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ANÁLISE DE GRADIENTES ECOLÓGICOS: DISTRIBUIÇÃO ESPACIAL E REGRAS DE MONTAGEM DAS COMUNIDADES DE AVES NO LITORAL SUL DO BRASIL

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RESUMO

Gradientes ecológicos são cenários ideais para avaliar como espécies interagem e respondem às alterações nas características ambientais. A teoria de nicho postula que gradientes ecológicos afetam a distribuição das espécies e até mesmo de linhagens evolutivas, pois a medida que se alternam as condições ambientais, diferentes espécies podem encontrar as condições adequadas para sua manutenção, crescimento e reprodução. Assim, havendo conservação filogenética de nicho, linhagens de espécies tendem a ser restritas às manchas de habitat adequado. A teoria neutra, por outro lado, pressupõe que as espécies são ecologicamente equivalentes, e que diferenças na composição de espécies resultam de eventos estocásticos associados a capacidade dispersora das espécies. Assim, é esperada autocorrelação espacial na composição de espécies, independentemente das características ambientais. Para avaliar o papel de processos neutros ou relacionados ao nicho sobre a distribuição das espécies e linhagens evolutivas de aves no sul do Brasil, avaliou-se a abundância das espécies ao longo de um gradiente ecológico formado por praia, dunas e campos. Em cada habitat foram alocadas 19 parcelas, totalizando 57, as quais foram visitadas uma vez por estação do ano. Nas mesmas parcelas foram avaliadas as características ambientais. Utilizou-se as coordenadas geográficas das parcelas para criarr descritores espaciais. Ao todo, foram registradas 102 espécies de aves ao longo do ano. No primeiro capítulo ficou claro que há uma grande variação na composição de espécies de aves ao longo do gradiente, apesar da justaposição dos habitats. Variação temporal na composição de espécies ocorreu tanto devido às alterações abióticas ao longo do ano como ao intercâmbio de espécies migratórias. No segundo capítulo foi demonstrada a importância das feições ambientais estruturando a diversidade beta, o que corrobora a importância de processos relacionados ao nicho sobre a composição de espécies. Os processos neutros são de menor importância na composição de espécies de aves na escala considerada. No terceiro capítulo, ao incluir as relações filogenéticas das espécies nas análises de comunidades ecológicas, demonstrou-se que grupos de espécies evolutivamente relacionadas exploram habitats com características ambientais semelhantes. Além disso, agrupamento filogenético foi observado nos hábitats com características ambientais mais estressantes.

Palavras-chave: Diversidade-beta, teoria neutra, estrutura filogenética.

ABSTRACT

Ecological gradients represent ideal scenarios to assess how interacting species respond to environmental changes. According to niche theory, species and lineages distributions are affected by ecological gradients because environmental changes allow different species to thrive under distinct ecological conditions. Thus, if phylogenetic niche conservatism is a prevalent pattern, species lineages tend to be restricted to adequate environmental habitat patches. Neutral theory, on the other hand, assumes ecological equivalence among species, and postulates that differences in species composition are caused by sthocastic events in combination with differences in dispersal rates among species. Thus, spatial autocorrelation in species composition emerges, irrespective of environmental quality. In order to assess the importance of neutral and niche related process affecting avian species and lineages distribution in southern Brazil, we gathered species abundance data across a coastal gradient formed by sandy beach, dunes and grasslands. We allocated 19 samples in each habitat, in a total of 57, which were visited once per season. Inside each sample we also assessed environmental variables. Geographic coordinates of the samples were used to create spatial descriptors. Considering all habitats and seasons, we recorded 102 avian species. In the first chapter we demonstrated that, although the coastal habitats are justaposed, there is a great turnover in species composition across the ecological gradient. High temporal variation in species composition occurred due to environmental changes along the year as well as interchanges of migratory species. In the second chapter we demonstrated the prevalence of niche related processes affecting beta-diversity, since environmental features respond to high variation in species composition data. Neutral factors presented a minor impact in avian species composition in the scale considered. In the third chapter, by the inclusion of species phylogeny in the analysis of community ecology, we demonstrated that evolutionary closely related species explored habitats with similar environmental conditions. In addition, habitats with stressing environmental conditions led to phylogenetic clustering in relation to phylogenetic poll.

Keywords: Beta-diversity, neutral theory, phylogenetic structure.

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APRESENTAÇÃO

Os estudos em ecologia de comunidades buscam descrever os padrões de diversidade, abundância e distribuição dos organismos na natureza, bem como entender os mecanismos que permitem que diferentes espécies co-ocorram em um determinado local ou região. A teoria ecológica prevê uma série de processos aninhados, os quais atuam como filtros sobre a organização e estruturação das comunidades em diferentes escalas espaciais e temporais. Dentre os processos que ocorrem em amplas escalas de espaço e tempo estão a especiação e a extinção, os quais atuam como um balanço para determinar o número de espécies em diferentes regiões biogeográficas do planeta. Quando a dispersão não é limitada, espécies são potencialmente capazes de colonizar novas áreas distantes do seu centro de origem. No entanto, em escalas menores, o que vai determinar a permanência de uma espécie na comunidade são as condições abióticas do local e as interações com as espécies que já estavam presentes naquela comunidade.

Definir limites para o estudo de comunidades ecológicas é uma decisão arbitrária, a qual depende dos interesses do pesquisador e do tipo de organismos alvo, pois na maioria das situações naturais ocorre uma substituição lenta e gradual de organismos ao longo de gradientes ecológicos, os quais se caracterizam pela ausência de barreiras ou limites bem definidos. Portanto, gradientes ecológicos são um cenário adequado para avaliar como diferentes espécies interagem e respondem às alterações nas características ambientais. A teoria de gradientes ecológicos postula que as espécies atingem um pico de abundância no local onde as condições ambientais são ótimas para sua manutenção, crescimento e reprodução. Assim, a medida que a distância deste local adequado aumenta e as condições ambientais se alternam, estas espécies diminuem em números, sendo substituídas por outras mais aptas a ocorrer nesta nova situação.

Uma propriedade bastante conhecida das variáveis ecológicas é a auto-correlação espacial, que pode ser definida como a probabilidade de um conjunto de amostras vizinhas serem mais semelhantes em suas características ambientais do que em relação às amostras mais distantes. Assim, uma vez que as espécies respondem às características físico-químicas do ambiente, há uma probabilidade maior de que a composição de espécies seja similar entre amostras situadas próximas. Se as amostras são distribuídas espacialmente ao longo de um gradiente ecológico, é esperado que tanto as variáveis ambientais como a distribuição das espécies sejam espacialmente estruturadas. No entanto, em situações onde duas amostras espacialmente próximas possuem características ambientais distintas, por exemplo devido à descontinuidades ecológicas, é esperado que a composição de espécies também seja diferente. Da mesma forma, duas amostras colocadas muito distantes entre si, mas que compartilhem semelhantes condições ambientais, podem ainda apresentar diferenças na composição de espécies caso haja limitações à dispersão dos taxa. Assim, é importante analisar os dados ecológicos de forma a remover os efeitos conflitantes capazes de gerar confusão nos resultados, como é o caso dos efeitos espaciais e ambientais sobre a distribuição das espécies.

Quando se analisa um gradiente estrutural de complexidade de habitats, como é o caso do presente estudo, é previsível que a porção estruturalmente mais heterogênea possua maior número de espécies, pois estas são capazes de explorar diferentes recursos de maneiras variadas. Por outro lado, no ambiente mais homogêneo as espécies tendem a ser mais semelhantes em sua morfologia e estratégias de forrageio, pois costumam competir por uma mesma base de recursos. No entanto, a co-ocorrência de espécies em um ecossistema reflete tanto as condições ambientais atuais e a disponibilidade dos recursos presentes, como também suas histórias evolutivas, que permitiram que cada espécie evoluísse atributos morfológicos, fisiológicos e comportamentais para sobreviver em determinadas situações. Restrições filogenéticas impedem o surgimento de novidades morfológicas em grupos de espécies aparentadas, o que resulta na similaridade fenotípica de espécies proximamente relacionadas. Por sua vez, as características fenotípicas restringem o tipo de ambientes que as espécies podem explorar. Assim, incluir a filogenia das espécies nas análises de gradientes ecológicos permite avaliar não apenas as relações das espécies com seu ambiente mas também rastrear seu passado evolutivo para entender melhor como as comunidades se organizam. Por exemplo, utilizar índices de diversidade beta taxonômico para comparar comunidades de aves de praias arenosas do litoral da África do Sul e do sul do Brasil poderá resultar em um elevado turnover na composição de espécies. No entanto, comparar a diversidade beta filogenética entre estas comunidades pode resultar em grande similaridade, pois a maioria das espécies pertence à mesma ordem, família ou gênero. No entanto, comunidades situadas espacialmente próximas, como em campos litorâneos e praias arenosas adjacentes, podem apresentar grande diversidade beta filogenética, desde que a evolução de atributos funcionais das espécies de aves de praia e campos tenha ocorrido entre linhagens distantes.

O objetivo maior deste trabalho é descrever os padrões e entender os processos que promovem a diversidade das comunidades de aves ao longo de um gradiente ecológico formado por diferentes ecossistemas costeiros no sul do Brasil. No primeiro capítulo, objetivou-se especificamente relacionar a abundância, a riqueza e a composição de espécies com um gradiente de complexidade de habitats formado por campos litorâneos, dunas costeiras e praia arenosa no sul do Brasil. Foi avaliado, ainda neste capítulo, se a mudança abrupta nas características físicas entre os habitats e entre estações climáticas resulta em elevada variabilidade espaço-temporal das comunidades de aves. Se este é o caso, um conjunto de espécies deve ser responsável por estes padrões. Procurou-se então apontar quais espécies são mais associadas a cada um dos ecossistemas em diferentes estações climáticas. No segundo capítulo o principal objetivo foi testar diferentes modelos de metacomunidades, separando os efeitos das características ambientais e do espaço sobre a estruturação das comunidades de aves. Por fim, no capítulo três objetivou-se avaliar como as relações evolutivas das espécies de aves podem limitar os tipos de ambientes utilizados por estas.

No capítulo um ficou demonstrado que os ecossistemas de dunas costeiras e campos litorâneos possuem maior riqueza e equitabilidade de aves ao longo do ano se comparado à praia arenosa, o que sugere a importância da complexidade do habitat sobre a organização destas comunidades. Além disso, foi reportada uma grande variação na composição de espécies entre os ecossistemas, apesar de serem espacialmente justapostos. Isso demonstra que a variação nas características ambientais ao longo do gradiente costeiro possui papel preponderante na determinação de quais espécies de aves podem ocorrer em cada habitat. Além disso, houve importante variação na composição de espécies em cada ecossistema ao longo do ano, o que se deve tanto às alterações nas condições ambientais provocadas pelos ciclos sazonais como também à chegada de espécies migratórias de inverno e verão, conforme foi possível apontar por meio de uma análise de espécies indicadoras.

No capítulo dois foi demonstrado o papel preponderante das características ambientais na determinação da distribuição das espécies de aves, corroborando a perspectiva de “species sorting”, como processo estruturador da metacommunidade estudada. Além disso, foi possível demonstrar que boa parte da variação na composição das espécies de aves e das características ambientais são espacialmente estruturadas ao longo do gradiente costeiro. A distância entre as amostras por si própria, pouco afetou a variação na composição de espécies, enfraquecendo a perspectiva da importância de processos neutros sobre a organização de comunidades de aves em uma região subtropical do Brasil.

Pela inclusão das relações filogenéticas entre as espécies de aves nas análises, foi possível demonstrar, no capítulo três, que a praia arenosa, ou seja, a porção de hábitat com condições ambientais mais severas devido ao spray salino, maior exposição ao vento e ações de marés, possui espécies filogeneticamente mais próximas entre si do que o esperado ao acaso. Este resultado corrobora a hipótese de “phylogenetic clustering” ao longo de gradientes ambientais limitantes, mas estudos observacionais semelhantes tem apontado resultados conflitantes. Além disso, foi demonstrado no capítulo 3 o quanto espécies com histórias evolutivas semelhantes são limitadas a explorar ambientes com características ambientais semelhantes, provavelmente devido a conservação filogenética de nichos.

CAPÍTULO 1

Este manuscrito segue as normas de formatação da revista ornitológica *The Condor*

AVIAN COMMUNITIES IN COASTAL ECOSYSTEMS

SPATIAL AND TEMPORAL VARIABILITY OF AVIAN COMMUNITIES ALONG A GRADIENT OF COASTAL ECOSYSTEMS IN SOUTHERN BRAZIL

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Abstract. Beta-diversity was defined as the variation in species composition among sites within a region of interest. Abiotic conditions and species interactions are the main drivers of local communities assembly. A turnover in species composition is expected to occur as environmental conditions changes across ecological gradients. Birds are an ideal group to assess ecological issues, because they are very mobile organisms and avian communities are comprised by many potentially interacting species. In addition, many bird species are sensitive to environmental changes. We present information about avian communities structure across a gradient of coastal ecosystems in southern Brazil (sandy beach, coastal dunes and grasslands). Specifically, we assessed species richness and evenness in these structurally distinct, juxtaposed coastal habitats. We also evaluated the magnitude of spatial and temporal variation in species composition among habitats and climatic seasons, highlighting the indicator species in each habitat type during each season. We found higher species richness in grasslands and dunes than in sandy beach. Evenness values were higher in dunes. The more contrasting species composition occurred between sandy beach and grasslands (the endpoints of the gradient). Temporal variation was strong between seasons. These founds suggest that species richness was positively related to habitat complexity and negatively related to environmental stressing conditions. Abiotic instability, food limitation and habitat heterogeneity likely reflected higher evenness values on dunes. Our results demonstrated that abrupt environmental changes across the sea distance gradient causes higher species turnover and each habitat type must be preserved to maintain the regional species diversity.

Keywords. Beta-diversity, dunes, grassland birds, sandy beach, shorebirds.

Variabilidad Espacial y Temporal de las Comunidades de Aves a lo Largo de un Gradiente de Ecosistemas Costeros en el Sur de Brasil

Resumen. La diversidad-beta ha sido definida como la variación en la composición de especies entre sitios dentro de una región de interés. Condiciones abióticas e interacciones de especies son los conductores de una asamblea de comunidades locales. Un reemplazo en la composición de especies es esperada en la medida que las condiciones ambientales cambian a lo largo de gradientes ecológicos. Las aves son un grupo ideal para evaluar tópicos ecológicos, porque son organismos muy móbiles y porque las comunidades de aves tienen muchas especies en potencial interacción. Además, muchas especies de aves son sensibles a los cambios en el ambiente. Presentamos informaciones sobre la estructura de la comunidad de aves a lo largo de un gradiente de ecosistemas costeros en el sur de Brasil (playa arenosa, dunas costeras y campos). Evaluamos la riqueza y equitabilidad de especies en estos hábitats costeros contíguos y estructuralmente distintos. También evaluamos la magnitud de la variación espacial y temporal en la composición de especies entre los hábitats y las estaciones climáticas, destacando las especies indicadoras en cada tipo de hábitat durante cada estación. Encontramos una riqueza más alta de especies en campos y dunas que en la playa arenosa. Los valores de equitabilidad fueron más altos en las dunas. La composición más contrastante de especies ocurrió entre playa arenosa y campos (puntos extremos del gradiente). La variación temporal fue fuerte entre las estaciones. Estos resultados sugeren que la riqueza de especies es positivamente relacionada con la complexidad del hábitat y negativamente relacionada con las condiciones ambientales estresantes. La inestabilidad abiótica, limitación de alimentos y heterogeneidad del hábitat posiblemente reflejan los mayores valores de equitabilidad en las dunas. Los resultados demostraron que los cambios ambientales abruptos a lo largo del gradiente de distancia del mar, originan un alto reemplazo de especies y que cada tipo de hábitat tiene que ser preservado para mantener la diversidad de especies regional.

Palabras clave. Aves costeras, aves de pastizales, diversidad-beta, dunas, playas arenosas.

INTRODUCTION

Beta-diversity was first defined by Whittaker (1960) as the variation in species identities among sites within a region of interest, and since then, there was an increase in the number of publications referring to this concept, especially in the last two decades (Tuomisto 2010a,b, Anderson et al. 2011). In fact, understanding which processes makes species composition to vary across space and time is a central question in community ecology (Vellend 2010). Ecological theory suggests a series of hierarchical or nested processes, acting on communities' assembly, as rules that determine species composition in different scales (Weiher and Keddy 1999, Holyoak et al. 2005). The "species sorting hypothesis" is based on theories of community variation across environmental gradients (Whittaker 1962), and postulate that, at small spatial scales, abiotic conditions and species interactions (i.e., competition, predation, mutualism) represent the main drivers of community composition (Leibold et al. 2004). According to this perspective, habitats serve as "filters" that select from a regional species poll a subset of them containing the adequate traits that maximize their fitness, which results in the local extinction of the less adapted ones (Weiher and Keddy 1999). Temporal variability in the abiotic environment can act as a selective force on species composition changes, ensuring different species to thrive in each system at each point in time (Loreau et al. 2003). Dispersal allows species to track environmental changes across ecological gradients, and have the role of potentially bring together some species that otherwise would not interact (Leibold et al. 2004).

Currently, it is well established that there are not well-defined boundaries delimitating natural communities (Leibold et al. 2004) and therefore a gradual substitution of life forms across environmental gradients is expected (Whittaker 1962). Species tend to exhibit a peak of abundance where optimum conditions occur and abundance decays as environmental conditions change, resulting in a turnover of species composition (Qian and Ricklefs 2007). Thus, a start point to assess how habitat features affect community structure is to consider ecological gradients as sampling scenarios, and this is the context of our study.

Together with the term beta-diversity, Whittaker (1960) also introduced the concept of alpha and gamma diversity. Both are diversity measures, but the former represents the species diversity per virtual sampling units (i.e., within sites or within habitat diversity) and the latter is a measure of the total, regional or landscape scale species diversity. Although the problem of arbitrariness in scales definition still remains, because of the absence of well-defined boundaries in ecological communities, a common pattern of alpha and gamma diversity is their positive relationship with habitat complexity (MacArthur and MacArthur 1961, Roth 1976, Tews et al. 2004). The "habitat heterogeneity hypothesis" assumes that structurally complex habitats provide different kinds of food resources, shelter from predators and nest sites allowing different ways of resources exploitation and higher possibility of predator's avoidance, leading to an increase in species diversity (MacArthur and Wilson 1967, Tews et al. 2004).

Considering a hypothetical ecological gradient, higher values of alpha diversity (i.e., within habitat diversity) are expected to occur on the most heterogeneous habitat embedded in it. On the other hand, all the extent of the gradient, including distinct habitat patches, provides environmental heterogeneity on a regional scale, which may inflate gamma diversity in comparison with another area similar in size but most structurally homogeneous. Actually, alpha and beta diversity are distinct components of the total (gamma) diversity (Tuomisto 2010 a,b). Thus, one must expect that, as higher is the species diversity within sites (alpha) and the less similar are species identities among sites (high beta diversity), the larger will be the regional (gamma) species diversity (Tuomisto 2010).

