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 can be explained by different metacommunity paradigms, which are not mutually exclusive. While species sorting emphasizes the role of habitat features in affecting species composition, the neutral model suggests that constraints on dispersal are key assembly factors. We assessed the role of environmental features and spatial descriptors at multiple scales, in affecting avian beta diversity across a gradient of coastal habitats in southern Brazil. During the winter 2008 and summer 2009, we counted birds in 57 plots on a sandy beach and in coastal dunes and coastal grasslands (19 plots per habitat). We measured the structure of the herbaceous vegetation, the number of individual cactuses and shrubs, and the percentages of sand and water cover on each plot. We generated spatial filters by means of principal coordinates of neighbour matrices. We used variation partitioning based on redundancy analysis to decompose the fraction of beta diversity explained by environmental features and spatial descriptors at the scale of the entire gradient and within each habitat type. In both seasons, environmental variables explained 33% of beta diversity across the entire gradient. A third of this amount could also be explained by space, representing the fraction of species and environmental variables that were spatially structured. Pure environmental processes explained about 22% of beta diversity. Pure spatial control was weak at this larger scale. The opposite pattern was found within each habitat type, as there was no environmental control and neutral processes became dominant at this smaller scale. Our study thus presents a case where the strong environmental gradient filters out different species at the largest scale, whereas stochastic processes and spatial autocorrelation increase with loss of environmental heterogeneity within habitat types.

Key words: metacommunity, neutral dynamics, spatial descriptor, species sorting, variation partitioning.

INTRODUCTION

An ecological community is viewed as the result of a series of nested processes occurring on multiple scales and determining which species co-occur in space and time. Basically, these processes refer to: (i) dispersal capacity of species from the regional pool (Louette & De Meester 2005); (ii) environmental conditions in the local habitat patch (Cottenie *et al.* 2003); and (iii) species interactions (Cottenie & De Meester 2004). Traditionally, however, much of formal community theory has been focused on a single scale, assuming that local communities are closed and isolated. During the past decade, the 'metacommunity' concept has gained much attention, uniting regional and local dynamics in a more inclusive theory, allowing new insights about community assembly by explicitly recognizing that the processes determining the distribution, abundance and interactions of organisms occur at multiple scales (Leibold *et al.* 2004). Further empirical studies focusing on these questions are necessary to increase our comprehension of the organization and functioning of ecological communities, as well as to provide a sound theoretical basis for their management and conservation (Legendre *et al.* 2005).

A central concept in ecological community theory is beta diversity, which was first defined as the differences in species identities among sites within a region of interest (Whittaker 1960). Recent advances in metacommunity theory have led to a better understanding of the underlying causes of beta diversity. One of the most important was the definition of four perspectives on the organization of metacommunities: neutral model, patch dynamics, mass effects and species sorting (Leibold *et al.* 2004), which are not mutually

exclusive. These models can be used to assess the origin and maintenance of beta diversity, as they place different weights on the importance of dispersal constraints, environmental heterogeneity and biotic and abiotic interactions for local species persistence. A recent review by Logue et al. (2011), however, pointed out the difficulties involved in disentangling the metacommunity models, because of some overlap in their predictions. Winegardner et al. (2012) recently proposed that patch dynamics and mass effects should be viewed as special cases of species sorting, as both models postulate asymmetrical competitive abilities among species, but patch dynamics assumes limited dispersal rates, whereas mass effects postulates excessive dispersal rates. Thus, the neutral model and species sorting can be viewed as the endpoints of a continuum of processes acting on the organization of communities on different scales.

According to the neutral model, all species are competitively equal and not specialized in specific environmental conditions, so differences in distributions are created by differences in demographic and dispersal rates (Hubbell 2001). Thus, irrespective of environmental features, contagious biotic processes including birth, death and migration might lead to autocorrelation in species composition patterns, because the colonization probability of a site would decay with the distance from species 'origins' (Rosindell et al. 2011). Accordingly, the greater the distance among sites, the greater will be the variation in species composition among them.

