait change in the biotic and environmental setting in which the species are sympatric. If, on the other hand, the trait-states of the two species diverged prior to secondary sympatry, then there is no need to ascribe trait similarity or difference to biotic interactions or environmental influences within that assemblage. As with the influence of history on expectations of co-occurrence, if spatially-explicit phylogenetic analyses of trait evolution are not incorporated into studies of biotic assembly, patterns of trait convergence or divergence might be interpreted as outcomes of ecological interactions rather than historical contingency.

The *Pteroglossus* at Cocha Cashu provide an example of how one might take an historical approach to understanding trait evolution. Body sizes of co-occurring species could be interpreted as the outcome of character displacement that reduced interspecific competition (Schluter & McPhail 1992; Grant & Grant 2006). The genus *Pteroglossus* can be divided into large- and small-bodied taxa (based on weight data from Short & Horne, 2002). Using standard ancestral character estimation techniques (Schluter et al. 1997), we reconstructed the evolution of

body size (large- and small-bodied) onto the *Pteroglossus* phylogeny. Based on this reconstruction, we concluded that three *Pteroglossus* taxa at Cocha Cashu retained ancestral body sizes, the most recent transition having occurred roughly 2 Ma. This finding suggests that history can explain much of the variation in body size of the taxa at Cocha Cashu, and can serve to focus ecological study of this trait on the single taxon that has a derived trait state.

Challenges to conducting historical assembly analysis

Although conceptually simple, resolving patterns of co-speciation across clades requires extensive phylogenetic and distributional data, and faces some well-known challenges (Nelson & Platnick 1981; Sanmartín & Ronquist 2002), even assuming data are available and estimates of relationships are accurate. In some groups a vicariant event may not lead to speciation, thus creating a widespread species in two or more areas. Long-distance dispersal can result in areas sharing species when those areas are not historically related, or dispersal can produce allopatry and speciation, in which case the geographic pattern of sister-species might not reflect the true historical connections among areas. In addition, species may be missing from areas due to extinction, even on relatively short timescales (Oswald & Steadman 2011), thus confounding area-relationships. Finally, barriers themselves are not necessarily stable over time and can arise and disappear (Fig. 1), thus making the reconstruction of the history of area-relationships difficult based on extant species alone (Ronquist & Sanmartín 2011). These factors combine to create complex relationships between areas and speciation events that can be specific to individual clades, necessitating reconstruction of biogeographic histories on a clade-by-clade basis (Bates et al. 1998). Yet even in complex systems such as Amazonia, historical biogeographic analysis can recover congruent temporal and spatial patterns of speciation and

diversification (Ron 2000; Eberhard & Bermingham 2005; Patel et al. 2011). Integrating independent knowledge from geological or environmental history can add critical information for, or against, inferences about biotic history, highlighting the need for an interdisciplinary approach that involves specialists across disciplines who understand the biotic results and recognize the importance of trying to reconcile biotic and Earth history events (e.g. Ribas *et al.*, 2012).

Conclusions

The integration of community ecology, phylogenetics and biogeographic analysis has the potential to elucidate the mechanisms by which ecological assemblages are formed. HAA places assemblages within an historical context characterized by a history of allopatry, speciation and dispersion, as well as the explicit understanding that areas are dynamic, hierarchical, and described by the joint evolutionary histories of their constituent species. We have endeavoured to outline a conceptual framework for using HAA to reconstruct biotic assembly in any system amenable to phylogenetic and historical biogeographic analyses (Table 1). Using historical approaches to frame the context of ecological processes will enable community phylogenetics to benefit from growing knowledge of phylogenetic history. This can facilitate the incorporation of time as well as the environmental and ecological background into assembly analysis. HAA also places assemblages in historical context, and would allow for comparative studies (e.g. Liu *et al.*, 2013; Troia & Gido, 2015) to be conducted at large extents and with explicit consideration of specific historical areas.

By applying an historical approach, the role of ecological interactions is circumscribed to their mechanistically proper scale, namely among individual organisms, not among species and

higher taxa (Cracraft 1989). Constraining the analyses of trait evolution to changes that occurred in the context of the assemblage being examined makes it possible to examine the influence of ecological interactions on those traits. As with co-occurrence, additional research is needed to quantify the importance of history for interpretations of trait evolution and, consequently, the role of traits in structuring assemblages.

Although HAA requires a significant amount of data, the rapid accumulation of detailed phylogenies for a wide array of taxa, as well as data about Earth history, are making it increasingly feasible to build historical models based on the processes that drive diversification and distributions. As phylogeneticists build trees at increasingly fine resolution and with larger taxonomic sampling, the ability to examine the phylogenetic relationships of entire guilds or assemblages at the species-level is no longer a distant reality for some taxa (e.g. Tobias *et al.*, 2014), making HAA an increasingly powerful tool for studying assembly

Taking an evolutionary approach to understanding assembly is important, not just because evolutionary processes have the potential to act at smaller spatial and temporal scales than previously appreciated (Hendry et al. 2000), but primarily because current patterns of co-occurrence are the results of a history of speciation, dispersion of biotas, ecological interactions, and phenotypic evolution. Our call for an historical approach to examining assembly is intended to stimulate discussion regarding the incorporation of evolutionary processes in a more explicit way, and to urge restraint in interpreting results of community structure studies without controlling for the effects of history. This view also implies a need for collaboration across disciplines. No single discipline can be expected to bring the expertise needed to link Earth history and biotic history in order to understand patterns of co-existence and trait variation, and to understand how they might be relevant for the assembly process. How biotas have evolved

and assembled into ecological communities across time and space is a complex problem, but a plethora of new methods, information, and conceptual approaches make this an exciting time to study the assembly process, and suggest that many new insights are sure to come.

Acknowledgements

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Figure 1.1. Biotic assemblages are structured by evolutionary history. (a) Nonhistorical approaches to assembly analysis typically view assemblages of species as a subsample of a "regional species pool", with local composition interpreted as the result of ecological processes. (b-d) An historical approach, in contrast, may discover that local species composition is evolutionarily contingent. (b) Landscapes are dynamic, and if a vicariant barrier (line 1) divides a region, it can induce congruent patterns of speciation in some species, resulting in sister-species distributed in separate historical areas and phylogenetically-overdispersed patterns. (c) If the region is further divided by a second vicariant event (line 2), the historical signature is stronger because now there is three-taxon and three-area congruence. (d) If a barrier breaks down (e.g., barrier 2), secondary sympatry can occur, resulting in phylogenetic-clustering locally. Allopatry, speciation, and dispersion after barriers decay create complex patterns as historical events are layered on top of one another.

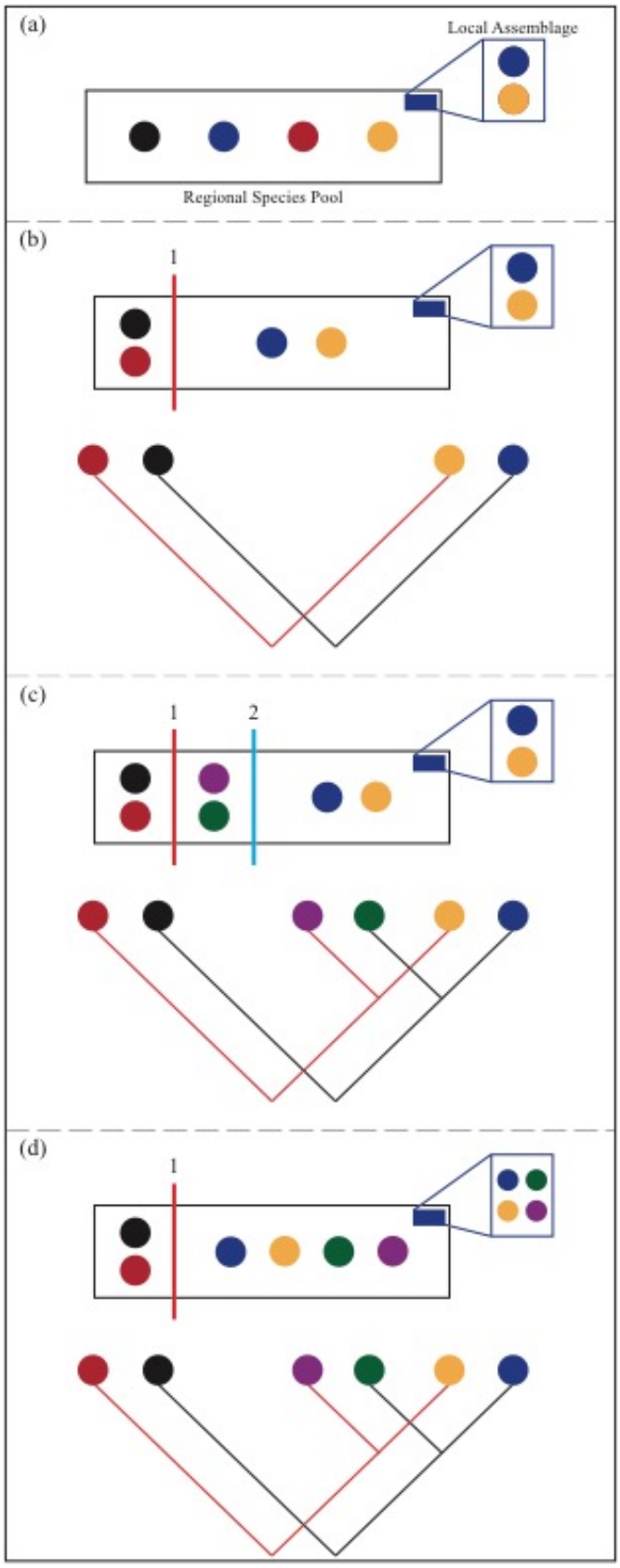

(a)
Local Assemblage
Regional Species Pool
(b)
1
(c)
1
2
(d)
1

Figure 1.2. Conceptual diagram of historical biotic assembly. A study usually begins with the choice of an area ("Study Area") and group of organisms ("Target Species") to study. Historical analysis depends on understanding the historical area for each target species. The size of these areas is typically constrained by the barriers that induced speciation, which may be different across species even within a given taxon (e.g., birds). However, historical areas are often congruent across multiple taxa, resulting in an area of endemism. Assemblages are outcomes of allopatry, speciation, and dispersal, and must be reconstructed by identifying the historical areas for individual target species. Ecological processes may only be responsible for filtering species with historical areas that contain the study area.

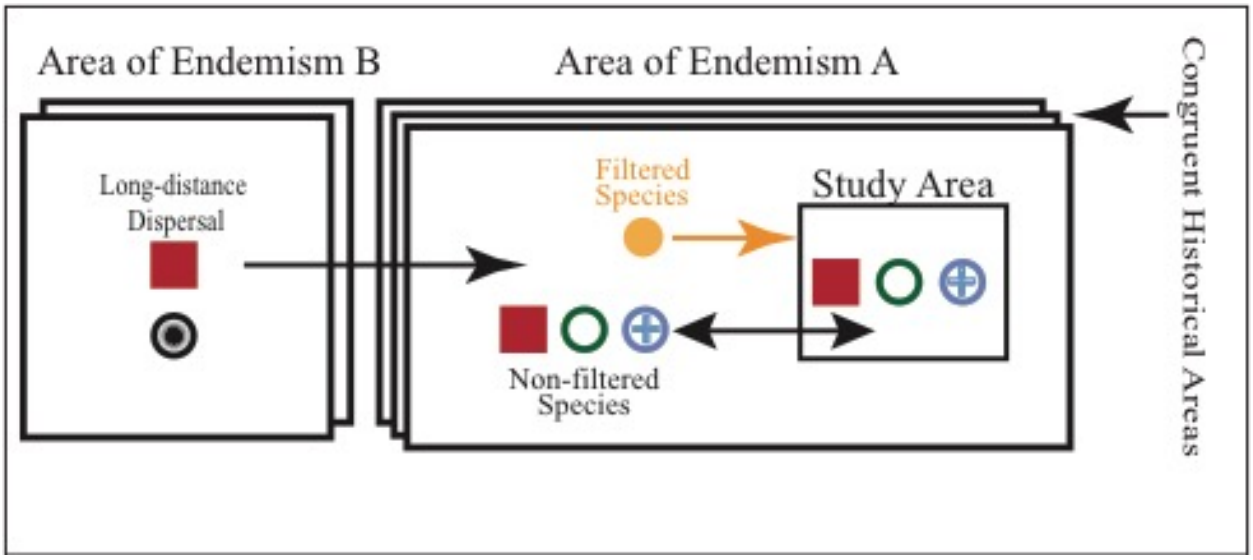
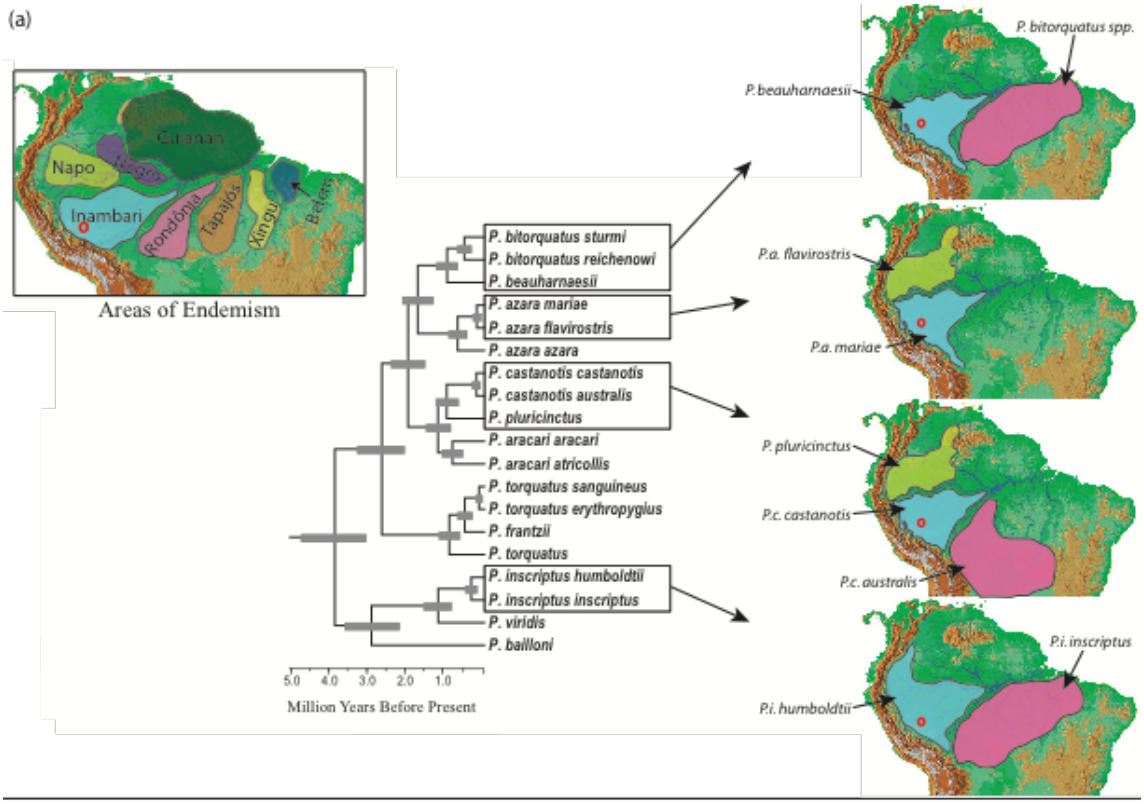


Figure 1.3. The imprint of history on an assemblage. The Cocha Cashu research station (red circle) is located within the Amazonian Inambari area of endemism. (a) Four species of *Pteroglossus* toucans co-occur there: *P. inscriptus*, *P. mariae*, *P. castanotis*, and *P. beauharnaesii* (Terborgh et al. 1990). Sister-taxa of these species are not found at Cocha Cashu, a pattern that might be interpreted as evidence of competitive exclusion. Yet, allopatry is expected based on the congruent speciation histories within *Pteroglossus*. For taxa endemic to the Inambari area, the Rio Madeira (separating the Inambari and Rondônia areas) and the Rio Solimões (separating the Inambari and Napo areas) are commonly associated with allopatric distributions for many of the sister-taxa of species at Cocha Cashu, including *Pteroglossus*. (b) These highly congruent patterns also exist in other taxonomic groups, such as trumpeters (*Psophia*), antwrens (*Myrmeciza*), and woodcreepers (*Xiphorhynchus*). While congruent patterns of relatedness are common, these patterns can be obscured by the failure of some taxa to speciate, long distance dispersal, a dynamic landscape that can generate complex patterns even within groups, and, importantly, the application of different taxonomic practices. (c) For example, *Tangara chillensis* and its pair of sister-taxa *(T. callophrys* and *T. velia*) are all found at Cocha Cashu. Thus, phylogenetic history is present within Amazonia and should be taken into account when reconstructing assembly processes. Taken together, these examples show a pervasive and largely congruent imprint of speciation history on the distribution of taxa, and also demonstrate the danger of capturing the complexity of diversification histories in a single "species pool".



Phylogeny in (a) from Patel et al. (2011); sister relationships in (b) from Ribas et al. (2012), Fernandes et al. (2012), and Aleixo and Prum (2002), from left to right; sister relationships in (c) and (d) from Burns and Naoki (2004).

Figure 1.4. Community phylogenetic analysis of the assembly of Pteroglossus sp. of Amazonia across scales and species pools. Phylogenetic clustering vs. overdispersion is measured as: [observed mean nearest taxon distance (MNTD) of an assemblage – the MNTD for randomly selected taxa from the regional species pool]/standard deviation of MNTD of randomly selected taxa, and calculated using Phylocom. Positive values indicate that the MNTD of the species in an assemblage is greater than expected by chance (i.e. the species are less-closely related than expected be chance; phylogenetic overdispersion), while negative values indicate the MNTD of species in an assemblage is less than expected by chance (i.e. the species are phylogenetically clustered). When all species in *Pteroglossus* are included in the regional species pool (black points), all assemblages appear to be more clustered than if only the *Pteroglossus* east of the Andes are included in the regional species pool (red points). Additionally, if the local assemblage is expanded from the *Ptreroglossus* found at Cocha Cashu (the first point), to the *Pteroglossus* species found in areas west of the Rio Madeira and Rio Negro (second point), or areas west of the Rio Madeira and south of the Amazon River (third point), or even all of Amazonia (fourth point), the local assemblage begins to encompass multiple areas of endemism. As the local assemblage increases in size in relation to the regional species pool, there is a clear shift from phylogenetic overdispersion toward clustering, as would be expected if speciation were driving patterns of relatedness across the landscape. This pattern is sensitive to the order that areas are added, but there is a consistent pattern toward phylogenetic clustering as the local assemblage is expanded in scope.

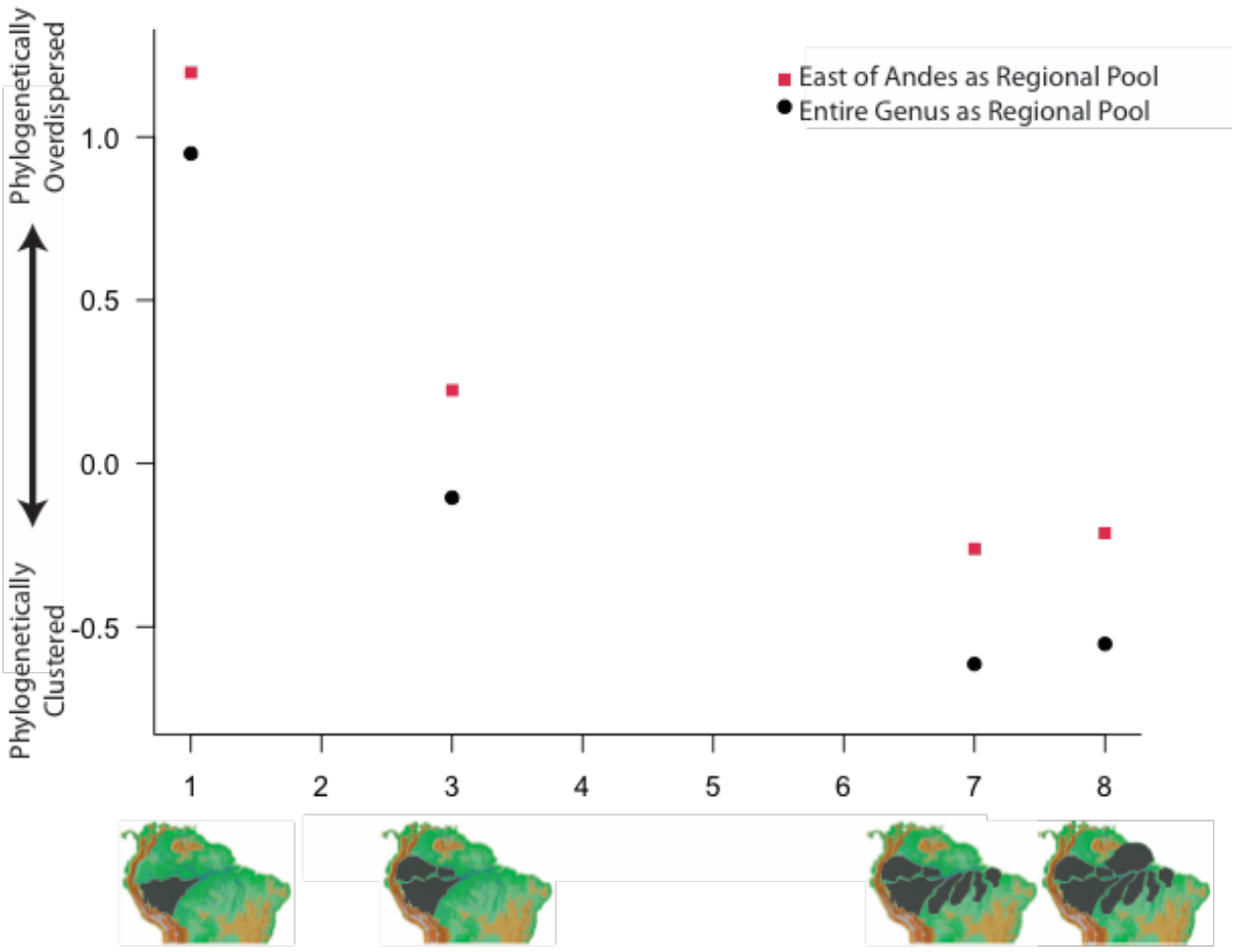

Phylogenetically Overdispersed
Phylogenetically Clustered
1.0
0.5
0.0
-0.5
East of Andes as Regional Pool
Entire Genus as Regional Pool
1
2
3
4
5
6
7
8
Number of Areas of Endemism included in the Local Assemblage

Figure 1.5. Historical assembly analysis provides essential context for understanding trait evolution. In this example, each shape represents a trait state: smaller black squares represent small body-size and larger red ovals represent large body-size. (a) In Area A, the species evolves a large body, whereas in Area B the ancestral small body size is retained. (b) If a vicariant event divides Area A (line 2), it is possible that both species will retain the ancestral state of "large-bodied". (c) If the initial barrier (line 1) breaks down, the assemblage will have two closely-related species, one with a large body and one with a small body. It would be inappropriate to consider biotic interactions (such as competition) between the two local species as a driver of trait divergence, as the different body sizes are the ancestral states of both species: the origin of large body size predates sympatry of the large and small-bodied species.