Beyond the theoretical importance around these questions, which has conducted to many improvements on analytical methods (Magurran 2004), there is also an important applied concern to assess and synthesize the information of ecological communities. If species composition is strongly correlated to local abiotic environment, areas for biological conservation must be delineated and managed considering the mosaic of environmental patches or the distinct portions of an environmental gradient in order to contemplate the total species diversity and to ensure ecosystems functioning (Primack and Rodrigues 2001, Legendre et al. 2005). Moreover, patches must be large enough to support considerable populations size and dispersal routes must be conserved or created to allow species movement across inhospitable habitats (Primack and Rodrigues 2001).

The composition of avian communities is known to vary substantially in time and space, since birds are very mobile organisms capable to be involved in many potential interactions (Bennett and Owens 2006). Moreover, birds represent a very diverse group with many species responding promptly to subtle changes in environmental conditions

(Bennet and Owens 2006). Thus, they constitute appropriate tools for exploring ecological issues like the role of environmental changes across ecological gradients on community structure.

In the last decades, many coastal areas around the world have experienced a rapid increase in urban development and economic activities, which in turn has resulted in biodiversity loss and deterioration of ecological services (Brown and Mclachlan 2002, Defeo et al. 2009). The southernmost Brazilian littoral includes a set of juxtaposed coastal habitats, like sandy beaches, coastal dunes and littoral grasslands, which constitute a remarkable physical gradient and harbor diversified avian communities that include seabirds, shorebirds and grassland birds (Vooren and Chiaradia 1990, Belton 1994). In addition, the region is under subtropical climate regime (Klein 1997), which makes environmental conditions to change according to the four well-defined seasons. These combined characteristics allow us to assess the spatial and temporal variability of the avian communities across an environmental gradient of coastal ecosystems along the year.

Specifically, we intended with this study: 1) to characterize the structure of coastal avian communities, basically in terms of species richness and evenness, in response to environmental changes across a gradient from sandy beach trough coastal dunes to littoral grasslands and 2) to assess the variation in avian species composition among habitats and between seasons (beta-diversity), as well as to determine which species are associated with each coastal habitat type in each season.

According to the "habitat heterogeneity hypothesis", we expect that the most homogeneous sandy beach will present lower species richness than dunes and grasslands. We also predict that, due to ecological discontinuities, species' populations occurring in the most heterogeneous habitats will be better distributed in abundance, rendering a positive relationship between habitat complexity and evenness. According to the "species sorting hypothesis", we expect that environmental changes across the coastal gradient will affect community composition, due to differences in species requirements and their adaptive strategies. If this is the case, the highest contrast in species composition is expected to occur between sandy beach and littoral grasslands, i.e., the endpoints of the coastal gradient. On the other hand, variation in total abundance and species composition through time is expected via two interacting factors: 1) the fluctuation of environmental conditions because of the well-defined climate seasons; and 2) the arriving of long distant migrants, like Nearctic or Patagonian coastal bird species (Vooren and Chiaradia

1990) as well as many Neotropical migrants (Sick 1994), that increment the species pool around the year.

METHODS

STUDY AREA

This study covered a portion of sandy beaches, coastal dunes and natural grasslands located in Cassino seaside resort (32° 11' S, 52° 10' W), Rio Grande, RS, Brazil. There is a remarkable physical gradient mainly portrayed by highly homogeneous sandy beach at an extreme, an intermediate situation represented by partially vegetated dunes and the herbaceous grasslands in the landwards extreme.

Climate in the region is subtropical, with rain distributed along the year, although mean monthly rainfall is highest during the winter and spring, whilst summer months can be associated with a seasonal water deficit. Total mean annual precipitation is about 1200-1500 mm and may vary from year to year. This variation in precipitation, with either a high amount of rainfall or dry periods, seems to be a consequence of the effect of the El Niño-Southern Oscillation cycle (Klein, 1997).

HABITATS DESCRIPTION

1. Sandy beach. The beach is very extensive, gently sloping and fine grained, presenting a wide intertidal zone. These conditions favor the occurrence of an abundant and diverse invertebrate fauna that represents important food resources for coastal birds both residents and migrants (Gianuca 1983, Vooren e Chiaradia 1990). During low tide periods, beach width achieves around 130 meters.

2. Coastal dunes. The upper part of the beach presents a system of coastal dunes partially stabilized by native herbaceous vegetation. Low embryo dunes are vegetated by the sand-fixing pioneer *Blutaparon portulacoides* (A. St. Hil.) Miers, whilst primary dunes are much higher and covered by the most important dune-building plant, the perennial grass *Panicum racemosum* (Beauv.) (Gianuca 1997). Other important species are *Spartina ciliata* (Kunth.), *Hydrocotyle bonariensis* (Lam.), *Andropogon arenarius* (Hack.) and *Androtrichum trigynum* (Spr.) (Seeliger 2004). Two introduced species of shrubs, *Acacia longifolia* (Andr.) Willd and *Tamarix gallica* (L.), can be found scarcely in some points. During rainy periods there is the for-

mation of seasonally flooded areas in the slacks and other lower parts of the dune system. In general, the line of coastal dunes presents around 150 meters in width.

3. Littoral grasslands. The littoral grasslands are located immediately behind the coastal dunes and are characterized by many species of native herbaceous plants. All the grasslands surveyed were private property and used for cattle grazing. Although we observed that many portions of the grasslands were overgrazed, the rotation system employed by some ranchers ensures a diversified vegetation structure on a regional scale, conferring a mosaic of low and tall vegetation strata that constitute distinct degrees of habitat heterogeneity and complexity. Depending of the management practices, the vertical structure of vegetation varies from 1 cm to 90 cm and is predominantly composed by several species of grasses, Cyperaceae, Juncaceae, Leguminoseae, and Umbelliflorae. That is the reason why some of our sampling plots were allocated in high vegetation grasslands, others included low vegetation strata and several were placed in mixed grasslands. In some places there are a few scarce shrub species such as *Schinus terebinthifolius* and *Acacia longifolia* and also cactuses. Many lower areas of the littoral grasslands are seasonally flooded during the rainy periods, forming ponds and temporary marshes, mainly in winter (Seeliger et al. 2004). Grasslands are the wider habitat surveyed; extendind from the edge of dunes to marshes located around 6 km landwards.

BIRD SAMPLING

From July 2008 to April 2009 we performed four avian censuses, corresponding to one in each climatic season. We counted birds in 19 plots (500 x 120 meters) allocated in each habitat. To ensure survey independence (Gotelli and Elisson 2004) we stipulated a buffer of at least 200 meters among samples. We used the area-search method (Ralph *et al.* 1993) to count birds. However, in order to achieve a better performance in our study area, we modified the size and shape of the plot and we did not use a time-based stopping-rule (*sensu* Watson 2003). One of the principal advantages of the area-search is the high detectability of secretive species in grassland-like ecosystems, because one can free-walk around the patches of tall vegetation as well as the crests and slacks of dunes while seeking for birds (Dieni and Jones

2002, Atkinson *et al.* 2006, Roberts and Schnell 2006). Although distance methods represent a straightforward technique to calculate species densities, an obstacle emerges in multiple species studies such as ours, because rare species makes impossible to achieve an adequate sample size of bird detections for the entire community (see Rosenstock et al. 2002).

Two observers covered simultaneously each plot, being each one responsible for sampling a half-section while progressing through the full length of the plot. As recommended by Roberts and Schnell (2006), we covered all points located 10 m inside the perimether of the plots. We walked at the same rhythm and communicated frequently to ensure that individual birds were not double-counted.

We counted all individuals seen or heard within the plot area. Birds in flight were considered only if foraging up to 30 m above the plot. In order to avoid sampling bias, surveys were realized only in the first four hours after sunrise in clear days with wind speed lower than 5 on the Beaufort scale (Bibby *et al.* 1992, McCoy *et al.* 2001). In each season, we spent two days to sampling in grasslands, another two days to sampling in dunes and only one day on the beach due logistic reasons. We used 12 x 50 binoculars to help find and identify birds and a handheld GPS unit with a 5 m error to assess distances. Scientific nomenclature and taxonomic sequence follows South American Classification Committee (SACC, Remsen et al. 2011).

DATA ANALYSIS

Species richness. We have calculated species richness in each habitat type considering each season separately. We used the total number of species found in all samples in each habitat. We compared the rates of species accumulation across habitats and seasons through rarefaction analyses based on Mao Tau method (Magurran 2004). We also calculated an estimate of species richness on the basis of the Chao 1 estimator, because it is more appropriate for abundance data (Magurran 2004). Chao 1 estimator is based on the ratio between singletons (i.e., species represented by a single individual in the survey) and doubletons (i.e., species represented by exactly two individuals in the survey). As greater is the number of singletons recorded, greater will be the estimated value of species richness in relation to the observed one. If no singleton is recorded, the survey effort is considered sactisfatory, and the estimated and observed richness values became the same. As the rarefaction method is based in interpolation and the estimated method is an extrapolation technique, we compared rarefied species richness (here after RSR) ± C.I. (confidence intervals) with the estimated species richness (here after ESR) ± C.I. in order to obtain a parameter of survey sufficiency. Both analyses were run in EstimateSMac8.2.0 (Colwell 2006).

Diversity, abundance and community composition. We used the Shannon index as a measure of alpha diversity (Magurran 2004). We calculated the Smith and Wilson evenness index for each habitat and season. We used species' abundance data over all sampling periods in each habitat to calculate Bray–Curtis similarity coefficients among habitat types. Then, data from the similarity matrix were used to assess differences in species composition among habitats and seasons by means of multi-factorial PERMANOVA (Anderson 2001, McArdle and Anderson 2001). Multi-factorial PERMANOVA determines whether samples (i.e., transects) within each habitat type (and also within each season) are more similar to each other in comparison with samples taken randomly from the entire sample pool (i.e., 228 transects). This analysis compares the level of similarity among transects of a given habitat (and within a given sampling period) to that among transects of all habitats (and all sampling periods) and determines if the former is greater than expected by chance. Multi-factorial PERMANOVA originated P-values by tests of significance based in Monte Carlo randomization technique, and also estimates pairwise comparisons. Thus, we used it to determine contrasts in species composition at a spatial scale (comparisons among habitats) and at a temporal scale (comparisons among seasons). Afterwards, we used nonmetric multidimensional scaling (NMDS) to visualize the similarities and differences among samples based on species' abundance data; thus, points that are closer in the ordination space are more similar in terms of species composition. Multi-factorial PERMANOVA was run in MULTIV 2.63b statistical software (by V. Pillar, available at http://ecoqua.ecologia.ufrgs.br/ecoqua/software.html, user's guide included) and NMDS was run in PRIMER-Beta 6.0 statistical package (Clarke and Gorley 2006)

In order to identify characteristic species of each habitat type in each season, we used an indicator-species analysis (Dufrêne and Legendre 1997). This analysis, which we did in PC-ORD version 4 (McCune and Mefford 1999), calculates an indicator value for species, based on its relative frequency and relative abundance in all treatment categories (i.e., habitat types). Indicator values can range from 0 (no indication) to 100 (perfect indication). Indicator values were tested for significance with a Monte Carlo randomization procedure, which compares the observed indicator values to alternative values calculated randomly from the same data. Only species with indicator values higher than 25% and that were significant ($P < 0.01$) are reported in the text.

RESULTS

VARIATION IN SPECIES RICHNESS AMONG HABITATS

According to rarefaction analyses, in winter and in spring, the highest and lowest values of species richness were recorded on grasslands and sandy beach, respectively (Table 1 to Table 3 and Fig. 1). Avian communities in dunes presented intermediary number of species richness, generating an ascending continuum from beach trough dunes to grasslands (Table 1 to Table 3 and Fig. 1). In summer and autumn, sandy beach presented again the lowest value of species richness, but in these seasons, grasslands and dunes presented a similar number of species recorded (Table 1 to Table 3 and Fig. 1).

ABUNDANCE AND EVENNESS

Considering all the sampling period togheter, the highest avian abundance values were recorded on the beach (4.141 detections), followed by grasslands (3.913 detections) and finally for dunes (3.062 detections). Along the year, the highest values of Smith and Wilson evenness index were obtained for coastal dunes, with the exception of spring (Table 2), when *Sicalis luteola* dominated the avian community with near 75% of total species abundance recorded in this habitat. This breaking in the pattern is still more impressive considering that *S. luteola* was virtually absent of coastal dunes in the other seasons, but was the second most abundant bird on littoral grasslands in winter. In the other extreme, sandy beach was marked by lowest values of the evenness index, irrespective of the season considered (Table 3). Littoral grasslands exhibited intermediary values of evenness along the year (Table 1).

Table 1. Descriptive overview of the avian communities occurring in littoral grasslands in southern Brazil. Abbreviations correspond to: N = total number of bird' detections; OSR = Observed Species Richness RSR = Rarefied Species Richness; ESR = Estimated Species Richness; CI = Confidence Intervals; H = Shannon index; E = Smith and Wilson evenness index.

Community descriptors	Grasslands			
	Winter	Spring	Summer	Autumn
N	1.132	998	1.081	702
OSR	45	46	33	31
RSR (95% CI)	45 (37-53)	46 (39-53)	33 (27-39)	31 (27-35)
ESR (95% CI)	63 (49-121)	57 (49-90)	34 (33-44)	31 (Null)
H	2.598	2.636	2.296	2.414
E	0.257	0.263	0.281	0.345
Singletons	11	11	3	0
Doubletons	2	4	2	7
Uniques	15	15	10	9
Duplicates	4	5	4	9
Total RSR (95% CI)	63 (57-69)			

Table 2. Descriptive overview of the avian communities occurring in coastal dunes in southern Brazil. Abbreviations correspond to: N = total number of bird' detections; OSR = Observed Species Richness RSR = Rarefied Species Richness; ESR = Estimated Species Richness; CI = Confidence Intervals; H = Shannon index; E = Smith and Wilson evenness index.

Community descriptors	Coastal Dunes			
	Winter	Spring	Summer	Autumn
N	380	1.881	489	312
OSR	33	36	34	31
RSR (95% CI)	33 (27-39)	36 (32-40)	34 (31-37)	31 (25-37)
ESR (95% CI)	36 (33-51)	40 (37-58)	34 (34-37)	32 (31-42)
H	2.918	1.315	3.02	2.88
E	0.360	0.261	0.389	0.400
Singletons	6	6	2	5
Doubletons	4	3	8	6
Uniques	11	9	7	11
Duplicates	4	7	10	5
Total RSR (95% CI)	61 (52-68)			

Table 3. Descriptive overview of the avian communities occurring in a sandy beach in southern Brazil. Abbreviations correspond to: N = total number of bird' detections; OSR = Observed Species Richness RSR = Rarefied Species Richness; ESR = Estimated Species Richness; CI = Confidence Intervals; H = Shannon index; E = Smith and Wilson evenness index.

Community descriptors	Sandy Beach			
	Winter	Spring	Summer	Autumn
N	1.344	645	865	1.287
OSR	21	32	20	23
RSR (95% CI)	21	32	20	23
	(17-25)	(24-40)	(17-23)	(18-28)
ESR (95% CI)	22	54	21	28
	(21-32)	(37-129)	(20-35)	(24-52)
H	1.619	2.542	2.218	1.771
E	0.195	0.240	0.223	0.164
Singletons	3	10	3	6
Doubletons	2	1	1	2
Uniques	5	15	4	8
Duplicates	2	3	3	3
Total RSR	45			
(95% CI)	(35-54)			

TEMPORAL VARIATION IN SPECIES RICHNESS WITHIN HABITATS

On littoral grasslands, values corrected by rarefaction analysis demonstrated that winter and spring presented higher species richness than summer and autumn (Table 1). According to Chao 1 estimator, there are still more species to be recorded on winter and spring in this habitat with an increase in sampling effort. On the other hand, it is evident that on summer and autumn, besides the lower species number recorded in comparison with the other seasons, the coincident values of

RSR and ESR suggest a sufficient survey effort (Table 1 and Fig. 1). Note that, for autumn, the ESR was equal to the observed value of species richness because there were no singletons in grasslands during this sampling period (Table 1).

On coastal dunes, apart from the absence of statistical differences in species richness along the year, values of ESR were similar to those of RSR, indicating a good sampling effort along all the sampling period in this habitat (Table 2 and Fig. 1).

On sandy beach, the highest value of species richness (32 spp.) was recorded on spring. However, according to rarefaction analysis, the number of species recorded in autumn is only marginally lower than that of spring due to the high confidence interval associated with this season (Table 3 and Fig. 1). Winter and summer presented species richness values statistically lower than that for spring, but similar to that of autumn (Table 3 and Fig. 1). Differently of the other seasons, values of ESR for spring also presented a considerable discrepancy in relation with RSR, suggesting an insufficient sampling effort in this season (Table 3 and Fig. 1).

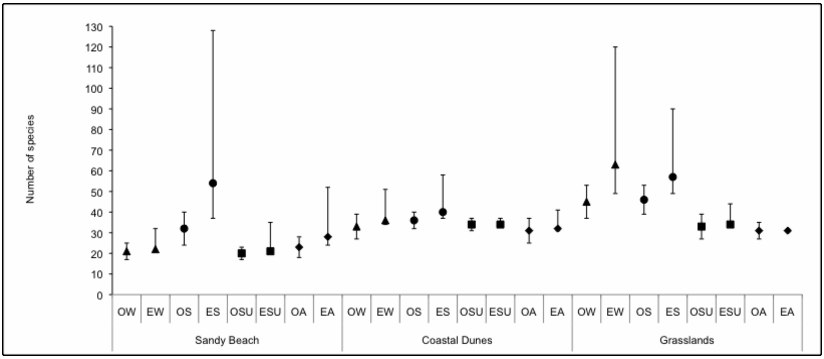

Figure 1: Observed Species Richness (OSR) corrected for rarefaction analysis and Estimated Species Richness (ESR) with 95% confidence intervals for avian communities occurring in sandy beach, coastal dunes and grasslands in each season. OW = (OSR) for Winter; EW = (ESR) for Winter; OS = (OSR) for Spring; ES = (ESR) for Spring; OSU = (OSR) for Summer; ESU = (ESR) for Summer; OA = (OSR) for Autumn; EA = (ESR) for Autumn.

BETA-DIVERSITY

The result of PERMANOVA indicated high divergence in species composition among habitats (global Qb = 25, P = 0.001), and such differences are highlighted in the NMDS graphical representation (Fig. 2). Figure 2 considers the samples surveyed during all the sampling period, that is the reason why 76 points for each habitat are represented (and not 19). It is clear that, variations in species composition within habitats are lower than that among habitats (Fig. 2), although some differences in species composition (within each habitat) caused by temporal variability is noticeable. The grasslands and sandy beach were the most different habitats in respect of species composition (Qb = 15, P = 0.001) (Table 4).

