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Dissertação de Mestrado

Community Assembly of Waterbirds on the Coast of Rio Grande do Sul, Brazil

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Aluno de IMAE

Porto Alegre, Setembro 2016

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RESUMO

As comunidades ecológicas formam-se a partir de pools regionais de espécies, mas contendo apenas um subconjunto da diversidade total da região envolvente. Quando comparadas com simulações aleatórias, as comunidades ecológicas reais mostram frequentemente evidências de estrutura não-aleatória. Esta estrutura pode incluir interações ambientais e/ou interespecíficas determinando os conjuntos de espécies e atributos que co-ocorrem, sendo a importância relativa dos efeitos ambientais vs. interespecíficos mediada pela qualidade de habitat. Além disso, as comunidades podem também revelar estrutura filogenética se, por exemplo, determinados atributos forem conservados dentro das linhagens, ou se espécies próximas se diversificarem rapidamente. Neste estudo, comparámos comunidades de aves aquáticas amostradas ao longo de 10 anos em lagoas costeiras e praias do Rio Grande do Sul, Brasil, oriundas de dois pools distintos de espécies contendo migradores estivais ou invernais – já que as espécies de aves que ocorrem sazonalmente, em particular as limícolas migradoras, constituem uma grande porção (c.25%) do total das espécies e indivíduos presentes. As comunidades foram comparadas em termos da sua composição taxonômica e ecologia funcional com base em dados existentes na literatura relativa a comportamento de forrageamento, dieta e morfologia de cada uma das espécies. Enquanto a composição taxonômica parece depender do pool de espécies a partir da qual a comunidade se formou, a composição funcional não diferiu entre estações. As comunidades dos lagos mostraram ser funcionalmente mais ricas e mais equitativas que as comunidades no ambiente mais homogêneo de praia, sugerindo que as comunidades são estruturadas pelo ambiente que limita as funções por si suportadas. Os resultados da comparação da diversidade funcional das comunidades com modelos nulos sugerem que a ocorrência das espécies é mediada pela competição interespecífica, ao passo que a abundância de indivíduos de cada uma das espécies está relacionada com as condições abióticas. Os atributos funcionais apresentaram sinal filogenético ao nível do pool de espécies, mas não foi encontrada evidência de influência da filogenia sobre a montagem de comunidades. Apesar de as comunidades variarem na sua composição filogenética relativamente ao ambiente, esta relação foi mediada pelos atributos. Tal como ocorreu com os atributos funcionais, também a variação filogenética foi maior em ambiente de lago do que em ambiente de praia, sendo que as praias mostraram agrupamento filogenético significativo. No seu conjunto, estes resultados evidenciam um forte papel do ambiente sobre a composição funcional das comunidades de aves aquáticas, o que por sua vez determina as composições taxonômica e filogenética. A composição taxonômica está associada ao pool de espécies, mas as comunidades são funcionalmente similares nas duas estações consideradas e as linhagens migratórias não são suficientemente distintas evolutivamente para revelar sinal filogenético associado à estação. Estes resultados contribuem para o nosso entendimento teórico sobre as regras de montagem de assembleias, um tema controverso em ecologia há décadas. Por último, a compreensão do modo como as comunidades de aves limícolas se constituem e tem aplicações na restauração ecológica e no delineamento de áreas protegidas, o que é de extrema importância dada a perda continuada de áreas húmidas e o subsequente declínio populacional de muitas espécies de aves aquáticas e migradoras.

ABSTRACT

Ecological communities are assembled from regional species pools, but contain only a subset of the total diversity from the surrounding region. Compared with random simulations, real ecological communities often show evidence of non-random structure. This structure may include environmental and/or interspecific interactions determining the sets of species and traits that co-occur, with the relative importance of environmental vs. interspecific effects mediated by habitat quality. Furthermore, communities may also show evidence of phylogenetic structure, for example if certain traits are conserved within lineages, or closely-related species diversify rapidly. In this study we compared waterbird communities sampled over 10 years at coastal lakes and beaches in Rio Grande do Sul, Brazil, from two distinct species pools containing summer and winter migrants – as seasonally occurring bird species, mainly migratory waders, form a large portion (c.25%) of the total species and individuals present. Communities were compared in terms of their taxonomic composition and functional ecology by collecting data on each species' foraging behaviour, diet and morphology from literature. While taxonomic composition depended on the species pool from which the community was drawn, functional composition did not differ between seasons. Communities in lakes were functionally richer and more even than communities in the more homogeneous beach environment, suggesting that communities are structured by their environment through limiting the functions they can support. Comparing communities' functional diversity with null models suggests that while species occurrence is mediated by interspecific competition, the abundance of individuals of each species is related to abiotic conditions. While functional traits had a phylogenetic signal at the species-pool level, there was no evidence of phylogenetic influence on community assembly. Although communities varied in their phylogenetic composition with respect to the environment, this relationship was mediated by traits. As occurred with functional traits there was considerably greater phylogenetic variation in lake habitats, with beach sites showing significant phylogenetic clustering. Together, these results are evidence of a strong environmental role in driving the functional composition of waterbird communities, which in turn determines the taxonomic and phylogenetic compositions. Taxonomic composition is sensitive to species pool, but communities were functionally similar in both seasons and migratory lineages were not evolutionarily distinct enough to cause a phylogenetic signal with respect to season. These results contribute to our theoretical understanding of community assembly, which has been a controversial issue in ecology for decades. Also, understanding how waterbird communities are assembled has applications to ecological restoration and reserve design, which is valuable given ongoing loss of wetlands and consequent population declines of many wetland and migratory species.

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General introduction

Intellectuals have long been concerned with categorizing the diversity of living organisms, since long before Biology, as we know it today, existed as an academic discipline. For example, Aristotle's *History of Animals* (4th Century BCE) sought both to describe types of organisms and describe patterns and generalities among them (Leroi 2014). However, for a long time species were considered immutable, until the Darwinian and Wallacean revolution added a temporal component to our understanding of biological diversity (Dennett 1995), changing forever our understanding of the natural world (Dobzhansky 1973; Kuhn 2012).

Species change over time as their ecological context selects between randomly-generated varieties (Darwin 1859). Thus, two processes become important for understanding species and the communities they form. In the short term (i.e., within an organism's lifespan), we are concerned with species' ecological function(s): how they interact with their environment and other individuals and species. Over a (generally much) greater time frame we consider evolution: how variation in those ecological functions affected the survival and reproduction of individual organisms, and how selection acting on that variation altered species' characteristics.

Through this lens, communities must be understood as resulting from two types of process: the immediate, and the contingent (Emerson & Gillespie 2008; Fukami 2015). In the immediate realm are the ways in which the environment and other organisms determine which species can coexist, and in what proportions.

A critique of the focus on immediate processes and adaptationism focussed on the role of contingency in determining which interactions can occur in the first place, as well as prejudicing their outcomes, and was made most forcefully by Marxist thinkers such as Stephen Jay Gould, Richard Lewontin and Richard Levins (e.g. Gould & Lewontin 1979; Lewontin & Levins 2007). When contingency is important, processes are influenced by factors external to the structures of interest, for example if historical demographic processes determine contemporary adaptability (Piersma 2003; Piersma & van Gils 2011), in addition to whatever immediate factors are at play.

What are communities?

If species are the 'elements' of ecology, are communities mixtures or compounds? That is, to what extent is the combination of these elements transformational: do properties intrinsic to the community emerge from the interactions between components, or are communities simply collections of non-interacting parts which could be modified, replaced or removed without affecting the whole?

Recent authors have tended towards the latter view. Slobodkin (2001) considered that image of communities as comprising a set of parts each of which is vital for the functioning of the whole was not merely an unsupported assumption but a 'reification', a process involving 'premature acceptance of the validity of a hypothesis'. Reified concepts 'are as likely to generate confusion as enlightenment' (*ibid.*).

Ricklefs (2008) too expressed concern that the view of communities as integral assemblages of interacting components is an encumbrance to progress in ecology. Long thought a valid construct that could be used to understand regional-scale processes, Ricklefs (*op. cit.*) argued that the community concept is merely an 'epiphenomenon' lurking between two legitimate ideas. At the local scale, populations of species have clear boundaries, and at the regional scale we can distinguish species' distributions; the community, however, merely emerges from the overlapping of differently-distributed populations and thus has no predictive power (Ricklefs 2008).

However, direct interaction between all (or even most) components is not necessary for the concept of communities to have utility. In a system of dynamic variables linked by first-order differential equations, at equilibrium or fluctuating within bounds, diffuse control can lead unlinked variables to determine each others' average values purely by means of mutual shared components; for example in an ecosystem, various trophically equivalent organisms with no direct interaction may determine each others' abundances at equilibrium if they merely exploit a common resource or are preyed upon by the same predator (Lewontin & Levins 2007b).

These conditions may be met quite frequently in nature under certain conditions. For example, insular habitats such as islands or lakes tend to have clear boundaries that are rarely crossed by organisms. Furthermore, it is often easier to demonstrate interactions between organisms in a bounded locale than in contiguous habitat. Thus, the study of such habitats offers opportunities to study ecological processes in tractable, ready-made macrocosms (Rigler & Peters 1995). The work in this dissertation focussed on two such habitats, lakes and beaches. As linear habitats, beaches are bounded in only one dimension, but nevertheless I consider them more amenable to focussed community studies than a contiguous expanse, such as a forest (Rigler & Peters 1995; Slobodkin 2001).

An operational definition

When terms are ambiguous or refer to contentious theories it can be helpful to clarify in what sense they are being used (Slobodkin 1987; Regan, Colyvan & Burgman 2002). Herein, the 'community' is therefore operationally defined as an assemblage of organisms overlapping in space and time in a discrete area and exploiting resources in common. This somewhat loose definition does not imply an integral whole nor require that all organisms interact with all others; these caveats should be borne in mind in the discussion below.

Niches in communities

´Community assembly´ refers to the process(es) by which the abovementioned organisms come to co-exist. Generally, these processes are considered at numerous levels of a hierarchy of organization. At the largest scale, the regional species pool, influenced by historical processes of evolution, determines the potential set of species that can coexist (Emerson & Gillespie 2008; Ricklefs 2008). From these species, only a subset forms the community. They are selected by two processes according to their traits. One, known as environmental filtering, is the selection of organisms capable of withstanding, or optimally exploiting, prevailing environmental conditions (Fukami 2015). The other deterministic force is that of interspecific interactions, where interactions amongst organisms (generally considered at the inter-specific scale) determine potential co-existence. Competition, predation and parasitism may all cause repulsion between taxa; coexistence can also be facilitated by mutual beneficial interactions (Gotelli & McCabe 2002). Finally, assembly occurs along a trajectory that is often sensitive to initial conditions, such that small variations, even stochastic ones, may have large impacts on some aspects of the community´s composition (Helson, Hermy & Honnay 2012).

Competition is likely to be more intense between functionally similar species, as they are dependent on a set of shared and limited resources. There is therefore thought to be a limit to the similarity between co-existing organisms (MacArthur and Levins 1967). Therefore, when we observe organisms sharing a set of resources, it is reasonable to expect that those resources are partitioned between them in some way, so as to minimize conflict to a level that permits coexistence. So, when species overlap in their use of a resource along one axis they are deemed to show differences in their use along another axis. For example, species may explore the same resources in different ways (e.g. Granadeiro *et al.* 2007, Denzinger *et al.* 2016), or else exploiting them at different times of the day (e.g. Lourenço *et al.* 2008, Hofmann *et al.* 2016) or year (Newton 2008; Somveille et al. 2015).

Waterbirds and migration in Rio Grande do Sul

Waterbirds are one such suite of organisms that share resources, occupying the same type of habitat (aquatic) and similar ways of obtaining food (in this study, any bird principally foraging on or in water is considered a waterbird). These species exhibit a wide range of morphological and behavioural traits enabling them to exploit their shared environmental resources in different ways (e.g. Mendez *et al.* 2012). Therefore, we might expect to see communities comprising species distributed throughout the multidimensional functional space.

However, aquatic environments can impose various forms of stress, such as salinity, thermoregulatory stress and the simple fact that birds cannot breathe underwater. There are, therefore, restrictions on which functions will be optional in a given site, and these limitations will vary between locations (for example according to water depth or salinity). Previous work has found that abundance and species richness are causally independent in waterbirds, suggesting that species richness is limited by environmental heterogeneity, while abundance is a function of species' responses to the availability of particular resources (Guan *et al.* 2016).

One way that waterbirds share resources is through migration. Many species exploit environments only seasonally, avoiding the chronic challenge of seasonal resource-scarcity by means of the acute challenge of migration (Newton 2008; Somveille *et al.* 2015). Thus, when resources are diverse, species richness increases, while competition is reduced by a decline in the number of individuals and/or species in the region when resources are less available (van der Graaf *et al.* 2006).

These seasonal movements, which include but are not limited to inter-regional migration, provide a natural experiment for studying the role of competition, environment and historical contingency in the assembly of communities. Communities in summer and winter, outside of the usual period during which species migrate, tend to have fairly consistent taxonomic composition. However, as many of the species are not locally present during that season it is fair to consider those communities as having been drawn from independent, or at least distinct, pools of species.

Nevertheless, the sites themselves remain sufficiently similar during both seasons to enable comparison along an environmental gradient, so long as a severe enough cline is chosen that environmental differences are greater between seasons than within them. The role of traits can be assessed directly, as well as indirectly. Using the simplifying assumption of constant diversification rates across clades, the phylogenetic distance between two taxa should correlate with the ecological difference between them. Therefore, while investigators can use a hypothesis-driven approach to select traits most relevant to coexistence and thus community assembly, incorporating phylogenetic data enables an evaluation of the role of traits potentially not measured, as well as directly providing insight into evolutionary mechanisms (Cadotte, Albert & Walker 2013).

This dissertation aimed to combine these sources of information to better understand the process of community assembly in waterbirds. By understanding how these unique assemblages are formed we gain insight into the process of community assembly in general. Furthermore, a better understanding of habitat requirements and interspecific interactions in waterbirds can help decision-making in the management and setting conservation priorities for a group of species affected globally by habitat loss, and additionally in some locations by the introduction of closely-related species (e.g. the endangered White-headed Duck *Oxyura leucocephala* in Iberia; Birdlife International 2012).

Dissertation structure

This dissertation is composed of two main articles. In the first article - *Environmental and interspecific interactions structure community assembly of waterbirds* – I tested the hypotheses that community functional composition is environmentally driven, and therefore independent of the species pool from which communities are drawn. I also examined evidence that functional diversity differs between habitats according to the diversity of resources.

In the second article - *Phylogenetic legacies in the community assembly of waterbirds?* - I tested the hypotheses that functional composition of communities is non-independent of the evolutionary history of the lineages comprising them. First I determine whether phylogenetic composition, like functional composition, responds to environmental differences. Following this, I test whether the association between certain lineages and habitats is mediated by the traits included in this study, or whether there is an additonal role of trait convergence, divergence or niche conservatism during evolutionary history.

The data used for the two chapters consists of survey data collected for an international waterbird monitoring scheme, subsequently re-purposed for community analysis. Trait data was derived from published literature and phylogenetic data was downloaded from an online resource based on a published tree of all bird species.

In the last chapter of the dissertation I present the main conclusions of the work, including the potential implications for conservations of my main findings and I indicate future directions for research into waterbird communities, and suggest how the study of these birds gives insight into generalizable principles of community assembly processes.

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Article 1: Environmental and interspecific interactions structure community assembly of waterbirds

Introduction

How are communities assembled?

The extent to which local communities are determined by deterministic *versus* stochastic processes, and the strength of influence of the regional species pool, are considered fundamental questions in ecological research (Gotelli & McCabe 2002; Emerson & Gillespie 2008; Sutherland et al. 2013; Fukami 2015). Approaches to these questions have often focussed on studying species' co-occurrences: are they more or less frequent than expected by chance? What characteristics allow them to do so?