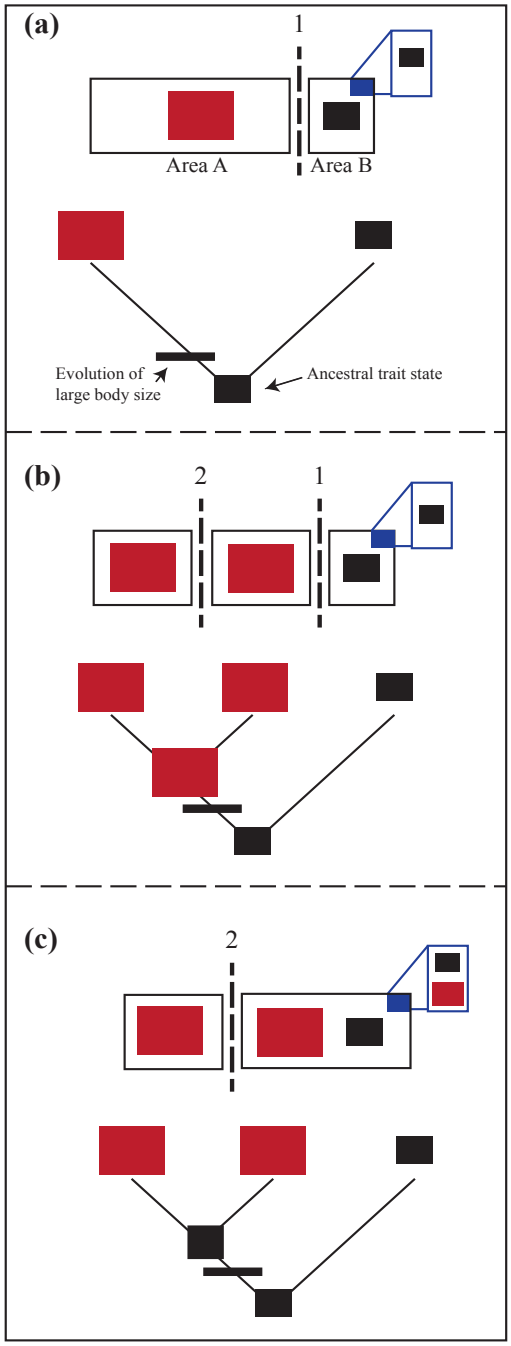

(a)
1
Area A
Area B
Evolution of
large body size
Ancestral trait state
(b)
2
1
(c)
2

Table 1. Using Historical Assembly Analysis (HAA): proposed steps to understand the influences of evolutionary histo assembly across spatial and temporal scales

Protocol	Objectives	Methods and approaches	Ref
1. Delimit the area of interest ("study area") and identify the relevant species ("target species") within the assemblage.	• Set the spatial and taxonomic context for subsequent steps, linking HAA to the specific questions of the study and beginning to establish the spatial and temporal scales of the analysis.	Use ecological and taxonomic background knowledge. Employ biodiversity assessments and/or species inventories.	Magurran & Morin (201
2a. Understand the general hierarchical-historical and spatial context of the study area and the target species.	• Identify the spatial extent of distributions for the target taxa and their potential close relatives.	Map distributions of target species and close relatives. Identify patterns of distributional congruence (areas of endemism). When relevant use distributional modeling.	Cracraft (19 Goloboff (2 Kreft & Jetz Arias et al. (
2b. Reconstruct the phylogenetic history of the target species in the assemblage and their close relatives (as determined in 2a), and estimate the timing of their clade's diversification.	• Provide an historical hypothesis for all relevant taxa and estimate their timetree. • Identify the original ranges of species, thus identifying likely historical areas for each target taxon's lineage.	Conduct a phylogenetic analysis using parsimony, likelihood, or other model-based methods. Construct a fossil calibrated timetree using Bayesian or likelihood methods.	Swofford et Arbogast et Felsenstein Yang & Rai Drummond

2c. Reconstruct the biogeographic history across clades.	• Understand the area relationships for the target species and their relatives. • Identify potential barriers responsible for allopatry. • Reconstruct the history of vicariance, dispersal, and extinction	Carry out a biogeographical area analysis, testing hypothesized histories. Conduct an ancestral-area reconstruction.	Nelson & P Hovenkamp Porzecansk (2005) Ree & Smit et al. (2011 Ronquist & (2011)
3. Reconstruct environmental change within and across all relevant historical areas.	• Identify and describe changes in Earth history (geomorphology, sedimentary, climatic, palynological, etc.) relevant to the biotic history of the assemblage. • Identify physical factors that have influenced the landscape within which the assemblage is embedded. • Integrate data on distributional patterns to identify barriers, their timing, and their potential loss.	Perform tectonic, paleohydrology, and geomorphological analyses. Examine paleontological and palynological studies. Leverage remotely-sensed data to understand potential changes in the landscape (e.g. Shuttle Radar Topography Mission data). Conduct paleoclimate modeling.	Campbell e Badgley et Picard et al Cheng et al
4. Synthesize across steps 2-3	• Partition causation for co-occurrences into historical and	Match the temporal patterns of biotic and Earth history and	Picard et al Moen et al.

CHAPTER 2. DISPERSAL HAS INHIBITED AVIAN DIVERSIFICATION IN AUSTRALASIAN ARCHIPELAGOES

B.C. Weeks and S. Claramunt

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Abstract

Different models of speciation predict contrasting patterns in the relationship between the dispersal ability of lineages and their diversification rates. This relationship is expected to be negative in isolation-limited models and positive in founder-event models. In addition, the combination of negative and positive effects of dispersal on speciation can result in higher diversification rates at intermediate levels of dispersal ability. Using molecular phylogenies to estimate diversification rates, and wing morphology to estimate dispersal ability, we analyzed the influence of dispersal on diversification in the avifauna of Australasian archipelagoes. Contrary to expectations given the fragmented nature of island systems, the relationship between dispersal ability and diversification rate was monotonically negative. While multiple mechanisms could generate this pattern, they all share a phase of range expansion that is decoupled from speciation.

Introduction

The role of dispersal in controlling rates of diversification remains poorly understood. For most traditional modes of allopatric speciation, such as vicariance, an increase in dispersal ability should decrease speciation rates because barriers become less effective in limiting gene flow (Mayr 1963; Bohonak 1999; Coyne & Orr 2004), resulting in a negative relationship between dispersal and diversification. However, if speciation is predominantly the result of a colonization event (founder-event speciation *sensu* Matzke 2013), an increase in dispersal ability should raise speciation rates because it increases the chances of colonization of new areas. Speciation after colonization can be triggered by founder effects (Templeton 2008; Wessel et al. 2013) or ecological speciation due to exposure to new habitats and selective pressures (Rosenzweig 1995; Schluter 2001; Price 2007). In addition, the relationship between dispersal ability and diversification may not be monotonic; instead, speciation rates may be maximized at intermediate levels of dispersal, as in the intermediate dispersal model (Diamond et al. 1976; Mayr & Diamond 2001; Claramunt et al. 2012). According to this model, lineages with the highest dispersal abilities have lower chances of speciation due to high levels of gene flow between populations, whereas lineages with the lowest dispersal abilities have lower chances of speciation due to lower rates of origination of barriers within their restricted geographical ranges. In contrast, lineages with intermediate dispersal abilities experience a combination of geographic expansion and subdivision that results in high speciation rates (Mayr 1963; Diamond et al. 1976; Mayr & Diamond 2001; Price & Wagner 2004; Claramunt et al. 2012).

Empirical examination of the relationship between dispersal ability and diversification has been challenging because of the difficulties in quantifying both dispersal ability and diversification rates. Recent studies of birds have found negative, positive, and unimodal

relationships between dispersal and diversification. For example, in the continental radiation of the Furnariidae, a diverse family of suboscine passerines from the Neotropics, there is a predominantly negative relationship between dispersal ability, as inferred from wing shape, and speciation rates estimated using a calibrated phylogeny (Claramunt et al. 2012). In contrast, a macroevolutionary analysis of all bird families recovered a positive relationship between diversification rates and an index of dispersal propensity based on ecological characteristics (Phillimore et al. 2006). Finally, the avifauna of Northern Melanesia inspired the intermediate dispersal model by showing a unimodal relationship between an index of intraspecific differentiation and assessments of dispersal ability based on behavior and biogeography (Mayr & Diamond 2001).

The discrepancies between these studies may be caused by the differences in the methods used for estimating dispersal and/or diversification. For example, the index of diversification used for the study of the Melanesian avifauna was a count of the number of subspecies and allospecies within each species; because this index does not take clade age into account, it is a measure of clade diversity, not diversification rate. Alternatively, the varied findings across studies may reflect real differences in the relationship between dispersal and diversification. In particular, the degree of discontinuity of the geographical setting may determine the relationship between dispersal and speciation rate (Claramunt et al. 2012). Within continents, dispersal may have a predominantly negative effect because even poor dispersers can colonize remote areas, and increased dispersal results in elevated levels of gene flow across weak or moderate barriers. In contrast, in highly discontinuous geographies such as archipelagoes, because range expansion may be a limiting factor, long distance dispersal may enhance speciation by allowing lineages to colonize new regions and subsequently diversify (Mayr & Diamond 2001).

Here we revisit the relationship between dispersal ability and diversification rates in the avifauna of Australasian archipelagoes with a focus on Northern Melanesia, using new estimates of dispersal ability and diversification rates. Because of the highly discontinuous geography of Australasian archipelagoes, we predict that colonization is a limiting factor controlling rates of diversification, resulting in either a positive or a unimodal relationship between dispersal ability and diversification rates (Mayr & Diamond 2001; Claramunt et al. 2012).

Methods

The study region consisted of archipelagoes east of Wallace's line, including Eastern Wallacea, Melanesia, Micronesia, and Polynesia, but excluding islands on the Australopapuan continental shelf. We used a standardized methodology for defining the clades to be included in this study in order to avoid sampling biases and ensure that the clades had diversified mostly in island systems within the study region. We first identified species endemic to Northern Melanesia that had been included in molecular phylogenetic studies. For each of these endemics, we used phylogenetic information to identify the largest clade that included the endemic and did not contain more than one species distributed outside the study region. In cases of incomplete phylogenies, we also used taxonomic information such as generic limits or superspecies complexes to determine if species not included in the published phylogeny belonged to the focal clade.

We estimated the net diversification rate of each clade as:

$$\log(N)/A \qquad \text{Equation 1}$$

where N is the number of species in the clade and A is the stem age for the clade (Kendall 1949). Some assessments suggest that current taxonomies underestimate true species diversity in the

region by considering basal evolutionary lineages as subspecies of widespread polytypic species (Cracraft 1983; Moyle et al. 2005; Reddy & Moyle 2011). Therefore we assessed the robustness of our results to species limits by also estimating diversification rates using subspecies counts. The number of subspecies in each species was taken from (Dickinson 2003).

We estimated the stem age of each clade using a relaxed mitochondrial molecular clock. We obtained sequences of the cytochrome b (cytb) gene or NADH dehydrogenase subunit 2 (ND2) gene for each focal clade and a closely related outgroup from Genbank (www.genbank.gov). We estimated divergence times using Bayesian methods in the program BEAST (Drummond et al. 2012). Substitution rates were modeled using a GTR + Gamma model and rate heterogeneity across lineages was modeled using a relaxed lognormal clock (Drummond et al. 2006). The prior for the overall substitution rate was set to match the distribution of rates observed in mitochondrial sequences of a wide variety of avian groups (Weir & Schluter 2008), log-normal distribution: log-mean = -4.6, log-standard deviation = 0.25). We determined burn-in and convergence by examining traces and ESS values for model likelihood and divergence time estimates using Tracer v1.5 (Rambaut & Drummond 2009).

Dispersal ability is notoriously difficult to estimate. Here we assume that dispersal ability in birds is at least partially determined by their flight capabilities. Although behavioral factors may also have a strong influence on dispersal tendencies (Diamond 1981) behavioral predisposition for long distance dispersal should be associated with strong flight capabilities, generating a correlation between behavioral, physiological, and biomechanical aspects of dispersal. Therefore, we used the hand-wing index (HWI, Kipp 1958), a proxy for the aspect ratio of the wing, as an index of dispersal ability. The advantage of focusing on the flight apparatus is that it can be measured using specimens. In particular, the aspect ratio of the wing is

a key determinant of the efficiency of long distance flight (Pennycuick 2008; Claramunt et al. 2012). Moreover, there is empirical evidence linking HWI to the dispersal process: HWI is well correlated with migration distance among a variety of Palearctic birds (Lockwood et al. 1998), average distance flown over water estimated through dispersal experiments in tropical forest birds (Moore et al. 2008; Claramunt et al. 2012), and natal dispersal distances among British passerines (Dawideit et al. 2009). The hand-wing index is calculated as:

$$HWI = 100(WL - SL)/WL \qquad \text{Equation 2}$$

in which WL is the standard measure of wing length, and SL is a measure of the distance from the carpal joint to the tip of the first secondary feather (Claramunt et al. 2012). For all species in our clades, three adult males - when available - were measured at the American Museum of Natural History. The average of each species was used for calculating an average HWI for each clade.

We used phylogenetic comparative methods and statistical modeling techniques to determine the function that best described the relationship between dispersal ability and diversification rate. In order to account for phylogenetic non-independence among clades, we used a phylogenetic generalized least squares regression method (Freckleton et al. 2002) which uses a correlation structure derived from a lambda transformation of the phylogenetic tree of relationships among clades. To obtain the tree, we used sequences of cytb, ND2, and the recombination activating gene 1 (RAG-1) for a representative of each clade. We then generated a maximum likelihood tree in RAxML (Stamatakis 2006), and transformed the tree into a chronogram in which branch lengths are proportional to time using a maximum likelihood approach (Paradis 2013).

Models of the relationship between the hand-wing index and diversification rates were optimized using the pgls function in the R package Caper (Orme et al. 2012). We used a logarithmic transformation of both the hand-wing index and the diversification rate because it resulted in a better fit to model assumptions. We compared constant, linear and quadratic models using Akaike Information Criterion (AIC) scores; reported p-values are calculated based on an F-test comparison with a model in which rates are constant, and all reported R^2 values are adjusted values. For comparison, we also analyzed the relationship between dispersal and diversification using Mayr & Diamond's (2001) index of diversification: the number of subspecies and allospecies of each species. We then calculated an index for each clade as the average value of the contained species.

Results

A total of 28 clades from 21 families of birds distributed across Australasian archipelagoes satisfied our clade-selection criteria. The clades range from 2 to 22 species, 2.4 to 24.9 million years in age, and represent a wide range of dispersal abilities (table 1). Wing morphology data were collected for 338 specimens representing 157 species (electronic supplementary material [ESM]).

The relationship between dispersal ability and diversification rates was monotonically negative (figure 1). A linear model (AIC = 67.4, $p = 0.005$, $R^2 = 0.17$) fit marginally better than a quadratic model (AIC = 68.6, $p = 0.03$), but both curves are very similar, with the quadratic model showing a monotonically decreasing relationship within the range of dispersal values (figure 1). A constant model had the lowest support (AIC = 71.7). The use of subspecies rather than species to estimate diversification rates produced similar results: a negative linear model

(AIC=66.4, $p < 0.001$, $R^2 = 0.28$) was better than a quadratic model (AIC = 68.2, $p = 0.004$), which declined monotonically, and both were better than a constant rate model (AIC = 73.0; supplementary figure 1, ESM).

Using a simple count of species and allospecies as an index of diversification, as done by Mayr & Diamond (2001), resulted in the best-fitting quadratic model assuming a unimodal shape, in which clades with intermediate dispersal abilities have the maximum diversification rates, consistent with the intermediate dispersal model (figure 2). However, quadratic (AIC = 62.7) and linear models (AIC = 62.4) were statistically indistinguishable and neither was better than a constant rate model (AIC = 61.3).

Discussion

We found a negative relationship between dispersal ability and diversification rates among bird clades that diversified in the discontinuous geography of Australasian archipelagoes. If opportunities for speciation were limited by dispersal across barriers, increased dispersal ability would have led to higher rates of speciation, resulting in a positive relationship between dispersal ability and diversification rate. Our discovery of a negative relationship implies that the limiting factor for speciation in this avifauna was not the chance of colonization of new islands, but the effectiveness of geographic barriers in limiting gene flow, which decreases as dispersal ability increases.

These results do not corroborate previous findings of an intermediate dispersal pattern in the avifauna of Australasian archipelagoes in which diversification was highest at intermediate levels of dispersal ability (Diamond et al. 1976; Mayr & Diamond 2001). When we used Mayr & Diamond's (2001) taxonomy-based index of diversification that does not take clade age into

account, a unimodal pattern emerged (albeit not significant, figure 2). This suggests that the discrepancy between our results and Mayr & Diamond's (2001) is not due to differences in taxonomic sampling or dispersal ability estimates. Rather, it is the direct estimation of diversification rates that revealed a negative relationship. Taxonomy-based indices of speciation across clades that do not consider clade age are measures of total lineage richness rather than a proxy for diversification rates and can be misleading because they are sensitive to differences in clade age.

While the influence of extinction is not directly testable, we expect extinction to have weakened the negative relationship we found between dispersal ability and net diversification rates. This is because species that are poor dispersers are expected to experience higher rates of extinction (and thus, lower net diversification rates) due to reduced range size (Stanley 1990; Reinhardt et al. 2005; Powell 2007) or reduced rates of recolonization in metapopulation dynamics (Hanski 1998). Therefore, extinction is most likely dampening a potentially steeper negative relationship.

A negative relationship between dispersal ability and diversification rates suggests a predominant role for modes of speciation limited by isolation, rather than range expansion (Claramunt et al. 2012). One such mode is vicariance, which is based on the subdivision of widespread ancestral biotas. Vicariance has not been considered to be a significant process of speciation in archipelagoes because many islands were never connected to other landmasses in the past (i.e. isolated volcanic islands). However, at least two factors make vicariance a plausible and potentially common mode of speciation in island settings. First, most islands have not been completely isolated throughout their history, but are part of tectonically dynamic archipelagoes with complex geological histories of fragmentation and collision; this is particularly true for

Wallacean and Melanesian archipelagoes (Hall 2002). Second, fluctuations in sea level can result in subdivision and reconnection of islands separated by shallow water gaps (Ali & Aitchison 2014). In addition, whereas a single long distance dispersal event usually involves an individual lineage, a single vicariance event can affect entire biotas, potentially leading to multiple speciation events. As a consequence, even if not common, vicariance can be responsible for a substantial portion of speciation events in archipelagoes. For example, a detailed analysis of *Aethopyga* sunbirds from the Philippines revealed that intra-island and shallow-water barrier vicariant events may have contributed as much as dispersal over deep water to the generation of the group's diversity (Hosner et al. 2013).

In addition to vicariance, evolutionary changes in dispersal ability could also generate a negative relationship between dispersal ability and diversification rates. Lineages may expand their geographic ranges and colonize new islands during evolutionary phases of high dispersal ability, and then differentiate and speciate during phases of reduced dispersal ability (Diamond et al. 1976; Moyle et al. 2009). While this process may be important at smaller taxonomic scales, it cannot entirely explain the negative pattern found across clades because of the magnitude of dispersal ability differences between clades. Strong phylogenetic inertia in HWI values across clades (Pagel's lambda = 0.99) and limited variation within clades (supplementary table 1, ESM) suggests that dispersal ability is relatively conserved in this avifauna. However, it is still possible that changes in dispersal ability may play a role at smaller scales. For example, rails show pronounced variation in wing shape (supplementary table 1, ESM). The widely distributed *Gallirallus philippensis*, with relatively high aspect ratio (HWI = 27) compared to other rails and most passerines, may represent a lineage in the dispersive phase. *G. philippensis* belongs to a clade of mostly flightless rails (Kirchman 2012) that has one of the highest diversification rates

in the dataset. Analyses of wing shape evolution within clades and comparisons between continental and island clades may provide further insights into the macroevolutionary effects of changes in dispersal ability.

What the scenarios of vicariance and changes in dispersal ability have in common is that lineages go through a phase of range expansion that is decoupled temporally from a phase of geographic isolation that can result in speciation. In the vicariance model, range expansion occurs when terrains are connected and speciation when terrains are divided by a barrier, usually the results of climatic, tectonic or geographic processes that operate over geological timescales. In the model of changes in dispersal ability, range expansion occurs when a lineage has high dispersal ability, and speciation occurs only after the evolution of a low dispersal phenotype. It is possible to conceive of other models with decoupled periods of range expansion and isolation. For example, lineages in an archipelago composed of islands that were never connected can go through a phase of range expansion during lower sea levels, when water gaps between islands become narrower, and a phase of isolation during high sea levels, when speciation is more likely (Ali & Aitchison 2014). This scenario provides a mechanism for the generation of a negative relation between dispersal ability and diversification rates across oceanic islands that were never connected to other islands.

In contrast, in founder-event speciation, long-distance dispersal produces both range expansion and speciation, coupling the two processes. For example, if a rare phenomenon like a hurricane transports individuals from a lineage to a new island that they cannot reach under normal circumstances, the new population is immediately isolated from the source population, and speciation occurs soon thereafter. Whereas long-distance dispersal may be an important phenomenon determining patterns of distribution of taxa (de Queiroz 2005; Gillespie et al.

2012), our data suggest that it is not a dominant force in the generation of diversity, at least for the avifauna of Australasian archipelagoes.

Our data suggest that diversification in this region has predominantly occurred via modes of speciation in which phases of colonization are decoupled from periods of isolation. This decoupling could have occurred as a result of a dynamic geography (i.e. a vicariance model), evolutionary changes in dispersal ability, or fluctuations in the permeability of barriers (e.g. sea level fluctuations). While we cannot distinguish between these mechanisms, our data do confirm that the limiting factor in speciation for these groups has been isolation, and that dispersal has inhibited diversification.

Conclusion

At a regional scale, and for a diverse group of birds, we found that dispersal ability is negatively related to diversification rates, suggesting that dispersal has inhibited avian diversification across Australasian archipelagoes. We attribute this negative relationship to a reduction in speciation rates caused by reduced efficacy of barriers to gene flow as dispersal ability increases. This also suggests that long distance dispersal, although important for range expansion in Australasian archipelagoes, was not the limiting factor in the diversification of this avifauna. Instead, isolation has played a more important role in controlling diversification rates. The fact that dispersal has not stimulated diversification even in an extremely discontinuous geography such as Australasian archipelagoes, suggests a general inhibitory effect of dispersal on rates of global avian diversification; the expansion of empirical work beyond Australasia is needed to confirm this hypothesis, and promises to be an exciting avenue of future research.