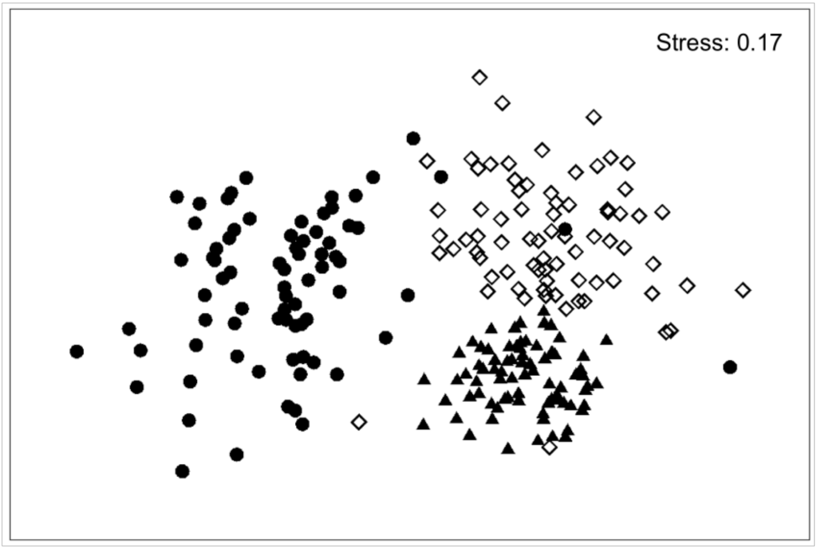

Figure 2: Nonmetric multidimensional scaling from a distance pairwise matrix based on Bray-Curtis similarity index. Symbols represent samples in: Littoral Grasslands (filled triangles); Coastal dunes (open diamonds); and Sandy Beach (filled circles).

In the assessment of temporal turnover within each habitat, the results of PERMANOVA indicated that, in all habitats, differences in species composition by sampling period were significant (global Qb = 4.5, P = 0.001). In terms of temporal turnover, spring vs. autumn and winter vs. spring were the most different in species composition (Table 4).

Table 4: Pairwise comparisons in species composition among habitats based on abundance data. Values are pairwise based on sum of squares between groups (Qb) from multi-factorial PERMANOVA based on Bray–Curtis similarity.

Factor	Sum of squares (Qb)
Habitats	24.6*
Grasslands vs. dunes	10.8*
Grasslands vs. beach	15.0*
Dunes vs. beach	10.6*
Seasons	4.5*
Winter vs. spring	2.0*
Winter vs. summer	1.2*
Winter vs. autumn	0.9*
Spring vs. summer	1.4*
Spring vs. autumn	2.0*
Summer vs. autumn	1.3*
Season vs. habitat	6.5*

* *P* (Qb NULL ≥) = 0.001.

INDICATOR SPECIES

The indicator-species analysis identified 14 species more associated with grassland habitats, 12 appear as dunes indicator species and other 12 as sandy beach indicators (Tables 5 to 8). These were the main species driving beta-diversity between habitats in our study system. According to these results, four passerine species were considered dune specialists along the year: *Geositta cunicularia*, *Alopochelidon fucata*, *Embernagra platensis* and *Anthus helmayri*. The most consistent indicator species on grasslands were *Vanellus chilensis, Anumbius annumbi, Pseudoleites virescens* and *Anthus furcatus*, which appear in at least three seasons. On sandy beach, *Haematopus palliatus*, *Himantopus melanurus, C. maculipennis*, *L. dominicanus* and *Sterna trudeaui* appear as strong indicator species along the year.

Indicator species in different seasons. In winter, *Plegadis chihi* was an indicator species of grasslands, while *Spartonoica maluroides* appears associated with dunes, and two terns (*Sterna hirundinacea* and *Thalasseus maximus*) were indicators of sandy beach (Table 5). *Sicalis luteola* and *Pitangus sulphuratus* were found associated with grasslands in winter, but appear as strong indicator species of dunes habitat in spring (Table 5).

On spring, *Anthus lutescens*, *Anthus correndera* and *Molothrus bonariensis* were associated with grasslands while in summer two migratory swallows, *Tachycineta leucorrhoa* (from neotropics) and *Hirundo rustica* (from neartic region), were indicator species of this ecosystem (Table 6). There were also two Neotropical migrants classified as indicators species in summer on coastal dunes (*Tyrannus savana* and *Progne chalybea*) (Table 7). The grassland sparrow *Ammodramus humeralis* occurred associated with coastal dunes in spring and summer (Tables 6 and 7).

The shorebirds *Pluvialis dominica* and *Tringa melanoleuca* were indicators of sandy beach in spring and summer (Tables 6 and 7). *Calidris fuscicolis* was associated with this habitat only in summer and *Calidris alba* in autumn (Table 8). These four shorebird species are migratory from Neartic region (Vooren and Chiaradia 1990).

Table 5: Indicator values (as percentage of perfect indication) and values of Monte Carlo test of significance based on habitats in winter. Only values significant at least at P < 0.01 are shown.

Species	Winter		
	Indicator values based on habitats		
	Grasslands	Dunes	Beach
Plegadis chihi	45	0	0
Vanellus chilensis	92	3	0
Charadrius collaris	0	0	53
Haematopus palliatus	0	0	37
Himantopus melanurus	5	0	41
Chroicocephalus maculipennis	0	0	100
Larus dominicanus	0	0	42
Sternula superciliaris	0	0	42
Sterna hirundinacea	0	0	47
Sterna trudeaui	0	0	37
Thalasseus maximus	0	0	26
Geositta cunicularia	2	75	3
Spartonoica maluroides	0	26	0
Anumbius annumbi	36	2	0

Pitangus sulphuratus	40	7	0
Machetornis rixosa	29	2	0
Alopochelidon fucata	0	60	0
Troglodytes musculus	0	37	0
Anthus hellmayri	2	66	0
Zonotrichia capensis	0	32	0
Sicalis luteola	26	0	0
Embernagra platensis	9	38	0
Pseudoleistes virescens	42	0	0

Table 6: Indicator values (as percentage of perfect indication) and values of Monte Carlo test of significance based on habitats in spring. Only values significant at least at P < 0.01 are shown.

Species	Spring		
	Indicator values based on habitats		
	Grasslands	Dunes	Beach
Vanellus chilensis	84	10	0
Pluvialis dominica	13	0	42
Haematopus palliatus	0	8	39
Himantopus melanurus	0	0	26
Tringa melanoleuca	0	0	37

Calidris fuscicolis	0	0	26
Chroicocephalus maculipennis	0	0	63
Larus dominicanus	0	0	37
Geositta cunicularia	3	73	0
Pitangus sulphuratus	3	52	0
Machetornis rixosa	26	0	0
Alopochelidon fucata	4	48	0
Anthus lutescens	63	0	0
Anthus furcatus	74	0	0
Anthus correndera	32	0	0
Zonotrichia capensis	0	37	0
Ammodramus humeralis	1	33	0
Sicalis luteola	3	94	0
Embernagra platensis	3	43	0
Pseudoleistes virescens	52	0	0
Molothrus bonariensis	35	0	0

Table 7: Indicator values (as percentage of perfect indication) and values of Monte Carlo test of significance based on habitats in summer. Only values significant at least at P < 0.01 are shown.

Species	Summer		
	Indicator values based on habitats		
	Grasslands	Dunes	Beach
Vanellus chilensis	93	3	0
Pluvialis dominica	3	0	63
Haematopus palliatus	0	5	34
Himantopus melanurus	0	0	37
Tringa melanoleuca	0	0	42
Chroicocephalus maculipennis	0	0	89
Larus dominicanus	0	0	58
Sterna trudeaui	0	0	47
Athene cunicularia	44	11	0
Geositta cunicularia	3	84	0
Anumbius annumbi	44	0	0
Tyrannus savana	4	37	0
Progne chalybea	1	32	0
Tachycineta leucorrhoa	43	15	0

Hirundo rustica	51	12	0
Anthus furcatus	53	0	0
Anthus hellmayri	7	43	0
Ammodramus humeralis	0	42	0
Embernagra platensis	1	31	0

Table 8: Indicator values (as percentage of perfect indication) and values of Monte Carlo test of significance based on habitats in autumn. Only values significant at least at $P < 0.01$ are shown.

Species	Autumn		
	Indicator values based on habitats		
	Grasslands	Dunes	Beach
Vanellus chilensis	96	0	0
Charadrius collaris	0	0	42
Calidris alba	0	0	58
Haematopus palliatus	0	0	42
Himantopus melanurus	0	0	37
Chroicocephalus maculipennis	0	0	63
Larus dominicanus	0	0	32
Sternula superciliaris	0	0	26

Sterna trudeaui	0	0	26
Rynchops niger	0	0	37
Athene cunicularia	53	8	0
Geositta cunicularia	2	70	0
Anumbius annumbi	26	0	0
Alopochelidon fucata	1	51	0
Troglodytes musculus	0	32	0
Anthus furcatus	79	0	0
Anthus hellmayri	11	44	0
Embernagra platensis	0	39	0
Pseudoleistes virescens	32	0	0

DISCUSSION

SPECIES RICHNESS

During winter and spring, an ascending continuum pattern of species richness was observed from sandy beach trough coastal dunes to littoral grasslands. Altough in summer and autumn the avian communities in grasslands and dunes presented similar values of species richness, the lowest number of species was recorded in the structurally homogeneous sandy beach during all the sampling period. These results corroborate the predictions of "habitat heterogeneity hypothesis", which assumes that habitat complexity allows a higher number of species to co-occur due to resources partitioning and predators avoidance, leading to an increase in species diversity (MacArthur 1961, MacArthur and Wilson 1967, Tews et al. 2004).

If comparing to dunes, littoral grasslands are more flatted in form, but still present very slightly undulating relief, a consequence of the transgressions and regressions of sea level during the Pleistocene (Seeliger et al. 1997). As a result, several temporary ponds are formed during winter' rainy periods, which attract many waterbird species (Belton 1994, Sick 2001). In fact, the increment in species richness in winter on grasslands was mainly related to the presence of waterbird species. The non-floodable portions that interspaced the ponds represent the adequate habitat for many grassland birds (Vickery 1999). Satellite images, in winter, showed a mosaic of flooded/non-flooded grasslands, which represent a heterogeneous situation *per se*. In addition, some of our transects cover low vegetation grasslands, others high strata vegetation, and several were located on distinct mixed situations. A scenario like this is favorable to maintain distinct species of grassland birds, which select sites for reproduction, foraging and resting based on very specific vegetation characteristics (Cody 1985, Coppedge et al. 2008). When spring arrives, temporary ponds evaporate and diverse annual grasses thrive on the moist lowlands, creating adequate conditions for macroinvertebrates and pollinator insects that represent food resources for many insectivorous birds (e.g., *Pseudoleistes virescens*, *Heteroxolmis dominicanus*, *Machetornis rixosus*, *Anthus* spp) (del Hoyo et al. 2004).

The crest of dunes serve as observatory for birds of prey, like *Caracara plancus*, *Milvago chimango* and *Athene cunicularia*, as well as adequate habitat for cursorial species that seek insects or forage upon the seeds of *P. racemosum* (e.g., *Geositta cunicularia*, *Anthus helmayri* and *Sicalis luteola*). On the other hand, the moist slacks characterized by dense vegetation (i.e., *Juncus acutus* and *Androtrichum tryginum*) provide habitat for many passerine species, which look for refuge and food resources in it (e.g., *Spartonoica maluroides*, *Cistothorus platensis*, *Embernagra platensis*, *Asthenes hudsoni, Phleocryptes melanops*) (Belton 1994, Bencke et al. 2003, del Hoyo et al. 2004). We also noticed the presence of scattered shrubs in some portions of the dunes (although exotic in this ecosystem), which form microclimatic conditions and increase heterogeneity. In fact, several authors have demonstrated that variation in vegetation types and their associated microclimatic conditions within dunes are more important to faunal distribution than its form or relief *per se* (Mclachlan 1991).

Temporal variation in species richness within habitats. Rarefied species richness indicates significant higher species richness on sandy beach in spring than in any other season. This difference was caused by 11 species that were exclusively recorded during spring. Five of these are migratory Nearctic shorebirds, two are migratory Neotropical swallows, two are Anatidae species, one is a resident wading bird, and other a resident swallow. Vooren and Chiaradia (1990) also observed these five Nearctic shorebirds (*Calidris canutus*, *Arenaria interpress*, *Tringa flavipes, Calidris melanotos and Charadrius semipalmatus*) on Cassino beach during spring, summer and autumn. The absence of these species in other seasons in our study may be a consequence of the increase in human disturbance, mainly in summer months, forcing them to select other foraging areas along the littoral of Rio Grande do Sul, before starting their northward migration in early autumn (Blanco et al. 2006). As a group, shorebirds are very sensible to human disturbances, like urbanization, vehicle traffic on beaches and presence of dogs (International Wader Study Group 2003, Steidl and Polwell 2006). Sherer (2010) demonstrated the detrimental effects of urbanization on shorebirds abundance on the central portion of Rio Grande do Sul' littoral, including some of the species cited above.

Coastal dunes. Avian ecological communities on coastal dunes of South America are poorly studied. The only mention in the literature that we are aware is a checklist for the Uruguayan coast, but this study was a result of compilations and sporadic records on dunes, without a methodological approach designed to assess avian communities (Aldabe et al. 2006). Possibly, this can explain why so few species were recorded (25 species) on coastal dunes of the entire south and east coast of Uruguay, across 50 years, in relation to our study (61 species in a single year data-base).

We observed that there were no fluctuations in species richness along the year on coastal dunes of Cassino beach, although species composition varies substantially between seasons. Coastal dunes present few exclusive species, because: 1) they are geological young ecosystems molded by recent changes in sea level during Pleistocene; and 2) they are ecosystems inherently small in area and narrower in form, with extensive sea and landwards boundaries, which allow free exchange of fauna (McLachlan 1991). Our results suggest that changes in environmental conditions in coastal dunes in addition to the high exchange of avian species with surrounded habitats, results in a turnover in species composition, but not in an increase in species richness. That is, since dispersal is not a limitation for many bird species, temporal variability in the abiotic environment can act as a selective force on species composition along the year, ensuring different species to thrive in each system at each point in time (see Loreau et al. 2003). So, we suggest that, as the environmental conditions change and surrounding habitats could export species to coastal dunes, a turnover in species composition took place, allowing more adapted species to thrive under new conditions.

Littoral grasslands. Although many studies on grasslands in the Uruguayan and Argentinean Pampa's Biome indicated a higher species number in spring and summer (e.g., Isacch and Martínez 2001, Isacch et al. 2003, Azpiroz and Blake 2009), the littoral grasslands considered in our study supported more species during winter and spring. On the one hand, the southern austral migrants that come from these neighbor countries looking for less severe climatic conditions (Joseph 1997), like *Cinclodes fuscus*, *Lessonia rufa* and *Charadrius modestus*, respond by this pattern. On the other hand, many temporary ponds, containing abundant food resources in winter, attract several waterfowls and some wading birds for littoral grasslands (Belton 1994), resulting in an increase in species richness. It is clear that waterfowls are only capable to occur where ponds or lakes with abundant resources are available (Belton 1994), and that is the reason why they leaved the littoral grasslands during spring, summer and early autumn.

EVENNESS

Our results shown that the highest and lowest values of evenness were achieved for coastal dunes and sandy beach, respectively. Ecological theory predicts an increase in evenness values under three distinct situations: 1) limitation in basic resources (Tokeshi 1993); 2) an increase in habitat complexity (Tanigushi et al. 2003); and 3) an increase in instability (Rotenberry 1978, Jackson et al. 2001). Thus, the opposite situations lead to an increase in dominance. As a matter of fact, these predictions are based on competition models, which suggest that superior competitors exploit more efficiently the abundant resources on homogeneous habitats under long-term predictable situations, increasing their fitness and leading to an exclusion of poor competitors or simply making them rare in the community. We suggest that an interaction between habitat complexity and resource limitation caused the highest evenness values observed on coastal dunes. Littoral grasslands also present a complex architecture, but usually provide more abundant food resources for birds than dunes, which are under higher stressing conditions due to saline spray, sand motion, aridity etc. The exception was on spring, when occur the flourishing of *Panicum racemosum* on dunes leading to a peak of seed production (Gianuca 1997), which provides abundant resources for seedeaters. Indeed, this increment in seed availability caused an increase in *S. luteola* abundance (a seedeater species), resulting in similar evenness values on coastal dunes and littoral grasslands in spring. Even so, the structurally homogeneous habitat of the sandy beach presents the lowest values of evenness during all the sampling period considered.

BETA-DIVERSITY

We observed a high variation in species composition among all habitat types. Sandy beach and littoral grasslands, which were the most distinct habitats in terms of environmental conditions, also presented the most contrasting species composition. These results are in concordance with the predictions of “species sorting hypothesis”, which postulates that, in the absence of dispersal limitations, changes in environmental conditions and species interactions are the main processes underlining communities organization (Leibold et al. 2004). In general, there are not important barriers to avian dispersal in the coastal plain of Rio Grande do Sul, especially across the coastal gradient considered in this study. On the other hand, abrupt changes in environmental conditions across coastal gradients are, probably, the most important determinant of species distributions. A revision made by Cottenie (2005) demonstrated that species sorting is the most common process structuring ecological communities, at least in temperate regions.

The pattern of less contrasting species composition on dunes in comparison with the other two communities may be explained by at least two distinct hypotheses: 1) As mentioned above, coastal dunes present few exclusive species, because of its recent geological history as well as its narrower form, which permits free exchange of fauna (McLachlan 1991). So, the surrounding habitats potentially serve as sources for many species that occurs on dunes, and some of them are capable to thrive in some portions that contain adequate environmental conditions for them; 2) According to the predictions of ecological gradients theory (Whittaker 1960), coastal dunes are a transitional habitat that present mixed environmental characteristics with beach and grasslands, and not a well defined ecotone with impermeable boundaries. Thus, some portions of the habitat are adequate for birds from the beach and other portions for birds from grasslands.

INDICATOR SPECIES

The indicator species analysis had the potential to unravel many species that presented high association to one habitat type in detriment of the others. The indicator species are the main drivers of beta-diversity among habitats and seasons These results are in agreement with the "environmental habitat filtering" perspective, which postulates that habitats serve as filters that select from a regional species poll a subset of them containing the adequate morphological and physiological traits that maximize their fitness, which results in the elimination of the inferior competitors (Keddy 1992, Weiher and Keddy 1999).

Finally, we demonstrated in this study that, the well-marked changes in environmental conditions along the gradient of coastal habitats results in "inflated" gamma diversity, since no habitat alone has an approximation of the total species richness recorded when all the habitats are considered together. Thus, in order to preserve the potential species pool of coastal avian communities in southernmost Brazil, one must consider holistically the distinct portions (and processes) embedded within the gradient of sandy beaches, coastal dunes and littoral grasslands.