For example, by comparing island bird communities in the Bismarck Archipelago, Diamond (1975, apud Gotelli & McCabe 2002) argued that while the assembly process is essentially stochastic, biotic interactions (interspecific competition) determine which co-occurrences, and therefore which communities, are stable over time. While the patterns detected by Diamond (1975) – lower-than-expected co-occurrence, fewer observed species pairs and 'checkerboards' of 'allowed' or 'forbidden' pairs of species – have been found consistently in a variety of systems, the processes underlying the pattern remain controversial (Gotelli & McCabe 2002)

Whilst competition and other biotic interactions (e.g. resource availability; predation risk; parasite pressure: Mitchell & Power 2003; Fincher & Thornhill 2008; Laundré, Hernández & Ripple 2010; Quaintenne et al. 2011) may limit which combinations are stable, abiotic conditions also present limits to which species can inhabit a given area (Piersma 2007; Sunday, Bates & Dulvy 2012; Fjeldså, Bowie & Rahbek 2012). There are therefore two competing ecological pressures affecting functional similarity of co-occurring species: competition limiting similarity (MacArthur & Levins 1967), and environmental filtering that restricts occurrence to certain phenotypes, necessarily increasing organisms' similarity (e.g. Mendez et al. 2012).

A variety of methods have been employed in the attempt to isolate environmental effects from those of species pools. The method used by Diamond (1975) has been criticised for its *post hoc* nature, analysing communities that have already assembled (Cadotte et al. 2015). Though this shortcoming was remedied in part through comparing observed patterns with expectations from null models, the details of this approach have been somewhat controversial (Gotelli 2000). Isolating pattern from process would benefit from studying communities as they assemble from *tabula rasa*.

The majority of previous work on community assembly and related topics has focussed on vegetation communities, especially herbaceous species (but see e.g. Mendez et al. 2012; Mims & Olden 2013). While herbaceous plants offer a number of advantages to researchers – for instance, they can be planted or otherwise experimentally manipulated with ease and without ethical considerations – their sessile nature limits the wider applicability of these results, for example to animals. In addition, primary producers often have simpler trophic interactions than consumers, and lack complex behaviour.

Animals, and migratory ones in particular, therefore offer an opportunity to investigate relative importance of stochastic and deterministic factors without one of the main limitations in plant studies, dispersal: travelling from other biogeographical regions, migratory individuals can be reasonably assumed to have the ability to reach any site in the study region (Quaintenne et al. 2011). Volant taxa in general are less likely to be limited by dispersal than passively-transported organisms such as plants, especially as they can fly directly over unfavourable habitat areas (Lok, Overdijk & Piersma 2013). Due to this dispersal limitation, species composition of plant communities is often highly stochastic and subject to a ‘priority effect’, whereby the first-arriving suitable species rapidly become dominant, and influence the future course of community development (Fukami et al. 2005; Helsen, Hermy & Honnay 2012; Kardol, Souza & Classen 2013; Plückers et al. 2013; Fukami 2015).

For this reason, newly-established plant communities often diverge from each other in terms of species composition, becoming more dissimilar over time (Fukami et al. 2005; Helsen, Hermy & Honnay 2012). Nevertheless, the same studies found that communities became functionally more similar as they established, attesting to the influence of environmental filtering: the environment offers a restricted range of niches which can be filled, constraining the possible traits that additional members of a community can occupy. On the other hand, species identity does not relate to the filling of niches (Fukami et al. 2005).

Objectives

In this dissertation, I use waterbird census data to test community assembly processes. The presence of a number of seasonally migratory species in the study region causes annual alternation between two distinct seasonal pools, one of resident species plus boreal migrants (during the local summer: December to February) and one of resident species and austral migrants (during local winter: June to August). By calculating and comparing trends in species and functional composition of communities between seasons, we can explore the following questions:

1. Is the seasonal difference in species composition statistically detectable? If a significant proportion of species and individuals are migratory in a given community, then it is fair to consider summer and winter communities as partially independent, and we can therefore characterise these communities as having assembled from distinct (though partially overlapping) species pools.

2. Are there functional differences between summer and winter communities? If so, this would imply that the differences in species pool override environmental determinants of community composition. Alternatively, if both communities are functionally equivalent, this suggests that trait-environment linkages are driving assembly processes.

3. Do these trends differ between habitat types? For example, is the role of environmental filtering stronger in environments that offer fewer niches?

4. How does functional ecology differ between austral and boreal migrants, and between migrant and resident species?

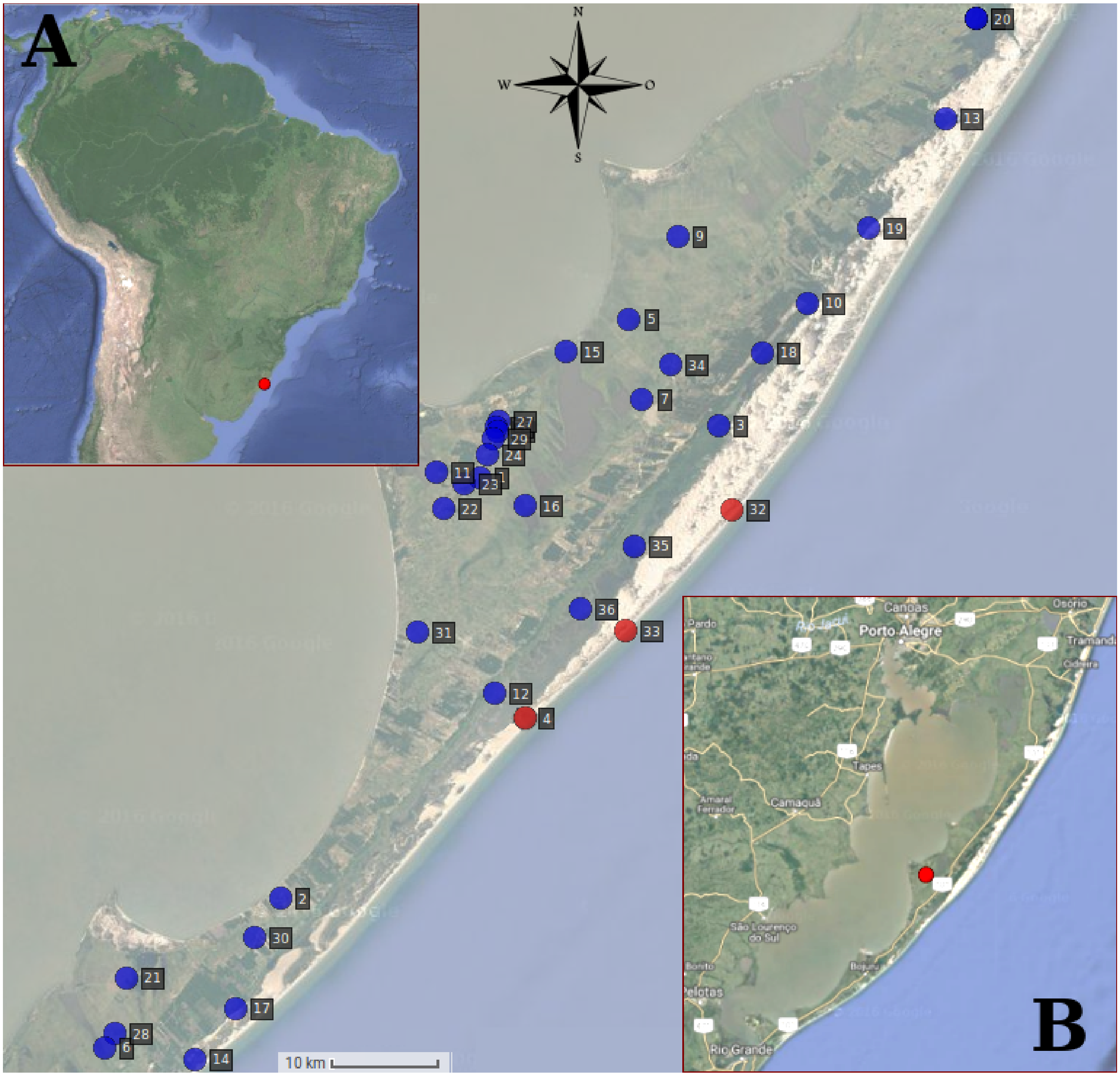

Figure 1: Location of study sites. Inset A: location in Brazil; Inset B, location in relation to Porto Alegre and the Lagoa dos Patos; main figure: distribution of sites surveyed for the CNAA. For site names, see Table 1.

Materials and methods

Survey data

This study used survey data collected for the Neotropical Waterbird Census (Censo Neotropical de Aves Aquáticas; CNAA), co-ordinated by Wetlands International. These censuses were conducted at wetland sites on the Mostardas peninsula, on the coast of Rio Grande do Sul, Brazil. The censuses in this study were conducted during the austral summer (February or March) and winter (July or August), from winter 2005 to summer 2016.

Two distinct habitat categories were sampled, the coastal beach and inland lakes. Surveys on the *beach* recorded all birds seen inshore as well as any on the ground including the intertidal sediments and foredunes. The estuary area of Lagoa do Peixe – the *Barra da Lagoa* – is also considered a beach habitat as it shares many characteristics in common, such as saline water and exposed sediment (Lara Resende 1988). Surveys in *lake* habitats included all birds seen in the water or adjacent vegetation (typically grazed grassland).

Some sites were sampled very frequently (almost every season); others less frequently and several only once. Surveys were conducted at varying times of day and for varying durations. The effect of survey effort (duration, number of observers) or other characteristics (such as weather, human disturbance) was neither analysed nor corrected for as these data were not available for all surveys. The analysis therefore does not assume equality of survey effort. See … for a summary of site visits. Surveys which detected <3 species were excluded from the analysis, as such atypically low numbers are unlikely to be representative of the total community habitually present at a site.

Table 1: Sites on the Mostardas peninsular that were surveyed for the CNAA, with the number of visits to that site which where included in these analyses. Numbers refer to Figure 1.

Number	Site name	Latitude	Longitude	Habitat	Visits
1	Banhado da Alemoa	-31.156	-51.078	Lake	3
2	Banhado da Ronda	-31.498	-51.268	Lake	1
3	Banhado do balneário	-31.114	-50.853	Lake	7
4	Barra da Lagoa	-31.262	-50.983	Beach	3
5	Caieira	-31.028	-50.937	Lake	6
6	Canal da Lagoa	-31.618	-51.434	Lake	6
7	Capão do Fundo	-31.092	-50.925	Lake	12
8	Figueiras	-30.785	-50.611	Lake	1
9	Granja do Pântano	-30.961	-50.891	Lake	6
10	Lagoa da Veiana	-31.015	-50.769	Lake	1
11	Lagoa do Bonito	-31.152	-51.119	Lake	1
12	Lagoa do Meio	-31.330	-51.065	Lake	3
13	Lagoa do Papagaio	-30.865	-50.638	Lake	5
14	Lagoa do Paurá	-31.627	-51.349	Lake	-
15	Lagoa do Rincão	-31.055	-50.998	Lake	12
16	Lagoa do Sangradouro	-31.179	-51.035	Lake	3
17	Lagoa João Dias	-31.586	-51.311	Lake	1
18	Lagoa Pai João	-31.055	-50.811	Lake	1
19	Lagoa São Simão	-30.954	-50.712	Lake	1
20	Paulo Santana	-30.785	-50.611	Lake	2
21	Ponto1	-31.562	-51.413	Lake	1
22	Ponto10	-31.181	-51.112	Lake	-
23	Ponto11	-31.162	-51.093	Lake	-
24	Ponto13	-31.138	-51.071	Lake	-
25	Ponto14	-31.119	-51.062	Lake	-
26	Ponto15	-31.115	-51.063	Lake	-
27	Ponto17	-31.111	-51.060	Lake	-
28	Ponto2	-31.607	-51.424	Lake	1
29	Ponto20	-31.125	-51.066	Lake	1
30	Ponto4	-31.530	-51.292	Lake	-
31	Ponto7	-31.281	-51.138	Lake	-

Number	Site name	Latitude	Longitude	Habitat	Visits
32	Praia do Balneário	-31.182	-50.841	Beach	6
33	Praia do PNLP	-31.280	-50.941	Beach	12
34	Saída da Caieira	-31.065	-50.899	Lake	1
35	Trilha das Dunas	-31.211	-50.933	Lake	1
36	Trilha do Talhamar	-31.350	-51.037	Lake	9

Species data

Species names and taxonomy followed van Perlo (2009). Only species recorded on >5% of surveys were included, as species detected on fewer occasions are unlikely to be regular members of a given community.

Species were classified as resident, summer migrants or winter migrants based on the account in van Perlo (2009). However, this source contains numerous errors for this region; for example, Semipalmated Plover *Charadrius semipalmatus* is listed as a 'rare or vagrant' species, when in fact it is regularly recorded on the coast in large numbers (Sanabria & Müller Brusco 2011; Scherer & Petry 2012 and pers. obs). Therefore, information on the local status of birds was supplemented using a checklist published for Parque Nacional da Lagoa do Peixe, a large protected site in the study area (Nascimento 1995).

Trait data

There is currently no agreed standard for which functional traits to analyse in birds. Plant studies tend to focus on morphology and life history (e.g. Helsen, Hermy & Honnay 2012), and a recently-developed framework for terrestrial beetles focuses on the same (Fountain-Jones, Baker & Jordan 2015). However, in both cases these traits tend to be assessed from collected specimens, whereas behavioural data, derived from field observations, is available for most bird species in compendia such as del Hoyo et al. (2016).

In previous studies of functional traits in birds, the traits analysed have often been tailored to the question under focus. For example, studying which traits facilitate birds' breeding in urban areas, Croci, Butet & Clergeau (2008) included traits relating to life history, diet and nesting, explicitly because those traits pertain to tolerance of new environments. Conversely, studying non-breeding waders in estuaries, a habitat used primarily for foraging, Mendez et al. (2012) selected traits relating to waders' use of food resources.

This study included census data from outside the focal species' breeding periods (Nascimento 1995), and so traits to do with life history or reproduction have been omitted. Instead, traits related to foraging are included, from three categories: diet composition, foraging behaviour and morphology. These categories were based on a previous analysis of wader functional diversity (Mendez 2012), but have been refined for the details of this study, primarily by expanding the categories to account for waterbirds other than waders. These traits have associations with both foraging behaviour (Barbosa & Moreno 1999; Durell 2000) and habitat use (Baker 1979; Cartar & Morrison 2005).

Data were initially gathered from del Hoyo et al. (2016); however, this source does not include bill or tarsus lengths, and does not have detailed diet and/or behaviour information for all species (resident species with small ranges are especially poorly covered). Therefore, where the species account in del Hoyo et al. (2016) reported that information was scarce, additional data were used from other published accounts. A full reference list for each trait is available in Appendix 1A.

Morphological data

Body mass, Bill length, Tarsus length

Where mean values were reported, these were used; for sexually dimorphic species, each sex's mean was used to calculate an overall mean for the species. Where a range was reported, the median value of this range, or of both ranges for sexually dimorphic species, was used. Previous studies have also averaged sexually dimorphic traits (Barbosa & Moreno 1999; Mendez et al. 2012). Data for adult birds was used in preference to juveniles, and local subspecies if geographical variation was reported. These continuous data were ln(x)-transformed prior to analysis as they ranged over an order of magnitude.

Bill shape

As in Mendez et al. (2012) bills were classified as straight, up-curved or down-curved, based on illustrations in del Hoyo et al. (2016).