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Figure 2.1. The relationship between dispersal ability and diversification rates for 28 clades of birds from Australasian archipelagoes. Dispersal abilities were estimated using the average hand-wing index for each clade, and diversification rates were estimated using equation 1. The best fitting model is a negative linear model (solid line, log(diversification rate) = 2.18 – 1.13 * log(dispersal)) followed by a quadratic model (dashed line, log(diversification rate) = 11.52 - 6.96 * log(dispersal) + 0.9 * log(dispersal)^2).

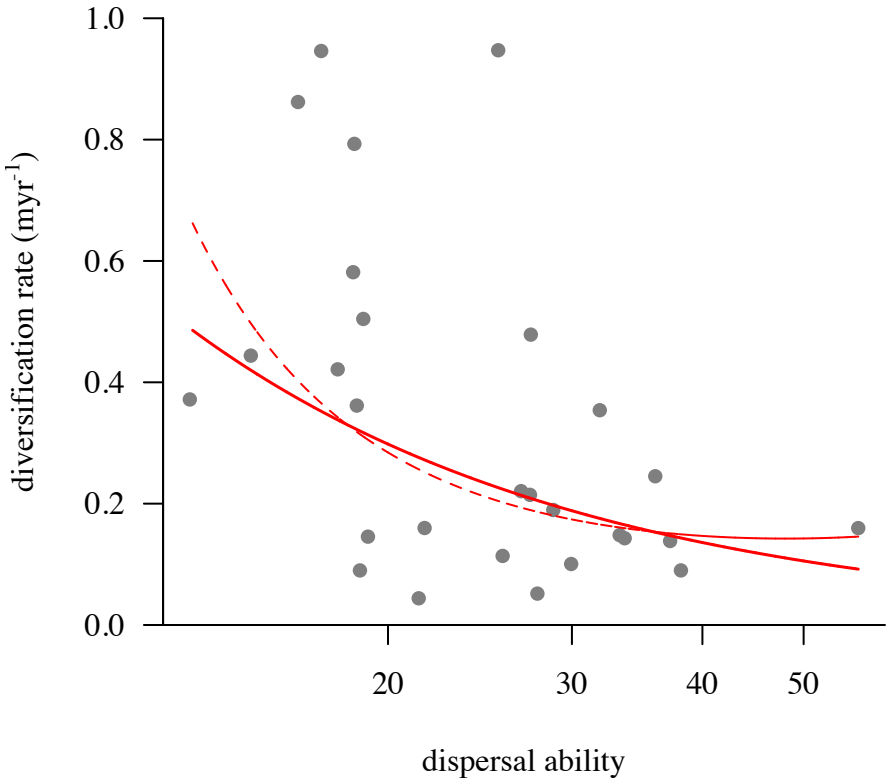


Figure 2.2. The relationship between a taxonomic index of diversification and dispersal ability results in the best-fitting quadratic model assuming a unimodal shape, but the model is not significantly different from a constant model.

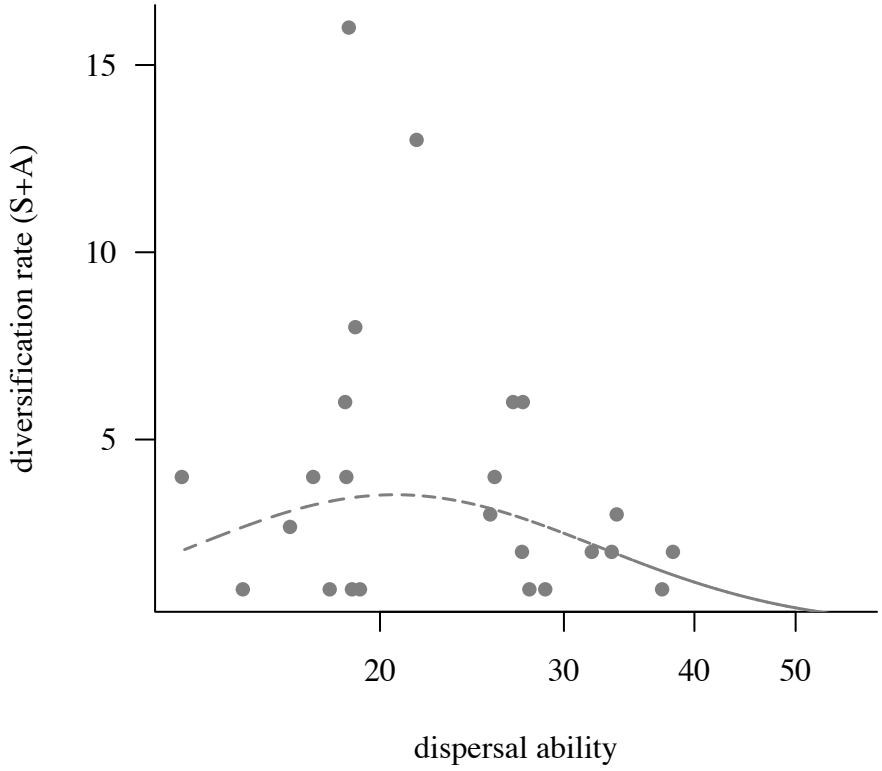


Table 2.1. Clades that diversified in Australasian archipelagoes that were included in the analysis. The reference listed for each family is the reference from which the phylogeny or the sequence data used to measure diversification rates were taken. The hand-wing index listed is the average for the species in the clade.

family	clade*	number of species	stem age (myr)	diversification rate (log(N)/A)	hand-wing index	reference
Accipitridae	*Haliaeetus*	2	7.70	0.09	38.15	(Wink et al. 1996)
Accipitridae	*Henicopernis*	2	5.01	0.14	37.25	(Barrowclough et al. 2014)
Aegothelidae	*Aegotheles*	2	6.90	0.10	29.95	(Dumbacher et al. 2003)
Alcedinidae	*Ceyx*	12	4.93	0.50	18.94	(Andersen et al. 2013b)
Cacatuidae	*Cacatua*	5	8.49	0.19	28.79	(White et al. 2011)
Cettiedae	*Cettia*	5	3.63	0.44	14.78	(Lecroy & Barker 2006)
Columbidae	*Alopecoenas*	5	3.36	0.48	27.4	(Moyle et al. 2013)
Columbidae	*Reinwardtoena*	3	7.68	0.14	33.7	(Pereira et al. 2007)
Columbidae	*Ptilinopus eugeniae*	2	3.23	0.21	27.35	(Cibois et al. 2014)
Columbidae	*Ptilinopus roseicapilla*	16	2.93	0.95	25.5	(Cibois et al. 2014)
Columbidae	*Henicophaps*	2	13.40	0.05	27.8	(Pereira et al. 2007)
Corvidae	*Corvus*	4	3.92	0.35	31.9	(Jonsson et al. 2012)
Dicruridae	*Dicrurus*	2	6.09	0.11	25.75	(Pasquet et al. 2007)
Meliphagidae	*Meliarchus*	9	24.43	0.09	18.8	(Andersen et al. 2013a)
Meliphagidae	*Glycifohia*	3	24.97	0.04	21.4	(Andersen et al. 2013a)
Monarchidae	*Clytorhynchos*	14	6.26	0.42	17.9	(Filardi & Moyle 2005)
Monarchidae	*Myiagra*	9	3.78	0.58	18.52	(Fabre et al. 2014)
Pachycephalidae	*Pachycephala*	4	3.83	0.36	18.67	(Andersen et al. 2014)
Sylviidae	*Phylloscopus*	3	2.96	0.37	12.92	(Olsson et al. 2005)
Pittidae	*Pitta*	3	1.39	0.79	18.57	(Irestedt et al. 2013)
Procellariidae	*Pseudobulweria*	4	8.68	0.16	56.4	(Gangloff et al. 2012)
Psittacidae	*Eunymphicus*	2	2.83	0.25	36.05	(Boon et al. 2008)
Rallidae	*Gallirallus*	10	2.43	0.95	17.26	(Kirchman 2012)
Rhipiduridae	*Rhipidura*	3	6.87	0.16	21.68	(Nyári et al. 2009)
Sturnidae	*Mino*	2	4.76	0.15	19.14	(Lovette & Rubenstein 2007)
Turdidae	*Zoothera*	2	3.14	0.22	26.82	(Klicka et al. 2005)
Tytonidae	*Tyto*	5	10.87	0.15	33.33	(Jonsson et al. 2013)
Zosteropidae	*Zosterops*	22	3.59	0.86	16.4	(Moyle et al. 2009)

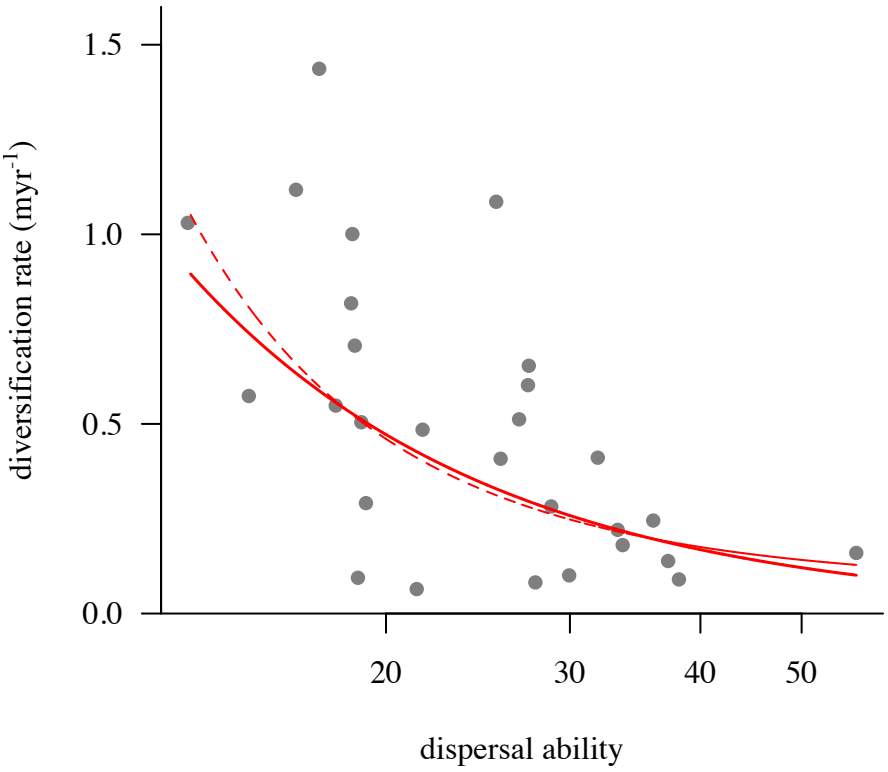
*The clade name corresponds to the focal genus or species (that is endemic to Melanesia); some clades contain multiple genera, see supplementary table 1 (ESM) for a list of species included in the analysis.

Supplemental Material

Robustness to Species Limits

To confirm that our results are robust to uncertainty in species limits, we repeated our analysis of the relationship between dispersal ability and diversification rate using the total number of basal taxa (sub-species and monotypic species) for each clade included in the analysis (supplementary table 1). We used equation 1 but with the number of basal taxa per clade rather than the number of species per clade to estimate a net diversification rate. The results were qualitatively the same. The best-fitting model was a negative linear model (log(diversification rate) = 3.7 – 1.49 * log(dispersal), AIC = 66.42, $R^2 = 0.28$, $p < 0.001$), which fit the data better than the best-fitting quadratic model, which was a monotonically negative curve (log(diversification rate) = 8.55 – 4.51 * log(dispersal) + 0.47 * log(dispersal)^2, AIC = 68.2, $R^2 = 0.26$, $p = 0.004$). Both models were better than a constant rate model (AIC = 73.0) and show a monotonically negative relationship between dispersal ability and diversification (supplementary figure 1). These results demonstrate that the negative relationship between dispersal ability and diversification rates is robust to uncertainties regarding species limits.

Supplementary figure 1. Dispersal ability and diversification rate estimated using basal taxa (subspecies and monotypic species). Lines represent the best fitting model (a negative linear model, solid line) and a quadratic model (dashed line). Both models suggest a monotonically negative relationship.



Supplementary table 1. Clade composition, dispersal ability, and historical diversification rate estimates included in the analyses. The species included in each clade for our analyses are listed below. The Mayr & Diamond (2001) speciation index (number of sub-species and allospecies per species) is taken from Appendix 5 in Mayr and Diamond (2001). Hand-wing index estimates are the average estimate of 3 adult male specimens when available (raw data available from BCW upon request).

Family	Species In Clade	Number of Species	Number of Sub-species	Hand-wing Index	Mayr and Diamond (S+A)
Accipitridae		2	2	38.15	2
	Haliaeetus sanfordi	*1*	*1*	*35.10*	-
	H. leucogaster	*1*	*1*	*41.20*	*2*
Accipitridae		2	2	37.25	1
	Henicopernis infuscatus	*1*	*1*	*37.4*	*1*
	H. longicauda	*1*	*1*	*37.1*	-
Aegothelidae*		2	2	29.95	-
	Aegotheles savesi	*1*	*1*	*31.3*	-
	A. novaezealandia	*1*	*1*	*28.6*	-
Alcedinidae		12	12	18.94	8
	Ceyx lepidus	*1*	*1*	*20.23*	*8*
	C. uropygialis	*1*	*1*	*21.79*	-
	C. pallidus	*1*	*1*	*17.40*	-
	C. meeki	*1*	*1*	*17.82*	-
	C. malaitae	*1*	*1*	-	-
	C. collectoris	*1*	*1*	*18.13*	-
	C. nigromaxilla	*1*	*1*	*21.32*	-
	C. dispar	*1*	*1*	*16.29*	-
	C. mulcatus	*1*	*1*	*18.55*	-
	C. solitarius	*1*	*1*	*19.41*	-
	C. gentiana	*1*	*1*	*17.44*	-
	C. sacerdotis	*1*	*1*	*19.95*	-
Cacatuidae		5	11	28.79	1
	Cacatua galerita	*1*	*4*	*26.99*	*1*

C. sulphrea	*1*	*4*	*30.90*	-
C. alba	*1*	*1*	*31.79*	-
C. ophthalmica	*1*	*1*	*27.84*	-
C. moluccensis	*1*	*1*	*26.41*	-
Cettiidae	5	8	14.78	1
Cettia annae	*1*	*1*	*15.47*	-
C. parens	*1*	*1*	*16.38*	*1*
C. ruficapilla	*1*	*4*	*14.83*	-
C. haddeni	*1*	*1*	*12.43*	-
C. carolinae	*1*	*1*	-	
Columbidae	5	9	27.40	6
Alopecoenas stairi	*1*	*1*	*29.70*	-
A. sanctaecrucis	*1*	*1*	*30.18*	-
A. beccarii	*2*	*6*	*23.97*	*6*
A. canifrons	*1*	*1*	*25.78*	-
Columbidae	2	3	27.8	1
Henicophaps foersteri	*1*	*1*	*28.0*	*1*
H. albifrons	*1*	*2*	*27.6*	-
Columbidae	2	7	27.35	2
Ptilinopus eugeniae	*1*	*1*	*27.4*	-
P. viridis	*1*	*6*	*27.3*	*2*
Columbidae	16	24	25.50	3
Ptilinopus richardsii	*1*	*2*	*25.76*	-
P. roseicapilla	*1*	*1*	*24.12*	-
P. pelewensis	*1*	*1*	*22.33*	-
P. porphyraceus ponapensis	*1*	*4*	*27.84*	-
P. greyi	*1*	*1*	*26.09*	-
P. porphyraceus Eua Tonga	*1*	-	-	-
P. perousii	*1*	*2*	*27.30*	-
P. huttoni	*1*	*1*	*24.48*	-
P. insularis	*1*	*1*	*21.89*	-
P. chalcurus	*1*	*1*	-	-
P. coralensis	*1*	*1*	*22.88*	-
P. purpuratus chrysogaster	*1*	*3*	-	-
P. rarotongensis	*1*	*2*	*23.27*	-
P. purpuratus purpuratus	*1*	-	*28.08*	*3*
P. dupetithouarsi	*1*	*2*	*29.00*	-
P. mercieri	*1*	*2*	*28.46*	-

Columbidae	3	4	33.7	3
Reinwardtoena browni	*1*	*1*	*34.3*	*3*
R. crassirostris	*1*	*1*	*31*	-
R. reinwardtii	*1*	*2*	*35.8*	-
Corvidae	4	5	31.91	2
Corvus meeki	*1*	*1*	*31.51*	-
C. moneduloides	*1*	*1*	*24.42*	-
C. woodfordi	*1*	*2*	*33.27*	*2*
C. validus	*1*	*1*	*38.43*	-
Dicruridae	2	12	25.75	4
Dicrurus megarhynchus	*1*	*1*	*25.92*	*4*
D. bracteatus	*1*	*11*	*25.58*	-
Meliphagidae	3	5	21.4	-
Glycifohia notabilis	*1*	*2*	*18.7*	-
G. undulata	*1*	*1*	*21*	-
Gliciphila melanops	*1*	*2*	*24.5*	-
Meliphagidae	9	10	18.81	1
Meliarchus sclateri	*1*	*1*	*15.74*	*1*
Guadalcanaria inexpectada	*1*	*1*	*17.97*	*1*
Gymnomyza viridis	*1*	*2*	*19.14*	-
Xanthotis provocator	*1*	*1*	*18.05*	-
Gymnomyza samoensis	*1*	*1*	*18.16*	-
Foulehaio procerior	*1*	*1*	*20.96*	-
F. taviuensis	*1*	*1*	*19.42*	-
F. carunculatus	*1*	*1*	*21.05*	-
Gymnomyza aubryana	*1*	*1*	-	-
Monarchidae	14	31	17.90	1
Clytorhynchos pachycephaloides	*3*	*16*	*17.33*	-
C. hamlini	*1*	*1*	*15.55*	*1*
Mayornis lessoni	*3*	*4*	*16.65*	-
Neolalage banksiana	*1*	*1*	*19.29*	-
Pomarea iphis	*5*	*6*	*21.64*	-
Chasiempis sandwichensis	*1*	*3*	*16.92*	-
Monarchidae	9	22	18.52	6
Myiagra ferrocyanea	*1*	*4*	*19.57*	*6*

Myiagra pluto	*1*	*1*	*19.39*	-
Myiagra cervinicauda	*1*	*1*	*17.10*	-
Myiagra caledonica	*1*	*5*	*19.1*	-
Myiagra vanikorensis	*1*	*5*	*20.33*	-
M. albiventeris	*1*	*1*	*19.22*	-
M. atra	*1*	*1*	*15.9*	-
M. freycineti	*1*	*1*	*19.3*	-
M. galeata	*1*	*3*	*16.80*	-
Pachycephalidae	4	15	18.67	
Pachycephala feminina	*1*	*1*	*16.54*	*16*
P. flavifrons	*1*	*1*	*18.2*	-
P. graeffi/vitiensis	*1*	*12*	*21.28*	-
P. jacquinoti	*1*	*1*	-	-
Pittidae	3	4	18.57	4
Pitta splendida	*1*	*1*	*16.97*	*4*
P. gazellae	*1*	*1*	*20.24*	-
P. novaehibernicea	*1*	*2*	*18.5*	-
Procellariidae	4	5	*56.40*	
Pseudobulweria becki	*1*	*1*	-	-
P. rostrata	*1*	*2*	*56.4*	-
P. macgillivrayi	*1*	*1*	-	-
P. aterrima	*1*	*1*	-	-
Psittacidae	2	2	36.05	-
Eunymphicus cornutus	*1*	*1*	*36.79*	-
E. uvaeensis	*1*	*1*	*35.30*	-
Rallidae	10	33	17.26	4
Gallirallus philippensis	*1*	*21*	*27.09*	*8*
G. rovianae	*1*	*2*	*17.35*	-
Tricholimnas sylvestris	*1*	*1*	*14.61*	-
Nesoclopeus poecilopterus	*1*	*3*	*13.10*	*3*
G. owstoni	*1*	*1*	*15.50*	-
G. wakensis	*1*	*1*	*28.20*	-
G. dieffenbachii	*1*	*1*	-	-
G. pendiculentus	*1*	*1*	-	-
G. ripleyi	*1*	*1*	-	-
Habropteryx insignis	*1*	*1*	*5.00*	*1*
Rhipiduridae			21.68	13

Rhipidura cockerelli	*1*	*7*	*22.8*	-
R. rufiventris	*1*	*20*	*19.65*	*13*
R. fuscorufa	*1*	*1*	*22.6*	-
Sturnidae	2	4	19.14	1
Mino kreffti	*1*	*3*	*20.27*	-
M. dumontii	*1*	*1*	*18*	*1*
Sylviidae	3	21	12.92	4
Phylloscopus amoenus	*1*	*1*	*13.34*	*1*
P. poliocephalus	*1*	*19*	*12.72*	*7*
P. makirensis	*1*	*1*	*12.7*	-
Turdidae	2	5	26.82	6
Zoothera heinei	*1*	*4*	*30.16*	*6*
Z. talaseae	*1*	*4*	*23.48*	-
Tytonidae	5	11	33.33	2
Tyto manusi	*1*	*1*	*31.6*	-
T. novaehollandiae	*1*	*6*	*41.3*	*2*
T. sororcula	*1*	*2*	-	-
T. almae	*1*	*1*	-	-
T. aurantia	*1*	*1*	*27.1*	-
Zosteropidae	22	55	16.40	2.67
Zosterops metcalfi	*1*	*3*	*15.9*	*2*
Z. stressemani	*1*	*1*	*12.92*	*1*
Z. ugiensis	*1*	*3*	*17.2*	*3*
Z. vellalavella	*1*	*1*	*14.48*	-
Z. fuscicapillus	*1*	*2*	*17.4*	-
Z. splendidus	*1*	*1*	*16.64*	-
Woodfordia superciliosa	*2*	*2*	*14.3*	*1*
Z. flavifrons	*1*	*7*	*16.2*	-
Z. cinerea	*1*	*3*	*16.8*	-
Rukia oleaginea	*3*	*3*	-	-
Z. luteirostris	*1*	*1*	*16.43*	-
Z. rendovae	*1*	*1*	*19.41*	-
Z. kulambangrae	*1*	*1*	*14.01*	-
Z. teteparius	*1*	*1*	*12.85*	-
Z. lateralis	*1*	*17*	*22.5*	-
Z. rennelliana	*1*	*1*	*15.5*	-
Z. inornatus	*1*	*1*	*14.5*	-
Z. griseotincta	*1*	*5*	*20.27*	*8*

Z. murphyi	*1*	*1*	*17.91*	*1*

*Because specimens were not available for *Aegotheles savesi* or *novaezealandia,* they were given HWI values obtained from specimens of *A. wallacii*, and *A. insignis*, respectively.