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Appendix 1. List of the species recorded in grasslands, coastal dunes and sandy beach during each climatic season (from July 2008 to April 2009). Symbols represent: X = species presence in the season considered; - = species absence; Win = winter; Spr = spring; Sum = summer; Aut = autumn.

Táxon	Grasslands				Coastal Dunes				Sandy Beaches			
	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut
TINAMIFORMES												
TINAMIDAE												
Nothura maculosa	X	X	X	X	X	X	X	X	-	-	-	-
ANSERIFORMES												
ANHIMIDAE												
Chauna torquata	X	-	-	-	-	-	-	-	-	-	-	-
ANATIDAE												
Amazonetta brasiliensis	X	-	-	-	X	-	-	-	-	X	-	-
Anas flavirostris	X	-	-	-	-	-	-	-	-	-	-	-
Anas georgica	X	X	-	-	-	X	-	-	-	X	-	-
Anas versicolor	X	-	-	-	-	-	-	-	-	-	-	-
CICONIIFORMES												
CICONIIDAE												
Ciconia maguari	-	-	-	-	-	X	-	-	-	-	-	-
SULIFORMES												
PHALACROCORACIDAE												
Phalacrocorax brasilianus	-	-	-	-	-	-	-	-	-	-	X	-
PELECANIFORMES												
ARDEIDAE												
Bubulcus ibis	-	X	-	-	-	-	-	-	-	-	-	-
Ardea cocoi	-	-	-	-	X	X	X	X	X	X	X	-
Ardea alba	-	-	-	-	-	-	-	-	-	X	-	-
Syrigma sibilatrix	X	X	X	X	-	-	-	X	-	-	-	-
Egretta thula	-	X	-	-	-	X	-	-	X	X	X	-
THRESKIORNITHIDAE												

Plegadis chihi	X	X	-	X	-	X	-	-	X	-	-	-
Phimosus infuscatus	X	-	-	X	-	-	-	-	-	-	-	-
Theristicus caerulescens	X	-	-	-	-	-	-	-	-	-	-	-
ACCIPITRIFORMES												
ACCIPITRIDAE												
Circus cinereus	-	-	-	-	X	-	-	-	-	-	-	-
Circus buffoni	X	-	-	-	-	-	-	-	-	-	-	-
Heterospizias meridionalis	-	X	-	X	-	-	X	-	-	-	-	-
FALCONIFORMES												
FALCONIDAE												
Caracara plancus	X	X	X	X	X	X	X	X	X	-	X	X
Milvago chimango	X	X	X	X	X	X	X	X	X	X	X	X
Falco sparverius	-	X	X	-	-	-	-	X	-	-	-	-
CHARADRIIFORMES												
CHARADRIIDAE												
Vanellus chilensis	X	X	X	X	X	X	X	X	X	X	-	X
Pluvialis dominica	-	X	X	-	-	X	-	-	-	X	X	-
Pluvialis squatarola	-	-	-	-	-	-	-	-	-	-	-	X
Charadrius semipalmatus	-	-	-	-	-	-	-	-	-	X	-	-
Charadrius collaris	-	-	-	-	-	X	X	-	X	X	X	X
Charadrius modestus	X	-	-	-	-	-	-	-	X	-	-	X
HAEMATOPODIDAE												
Haematopus palliatus	-	-	-	-	-	X	X	-	X	X	X	X
RECURVIROSTRIDAE												
Himantopus melanurus	X	-	-	-	-	-	-	-	X	X	X	X
SCOLOPACIDAE												
Gallinago paraguaiae	X	-	-	-	-	-	-	-	-	-	-	-
Tringa melanoleuca	X	-	-	-	-	-	-	-	-	X	X	X
Tringa flavipes	-	-	-	-	-	-	-	-	-	X	-	-
Arenaria interpres	-	-	-	-	-	-	-	-	-	X	-	-
Calidris canutus	-	-	-	-	-	-	-	-	-	X	-	-
Calidris alba	-	-	-	-	-	-	-	-	-	X	X	X

Calidris fuscicollis	-	-	-	-	-	-	-	-	-	X	-	X
Calidris melanotos	-	-	-	-	-	-	-	-	-	X	-	-
STERCORARIIDAE												
Stercorarius parasiticus	-	-	-	-	-	-	-	-	-	-	-	X
LARIDAE												
Chroicocephalus maculipennis	-	-	-	-	-	-	-	-	X	X	X	X
Chroicocephalus cirrocephalus	-	-	-	-	-	-	-	-	X	X	-	X
Larus dominicanus	-	-	-	-	-	-	-	-	X	X	X	X
STERNIDAE												
Sternula superciliaris	-	-	-	-	-	X	-	-	X	X	X	X
Sterna hirundo	-	-	-	-	-	-	-	-	-	X	X	-
Sterna hirundinacea	-	-	-	-	-	-	-	-	X	-	-	X
Sterna trudeaui	-	-	-	-	-	-	-	-	X	X	X	X
Thalasseus acuflavidus	-	-	-	-	-	-	-	-	-	X	X	X
Thalasseus maximus	-	-	-	-	-	-	-	-	X	-	X	-
RYNCHOPIDAE												
Rynchops niger	-	-	-	-	-	-	-	-	-	-	X	X
COLUMBIFORMES												
COLUMBIDAE												
Zenaida auriculata	X	-	-	-	-	X	X	-	-	-	-	-
PSITTACIFORMES												
PSITTACIDAE												
Myiopsitta monachus	-	X	X	X	-	-	-	-	-	-	-	-
CUCULIFORMES												
CUCULIDAE												
Guira guira	X	X	-	X	-	X	X	X	-	-	-	-
STRIGIFORMES												
STRIGIDAE												
Athene cunicularia	X	X	X	X	X	X	X	X	-	-	-	-
CAPRIMULGIFORMES												
CAPRIMULGIDAE												
Chordeiles nacunda	-	-	X	-	-	-	-	-	-	-	-	-

PICIFORMES												
PICIDAE												
Colaptes campestris	X	X	X	X	-	-	-	-	-	-	-	-
PASSERIFORMES												
SCLERURIDAE												
Geositta cunicularia	X	X	X	X	X	X	X	X	X	X	-	-
FURNARIIDAE												
Cinclodes fuscus	X	-	-	-	-	-	-	-	-	-	-	-
Furnarius rufus	X	X	X	X	-	-	X	X	-	-	-	-
Phleocryptes melanops	-	-	-	-	X	-	-	-	-	-	-	-
Spartonoica maluroides	-	-	-	-	X	-	-	X	-	-	-	-
Phacellodomus striaticollis	-	X	-	X	-	-	X	X	-	-	-	-
Anumbius annumbi	X	X	X	X	X	X	X	-	-	-	-	-
Schoeniophylax phryganophilus	-	-	-	-	X	-	-	-	-	-	-	-
Synallaxis spixi	-	-	-	-	-	X	-	-	-	-	-	-
Asthenes hudsoni	-	X	-	-	-	-	-	X	-	-	-	-
TYRANNIDAE												
Serpophaga nigricans	-	-	-	-	-	-	-	-	-	-	-	-
Pitangus sulphuratus	X	X	X	X	X	X	X	X	X	X	-	X
Machetornis rixosa	X	X	X	X	X	-	X	-	-	-	-	-
Tyrannus savana	-	X	X	-	-	X	X	-	-	-	-	-
Lessonia rufa	X	-	-	X	X	-	-	-	X	-	-	X
Hymenops perspicillatus	X	-	-	X	X	-	-	-	-	-	-	-
Satrapa icterophrys	-	X	-	-	X	-	-	-	-	-	-	-
Xolmis irupero	X	X	X	X	X	-	X	X	-	-	-	-
Xolmis dominicanus	X	X	-	X	-	-	-	-	-	-	-	-
Agriornis murinus	-	-	-	-	-	-	-	-	-	-	-	X
HIRUNDINIDAE												
Pygochelidon cyanoleuca	-	X	-	-	-	-	-	X	-	X	-	-
Alopochelidon fucata	X	X	X	X	X	X	-	X	-	-	-	X
Progne tapera	-	X	X	-	-	X	X	-	-	X	-	-
Progne chalybea	-	X	X	-	-	X	X	-	-	-	-	-

Tachycineta leucorrhoa	X	X	X	X	X	X	X	X	-	X	X	-
Tachycineta leucopyga	-	-	-	-	X	-	-	-	X	-	-	-
Riparia riparia	-	X	-	-	-	-	-	-	-	-	-	-
Hirundo rustica	-	X	X	-	-	X	X	X	-	X	-	-
TROGLODYTIDAE												
Troglodytes musculus	-	-	X	-	X	X	X	X	-	-	-	-
Cistothorus platensis	-	-	-	-	X	-	-	X	-	-	-	-
TURDIDAE												
Turdus amaurochalinus	-	-	-	-	X	-	-	-	-	-	-	-
MIMIDAE												
Mimus triurus	-	-	-	-	-	-	X	-	-	-	-	-
MOTACILLIDAE												
Anthus lutescens	X	X	X	-	-	-	-	-	-	-	-	-
Anthus furcatus	X	X	X	X	-	-	-	-	-	-	-	-
Anthus correndera	X	X	X	X	X	-	X	X	-	-	-	-
Anthus hellmayri	X	X	X	X	X	X	X	X	-	-	-	-
EMBERIZIDAE												
Zonotrichia capensis	-	-	-	-	X	X	X	X	X	X	X	X
Ammodramus humeralis	X	X	-	-	X	X	X	X	-	-	-	-
Donacospiza albifrons	-	-	-	-	X	-	-	X	-	-	-	-
Sicalis flaveola	X	-	-	-	X	X	-	X	-	-	-	-
Sicalis luteola	X	X	X	X	-	X	X	X	-	-	-	-
Embernagra platensis	X	X	X	X	X	X	X	X	-	-	-	-
ICTERIDAE												
Agelasticus thilius	X	X	-	-	-	-	-	-	-	-	-	-
Pseudoleistes virescens	X	X	X	X	-	X	-	-	-	-	-	-
Molothrus bonariensis	X	X	X	X	-	X	-	-	-	-	-	-
Sturnella superciliaris	-	X	-	-	-	X	X	-	-	-	-	-
PASSERIDAE												
Passer domesticus	-	-	-	-	-	X	X	X	-	-	-	-

CAPITULO 2

Este artigo segue as normas de formatação do periódico *Austral Ecology*

INDEPENDENT AND SHARED EFFECTS OF ENVIRONMENTAL FEATURES AND SPACE DRIVING AVIAN COMMUNITY BETA-DIVERSITY ACROSS A COASTAL GRADIENT IN SOUTHERN BRAZIL

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ABSTRACT

Beta-diversity is defined as the variation in species composition among sites within a region of interest. This variation could be explained by niche theory or neutral theory, which are not mutually exclusive. The former emphasizes the role of habitat features on species composition. The latter suggests space and geographical barriers as drivers of species composition. In order to contribute with some of these issues we assessed the role of environmental features and spatial descriptors on avian community beta-diversity on three juxtaposed coastal habitats in southern Brazil. During 2008 autral winter and 2009 summer season we allocated 57 transects on sandy beach, coastal dunes and littoral grasslands (19 transects in each habitat). In the same transects we assessed herbaceous vegetation structure, the number of cactuses and shrubs and the percentage of sand cover and water cover. The geographical coordinates obtained *in situ* were used to generate spatial filters by means of Principal Coordinates of Neighbour Matrices. We used variation partitioning based on CCA to decompose the fraction of beta-diversity explained by environmental features and spatial descriptors. Both, in winter and summer, environmental variables explained near to 30% of the variation in species composition. A third of this variation could also be explained by space, representing the fraction of species and environmental variables that were spatially structured. Near to 20% of the variation in species composition were affected only by environmental features. Spatial descriptors *per se* explained only 3% of beta diversity. We concluded that environmental features were the key driver of avian species distribution on coastal ecosystems, which are in accordance with niche theory. However, the absence of significant dispersal barriers for birds on southern Brazilian coastal plain and the spatial scale considered makes difficult to assess neutral/historical processes adequately.

Keywords: Neutral theory, species sorting, metacommunities.

INTRODUCTION

Understanding the patterns of distribution, abundance and interactions of species is a central question in community ecology. Ecological theory predicts that different processes act as filters on communities' assembly at different scales (Leibold et al. 2004, Holyoak et al. 2005). A metacommunity is defined as a set of local communities linked by dispersal of multiple potentially interacting species (Wilson 1992, Leibold et al. 2004). Leibold and collaborators (2004) proposed four perspectives about the organization of metacommunities: neutral model, patch dynamics, mass effect and species sorting, which are not mutually exclusive. As a matter of fact, neutral model and species sorting represent the endpoints of a continuum of processes acting on communities organization in different scales, and the four perspectives present certain overlap in their predictions (Cottenie 2005, Driscoll and Lindenmayer 2009). While neutral model emphasizes the role of dispersal on communities assembly and species sorting focus on the importance of local environmental conditions on species distributions, patch dynamics and mass effect are a mixed of both perspectives.

From a neutral perspective, species composition may be randomly associated with environmental conditions but autocorrelated in space. From neutral expectations all species are competitively equal and not specialized in specific environmental conditions, but differences on distributions are created by distinctive dispersal rates occurring randomly among species (Hubbell 2001). Thus, irrespective of environmental conditions, contagious biotic processes like birth, death and migration, might lead to autocorrelated species composition, because the colonization probability of a site will decay with the distance of species origins (Rosindell et al. 2011). According to neutral theory predictions, as greater the distance among sites, greater will be the divergence in species composition among them.

The species sorting perspective arises from the niche theory and predicts that species are only capable to occur where their required set of resources and conditions are available (Hutchinson 1959, Leibold et al. 2004). Thus, habitats may be considered as filters that select from a regional species pool a subset of them containing the adequate morphological and physiological traits that permit a good performance concerning resources exploitation (Keddy 1992, Weiher and Keddy 1999). If there are not restrictions to dispersal, differences in environmental conditions among sites will result in differences of species composition, irrespective of the distance among them.

A start point to assess if species sorting, neutral model or both are acting on communities assembly is to consider environmental and isolation gradients as sampling scenarios, and this is the context of our study (Legendre et al. 2005, Driscoll and Lindenmayer 2009). Ecological gradients theory predicts that species tend to present a peak of abundance where optimum conditions occur and abundance decays as environmental conditions change, leading to a gradual substitution of taxa (Whittaker 1975, Qian and Ricklefs 2007). On the other hand, variation in species composition among samples within the same habitat type is expected to increase as distance among samples augments (Jankowski et al. 2008), which unravel the potential role of dispersal as an important driver of species assembly. Thus, a solution to disentangling the confounding processes causing species composition to vary across ecological gradients is taking into account the role of space and environmental features as drivers of ecological communities (Legendre 1993, Cottenie 2005).

To better understand how these hypotheses (species sorting vs. neutral model) are driving beta-diversity – i.e., the variation in species composition among samples across a gradient (Whittaker 1960) – spatial-based functions should be incorporated as descriptors in ecological models as well as environmental variables (Legendre et al 2005). The principal coordinates of neighbor matrices method (PCNM) represent a straightforward way to assess spatial structure in ecological data at different scales across a gradient of geographical distances (Borcard and Legendre 2002). The method of variation partitioning allows one to decompose the percentage of variation on community composition data explained by environmental variables alone, plus the fraction corresponding to spatially-structured environmental variables, another portion explained by a set of spatial descriptors based on geographical coordinates (e.g., PCNMs), and the variance that remains unexplained (Borcard 1992). Legendre et al. (2005) argued that the correct way to test the variation on community composition data among samples, by means of variation partitioning, is based on raw-data approach in detriment of distance matrix (i.e., Mantel) approach. By doing so, one can corroborate the hypothesis that neutral assumptions are driving beta diversity if the community composition is autocorrelated in space but independent of environmental variables. In the same way, if species composition is not spatially structured but strikingly associated to environmental conditions it strengthens niche hypothesis. However, if community composition is autocorrelated and environmental conditions are also spatially structured, niche and neutral hypothesis becomes compatible answers (Legendre et al. 2005).

Although metacommunity theory is based on important theoretical studies, there is limited empirical research about their predictions (Leibold et al. 2004, Holyoak et al. 2005, Driscoll and Lindenmayer 2009). Studies focusing these questions are of interest to increase our comprehension of ecological communities' organization and functioning, as well as for practical reasons like planning and management of biological reserves (Legendre et al. 2005). If beta-diversity is high and species composition is closely related to environmental features, reserves must be planned considering the mosaic of environmental conditions (Primack and Rodrigues 2001, Legendre et al. 2005). If species' distributions are autocorrelated in space but randomly related to environmental characteristics, each increment in reserve's size would probably encompass new species (Legendre et al. 2005). In a situation like this, reserves must be as large as possible to contemplate higher species diversity.

In order to contribute with these issues, we intended to assess in this study the independent and shared effects of environmental variables and spatial descriptors on avian communities' organization across a gradient of coastal ecosystems. Birds perform important roles in ecosystem functioning. They act for example as top predators that control potential plagues, genetic linkers by seed and pollen dispersal and resources linkers contributing to material flux within and among ecosystems (Sekercioglu 2006). Avian communities' composition is known to vary substantially in time and space, since bird species are individually involved in many potential interactions (Bennett and Owens 2006). Moreover, birds represent a very diverse group with many species responding promptly to subtle changes in environmental conditions (Bennet and Owens 2006). Thus, they constitute appropriate tools for exploring ecological issues like the role of niche and neutral models underlining communities' organization.

Our predictions are as follows: 1) since birds are sensitive organisms to habitat quality, the remarkable changes in environmental conditions across a coastal gradient will result in a high beta diversity; 2) because of differences in physical and chemical stressors from the most exposed sandy beach to landwards sheltered habitats across the gradient, species composition and environmental features should be spatially structured in coastal ecosystems; 3) as birds are very mobile organisms and there are not well defined barriers to dispersal in southern Brazilian coastal plain, space alone should not have an important role in avian communities assembly.

MATERIAL AND METHODS

Study area. This study was conducted on three juxtaposed coastal ecosystems (Sandy Beach, Coastal Dunes and Littoral Grasslands) located south of the Lagoa dos Patos mouth, near Cassino seaside resort (32° 11’ S, 52° 10’ W), Rio Grande municipality, RS, Brazil. There is a remarkable physical gradient mainly portrayed by highly homogeneous sandy beach at an extreme, an intermediate situation represented by partially vegetated dunes and the herbaceous grasslands in the landwards extreme.

The beach is very extensive, gently sloping and fine grained, presenting a wide intertidal zone. These conditions favor the occurrence of an abundant and diverse invertebrate fauna that represents an important food source for coastal birds, several of them are Nearctic northern migrants and others are Patagonic southern migrants (Gianuca 1983, Vooren and Chiaradia 1990).