Behavioural data

Whether or not (1/0) the species is recorded as using the following behaviours to forage:

Pecking Taking an item from the surface of the substrate

Probing Inserting the bill below the surface of the sediment

Jabbing Repeatedly pecking at a prey item

Hammering Striking repeatedly with the bill in order to break an object

Scything Moving the bill from side to side through the water or sediment

Turning Turning over objects to locate prey

Foot trembling Inserting a foot into the sediment and vibrating it to disturb invertebrates

Swimming Foraging while swimming on the surface of water

Dipping Inserting the entire head beneath the surface of the water

Diving Foraging entirely below the surface of the water

Skimming Flying with the lower mandible of the bill inserted into the water or sediment

Aerial Jumping or flying to catch prey before landing

Kleptoparasitism Stealing prey caught by individuals of other species

Scavenging Consuming animal matter or waste discarded by other species, including humans

Diet data

If (1/0) the species is recorded as consuming:

Insects Adult or larval insects

Crabs, Crustaceans Crabs (and other large Decapoda, such as shrimp) were considered separately to smaller crustaceans such as Amphipoda

Worms A highly polyphyletic grouping: any long, legless, soft-bodied invertebrate

Snails, Molluscs Snails (and other small Gastropoda) were considered separately to larger, harder-shelled molluscs such as clams

Herps Herpetofauna: amphibians and reptiles

Fish Fish

Plant Any plant material, including leaves, seeds and other parts

Eggs Eggs of any taxon, including birds, fish and horseshoe crabs

Diatoms Microscopic, unicelluar phytoplankton characterised by a cell wall composed of silicon dioxide

Other Any other diet component not included in the above categories, but insufficiently distinct or common to warrant its own; for example, bird nestlings, human rubbish, faeces

If a given behaviour or dietary component was not recorded in the literature, it was assumed not to occur commonly enough to be considered a trait of the species. For one species, the Spot-flanked Gallinule *Gallinula melanops*, no dietary information was found in the literature. Also, no morphological data was available in the literature for some species (no bill: *Rollandia rolland*; no tarsus: *Cygnus melanocoryphus, Jacana jacana*; no bill or tarsus: *Chauna torquata, Podiceps major*). However, the analytical methods used are able to function with small amounts of missing data (Pavoine et al. 2009; Laliberté, Legendre & Shipley 2014).

Trait differences between species

Due to the inclusion of categorical variables, Gower distance was used for the trait data (Pavoine et al. 2009; Borcard, Gillet & Legendre 2011), using the `gowdis` function of the `FD` package for `R` (Laliberté, Legendre & Shipley 2014).

In order to give equal weight to the three categories of trait variables (behaviour, diet and morphology), despite their unequal number of variables, I first constructed separate distance matrices for each category. The mean of those matrices gave an overall trait distance matrix. Correlation between these four matrices was evaluated using Spearman's correlation coefficient, testing significance with Mantel tests with 999 permutations (significance tests were not conducted with the overall-mean matrix due to non-independence).

The functional diversity metrics used in this analysis were based on PCoA (Laliberté & Legendre 2010) of the trait distance matrix. For these analyses, a Euclidian trait distance matrix is required, calculated from untransformed species abundances. Negative eigenvalues (imaginary axes) were made Euclidian using the Cailliez transformation, which adds the smallest possible constant to the distances (Borcard, Gillet & Legendre 2011).

Species differences between sites

The functional diversity analyses include species abundances as a simple weighting. For all other analyses, species dissimilarity between sites used the Cao index implemented by the `vegdist` function of `vegan` (Oksanen et al. 2016). This measure minimises bias in data with high beta diversity and variation in sampling intensity, and therefore has higher success in correctly classifying sites (Cao, Williams & Bark 1997). This implementation of the index is based on ln(x)-transformation of abundances; zero counts are arbitrarily replaced with 0.1.

Predicting community composition and function

Overall changes in taxonomic and functional composition across habitat and season

Using the distance matrix of species composition as a response variable, I used PERMANOVA to partition the variance explained by two potential sources of variation in inter-survey dissimilarity/distance, habitat and season. This used the `adonis` function of vegan (Oksanen et al. 2016).

To compare between-survey differences in functional composition, it was first necessary to measure the functional composition of each survey. For this, I used community weighted means (CWMs: Lavorel et al. 2008), as computed by the `functcomp` function of the `FD` package.

For continuous trait variables (such as the morphological measures in this analysis) the CWM is simply the mean trait value for each species present, weighted by that species' abundance. For categorical variables with >2 categories, such as bill shape, the CWM is the most frequent category. Binary variables' CWMs can be computed as either the dominant value (0 or 1) or a mean, treating the 0s and 1s numerically. I used the latter approach for its more intuitive interpretation (as the proportion of individuals possessing that trait), although repeating the analysis using the former method did not change results.

Functional composition distances were tested for their response to habitat and season, as described above for dissimilarity in taxonomic composition. Distance matrices for the CWM traits in each category (behaviour, diet and morphology) were tested independently, as was the overall mean.

I also compared the frequency of individual traits between habitats. For binary traits I used a series of χ^2 tests (controlling for the FDR: Benjamini & Hochberg 1995); the three continuous morphological were compared with Mann-Whitney *U* tests.

Functional dissimilarity was then calculated between each migrant-only community, and analysed according to season and habitat as the total community was above.

Functional differences between austral and boreal migrant communities

To compare average trait values between migratory birds only, resident species were eliminated from census results. Following species removal, any censuses which recorded fewer than three species were excluded from analysis, as calculating Community Weighted Means requires at least three (Lavorel et al. 2008).

Functional differences between migrant and resident communities

Having calculated CWMs for the above migrant-only censuses, I repeated the process excluding migrants, and including only resident species. I then compared average trait values between migrant and resident species using a series of FDR-adjusted Mann-Whitney *U* tests.

Functional diversity metrics

Functional diversity is a complex and evolving concept. Modern approaches acknowledge that diversity is a multifaceted issue, and that therefore using several metrics in a single analysis is the preferred approach (Laliberté & Legendre 2010). The approach used in this analysis is based on the distance between communities in multivariate trait space (based on the PCoA axes of a Gower distance matrix), and incorporates information about species' relative abundances (Villéger, Mason & Mouillot 2008).

Five independent functional diversity metrics were used in this analysis:

Functional richness is the minimum convex-hull volume, which can include all species in multivariate space. Proposed as a multivariate analogue of the range of a single trait (Villéger, Mason & Mouillot 2008), it is unweighted by abundance and therefore sensitive to outliers (Laliberté & Legendre 2010).

Functional evenness is a description of the abundance distribution within a community's convex hull. Higher values indicate that distances between all nearest-neighbour pairs are similar; values tend towards zero with increasingly clustered points.

Functional divergence describes the abundance distribution of species relative to the centre of the convex hull. As noted above, the vertices of the convex hull may be formed by common species or by very rare outliers. High values indicate that the abundant species are close to the vertices of the hull; values approach zero as abundant species approach the centre of the hull.

Functional dispersion was proposed to combine the strengths of the first three measures (Laliberté & Legendre 2010). Like evenness and divergence, it incorporates abundance information; unlike those measures, but like richness, it considers the dispersion of species in trait space (rather than within a convex hull textitindependently of its volume). In essence, dispersion is the mean distance of each individual to the centroid of the community.

Number of functionally distinct species in this analysis is equal to the number of species recorded in a community, as all included species were functionally distinct.

Observed functional diversity

As all the diversity metrics (except for species count data) were bounded between 0 and 1 and often had skewed or bimodal distributions, I used non-parametric testing to compare measures between categories. Functional diversity metrics were compared between habitats and seasons using Mann-Whitney *U* tests. Due to the multiple comparisons in each analysis, *p*-values were adjusted using the false discovery rate (FDR) correction (Benjamini & Hochberg 1995).

In addition to these analyses, I tested for an interaction between habitat and seasonal effects using analysis of variance. For each functional diversity metric I tested models allowing different intercepts for each group, and models allowing different slopes and intercepts for each group. Models which included a significant term for at least one habitat and a seasonal effect were considered significant.

Testing for processes of community assembly

To evaluate trait convergence or divergence in the waterbird community I compared the observed functional diversity metrics to the 'expected' functional diversity of randomly generated communities (Mendez et al. 2012). I first identified the separate species pools for summer and winter surveys. Then, for each survey included in the above analyses I drew 1000 random communities from the appropriate seasonal pool. Species and site totals were constrained within each seasonal pool. This method is equivalent to the IT algorithm of Ulrich & Gotelli (2010), and used the `r2dtable` function in `R`.

Following the same methods and trait data used to analyse the observed data (detailed above), all five functional diversity metrics were then calculated for each random community. As in Mendez et al. (2012), these values were used to calculate the standardised effect size (SES). Gotelli & McCabe (2002) give the formula as:

$$\mathbf{SES} = (\boldsymbol{I}_{\text{obs}} - \boldsymbol{I}_{\text{sim}}) / \boldsymbol{\sigma}_{\text{sim}}$$

where I_{obs} is the observed functional diversity index, I_{sim} is the mean of the 1000 indices calculated from random communities, and σ_{sim} is the standard deviation of those 1000 random indices.

If SES does not differ significantly from 0 then observed communities do not differ from random. Positive values indicate trait divergence, for example as might result from interspecific competition; negative values indicate trait convergence, for example as a result of ecological filtering by local habitat characteristics.

Software

All analysis used the `R` environment (R Core Team 2016). In addition to the packages cited above, the analysis used the `dudi.pco` function of `ade4` for principle co-ordinates analysis (Dray & Dufour 2007).

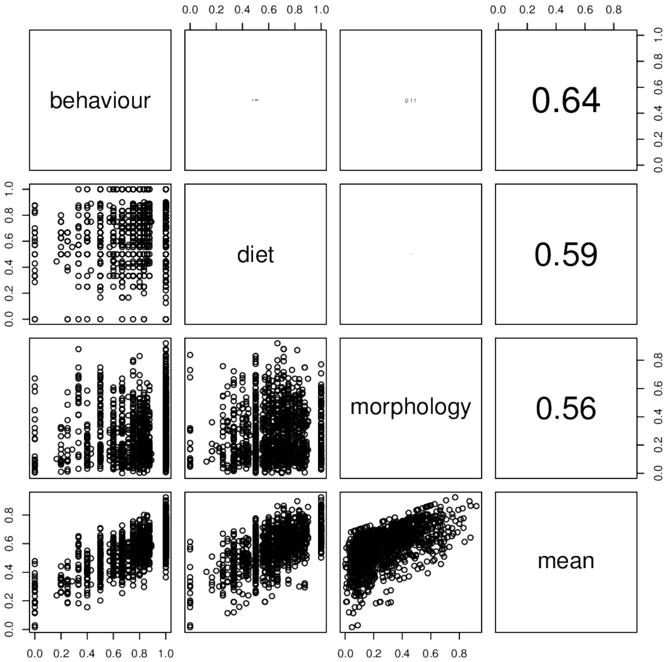

Figure 2: Correlation matrix between the behaviour, diet, morphology and mean distance matrices. Lower panels show scatter plots; upper panels show Spearman correlation coefficients, scaled according to their value.

Results

Out of a total of 141 surveys, 17 were excluded due to insufficient observations, leaving 124 surveys and 52 species that were included in the analysis (Table 2). While over half of surveys were conducted in lake habitats, an adequate number of beach surveys remained in the analysis. The seasonal division between summer and winter was more even, with 54.8% conducted in summer.

Table 2: Number of included surveys in each habitat and season category

	Summer	**Winter**	**Total**
Beach	17	11	28
Lake	51	45	96
Total	68	56	124

Predicting community composition and function

The three distance sub-matrices (behaviour, diet and morphology) were poorly correlated with each other (*behaviour and diet*: Spearman's r=0.08, p=0.07; *behaviour and morphology*: r=0.11, p=0.04; *diet and morphology*: r=0.05, p=0.24), suggesting that these variables captured different aspects of species' functional ecology. However, the overall distance matrix used in subsequent analysis, calculated from the mean of the three sub-matrices, had a Spearman correlation r > 0.56 with all three sub-matrices, suggesting that all of these aspects were represented in the matrix used for analysis (Figure 2).

Species assemblages were highly significantly more dissimilar between sites in different habitats ($p = 0.001$), with this relationship explaining 171% of variation. In addition, season was a significant predictor of community dissimilarity, though with very weak explanatory power ($R^2 = 0.02$). The interaction between habitat and season was not significant (Table 3). Differences in each species' occurrence and abundance between habitats are shown in Appendix 1B.

Table 3: Sources of variation in dissimilarity between waterbird community taxonomic composition from PERMANOVA with 999 permutations. Table reports degrees of freedom (d.f.), sums of squares (SS), mean squares (MS), F statistics, partial R^2 values and p values.

Variable	**d.f.**	**SS**	**MS**	**F**	**R^2**	**p**
Habitat	1	13.4	15.4	25.4	0.17	**0.001**
Season	1	1.9	1.9	3.1	0.02	**0.003**
Habitat × Season	1	1.0	1.0	1.7	0.01	0.063
Residuals	120	72.4	0.6		0.79	
Total	123	90.7				

Differences in community functional composition were also strongly related to habitat differences ($p < 0.001$), with a similar amount of variation explained by this relationship ($R^2 = 0.19$; Table 4). Unlike species composition, functional composition did not vary between seasons. The interaction between habitat and season was weakly significant ($p = 0.04$), explaining a tiny proportion of total variance ($R^2 = 0.02$).

Table 4: Sources of variation in distance between functional composition of waterbird communities, from PERMANOVA with 999 permutations. Table reports degrees of freedom (d.f.), sums of squares (SS), mean squares (MS), F statistics, partial R^2 values and p values.

Variable	d.f.	SS	MS	F	R^2	p
Habitat	1	0.75	0.75	28.7	0.19	**0.001**
Season	1	0.05	0.05	2.0	0.01	0.080
Habitat × Season	1	0.06	0.06	2.5	0.02	**0.037**
Residuals	120	3.1	0.03		0.78	
Total	123	4.0				

Considering each category of functional traits separately confirmed that birds' behaviour, diet and morphology all vary significantly between habitat, with this relationship explaining 20%, 25% and 13% of variation in behaviour, diet and morphology respectively (Table 5). On the other hand, the role of season was again weak, explaining 0-2% of variation and reaching weak significance (p=0.02) for behaviour only. The habitat × season interaction was also not a useful predictor, explaining 3% of variance in diet (p=0.003).

Table 5: Partitioning of variance via PERMANOVA between habitat and season (and an interaction term), explaining distance between the CWMs of waterbird communities. Table reports partial F, R^2 and p statistics.

	Behaviour			**Diet**			**Morphology**		
Variable	**F**	**R^2**	**p**	**F**	**R^2**	**p**	**F**	**R^2**	**p**
Habitat	31.0	0.20	**0.001**	42.1	0.25	**0.001**	18.4	0.13	**0.001**
Season	3.1	0.02	**0.021**	2.4	0.01	0.062	0.6	<0.01	0.472
Habitat × Season	1.6	0.01	0.162	5.1	0.03	**0.003**	0.64	<0.01	0.494
Residuals		0.77			0.70			0.86	

Individual traits considered in isolation also often differed between habitats: relative frequencies of foraging behaviours and diet items are presented and analysed in Table 6.

Table 6: Inter-habitat variation in dominant species traits (Community Weighted Means).For diet and behaviour traits, the value shown is the percentage of individuals in the community possessing that trait. The equality of proportions of species having a given traitin each habitat was tested with a series of χ^2 tests (d.f.= 1), the results of which are presented here with FDR-adjusted p-values. Data are presented in order of increasing statistical significance. Continuous variables were not compared. Mass was measured in grams (g), tarsus and bill lengths in millimetres (mm); though these values were ln(x) transformed for analysis, untransformed data are presented here.