Contrary to the relatively recently proposed neutral theory (Hubbell 2001), niche theory is deeply rooted in ecological community thinking (Hutchinson 1957; Leibold 1995). Its predictions assume that the presence and abundance of species in a community are determined by environmental conditions and species interactions (e.g. Keddy 1992; Cottenie et al. 2003). Niche theory is the basis of the species sorting metacommunity model (Leibold et al. 2004) and there is some evidence that this may be the most common process operating in nature (Cottenie 2005). According to species sorting, propagules of all species are able to reach all habitat patches, but they only survive and establish in sites that provide suitable environmental conditions (Cottenie & De Meester 2004). Therefore, community composition has a close association with environmental features, and does not show relationships to the spatial configuration of patches, unless the environmental conditions are also autocorrelated in space.

A starting point to assess the relative importance of the metacommunity processes for community assembly is to consider environmental and isolation gradients as sampling scenarios (Legendre et al. 2005), and this is the context of our study. The method of variation partitioning allows one to decompose the percentage of beta diversity explained by pure environmental control, pure spatial causes and their shared effects (Legendre et al. 2005). Accordingly, one can assume that: (i) a predominance of pure environmental control in affecting beta diversity indicates species sorting; (ii) a predominance of the pure spatial signal indicates dispersal constraints and strengthens neutral dynamics; and (iii) the shared effects of environmental and spatial control on beta diversity suggest species sorting, dispersal limitation or a combination of both (Cottenie 2005; Winegardner et al. 2012).

The relative importance of metacommunity processes is expected to be scale-dependent (Declerck et al. 2011) and also to vary among different ecosystems and different organism groups, because of changes in edge permeability and differences in dispersal rates among species (Logue et al. 2011). From an applied point of view, if beta diversity is high and species composition is closely related to environmental features, protected areas must be planned considering the mosaic of environmental conditions (Legendre et al. 2005). Conversely, if species distributions are autocorrelated in space but randomly related to environmental characteristics, each increase in the size of a reserve would probably encompass new species (Legendre et al. 2005). In a situation such as this, reserves must be as large as possible to include higher species diversity. There is limited empirical research on metacommunity organization in terrestrial coastal ecosystems, especially those involving highly mobile vertebrates, such as birds, which hinders generalizations (Logue et al. 2011). Furthermore, the relatively few studies on avian metacommunities have yielded contradictory results. For example, while environmental forces were the main drivers of avian beta diversity in temperate forests in Chile (Meynard & Quinn 2008), the opposite pattern was found for avian communities in Australia, which showed a strong spatial signal (Driscoll & Lindenmayer 2009).

Birds perform important roles in ecosystem functioning. They act, for example, as top predators that control potential pests, genetic linkers by seed and pollen dispersal, and resource linkers contributing to material flux within and among ecosystems (Sekercioglu 2006). The composition of avian communities varies substantially in time and space, as bird species are individually involved in many potential interactions (Bennett & Owens 2006). Moreover, birds are a very diverse group, with many species responding promptly to subtle changes in environmental conditions (Bennett & Owens 2006). Thus, they constitute an appropriate model group for exploring ecological issues such as assessing the relative roles of metacommunity models underlying community organization.

In order to contribute to the discussion of these issues, we assessed the independent and shared effects of environmental variables and space on avian beta

diversity at multiple scales across a gradient of coastal ecosystems. In a first set of analyses, we considered the entire length of the gradient formed by the sandy beach, dunes and grasslands. Our predictions were as follows: (i) as birds are sensitive to habitat quality, the strong environmental gradient will result in high beta diversity and a predominance of species sorting; (ii) because of differences in physical and chemical stressors across the gradient from the most exposed sandy beach to sheltered habitats landward, species composition and environmental features are expected to be spatially structured; and (iii) as birds are very mobile organisms and there are no well-defined barriers to dispersal in our study region, space alone will not play an important role in beta diversity. Additionally, by conducting a second set of analyses focused on beta diversity within each habitat type, we derived the following hypotheses: (iv) as environmental heterogeneity within each habitat type is much lower than between habitat types, the relative influence of species sorting on beta diversity would decrease at this scale; and (v) as the distance between habitats is shorter than the longest distance between plots within each habitat, the relative role of spatial structure will increase when the dataset is analysed within each habitat category.