The upper part of the beach presents a system of coastal dunes partially stabilized by native herbaceous vegetation. Low embryo dunes are vegetated by the sand-fixing pioneer *Blutaparon portulacoides*, whilst primary dunes are much higher and covered by the most important dune-building plant, the perennial grass *Panicum racemosum* (Gianuca 1997). Other important species are *Spartina ciliata*, *Hydrocotyle bonariensis*, *Andropogon arenarius* and *Androtrichum tryginum* (Seeliger 1997). Two introduced species of shrubs, *Acacia longifolia* and *Tamarix gallica*, can be found scarcely in some points. During rainy periods there is the formation of seasonally flooded areas in the slacks and other lower parts of the dunes system. A serious threat for the stability of these coastal dunes and their ecological communities is the impact represented by the ever increasing cattle pasture on the natural vegetation and the recreation with off-road vehicles, reducing plant cover and height, lowering species diversity and decreasing substrate stability which results in erosion and massive sand transport by the wind (Gianuca 1997).

The littoral grasslands are located immediately behind the coastal dunes and are characterized by many species of native herbaceous plants that form a mosaic of lower vegetation mixed with varied spots of taller herbaceous, such as *Androtrichum trigynum* and *Juncus acutus*, to constitute distinct degrees of habitat heterogeneity and complexity. The vertical structure of vegetation varies from near 1cm to about 90 cm and is predominantly composed by several species of grasses, Leguminoseae, Cyperaceae and Umbelliflorae. In some places there are a few scarce shrub species such as *Schinus terebinthifolius* and *Acacia longifolia* and also cactuses. Many lower areas of the coastal grasslands are seasonally flooded during the rainy periods, forming ponds and temporary marshes, mainly in winter. Climate in the region is subtropical, with rain distributed along the year, although summer months can be associated with a seasonal water deficit (Klein, 1997).

Bird sampling. Considering the great differences in abiotic conditions along the year that are supposedly capable to affect bird species abundance and distribution as well as the arrival of different migrants in different seasons, bird sampling took place during 2008 austral winter and during 2009 austral summer. In these seasons one can find major contrasts in abiotic conditions in subtropical coastal ecosystems. Moreover, we did not include spring and autumn in the analysis because many migrants coming from northern hemisphere just pass trough the area in direction of staging areas in Argentina during spring as well as during autumn when they return to breeding sites, with a very briefly permanency in the area (e.g. Vooren and Chiaradia 1990) and supposedly may cause noise in the analysis.

We counted birds in 19 plots (500 x 120 meters) allocated in each habitat. To ensure survey independence (Gotelli and Elisson 2004) we stipulated a buffer of at least 200 meters among samples. We used the area-search method (Ralph *et al.* 1993) to count birds. However, in order to achieve a better performance in our study system, we modified the size and shape of the plot and we did not use a time-based stopping-rule (*sensu* Watson 2003). One of the principal advantages of the area-search is the high detectability of secretive species in grassland-like ecosystems, because one can free-walk around the patches of tall vegetation as well as the crests and slacks of dunes while seeking for birds (Dieni and Jones 2002, Atkinson *et al.* 2006, Roberts and Schnell 2006). Although distance methods represent a straightforward technique to calculate species densities, an obstacle emerges in multiple species studies such as ours, because rare species makes impossible to achieve an adequate sample size of bird detections for the entire community (see Rosenstock et al. 2002).

Two observers covered simultaneously each plot, being each one responsible for sampling a half-section while progressing through the full length of the plot. As recommended by Roberts and Schnell (2006), we covered all points located 10 m inside the perimether of the plots. We walked at the same rhythm and communicated frequently to ensure that individual birds were not double-counted.

We counted all individuals seen or heard within the plot area. Birds in flight were considered only if foraging up to 30 m above the plot. In order to avoid sampling bias, surveys were realized only in the first four hours after sunrise in clear days with wind speed lower than 5 on the Beaufort scale (Bibby *et al.* 1992, McCoy *et al.* 2001). In each season, we spent two days to sampling in grasslands, another two days to sampling in dunes and only one day on the beach due logistic reasons. We used 12 x 50 binoculars to help find and identify birds and a handheld GPS unit with a 5 m error to assess distances. Scientific nomenclature and taxonomic sequence follows South American Classification Committee (SACC, Remsen et al. 2011).

Environmental variables. The environmental variables assessed inside each sample were: average of vegetation height, vegetation heterogeneity, sand cover, water cover and number of cactuses and shrubs.

In order to measure the vegetation height in each transect, we defined nine strips within it, separately by 50 meters from each other and oriented transversally in relation to bird survey direction. In each strip, we measured vegetation height in 24 points interspaced by 5 meters from an edge to another, to a total of 216 measures by transect, which were used to calculate the average of vegetation height in each transect.

To assess vegetation heterogeneity, we utilized the heterogeneity index proposed by Wiens (1974), based on the values of vegetation height, according with the following equation: $H.I.=\sum(\max - \min) / \sum \text{averages}$, where amplitudes inside each strip are summed and divided by the sum of averages in each strip.

The percentage of sand cover and water cover were visually estimated inside each transect. Shrubs and cactuses were considered a single variable and thus quantified as one.

Spatial descriptors. The geographical coordinates (latitude, longitude) of the samples were taken using a handheld GPS. Afterwards we generated spatial variables using the method of principal coordinates of neighbor matrices (PCNM) described by Borcard and Legendre (2002). The PCNM approach allows one to assess different spatial structures over the whole range of scales encompassed in the geographic sampling area. The firsts PCNMs generated in the analyses represent broader spatial scales and the last ones cover more and more finer spatial structures. The method consists in calculate a truncated Euclidean distance matrix from the geographical coordinates of the sampling sites and to perform a subsequent principal coordinates analysis to extract eigenvectors associated with positive eigenvalues from it, which could thus be used as explanatory variables in multiple regression analyses (Borcard and Legendre 2002). PCNM analyses were performed using SAM 4.0 software (Rangel et al. 2010).

Forward selection of explanatory variables. In order to avoid Type I error and the overestimation of the amount of explained variance on the species abundance data matrix, we followed the double selection criteria of explanatory variables recommended by Blanchet et al. (2008). As proposed for them, we first runed a global test including all explanatory variables and adjusting the $R^2_{(Y|X)}$ according to Ezekiel´s correction (Peres-Neto et al. 2006). The $R^2_{(Y|X)adj}$ of the global test is then used as a second criterion besides the alpha-value of 0.05 to select which explanatory variables will be kept in the following analyses. The next step consists in performing the forward routine, which we did in software CANOCO 4.5 (Ter-Braak and Smilauer 2002), starting by selecting the available explanatory variable that maximizes model fitting and computing a F-ratio for the analysis. Then, a *P*-value for the analysis is generated by permutation of residuals under the full model approach (Legendre and Legendre 1998), computing a $R^2_{(Y|X)adj}$ for the forward test whenever a *P*-value ≤ 0.05 is obtained. If the $R^2_{(Y|X)adj}$ of the forward test is lower than that of the global test, a new variable is added to the analysis and the permutation test is runed again, otherwise, the procedure is stoped. We performed the forward selection of both sets of explanatory variables (i.e., environmental vs. spatial) separetely.

Variation partitioning of environmental and spatial drivers of beta-diversity. The method of variation partitioning allows decomposing the variation in species composition into pure environmental components, pure spatial effects, spatially structured environmental variables and the unexplained causes of variation (Borcard 1992). We used a tree-step approach to disentangling environmental and spatial drivers of beta diversity based in canonical analyses, such as Canonical Correspondence Analysis (CCA) (Fig. 1). The portion of the explained variation in such analysis (CCA) is given by R^2, which is assessed dividing the sum of all canonical eigenvalues by the total inertia in the software CANOCO 4.5 (Ter-Braak and Smilauer 2002). In order to avoid the type I error and the overestimation of the total of explained variation, we adjusted the $R^2_{Y|X|}$ according to Ezekiels correction (Peres-Neto et al. 2006). Before running the series of CCAs, bird abundance values were square root transformed in order to eliminate the great disparity in magnitude among them. We also choose the option “down weighting for rare species” in the software CANOCO 4.5.

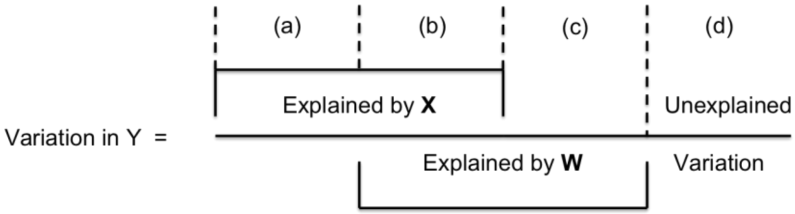

Figure 1. Scheme showing the steps used in variation partitioning of the species abundance matrix Y between two sets of explanatory variables X (environmental variables) and W (spatial predictors). The total variation in Y is partitioned into four portions as follows: (1) portion [a + b + c] based on both sets of predictor matrices [X,W] ([a + b + c] = $R^2_{Y|X,W|}$); (2) portion [a + b] based on matrix X ([a + b] = $R^2_{Y|X|}$); (3) portion [b + c] based on matrix W ([b + c] = $R^2_{Y|W|}$); (4) the fraction of variation explained only by X, [a] = [a + b + c] – [b + c]; (5) the portion of variation explained only by W, [c] = [a + b + c] – [a +b]; (6) the shared portion of explained variation based on X and W, [b] = [a + b + c] – [a] – [c]; and (7) the portion of variation that remains unexplained in the model, [d] = 1 – [a + b + c]. (Figure adapted from Borcard et al. 1992, Legendre et al. 2005, Peres-Neto et al. 2006).

RESULTS

Summer. In summer, we recorded 58 bird species distributed in 27 families (2.435 detections), including all transects (n = 57) and habitats. The number of species in each habitat was: 20 on sandy beach, 34 on coastal dunes and 33 on littoral grasslands.

A previous CCA using the forward procedure and taking into account the alpha-value of 0.05 selected four explanatory variables for summer, in decreasing order of importance: average vegetation height; vegetation heterogeneity index; sand cover and number of shrubs/cactuses ($R^2_{Y|X|adj}$ = 0.231, P = 0.001). However, the $R^2_{Y|X|adj}$ obtained for these four variables was higher than that of the global test ($R^2_{Y|X|adj}$ = 0.229), indicating a type I error in the forward selection procedure. For this reason we eliminated the fourth environmental variable (number of shrubs/cactuses), decreasing the $R^2_{Y|X|adj}$ to 0.222.

The analysis of spatial filters based on geographical coordinates generated fifteen PCNM descriptors for summer. After the two-step selection criteria, we kept in the subsequent analyses four spatial descriptors: PCNM1; PCNM2; PCNM3; and PCNM6 ($R^2_{Y|X|adj}$ = 0.113, P = 0.001). The first three PCNMs, which contain higher eigenvalues, cover the broader spatial scales, while PCNM 6 correspond to relatively finer spatial scales (i.e., containing lower eigenvalues).

Variation partitioning based on CCAs showed that space and environment together explained near to 26% of beta-diversity in our study area in summer ($R^2_{Y|X,W|adj}$ = 0.258, P = 0.001) (Fig. 2 left). Around to 23% of the variance in species composition data were explained by environmental variables (portion a + b in Figure 2) ($R^2_{Y|X|adj}$ = 0.222, P = 0.001). Since one-third of this contribution can also be predicted by PCNMs (fraction b in Fig. 2), we concluded that a significant portion of avian community organization and environmental data were spatially structured. Environmental features alone explained the largest portion of the variance (portion a in Fig. 2) ($R^2_{Y|X|adj}$ = 0.145, P = 0.001). The spatial descriptors alone represented the lowest portion of the explained variance (portion c in Fig. 2) ($R^2_{Y|W|adj}$ = 0.035, P = 0.001). The amount of variance that remained unexplained was around to 74% (fraction d on Fig. 2).

The best predictive variables in summer, organized along the first axis, were sand cover and herbaceous heterogeneity index, while the height of vegetation and PCNM2 were mainly correlated with the second axis. We generated a canonical ordination biplot based on samples, environmental variables and spatial descriptors (Fig. 3 left), which indicated that samples on dunes presented higher average of vegetation strata. Samples on the beach were characterized by high proportion of sand cover, while samples on grasslands presented high proportion of vegetation cover (i.e., the inverse of sand cover) and the highest values of herbaceous heterogeneity index. An additional ordination biplot based on species abundances including both, spatial and environmental descriptors, showed that Passeriformes (represented by the numbers 31 to 58 in the Figure 3 right) were mainly associated with grasslands and dunes while Charadriiformes (numbers 10 to 24 in the Figure 3 right) were typical indicators of sandy beach habitat during summer (Fig. 3 right).

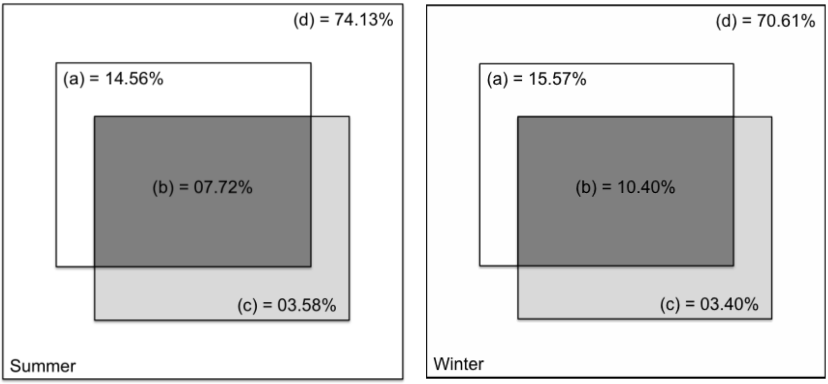

Figure 2: Venn diagrams representing summer (left) and winter (right) as the percentage of variance on species composition data explained by: (a) environmental variables; (b) the shared effects of space and environmental features; (c) spatial descriptors alone; and (d) the fraction that remain unexplained.

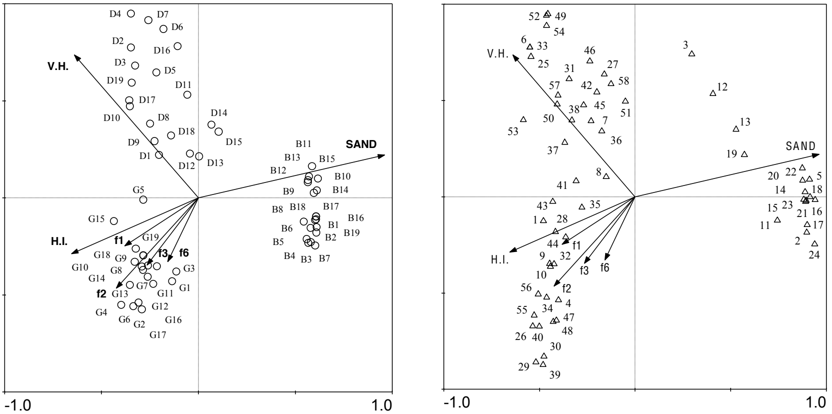

Figure 3: Canonical ordination biplot including spatial descriptors and environmental variables representing samples' distribution (left) and species' distribution (right) in summer. Arrows represent variables; unfilled circles represent samples (left); unfilled triangles are species (right). Abreviations correspond to: H.I. = Heterogeneity index; V.H. = Vegetation height; SAND = Sand cover; f1 to f6 are the four spatial filters (PCNMs) included in the model. G1 to G19 are the nineteen samples on grasslands; D1 to D19 are samples on dunes; B1 to B19 are samples on beach. Numbers represent species in taxonomic sequence: 1.*Nothura maculosa*; 2.*Phalacrocorax brasilianus*; 3.*Ardea cocoi*; 4.*Syrigma sibilatrix;* 5.*Egretta thula*; 6.*Buteogallus meridionalis*; 7.*Caracara plancus*; 8.*Milvago chimango*; 9.*Falco sparverius*; 10.*Vanellus chilensis*; 11.*Pluvialis dominica*; 12.*Charadrius collaris*; 13.*Haematopus palliatus*; 14.*Himantopus mexicanus*; 15.*Tringa melanoleuca*; 16.*Calidris alba*; 17.*Chroicocephalus maculipennis*; 18.*Larus dominicanus*; 19.*Sternula superciliaris*; 20.*Sterna hirundo*; 21.*S. trudeaui*; 22.*Thalasseus sandvicensis*; 23.*T.* maximus; 24.*Rynchops niger*; 25.*Zenaida auriculata*; 26.*Myiopsitta monachus*; 27.*Guira guira*; 28.*Athene cunicularia*; 29.*Chordeiles nacunda*; 30.*Colaptes campestris*; 31.*Geositta cunicularia*; 32.*Furnarius rufus*; 33.*Phacellodomus striatic*ollis; 34.*Anumbius annumbi*; 35.*Xolmis irupero*; 36.*Machetornis rixosa*; 37. *Pitangus sulphuratus*; 38.*Tyranus savana*; 39.*Pygochelidon cyanoleuca*; 40.*Alopochelidon fucata*; 41.*Progne tapera*; 42.*Progne chalybea*; 43.*Tachycineta leucorrhoa*; 44.*Hirundo rustica*; 45.*Troglodytes aedon*; 46.*Mimus triurus*; 47.*Anthus lutescens*; 48.*Anthus furcatus*; 49.*Anthus correndera*; 50.*Anthus hellmayri*; 51.*Zonotrichia capensis*; 52.*Ammodramus humeralis*; 53.*Sicalis luteola*; 54.*Embernagra platensis*; 55.*Pseudoleistes virescens*; 56.*Molothrus bonariensis*; 57. *Sturnella superciliaris*; 58.*Passer domesticus.*

Winter. In winter, we recorded a total of 68 species (2.856 detections) distributed among 25 families. The numbers of species recorded in each habitat separately were: 21 on sandy beach, 33 on coastal dunes and 45 on littoral grasslands.

The two-step selection criteria of explanatory descriptors indicated that all the five environmental variables assessed in the field during winter were significant. The same procedure selected five spatial descriptors for winter: PCNM1; PCNM2; PCNM3; PCNM6; and PCNM12. The first three PCNMs correspond to broader scales while the last two represent finer spatial scales.

Variation partitioning in winter. Although a significant turnover in species composition from summer to winter was noticed in a preliminary analysis (not showed here), our model based in spatial and environmental descriptors resulted in a very similar pattern, explaining near to 30% of avian beta-diversity in winter ($R^2_{Y|X,W|adj} = 0.293$, $P = 0.001$) (Fig. 2 right). Near to 26% of the variance in species composition data were explained by environmental variables (a + b in figure 2 right) ($R^2_{Y|X|adj} = 0.259$, $P = 0.001$). In comparison with summer, there was a slightly increase in the fraction corresponding to spatially structured environmental variables explaining beta-diversity in winter (fraction b in Fig. 2 right) ($R^2_{Y|X|adj} = 0.104$, $P = 0.001$). Probably, the occurrence of ephemeral ponds, which were spatially restricted to some portions of grasslands, contributed to this pattern. Slacks in coastal dunes also accumulated small portions of water and a dense vegetation cover, but their occurrence is rare, since sandy dunes are considerably more permeable and better drained than grasslands. Again, similarly to summer, environmental features *per se* represented the largest portion of the explained variance (fraction a in Fig. 2 right) ($R^2_{Y|X|adj} = 0.155$, $P = 0.001$). Also, the lowest portion of explained variance in the model was represented by spatial descriptors alone (portion c in Fig. 2 right) ($R^2_{Y|w|adj} = 0.034$, $P = 0.001$).