Trait	Beach	Lake	Chi.sq	p.value
Plant	15.4	77.4	74.8	**<0.001**
Crabs	53.9	5.4	54.1	**<0.001**
Dipping	5.8	54.9	54.7	**<0.001**
Snails	55.2	6.7	52.8	**<0.001**
Scavenging	46	2.4	49.5	**<0.001**
Scything	6.5	49.7	44.1	**<0.001**
Other	42.9	5.8	35.4	**<0.001**
Eggs	41.3	8.4	27.2	**<0.001**
Worms	69	36.2	20.3	**<0.001**
Kleptoparasitism	29.1	4.3	20.4	**<0.001**
Swimming	23.1	52.1	16.7	**<0.001**

Trait	Beach	Lake	Chi.sq	p.value
Herps	17.4	41.7	13	**0.001**
Molluscs	66.2	41	11.8	**0.001**
Foot trembling	25.3	6.5	11.8	**0.001**
Hammering	11.5	0.1	9.9	**0.003**
Diving	39.6	62.3	9.4	**0.003**
Insects	96.5	82.2	9.3	**0.003**
Jabbing	12	2.1	6	**0.019**
Fish	67.8	51	5.2	**0.029**
Probing	40.8	24.6	5.2	**0.029**
Crustaceans	82.2	68.4	4.4	**0.039**
Pecking	49.3	65	4.4	**0.039**
Aerial	12.2	3.2	4.5	**0.039**
Turning	0	0.9	0	1
Skimming	2.9	2.6	0	1
Mass	222.5	625.2	-	-
Bill length	40	57.9	-	-
Tarsus	40.5	60.6	-	-
Bill shape	Straight	Straight	-	-
Diatoms	0	0	-	-

Comparing austral and boreal migrants

In all surveys analysed, 23.1% of the 52 species recorded were migratory, comprising 30.9% of all individuals recorded. Of the migratory species, 3 were austral migrants (present in the study area during the austral winter) and 9 were boreal migrants (locally present during summer). In total, 27 surveys were included in the analyses comparing functional traits amongst migrants, and between migrant and resident species. The distribution of these surveys amongst habitats and seasons is shown by Table 7. There were significant differences in the functional ecology of summer versus winter migrants, and between migratory birds using each habitat; however, the interaction term was not significant (Table 8). Considering the functional subcategories, migratory birds differed significantly in their diet between seasons, and in their diet and foraging behaviour between habitats (Table 9).

Table 7: Sample sizes by survey habitat and season for bird census included in the comparative community analyses

	Summer	Winter	Total
Beach	12	7	19
Lake	7	1	8
Total	19	8	27

Table 8: Sources of variation in distance between functional composition of migratory waterbird communities, from PERMANOVA with 999 permutations. Table reports degrees of freedom (d.f.), sums of squares (SS), mean squares (MS), F statistics, partial R^2 values and p values.

Variable	d.f.	SS	MS	F	R^2	p
Habitat	1	0.16	0.16	5.2	0.16	**0.002**
Season	1	0.11	0.11	3.6	0.11	**0.011**
Habitat × Season	1	0.04	0.04	1.2	0.04	0.265
Residuals	23	0.70	0.03		0.70	
Total	26	1.01				

Table 9: Partitioning of variance via PERMANOVA between habitat and season (and an interaction term), explaining distance between the CWMs of migrant waterbird communities. Table reports partial F, R^2 and p statistics.

	Behaviour			Diet			Morphology		
Variable	F	R^2	p	F	R^2	p	F	R^2	p
Habitat	7.6	0.21	**0.007**	3.4	0.10	**0.027**	3.1	0.11	0.062
Season	2.6	0.07	0.090	7.7	0.22	**0.001**	1.3	0.05	0.281
Habitat × Season	2.6	0.07	0.080	0.9	0.02	0.500	1.0	0.03	0.335
Residuals			0.64		0.66			0.81	

Comparing migrant and resident communities

Overall, using the same surveys as the above analysis (Table 7), I found that 18 of 28 trait variables differed significantly between the migratory and resident species (Table 10). Behavioural, diet and morphological traits all included highly significant ($p < 0.001$) differences. While all morphological traits were highly significantly different ($p \leq 0.001$), there were diet and behaviour traits that did not differ between migrant and resident birds (Table 10).

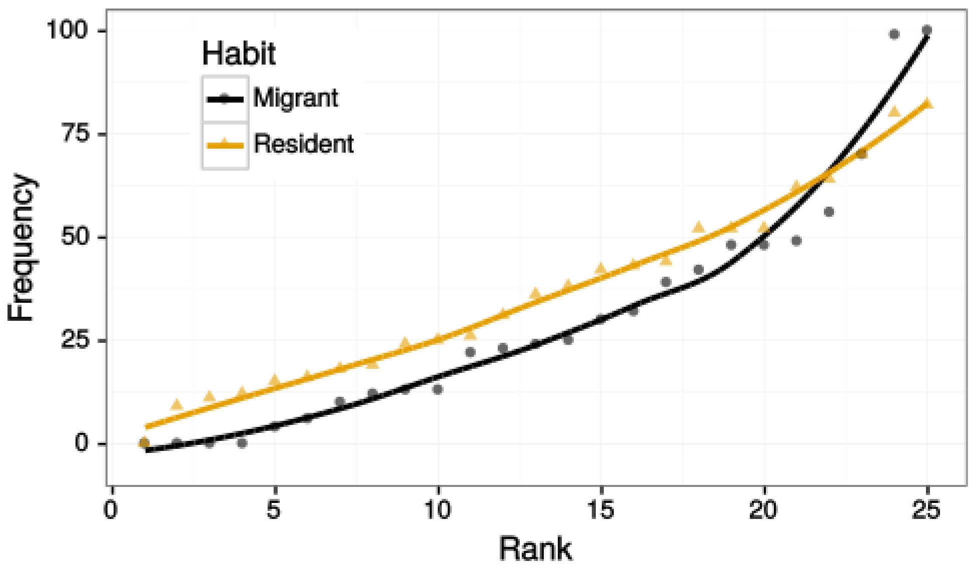

Figure 3: Trait accumulation profiles for migrant and resident waterbirds. Points show the absolute frequency of each behavioural and diet trait, ranked by frequency; lines depict a LOESS smooth.

Common and rare traits exhibited significant differences. There was no correlation between trait frequency and p-value for migrants (Spearman's $r = 0.02$, $p = 0.9$) nor residents (Spearman's $r = -0.4$, $p = 0.1$). Note that this analysis included only those traits whose values can be summarised as frequencies (i.e., morphological traits are excluded). Instead, traits that were relatively common in migrants tended also to be relatively common in resident species, and vice-versa (Spearman's $r = 0.62$, $p = 0.001$; $n = 25$ for all tests). However, rare traits in migrants tended to be rarer, and common traits nearer to universal, than in resident species, which showed a more even distribution of trait frequencies (Figure 3). However, in addition to the data presented in Table 10, there was no significant difference in the commonest bill shape, which was 'straight' for nearly all communities (data not shown).

Table 10: Mean trait values for migratory and resident birds, the difference between those means and the FDR-adjusted p-values from Mann-Whitney U tests of the difference between communities. Data are presented in order of increasing statistical significance. For diet and behaviour traits, the value shown is the percentage of individuals in the community possessing that trait. Mass was measured in grams (g), tarsus and bill lengths in millimetres (mm); though these values were ln(x) transformed for analysis, untransformed data are presented here.

Trait	Migrants	Residents	Difference	p.value
Mass	129	527	-398	<0.001
Bill length	34	58	-25	<0.001
Tarsus	35	65	-30	<0.001
Insects	99	82	17	<0.001
Crustaceans	100	64	36	<0.001
Snails	70	24	46	<0.001
Herps	0	44	-44	<0.001
Hammering	0	16	-16	<0.001
Swimming	6	52	-46	<0.001
Skimming	0	15	-15	<0.001
Pecking	39	62	-23	0.003
Kleptoparasitism	13	43	-30	0.003
Foot trembling	13	42	-29	0.004
Jabbing	4	18	-14	0.005
Diving	24	52	-28	0.009
Fish	49	80	-30	0.010
Other	23	38	-15	0.033
Probing	48	26	22	0.044
Worms	56	70	-13	0.099
Scything	22	11	10	0.183
Aerial	12	12	0	0.301
Eggs	30	25	5	0.423
Crabs	42	36	6	0.466
Molluscs	48	52	-5	0.466
Plant	25	19	6	0.478
Scavenging	32	31	1	0.697
Turning	0	0	0	1.000

Functional diversity of waterbird communities

In general, functional diversity appeared similar between habitats (Figure 4). Formal hypothesis testing confirmed this similarity. Only functional evenness and richness varied between habitats (Table 11). Pairwise Mann-Whitney U tests with the Benjamini-Hochberg (1995) correction showed that beach communities were less functionally even than lake ($p = 0$) communities. There was no apparent difference in any functional diversity metric between seasons (Figure 4), which was confirmed by formal hypothesis testing (Table 11): there was no significant difference in any metric between summer and winter (FDR-adjusted Mann-Whitney U tests: all $p > 0.05$). None of the two-way ANOVA models showed a significant interaction between habitat and season.

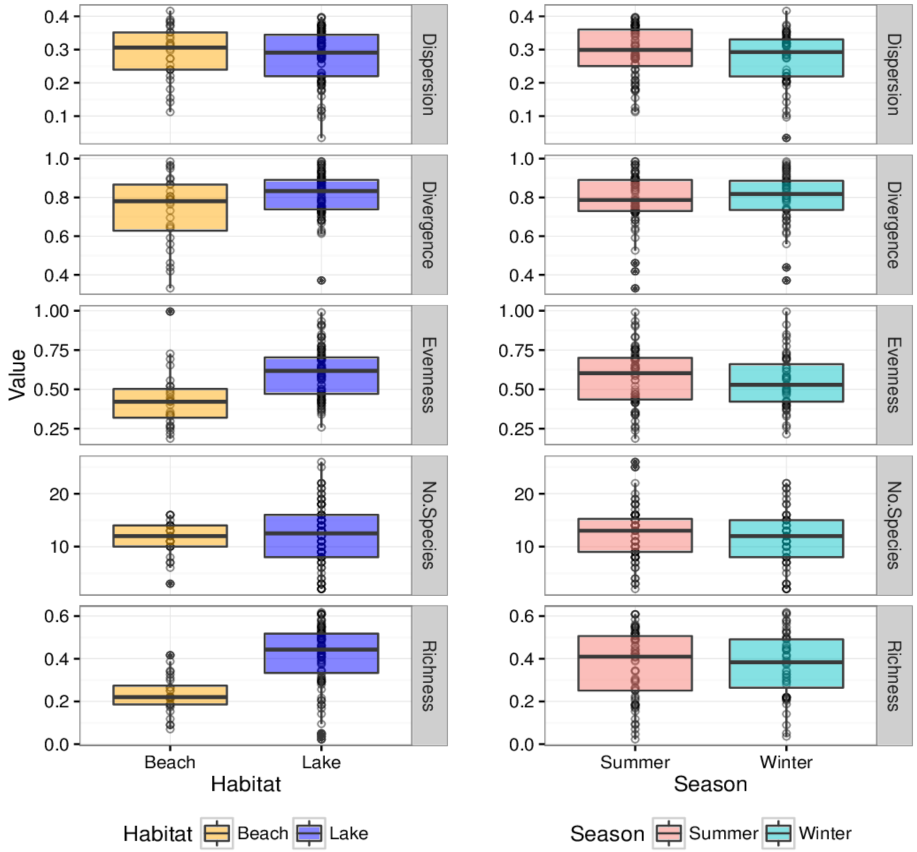

Figure 4: Functional diversity metrics according to habitat (left) and season (right). Note that the y-axis has a different scale in each plot facet. Only functional evenness and richness by habitat showed a significant difference, with beach communities significantly less even and less even than the others (see text for statistics).

Table 11: FDR-adjusted p values from Mann-Whitney U tests comparing each functional diversity metric between habitats and seasons.

Metric	**Habitat**	**Season**
Dispersion	0.682	0.62
Divergence	0.080	0.85
Evenness	<0.0001	0.62
Number of species	0.686	0.62
Richness	<0.0001	0.93

Testing for processes of community assembly

The observed communities had significantly lower functional diversity than expected for all metrics except for functional divergence, which did not differ from random. Beach communities showed SES strongly negative ($p<0.001$) for functional dispersion, evenness, richness and the number of functionally-distinct species; lake communities' functional richness was only slightly less than random ($p = 0.025$).

Table 12: Median SES score and its associated p-value for each functional diversity metric in each habitat

	Beach		Lake	
Metric	**Median**	**p value**	**Median**	**p value**
Dispersion	-28.5	**<0.001**	-10.7	**<0.001**
Divergence	-1.9	0.089	-0.2	1
Evenness	-3.5	**<0.001**	-1.4	**0.001**
No.Species	-16.4	**<0.001**	-6.2	**<0.001**
Richness	-1.5	**<0.001**	-0.1	**0.025**

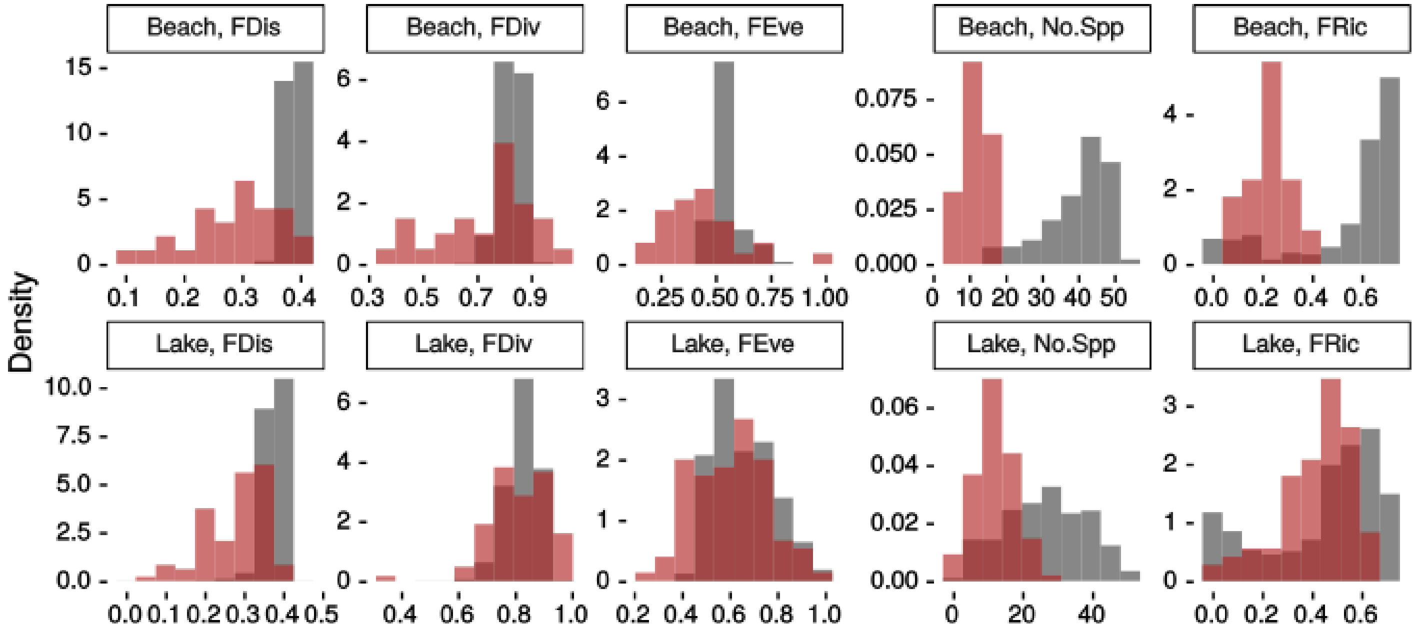

Figure 5: Histograms of observed (red) and simulated (grey) functional diversity metrics, comparing the results of waterbird surveys with 1000 randomly simulated communities

Discussion

Habitat filtering selects species composition from seasonal pools

Habitat explained 40% of the variance in species composition, with communities in different habitats tending to have a Cao dissimilarity index 0.3 greater (out of 1) than surveys conducted in the same habitat. In contrast, while season was also a statistically significant explanatory variable, the proportion of variance explained was negligible, and including season in the model with habitat halved the model's explanatory power compared with the habitat-only model.