METHODS

Study area

This study was conducted in three contiguous coastal ecosystems (sandy beach, dunes and grasslands) located south of the Lagoa dos Patos outlet, near the seaside resort of Cassino (32°11′S, 52°10′W), Rio Grande municipality, Rio Grande do Sul state, Brazil. There is a strong physical gradient from a highly homogeneous sandy beach on the seaward side, an intermediate situation consisting of partly vegetated sandy dunes, to well-vegetated grasslands on the landward side.

The beach is long, gently sloping and fine-grained, with a wide intertidal zone. These conditions favour the occurrence of an abundant and diverse invertebrate fauna that provides abundant food for coastal birds, several of them Nearctic and Patagonian migrants (Gianuca 1983; Vooren & Chiaradia 1990).

The upper part of the beach is a system of coastal dunes partly stabilized by native herbaceous vegetation. Low incipient dunes are covered by the sand-fixing pioneer *Blutaparon portulacoides*, and the much higher primary dunes are covered by the perennial *Panicum racemosum* (Gianuca 1997). Other important plant species are *Spartina ciliata*, *Hydrocotyle bonariensis*, *Andropogon arenarius* and *Androtrichum tryginum* (Seeliger *et al.* 1997). Two introduced species of shrubs, *Acacia longifolia* and *Tamarix gallica*, occur sparsely in some sectors.

The coastal grasslands are located immediately behind the dunes and support many species of native plants of the families Poaceae, Leguminoseae, Cyperaceae and Umbelliflorae that form a mosaic of prostrate vegetation mixed with variably sized patches of taller herbaceous plants, mainly *Androtrichum trigynum* and *Juncus acutus*. The vertical structure of the vegetation ranges from 1 to 90 cm. Shrub species such as *Schinus terebinthifolius* and *A. longifolia* and cactuses occur sparsely in some places.

The regional climate is warm-temperate (Klein 1997). Mean annual temperature is 17°C; July and January are the coldest and warmest months, with mean temperatures of 13°C and 24°C, respectively (Klein 1997). Precipitation is well distributed along the year and is slightly higher from June to October (Klein 1997). Evaporation is high during the summer (Klein 1997). These patterns result in the flooding of lower areas and depressions in the dunes and grasslands during the winter and spring, which develop into temporary ponds and marshes.

Bird surveys

To account for differences in abiotic conditions and the migratory behaviour of part of the avifauna, we restricted sampling to the 2008 austral winter and 2009 austral summer. In these seasons one can find major contrasts in abiotic conditions in local coastal ecosystems (Klein 1997; Seeliger *et al.* 1997). We did not include the spring and autumn in the analysis because many migrants merely pass through our study area while heading to and from staging areas in Argentina (see Vooren & Chiaradia 1990), which presumably could introduce noise into the analysis.

We counted birds in 19 plots (500 × 120 m) allocated in each habitat. Minimum and maximum distances among sampling plots were 0.2 km and 25 km, respectively. We used the area search method (Ralph *et al.* 1993) to count birds. In this method one or more observers walk for 20 min through three search areas inside a plot of variable size, tracking down unfamiliar calls and quiet birds (Ralph *et al.* 1993). One of the principal advantages of the area search method is the high detection rate of secretive species in open environments, because one can investigate different habitat features within the plot in search of secretive species (Dieni & Jones 2002; Atkinson *et al.* 2006; Roberts & Schnell 2006). In order to achieve a better performance in our study system, we modified the size and shape of the plot and the number of search areas, and did not use a time-based stopping rule (*sensu* Watson 2003).