Similar to summer, the best predictors of species composition in winter were sand cover and herbaceous heterogeneity. Jointly with vegetation height, however, water cover appeared as an important variable in winter, organized along the second axis, as well as PCNM3 and PCNM6. The canonical ordination biplot based on samples, environmental variables and spatial descriptors (Fig. 4 left), revealed a very similar pattern to that noticed for summer, although water represented an important feature of grasslands in winter. The ordination biplot based on species abundances, spatial descriptors and environmental variables, shown that waterfowls (numbers 3 to 6 in the Figure 4 right) presented high association with ponds distributed on grasslands, Passeriformes were mainly associated with grasslands and dunes (numbers 35 to 68 in the Figure 4 right) while Charadriiformes were again typically correlated with sandy beach habitat (numbers 17 to 30 in the Figure 4 right) (Fig. 4 right).

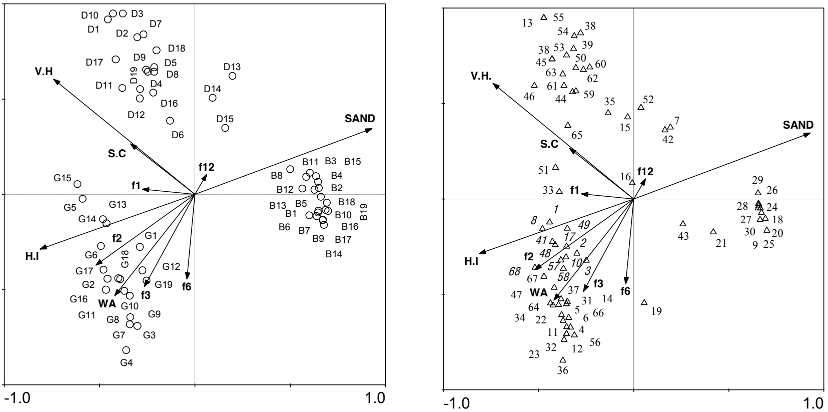

Figure 4: Canonical ordination plot including spatial descriptors and environmental variables representing samples' distribution (left) and species' distribution (right) in winter. Arrows represent variables; unfilled circles represent samples (left); unfilled triangles are species (right). Abreviations correspond to: WA = Water cover; H.I = Heterogeneity index; S.C = Number of shrubs and cactuses; V.H = Vegetation height; SAND = Sand cover; f1, f2, f3, f6 and f12 are the five spatial filters (PCNMs) included in the model. G1 to G19 are the nineteen samples on grasslands; D1 to D19 are samples on dunes; B1 to B19 are samples on beach. Numbers represent species in taxonomic sequence: 1.*Nothura maculosa*; 2.*Chauna torquata*; 3.*Amazonetta brasiliensis*; 4.*Anas flavirostris;* 5.*Anas georgica*; 6.*Anas versicolor*; 7.*Ardea cocoi*; 8.*Syrigma sibilatrix*; 9.*Egretta thula;* 10.*Plegadis chihi*; 11.*Phimosus infuscatus*; 12.*Theristicus caerulescens*; 13.*Circus cinereus*; 14.*Circus buffoni*; 15.*Caracara plancus*; 16.*Milvago chimango*; 17.*Vanellus chilensis*; 18.*Charadrius collaris*; 19.*Charadrius modestus*; 20.*Haematopus palliatus*; 21.*Himantopus mexicanus*; 22.*Gallinago paraguaiae*; 23.*Tringa melanoleuca*; 24.*Chroicocephalus maculipennis*; 25.*Chroicocephalus cirrocephalus*; 26.*Larus dominicanus*; 27.*Sternula superciliaris*; 28.*Sterna hirundinacea*; 29.*S. trudeaui*; 30.*Thalasseus maximus*; 31.*Zenaida auriculata*; 32.*Guira guira*; 33.*Athene cunicularia*; 34.*Colaptes campestris*; 35.*Geositta cunicularia*; 36.*Cinclodes fuscus*; 37.*Furnarius rufus*; 38.*Phleocryptes melanops;* 39.*Spartonoica maluroides*; 40.*Schoeniphylax phryganophilus*; 41.*Anumbius annumbi*; 42.*Serpophaga nigricans*; 43. *Lessonia rufa*; 44.*Hymenops perspicillatus*; 45.*Satrapa icterophrys*; 46.*Xolmis irupero*; 47.*Xolmis dominicanus*; 48.*Machetornis rixosa*; 49.*Pitangus sulphuratus*; 50.*Alopochelidon fucata*;

51.*Tachycineta leucorrhoa*; 52.*Tachycineta meyeni*; 53.*Troglodytes aedon*; 54.*Cistothorus platensis*; 55.*Turdus amaurochalinus*; 56.*Anthus lutescens*; 57.*Anthus furcatus*; 58.*Anthus correndera*; 59.*Anthus hellmayri*; 60.*Zonotrichia capensis*; 61.*Ammodramus humeralis*; 62.*Donacospiza albifrons*; 63.*Sicalis flaveola*; 64.*Sicalis luteola*; 65.*Embernagra platensis*; 66.*Agelasticus thilius*; 67.*Pseudoleistes virescens*; 68.*Molothrus bonariensis*.

DISCUSSION

Our results represent the first insight to a better comprehension of the avian metacommunities in the Brazilian subtropical coastal ecosystems. We showed that, independent of the climatic season considered, local effects of environmental variables on avian species composition represented the main driver of beta-diversity in the scale considered. These founds strengthen the species sorting perspective (Leibold et al. 2004), which predicts that, under a scenario of high dispersal rates, environmental habitat filtering is the main process determining species composition (Keddy 1992, Weiher and Keddy 1999). The absence of important barriers to avian dispersal in the Southern Brazilian coastal plain allows birds to track changes in environmental conditions across the well-marked ecological gradient (Holyoak et al. 2005). As a group, birds are very mobile organisms, with many species performing long distance migrations (Elphick and Lovejoy 2006), as is the case of many shorebird and tern species (Harrison 1985), which are know to fly from the Artic to Antartic in order to select foraging sites based on very specific environmental conditions (Morrison et al. 1987, Vooren and Chiaradia 1991, Blanco et al. 2006). A recent review by Cottenie (2005), demonstrated that, as finer the spatial scale considered, higher the occurrence of niche related phenomena in determining species composition, mainly when very mobile taxa are considered.

The shared effects of spatial and environmental forces explained near a third of the variation in species composition, representing the fraction of environmental variables and species abundance data that were spatially structured. While the neutral model, patch dynamics and mass effect frameworks predicts autocorrelation in species composition, species sorting perspective is the only type of metacommunity that disregard this premise, unless the environmental gradient is also autocorrelated in space (Leibold et al 2004, Holyoak et al. 2005). The pattern observed in this study may result of the negative impacts on vegetation properties across the gradient from the beach through dunes to grasslands. For instance, chemical and physical negative effects of salinity and wave impacts on plant establishment are expected across coastal ecosystems (e.g., Oosting 1945), and vegetation structure is known to affect directly and indirectly bird species occurrence and abundance (MacArthur and MacArthur 1961, Meynard and Quinn 2008).

Spatial descriptors alone responded by only 0.3% of the variance in species composition, and this proportion could be lesser than this, because space may be hiding some latent environmental variables not adequately assessed (Diniz-Filho and Bini 2005). For instance, human activities in summer are aggregated in the northern part of Cassino beach and this is a plausible hypothesis to ask why birds could be avoiding this area, even when favorable habitat is available. Continual human activities may be detrimental for sensitive birds, as is the case for many shorebird species (International Wader Study Group 2003, Steidl and Polwell 2006). Taking into account that there are not significant barriers to avian dispersion in the coastal plain of Southern Brazil, this low spatial signal in species composition data is not surprising. On the other hand, the large amount of unexplained variance in species composition may be a result of non-habitat related phenomena, like nest-predation (Morales and Traba 2009), agonistic interactions, intra-specific attraction and food-limitation (Morales and Traba 2009). These are all important drivers of habitat use and habitat selection in birds (Jones 2001), and all are possible assembly factors that were not assessed in the context of our study.

Metacomunity theory is alicerced on a solid theoretical field, but empirical research designed objectively to test their predictions are rare (Cottenie 2005, Driscoll and Lindenmayer 2009), many of them showing contradictory results. For example, while environmental forces were the main driver of variance in avian species composition on temperate forests in Chile (Meynard and Quinn 2008), the opposite pattern was found for avian communities in Australia, which presented a strong spatial signal (Driscoll and Lindenmayer 2009). Cottenie (2005) reviewed 158 databases to shown that, in temperate ecosystems, species sorting and species sorting combined with mass effect are the main processes assembling metacommunities. However, only four of the databases considered for him refer to birds, indicating a certain bias in the results. On the contrary, neutrality is advocated to perform an important role in forest tropical communities assembly (Hubbell 2001).

Independent of the metacommunity type considered, however, space has an important role in communities' structure, either directly by affecting species dispersal rates, or indirectly structuring environmental variables (Legendre 1993). Neutral theory and species sorting frameworks are the endpoints of a continnum of processes structuring metacommunities (Clark 2008), and studies representing different climatic regions, under distinct spatial scales and considering different taxa, will probably result in different mixes of metacommunities processes. In this paper, we demonstrated the importance of local environmental variables and the importance of the distinct habitats embedded across the coastal gradient to preserve a variety of avian species. Humam activities on sandy beach, eolic energetic business and civil construction will represent an increasing challenge to conserve biological diversity in coastal subtropical ecosystems.

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CAPÍTULO 3

Este manuscrito segue as normas do periódico *Journal of Animal Ecology*

Assessing environmental drivers of avian community phylogenetic structure across a coastal gradient in Southern Brazil

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Summary

1. The evolution of a particular trait, or combination of traits, within lineages may constrain subsequent evolutionary options, leading closely related species to exhibit phenotipc similarity. Niche theories postulate that phenotypes determine species distributions across environmental gradients, leading to phylogenetic signature in communities assembly. Environmental stressing conditions cause phylogenetic clustering due to habitat filtering processes. Communities controled by competition tend to exhibit phylogenetic overdispersion due to limiting similarity. In communities controled by neutral processes, phylogenetic randomness patterns are expected.

2. The integration of species' phylogeny in the analysis of community ecology allows to link broader spatial and temporal scale factors to local and current ecological processes to better understanding communities assembly.

3. We used net relatedness index to assess phylogenetic relationships among avian species across an environmental stressing gradient in coastal habitats, providing insigths about the factors structuring these communities. In adition, we evaluated phylogenetic beta diversity to test whether closely related species explore habitats with similar environmental conditions. For this, we scaled-up phylogenetic information from species to the site level, by means of phylogenetic-fuzzy weighting method, generating a matrix P containing degrees of relatedness among species. A PCoA on matrix P generates principal coordinates of phylogenetic structure (PCPS; synthetic response variables containing phylogenetic information). As explanatory descriptors, we used environmental variables describing the ecological gradient that are known to influence avian species distributions.

4. We found a pattern of phylogenetic clustering in the portions of habitats containing more stressing environmental conditions. In adittion, we observed strong effect of environmental variables on avian phylogenetic variation. Ancient lineages were associated to the

structurally homogeneous habitat, where stressing environmental conditions predominate. Derived clades occur in more complex habitats and were positively related to vegetation cover and height.

5. The observed pattern of phylogenetic clustering in relation to phylogenetic poll demonstrated the importance of stressing environmental conditions constraining the distribution of lineages. The role of environmental forces on phylogenetic variation demonstrated the prevailing of phylogenetic habitat filtering. Habitat patches embedded within ecological gradients must be considered in its plenitude to preserve distinct evolutionary options.

Key-words: Assembly rules; birds; habitat-filtering; habitat complexity; niche conservatism; phylogenetic beta-diversity.

Introduction

Community ecology is concerned with describing the patterns of distribution, abundance and evolution of interacting species and explaining the underlining processes that cause these patterns. Ecological theory predicts a series of nested processes acting as filters on communities' assembly in different spatial and temporal scales (Leibold et al. 2004, Vellend 2010). Speciation and extinction are historical processes that affect the balance of regional species diversity over a macro geographical and broad temporal scale (Ricklefs and Schluter 1993). However, species are known to evolve within communities and thus, evolutionary processes must be considered as a consequence of species interactions under shared environmental conditions, which occur in small spatial scales (Darwin 1859, Cavender-Bares 2006). As a consequence, the slow processes that lead to the evolution of morphological traits and physiological responses among lineages, determine current species distributions and communities' assembly (Ackerly 2003, Cavender-Bares 2006, Pillar et al. 2009).

Basically, there are three different perspectives concerning the assembly processes that underlie communities' structure. First, according to species sorting hypotheses, habitats are viewed as filters that select from a regional species pool a subset of them containing the adequate traits that increase their fitness, which provides good resource exploitation and leads to the exclusion of the less adapted ones (Weiher and keddy 1999, Leibold et al. 2004, Holyoak et al. 2005). Thus, if closely related species share more functional traits and present similar ecological requirements because of niche conservatism (Blomberg and Garland 2002, Blomberg et al. 2003, Bennett and Owens 2006), environmental filtering will tend to cause a higher co-occurrence of closely related species than expected by chance (phylogenetic clustering). In analogy with the term "environmental habitat filtering" (Weiher and Keddy 1999), Duarte (2011) proposed the term "phylogenetic habitat filtering" to describe a situation where traits' conservation in ancient clades and evolutionary novelties in others are capable to constrain the types of habitats that could be occupied by some lineages in relation to all habitats available in the landscape.

Differently of the habitat filtering hypotheses, which are expected to predominate under stressing environmental conditions, the second perspective is concerned with the importance of species interactions under benign environmental conditions, which may determine communities' assembly. If closely related species share more similar morphological traits and physiological responses, they tend to compete more strongly by the same base of resources than distantly related species, and this limiting similarity (MacArthur and Levins 1967) could result in patterns of phylogenetic overdispersion within communities (Cavender-Bares et al. 2004).

The third perspective emphasizes the role of dispersal, disturbance and stochastic processes in communities' assembly and has its roots in the theory of Island Biogeography (MacArthur and Wilson 1967), but these processes gained prominence under the Unified Neutral Theory of Biodiversity proposed by Hubbell (2001). According to the Neutral Theory, species are ecological equivalent in their resources requirements and differences in species distributions are created by stochastic processes, such as disturbance events occurring randomly in space and time, as well as distinctive dispersal rates among species. Thus, according to this perspective, differences in functional traits among species do not matter and species composition varies randomly across the space, irrespective of the environmental conditions. If stochastic/neutral processes are affecting species distribution, one could expect to found a pattern of phylogenetic randomness in ecological communities.

A usual way to assess whether habitat filtering, limiting similarity or neutral processes are affecting phylogenetic structure is by means of phylogenetic clustering/overdispersion indices (Cavender-Bares et al. 2004, Cavender-Bares et al. 2006, Graham, et al. 2009, Willis et al. 2010), which compares the observed level of phylogenetic relatedness in ecological communities to that expected by chance (Webb et al. 2000). However, such indices do not reveal which clades are responding by the observed patterns, even though this is a key information, because two communities exhibiting a similar pattern of phylogenetic relatedness could contain very distinctive phylogenetic clades. The approach of phylogenetic fuzzy-weighting (Pillar and Duarte 2010), followed by a Principal Coordinates of Phylogenetic Structure (Duarte 2011) represents a valuable tool to solve this problem. The method consists in scaling-up phylogenetic information from the species to the site level, generating a matrix P, which contains information on the abundance of all species co-occuring in a community in relation to their phylogenetic relationships. A principal coordinates analysis of sites defined by matrix P generates principal coordinates of phylogenetic structure (PCPS; Duarte 2011), which allow the visualization of phylogenetic structure patterns in a set of samples and, more importantly in the context of this study, which phylogenetic clades underlie the patterns.

Birds are very mobile organisms with a rapid radiation earlier in their evolutionary history that resulted in distinctive, morphologically cohesive orders and families (Bennett and Owens 2006, Hacket et al. 2008), although recent diversification within some lineages has occurred due to dispersal in new environments across the globe (Derryberry et al. 2011). These combined characteristics make birds an ideal group to study the relationship of phylogenetic structure and community organization. In addition, avian communities are normally comprised by many interacting species that present high levels of dietary specialization (Sick 2001), which finally affect their distribution when environmental changes occur across ecological gradients. Nonetheless, the majority of studies concerning phylogenetic structure (or phylogenetic signal; or phylogenetic clustering/overdispersion) in ecological communities refer to plants, and the small fraction of studies relating animal phylogenies with ecological gradients has shown contradictory results (e.g., Cooper, Rodríguez and Purvis 2008 for mammalians; Graham et al. 2009 for hummingbirds).

In this paper, we used net relatedness index to evaluate the patterns of avian phylogenetic community structure across a gradient of stressing conditions in coastal habitats. Complementarily, we used PCPS to assess the relationship between species clades and environmental variables.

We expect to find phylogenetic clustering in sandy beach, which is the most homogeneous portion of habitat, and presents more stressing environmental conditions. In the same way, phylogenetic overdispersion is expected to occur in the opposite extreme of the gradient, (i.e. the grasslands) which is caractherized by more abundant and varying food resources. If niche conservatism within lineages is the predominant pattern in the region, we expect to find a great variation in species clades across the coastal gradient due to a well-marked change in environmental conditions, which might result in phylogenetic habitat filtering among lineages.

Materials and methods

STUDY AREA

This study was conducted on three juxtaposed coastal ecosystems (Sandy beach, Coastal Dunes and Littoral Grasslands) located south of the Lagoa dos Patos mouth, near Cassino seaside resort (32° 11' S, 52° 10' W), Rio Grande municipality, RS, Brazil. There is a remarkable physical gradient mainly portrayed by highly homogeneous sandy beach at an extreme, an intermediate situation represented by partially vegetated dunes and the herbaceous grasslands in the landwards extreme.

The beach is very extensive, gently sloping and fine grained, presenting a wide intertidal zone. These conditions favor the occurrence of an abundant and diverse invertebrate fauna that represents an important food source for coastal birds, several of them are neartic northern migrants and others are patagonic southern migrants. (Gianuca 1983, Vooren and Chiaradia 1990).