While many of the waterbird species detected by these surveys have specific habitat requirements (del Hoyo et al. 2016), only around a quarter of species or individuals were migratory. Though seasonal movements do occur also in resident species, overall most of the species in this region can be observed year-round (Nascimento 1995). Therefore, while the seasonal difference in species composition is statistically detectable, it is not of any great biological significance in terms of overall community composition.

Functional composition driven by habitat filtering

While the Gower distance of functional composition between surveys was on average only 0.08 higher in different habitats, as an explanatory variable habitat explained 20% of the variance in community functional composition.

On the other hand, unlike species composition, functional composition did not vary according to season. This may be because of the small contribution of migratory species to the overall community, or may represent the filling of any niches vacated by departing migrants by resident species.

This relationship held true for each subcategory of functional trait, with habitat explaining 30% of the variance in communities' diets, 20% of the variance in the prevalence of behavioural traits but only 2% of the variance in morphology. This hierarchy reflects the extent to which these traits are environmentally mediated. Diet is entirely constrained by the food items available in the environment. The extent to which a behavioural strategy is adaptive depends in part on environmental conditions: what prey is present, where prey is located, and other factors such as water depth, presence of predators, among others. Morphology, on the other hand, is largely genetically determined via developmental processes, and cannot be adjusted by organisms to suit a particular habitat.

It should be borne in mind, however, that the traits analysed in this study were derived from published literature, chiefly the globally comprehensive (del Hoyo et al. 2016), rather than from direct observations of each species in the locations surveyed in this study. The diet and behaviour actually manifested by individuals in this region is likely to be a subset of those attributed to species in this analysis: for instance, diet in a given habitat and season can only reflect which prey items are present in that place and time. Behaviour is also known to be remarkably plastic, enabling rapid adjustment of foraging strategies as birds change environment, or as their environment changes (see Piersma & van Gils (2011) for examples including shorebirds, gulls, waterfowl and other birds).

In addition, detecting birds in a particular habitat does not necessarily imply that they are foraging there (Jones 2001). At one of the survey sites in this study (Lagoa do Peixe), birds of several species are known to roost in the lake, but forage preferentially on the beach (e.g. *Calidris alba*) or offshore (e.g. *Sterna hirundo*; Lara Resende 1988). The inclusion of non-foraging individuals likely weakens the association between habitat and function, as the traits included were those relevant to foraging.

Differences between migrant and resident species

While summer and winter communities were functionally similar, this was not caused by functionally-similar boreal and austral migrants seasonally occupying identical niches; rather, the continuity of average community trait values resulted from relatively continuous occupation of the same habitats by resident species throughout the year.

In fact, boreal migrant species had a distinct, and less diverse, array of ecological functions, suggesting that they occupy a distinct niche. By implication, either an area of niche-space is left seasonally unoccupied – which seems unlikely, given the usual efficiency of life in exploiting opportunity (Darwin 1859) – or else migratory waterbirds have evolved to exploit a seasonally-available niche in their non-breeding range, as they do in their breeding range (Newton 2008; Somveille, Rodrigues & Manica 2015). Boreal migrants have been shown to time their arrival to coincide to with maximum prey availability during both southward (Schneider & Harrington 1981) and northward (van der Graaf et al. 2006) migration at stopover sites. Locally, work by Fedrizzi (2008) has shown that the migratory shorebirds *Calidris alba* and *C. fuscicollis* have their peak abundance at Lagoa do Peixe at the same time their principal benthic macroinvertebrate prey reach peak abundances (see Chapter 2, Fedrizzi 2008).

Migratory birds made up a fairly small proportion of the total number of species or individuals detected, around 25% in both cases. Few surveys contained sufficient migratory species for the analysis (at least 3: Laliberté, Legendre & Shipley 2014). In particular, only one winter survey from a lake habitat was included. Any conclusions from these analyses must therefore be drawn very cautiously, and warrant testing on a considerably larger dataset.

Austral versus boreal migrant communities

Functional composition of migratory bird assemblages differed between habitats and between seasons, with the model including both predictors explaining the most variance (although only 8%). Focussing on subcategories of traits, behaviour and diet varied between season only, whereas morphology differed between habitats.

Of the species included in this analysis, one lineage (the Scolopacidae) is a boreal radiation. The 7 species of this lineage occur in the surveyed region only during the austral summer, and were often among the most abundant species in these surveys. These species' foraging strategy, with a substantial component of probing in the sediment, is highly distinct and has no equivalent in the austral migrant community. While the Scolopacidae therefore contribute a large amount of seasonal variation, these species occur in both habitats (Lara Resende 1988).

Conversely, the most numerous austral migrant is the Chilean Flamingo (*Phoenicopterus chilensis*), which occurs exclusively in lake habitats and is considerably larger than any species occurring on the beach. This species probably causes most of the variation in morphology. However, it is present year-round at Lagoa do Peixe – the only location Brazil where this is true (Nascimento 1995; van Perlo 2009) – and therefore does not cause seasonal variation in this dataset, as the only winter lake survey is from Lagoa do Peixe. Repeating this analysis with data from other areas could help to determine if there is an effect other than that caused by flamingoes.

Functional diversity

The bird community in lake habitats was functionally richer and more even than that of the beach, while there were no differences in functional dispersion or divergence. This is likely due to the presence of certain functionally unusual, but uncommon, species in lake habitats.

Functional richness reflects the total range of all traits simultaneously; however, it is not weighted by abundance, and so can be inflated even by a single individual with unusual characteristics. While in most cases traits were scored as 0 or 1, morphological measurements were continuous variables. Most of the largest species in this region, such as flamingoes, storks (Maguari Stork *Ciconia maguari*, Wood Stork *Mycteria americana*) and the larger herons (Cocoi Heron *Ardea cocoi*, Great Egret *Ardea alba*) were generally or entirely restricted to lake habitats. Furthermore, the nine species of waterfowl (Anatidae) and three grebes (Podicepidae) represent a distinct suite of functions – such as consuming plant material, and foraging by dipping while swimming – which are absent from almost all species on the beach, but appear on most lake surveys as species in these groups are locally common (Nascimento 1995 and pers. obs.). The presence of these additional traits would have the effect of expanding the vertices of the community's convex hull in trait-space, in other words increasing the functional richness.

Low functional evenness indicates clustering of species within that convex hull. This indicates that certain areas of trait-space are occupied more or less frequently than others. Ecologically this suggests that the extent to which some combinations of functions are more adaptive than others is greater in beach habitats. This is generally interpreted as representing environmental filtering: for example, there is almost no vegetation on the beaches in the study region (pers. obs.), so species depending on plant material would struggle. Similarly, wave action and the largely benthic distribution of marine invertebrates makes swimming a poorly adapted strategy. Conversely, these traits support many organisms in lakes, while the foraging strategies and dietary components found on the beach are mostly also present in lakes. The beach habitat is therefore shown to offer fewer niches, or require greater specialisation, than lakes.

There were no differences in functional divergence or dispersion. These metrics evaluate the abundance distribution of species relative to the weighted average of the total community. In this case, the majority of traits are binary. Species can therefore have a value of either 0 or 1 only, whereas the community average can be an intermediate rational number. In both habitats we therefore expect most species to occupy positions far from the centroid of most traits.

There were no seasonal differences in any metric of functional diversity, just as survey season did not explain any variation in functional distance between communities. This result lends further support to the notion that the summer and winter bird communities resemble each other functionally, despite statistically detectable differences in the species present.

Overall there were no seasonal or habitat differences in the number of species present. While this result may be valid, and therefore reflect ecological processes, I think it is more likely that the variation in species richness between survey dwarfed any difference there might be between habitats and/or seasons. This is another case where confronting ideas with a far larger dataset would be useful.

For all these metrics there was great variation in all the functional diversity metrics calculated for individual surveys, likely reflecting the variation in species richness between surveys. All species were functionally distinct, and so functional diversity is often partly a function of species richness.

Null communities and SES

As well as having a lower number of species, observed communities had lower functional richness, dispersion and evenness than random communities, although there was no difference in functional divergence. This combination of results indicates clustering of functional traits in waterbird communities. Many waterbird species occur in flocks, so while individuals of a given species were drawn independently in the null models, their occurrence in real life is not independent.

The only metric not showing a reduction in observed communities compared to randomness was functional divergence. Unlike dispersion, which showed a difference, divergence is calculated relative to the functional space each community occupies, rather than deriving from the absolute extent of that space. The traits showing the greatest numerical range – and therefore most likely to contribute to this disparity – were morphological (as all other traits were binary). It therefore seems likely that morphological differences between species are especially important in explaining their relative abundances in these habitats.

In general, beach habitats showed a greater reduction in functional diversity compared to randomness than the lake communities showed, indicating that environmental filtering operates more strongly at those sites. The greatest difference between the two habitat types was seen in functional richness, which is not sensitive to species' abundances, whereas abundance-weighted metrics showed similar reductions in both habitats. This suggests that abundant species are exploiting a restricted subset of the total functional space, but, in lake habitats, a small number of individuals from rarer, functionally-distinct species are able to co-exist by exploiting different resources.

These results may reveal that both competition and environmental filtering co-occur in these habitats. Though we have the tendency to separate these two processes behind patterns of community assembly, the fact is that environmental filtering and competition may act together, simultaneously or sequentially, and communities are not static though they may be more or less stable, while responding to a whole set of biotic and abiotic factors.

So, while the majority of individuals are clustered in a few, highly exploited niches, there nevertheless remains opportunity for ecologically dissimilar species to persist – but probably only in low numbers. For example, a given area may support many benthic-feeding insectivores, as their prey is numerous, but only a few piscivorous species which, feeding at a higher trophic level, face the challenge of finding less abundant prey.

Synthesis and conclusions

While species composition varied between both habitats and seasons, functional composition was similar in both seasons, but still varied between habitats. The same pattern was observed whether diet, behavioural or morphological traits were considered, or using a composite functional index. In other words, despite modest but statistically detectable differences in available species pools between seasons, surveyed communities remained functionally similar. Taken together, these results suggest that environmental filtering determines waterbird community assembly, at least at the local spatial scale considered here, while dispersal limitation seems unlikely given the geographic proximity and overlap of many of the surveyed sites.

Likewise, whilst functional diversity was similar between seasons, differences in diversity between habitats suggested that environmental filtering was stronger in beach habitats than lakes. Robust statistical results show that many individual traits have significantly different frequencies of occurrence in each habitat. Similarly, frequency and abundance of species varied significantly between habitats. While this latter result is not exactly surprising – species differences between habitats have been recorded locally (at Lagoa do Peixe) by a substantial body of previous work (Lara Resende 1988; Nascimento 1995; Fedrizzi 2008; Gonçalves 2009) – it is valuable to confirm that the dissimilarity-based methods used here detect known relationships, before attempting to draw inference from the non-detection of an unknown (in this case, a link between season and ecological function). The results of this study therefore provide a useful proof-of-concept that waterbird census data from areas including migratory species may be used to study processes of community assembly and environmental filtering in a variety of habitats. However, the limited quantity of data used in this study, owing to its restricted spatial scale, limits the strength and scope of conclusions that can be drawn.

While this study focussed on foraging and associated traits, differences in habitat use may also result from phenomena other than environmental conditions and foraging, in particular biotic interactions such as competition (Jones 2001). Furthermore, the habitats selected during the non-breeding period (as is the case for the boreal migrants in this study) may be partially determined by conditions during the breeding season, in another hemisphere. Reviewing evidence from shorebirds, gulls, terns, waterfowl and passerines, Piersma (Piersma 2007) makes a case that a positive feedback exists between breeding and non-breeding habitat specialism over evolutionary time: species breeding in the high Arctic may decrease investment in immunity due to the low environmental disease pressure in these regions, enabling higher energetic performance under demanding environmental conditions such as extreme thermoregulatory costs (Cartar & Morrison 2005; Piersma & van Gils 2011; McNab 2012) and perpetual daylight (Lesku et al. 2012).

Decreased immunity could also result from population bottlenecks caused by such extreme specialism during periods of environmental change (Piersma 2007). In either case, a comparatively weak immune system would restrict potential non-breeding habitats to saline, marine or coastal areas, which also have lower environmental disease pressure; for example, freshwater habitats have many more mosquitoes, which are vectors for avian malaria (Piersma 2003), Thus, further specialisation in habitat selection during the non-breeding period and migratory stopovers, would be necessary to mitigate this increased susceptibility, potentially causing further bottlenecks and constraining future adaptation (Piersma 2007). A pattern of correlated Arctic- and marine-specialisation is observed in many groups of waterbird (Piersma 2007).

In general, migration appears to be a strategy evolved by boreal-breeding taxa that shift their non-breeding range increasingly southward, as demonstrated convincingly for New World emberizoid passerines by Winger, Barker & Ree (Winger, Barker & Ree 2014). The migratory strategy likely evolved to enable breeding at latitudes and habitats that could not support large, long-term populations of the species (Newton 2008; but see Somveille, Rodrigues & Manica 2015). The effect of this (probable) boreal origin of most migratory waterbird lineages is the strong phylogenetic non-independence of migration: all but two of the migrants recorded on these surveys were Charadriiformes, and the other two were Phoenicopteriformes; the other seven orders of birds present contain no migratory taxa at these sites. In the southern hemisphere, therefore, migration is somewhat inseparable from both habitat use and evolutionary history.

Waterbird communities appear to be assembled via trait-environment interactions, with biotic interactions such as competiton playing a lesser role. However, given the apparent conservation of migratory habit and other ecological traits within lineages, the role of phylogeny in structuring waterbird communities should also be investigated.