CHAPTER 3. MIXED-SPECIES FORAGING FLOCKS OF BIRDS IN THE SOLOMON ISLANDS: DIFFERENCES IN MORPHOLOGY REFLECT VARIATIONS IN FORAGING BEHAVIOR ACROSS TAXONOMIC SCALE

Abstract

Understanding how co-occurring species divide ecological space is a central issue in ecology. Functional traits have the potential to serve as a means for quantitatively assessing niche partitioning by different species based on their ecological attributes, such as morphology, behavior, or trophic habit. This enables testing ecological and evolutionary questions using functional traits at spatio-temporal scales that are not feasible using traditional field methods. Rapid evolutionary change, however, may limit the utility of morphological functional traits as indicators of how niches are partitioned among species. Changes in behavior may occur more rapidly than morphological changes, decoupling morphological functional traits from behaviors that mediate ecological interactions, limiting the use of morphology as a proxy for behavior. This problem may be particularly relevant following the colonization of insular systems where species confront vastly different abiotic and biotic conditions, spurring rapid adaptive change, compared to rates of adaptive evolution on continents. Alternatively, parallel adaptive changes in behavior and morphology may maintain the correlation between morphology and behavior. Further, high intra-specific competition relative to inter-specific competition on islands can increase within-species morphological variation, potentially limiting the utility of morphology as an indicator for behavioral changes at small taxonomic scales. Bird species that forage in mixed-species flocks are exposed to inter-specific competition and facilitation that are especially likely to enhance rates of evolutionary adaptation in behavior. Island flocks are therefore an ideal system to test whether rapid evolutionary change, in conjunction with increased intra-specific morphological variation, has the capacity to decouple morphology and behavior. Our study explores this issue using observations of individual birds foraging within mixed-species foraging flocks in the

Solomon Islands; we use these data to develop quantitative characterizations of the foraging behavior of flocking species across four islands. Morphology is characterized using a suite of functional-trait measurements taken on museum specimens. We find that foraging behavior across all taxa and islands is significantly correlated with morphology. Further, we show that even within genera, shifts in morphology across islands are highly correlated with shifts in foraging behavior. Because morphology predicts foraging behavior despite the insular nature of our system and the extreme degree of inter-specific interactions within mixed-species foraging flocks, we suggest that bird morphology, which is more readily obtained than spatially and temporally comprehensive sets of behavioral data, can predict niche partitioning in bird communities across systems, and even within close relatives that are morphologically and behaviorally similar.

Keywords: mixed-species flocks, behavioral ecology, Melanesia, ornithology, morphology

Introduction

A central focus of ecology is to understand how and why species co-exist through the partitioning of resources. Classic studies with birds have tested niche partitioning hypotheses using detailed observations of behavior, and various methods of quantifying ecological space, to characterize the ecological niches of species (Grinnell 1917, MacArthur 1958). Traditionally, direct observations of how species exploit potentially limiting resources are used to uncover niche partitioning and overlap to determine community structure. These studies are usually focused on pairwise interactions centered on competition for limited resources. Functional traits have also been used to elucidate community structure through the analysis of partitioning of

niche space (e.g., by using hyper-volumes; Ricklefs and Travis 1980). Trait-based methods for determining community structure assume that morphological characterization of species reflects their biotic interactions as well as local adaptations. For example, traits have been correlated to complex foraging behaviors in various contexts, including across major taxonomic groups within a community (Miles and Ricklefs 1984), across major adaptive radiations (Fitzpatrick 1985a), and within single smaller clades (Botero-Delgadillo and Bayly 2012). A consensus has emerged through these studies: bird morphology is broadly correlated with foraging behavior, suggesting that morphology can be used as a proxy or indicator of foraging behavior, resulting in the use of functional traits as surrogates for ecological differences across spatial and temporal scales that are beyond the scope of direct observation (e.g. Weeks and Claramunt 2014, Weeks et al. 2016a).

Despite widespread use of morphology as a proxy for behavior, there are both specific examples of behavior and morphology being decoupled (e.g. behavioral flightlessness in some Melanesian birds, where birds have retained the morphological flight apparatus but have adapted their behavior to greatly reduce their flight; Diamond 1981), and broader syntheses that have found behavioral traits to be more evolutionarily labile than morphological traits (Blomberg et al. 2003). Together, these findings demonstrate that in some circumstances morphological adaptations may lag behind behavioral changes, potentially limiting the utility of morphology as a proxy for behavioral differences between recently diverged populations or taxa. It is not known how long this lag may last, potentially decoupling morphology and behavior and phylogeographic scales, but not phylogenetic scales. We test whether morphology is correlated to the position in the canopy and foraging maneuvers of species in mixed-species foraging flocks of birds in the Solomon Islands (Figure 1).

To explore the potential for morphology to predict complex behaviors, one needs multiple communities in which species clearly coexist and partition resources; in this respect, mixed species flocks of foraging birds are ideal. Birds form mixed-species flocks in virtually all habitats, and have been documented on every continent (Tubelis 2007). In Northern Melanesia, qualitative descriptions of mixed-species foraging flocks have characterized them as regular fixtures of the avifauna, and important components of the natural histories of many species (Diamond 1975b, Kratter et al. 2001, Dutson 2011). In the Solomon Archipelago, the participation of species in mixed-species foraging flocks of insectivorous birds has been noted (Dutson 2011), but holistic quantitative flock descriptions are lacking.

Participation in flocks can result in improved predator avoidance and improved foraging efficiency, though can also be ecologically costly (reviewed in Sridhar et al. 2009). Due to the intensity and complexity of inter-specific interactions in mixed-species flocks, constituent species are likely exposed to intense biotic selective pressures that may stimulate rapid behavioral adaptation, and can be characterized by behavioral flexibility across landscapes (Knowlton & Graham 2011). Here, we quantify foraging behavior for mixed-species foraging flocks from four islands in the Solomon Archipelago: Kolombangara, Choiseul, Makira, and Vangunu (Table 1; Figure 1) to test the relationship between morphology and foraging behavior. In assessing mixed-species foraging flocks of the Solomon Islands, we are examining a system that is characterized by biotic and abiotic conditions that are expected to be ideal for stimulating rapid behavioral adaptation.

We address two questions: 1) what is the potential for rapid adaptive evolution—for example following colonization of depauperate insular systems—to decouple morphology and foraging ecology across phylogenetic and phylogeographic scales, and 2) how well do shifts in

morphology characterize shifts in behavior of closely related taxa and populations across islands? To address the first question, we test the null hypothesis that behavior and morphology are not correlated. This lack of correlation may be the outcome of rapid behavioral adaptation in response to novel abiotic and biotic pressures, and more conserved morphologies. Alternatively, behavior and morphology may be correlated. Such a correlation would imply that behavior and morphology have changed in parallel, with any lag in morphological change fleeting enough that a correlation between morphology and behavior persists. To address the second question, we test the null hypothesis that within genera, recent and limited divergence between taxa across the islands will not be reflected in correlated shifts in behavior and morphology across islands. This may be the result of highly consistent behaviors and morphologies across islands, or rapid recent behavioral changes that are not yet reflected in morphology. Alternatively, it may be possible that even at phylogeographic scales, correlated shifts in morphology and behavior may be discovered; this suggests that even subtle and recent changes in behavior may be approximated using morphology.

Methods

Flock Characterization

Mixed-species flock descriptions and foraging data are based on targeted flock observations by BCW over the course of two field seasons (June 6-July 24, 2012 and June 6-July 9, 2016; Table 1). The limitations of observing birds in the rainforest canopy precluded collection of comprehensive lists of constituent species in each flock or precise estimates of relative abundances within flocks, but by pooling across all observations at a locality, we have developed qualitative descriptions of flock composition for each island. Flocks are characterized

based on typical species composition with notes on the foraging behavior, inter-specific interactions of note, estimated relative abundances within the flocks, and the perceived role of each species in the flock. The dominant call is noted, as is the consistency with which the flocks appeared to form around an individual species. The five most consistent genera from the flocks are analyzed.

Relating Foraging Behavior and Morphology

Two sets of analyses were conducted to test for correlations between shifts in morphology and foraging behavior. For all analyses the data are representative of a single taxon on a single island. This means that if a genus has a distinct species on each of the four islands, a data point was included for each species on each island. Similarly, if a genus were to have a single species found on all islands, the populations on each island were included as distinct data points (i.e. they were treated in the same way that two different species were treated). In intermediate cases (e.g. if a genus were to have one species found on two of the islands and different species on the remaining two islands), each island population was treated identically. For the first set of analyses, all populations (regardless of genus, species or subspecies) were analyzed at the same time (subsequently referred to simply as the correlation between morphology and behavior). For the second set of analyses, each genus was analyzed independently (subsequently referred to as the within-genus correlations between morphology and behavior).

Foraging Behavior

On each island, days were spent walking along ridgelines, and observations were collected whenever a flock was encountered. These observations were collected in low to mid-elevation forest, which varied in absolute elevation from island to island, but was considered to be the forest below stunted montane forest, a readily apparent transition on all islands. Observations were only made in forest that had not been recently impacted by humans; anecdotal evidence suggests that these village sites were largely abandoned as a result of conversion to Christianity, which happened in three waves: 1845-1855, 1898-1942, and 1946-1966 (Laracy 1969). While it is impossible to know exactly when these particular sites were abandoned, anecdotal evidence suggests that it was roughly around 1900, and much of the migration to the coast had occurred before World War II (at which point, limited migration back into the interior forests occurred as a result of the war). Historical impact was clearly very minimal, with relicts of extremely limited clearing for gardens and village sites; human activities appear to have been restricted to ridges due to inter-group conflict, and forest near ancient village sites was indistinguishable from distant forest. The only exception to this was the site on Choiseul, which was a village abandoned from roughly 1960-1980 (a date estimated by local landowners), meaning that there were still signs of the impacts of abandoned gardens on the forest plant composition and structure, and the village was quite large in extent and included some limited tree crops (ranging from limited cacao groves, to more subtle changes, e.g. increased relative abundances of mature tree nut species).

Upon encountering a flock, any foraging maneuver made by an individual was noted, and the elevation and time of encounter were recorded. Foraging maneuvers were characterized based on whether they occurred in the lower, middle, or upper stratum of the canopy, and the type of move that was made: picking (capturing food while perched or hopping along a branch),

gleaning (capturing food from a substrate while flying), or hawking (capturing food on the wing, in mid air) *sensu* Holmes et al. (1979). Because it was not always possible to determine if the same individual was being counted making multiple moves, multiple moves made by one individual may have been counted. We do not expect this was a frequent occurrence, and note that when multiple moves were made by single individuals in other systems, those moves were no more correlated than moves by multiple individuals of the same species (Holmes et al. 1979).

We used reciprocal averaging (RA) to ordinate foraging behavior in order to characterize both the foraging moves and the distribution of those moves through the canopy strata for each taxon on each island (following Miles and Ricklefs 1984). Reciprocal averaging was conducted using the detrended correspondence analysis and basic reciprocal averaging ("decorana") function in the Vegan package (Oksanen et al. 2016), implemented in R (R Core Team 2016).

For the general correlation between morphology and behavior, reciprocal averaging was used to ordinate the foraging data for all species across all islands. While there is no standard way to determine how many reciprocal axes should be used to characterize an RA ordination, we took the approach that all axes would be used until there was a significant change in the magnitude of the eigenvalue for an axis, and that species scores on these axes would be used to correlate with the morphological data. For the within-genus correlations between behavior and morphology across the four islands, RA was used to ordinate only the foraging behavior of a single genus at a time. Due to the limited sample size of each within-genus analysis, only the species scores on the first RA axis were retained.

In order to assess shifts in the distribution of foraging through the canopy strata, an additional analysis was conducted using the proportion of foraging in each stratum for each genus across all islands. Similarly, in order to assess changes in prey capture maneuver across

islands, the proportion of each prey capture maneuver on each island was calculated for each genus.

Morphological Dataset

In order to examine morphometric space within the species, we measured at least three adult male specimens of each species from each island, when available, at the American Museum of Natural History (for a mean of 4.3 specimens per island, and range of 2-10; Appendix 1). For each specimen, we measured wing length (length from the carpal joint to the tip of the longest primary), length from the carpal joint to the tip of the first secondary feather, tarsus length, toe length, tail length, bill width at the anterior edge of the nares, bill depth at the anterior edge of the nares, and bill length from the anterior edge of the nares to the tip of the bill. Morphology was characterized using a principle components analysis (PCA) based on: the hand-wing index (HWI; Claramunt et al. 2012), the ratio of tarsus to wing length, the ratio of tail to wing length, bill volume (approximated as the product of bill length, bill depth, and bill width), and toe length. All variables included in the PCA were first log-transformed, following Miles and Ricklefs (1984), and with the exception of toe length and bill volume, ratios to wing length were used to control for body size. These traits have been correlated to behavior in birds across a range of systems (Miles and Ricklefs 1984, Fitzpatrick 1985b, Botero-Delgadillo and Bayly 2012). Ordination was conducted using the "prcomp" function in the Stats package implemented in R (R Core Team 2016). The PCA was conducted using all individuals, and species average morphologies were calculated as the means of the individual scores on each PCA axis for each species (i.e. the scores of all individuals of a taxon on an island were averaged for each PCA axis). For the general correlation of morphology and behavior, a PCA was performed to ordinate

all of the morphology data together. We kept all of the axes needed to explain at least 90% of the variance in the data to test for a general correlation between morphology and behavior.

For the comparison of within-genus morphological change across the four islands, a separate PCA analysis was conducted to ordinate only the morphology of the taxa within each genus, and average scores were calculated for each island. Due to the limited sample size (n = 4-5), only the species scores on the first PCA axis were retained. In order to test how morphological distinctiveness shifted with taxonomic scale, we repeated this analysis on subsets of the dataset, assessing the ability to classify the island of each population within each genus, with the exception of *Rhipidura*, which had multiple taxa (*R. cockerelli ssp.* and *R. rufifrons ssp.*) on single islands. For *Rhipidura*, we assessed the ability to determine the subspecies identity of the individuals in the test data. Because these datasets have low sample sizes, we repeated the analysis 1,000 times for each genus, assigning the data to the training and testing subsets randomly each time, and taking the mean percentage of correct classifications across all repetitions; for the within-genus classifications, we used 50% of the data for training and 50% for testing.

In addition to the multivariate ordination-based characterization of morphology, we examined two morphological traits individually: relative tarsus length and the pointedness of the bill (which we characterized as bill length/bill width). These traits have been associated with the degree to which species capture prey on the ground (Fitzpatrick 1985b), so we tested their correlation to the proportion of non-aerial (i.e. picking) prey capture.

Correlating Morphology and Behavior

For the general correlation between morphology and behavior, we used canonical correlation analysis (CCA) based on the mean morphology of each taxon on each island (summarized using a PCA, as described above) and the foraging behavior of each taxon on each island (ordinated with RA, as described above). CCA was implemented using the "CCorA" function in the Vegan package (Oksanen et al. 2016) in R (R Core Team 2016). Significance of the correlation was assessed using an F-distribution of Pillai's Trace (as implemented in CCorA).

In order to test for within-genus correlations in the shifts of morphology and behavior across islands, the species scores of each taxon on each island on the first RA axis and the first PCA axis were correlated. Because these within-genus correlations have greatly reduced sample sizes, CCA and other multivariate analytical techniques were not feasible. Therefore, in order to compare these within-genus correlations to the general correlation between morphology and behavior, we also correlated the species scores of each taxon on each island for the first RA axis and the first PCA axis for all species in the general correlation analysis to provide context for interpretation of the within-genus results. For any genus with limited correlations, we explored the extent to which that may have been driven by correlated shifts in alternate axes of morphology and behavior (i.e. we correlated axes 2 from the RA and PCA analyses).

In order to test whether the relative tarsus length and bill volume predicted the proportion of non-aerial foraging, we regressed the proportion of picking foraging maneuvers onto these variables for all taxa across all islands.

Results

Flock Composition and Foraging Behavior

A total of 927 foraging observations were collected across the four islands (420 observations from Kolombangara, 249 from Vangunu, 115 from Choiseul, and 143 from Makira). There was not a clear break in the eigenvalues of the RA axes, which ranged from 0.66-0.26, with similar differences between all axes, so the scores for all four RA axes were used in the CCA.

Across the four islands there was relatively consistent participation of distantly related species (genera) in the mixed-species flocks, though their relative abundances within flocks and the nature of their roles varied greatly across the islands (Table 1). On Kolombangara, Vangunu, and Choiseul, the species of *Zosterops* were definitively the nuclear members of the flocks as they were consistently the loudest callers (for example, on Choiseul, *Z. metcalfii* was the dominant caller in 75% of the flocks), and flocks of the other species in the absence of *Zosterops* were exceedingly rare. However, on Makira, *Z. ugiensis ugiensis* was present in low relative abundances, and was not a vocal, consistent, or nuclear participant in the mixed-species flocks. This shift from being the core nuclear member of the flocks on Kolombangara, Choiseul, and Vangunu to a peripheral member on Makira is correlated with a shift from foraging throughout all strata to a total lack of foraging in the understory and a predominance of upper canopy foraging on Makira (Figure 2). The majority of flocks on Makira were dominated by *Symposiachrus vidua,* which was the main caller in 57% of the flocks.

In contrast to the flocks on Makira, the *Symposiachrus* species on Kolombangara, Vangunu and Choiseul were largely unobtrusive, though to varying extents. On Kolombangara, *S. browni* was present almost exclusively in the understory, and in low numbers, with extremely limited calling. On Vangunu, *S. browni* was still present in low numbers, but was less restricted to foraging in the understory, and was often observed foraging in higher strata than *M. richardsii*,

a scenario seldom found on Kolombangara. On Choiseul, *S. barbatus* was most similar in behavior to *S. browni* on Vangunu, though it was much more readily observed than *S. browni* on either Kolombangara or Vangunu. These qualitative assessments, which were noted in the field, are strikingly well correlated to the quantitative characterization of foraging shifts across the islands (Figure 2).

Differences were observed in the behavior of *Monarcha* across the islands. On Kolombangara and Vangunu, *M. richardsii* was apparent, and on Kolombangara it was frequently the second most vocal and abundant species in the flocks. Its behavior was noticeably different on Kolombangara and Vangunu, with a shift from largely picking across all strata to an increased presence in the lower canopy and a shift toward more aerial foraging, respectively. Again, this shift was significant enough that it was noted in the field, and later corroborated with quantitative characterization of both the distribution of foraging through the canopy strata (Figure 2) and the shift in prey capture maneuvers (Figure 3). The shift in canopy occupancy was inversely related to a corresponding shift in *Symposiachrus*; this was readily apparent in the field. The distribution of foraging through the canopy, and prey capture maneuver proportions were similar on Makira and Choiseul, where *Monarcha* behavior was more concentrated in the middle and upper strata, and shifted from picking to aerial foraging. In addition to the quantified changes in behavior, it was noted that *Monarcha* was significantly more difficult to observe on these islands, in particular on Makira where observing foraging by *Monarcha* was rarer than any other species, including *Z. ugiensis ugiensis*.

In contrast to the apparent shifts in the character of flock participation of *Zosterops, Monarcha,* and *Symposiachrus*, changes in the participation of *Rhipidura* were not apparent through qualitative observations. In particular, the behavior of *R. cockerelli* appeared upon

observation to be wholly consistent across all islands, with individuals quietly waiting on exposed branches in the middle stratum of the canopy to sally off the branch hawking prey. This behavior is best characterized by the *Rhipidura* data from Choiseul where *R. rufifrons* was absent, so only *R. cockerelli* behavior is summarized, and it is apparent that the majority of foraging was done via hawking in the middle or upper strata of the canopy (Figure 2; Figure 3). Similarly, the behavior of *R. rufifrons* appeared to be consistent across islands, however it was different from *R. cockerelli* in that its behavior was much less specialized. Based on the qualitative summary of field observations, *R. rufifrons* appeared to forage through all strata of the canopy, and using all manner of prey capture techniques, though gleaning appeared to be the predominant mode of capture. This is reflected in the Makira data in both Figure 2 and Figure 3, where only *R. rufifrons* was present.

Similar to *Rhipidura*, the distribution of foraging through the canopy and mode of capture employed by *Myiagra* were relatively consistent across islands. Based on qualitative observation alone, differences in *Myiagra* foraging across islands is not apparent; all populations appear to forage exclusively in the upper or middle strata, and almost entirely by hawking. *Myiagra* was often present in what appeared to be family groups, and occasionally was vocal, often noted as an apparent, but not dominant call in the flocks. While variations in foraging behavior of *Myiagra* across the islands was not stark enough to be characterized through qualitative observation alone, the quantitative characterization of foraging suggests slight variation in the proportion of foraging occurring in each stratum across the islands, and a major increase in picking on Kolombangara.

Natural History Notes of Interest and Peripheral Species

In addition to the five focal genera, several additional passerine and non-passerine species were occasional, peripheral members of flocks (Table 1). Some of these taxa are likely more regular fixtures of the flocks than suggested by our observations, because they are quite cryptic (e.g. *Micropsitta*). Additionally, the character of the participation of some of these peripheral members is uncertain. For example, *P. orioloides* was frequently observed moving with the flocks but often appeared to only join the flocks as they passed through individual territories. Several natural history observations of note were made while watching the flocks. Two observations suggested that occasionally *M. castaneiventris* and *P. orioloides* play the role of sentinel species. The first was an alarm call made by *M. castaneiventris* that coincided with a hawk species (*Acccipiter*) flying above the canopy. The second was what appeared to be an alarm call made by *P. orioloides* when BCW approached a flock noisily, immediately after which all of the species that had been making contact calls were silent for several minutes. In addition to warning calls, there were two apparent pairwise interactions. The first was the observation on Makira that an individual *R. rufifrons* followed roughly 50 cm behind a *P. orioloides* as it was flying through the lower canopy apparently attempting to glean prey; the *R. rufifrons* appeared to be following in order to hawk disturbed insects. Observations were also made of *Meliarchus sclateri* aggressively chasing species that were actively picking, chasing them away from where they were foraging. *M. sclateri* would then take over picking in the place where the species had been foraging. These notes should not be viewed as comprehensive, rather as an indication of complex inter-specific dynamics in need of detailed description.

Morphology

We measured eight morphometric variables on 92 specimens distributed across the four islands (Appendix 1). The first four axes of the PCA explained 95% of the variance in morphology, so average PCA scores on these axes were calculated for each taxon on each island and used in the CCA (n = 21; Table 2; Figure 4). Surprisingly, rather than PC1 reflecting size – a common assumption (Jolicoeur 1963) - the principal loadings on PC1 were the ratio variables: HWI, relative tail length, and relative tarsus length, whereas the principal loadings on PC2 were the size variables toe length and bill volume (Table 3). The morphologies of taxa within genera form clear clusters across all islands for some groups (*Zosterops, Symposiachrus,* and *Rhipidura rufifrons* and *Rhipidura cockerelli*), and to an intermediate extent for other groups (*Monarcha* and *Myiagra*; Figure 5). Using the knn algorithm, we were able to correctly assign species identity 83% of the time, and subspecies identity 61% of the time based on morphology. The ability to successfully classify the species, subspecies, and island of individuals within genera varied across genera (Table 4), reflecting different degrees of morphological differentiation across the islands within different genera (Figure 5).