Two observers covered each plot simultaneously. Each observer was responsible for sampling a half-section search area 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 perimeter of the plots. We walked at the same pace, 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 included only if foraging up to 30 m above the plot. In order to avoid sampling bias, surveys were conducted only in the first 4 h after sunrise on 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 2 days sampling in grasslands and 2 days sampling in dunes. Because of the high detection of birds on the beach, we moved by car along the sampling units, which allowed us to spend less time inside each plot and to avoid double-counts of highly mobile shorebirds. Thus, we spent only 1 day sampling on the beach. We used 12 × 50 binoculars to locate and

identify birds and a hand-held GPS unit with a 5 m error to assess distances. Scientific nomenclature and taxonomic sequence follow the South American Classification Committee (Remsen *et al*. 2011).

Environmental variables

In each plot we measured the following environmental variables: vegetation height, vegetation heterogeneity (as an index of vegetation heterogeneity, see below), sand cover, water cover and the number of individual cactuses and shrubs.

To determine the height of the vegetation in a given plot, we defined nine strips within it, separated by 50 m from each other and oriented transversely to the long axis of the plot. In each strip we measured the height of the vegetation at 24 points 5 m apart, totalling 216 measurements per plot. We then calculated the mean of all 216 measurements and used this value as an estimate of the height of the vegetation in a plot.

To assess the heterogeneity of the herbaceous vegetation, we used a heterogeneity index proposed by Wiens (1974) and based on the values of vegetation height, according to the following equation: $H.I. = \Sigma(max - min)/\Sigma means$, where amplitudes inside each strip are summed and divided by the sum of the means in each strip.

The percentages of sand cover and water cover were estimated visually within each plot. We counted all individual shrubs and cactuses present in a given plot and used the total value as a measure of the amount of woody vegetation per plot.

Statistical analyses

Generating spatial descriptors

The geographical coordinates (Universal Transverse Mercator) of the samples were taken using a hand-held GPS. We then generated spatial variables using the method of principal coordinates of neighbour matrices (PCNM) described by Borcard and Legendre (2002). The PCNM approach allows one to assess different spatial structures over the entire range of scales encompassed by the geographical sampling area. The first PCNMs generated in the analyses represent broader spatial scales, and the last ones cover finer spatial structures. The method consists of calculating a truncated Euclidean distance matrix from the geographical coordinates of the sampling sites and subsequently performing a principal coordinates analysis to extract eigenvectors associated with positive eigenvalues, which can be used as explanatory variables in multiple regression analyses (Borcard & Legendre 2002). We first generated spatial descriptors, taking into account the entire length of the gradient studied (including all 57 plots) and afterwards we also created PCNMs including only the subset of 19 plots within each habitat type. This allowed us to analyse different spatial scales across the gradient. PCNM analyses were performed in R (v2.15.0; R Development Core Team 2012).

Forward selection of explanatory variables

In order to avoid type I error and overestimating the amount of explained variance in the species abundance data matrix,

we followed the double selection criterion of explanatory variables recommended by Blanchet *et al*. (2008). We first ran a global redundancy analysis (RDA) 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 in addition to the alpha value of 0.05 to select explanatory variables which will be retained in the following analyses. The next step consists of performing the forward routine, starting with the selection of the available explanatory variable that maximizes model fitting and computing an F-ratio for the analysis. Then, a P-value for the analysis is generated by permutation of residuals under the full model approach (Legendre & 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 included in the analysis and the permutation test is repeated; otherwise, the procedure is stopped. We performed the forward selection of both sets of explanatory variables (environmental *vs*. spatial) separately in the R statistical package (v2.15.0; R Development Core Team 2012).