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Appendix 1A: List of references for trait data

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Appendix 1B: Habitat associations of migratory and resident birds: percentage occurrence and mean abundance

Species	**Life history**	**Frequency**		**Mean**	
		Beach	**Lake**	**Beach**	**Lake**
Amazonetta brasiliensis	Resident	3.6	76	0.1	11.8
Anas flavirostris	Resident	0	19.8	0	0.8
Anas georgica	Resident	0	22.9	0	3.1
Anas versicolor	Resident	0	43.8	0	3.4
Aramus guarauna	Resident	0	42.7	0	1
Ardea alba	Resident	10.7	68.8	0.8	4.4
Ardea cocoi	Resident	71.4	60.4	1.8	1.4
Bubulcus ibis	Resident	0	22.9	0	1.7
Calidris alba	Boreal	60.7	2.1	363.6	3.2
Calidris canutus	Boreal	28.6	4.2	82.1	2.5
Calidris fuscicollis	Boreal	35.7	4.2	171.2	6.9
Charadrius collaris	Resident	60.7	6.2	8.2	0.3
Charadrius falklandicus	Austral	21.4	0	4.6	0
Charadrius semipalmatus	Boreal	46.4	2.1	11.8	0.3
Chauna torquata	Resident	3.6	44.8	0.1	2
Chroicocephalus maculipennis	Resident	75	45.8	87.6	13.9
Ciconia maguari	Resident	3.6	39.6	0	1.2
Coscoroba coscoroba	Resident	14.3	32.3	38.4	7.3
Cygnus melanocoryphus	Resident	0	9.4	0	2.1
Dendrocygna bicolor	Resident	0	21.9	0	41.9
Dendrocygna viduata	Resident	0	40.6	0	82.3
Egretta thula	Resident	42.9	53.1	31.9	3.2
Fulica leucoptera	Resident	0	22.9	0	30.6
Gallinula chloropus	Resident	0	44.8	0	30.6
Haematopus palliatus	Resident	89.3	6.2	188	0.2
Himantopus mexicanus	Resident	39.3	38.5	11.5	8
Jacana jacana	Resident	0	54.2	0	4.3
Larus dominicanus	Resident	82.1	13.5	228.1	2.4
Mycteria americana	Resident	0	9.4	0	0.5
Netta peposaca	Resident	0	11.5	0	43.5
Nycticorax nycticorax	Resident	0	13.5	0	0.6
Phaetusa simplex	Resident	21.4	3.1	0.6	0.1
Phalacrocorax brasilianus	Resident	46.4	51	10.5	47.6
Phimosus infuscatus	Resident	0	47.9	0	4.1
Phoenicopterus chilensis	Austral	17.9	11.5	52.3	5.5
Platalea ajaja	Resident	0	26	0	2.1
Plegadis chihi	Resident	3.6	74	0.2	98
Pluvialis dominica	Boreal	25	3.1	5.1	0.5
Podiceps major	Resident	0	25	0	0.4

Species	**Life history**	**Frequency**		**Mean**	
		Beach	**Lake**	**Beach**	**Lake**
Podilymbus podiceps	Resident	0	15.6	0	0.3
Rollandia rolland	Resident	0	11.5	0	0.2
Rynchops niger	Resident	46.4	7.3	41.2	12.6
Sterna hirundinacea	Boreal	28.6	0	138.6	0
Sterna hirundo	Boreal	46.4	3.1	110.8	0.1
Sterna sandvicensis	Austral	35.7	0	8.6	0
Sterna trudeaui	Resident	53.6	3.1	20.6	0.2
Sternula superciliaris	Resident	50	13.5	3	0.9
Syrigma sibilatrix	Resident	3.6	7.3	0.1	0.1
Thalasseus maximus	Resident	39.3	1	5.7	0
Tringa flavipes	Boreal	10.7	9.4	2.8	2.2
Tringa melanoleuca	Boreal	21.4	7.3	1.5	0.6
Vanellus chilensis	Resident	14.3	14.6	0.9	2

Article 2: Phylogenetic legacies in the community assembly of waterbirds?

Introduction

The assembly of local communities from species pools is mediated by a combination of neutral and deterministic factors, the latter including environmental filtering and interspecific competition (Keddy & Weiher 2004; Vellend et al. 2014). Species pools themselves are determined by broad-scale, long-term processes such as evolutionary diversification, extinction and dispersal (Ricklefs 1987, 2006; Emerson & Gillespie 2008).

Assessments of local diversity are frequently used to infer broader-scale patterns at the regional level (Vellend et al. 2014). Nevertheless, investigators should consider considering regional and historical (i.e. phylogenetic) context when using local community-focused approaches (Kelt & Brown 2004; Ricklefs 2006). The contingency of observed patterns on the organisms, locales and timescales investigated is especially obfuscatory at the community scale, wedged uncomfortably between species, whose variation is generally manageable, and large-enough expanses of space or time to find a signal amongst the noise (Lawton 1999). It has even been argued that attempting to scale-up from communities to 'ecogeography' (*sensu* Vellend et al. 2014) is conceptually invalid, as local communities are the results, not the drivers, of regional patterns and therefore community diversity could have no predictive power (Ricklefs 2008).

However, it appears that the relationship between community ecology and species evolution is not so straightforward, with dynamic interplay between the two such that a species' community context may drive adaptive change (Johnson & Stinchcombe 2007; Cavender-Bares et al. 2009). Traits and phylogenies therefore provide distinct but complementary information regarding community assembly processes (Emerson & Gillespie 2008). Differences between areas in historical selection pressures result in differences in the strength of correlation between traits and phylogeny. Therefore, investigating both can enhance the ability to compare assembly patterns between habitats (Cadotte, Albert & Walker 2013).

In waterbird communities in coastal Rio Grande do Sul, Brazil, seasonal migration of many species causes the species pool from which communities are assembled to differ distinctly between summer and winter (Nascimento 1995; Bencke 2001). By comparing how communities are assembled in each season, it is possible to investigate which processes are dependent on the species pool, and which processes occur independently of regional biodiversity.

In Chapter 1 I investigated the strength of environmental mediation of waterbird community assembly. I compared taxonomic and functional community composition between two habitats on a gradient known to structure shorebird community taxonomic composition: a harsh, homogeneous habitat – sandy coastal beaches – and a more easily-tolerated, heterogeneous environment, freshwater lakes (Hill *et al.* 1993). Whereas the taxonomic composition of communities depended on the pool of species from which they are drawn, functional composition did not differ between seasons at any niche level, suggesting that trait-environment relationships are important in structuring waterbird communities. Both taxonomic and functional composition varied between habitat types, providing additional evidence of an environmental influence on community assembly: functional composition was richer and more even in the less harsh lake environment. Comparison of communities' functional diversity with null models suggests that while species occurrence is mediated by interspecific competition, the abundance of individuals of each species is related to abiotic conditions (Chapter 1).

Research focusing on the same environmental gradient, but in terrestrial habitats, found increased phylogenetic clustering in the harsher, more homogeneous beach environment (Gianuca et al. 2014), echoing results from aquatic habitats showing clustering functional traits (Chapter 1), which were not investigated in the previous work by Gianuca et al. (*op. cit.*). In this study I use data from the same region to test the hypothesis that phylogenetic clustering occurs in homogeneous, harsh environments, and if so if it can be explained by a purported relation to functional clustering.

Such an evolutionary restriction has been proposed as an explanation for biogeographical patterns observed in migratory shorebirds (Scolopacidae), where habitat specialisation is correlated between seasons (high-Arctic breeding and use of marine habitats in the non-breeding season). This is hypothesised to have had two evolutionary consequences: by severely limiting available habitat, specialisation has lead to historical population bottlenecks resulting in low present-day heterozygosity (Piersma 2003), and reduced investment in immunocompetency (permitted by the low parasite pressure in both Arctic and marine habitats) has rendered species incapable of colonising other habitats (Piersma 2007). Using the data from the present study, I test whether the acute pressure of migration exacerbates the ecological syndrome created by the chronic pressure of habitat-specialism, comparing evidence from both migratory and non-migratory habitat specialists of an association between phylogeny and ecological traits.

In this study, I examine the extent to which species' evolutionary history affects the community assembly process. This examination used traits related to foraging, drawn from three uncorrelated categories, which correspond to three levels of niche variation (Emerson & Gillespie 2008): behaviour (α: varies within habitats; e.g. Durell 2000), diet (β: varies between habitats; e.g. Lourenço et al. 2015) and morphology (γ: varies between regions; e.g. Prater, Marchant & Vuorinen 1977). The extent of intraspecific variation may reflect differing degrees of phylogenetic lability, in which case we would expect to observe present increasing degrees of phylogenetic signal from α to γ.

First, I test whether phylogenetic composition mirrors functional composition, by showing greater clustering in the beach habitat, as would be expected if functional and evolutionary distances correlate. I then look for any association between certain evolutionary lineages and certain habitats, to test for evidence of habitat specialism over evolutionary time. The role of season and environment in determining phylogenetic structure was examined, to see if phylogeny presents a pattern more similar to taxonomy (varying with species pool and environment) or functional ecology (varying with environment only). Finally I looked for phylogenetic signal in foraging traits at three niche levels, at both the metacommunity and species pool levels.

Methods

Community data

These analyses used data from 114 waterbird censuses conducted over 11 years (July 2005 – February 2016) on the Mostardas peninsula of Rio Grande do Sul, Brazil. These census were conducted in either summer (January or February) or winter (July or August), and surveyed all species present in either lake (n=87) or beach (n=27) habitats. A total of 24 sites were visited, though survey effort varied between years with a mean of 11.4 (range 2-24) sites surveyed each year. Data analysed included species' abundances, which varied from 1 to 4400 individuals, to reduce results' sensitivity to rare species. In total, 52 species were included. See Chapter 1 for further explanation.

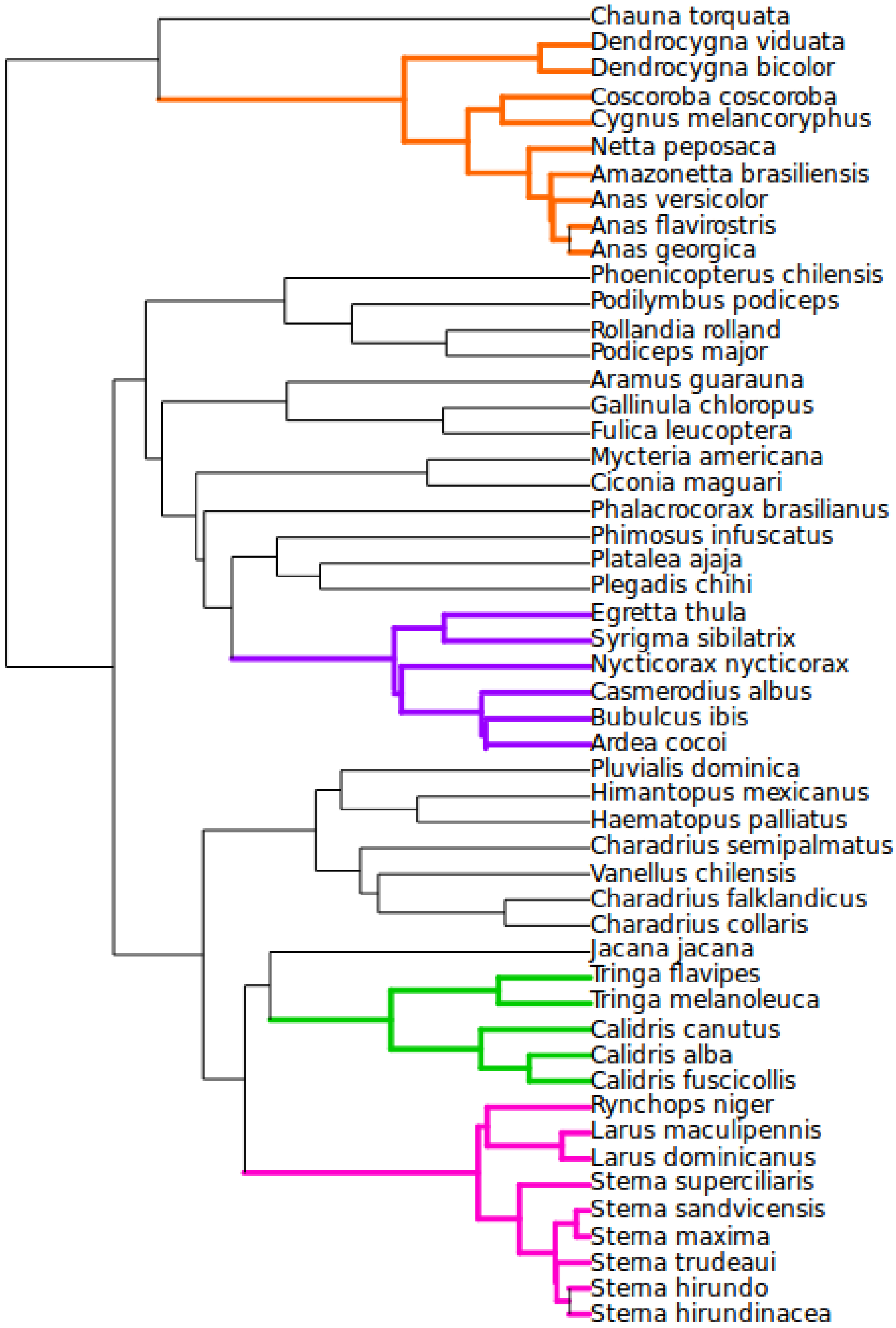

Figure 6: Ultrametric consensus tree of all species recorded in 106 waterbird surveys on the Mostardas peninsula, Rio Grande do Sul. Lineages referred to in the text are coloured as follows: ducks, **orange**; herons, **purple**; Scolopacidae (shorebirds), **green**; terns, gulls and skimmer, **pink**.

Phylogenetic data

Like Gianuca et al. (2014), I downloaded 5000 stage 2 trees with the Hackett et al. (2008) tree as a backbone from BirdTree.org (Jetz *et al.* 2012). Using the **consensus** function in the **ape** package version 3.5 (Paradis, Claude & Strimmer 2004) for R (R Core Team 2016), I generated a 50% majority-rule consensus tree. I then used the **consensus.edges** function from the **phytools** package version 0.5-38 (Revell 2012) to calculate branch lengths using non-negative least squares, resulting in an ultrametric tree (Figure 6).

Alpha diversity

I calculated the pairwise phylogenetic distance between each species, and then calculated NRI using the **ses.mpd** function of the **picante** package version 1.6-2 (Kembel *et al.* 2010). As in the earlier study (Gianuca *et al.* 2014), SES was calculated through comparison with null models generated under the 'richness' algorithm, which randomises species abundances within sites, thus maintaining species richness. The effect of habitat and season, and an interaction between the two, on NRI was tested for statistical significance using ANOVA.

Beta diversity

In order to test the role of seasonal and environmental restrictions on the species pool in structuring communities, I first calculated the Euclidean distance between each community's phylogenetically-weighted species composition (Pillar & Duarte 2010), using the **matrix.p** function in the package **SYNCSA** version 1.3.2 (Debastiani & Pillar 2012).Using this matrix as a response, I tested for effects of habitat, season, and an interaction between habitat and season effects as predictors. This analysis used PERMANOVA as implemented by the function **adonis** in **vegan** 2.3-4 (Oksanen *et al.* 2016).

To explore how phylogenetic structure varies among the communities I used principal coordinates of phylogenetic structure (PCPS) analysis (Duarte 2011), using the **pcps** function of the **PCPS** package version 1.0.3 (Debastiani 2016) with square-root transformed Bray-Curtis distances. I used PERMANOVA to test the predictive value of habitat, season and an interaction between them to explain variation in the first two principal coordinates, using Euclidian distance between sampling units (surveys) as a dissimilarity measure.

It is known that PERMANOVA is affected by differences in dispersion between groups in studies with unbalanced designs (Anderson & Walsh 2013). Due to the large differences in sample size between lake (n=27) and beach (n=87) habitats, I also used PERMDISP2 (Anderson 2006) via the **betadisper** function of **vegan** (Oksanen *et al.* 2016) to analyse multivariate homogeneity of group dispersions, using a permutational F-test of significance.

The relative contribution of species composition and the underlying environmental gradient (habitat type) to community phylogenetic composition was assessed with the function **pcps.sig** from **PCPS**, which first permutes sites across the environmental gradient, holding phylogeny constant, and then permutes phylogenetic distance between species, holding site totals constant (**taxaShuffle**; Kembel et al. 2010). Each permutation process generates an F statistic and thus a significance value reflecting the probability of obtaining the observed result under each null model. Significance is tested via redundancy anaylsis (RDA; Oksanen et al. 2016).

Phylogenetic signal

I tested phylogenetic signal at the metacommunity and species-pool levels using the framework of Pillar & Duarte (2010). At the metacommunity level I tested for trait-convergence assembly processes [TCAP; ρ(**PT**)]. I also tested for phylogenetic signal at the species pool level, the matrix correlation ρ(**BF**). In addition, I tested for evidence of niche conservatism using the partial Pearson correlation ρ(**TE.P**). A non-significant correlation indicates that traits are not correlated with the environment once phylogeny is accounted for: therefore, a combination of significant trait-environment correlation ρ(**PT**) and null ρ(**TE.P**) indicates phylogenetic niche conservatism (Pillar & Duarte 2010). These analyses used the **syncsa** function of **SYNCSA** (Debastiani & Pillar 2012), with its default settings.