Correlating Morphology and Behavior

Based on the canonical correlation, the morphology and foraging behavior of all taxa across all islands are significantly correlated (n = 21, Pillai's trace = 1.26, $P = 0.05$). Within the individual genera, the first axis of morphology was consistently highly correlated with foraging behavior, with absolute values of the correlations ranging from 0.17-0.83, with a mean absolute value of 0.61 (Figure 6). For comparison, the first axis of the morphology PCA from the general correlation between morphology and behavior analysis was highly correlated with the species scores from the first RA axis (r = -0.56; Figure 6). However, in addition to being below the mean

absolute value of the within-genus correlation coefficients, this value was lower than all but one (*Zosterops*) of the within-genus coefficients. In order to assess the extent to which the low correlation between morphology and behavior for *Zosterops* may have been driven by correlations between alternate axes of variation in morphology and behavior, the correlation between PC2 and RA2 was calculated, and found to be high (-0.74; Figure 7).

Relative tarsus length and bill pointedness were significantly positively related with the proportion of non-aerial foraging (r^2 = 0.25 and 0.35, and P = 0.01 and P = 0.003, respectively; Figure 8).

Discussion

While morphology has the potential to serve as a powerful tool for understanding how species partition niche space (Ricklefs & Travis 1980b), this is based on the presumption that differences in morphology coevolve with changes in behavior. In birds, testing this relationship has often taken the form of correlating functional trait measurements with ordinations of multivariate representations of complex foraging behaviors, but these efforts have focused on continental systems (Miles & Ricklefs 1984; Fitzpatrick 1985b; Botero-Delgadillo & Bayly 2012), and have often explored correlations between distantly related taxa (Miles & Ricklefs 1984). Our results suggest morphology and behavior are correlated in an island system, and across taxonomic scales, including closely related conspecific populations.

Because species encounter novel environmental conditions when they colonize new areas, and because of the relatively depauperate nature of insular systems, island birds are likely to have rapidly adapted to a suite of both abiotic and biotic pressures. Island colonization is associated with ecological shifts in birds of the Southwest Pacific, including shifts in distribution

through the canopy and changes in foraging technique (Diamond 1970). Although shifts in behavior in South Pacific birds appear to largely have been limited to those species that have diverged morphologically (Diamond 1970), the biotic pressures may be particularly powerful when species life histories include complex inter-specific interactions, for example foraging in mixed-species flocks, and more nuanced ecological study may reveal decoupling of morphology and ecology at finer scales (Bolnick et al. 2007).

In addition to directional selective pressures that may arise from the novel biotic and abiotic context encountered in islands, the increased strength of intra-specific competition relative to inter-specific competition on relatively depauperate islands can result in increased niche breadth, with concomitant increases in intra-population morphological variability (i.e. the niche variation hypothesis; Van Valen 1965). This broadening of the population niche can be decoupled from individuals' niches, with individuals either expanding their niches or increasing variation of individual niches without broadening of those niches (Bolnick et al. 2010). While this added within-taxon morphological variation is unlikely to obscure correlated morphologies and behaviors at coarse taxonomic scales (e.g. species in different families), it could be capable of breaking down the correlation between morphology and behavior within smaller taxonomic groups (e.g. correlations between the shifts in morphology and behavior between populations of the same species on different islands, or subspecies of the same species on different islands). As such, if morphology and behavioral ecology are likely to become decoupled due to differential rates of behavioral and morphological adaptation, this is likely to occur in isolated island settings.

Despite the Solomon Islands presenting an ideal setting for foraging behavior to be decoupled from morphology, we find that morphology is still correlated with foraging behavior

across a wide range of taxa ($P = 0.05$). Because this correlation persists even in the face of novel abiotic and biotic conditions, and in a relatively depauperate system – and in conjunction with qualitatively similar findings across a range of continental systems (Miles and Ricklefs 1984, Fitzpatrick 1985b, Botero-Delgadillo and Bayly 2012) – we argue that this finding suggests that bird morphology can reasonably be used as an indicator of behavior and behavioral shifts in birds across a wide range of systems. Further, we show that even within individual genera, shifts in morphology are highly correlated to shifts in nuanced multivariate representations of foraging behavior. Although these correlations tend not to be highly significant, we attribute this to the low sample size; this presumption is supported by the finding that when we conducted comparable analyses on the gross morphology dataset, we find a correlation coefficient that is lower, in absolute terms, than the mean correlation coefficient of within-genus morphology and behavior relationships (Figure 6).

Interestingly, the main loadings on PC1 are the morphological traits that are based on ratios, suggesting that the variance in morphology is largely driven by changes in shape, rather than size. This interpretation is supported by the biology of the birds. The distribution of taxa along PC1 separates three distinct groups: the fantails (*Rhipidura cockerelli* and *R. rufifrons*), the monarchs (*Monarcha, Symposiachrus*, and *Myiagra*), and the white eyes (*Zosterops*). These groups differ largely in shape, while *Myiagra* is more similar in body size to *Zosterops* and *Rhipidura* than either *Symposiachrus* or *Monarcha.*

Whereas one group, *Zosterops*, has a relatively low correlation coefficient, this is not due to a lack of morphological variation among islands (Figure 5). Rather, we attribute this to the necessity of taking a bivariate approach to analyzing the within-genus data. For example, when additional bivariate analyses are taken with the *Zosterops* data some correlations are extremely

high (e.g. the correlation between PC2 and RA2; Figure 8). We attribute this to the extreme consistency of prey capture maneuver in *Zosterops* (Figure 3), suggesting that changes in canopy stratum may be related to morphological changes captured in PC2, whereas changes along PC1 may reflect a combination of changes in canopy stratum and foraging maneuver. Presumably, had we had enough sampling to take a multivariate approach within *Zosterops*, the correlation between PC2 and RA2 would have resulted in a multivariate correlation between morphology and behavior.

The two traits that we examined individually (relative tarsus length and bill pointedness) are significantly correlated with percent of non-aerial foraging ($P < 0.05$). This is in line with similar findings for ground foragers within the very distantly-related Tyrannidae (Fitzpatrick 1985b), suggesting that similar morphologies may be well suited to ground foraging and picking, despite the extreme differences in ground-dwelling and arboreal species morphologies.

In addition to confirming that morphology and foraging behavior are correlated across the islands, our findings suggest that there are significant morphological and behavioral changes in taxa depending on the island where they occur. For example, the *Monarcha* and *Symposiachrus* taxa tend to occupy distinct niches, but those niches are not consistent across islands. This adds complexity to the longstanding observation that species ranges and ecologies shift depending on the presence of other – typically closely related – species (Diamond 1975a). The shifts in foraging ecologies of taxa, even closely related taxa (e.g. populations of the same species or subspecies) across islands suggest a strong role for an as-of-yet undetermined combination of abiotic, biological, and historical contingencies in the assembly of these communities driving rapid localized changes in behavior. Based on the abiotic and biological similarity of the islands in this study, it seems likely that historical contingency has played an important role in producing

the observed differences in ecologies of taxa across islands. The ecologies of the birds of the Solomon Archipelago have been found to reflect historical biogeographic processes, and as biologically and environmentally similar replicates with varied biogeographic histories, they represent an ideal system for exploring evolutionary priority effects (Weeks et al. 2016a). While the integration of phylogeography and phylogenetics and Earth history is needed to reconstruct the assembly history of mixed-species foraging flocks across the Solomon Islands in order to explore the impacts of historical contingency on contemporary ecology, it is clear that morphological functional traits can be a powerful tool for characterizing shifts in community structure across space and time.

Figure 3.1: The Solomon Archipelago, with the sampling locations marked with asterisks.

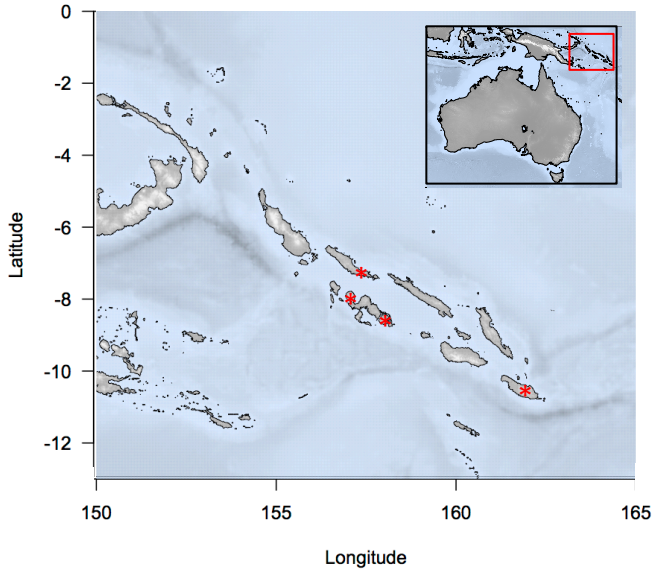


Figure 3.2: Distributions of foraging moves through the canopy. Each color represents the proportion of the total foraging behavior for each taxon that occurred on an island. These data are from 927 foraging observations across the islands; sample sizes for each taxon on each island are noted.

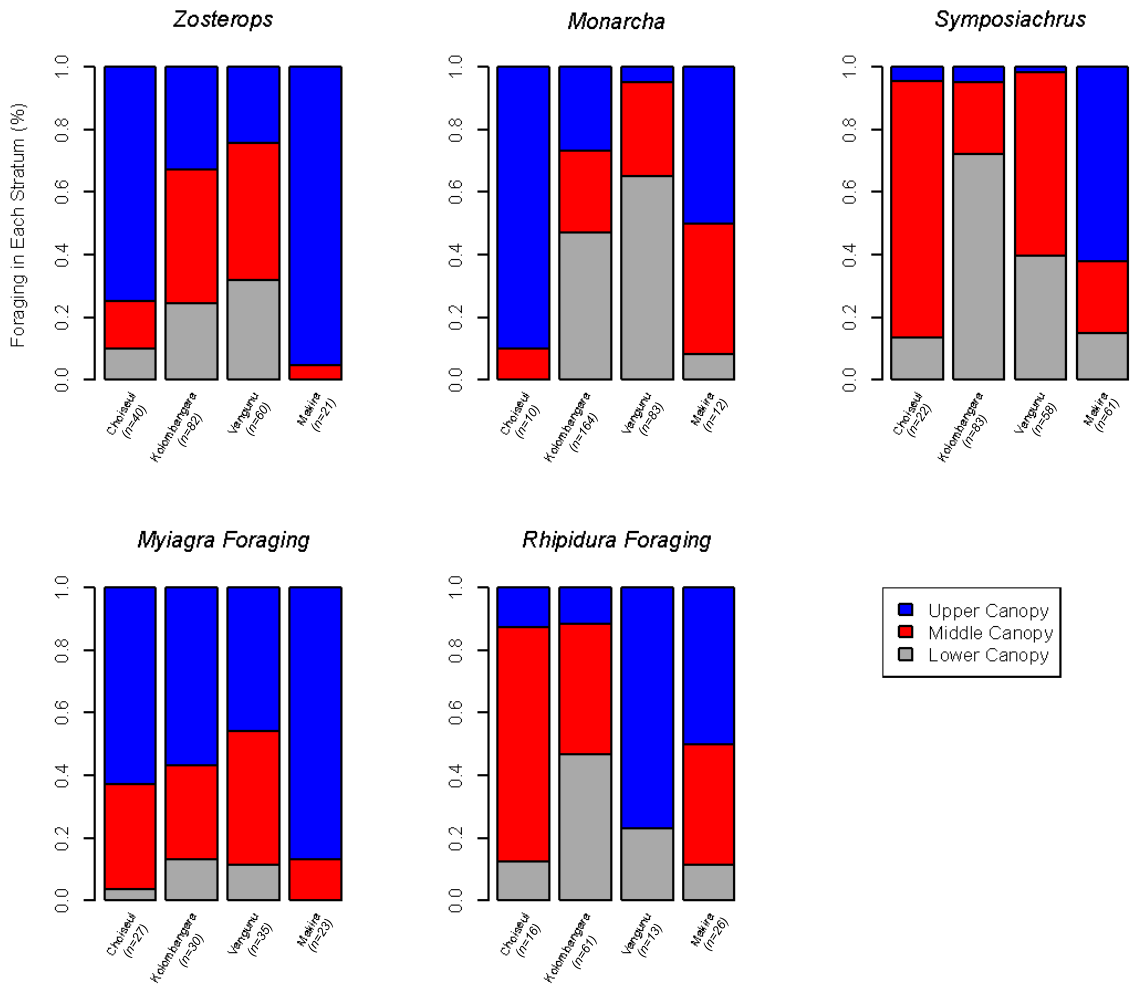


Figure 3.3: Proportion of foraging maneuver type across islands. Colors correspond to the proportion of total foraging effort comprised of each foraging maneuver for each taxon on each island. Sample sizes match those of Figure 3.2.

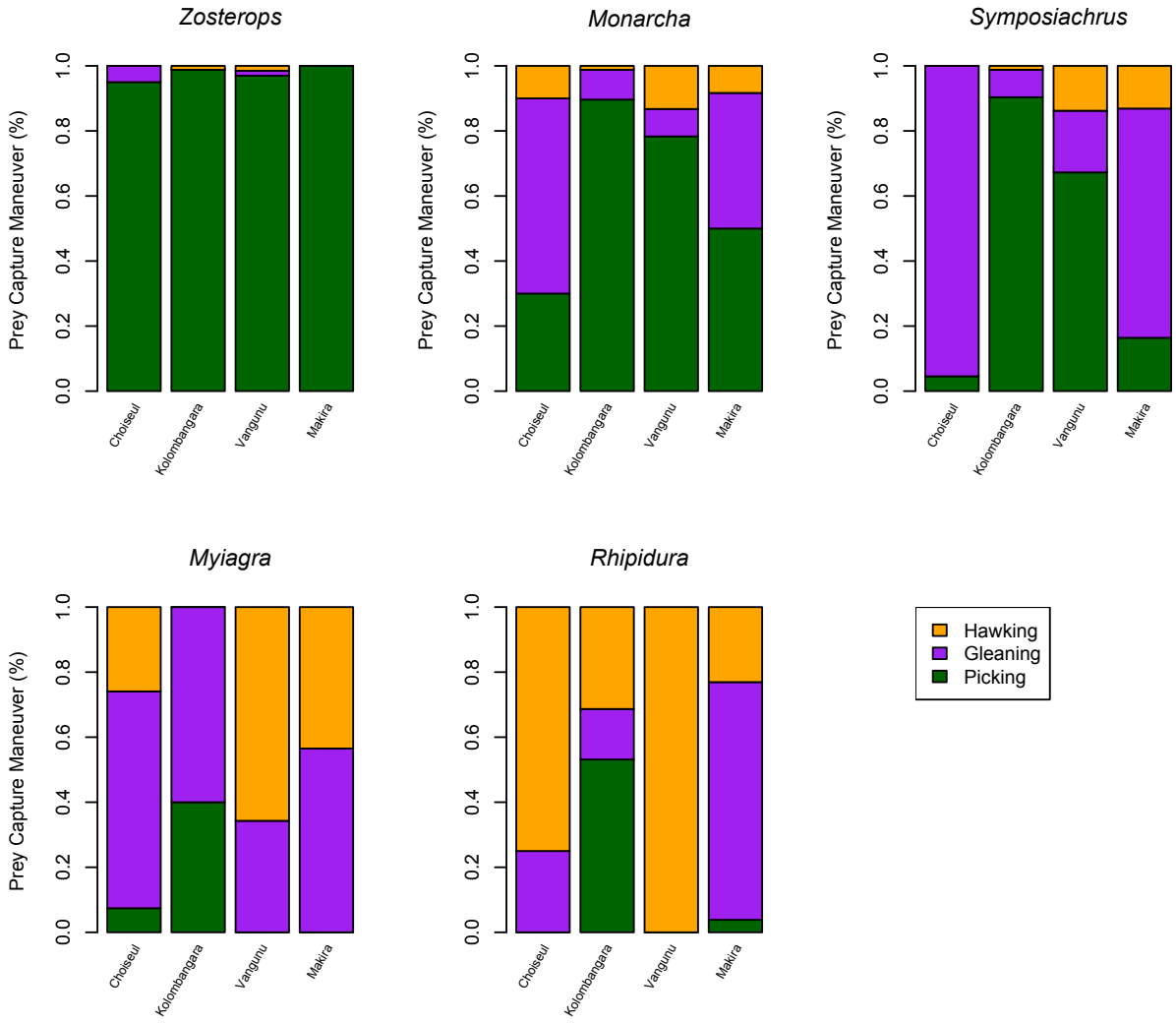


Figure 3.4: A PCA of morphology for all taxa across all islands. Each taxon on each island is a different color. Ellipses are normal data probability ellipses, using a normal probability of 68%. Loadings are represented by the arrows, scaled by each variable's loading on PC1 and PC2. Representatives of each genus are placed in proximity to their constituent taxa in the PCA.

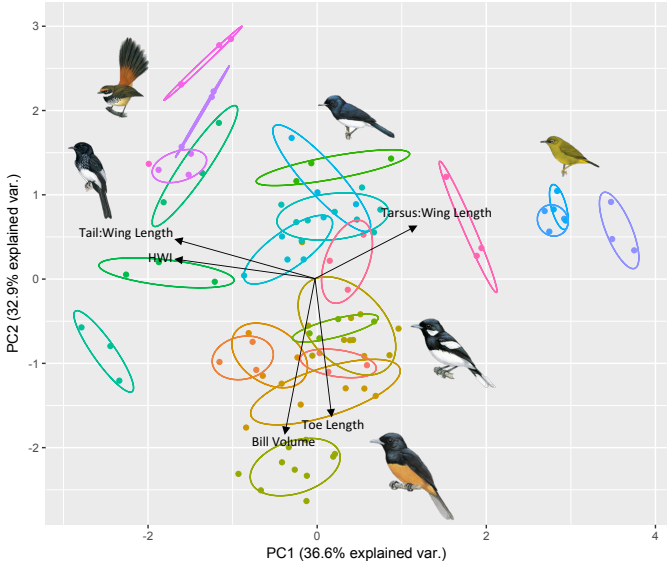


Figure 3.5: Morphological differentiation within genera across islands. Ellipses are included, showing the normal data probability distribution (68%); black dots have been added for each group, showing the mean scores for each group.

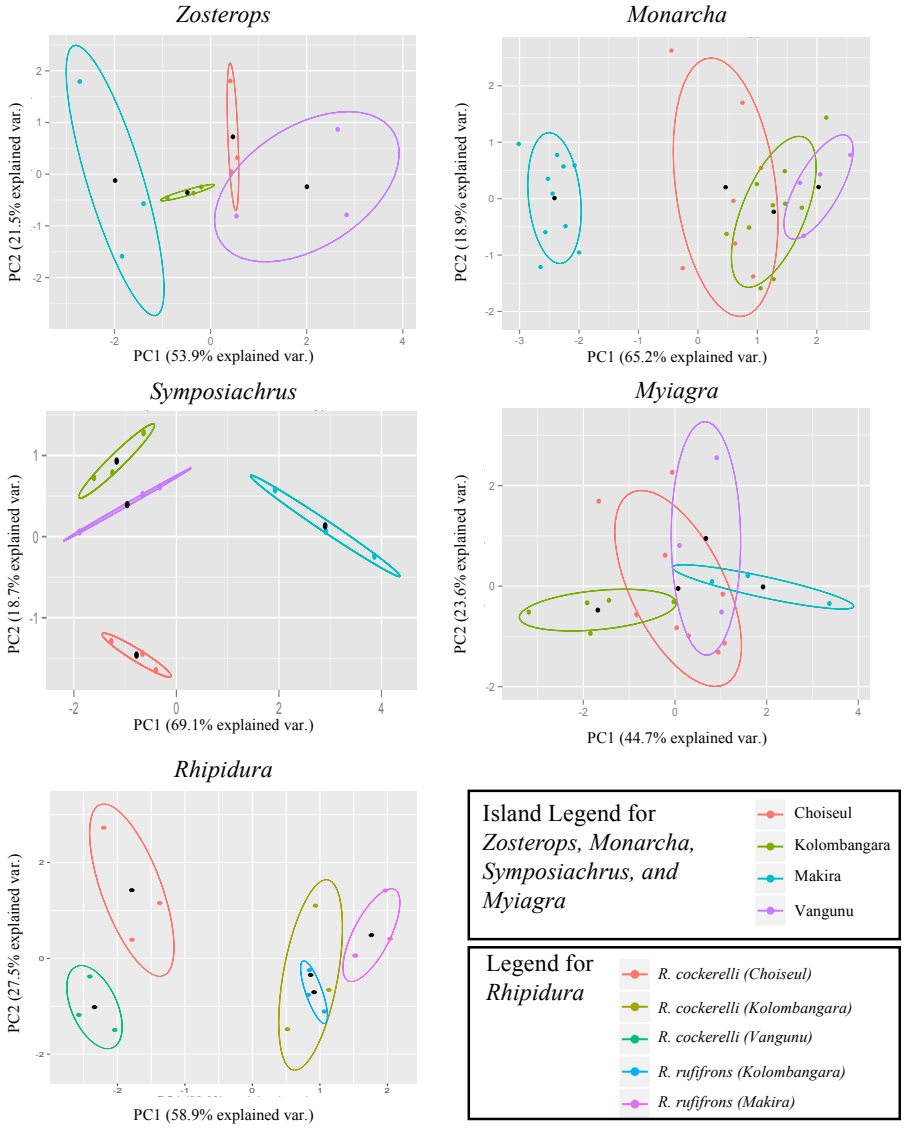


Figure 3.6: Within genus correlations. Each dot is a taxon within the genus on one of the four islands. The correlation coefficient is noted, and the correlation between PC1 and RA1 for all taxa on all islands (the "All Species" plot) is included for comparison. To help visualize trends, regression lines have been superimposed on the data; none of the individual genus regressions were significant.