The upper part of the beach presents a system of coastal dunes partially stabilized by autochthonous herbaceous vegetation. Low embryo dunes are vegetated by the sand-fixing pioneer *Blutaparon portulacoides*, whilst primary dunes are much higher and covered by the most important dune-building plant, the perennial grass *Panicum racemosum* (Gianuca 1997). Other important species are *Spartina ciliata*, *Hydrocotyle bonariensis, Andropogon arenarius and Androtrichum tryginum* (Seeliger 1997). Two introduced species of shrubs, *Acacia longifolia* and *Tamarix gallica*, can be found scarcely in some points. During rainy periods there is the formation of seasonally flooded areas in the slacks and other lower parts of the dunes system. A serious threat for the stability of these coastal dunes and their ecological communities is the impact represented by the ever increasing cattle pasture on the natural vegetation and the recreation with off-road vehicles, reducing plant cover and height, lowering species diversity and decreasing substrate stability which results in erosion and massive sand transport by the wind (Gianuca 1997).

The littoral grasslands are located immediately behind the coastal dunes and are characterized by many species of autochthonous herbaceous plants that form a mosaic of lower vegetation mixed with varied spots of taller herbaceous, such as Androtrichum trigynum and *Juncus acutus*, to constitute distinct degrees of habitat heterogeneity and complexity. The vertical structure of vegetation varies from near 1cm to about 90 cm and is predominantly composed by several species of grasses, Leguminoseae, Cyperaceae and Umbelliflorae. In some places there are a few scarce shrub species such as *Schinus terebinthifolius* and *Acacia longifolia* and also cactuses. Many lower areas of the coastal grasslands are seasonally flooded during the rainy periods, forming ponds and temporary marshes, mainly in winter. Climate in the region is subtropical, with rain distributed along the year, although summer months can be associated with a seasonal water deficit (Klein, 1997).

BIRD SAMPLING

Considering the great differences in abiotic conditions along the year that are supposedly capable to affect bird species abundance and distribution as well as the arrival of different migrants in different seasons, bird sampling took place during 2008 austral winter and during 2009 austral summer. In these seasons one can find major contrasts in abiotic conditions in subtropical coastal ecosystems. Moreover, we did not include spring and autumn in the analysis because many migrants coming from northern hemisphere just pass trough the area in direction of staging areas in Argentina during spring as well as during autumn when they return to breeding sites, with a very briefly permanency in the area (e.g. Vooren and Chiaradia 1990) and supposedly may cause noise in the analysis.

We counted birds in 19 plots (500 x 120 meters) allocated in each habitat. To ensure survey independence (Gotelli and Elisson 2004) we stipulated a buffer of at least 200 meters among samples. We used the area-search method (Ralph *et al.* 1993) to count birds. However, in order to achieve a better performance in our study system, we modified the size and shape of the plot and we did not use a time-based stopping-rule (*sensu* Watson 2003). One of the principal advantages of the area-search is the high detectability of secretive species in grassland-like ecosystems, because one can free-walk around the patches of tall vegetation as well as the crests and slacks of dunes while seeking for birds (Dieni and Jones 2002, Atkinson *et al.* 2006, Roberts and Schnell 2006). Although distance methods represent a straightforward technique to calculate species densities, an obstacle emerges in multiple species studies such as ours, because rare species makes impossible to achieve an adequate sample size of bird detections for the entire community (see Rosenstock et al. 2002).

Two observers covered simultaneously each plot, being each one responsible for sampling a half-section while progressing through the full length of the plot. As recommended by Roberts and Schnell (2006), we covered all points located 10 m inside the perimether of the plots. We walked at the same rhythm and communicated frequently to ensure that individual birds were not double-counted.

We counted all individuals seen or heard within the plot area. Birds in flight were considered only if foraging up to 30 m above the plot. In order to avoid sampling bias, surveys were realized only in the first four hours after sunrise in clear days with wind speed lower than 5 on the Beaufort scale (Bibby *et al.* 1992, McCoy *et al.* 2001). In each season, we spent two days to sampling in grasslands, another two days to sampling in dunes and only one day on the beach due logistic reasons. We used 12 x 50 binoculars to help find and identify birds and a hand-held GPS unit with a 5 m error to assess distances. Scientific nomenclature and taxonomic sequence follows South American Classification Committee (SACC, Remsen et al. 2011).

ENVIRONMENTAL VARIABLES

The environmental variables assessed inside each sample were: average of vegetation height, vegetation heterogeneity, sand cover, water cover and number of cactuses and shrubs.

In order to measure vegetation height we defined nine strips, separately by 50 meters from each other and oriented transversally in relation to bird survey direction. In each strip, we measured vegetation height in 24 points interspaced by 5 meters from an edge to another, totalizing 216 measures by transect.

To assess vegetation heterogeneity, we utilized the heterogeneity index proposed by Wiens (1974), based on the values of vegetation height, according with the equation $H.I.=\sum(\max - \min) / \sum \text{averages}$, where amplitudes inside each strip are summed and divided by the sum of averages in each strip.

The percentage of sand cover and water cover were visually estimated inside each sample. Shrubs and cactuses were considered a single variable and thus quantified as one.

BUILDING THE AVIAN PHYLOGENETIC TREE

The entire evolutionary history of birds remains unresolved and there is not a unique and unambiguously accepted source of avian phylogenetic tree. In order to eliminate this problem, our analyses have been performed using two avian phylogenies. The first phylogeny was Sibley and Alquist’s (1990) molecular “tapestry” based on DNA-DNA hybridization methods. We used a second phylogeny to compare the extent to which our results are sensitive to different reconstructions of avian evolutionary history. The second phylogeny was Hacket et al. (2008), which is based on phylogenomics. Although this robust methodology employed by Hacket and co-workers was able to corroborate some results of Sibley and Alquist's work, other unexpected differences were found, like the sister relationship between Passeriformes and Psittaciformes, with Falconidae as sister to this latter clade. Other important distinction among the phylogenies is the distance of separation between Accipitridae and Falconidae. Nonetheless, the main difference in these two phylogenies is the number of taxa assessed. While Sibley and Alquist's work is focused in almost the complete class, from orders through families and genera to species, Hacket et al. (2008) is restricted to families and rarely to some genera. Thus, when it was the case, we completed the absent information in Hacket et al. (2008) with other sources as follows: for Anatidae (Eo et al. 2009); for Threskiornithidae (Malaver 2011); for Ardeidae (Sheldon et al. 2000); for Charadriformes (Thomas et al. 2004); for Accipitridae (Griffiths et al. 2007); for Tyrannidae (Ohlson et al. 2008); for Furnaridae (Derryberry at al. 2011); for Hirundinidae (Sheldon et al. 2005); for Motacilidae (Voelker 1999); for Icteridae (Lanyon and Omland 1999); and for Emberizidae (Jonsson and Fjeldsa 2005).

PHYLOGENETIC STRUCTURE OF AVIAN COMMUNITIES

Based in the literature we constructed the phylogenetic relationships among species using the software Mesquite 2.74 (Madison and Madison 2010) and exported a matrix containing a phylogenetic pairwise distances (D_F) from it, based in the number of node counts (Fig. 1).

The phylogenetic structure of avian communities in habitats embedded along the coastal gradient (i.e., sandy beach, dunes and grasslands) was evaluated using the net relatedness index (NRI, Webb 2000), through the statistical software R (Version 2.11.1 for Mac). The statistical significance of each observed NRI value was tested by comparing it with 999 NRI values computed under "richness" null model, which randomize community data matrix abundances within samples, maintaining sample species richness (available at Picante package in R statistical software). All species in the metacommunity were included in the phylogenetic pool. For $\alpha = 0.05$, positive NRI values with $p \leq 0.025$

indicate phylogenetic clustering, while negative values with $p \geq 0.975$ indicate phylogenetic overdispersion. Otherwise ($0.025 > p < 0.975$), phylogenetic randomness in the community is assumed. NRI values for communities occurring in different habitats along the coastal gradient were compared through analysis of variance (ANOVA) using the Fisher's correction.

We also used a fuzzy set algorithm to ponder the information in matrix D_F with the values of species abundances per samples (W), generating a matrix P containing phylogeny-weighted species composition for each sample (Pillar and Duarte 2010). So that, matrix P determines degrees of phylogenetic relatedness among species co-occurring in the same samples, which means that species of the same genus receive a proportionally higher fraction of similarity from each other, than more distantly related species (e.g., from a different genus). Duarte (2011) proposed an improvement of this method by performing a principal coordinates analysis (PCoA, Legendre and Legendre 1998) on matrix P, based on square root of Bray-Curtis dissimilarities between samples to generate a principal coordinates of phylogenetic structure (PCPS). Thus, each PCPS is an eigenvector describing an independent phylogenetic gradient in the ecological community (Duarte 2011, Duarte, Prieto and Pillar in press.)

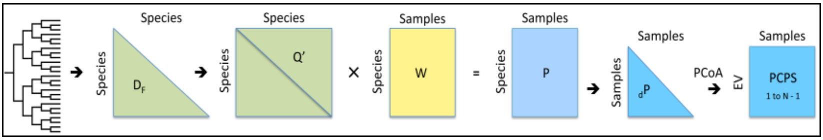


Figure 1: A schematic overview of the methodological steps used to calculate PCPS. Matrixes correspond to: D_F = distance pairwise matrix based on number of node counts in phylogenetic tree; Q' = a square matrix derived from D_F containing degrees of phylogenetic relatedness among species; W = species abundances by samples; P = information of phylogeny weighted species composition. At this point, a principal coordinates analyses on P generates the matrix containing PCPS, which contains eigenvectors (EV) by samples. Each PCPS could potentially be used in subsequent analyses as synthetic response variables containing phylogenetic information for the community. (Figure modified from Pillar and Duarte 2010 and Duarte, Prieto and Pillar in press).

SELECTING A SUBSET OF PCPS FOR POSTERIOR ANALYSIS

Although all PCPS generated in the analysis could potentially be used as dependent variables to assess the causal effects of environmental variables on phylogenetic structure, this practice must be avoided in order to minimize bias (Duarte, Prieto and Pillar in press). Since each PCPS is an orthogonal axis representing a phylogenetic gradient, some of them are likely residuals and thus, using all of them could introduce noise in the analysis. A selection procedure proposed by Duarte and co-workers (in press) consists in performing a series of distance-based redundancy analyses (db-RDAs) (Legendre and Legendre 1998) using an increasing number of PCPS, starting with that containing the largest percentage of variation in matrix P. Thus, one must keep in the posterior analysis the subset containing the number of PCPS that maximizes the F-value, which consequently minimize the residual sum of squares. The db-RDAs were runned using all the five environmental variables as explanatory descriptors.

FORWARD SELECTION OF EXPLANATORY VARIABLES

In order to avoid Type I error and the overestimation of the amount of explained variance on the species abundance data matrix, we followed the double-selection criteria of explanatory variables recommended by Blanchet et al. (2008). As proposed for them, we first ran a global test including all explanatory variables and adjusting the $R^2_{(Y|X)}$ according to Ezekiel´s correction (Peres-Neto et al. 2006). The $R^2_{(Y|X)adj}$ of the global test is then used as a second criterion besides the alpha-value of 0.05 to select which explanatory variables will be kept in the following analyses. The next step consists in performing the forward routine, which we did in software CANOCO 4.5 (Ter-Braak and Smilauer 2002), starting by selecting the available explanatory variable that maximizes model fitting and computing a F-ratio for the analysis. Then, a P-value for the analysis is generated by permutation of residuals under the full model approach (Legendre and Legendre 1998), computing a $R^2_{(Y|X)adj}$ for the forward test whenever a P-value ≤ 0.05 is obtained. If the $R^2_{(Y|X)adj}$ of the forward test is lower than that of the global test, a new variable is added to the analysis and the permutation test is ran again, otherwise, the procedure is stoped.

ASSESING THE RELATIONSHIP BETWEEN ENVIRONMENTAL FACTORS AND PHYLOGENETIC CLADES

The relationship between phylogenetic clades (described by a response matrix containing PCPS) and environmental variables was evaluated trough db-RDA in the statistical software CANOCO 4.5 (Ter Braak and Smilauer 2002). This analysis is based in Monte-Carlo statistics, and we performed 1000 permutations under the full model approach to assess the relationship between PCPS and the matrix of explanatory variables. The portion of the explained variation in such analysis (db-RDA) is given by $R^2_{Y|X|}$, which is called RDA trace in the software CANOCO 4.5 (Ter-Braak and Smilauer 2002). In order to avoid the type I error and the overestimation of the total of explained variation, we adjusted the $R^2_{Y|X|}$ according to Ezekiels correction (Peres-Neto et al. 2006).

RESULTS

Summer. In summer, we recorded 58 bird species distributed in 27 families (2.435 detections). Near a half of the species recorded in summer comprised the families Hirundinidae (10%), Sternidae (9%), Furnaridae (7%), Tyranidae (7%), Motacilidae (7%) and Emberizidae (7%) (Fig. 2). Species richness in each habitat was: 20 on sandy beach, 34 on coastal dunes and 33 on littoral grasslands.

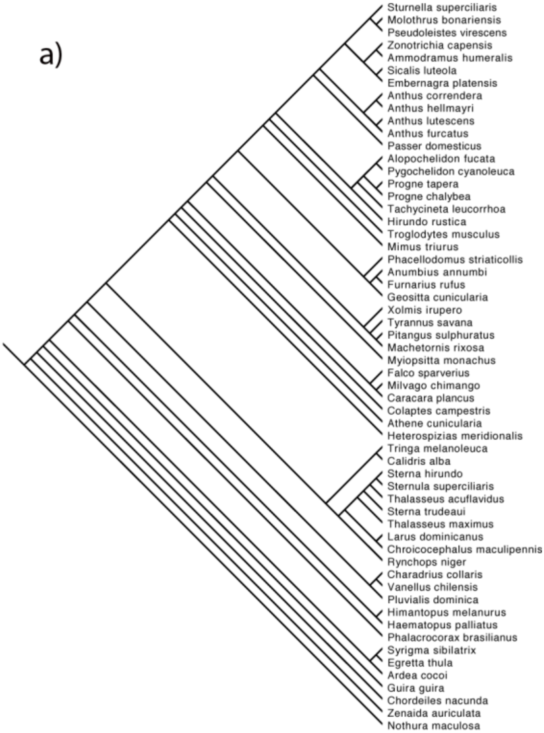
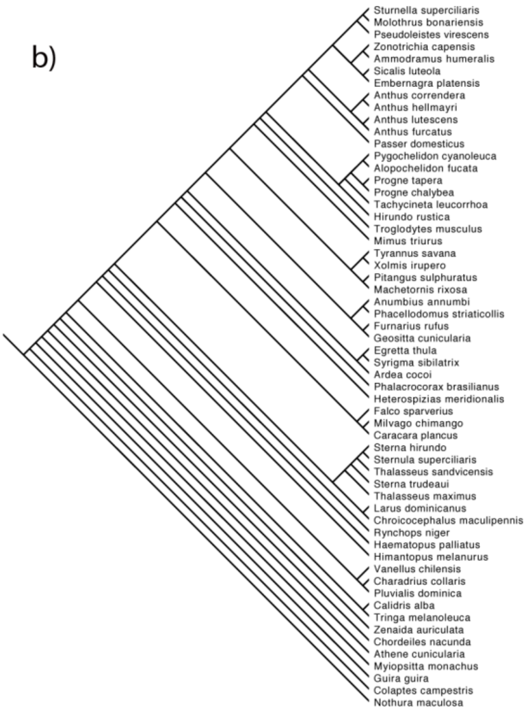


Figure 2. a) Phylogenetic tree based in the "tapestry phylogeny" proposed by Hacket and co-workers (2008); (and other sources; for details about phylogeny reconstruction see the respective section in methods); and b) (next page) phylogenetic tree based in Sibley and Alquist (1990) for avian communities occurring in summer across a gradient of coastal ecosystems in southern Brazil, namely sandy beach, coastal dunes and littoral grasslands.



The analyses of phylogenetic structure revealed that around 60% of the samples in the beach and near to 15% of the samples in coastal dunes presented phylogenetic clustering (i.e., positive NRI values, $p < 0.025$). All the samples in grasslands were phylogeneticaly random in relation to the phylogenetic pool as well as the remaining 85% of the samples in dunes and 40% of the samples in beach. Phylogenetic overdispersion was not observed in any sample. Furthermore, all the habitats differ significantly in respect to NRI values, forming a continuum of increasing positive values from grasslands through coastal dunes to sandy beach, which demonstrate a trend to phylogenetic clustering from grasslands to beach (Table 1 Fig. 3).

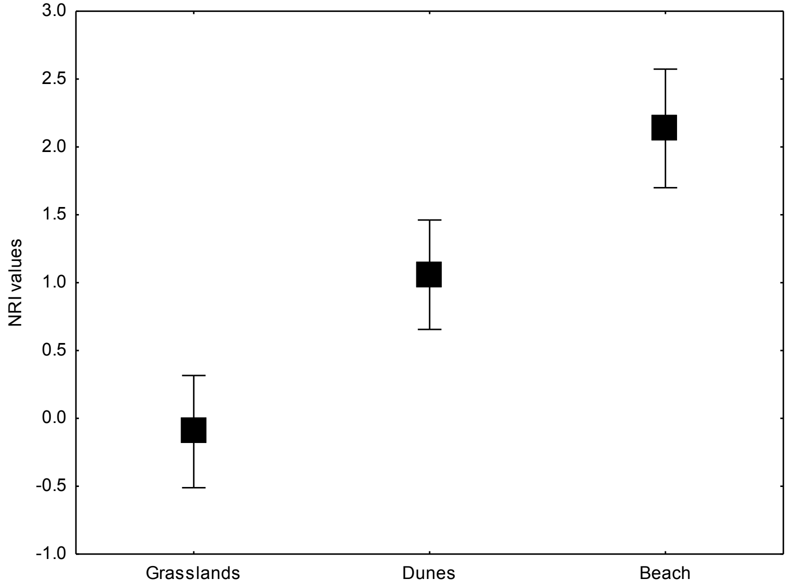


Figure 3. Analysis of variance for net relatedness index (NRI) in coastal habitats embedded across an ecological gradient in summer. Black boxes represented mean values; error bars represent standard errors.

Table 1. Analysis of variance for net relatedness index (NRI) in coastal habitats embedded across an ecological gradient in summer. Contrasts were performed through Fisher's correction.

	Grasslands	Dunes	Beach
Grasslands		***	***
Dunes	***		***
Beach	***	***	

*** $P < 0.0001$

The Principal Coordinates Analysis on matrix P (based in the phylogeny proposed by Hacket et al. 2008) generated 56 PCPS with eigenvalues higher than zero. The first PCPS represented 60.2% of the variation in matrix P, while the second increased 12.8% and the third only 5.5% of the total explained variation in P. Performing the pre-selection procedure of response variables through db-RDA, showed that, the first PCPS presented the lowest residual sum of squares (F = 31.28, $P = 0.001$), and thus, we kept only it as response variable for the subsequent analysis. Including both, the first and second PCPS in the pre-analysis, decreased the F-value to 25.95. The inclusion of the first three PCPS decreased F-values to 21.42, and each posterior increase in the number of PCPS in the forward analyses resulted in decreasing F-values.