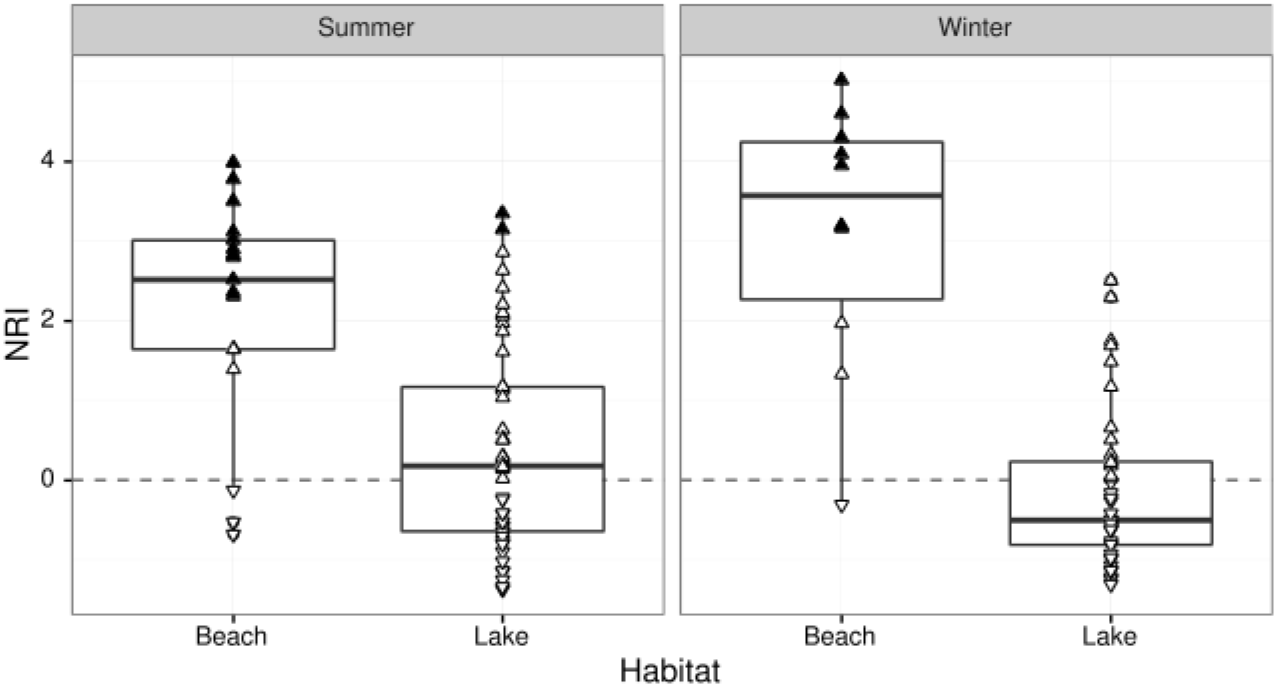

Figure 7: Net relatedness index (NRI) for waterbird communities in coastal habitats of Rio Grande do Sul, Brazil, during the austral summer and winter. Upward-pointing triangles indicate sites with phylogenetic clustering (NRI > 0); downward triangles phylogenetic overdispersion (NRI < 0). Filled shapes indicate that the NRI was significantly different to the null distribution at α = 0.05.Boxplots show median and IQR. Beach communities were significantly more closely related (higher NRI) than lake communities and the discrepancy was significantly greater in winter than in summer.

Results

Alpha diversity

Net relatedness index (NRI) was significantly higher on the beach than in lake habitats (Figure 7). While there was no significant difference between the seasons, the discrepancy between habitats was significantly greater in winter than in summer (Table 13). Only phylogenetic clustering occurred significantly, and the majority of communities expressing clustering were on the beach. Nevertheless most communities did not show a pattern of relatedness that differed significantly from null expectations (Figure 7).

Table 13: ANOVA predicting net relatedness index (NRI) of waterbird communities in Rio Grande do Sul. Model statistics: $F_{3,110}$ = 25.6, p < 0.001; R^2 = 0.41.

Coefficient	**Estimate**	**Standard error**	**t**	**p**
Intercept	2.13	0.30	6.98	<0.001
Habitat: Lake	-1.71	0.35	-4.83	<0.001
Season: Winter	0.96	0.50	1.92	0.057
Lake × Winter	-1.48	0.57	-2.61	0.010

Beta diversity

Communities within the same habitat were phylogenetically more similar to each other than communities in different habitats, although the proportion of variance partitioned to the habitat predictor was only 3.2% (Table 14). There was no significant effect of season, nor was there an interaction between season and habitat.

Table 14: ADONIS partitioning of variance in phylogenetic distance between waterbird communities in Rio Grande do Sul

Variable	**Sums of squares**	**Mean squares**	**R^2**	***p***
Habitat	0.03	0.03	0.03	0.014
Residuals	0.87	0.01	0.97	
Total	0.90		1.00	

The first two principal coordinates explained 43.7% and 18.9% (total 62.5%) of variation collectively. All others represented <7% of the variation in matrix P. The first coordinate was strongly negatively related to the Anseriformes clade, containing ducks (score -0.56) and the screamer (score -0.43), and positively with the Charadriiformes (scores 0.25-0.29). The second principal coordinate was negatively related to the Pelecaneformes lineage, which includes ibises (score -0.23) and herons (-0.22), whereas the strongest positive relations were again with some lineages within the Charadriiformes (Laridae: 0.15; Scolopacidae: 0.11).

Both PCPS varied significantly between habitats ($p < 0.001$) but not between seasons ($p > 0.4$; Tables 15 and 16), with habitat explaining about a third of the variation in phylogenetic composition. In addition, there was significantly greater dispersion between lake sites than between beach sites ($F = 36.6$; $p = 0.001$). Beach sites were mainly tightly clustered, and all were restricted to a small subset of the region occupied by lake sites; nevertheless the two habitat types overlapped almost completely (Figure 8). Site scores on the first two PCPS axes were significantly related to both the environmental gradient ($F = 51.7$; $p = 0.001$) and species composition ($p = 0.018$).

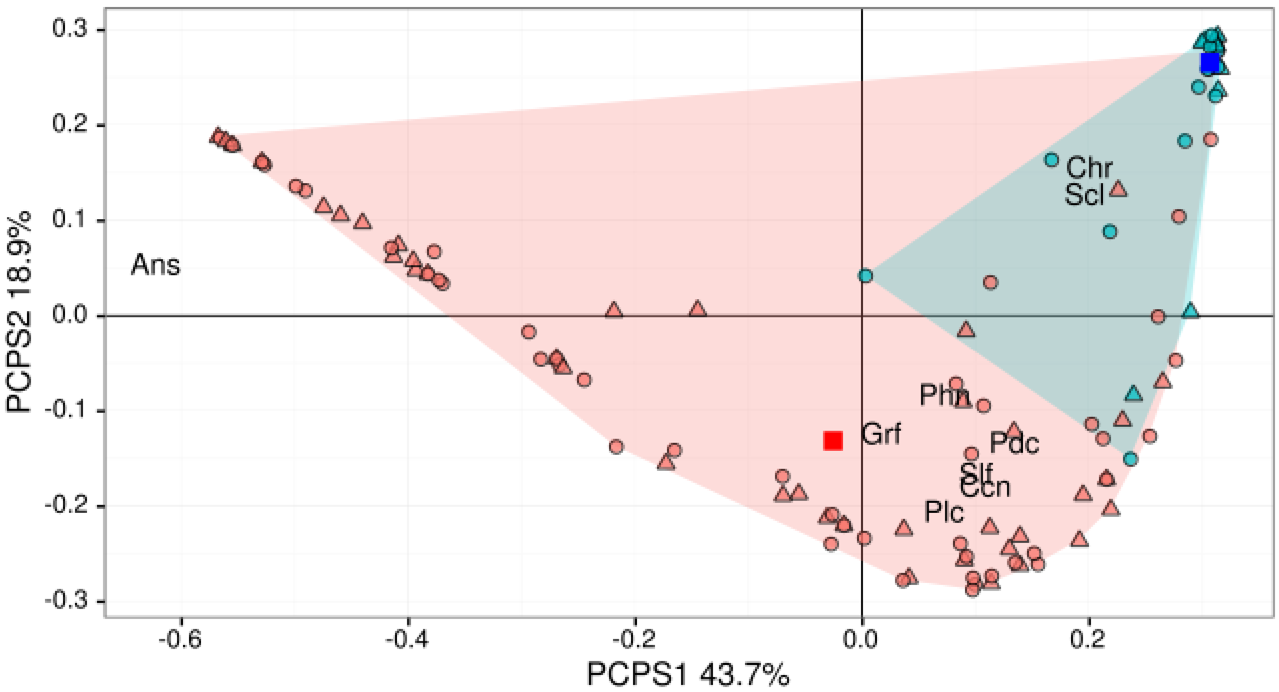

Figure 8: Ordination biplot of the first two axes of a PCPS analysis, showing phylogenetic composition of waterbird communities from lake (red) and beach (blue) habitats, surveyed during summer (circles) or winter (triangles). Squares indicate the centroid of each group. Also shown are convex hulls representing total dispersion of each habitat group. Text represents the location of each clade; abbrevations: Ans = Anseriformes; Ccn = Ciconiiformes; Chr = Charadriiformes; Grf = Gruiformes; Pdc = Podicepiformes; Phn = Phoenicopteriformes; Plc = Pelecaniformes; Scl = Scolopacidae (migratory Charadriiformes); Slf = Suliformes.

Table 15: PERMANOVA predicting seasonal and inter-habitat differences in waterbird communities' scores on the PC1 of a PCPS analysis. Table shows sources of variation, degrees of freedom (df), sequential sums of squares (SS), mean squares (MS), F statistic, partial R² and p-value, based on 999 permutations.

Coefficient	**df**	**SS**	**MS**	**R²**	**F**	**p**
Season	1	0.05	0.05	<0.01	0.9	0.3
Habitat	1	2.99	2.99	0.31	49.8	0.001
Season × Habitat	1	0.02	0.02	<0.01	0.4	0.6
Residuals	110	6.60	0.06	0.68	-	-

Table 16: PERMANOVA predicting seasonal and inter-habitat differences in waterbird communities' scores on the PC2 of a PCPS analysis. Table shows sources of variation, degrees of freedom (df), sequential sums of squares (SS), mean squares (MS), F statistic, partial R² and p-value, based on 999 permutations.

Coefficient	**df**	**SS**	**MS**	**R²**	**F**	**p**
Season	1	0.02	0.02	<0.01	0.6	0.5
Habitat	1	1.88	1.88	0.34	57.8	0.001
Season × Habitat	1	<0.01	<0.01	<0.01	0.1	0.8
Residuals	110	3.58	0.03	0.65	-	-

Testing the PCPS 1 and 2 against null models suggested that both the environmental gradient (beach vs lake habitat) and species composition were important in generating the observed patterns. Randomising sites across the environmental gradient resulted in a very low probability of obtaining the observed pattern (p=0.001). Furthermore, randomising phylogenetic distance between taxa showed a significant influence of species composition on PCPS scores (p=0.018).

Phylogenetic signal

All trait categories, and the ensemble, showed significant phylogenetic signal at the species pool level (Table 17), but none at the metacommunity level. There was no evidence of niche conservatism.

Table 17: Tests for phylogenetic signal and niche conservatism in all waterbird communities and species recorded (*n*=114 censuses), following the framework of (Pillar & Duarte 2010). At the metacommunity level I tested for trait-convergence assembly processes [TCAP:: ρ(**PT**)]. Test results in **bold** indicate that the signal was detected statistically: note that for niche conservatism, the signal is detected *via* a combination of significant ρ(**PT**) and non-significant ρ(**TE.P**) (see text for details). Asterisks indicate that matrix correlations were significant at *p<0.05; **p<0.01; ***p≤0.001.

Signal	All traits	Behaviour	Diet	Morphology
Phylogenetic signal at metacommunity level: ρ(**PT**)	0.30	0.23	0.37	0.06
Phylogenetic signal at species pool level: ρ(**BF**)	**0.32*** **	**0.23*** **	**019*** **	**0.15***
Niche conservatism: ρ(**TE.P**)	0.27*	0.24*	0.35**	-0.02

When only the Scolopacidae were analysed, considerably less phylogenetic signal was detected. No test was significant at the p < 0.05 level (Table 18). Perhaps due to the small number of surveys with sufficient Scolopacidae species detected (n=35 surveys), even strong correlation coefficients such as ρ(**PT**)=0.78 for TCAP in behaviour at the metacommunity level, had p values in the range 0.05 < x < 0.1.

Table 18: Tests for phylogenetic signal and niche conservatism in shorebird of the family Scolopacidae, following the framework of (Pillar & Duarte 2010). All communities containing at least one species were included (*n*=35 censuses). At the metacommunity level I tested for trait-convergence assembly processes [TCAP:: ρ(**PT**)]. Test results in **bold** indicate that the signal was detected statistically: note that for niche conservatism, the signal is detected *via* a combination of significant ρ(**PT**) and non-significant ρ(**TE.P**) (see text for details). Superscript characters indicate that matrix correlations were significant at †p<0.01; *p<0.05; **p<0.01; ***p≤0.001.

Signal	All traits	Behaviour	Diet	Morphology
Phylogenetic signal at metacommunity level: ρ(**PT**)	0.65	$0.78^{\dagger}$	0.58	0.02
Phylogenetic signal at species pool level: ρ(**BF**)	0.41	0.47	0.26	0.15
Niche conservatism: ρ(**TE.P**)	0.02	-0.05	0.08	-0.01

Discussion

Communities on the beach exhibited significant phyogenetic clustering, suggesting that this habitat acted to filter the lineages which could occur there, reinforcing results from terrestrial habitats in this region (Gianuca *et al.* 2014). This demonstrates a lack of convergent evolution amongst these species for the traits necessary to occur in sandy beach habitats, which may reflect that, amongst highly dispersive taxa such as birds, its is almost always more likely for a niche to be filled through dispersion of pre-adapted taxa than by *in-situ* adaptation (Emerson & Gillespie 2008).

There is a detectable overall difference in the phylogenetic composition of beach versus lake habitats, in that similarities between communities' phylogenetic compositions were greater when the communities compared were both from the same habitat. This reinforces the idea that distinct lineages inhabit certain types of habitat only. Unfortunately, the sample size was not sufficient to obtain meaningful results for the extreme-specialist Scolopacidae lineage. While it would be instructive to test the idea that niche conservatism increases with habitat specialism, this study lacked statistical power as few communities had enough Scolopacidae. Instead, a family-wide comparative analysis could be conducted. The rest of this discussion focuses only on the results from the total waterbird community.

Beach communities, which are dominated by Charadriiformes, were located almost exclusively in the quadrant of Figure 8 where both axes had positive loadings from Charadriiformes. Lake communities were more dispersed, exhibiting a general negative correlation between the axes, which suggested that these communities tend to be dominated by either ducks or Pelecaniformes. The relative abundance of these groups likely reflects an environmental gradient related to depth of water: ducks mainly forage while swimming (del Hoyo *et al.* 2016), and therefore can inhabit even the deepest lakes. Conversely, Pelecaniformes forage while standing on the ground, and many also probe into the sediment with their bills (del Hoyo *et al.* 2016), requiring a shallower body of water. Overall, the majority of phylogenetic variation was within lake communities, rather than between the two habitat types, reflecting the greater heterogeneity of lake communities (and the larger number of sites surveyed) compared with the beach. The environmental drivers of phylogenetic community structure warrant further investigation with more detailed environmental data.

The principal components of phylogenetic structure in waterbird communities varied significantly between habitats, indicating consistent associations between certain lineages and habitats, which is perhaps evidence that habitat-specialism has been a conserved trait in those lineages over evolutionary time. However, this signal is sensitive to changes in species composition at the metacommunity level. Examination of the PCPS biplot (Figure 8) leads to the inference that this is because of within-habitat variation in species composition: specifically, that within lake habitats there is variation in the relative dominance of the Anseriformes clade (the most basal node in the species-pool phyloegeny). Research from elsewhere in south Brazil investigated the environmental and anthropogenic drivers that structure waterbird communities at the guild level (Tavares *et al.* 2015). While the Anseriformes in their analysis were sensitive to lagoon size and grazing pressure from cattle, the Ciconiiformes and Pelecaniformes responded most strongly to water depth, salinity and distance from human settlements.