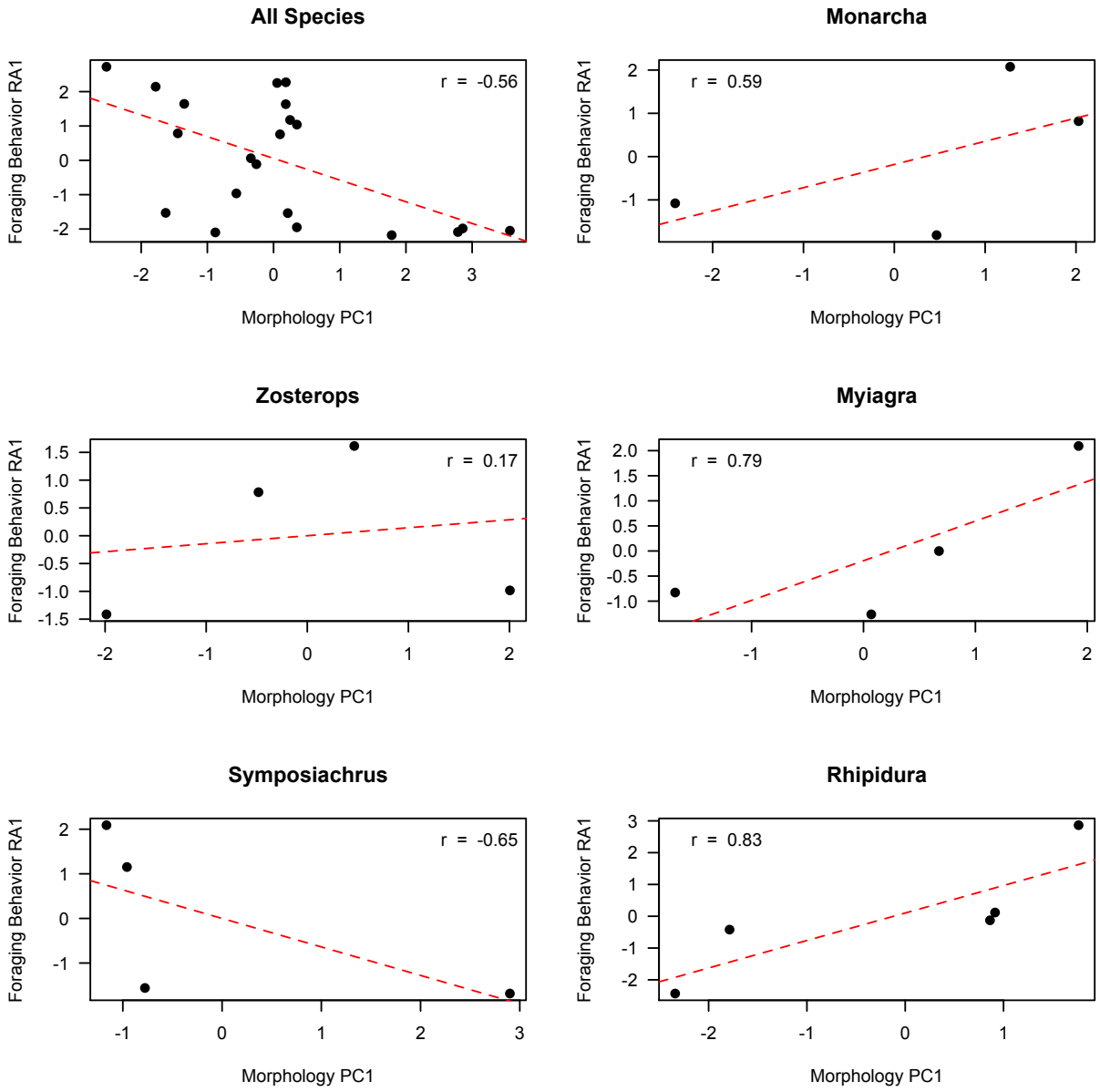


Figure 3.7: Exploring within-Zosterops morphological variation and correlation between PC2 and RA2. The low correlation coefficient for *Zosterops* between PC1 and RA1 (Figure 6) is not due to limited inter-island morphological differentiation (Figure 3), rather, it appears to be because the morphological change that is correlated with behavioral change is captured in PC2 for this group, rather than PC1. A trend line has been added.

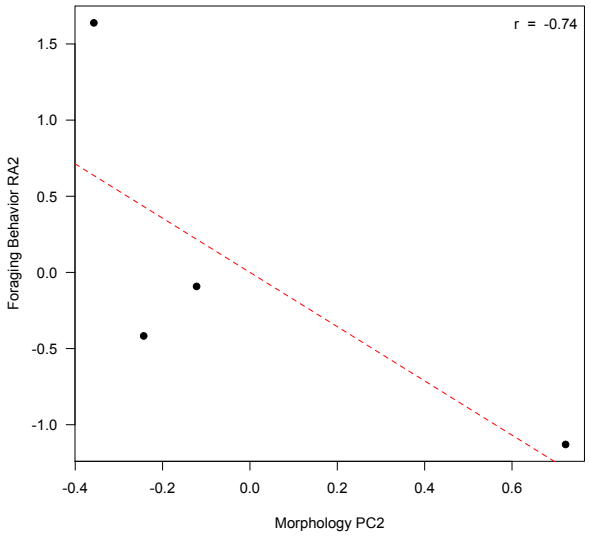


Figure 3.8: Decomposing the morphological traits associated with aerial foraging. Increased relative tarsus length (the ratio of tarsus length to wing length) and increased bill pointedness (bill length divided by bill width) have been associated with increased ground foraging in Tyrannidae flycatchers.

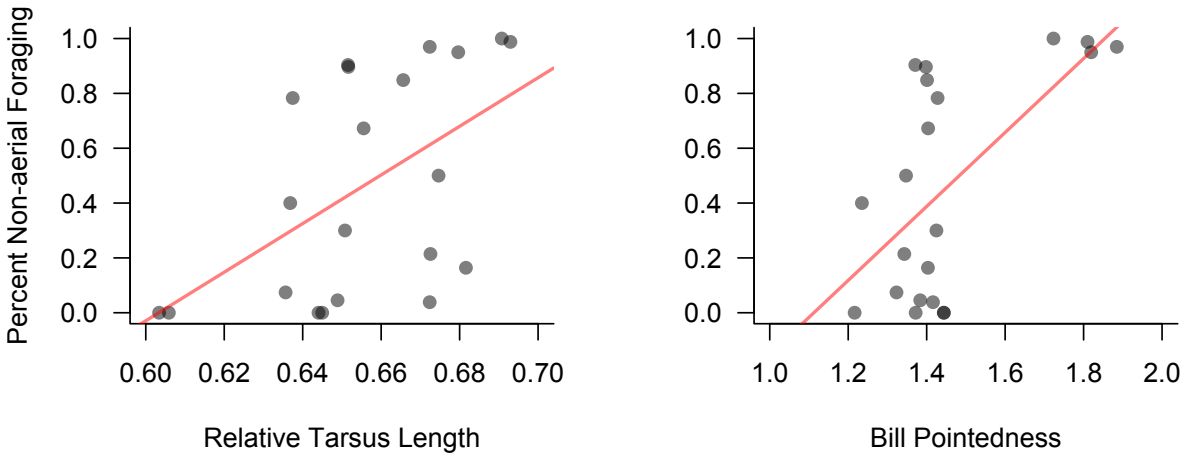


Table 3.1. Flock species composition across islands. All constituent species are noted, and dominant species are identified.

Genus	Island			
	Choiseul	Kolombangara	Vangunu	Makira
Zosterops	*Z. metcalfii exiguus*	*Z. kulambangrae kulambangrae*[1]	*Z. kulambangrae kulambangrae*[1]	*Z. ugiensis ugiensis*
Monarcha	*M. castaneiventris castaneiventris*	*M. richardsii*[2]	*M. richardsii*	*M. castaneiventris megarhynchus*
Symposiachrus	*S. barbatus barbatus*	*S. browni browni*	*S. browni browni*	*S. vidua vidua*[1]
Rhipidura	-	*R. rufifrons granti*	*R. rufifrons granti*	*R. rufifrons russata*
	R. cockerelli interposita	*R. cockerelli albina*	*R. cockerelli albina*	-
Myiagra	*M. ferrocyanea ferrocyanea*	*M. ferrocyanea feminina*	*M. ferrocyanea feminina*	*M. cervinicauda*
Pachycephala	*P. orioloides orioloides*	*P. orioloides centralis*	*P. orioloides centralis*	*P. orioloides cristophori*
Myzomela	*M. lafargei*	*M. eichhorni eichhorni*	*M. eichhorni eichhorni*	*M. tristrami*
Micropsitta	*M. finschii nanina*	*M. finschii tristrami*	*M. finschii tristrami*	*M. finschii finschii*
Meliarchus	-	-	-	*Meliarchus sclateri*[2]
Dicaeum	*D. aeneum aeneum*	-	-	-
Aplonis	*A. grandis grandis*			*A. dichroa*
Coracina	*C. tenuirostris saturatior*	*C. tenuirostris saturatior*	*C. tenuirostris saturatior*	*C. salamonis*
		C. lineata ombriosa		
Phylloscopus		*P. poliocephalus pallescens*		*P. poliocephalus makirensis*
Dicrurus				*D. bracteatus*

[1] Dominant nuclear species; [2] Second most abundant/core species

Table 3.2. Morphology Principal Component Analysis

Principal Component Axis	PC1	PC2	PC3	PC4	PC5
Proportion of Variance Explained	0.37	0.33	0.19	0.06	0.05
Cumulative Variance Explained	0.37	0.70	0.88	0.95	1

Table 3.3. Principal Component Analysis Loadings

Trait	PC1	PC2	PC3	PC4	PC5
Hand-wing Index	-0.63	0.09	-0.32	-0.66	-0.25
Relative Tail Length	-0.62	0.18	-0.26	0.71	0.12
Relative Tarsus Length	0.44	0.25	-0.72	0.14	-0.45
Toe Length	0.06	-0.63	-0.54	-0.08	0.55
Bill Volume	-0.14	-0.71	0.12	0.21	-0.64

Table 3.4. Morphology-based classification.

Group	Correct Species	Correct Island	Correct Subspecies
All Taxa	83%	NA	61%
Zosterops	100%	70%	29%
Monarcha	100%	25%	77%
Symposiachrus	100%	50%	59%
Myiagra	100%	37%	42%
Rhipidura	100%	NA	45%

Appendix 1

Genus	Species	Subspecies	Island	AMNHID	WingLength	Secondary	BillHeight	BillWidth	BillLength	Tarsus	Toe	Tail
Monarcha	castaneiventris	castaneiventris	Choiseul	219722	77.62	65.78	5.48	6.07	13.05	17.81	15	66.4
Monarcha	castaneiventris	castaneiventris	Choiseul	219719	78.59	67.3	5.42	5.5	12.09	16.87	14	67.4
Monarcha	castaneiventris	castaneiventris	Choiseul	219721	82.03	69.85	5.89	5.99	12.22	18.09	15	67.5
Monarcha	castaneiventris	castaneiventris	Choiseul	219723	84.08	70.54	5.53	5.76	12.16	18.33	15	68.9
Monarcha	castaneiventris	castaneiventris	Choiseul	228488	85.02	68.05	6.07	6.63	13.79	18.09	15	68.2
Monarcha	castaneiventris	castaneiventris	Choiseul	228489	85.22	71.44	6.2	5.91	na	15.82	14	71.4
Monarcha	castaneiventris	castaneiventris	Choiseul	219720	86.18	72.23	5.56	5.6	12.11	16.83	15	72.2
Monarcha	castaneiventris	castaneiventris	Choiseul	228486	86.84	71	6.32	5.67	11.91	18.03	15	69.8
Monarcha	richardsii		Kolombangara	225967	75.41	61.98	5.33	5.5	11.18	16.93	12	62.4
Monarcha	richardsii		Kolombangara	225974	76.64	64.88	5.57	5.68	11.68	16.17	14	62.2
Monarcha	richardsii		Kolombangara	219759	77.04	65.99	5.61	5.52	11.37	17.76	14	64.1
Monarcha	richardsii		Kolombangara	225966	77.09	66.34	5.84	5.82	10.86	16.82	14	64.3
Monarcha	richardsii		Kolombangara	219757	77.17	64.66	5.32	5.8	10.49	17.56	14	64.1
Monarcha	richardsii		Kolombangara	219758	77.28	64.17	5.32	5.62	11.2	16.52	14	64.8
Monarcha	richardsii		Kolombangara	225969	79.38	66.79	6.14	5.48	11.65	17.34	14	64.6
Monarcha	richardsii		Kolombangara	655275	79.6	66.69	5.33	5.32	11.03	17.93	15	67.3
Monarcha	richardsii		Kolombangara	225972	79.87	66.97	5.45	5.62	11.14	17.99	13	64
Monarcha	richardsii		Kolombangara	225963	80.38	66.95	6.31	6.04	11.55	16.05	13	62.8
Monarcha	castaneiventris	megarhynchus	Makira	217852	82.06	68.57	6.82	7.59	14.57	20.2	16	73.1
Monarcha	castaneiventris	megarhynchus	Makira	228053	86.13	70.35	6.94	7.46	15.19	20.26	15	73.4
Monarcha	castaneiventris	megarhynchus	Makira	217882	86.29	71.45	6.57	7.39	14.62	20.41	16	76.4
Monarcha	castaneiventris	megarhynchus	Makira	217873	86.34	70.55	6.77	7.52	14.58	20.33	16	73.4
Monarcha	castaneiventris	megarhynchus	Makira	655315	86.66	70.84	6.6	7.55	16.1	20.34	16	75.6
Monarcha	castaneiventris	megarhynchus	Makira	217853	87.71	71.36	6.45	7.3	14.61	18.92	16	78.8
Monarcha	castaneiventris	megarhynchus	Makira	217872	88.03	72.42	6.88	7.07	15.56	20.93	16	75.7
Monarcha	castaneiventris	megarhynchus	Makira	217856	88.79	74.37	6.04	7.34	14.44	20.86	16	78.2
Monarcha	castaneiventris	megarhynchus	Makira	217861	89.7	72.47	7.34	7.57	15.44	21.01	17	77.9
Monarcha	castaneiventris	megarhynchus	Makira	217866	90.73	75.68	6.8	7.73	14.59	20.6	17	81.1
Monarcha	richardsii		Vangunu	225914	77.13	65.52	5.43	5.12	11.12	16.83	14	62.7
Monarcha	richardsii		Vangunu	225929	77.27	64.9	5.76	5.97	11.44	16.23	13	61.7
Monarcha	richardsii		Vangunu	225940	79.26	66.46	5.07	5.49	11.69	15.91	14	66.2
Monarcha	richardsii		Vangunu	225941	80.6	67.8	5.19	5.5	11.42	15.63	14	64.7
Myiagra	ferrocyanea	ferrocyanea	Choiseul	225693	65.23	56.03	4.55	5.3	9.32	14.26	12	56.6
Myiagra	ferrocyanea	ferrocyanea	Choiseul	219658	66.13	55.19	4.91	5.52	8.67	14.32	12	57.7
Myiagra	ferrocyanea	ferrocyanea	Choiseul	228455	66.46	55.7	4.1	5.24	8.2	14.2	12	55.6
Myiagra	ferrocyanea	ferrocyanea	Choiseul	653165	67.03	57.39	4.17	5.27	8.86	14.77	12	56.9
Myiagra	ferrocyanea	ferrocyanea	Choiseul	228456	67.24	57.2	4.77	4.75	9.07	14.89	12	58.8
Myiagra	ferrocyanea	ferrocyanea	Choiseul	228452	67.84	57.57	4.06	4.92	8.23	14.06	12	NA
Myiagra	ferrocyanea	ferrocyanea	Choiseul	225692	69.34	57.78	4.21	5.29	8.56	14.38	13	59.9
Myiagra	ferrocyanea	ferrocyanea	Choiseul	228459	69.46	57.86	4.65	5.36	8.89	14.69	12	60.9
Myiagra	ferrocyanea	ferrocyanea	Choiseul	228450	69.97	59.14	4.04	4.33	8	14.69	12	56.7

Myiagra	ferrocyanea	ferrocyanea	Choiseul	228453	70.62	57.16	4.63	5.28	8.67	15.27	12	56.4
Myiagra	ferrocyanea	feminina	Kolombangara	225681	67.71	55.16	4.49	5.94	9.01	14.84	13	56.4
Myiagra	ferrocyanea	feminina	Kolombangara	225679	68.78	56.15	4.54	6.05	9.1	15.13	13	57.5
Myiagra	ferrocyanea	feminina	Kolombangara	219649	69.11	57.4	4.23	5.07	9.08	15.45	13	58.8
Myiagra	ferrocyanea	feminina	Kolombangara	225680	69.35	57.45	4.67	6.09	8.58	14.49	13	57.3
Myiagra	ferrocyanea	feminina	Kolombangara	225678	71.75	58.14	4.67	6.76	9.27	14.46	13	59.3
Myiagra	cervinicauda		Makira	228039	60.51	51.97	3.62	5.76	8.59	14.2	12	53.4
Myiagra	cervinicauda		Makira	653114	62.59	51.64	3.74	6.06	8.81	14.53	12	54.1
Myiagra	cervinicauda		Makira	653117	63.75	52.43	4.08	5.92	8.65	14.36	12	54.9
Myiagra	ferrocyanea	feminina	Vangunu	225690	65.95	55.37	4.77	4.52	9.01	15.35	12	56.3
Myiagra	ferrocyanea	feminina	Vangunu	225691	69.16	57.15	3.78	5.14	8.46	15.34	12	58.1
Myiagra	ferrocyanea	feminina	Vangunu	225687	71.83	59.16	3.8	3.97	8.71	15.13	12	60.9
Rhipidura	cockerelli	interposita	Choiseul	219436	81.16	65.81	4.43	5.73	9.92	14.75	13	77.8
Rhipidura	cockerelli	interposita	Choiseul	651711	86.03	68.56	4.53	5.31	10.69	14.75	13	78.1
Rhipidura	cockerelli	interposita	Choiseul	219434	89.3	74.12	4.65	5.12	9.56	14.9	13	78.1
Rhipidura	cockerelli	albina	Kolombangara	225288	71.08	57.16	4.01	4.47	7.86	18.26	14	81.3
Rhipidura	cockerelli	albina	Kolombangara	225286	75.24	60.96	3.68	4.35	7.45	17.87	13	79.6
Rhipidura	cockerelli	albina	Kolombangara	225294	77.46	61.26	4.14	4.89	7.7	18.37	14	83.8
Rhipidura	rufifrons	granti	Kolombangara	225288	71.93	57.23	3.59	4.32	7.9	16.95	14	81.7
Rhipidura	rufifrons	granti	Kolombangara	226291	75.44	60.33	3.67	4.5	7.55	18.08	14	82.4
Rhipidura	rufifrons	granti	Kolombangara	225287	76.7	61.42	3.88	3.99	7.4	17.95	13	82.1
Rhipidura	rufifrons	russata	Makira	217545	64.47	51.88	3.49	3.81	7.23	17.12	12	70.2
Rhipidura	rufifrons	russata	Makira	217559	66.75	53.21	2.36	4.24	7.57	17.55	12	72.2
Rhipidura	rufifrons	russata	Makira	217552	69.22	54.96	2.93	4.17	7.3	16.59	13	74.5
Rhipidura	rufifrons	russata	Makira	217552	69.22	54.96	2.93	4.17	7.3	16.59	13	74.5
Rhipidura	rufifrons	granti	Vangunu	225274	70.61	57.68	NA	NA	NA	16.98	14	81.1
Rhipidura	rufifrons	granti	Vangunu	225275	74.94	59.59	4.26	4.4	7.43	17.39	13	85
Symposiachrus	barbatus	barbatus	Choiseul	219556	82.1	70.03	4.82	5.32	10.13	18.03	16	71.8
Symposiachrus	barbatus	barbatus	Choiseul	219555	83.61	70.06	4.61	5.39	10.3	17.51	16	70.6
Symposiachrus	barbatus	barbatus	Choiseul	655038	83.77	70.43	4.61	5.43	10.35	17.3	15	72.5
Symposiachrus	browni	browni	Kolombangara	225565	83.14	67.88	4.67	5.56	10.5	17.91	16	75.7
Symposiachrus	browni	browni	Kolombangara	225563	83.92	67.78	4.63	5.46	9.19	18.72	16	75.7
Symposiachrus	browni	browni	Kolombangara	225560	85.39	68.94	5.03	5.17	10.58	17.27	15	76.3
Symposiachrus	vidua	vidua	Makira	654923	72.33	61.24	4.04	4.9	9.21	18.51	14	70
Symposiachrus	vidua	vidua	Makira	654925	74.02	61.75	4.58	5.31	9.37	19.49	15	70.5
Symposiachrus	vidua	vidua	Makira	228049	77.74	65.27	4.69	4.46	9.04	18.74	14	74.8
Symposiachrus	browni	browni	Vangunu	225524	84.7	69.71	4.68	5.23	10.17	19.32	16	76.2
Symposiachrus	browni	browni	Vangunu	225529	85.88	70.02	4.47	5.42	9.87	18.19	15	78.1
Symposiachrus	browni	browni	Vangunu	225528	89.37	72.92	5.15	4.98	10.33	18.39	16	76.8
Zosterops	metcalfii	metcalfii	Choiseul	220052	60.16	52.03	3.51	3.48	9.28	16.08	13	41.5
Zosterops	metcalfii	metcalfii	Choiseul	220053	60.58	51.77	3.58	3.47	8.98	16.27	14	39.8
Zosterops	metcalfii	metcalfii	Choiseul	700646	60.74	52.17	3.44	3.3	9.75	16.41	14	40.1

Zosterops	kulambangrae	kulambangrae	Kolombangara	221861	61.65	52.18	3.35	3.67	9.5	17.48	15	41
Zosterops	kulambangrae	kulambangrae	Kolombangara	221863	62.52	52.69	3.72	3.38	10.15	17.48	14	40.1
Zosterops	kulambangrae	kulambangrae	Kolombangara	700750	63.07	53.74	3.67	3.46	9.29	17.66	14	41.1
Zosterops	ugiensis	ugiensis	Makira	700669	57.62	46.49	3.46	3.55	9.45	17.2	14	40.5
Zosterops	ugiensis	ugiensis	Makira	228096	63.55	52.32	3.89	3.81	9.77	17.17	15	41.9
Zosterops	ugiensis	ugiensis	Makira	700668	66.52	55.28	3.79	3.63	8.87	17.78	15	45.6
Zosterops	kulambangrae	kulambangrae	Vangunu	222006	59.59	52.54	3.44	3.32	9.32	16.53	15	39.3
Zosterops	kulambangrae	kulambangrae	Vangunu	222002	62.44	55.15	3.39	3.22	9.31	15.4	14	39.7
Zosterops	kulambangrae	kulambangrae	Vangunu	222004	62.48	55.19	3.17	3.27	9.34	15.93	13	40.8

CHAPTER 4. BIRD ASSEMBLAGE VULNERABILITY DEPENDS ON THE DIVERSITY AND BIOGEOGRAPHIC HISTORIES OF ISLANDS

B.C. Weeks, N. Gregory, and S. Naeem

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Abstract

Biodiversity is widely acknowledged to influence the magnitude and stability of a large array of ecosystem properties, with biodiverse systems thought to be more functionally robust. As such, diverse systems may be safer harbors for vulnerable species, resulting in a positive association between biodiversity and the collective vulnerability of species in an assemblage, or assemblage vulnerability. We find that for 35 islands across Northern Melanesia, bird assemblage vulnerability and biodiversity are positively associated. This relationship is highly contingent on Pleistocene connectivity, suggesting that biogeographic history—a factor often overlooked in biodiversity and ecosystem functioning studies—may influence contemporary ecological processes. In the face of biodiversity loss attributable to anthropogenic drivers, reduced ecosystem functioning may erode the safe harbors of vulnerable assemblages. Paradoxically, these results suggest that biodiverse systems, as more robust systems, may experience greater biodiversity loss over ecological time because they harbor more vulnerable species accumulated over evolutionary time.