Keeping only a single PCPS as response variable resulted in only one axis of ordination in db-RDA. A previous db-RDA on first PCPS, using the forward procedure and taking into account the alpha-value of 0.05, selected two explanatory variables for summer, in decreasing order of importance: average of vegetation height and sand cover ($R^2_{Y|X|adj}$ = 0.726, P = 0.001). Furthermore, the $R^2_{Y|X|adj}$ obtained for that two variables was lower than that of the global test ($R^2_{Y|X|adj}$ = 0.729), which allow us to keep both variables in the model. Thus, we concluded that average of vegetation height and sand cover explained more than 70% of the variation in phylogenetic structure across the gradient of coastal habitats.

The correlation scatter plot shows that phylogenetic clades are segregated across a gradient marked mainly by highest proportion of sand cover in an extreme to a highest proportion of vegetation cover and height in the other (Fig. 4). Basically, derived species clades, such as many families of Passeriformes, were highly associated with habitats more structurally complex, which presented high vegetation cover and height while basal clades, such as Ciconiiformes and Charadriiformes shown the inverse pattern. The observed paterns for both phylogenies sources were very similar, which demonstrate very consistency in the main results independent of phylogenetic tree considered. Thus, we presented the results of Sibley and Alquist (1990) in a supplementary material.

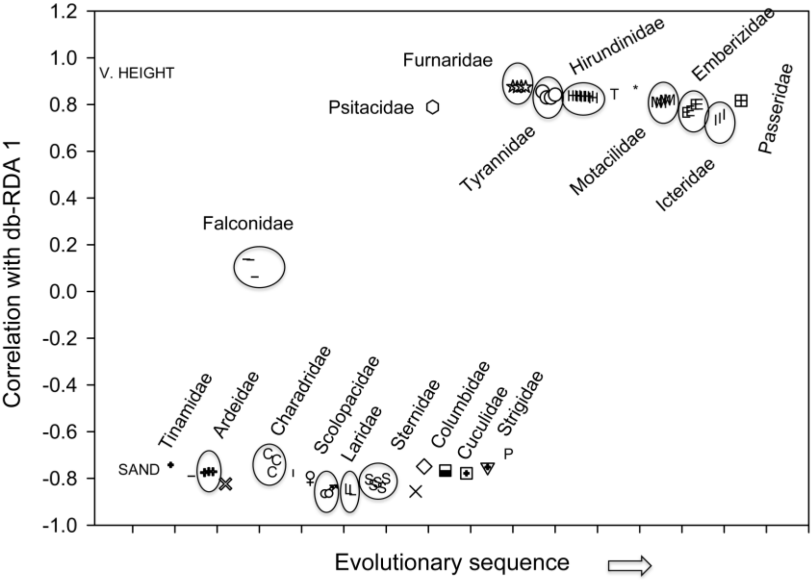


Figure 4. Correlation scatter plot for avian phylogenetic clades and environmental variables showing correlation values with the first axis of distance-based Redundancy Analysis (db-RDA). The X-axis starts with environmental variables (V. HEIGTH = vegetation height; SAND = sand cover) and follow by phylogenetic clades in evolutionary sequence.

Winter. In winter, we recorded a total of 68 avian species distributed in 25 families (2.856 detections), including all transects (n = 57) and habitats. Near half of the total species recorded in winter comprised the families Tyranidae (12%), Furnaridae (10%), Emberizidae (9%), Anatidae (6%), Motacilidae (6%) and Sternidae (6%) (Fig. 4). The number of species recorded in each habitat in winter was: 21 on sandy beach, 33 on coastal dunes and 45 on littoral grasslands.

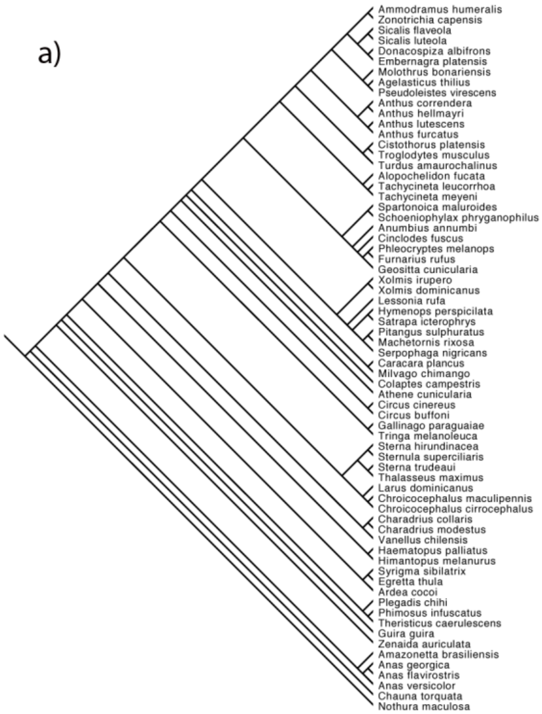
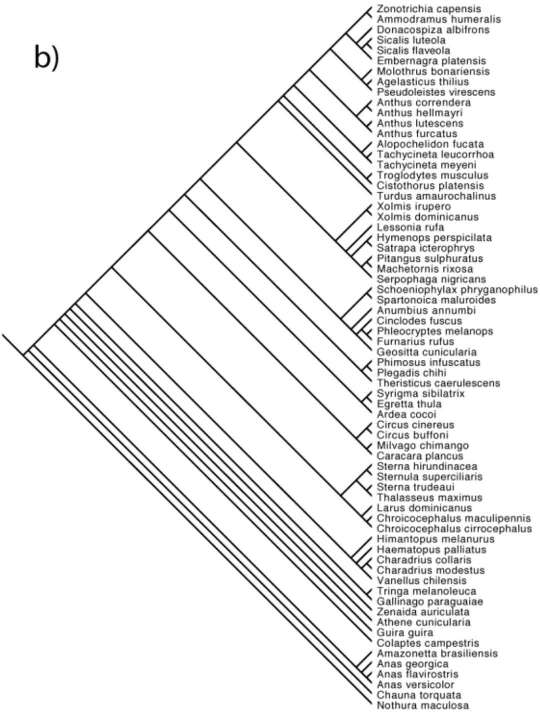


Figure 5. a) Phylogenetic tree based in the “tapestry phylogeny” proposed by Hacket and co-workers (2008) (and other sources; for details about phylogeny reconstruction see the respective section in methods); and b) (next page) phylogenetic tree based in Sibley and Alquist (1990) for avian communities occurring in winter across a gradient of coastal ecosystems in southern Brazil, namely sandy beach, coastal dunes and littoral grasslands.



The net relatedness index revealed that around 58% of the samples in the beach and 26% of the samples in coastal dunes presented phylogenetic clustering (i.e., positive NRI values, $p < 0.025$). All the samples in grasslands were phylogeneticaly random in relation to the phylogenetic pool as well as the remaining 74% of the samples in dunes and 42% of the samples in beach. Phylogenetic overdispersion was not observed in any sample. In addition, there were not differences in NRI values between sandy beach and coastal dunes, but NRI values in grasslands were significantly lower than that of the other two habitats, indicating a trend to phylogenetic clustering from grasslands to coastal dunes and sandy beach (Table 2 Fig. 5).

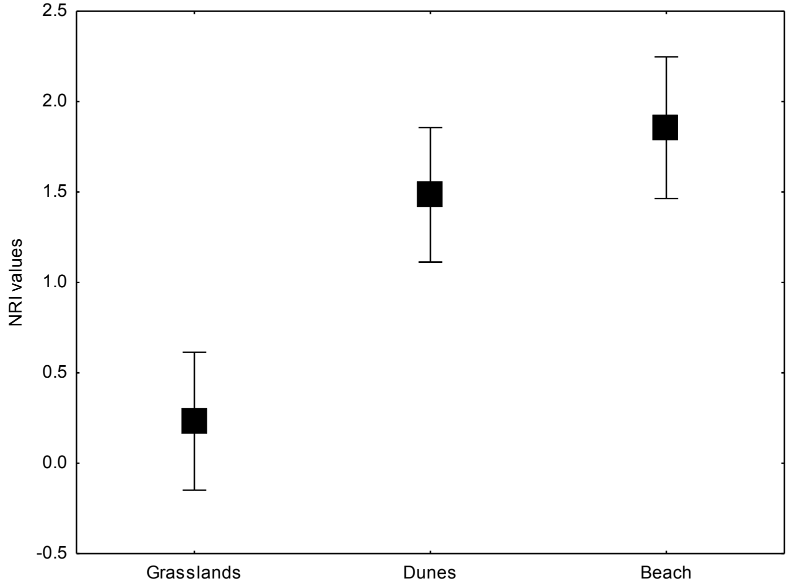


Figure 6. Analysis of variance for net relatedness index (NRI) in coastal habitats embedded across an ecological gradient in winter. Black boxes represented mean values; error bars represent standard errors.

Table 2. Analysis of variance for net relatedness index (NRI) in coastal habitats within an ecological gradient in winter. Contrasts were obtained through Fisher correction.

	Grasslands	Dunes	Beach
Grasslands		***	***
Dunes	***		0.174
Beach	***	0.174	

*** $P < 0.0001$

The Principal Coordinates Analysis on matrix P (based in Hacket et al. 2008) generated 56 PCPS with eigenvalues higher than zero for winter. The first PCPS represented 62.5% of the variation in matrix P, while the second 10.2% and the third increased only 4.5% of the total explained variation in P. Performing the pre-selection procedure of response variables through db-RDA, showed that, the first PCPS presented the lowest residual sum of squares (F = 27.70, $P = 0.001$), and thus, we kept only it as response variable for the subsequent analysis. Including both, the first and second PCPS in the pre-analysis, decreased the F-value to 19.99. The inclusion of the first three PCPS decreased F-values to 18.82, and each increase in the number of PCPS forward analyses resulted in decreasing F-values.

Keeping only a single PCPS as response variable resulted in only one axis of ordination in db-RDA. For winter, only a single explanatory variable was selected, out of five, when the two-criteria selection approach proposed by Blanchet et al. (2008) was performed. Vegetation height was the unique explanatory variable considered, forming a single axis that explained near 65% of the variation in phylogenetic structure across the coastal gradient ($R^2_{Y|X|adj} = 0.645$, $P = 0.001$).

The correlation scatter plot shows that phylogenetic clades are segregated across a gradient marked mainly by high proportion of vegetation cover and height in an extreme to low proportion of vegetation cover and height in the other (Fig. 6). Basically, derived species clades such as many families of Passeriformes were highly associated with habitats more structurally complex, which presented high vegetation cover and height while basal clades, such as Anseriformes, Ciconiiformes and Charadriiformes shown the inverse pattern. Falconidae was the only non-passeriforme family also positively correlated to PCPS1.

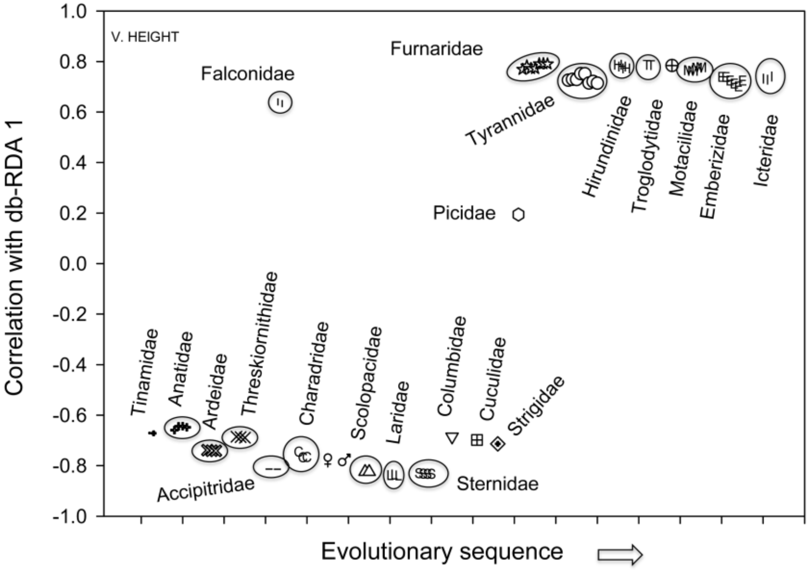


Figure 7. Correlation scatter plot for avian phylogenetic clades and environmental variables showing correlation values with distance-based Redundancy Analysis (db-RDA) axis. The X-axis starts with the environmental variable included in the model (V. HEIGTH = vegetation height) and follow by phylogenetic clades in evolutionary sequence.

Discussion

The integration of species' phylogeny in the analysis of community ecology allows the linkage between continental and global processes to that occurring at small spatial and temporal scales, like the role of species interactions and local environmental conditions driving communities' assembly (Cavender-Bares et al. 2009). Here we presented a first essay to a better comprehension of avian communities phylogenetic relationships in subtropical coastal habitats of Southern Brazil. Our results showed that there is a trend to avian phylogenetic clustering from grasslands, which is the more sheltered habitat, through coastal dunes to sandy beach. In our study area, a gradient of stressing conditions emerges from landwards to seawards, due to an increase in salinity spray, strong wind conditions and wave impacts near the sea. These stressing conditions, combined with the simplified habitat structure in the sandy beach, limit the kind of food resources that are available for bird species in comparison to other adjacent habitats, resulting in phylogenetic clustering. Gradients of stressing environmental conditions could lead to phylogenetic clustering due to environmental filtering processes (Graham et al. 2009), although contradictory results have been reported when species interactions represent a major force (e.g., Cavender-bares et. al. 2004 for Oak communities). Besides the inconsistency in phylogenetic clustering/overdispersion paterns across stressing gradients that have benn reported in the literature, the largest amount of studies relating communities' assembly and phylogenetic structure has focused on plants, and a little proportion of the studies considering vertebrates has focused on birds, which makes difficult to draw generalizations (Vamosi et al. 2009, Cavender-Bares 2009). In this way, our results represents an approximation of the need to evaluate a broader range of taxonomic groups to unravel patterns about variation in community structure along ecological gradients.

While taxonomic beta diversity indices captures the amount of variation in species composition between sites (e.g., plots, habitats, landscape types) (Anderson et al. 2011), it does not provide information about the evolutionary relationships among these lineages, which can provide different insights about the ecological and historical mechanisms underlining communities assembly (Hardy and Senterre 2007, Graham and Fine 2008). Here, we demonstrated that avian phylogenetic variation across the coastal gradient is strongly related to changes in vegetation cover and structure, even though in so juxtaposed habitats, which means that some avian lineages have differentiated earlier in their life history to exploit resources in sandy beaches and other in grasslands and did not have changed their traits enough to allow a good performance in the other habitat type. In addition, it was clear that ancient lineages, like Ciconiformes and Charadriformes are related to the structurally homogeneous sandy beach, while recent derived lineages like many families of Passeriformes occupy habitats with higher proportion of vegetation cover and height. Habitat heterogeneity and vegetation structure provide different food resources, perches, nest sites and refuge from predators (Wiens 1994). Passerine birds have evolved different mechanisms and behaviors to explore many kinds of food items, such as seeds (e.g., Emberizidae), insects in the ground (e.g. Icteridae, Motacilidae) and in the air (e.g. Hirundinidae, Tyranidae) flying over grasslands and dunes. These varieties of diet specializations and behaviors allow niche partitioning in more complex habitats (Mac Arthur 1961, Mac Arthur and Wilson 1967, Tews et al. 2004). Although some shorebird species can use littoral grasslands as staging areas during non-reproductive periods (Blanco 2006, Belton 1994) the majority of them are mainly associated to mudflats and sandy shores ecosystems, where they feed upon benthic macro invertebrates (Vooren and Chiaradia 1990). Indeed, many Charadriiformes such as shorebird species (Charadriidae an Scolopacidae) and seabird species (Laridae and Sternidae) are diet specialists that present little diversification within families and genus (Harrison 1986), i.e., they present strong niche conservatism (Bennet and Owens 2006).

Through the analysis of phylogenetic variation in the structure of local communities within an ecological gradient framework we started to evaluate the interaction between patterns caused by historical processes associated with traits evolution and local processes ocuuring nowadays such as competition and environmental filtering. Here, we have focused on a local scale view in an attempt to quantify the environmental forces structuring avian communities in coastal ecosystem. However, broader scale analyses including explicitly modeling spatial patterns could yield different insights into what factors might structure ecological communities. In addition, future research should evaluate how abiotic and biotic factors shape avian communities by explicitly incorporating traits associated with food exploitation, competition, and flight performance into analyses of community structure.

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APPENDIX 1. Suplementary material showing the percentage of explained variation on phylogenetic clades across the ecological gradient considering the phylogenetic tree proposed by Sibley and Alquist (1990).

a) Percentage of explained variation on matrix P considering the first three individual PCPS.

Axis	Percentage of explained variation on matrix P
First – PCPS 1	55.34%
Second – PCPS 2	10.60%
Third – PCPS 3	8.08%

b) Total of explained variation on PCPS 1 considering environmental variables of interest that maximizes F - value.

Number of PCPS	Environmental Variables considered	$R^2_{(Y\|X)adj}$
1 – PCPS 1	Vegetation height; percentage of sand cover	0.616

CONCLUSÕES GERAIS

Neste estudo, ficou demonstrado que as aves, apesar de serem organismos altamente móveis, possuem distribuições restritas às porções de habitats que abrigam as condições e os recursos de que necessitam. Gradientes ecológicos bem definidos resultam em grande variação na composição de espécies de aves. Ademais, porções de hábitat mais heterogêneas possuem maior riqueza em espécies do que locais estruturalmente mais simples. Maiores valores de equitabilidade ocorreram associados a ambientes mais heterogêneos, instáveis e com escassez de recursos alimentares. A chegada de espécies migratórias neárticas, neotropicais e patagônicas em distintas épocas do ano, somada a alterações nas características ambientais provocadas por ciclos sazonais, características de regiões subtropicais, acarretam uma grande variação na composição de espécies ao longo do ano.

Foi possível demonstrar ainda que as variáveis ambientais exercem importante influência na distribuição das espécies de aves. O arranjo espacial das amostras, definido em nosso delineamento amostral, demonstrou que a estrutura dos habitats em ambientes costeiros seguem um padrão espacialmente estruturado, possivelmente em função de fatores de estresse ao longo do gradiente de distância do mar. Por sua vez, esse gradiente exerce efeitos diretos e/ou indiretos sobre as comunidades de aves.

Concluiu-se que as respostas das espécies de aves ao longo do gradiente costeiro é reflexo de suas histórias evolutivas. Houve um forte sinal filogenético na estruturação das comunidades de aves, o que demonstra que espécies filogeneticamente relacionadas exploram semelhantes porções de hábitat ao longo do gradiente costeiro.