While the environmental gradient caused dissimilarity between communities, there was no significant effect of the seasonal change in species pool on community dissimilarity, with more variation within seasons than between them. This likely reflects that the migratory species, limited to a few clades, represent only a small portion of the total phylogenetic variation present at these sites. In addition, migratory taxa at these sites all have sedentary close relatives (Nascimento 1995; Bencke 2001). The construction of fuzzy sets to generate the matrix of phylogenetically-weighted species composition characterises species by their evolutionary history in common with other species in the pool (*cross-belonging*), as well as by their own unique evolutionary history (*self-belonging*; Duarte et al. 2016), minimizing the seasonal influence that these migratory species have at the community level. Thus, the pattern shown by phylogenetic composition is similar to that shown by functional composition: seasonal changes to the species pool are not detectable due to the presence of species with similar evolutionary histories.

The data in this study found significant phylogenetic signal for all niche levels at the species pool level, showing that certain traits are indeed associated with certain lineages. However, there was no evidence of niche conservatism, and nor did the species-pool signal scale down to a relationship between phylogenetic distance and trait dissimilarity at the metacommunity level. As shown in Chapter 1, there is a strong relationship between traits and habitat, and herein the trait-environment relationship remained strong when phylogeny was accounted for (Table 17).

Many previous published studies have found varying strengths of phylogenetic signal when considering different kinds of traits. A previous review from multiple taxa found a hierarchy in the strength of phylogenetic signal between categories of traits, with morphology showing the strongest signal, behaviour the most labile, and physiological and ecological traits showing an intermediate level of phylogenetic signal (Blomberg, Garland & Ives 2003). Similarly, in birds, phylogeny explained a large amount of variation in diet and morphology, but very little variation in behavioural traits. Traits tended to be more similar within families, but differed significantly between orders (Böhning-Gaese & Oberrath 1999). The general pattern of morphological traits showing stronger phylogenetic signal is supported by numerous studies from diverse taxa (Kamilar & Cooper 2013), but the result was not replicated in this study, where all trait categories showed signal at the species pool level, but morphology had the weakest correlation.

Instead, these results point to another way in which scale is crucial for understanding ecological mechanisms (Swenson *et al.* 2006; Münkemüller *et al.* 2014; Li *et al.* 2016). At the species pool level, traits are manifestations of evolutionary history and determine which species can inhabit which habitats. However, at the level of metacommunities, traits are related to the environment independently of phylogeny. This indicates a process of niche-filling in community assembly (Fukami 2015), wherein niches are filled by species according to their traits and co-occurrence is therefore limited by similarity (MacArthur & Levins 1967). Where closely-related species have similar traits we would expect them *not* to co-occur (Silvertown *et al.* 2006; Fukami 2015), breaking the regional-level correlation between traits and environment (but see Godoy, Kraft & Levine 2014). Furthermore, results from a similar bird community showed that while environmental effects were important in community taxonomic composition at the regional scale, local dynamics were dominated by neutral/stochastic processes and lacked a clear environmental signal (Gianuca *et al.* 2013). Site occupancy by one of several ecological equivalent close relatives, selected from within a pre-adapted lineage (Emerson & Gillespie 2008), would explain the observed pattern. Alternatively, given the broad taxonomic scale of this study, it may be that the phylogenetic signals detected refer to conserved traits, which are important at broad scales, but derived traits are more important for determining local coexistence.

The choice of species that comprise the ‘regional pool’ also affects the results of analyses, with broader geographic scales tending to show increased phylogenetic clustering (Swenson *et al.* 2006). This study used only species recorded in the censuses used for the analysis – the smallest possible resolution – and still observed positive or null NRI values (indicating a tendency towards clustering). It is therefore unlikely that the ultimately subjective choice of species pool (Swenson *et al.* 2006; Münkemüller *et al.* 2014) affected our results.

It should also be borne in mind that no genetic data was collected for this study, which instead relied on previous work by Jetz et al. (2012). However, genetic data was not available for one species in this study (*Fulica leucoptera*), which therefore had to have its position in the tree estimated using stochastic simulations of birth-death processes to estimate clade diversification rates (Stadler 2011). Such neutral assumptions ignore trait values, and therefore when traits are phylogenetically conserved or overdispersed can lead to clade positioning that varies greatly from the most likely placement were trait data included in the analysis. Rabosky (2015) demonstrates that this effect can lead to biased results, with both continuous and discrete traits, and that bias increases with decreasing sample coverage. Therefore, to have confidence in these results, the analysis should be repeated including only species for which genetic data was included in

Jetz et al. (2012), assuming that sample coverage is unbiased with respect to phylogeny (Rabosky 2015). Nevertheless, given that only one species is affected in this manner, it seems unlikely that a re-analysis would have radically different results.

Conclusion

Waterbirds exhibit clear functional groupings which concord with evolutionary clades (e.g. Tavares et al. 2015). However, waterbird communities are assembled by trait-environment associations independently of phylogeny, despite showing strong phylogenetic signal, of all niche levels, at the species-pool scale. Waterbird community assembly shows little evidence of being contingent on historical processes, as species can colonise suitable sites rapidly, by flying, before other lineages have time for adaptive evolution. That there was also little evidence of sensitivity to changes to the regional pool suggests that this situation of colonisation taking precedence over adaptation may have been persistent during recent evolutionary time (Emerson & Gillespie 2008). These results stand in contrast to many showing contingency in vegetation communities, and highlight the importance of testing ecological theories in as diverse a selection of organisms as possible.

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Final considerations

This study found evidence that community assembly in waterbirds is trait-based, with environmental conditions determining the suite of species which can inhabit a given locale according to their diet and their morphological and behavioural strategies for obtaining food. The habitats studied in this work were beaches, a somewhat homogeneous habitat with strong environmental limitations, and coastal lakes and lagoons with a wide variety of ecologies. We found that the beach habitat contains a more clustered set of traits than the lagoons, and a more restricted set of evolutionary lineages.

Certain traits are associated with certain lineages; certain lineages with certain habitats; and certain habitats with certain traits. An association between phylogeny and the environment can arise from two mechanisms (Pillar & Duarte 2010). The environment (E) may select a set of ecological traits (T), resulting in a phylogenetic signal (P) due to phenotypic similarities between species with shared ancestry. In such a situation, where the traits involved are phylogenetically conserved, ancestry is partly responsible for the relationship between environment and traits, acting as a middle-man in the chain of command: E → P → T. However, if the traits selected by the environment are more labile, the relationship between the environment and traits may not depend on phylogeny; equally, a relationship between the environment and phylogeny may be mediated by traits other than those measured by investigators. In this case traits would have two independent relationships, one with the environment and one with phylogeny, without environment and phylogeny interacting directly: E → T ← P.

The latter pathway is supported by these analyses. Most traits had an association with one habitat or the other, with functionally similar communities being assembled in similar environments even when drawn from distinct species pools. Whereas the environment explained a large proportion of variation in functional ecology, phylogenetic distance was largely unexplained by habitat. Furthermore there was no correlation between communities' functional and phylogenetic dissimilarities, while the trait-environment correlation was supported, albeit modestly, after controlling for phylogenetic variation.

Nevertheless, there are some clear instances where phylogeny appears to limit habitat colonisation. The most basal split in these communities was between the Anseriformes (ducks, geese and swans), and all others. While pelagic piscivorous ducks have evolved, they are chiefly a boreal radiation (Kear 2005), and the Brazilian representative of the clade is one of the most threatened waterfowl in the world, with a wild population of around 250 (Birdlife International 2016).

The remainder, mainly terrestrial or dabbing herbivores, would have to change simultaneously their diet and behaviour in order to utilise beach habitats; the majority of other species here eat fish or invertebrates, and feed by diving or probing in sediment, which could be applied to either habitat. Indeed, many species are recorded in both, but with differing degrees of frequency. Changes to environmental conditions or competitive release could therefore alter habitat use more rapidly in the non-Anseriformes lineages in this study. This likely explains why the Anseriformes drove the main principal component of phylogenetic structure, and their absence from the beach probably explains the greater phylogenetic clustering observed there.

It is also possible that traits unmeasured in this work contribute to a species' suitability for occurring in a given assemblage. For example, specialised glands for salt excretion facilitate occupancy of marine (or otherwise saline) habitats, and interspecific variation in investment in their maintenance is accordingly much higher in marine than nonmarine species, and also varies according to dietary salt intake (Gutiérrez et al. 2012). Perhaps underappreciated, in addition, are the challenges of foraging in the strong, unpredictable winds that characterise marine habitats in this region. Controlling aerial locomotion - for example for foraging – in a constantly changing medium requires a raft of behavioural, morphological and sensory adaptations (Shepard, Ross & Portugal 2016), which were not considered in this study.

It should also be borne in mind that the survey data on which these analyses were based depend upon detection and correct identification of species. Our estimates of functional and phylogenetic composition depend on correct characterisation of the taxonomic composition, which cannot be taken for granted (Cao, Williams & Larsen 2002). However, there are two important caveats which limit confidence in this assumption.

One is that detectability varies between habitats and sites (e.g. Boulinier et al. 1998). It is likely, for example, that more individuals go undetected in the densely-vegetated lake habitats than on the beach, where observers typically have an unobstructed view of birds. It may therefore be that taxonomic (and therefore other forms of) richness was underestimated in lake habitats, so the relationships detected in this study may in fact be more pronounced. On the other hand, imperfect detection is know to bias estimates of betadiversity upwards (Kéry & Schmid 2004).

Detection may also vary with levels of observer experience (Boulinier et al. 1998). Observer identity varied between years, but was not accounted for in these analyses. Finally, survey coverage was not randomised between sites, but rather focussed on the Parque Nacional da Lagoa do Peixe protected area. The analysis of taxonomic composition *per se* may not be strongly affected, as the dissimilarity measure used was designed to correctly classify sites despite variation in sampling intensity (Cao, Williams & Bark 1997).

If detectability is non-random with respect to ecology or phylogeny, however, the relationships observed may also be biased. Rails (Gruiformes: Rallidae), for example, are often difficult to detect (Taylor 1998). Studies from forest habitats have observed a tendency of bird counts to undersample understorey species (Whitman, Hagan & Brokaw 1997; Wang & Finch 2002) and to have biases with respect to taxonomic families (Martin, Blackburn & Simcox 2010), and therefore, by inference, to phylogeny. This is especially a problem with abundance, as opposed to presence-absence, records (Blake & Loiselle 2001). In general, aerial or openwater species seem more likely to be detected than those that forage amongst vegetation, for example, though detectability issues are less well studied in aquatic habitats than forests. Therefore, some of the environmental gradient observed, particularly within lake habitats, may in fact reflect detection differences caused by vegetation structure; this is, however, a thorny issue as vegetation structure also affects waterbird communities (Tavares et al. 2015). The issue of detection is important, though, as rare community members can have unique and important roles in ecosystem functioning (Lyons et al. 2005).

Two approaches are suggested for testing sample representativeness for which the data used herein would be suitable. One is autosimilarity: using data from repeat visits to the same site one can compare the similarity between the communities as assessed by each sampling instance (Cao, Williams & Larsen 2002). Sites with lower autosimilarity, typically those with higher taxon-richness, can then be sampled further. These data would also be amenable to traditional occupancy-modelling approaches that fit two parameters to the data, one for occupancy and one for detection-probability. The advantage of this latter approach is that covariates can be fit to test hypotheses regarding influences on detectability (Bailey, Mackenzie & Nichols 2014): e.g., whether or not it is random with respect to traits and ancestry.

Future Directions

Scale-dependency of conclusions is a common finding in ecology, and community assembly is no exception (Swenson et al. 2006; Münkemüller et al. 2014; Li et al. 2016). In terms of spatial scale, this study assumed that all birds were free to disperse across the entire study area, and certainly within habitats. This seems a reasonable assumption (e.g. Quaintenne et al. 2011). On the other hand, the entire waterbird community was included, covering many distantly-related clades and trophic levels. Equivalent data, gathered for the same CNAA surveys, is available for the whole continent of South America with data going back 25 years. A larger-scale database would enable the testing of ideas from this dissertation in new scenarios.

For example, migratory shorebirds have a very concentrated spatial distribution in South America (Myers, Maron & Sallaberry 1985; Baker et al. 1997). This study found evidence that communities were structured by environmental factors, resulting in functional convergence, rather than by abiotic interactions driving divergence. It would be valuable to know, for intellectual and conservation reasons, whether this pattern holds at a flyway scale. With data on entire communities one could test the hypothesis that the largest populations are found where environmental conditions are most suitable, versus another model explaining species' distributions in terms of functional uniqueness or overlap with the rest of the community. More data would also permit tests of the ecological roles of migrants versus resident species, which were hampered in this analysis by small sample size.

Shorebirds are a well-studied group of migratory birds. Recent work on the evolutionary origins and macroecology of migration have suggested broadly-applicable rules (Somveille, Rodrigues & Manica 2015). The challenge of distinguishing adaptations to breeding and non-breeding conditions is very important. By combining traits related to foraging and breeding with phylogeny (see Cadotte, Albert & Walker 2013) and a knowledge of distributions in both seasons, a large scale approach could test the hypothesis that it is sympatric *breeding* specifically, not just co-occurrence (Lovette & Hochachka 2006), that drives within-clade diversification. Close relatives that co-occur in non-breeding areas do not face the same need for reproductive isolation, and I would therefore expect non-breeding assemblages to be environmentally driven, and show trait convergence, while co-occurrence on breeding grounds would show close relatives avoiding one another or diverging ecologically.

Implications for conservation

These results have implications for the choice or design of reserves for waterbirds in general, and non-breeding migrants in particular. Conservation projects targeting particular species should ensure that as many as possible of that species' ecological functions are supported by the environment sufficiently to bear the target population size. Where competitive exclusion by other species is a threat, enhancing environmental characteristics that exploit any functional differences between the competitors may be of benefit. Alternatively, for projects aiming to enhance waterbird diversity in general, environmental conditions that support as wide a diversity of ecological functions as possible should be sought.

In addition, the detection of habitat differences in functional diversity suggest that waterbird survey data could be used to monitor the success of wetland restoration projects *via* a functional framework. Whereas differences in abundances of certain species between sites may lack a clear ecological interpretation, comparing functional diversity of communities between natural and restored/created sites may give a clearer indication of the project's success. While an individual species may depend on multiple criteria, analysing the functional composition of entire communities makes it possible to detect trends in individual functions across all species, as seen in this study. If a given function is found to be unsupported by a restored site, targeted planning can be undertaken to address what is lacking. For example, a dearth of probing species compared with surface-feeders would suggest a lack of benthic infauna compared with epifauna (McLusky & Elliott 2004). This approach has already been used to determine recovery of biogeochemical functioning and biological (though mainly vegetation) structure (Moreno-Mateos et al. 2012), finding that even 100 years from establishment restored wetlands are functionally distinct from reference sites. However, where the goal of restoration is directly the offsetting of threats to biodiversity from habitat loss, testing effects on the target biota directly may be more appropriate.

Conclusion

The results of this study represent progress in understanding of community assembly. Southern-Hemisphere bird assemblages containing seasonal migrants provide a valuable natural experiment to investigate species-pool effects on community compositions. While we found that the influence of differing species pools was statistically detectable using these methods, season explained little variation in taxonomic composition, and none in overall functional or phylogenetic composition. Although similar traits were often found in close relatives, communities themselves did not show evidence of phylogenetic conservatism. Instead, communities were assembled via a niche-based process, with environmental homogeneity and harshness predicting the presence of fewer functions, and greater functional and phylogenetic clustering.

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