Significance statement: Biodiversity is broadly thought to be positively associated with a wide array of ecosystem functions and properties. Because these properties may reduce extinction risk, for example by making functioning more stable and ecosystems less prone to invasion,

biodiverse islands have the potential to accumulate species over evolutionary time that are more vulnerable to extinction. We find that bird diversity is positively related to the collective vulnerability of species in a set of assemblages. This relationship is highly contingent on biogeographic history, a factor often overlooked in biodiversity and ecosystem functioning studies. Our findings expose a paradox: biodiverse systems, as more robust systems, may experience greater biodiversity loss over ecological time because they accumulate more vulnerable species over evolutionary time.

Introduction

There is a growing body of evidence that increased levels of biodiversity can impact ecosystem functions in predictable ways. Biodiversity is widely acknowledged to significantly influence the magnitude and stability of a large array of ecosystem properties, with stronger impacts evident when larger scales (Reich et al. 2012) and multiple functions are considered (Zavaleta et al. 2010; Pasari et al. 2013). These findings provide compelling support for biodiverse systems being functionally robust, with greater stability of function (Haddad et al. 2011; Tilman et al. 2014; Hautier et al. 2015), resistance to invasion (Naeem et al. 2000; Levine et al. 2004; Fargione & Tilman 2005; Byun et al. 2013), and resistance to pathogen spread (Guilherme Becker et al. 2014). Some of the impacts of higher levels of biodiversity on ecosystem properties that are apparent at ecological timescales (e.g. greater resistance to invasion) may influence evolutionary processes, like extinction rates. In natural assemblages, such a relationship would require the persistent influence of ecosystem functionality on extinction risk across evolutionary time; as such, it may be influenced by biogeographic history.

In order to quantify the persistent effects of increased ecosystem function in diverse systems, we explore the relationship between biodiversity and an ecosystem property: assemblage vulnerability. Assemblage vulnerability is the composite of the individual vulnerabilities of an assemblage's constituent species based on a suite of geographic, ecological, and anthropogenic factors. We used five indicators of species vulnerability: range size, dispersal ability, clutch size, body size, and Union for the Conservation of Nature (IUCN) threat status. Range size is a strong predictor of extinction risk for birds globally (Lee & Jetz 2011). Dispersal ability, body size, and clutch size are species' traits (*sensu* Violle et al. 2007) associated with extinction probability, with poor dispersal, large body size, and low clutch size correlated to elevated extinction risk (Bennett & Owens 1997; Reinhardt et al. 2005). IUCN threat status represents a widely accepted estimate of vulnerability to human and other contemporary environmental pressures that may not be reflected in ecologically-relevant traits. Species vulnerability was considered inversely associated with range size, dispersal ability and clutch size, and positively associated with IUCN threat status. Thus, assemblages composed of species with similarly restricted range size, poor dispersal ability, small clutch size, and high IUCN threat status, would have the highest assemblage vulnerability value.

Though often excluded in ecological studies, biogeographic history plays a significant role in determining species composition (Wiens & Donoghue 2004) and, by extension, has the potential to influence properties of species assemblages and the ecosystem functions they govern. Species in an assemblage frequently share diversification histories (Morrone 2014), and when conducting studies across multiple sites at larger scales, it is likely that communities with different assembly histories will be compared (e.g. assemblages characterized by high levels of *in situ*

diversification as opposed to high levels of colonization). Climate-driven sea level change is an example of a key historical biogeographic process that is of particular relevance in island systems. Changes in island connectivity as a result of sea level fluctuation have been invoked to explain relationships between fundamental evolutionary processes (e.g. the relationship between dispersal diversification rates; Weeks & Claramunt 2014), and have been related to key evolutionary outcomes (e.g., species richness and endemism; Weigelt et al. 2016). In the Solomon Archipelago, throughout the Pleistocene, fluctuations in sea level have connected and isolated some islands repeatedly, while others have remained isolated throughout their histories; these historical connections are clearly evident in the distributions of diversity in the Archipelago, with taxa typically endemic to islands that formed single landmasses at the Last Glacial Maximum (LGM; Mayr & Diamond 2001).

Island systems present opportunities to test for the impact of history over evolutionary time on present-day community and ecosystem properties by providing replicate systems with varied histories. In particular, the Solomon Archipelago has long been recognized as a series of islands that can be divided into two groups based on connectivity at the LGM (Diamond & Mayr 1976) and, as such, serves as an ideal system for testing hypotheses concerning patterns and processes across ecological, evolutionary, and biogeographical scales (Diamond & Mayr 1976).

The ability of alternate assembly histories over ecological time to influence biodiversity and ecosystem functioning has been demonstrated experimentally (Fukami & Morin 2003), and while the persistence of assembly history's influence on ecological processes over evolutionary time remains relatively unstudied, there is increasing evidence that this may occur (Leopold et al.

2015). As such, it is likely that persistent ecological impacts of assembly history may influence evolutionary processes acting at long time scales (e.g. extinction probability).

In order to quantify the relationship between diversity and assemblage vulnerability, we use structural equation modeling (SEM) to model the influence of species richness, functional richness, and the distribution of functional traits through trait space on assemblage vulnerability (*Methods*; Fig. 1). We quantify assemblage vulnerability using an index of the individual vulnerabilities of an assemblage's constituent species (i.e. all resident land birds on an island) based on the aforementioned indicators, which we expect to be strongly indicative of species' extinction risks on islands of the Solomon Archipelago (see *Methods*). In addition to looking at the relationships between diversity and assemblage vulnerability across all assemblages, following classic studies in the Archipelago (Mayr & Diamond 2001; Diamond & Mayr 1976), we divided the islands into two groups: those that were connected to other major islands at the LGM (land bridge islands), and those that have been isolated throughout their history (isolated islands). By comparing across these alternate histories, we evaluate the influence of biogeographical history on a contemporary relationship between biodiversity and an ecosystem property. This study is the first test of hypothetical relationships between biodiversity, assemblage vulnerability, and biogeographic history.

Results

When all islands are analyzed together, regardless of biogeographic history, the model is significantly better than a null model ($N = 35$, $\chi^2 = 38$, $df = 5$, $p < 0.001$), and species richness is positively associated with assemblage vulnerability (0.47 ± 0.194, $z = 2.4$, $p < 0.05$; Fig. 1). The

relationships between functional richness and the distribution of functional traits to assemblage vulnerability were not significant. For this complete dataset, the SEM explained 40% of the variance in assemblage vulnerability. For the land bridge islands, the model was significantly better than a null model ($N = 18$, $\chi^2 = 26.3$, $df = 5$, $p < 0.001$), but none of the diversity metrics were significantly related to assemblage vulnerability, and the SEM only explained 23% of the variance in assemblage vulnerability (Fig. 2A). For the isolated islands, the model was significantly better than a null model ($N = 17$, $\chi^2 = 25.3$, $df = 5$, $p < 0.001$), the distribution of functional traits was significantly positively related to assemblage vulnerability (0.54 ± 0.22, $z = 2.4$, $p = 0.01$), and functional richness was positively related to assemblage vulnerability, though the relationship was not significant (0.51 ± 0.29, $z = 1.79$, $p = 0.07$; Fig. 2B). For the isolated islands, the SEM explained 62% of the variance in assemblage vulnerability. For all three analyses, the covariance of functional richness and SR was consistently high (0.64-0.75) and significant ($p < 0.05$).

The bootstrap analysis to compare the assemblage vulnerability r^2 on isolated islands and land bridge islands showed that the amount of variance in assemblage vulnerability explained by the SEM of the two groups was significantly different ($p < 0.001$; Fig. 3A). Our comparison of the island groups to random groups of 18 islands revealed that assemblage vulnerability r^2 for the land bridge islands falls within the lowest 2.5% of the distribution, suggesting it is significantly different from a random grouping. The assemblage vulnerability r^2 of the isolated islands is larger than the mean assemblage vulnerability r^2 for random island groups, but does not fall outside of the 95% limits of the distribution (Fig. 3B).

Correlations within the vulnerability data (intrinsic biology, range size, and response to anthropogenic pressures) were minimal. Range size and response to anthropogenic pressure (IUCN status) were not significantly correlated, nor were IUCN status and intrinsic biology. Range size was significantly correlated with intrinsic biology ($p < 0.001$), however the correlation coefficient was low enough (0.3) that all three variables were retained in the calculation of vulnerability scores.

Discussion and conclusion

Our results demonstrate that across biogeographic groups of islands, increased species richness on islands is associated with more vulnerable avian assemblages in the Solomon Archipelago. We expect that this relationship also exists in non-island systems, in large part because more diverse continental systems are characterized by higher proportions of rare species, which are likely more vulnerable (Manne et al. 1999). The expectation that more diverse islands are likely to experience greater rates of species loss is in agreement with predictions based on the theory of island biogeography (MacArthur et al. 1967). However, because the accumulation of diversity has been accompanied by an ecological shift toward vulnerable assemblages, our findings suggest that diversity-related ecosystem properties and functions have altered the ecologies of diverse assemblages. This ecological shift has the potential to impact the responses of diverse islands to anthropogenic extinction pressures at shorter timescales, potentially resulting in disequilibrium between colonization and extinction not predicted by island biogeography theory. An additional consideration is the possibility that species richness may be associated with species population sizes, which would further link diversity with assemblage vulnerability. The character of this relationship is likely system-specific, with species on more diverse islands

potentially having smaller population sizes; however, in some systems, increases in density can compensate for increased species richness (MacArthur et al. 1972). The limited data available for the birds of Northern Melanesia suggest that the relationship between species richness and population sizes may have a limited impact on vulnerability, because total bird density increases linearly with species richness (Diamond 1970).

Surprisingly, species richness is a better predictor of assemblage vulnerability than functional diversity when all islands are considered together. This may be because the morphologies of close relatives across this system are relatively highly conserved (i.e. adaptive divergence appears minimal), limiting the variation of functional diversity across the islands; in contrast, speciation drives changes in species richness and has occurred quite rapidly for some groups (e.g., Moyle et al. 2009). Alternatively, this may be because of conflicting relationships between the different dimensions of diversity and assemblage vulnerability among groups of islands with different biogeographic histories. For example, the relationship between the distribution of functional traits and assemblage vulnerability is positive on isolated islands, and negative on land bridge islands. Species richness, however, is positively related to assemblage vulnerability across island groups.

An important outcome is that the relationship between diversity and assemblage vulnerability is mediated strongly by the Pleistocene connectivity of the islands studied. There is a significant difference in the amount of variation in assemblage vulnerability explained by the SEM of the two island groups. The stronger relationship between diversity and assemblage vulnerability on isolated islands could be due to the limited opportunities for extirpated populations to be re-

established during periods of low sea level. The accumulation of diversity on isolated islands, which by definition do not have periods of connectivity between islands, may be more dependent on *in situ* protection of vulnerable species via greater ecosystem functioning as a result of higher diversity. While historic changes in island size and connectivity have been linked to species richness and proportion of endemic species in an assemblage (Weigelt et al. 2016), our findings reveal a distinct example of a contemporary ecological relationship that is highly influenced by an historical biogeographic process.

Our findings suggest that the ecological impacts of community assembly history on contemporary ecological processes may span evolutionary timescales. Therefore, aspects of assembly history that are important at ecological timescales, such as the order of arrival of species to a community (Fukami & Morin 2003), warrant further examination in natural systems (e.g. Leopold et al. 2015). Effects of assembly history that span evolutionary timescales may result in complex interactions with evolutionary processes (e.g. speciation) influencing ecology, and ecology in turn, influencing evolutionary processes (e.g. extinction). More generally, our results suggest that global processes like sea level fluctuations, which influence biogeographic history and community assembly, can influence contemporary ecological processes. This relationship may complicate the comparison of ecological findings across biogeographic areas, providing compelling evidence for the necessity of integrating historical biogeography and ecology.

Our findings have important and surprising implications for conservation, especially for the globally-significant biodiversity on islands, which is characterized by significantly higher

endemism richness than mainland areas (Kier et al. 2009). While biodiverse islands might be expected to have lower background rates of extinction because of their higher ecosystem stability (Tilman et al. 2014; Hautier et al. 2015), resistance to invasion (Naeem et al. 2000; Levine et al. 2004; Fargione & Tilman 2005; Byun et al. 2013) and resistance to pathogen spread (Guilherme Becker et al. 2014), this prediction is complicated by decreased population-level stability of individual species within diverse communities (May 1973; Mcnaughton 1978; Tilman & Downing 1994; Tilman 1996; Tilman et al. 2006). In order for diverse islands to accumulate vulnerable species, the beneficial effects of ecosystem stability and increased ecosystem function that come with greater diversity must outweigh the costs of increased species-level instability as a result of high diversity. Our results suggest that this is the case, with more diverse assemblages providing the necessary conditions for the accumulation of vulnerable species over evolutionary time, resulting in vulnerable assemblages. As such, more diverse islands are likely to lose species in response to anthropogenic pressures, reducing ecosystem functionality, further reducing their ability to sustain vulnerable species. Predicting changes in the vulnerability of island endemic assemblages can be significantly improved when using historical biogeography to characterize islands. It is clear that diversity and assemblage vulnerability are more tightly coupled on islands with histories of isolation, highlighting the potential for historical contingency to play a strong role in shaping contemporary ecological processes.

Methods

The biota of Northern Melanesia have been foundational to the development of key theories of community assembly (Wilson 1961; MacArthur & Wilson 1967; Diamond 1975).

The birds of the Solomon Archipelago continue to serve as the empirical basis for understanding the origins and assembly of diversity within communities (Filardi & Moyle 2005; Sanderson et al. 2009), making them an ideal system within which to examine the impacts of alternative assembly histories on contemporary ecological relationships.

Our analyses include 35 islands in the Solomon Archipelago that have been used in classic studies in the Archipelago as representatives of this system (Diamond & Mayr 1976; Mayr & Diamond 2001). We only included islands larger than 2.6 km^2, which is the threshold below which species-area relationships become more complicated for these bird communities (Diamond & Mayr 1976). Assemblage vulnerability was calculated at the island level, based on the resident land birds that are found on each island (Table S1 and Dataset S1; 20). In order to calculate assemblage vulnerability, a species-level vulnerability score was calculated for each resident species in the archipelago using hypothesized indicators of vulnerability, and then for each island these species-level scores were combined to create an island-level assemblage vulnerability score.

Species-level vulnerability was quantified, using z-scores to standardize across variables, and incorporated intrinsic biology, range size, and response to anthropogenic pressures. Vulnerability as a function of the species' intrinsic biology was calculated as:

$$V_s(T) = 1/3(-z_{\text{clutch size}} + z_{\text{body size}} - z_{\text{dispersal ability}}) \qquad \text{eqn 1.1}$$

where clutch size is the mean number of eggs laid per year, body size is the length of each species (Dutson 2011), and dispersal ability is quantified using the hand-wing index (HWI). HWI is a measure of the aspect ratio of a wing, which is linked to flight efficiency, and is calculated as:

$$HWI = 100(WL - SL)/WL \qquad \text{eqn 1.2}$$

in which WL is the standard measure of wing length, and SL is a measure of the distance from the carpal joint to the tip of the first secondary feather (Claramunt et al. 2012; Weeks & Claramunt 2014). For each species, HWI was based on the measurement of 3 adult male specimens, when available, at the American Museum of Natural History (AMNH). Vulnerability as a function of each species' range size was calculated as:

$$V_s(H) = (-z_{\text{total range area}}) \quad \text{eqn 2}$$

Total range area for each species was obtained from Birdlife International (BirdLife International 2015). Finally, species vulnerability based on the impacts of anthropogenic pressures was estimated as:

$$V_s(A) = (-z_{\text{IUCN status}}) \quad \text{eqn 3}$$

where IUCN status was converted to a numerical value, with 1 being species of least concern and, and 5 being those species that are critically endangered. These three metrics of species vulnerability were then combined into a single species vulnerability index by taking the unweighted mean:

$$V(S) = 1/3(V_s(T) + V_s(H) + V_s(A)) \quad \text{eqn 4}$$

In order to calculate the assemblage vulnerability of the avifauna on each island, we calculated the unweighted mean species scores for the constituent species:

$$F_a(I) = 1/n\ (V(S)_1 + V(S)_2 \ldots V(S)_n) \quad \text{eqn 5}$$

where $F_a(I)$ is the assemblage vulnerability for island I, n is the number of species on island I, and $V(S)_n$ is the species vulnerability index for species "n" on the island (as per eqn 4).

In addition to assemblage vulnerability, species richness (SR) and functional diversity (FD) were calculated for each island using all of the resident land bird species on each island. For each species, bill length, bill depth, and tarsus length were measured for 3 adult male specimens,

when available, at AMNH. These traits are relevant to the natural histories of birds (Ricklefs & Travis 1980a; Miles & Ricklefs 1984; Botero-Delgadillo & Bayly 2012). A principal component analysis (PCA) was used to summarize bill morphology. Functional evenness, functional divergence, and functional richness (Villéger et al. 2008) were calculated using the R package FD (Laliberté & Legendre 2011), based on the functional trait values for all birds on each island (the position of each species on axis 1 and axis 2 of the PCA summary of bill morphology, tarsus length, and body size). These traits were chosen because they are commonly used indicators of resource use and energy constraints (body size; Brown 1995; Ding et al. 2013), and foraging behavior in birds (bill morphology and tarsus length; Ricklefs & Travis 1980; Miles & Ricklefs 1984). Species richness (SR) for each island was calculated using the land birds on each island. In order to ensure that we were not biasing our metric of assemblage vulnerability by duplicating the same information across aspects of vulnerability (e.g., a high correlation between range size and IUCN status might be expected because changes in range size can drive listing status), correlations between intrinsic biology, range size, and anthropogenic impact scores were examined.

The influence of functional diversity and species richness on assemblage vulnerability was then modeled using structural equation modeling (SEM), implemented in the R package lavaan (Rosseel 2012). The distribution of functional traits through trait space was modeled as a latent variable (which we will call *functional trait distribution*), measured using functional evenness and functional divergence, with the latent variable variance fixed to 1 and the loading on functional evenness constrained to be 1. SR and functional richness were considered exogenous variables. Assemblage vulnerability was regressed onto functional trait distribution, functional richness, and SR (Fig. 1).

In order to compare the relationship between diversity and vulnerability across biogeographical groupings, the data were divided into two groups of islands: those that were connected to form major land masses at the LGM (land bridge islands), and those that were isolated at the LGM (isolated islands; Fig. 2; Table S1 and Dataset S1; Diamond & Mayr 1976). To evaluate the sensitivity of the inter-biogeographical group differences to outliers, we employed a bootstrap method in which 1,000 sets of 35 islands were randomly sampled (with replacement) from each of the island groups. The SEM was fit to each random sample, and the assemblage vulnerability r^2 was calculated. The distributions of assemblage vulnerability r^2 values were compared across biogeographic groups using a t-test (Fig. 3A). In order to test whether the groups based on biogeographic history were significantly different from a random subset of the total dataset, we drew 1,000 random samples of 18 islands without replacement, and without regard to their biogeographic history, from the total dataset. We then compared the actual values of assemblage vulnerability r^2 of the biogeographic subsets to the distribution of r^2 values for random groups of islands (Fig. 3B).

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Figure 4.1. Assemblages with greater diversity are more vulnerable. A structural equation model of the relationship between the distribution of functional traits, functional richness, and species richness and assemblage vulnerability shows a positive relationship between species richness and assemblage vulnerability. Parameter estimates are standardized and the paths are scaled to reflect effect size. Significant relationships are denoted with asterisks, and the fixed loading of the distribution of traits on functional evenness is shown as a dashed line. The three dimensions of diversity explain 40% of the variance in assemblage vulnerability.

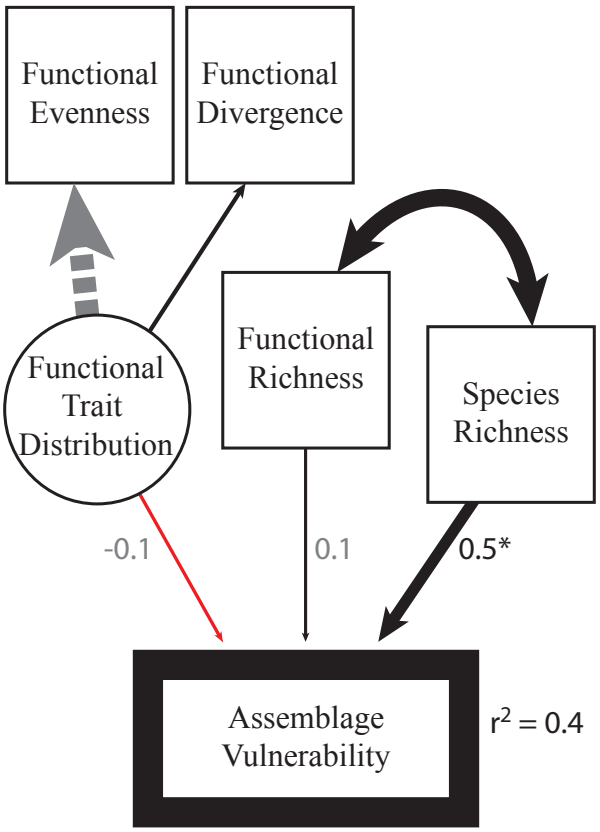


Figure 4.2. Alternate histories change the relationships between diversity and assemblage vulnerability. Parameter estimates are standardized, black lines represent positive relationships, red lines represent negative relationships, the paths are scaled to reflect parameter size, significant relationships are denoted with asterisks, and the boxes around assemblage vulnerability are scaled to the amount of variance in assemblage vulnerability explained by the model. For land bridge islands (A), the ability of diversity to explain variance in assemblage vulnerability is greatly reduced ($r^2 = 0.23$) and none of the path coefficients are significant. When only isolated islands are considered (B), the model has much higher explanatory power (assemblage vulnerability $r^2 = 0.62$) and the relationship between the distribution of functional traits and assemblage vulnerability is significant and positive ($p = 0.01$), and the relationship between functional richness and assemblage vulnerability is positive and nearly significant ($p = 0.07$).

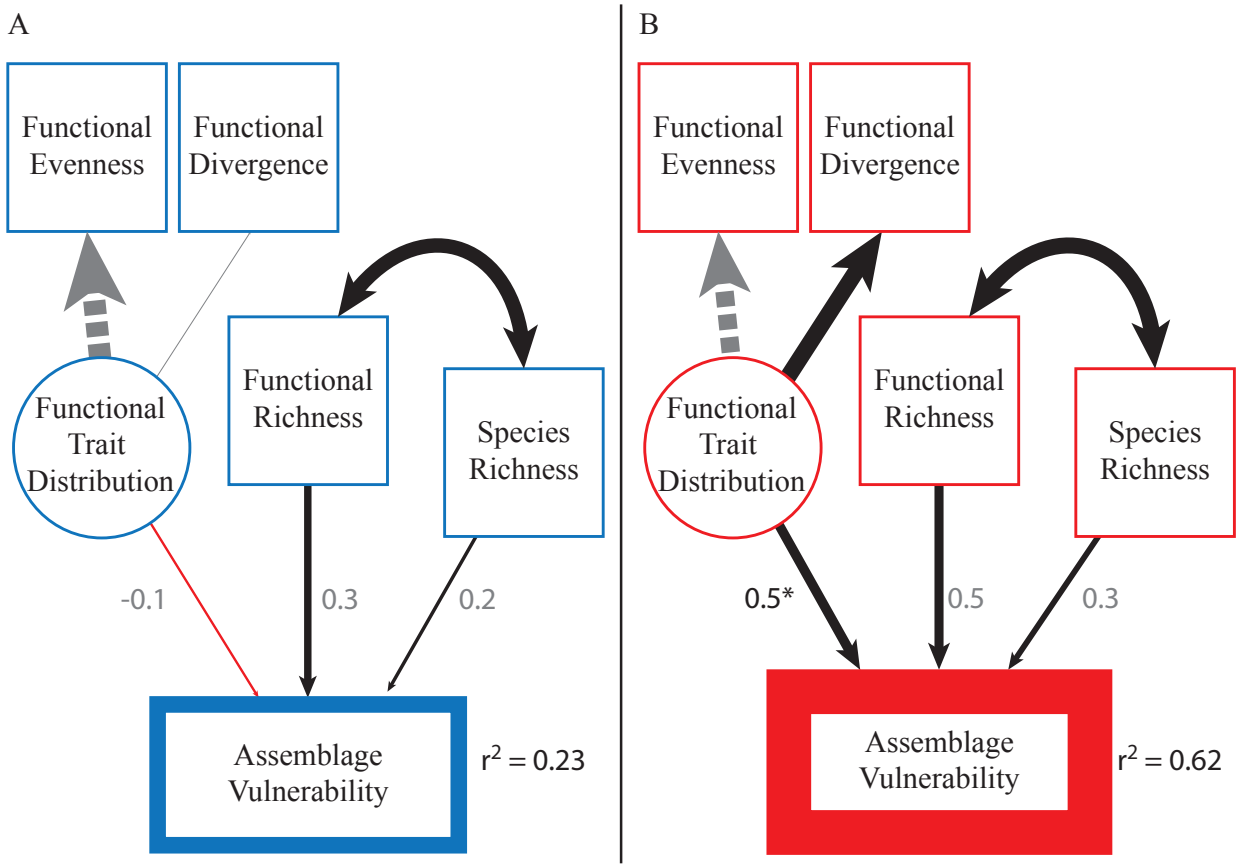
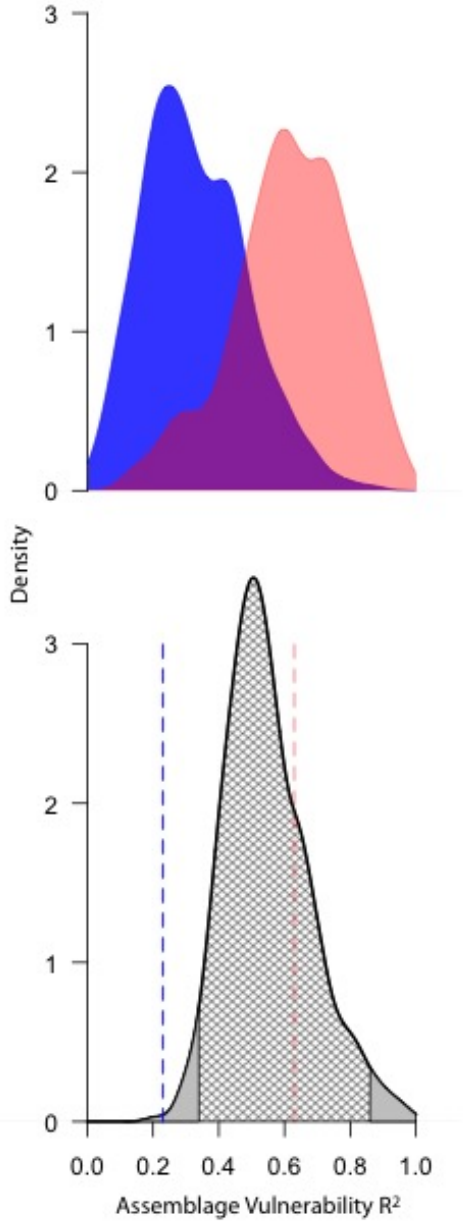

A
Functional Evenness
Functional Divergence
Functional Trait Distribution
Functional Richness
Species Richness
-0.1
0.3
0.2
Assemblage Vulnerability
r2 = 0.23
B
Functional Evenness
Functional Divergence
Functional Trait Distribution
Functional Richness
Species Richness
0.5*
0.5
0.3
Assemblage Vulnerability
r2 = 0.62

Figure 4.3. Robustness to outliers and comparison to random island groupings. When assemblage vulnerability r^2 is calculated across 1,000 bootstrap replicates of 35 islands (A), the distributions of variance in assemblage vulnerability explained by the SEM is significantly different ($p < 0.001$), with the assemblage vulnerability r^2 values lower on land bridge islands (blue distribution) than on isolated islands (red distribution). When the island groups based on biogeographic history are compared to random groups (B), the assemblage vulnerability r^2 of the land bridge islands (blue dashed line) falls within the lowest 2.5% of the distribution of random groupings while the assemblage vulnerability r^2 of the isolated islands (red dashed lines) lies above the mean of the distribution, but does not fall in the top 2.5% of all groups.


3
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Assemblage Vulnerability R²

Supplementary Table 1. Species-vulnerability data. When possible, three adult male specimens were measured to obtain the morphological data; in total, 447 specimens were measured (a mean of 2.84 specimens/species). For those species for which specimens were not available (noted with a[‡]), mean values for congeners were used. Clutch size data are from Jetz et al. (2008)[1] unless noted (b); when clutch size data for a particular species were not available, mean clutch size for a taxon considered to be congeneric or within the same super-species[19] was used (φ), or the genus average from Jetz et al. (2008) was used (*). Clutch size for brood parasites was not estimated due to uncertainty, and is noted (BP) Body size data and taxonomic treatment are from Dutson (2011)[22].

Genus	Species	Tarsus (mm)	Hand-wing Index	Bill Length (mm)	Bill Width (mm)	IUCN Status	Range Size (km^2)	Clutch Size	Body Size (cm)
Accipiter	*albogularis*	61.60	33.50	15.22	9.73	1	38100	2.4*	36
Accipiter	*fasciatus*	74.55	38.63	13.57	9.53	1	8180000	3.0	45
Accipiter	*hiogaster*	58.64	26.93	15.23	10.96	1	795000	2.4*	40
Accipiter	*imitator*	53.96	27.90	15.36	10.66	3	10100	2.4*	30
Accipiter	*meyerianus*	73.71	34.14	20.33	13.26	1	263000	3.0	52
Aceros	*plicatus*	63.33	22.83	166.31	43.52	1	754000	1.4	75
Acrocephalus	*australis*	24.13	18.29	12.10	4.23	1	3890000	2.4	16
Actenoides	*bougainvillei*	20.24	16.90	41.59	14.86	3	6400	2[φ]	32
Aerodramus	*esculenta*	8.30	67.22	2.32	1.75	1	2750000	1.4	9
Aerodramus	*orientalis*[‡]	6.70	66.23	2.83	1.55	NA	6500	1.5[a]	14
Aerodramus	*spodiopygius*	6.40	65.22	2.89	1.47	1	136000	1.4	10
Aerodramus	*vanikorensis*	6.99	65.41	3.29	1.43	1	1210000	1.4	13
Alcedo	*atthis*	11.35	26.26	33.75	6.60	1	17900000	6.5	16
Amaurornis	*moluccana*	51.07	22.23	16.31	5.23	1	1270000	5.3	26
Aplonis	*brunneicapillus*	21.92	30.47	13.45	5.58	4	15900	2.5[φ]	21
Aplonis	*cantoroides*	20.28	29.81	14.15	6.07	1	831000	2.4	19
Aplonis	*dichroa*	28.75	22.29	16.28	6.74	1	3300	2.5[φ]	20
Aplonis	*feadensis*	25.72	22.43	15.27	6.20	2	44	2.5[φ]	20
Aplonis	*grandis*	28.75	22.55	16.69	7.24	1	31200	2.5[φ]	25
Aplonis	*insularis*	24.23	22.28	14.45	5.69	1	540	2.5[φ]	17
Aplonis	*metallica*	20.94	31.95	13.78	5.96	1	770000	1.7	24
Aviceda	*subcristata*	38.58	31.59	19.46	11.59	1	1720000	2.4	39
Cacatua	*ducorpsii*	23.28	29.40	30.30	17.77	1	33000	2.4*	34
Cacomantis	*variolosus*	12.43	41.99	11.96	4.47	1	3710000	BP	25
Caloenas	*nicobarica*	39.56	33.24	15.61	7.92	2	476000	1.0	34
Centropus	*milo*	66.59	7.43	44.90	16.07	1	11000	2*	64
Cettia	*haddeni*	25.69	12.43	9.95	3.78	2	550	3.49[φ]	13
Cettia	*parens*	23.41	16.38	10.28	3.26	1	200	3.49[φ]	12
Ceyx	*lepidus*	11.86	20.23	31.82	7.69	1	43800	2.0	14
Ceyx	*pusillus*	8.66	21.83	24.11	5.01	1	910000	3.9	11
Chalcophaps	*stephani*	22.18	31.83	11.12	3.18	1	902000	2.0	23
Chalcopsitta	*cardinalis*	21.49	47.50	21.28	11.54	1	37500	2.08[φ]	31
Charmosyna	*margarethae*	12.23	48.11	13.55	7.75	2	27000	2[φ]	20
Charmosyna	*meeki*	11.05	45.24	12.27	6.71	2	6200	2[φ]	16
Charmosyna	*placentis*	11.04	40.55	12.30	6.79	1	821000	2[φ]	17
Chrysococcyx	*lucidus*	14.31	38.35	11.36	5.01	1	935000	BP	17
Cinnyris	*jugularis*	15.77	14.52	16.40	3.01	1	5200000	2.4	11
Clytorhynchus	*hamlini*	26.12	15.55	20.41	5.89	1	680	2[φ]	19
Columba	*pallidiceps*	27.45	20.07	17.21	8.32	3	49300	1.37[φ]	37
Columba	*vitiensis*	26.58	23.73	14.61	7.07	1	1130000	1.0	37
Coracina	*holopolia*	21.43	26.09	15.57	7.02	2	28400	1.8[φ]	21
Coracina	*lineata*	23.94	30.32	11.97	6.73	1	636000	2.0	23
Coracina	*papuensis*	24.46	28.62	18.04	9.79	1	4450000	2.4	25
Coracina	*salomonis*	25.12	25.10	17.22	7.77	1	3300	1.8[φ]	23
Coracina	*tenuirostris*	22.48	31.83	16.46	7.43	1	2310000	1.0	25
Coracina	*welchmani*	28.46	30.08	24.28	14.15	1	69200	1.8[φ]	32
Corvus	*meeki*	56.90	28.76	44.01	19.98	1	9700	3.9[φ]	41
Corvus	*woodfordi*	49.20	33.27	46.34	16.99	1	13000	3.9[φ]	41
Dicaeum	*aeneum*	12.19	20.40	8.76	3.92	1	27400	2.4[φ]	8
Dicaeum	*tristrami*	12.86	21.92	7.18	4.15	1	3300	2.4[φ]	9
Dicrurus	*bracteatus*	22.84	25.58	21.78	10.25	1	2100000	3.9	30
Ducula	*brenchleyi*	30.19	33.07	15.12	6.56	3	10900	1*	38
Ducula	*pacifica*	33.04	31.31	17.00	6.54	1	29600	1.0	39
Ducula	*pistrinaria*	31.45	29.56	18.06	7.89	1	85400	1.0	43
Ducula	*rubricera*	31.34	29.85	21.59	9.06	2	72400	1.0	41

Eclectus	*roratus*	24.00	30.39	38.22	21.00	1	1690000	2.0	31
Erythrura	*trichroa*	17.32	17.41	9.85	6.59	1	875000	3.5	12
Eudynamys	*orientalis*	32.01	29.86	22.51	12.31	1	2670000	BP	41
Eurostopodus	*nigripennis*	20.52	49.53	7.72	5.93	4	24000	1.06[o]	27
Eurystomus	*orientalis*	19.38	30.46	20.59	14.14	1	13900000	3.9	27
Falco	*peregrinus*	52.43	55.51	18.72	12.78	1	38100000	2.8	44
Falco	*severus*	33.47	61.56	12.63	8.52	1	4010000	2.8	28
Gallicolumba	*beccarii*	26.79	28.62	8.98	2.62	1	167000	1.0	19
Gallicolumba	*jobiensis*	25.10	34.46	12.72	3.66	1	647000	2.0	23
Gallinula	*silvestris*	55.87	11.18	23.43	5.90	5	3300	6.4[o]	26
Gallirallus	*philippensis*	44.58	27.09	17.83	4.05	1	1950000	5.7	28
Gallirallus	*rovianae*	53.38	17.35	21.02	5.41	2	3400	2.4	30
Geoffroyus	*heteroclitus*	17.88	50.38	19.71	12.46	1	79000	3.54[o]	24
Gerygone	*flavolaterialis*	18.58	14.80	7.94	2.66	1	30000	2.5[o]	10
Guadalcanaria	*inexpectata*	28.70	17.50	17.62	4.10	1	620	2[o]	20
Gymnophaps	*solomonensis*	34.45	30.96	12.76	5.00	1	6200	1.0	38
Haliaeetus	*leucogaster*	99.62	33.10	39.43	17.30	1	5130000	2.0	73
Haliaeetus	*sanfordi*	104.90	33.92	38.02	17.68	3	36300	1.97[o]	73
Haliastur	*indus*	55.35	38.50	22.99	12.30	1	8730000	1.4	48
Hemiprocne	*mystacea*	12.73	61.35	6.44	5.65	1	806000	1.0	29
Hirundo	*tahitica*	10.41	54.38	6.72	5.68	1	3360000	2.0	13
Lalage	*leucopyga*	21.82	28.74	9.98	4.58	1	34400	2.0	17
Lonchura	*melaena*	16.15	16.46	10.88	9.41	1	11400	4.2	11
Lorius	*chlorocercus*	18.19	40.62	22.75	10.87	1	14000	3.13[o]	28
Macropygia	*mackinlayi*	17.01	32.51	8.34	2.57	1	54500	1.4	32
Megalurulus	*llaneae*	25.47	11.31	10.51	3.49	2	47	2.3[o]	17
Megalurulus	*turipavae'*	25.03	11.31	10.52	3.37	2	4200	2[o]	18
Megapodius	*eremita*	67.53	20.34	13.49	5.92	1	84900	14.9[o]	34
Meliarchus	*sclateri*	36.12	15.76	21.25	5.34	1	6700	2[o]	25
Micropsitta	*bruijnii*	8.31	36.50	7.50	4.85	1	269000	3.59[o]	9
Micropsitta	*finschii*	7.41	35.98	9.03	6.87	1	42700	3.59[o]	9
Mino	*kreffti*	37.66	17.48	21.98	9.60	1	701000	1.4*	28
Monarcha	*castaneiventris*	18.72	19.03	13.10	5.72	1	21600	3.0	17
Monarcha	*cinerascens*	19.26	15.48	14.77	6.63	1	132000	1.4	18
Monarcha	*erythrostictus*	20.09	16.30	13.02	6.06	1	9600	2.4*	17
Monarcha	*richardsii*	19.28	17.06	11.48	5.48	1	5100	2.4*	17
Myiagra	*caledonica*	18.27	19.10	10.79	8.29	1	31500	2.4	14
Myiagra	*cervinicauda*	16.89	17.10	8.33	6.20	2	3300	2.4*	14
Myiagra	*ferrocyanea*	16.22	19.57	9.08	5.68	1	32600	2.4*	14
Myzomela	*cardinalis*	20.50	21.18	13.43	2.87	1	22300	3.9	12
Myzomela	*eichhorni*	17.70	18.31	15.26	3.00	1	5100	2.3[o]	12
Myzomela	*lafargei*	15.36	13.70	13.48	2.93	1	17300	2.3[o]	12
Myzomela	*malaitae*	17.33	14.83	12.51	2.90	2	4300	2.3[o]	13
Myzomela	*melanocephala*	16.67	17.37	12.73	3.03	1	5900	2.3[o]	12
Myzomela	*tristrami*	21.08	20.68	13.24	2.90	1	3400	2.3[o]	12
Nesasio	*solomonensis*	51.23	21.63	23.43	14.45	3	13200	4.1[o]	37
Nesoclopeus	*woodfordi*	62.82	13.40	24.79	5.98	2	4000	4[b]	30
Ninox	*granti*	38.54	25.99	14.92	9.00	1	5500	2*	24
Ninox	*jacquinoti*	40.66	24.57	16.29	8.14	3	17200	2*	26
Ninox	*malaitae*	40.53	24.36	14.79	8.25	1	4400	2*	22
Ninox	*roseoaxillaris*	33.49	28.84	14.44	8.72	3	3300	2*	21
Pachycephala	*feminina*	27.08	16.54	11.79	5.16	1	37111	1.4*	15
Pachycephala	*implicata*	26.01	15.64	10.49	5.29	1	20660	2.1[o]	16
Pachycephala	*melanura*	22.41	19.37	10.09	4.14	1	525000	2.4	16
Pachycephala	*orioloides*	25.96	16.89	12.87	6.33	1	1926141	1.4*	17
Pachycephala	*richardsi*	26.53	19.05	11.42	5.42	1	28510	2.1[o]	16
Pandion	*cristatus*	60.74	45.33	26.82	16.20	1	31500000	3*	57
Petroica	*multicolor*	16.17	19.39	7.64	3.69	1	594000	3.5	10
Phylloscopus	*amoenus*	21.77	13.34	9.13	3.68	3	38	2*	11
Phylloscopus	*poliocephalus*	18.98	21.25	6.74	2.71	1	473000	2*	10
Pitta	*anerythra*	50.08	9.37	17.02	7.50	3	13200	4.9	16
Porphyrio	*porphyrio*	89.05	25.12	25.81	10.47	1	18400000	3.7	41
Porzana	*cinerea*	32.22	22.27	11.63	3.97	1	3640000	4.6	17
Porzana	*tabuensis*	31.46	19.13	10.23	2.54	1	2320000	3.5	17
Ptilinopus	*eugeniae*	21.44	24.22	9.44	3.80	2	3400	1*	20
Ptilinopus	*richardsii*	21.87	25.76	9.24	3.96	1	770	1.06[o]	21
Ptilinopus	*solomonensis*	19.42	25.66	9.24	3.73	1	20700	1.0	21
Ptilinopus	*superbus*	18.76	29.13	9.63	5.15	1	1530000	1.0	23
Ptilinopus	*viridis*	25.02	29.65	8.54	4.07	1	95400	1.0	21
Reinwardtoena	*crassirostris*	26.38	31.32	13.35	7.28	2	29200	1.1[o]	45

Rhipidura	*albiscapa*	16.41	21.49	5.19	3.42	1	1400000	2.2*	15
Rhipidura	*cockerelli*	16.91	22.91	11.80	6.26	2	31800	2.4*	17
Rhipidura	*drownei*	19.71	17.19	7.32	4.50	1	2900	2*	16
Rhipidura	*leucophrys*	26.43	18.19	11.66	6.26	1	8400000	2.8	20
Rhipidura	*malaitae*	17.80	15.05	7.40	3.90	3	20	2*	16
Rhipidura	*rennelliana*	20.40	17.04	8.16	4.06	1	680	2*	16
Rhipidura	*rufifrons*	17.93	17.93	7.36	4.64	1	1230000	2.4	15
Rhipidura	*tenebrosa*	21.70	18.24	8.96	4.70	2	3300	2*	17
Rigidipenna	*inexpectata*	26.17	23.95	26.89	39.82	2	16700	1*	37
Stresemannia	*bougainvillei*	28.32	14.89	18.69	3.91	1	2000	2.02[o]	17
Symposiachrus	*barbatus*	20.32	17.10	10.33	5.17	2	26000	2.0	15
Symposiachrus	*browni*	20.32	17.30	10.95	5.32	2	4600	2*	15
Symposiachrus	*vidua*	21.10	18.86	9.32	4.60	1	3400	2.0	15
Todiramphus	*chloris*	17.13	27.23	41.94	13.87	1	3940000	3.2	23
Todiramphus	*leucopygius*	13.50	26.27	32.45	11.59	1	23200	3.0	21
Todiramphus	*sanctus*	12.37	27.33	31.84	10.95	1	5320000	4.5	19
Todiramphus	*saurophagus*	20.15	23.92	51.24	14.79	1	134000	2.8	30
Trichoglossus	*haematodus*	16.76	46.74	21.78	11.62	1	875000	1.7	27
Turdus	*poliocephalus*	30.80	24.91	13.70	4.97	1	253000	1.7	20
Turnix	*maculosus*	18.88	11.21	6.58	2.76	1	1110000	4.0	14
Tyto	*javanica*	72.95	38.28	19.88	10.60	1	63300000	5.3*	33
Woodfordia	*superciliosa*	24.56	12.68	11.98	4.18	1	680	2.5[o]	14
Zoothera	*atrigena*‡	39.40	14.02	15.37	6.01	2	5300	2*	20
Zoothera	*heinei*	28.13	30.16	20.94	5.65	1	469000	2.4	20
Zoothera	*margaretae*	39.40	14.02	15.33	5.71	2	3188	3.5*	23
Zoothera	*turipavae*	39.40	14.02	15.36	6.01	3	100	3.5*	20
Zosterops	*griseotinctus*	20.03	20.30	9.52	3.54	1	1000	2*	12
Zosterops	*kulambangrae*	18.47	17.52	9.44	3.30	1	4200	2*	12
Zosterops	*luteirostris*	17.28	16.01	10.45	4.10	4	35	2*	12
Zosterops	*metcalfii*	17.17	15.90	9.36	3.82	1	16900	2.5[o]	11
Zosterops	*murphyi*	19.44	17.91	11.11	3.98	1	110	2.5[o]	12
Zosterops	*rennellianus*	19.60	15.50	10.50	3.84	1	680	2*	12
Zosterops	*splendidus*	17.04	16.64	10.85	3.65	3	150	2*	12
Zosterops	*stresemanni*	19.84	14.28	11.03	3.80	1	4400	2.5[o]	13
Zosterops	*ugiensis*	20.01	16.74	9.32	4.03	1	1700	2.5[o]	12
Zosterops	*vellalavella*	17.29	14.84	9.90	3.56	2	670	2*	12

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