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 *et al*. 1992). As proposed by Peres-Neto *et al*. (2006), we used a three-step approach to disentangle environmental and spatial drivers of beta diversity based on RDA: (i) we ran a first RDA based on both sets of predictor matrices ($\mathbf{X}$ = environmental; $\mathbf{W}$ = spatial); (ii) a second RDA based on matrix $\mathbf{X}$ and removing the effect of $\mathbf{W}$; and (iii) a third RDA based on matrix $\mathbf{W}$ and removing the effect of $\mathbf{X}$. The proportion of the explained variation in this analysis (RDA) is given by R^2. In order to avoid type I error and overestimating the total explained variation, we adjusted the $R^2_{Y|X|}$ according to Ezekiel's correction (Peres-Neto *et al*. 2006). Before running the series of RDAs, bird abundance values were Hellinger-transformed in order to eliminate the wide disparity in magnitude among them and to increase the ecological meaning of the analysis (Legendre & Gallagher 2001). The variation partitioning technique, which we performed in R (v2.15.0; R Development Core Team 2012), was first used to assess the environmental and spatial drivers of beta diversity across the entire length of the gradient (i.e. by considering all 57 plots together), and afterwards considering only the subset of 19 plots sampled within each habitat category.

RESULTS

Variation partitioning across the entire gradient

Summer

In the summer we recorded 58 bird species distributed in 27 families (2435 detections in 57 plots). We
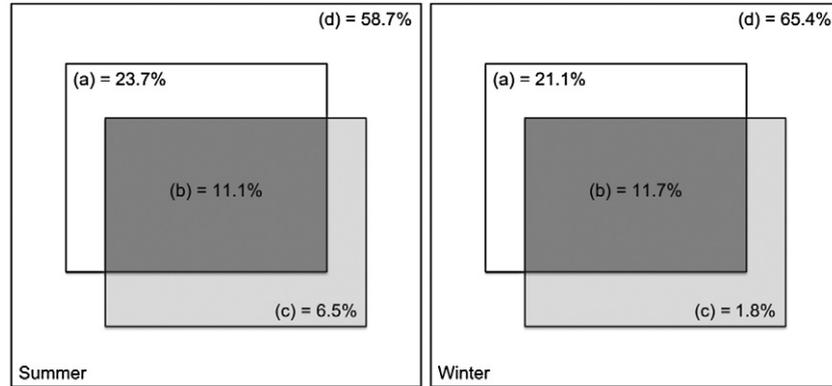
Fig. 1.   Venn diagrams representing the percentage of variance in species composition data in summer (left) and winter (right) explained by: (a) environmental variables; (b) the shared effects of space and environmental features; (c) spatial descriptors alone; and (d) the fraction that remained unexplained.

recorded 20 species on the beach, 34 in dunes and 33 in grasslands (see Appendix S1).

A previous RDA using the forward procedure and taking into account the alpha value of 0.05 selected three explanatory variables in decreasing order of importance: sand cover, vegetation height and vegetation heterogeneity ($R^2_{Y|X|adj} = 0.348$, $P = 0.001$). The P-values for the fourth and fifth variables were higher than 0.05.

The analysis of spatial filters based on geographical coordinates generated 18 spatial descriptors (PCNMs). The forward procedure initially selected five spatial descriptors in decreasing order of importance: PCNM3, PCNM1, PCNM2, PCNM4 and PCNM6 (accumulated $R^2_{Y|X|adj} = 0.193$, $P = 0.001$). However, the $R^2_{Y|X|adj}$ obtained for these five PCNMs was higher than that of the global test ($R^2_{Y|X|adj} = 0.177$), indicating a type I error. For this reason we eliminated the fifth spatial descriptor (PCNM6), decreasing the $R^2_{Y|X|adj}$ to 0.175.

Variation partitioning based on RDAs showed that space and environment together explained around 41% of the beta diversity in our study area in the summer ($R^2_{Y|X,W|adj} = 0.413$, $P = 0.001$) (Fig. 1 left). Approximately 35% of the variation in the species composition data was explained by environmental variables (fraction $a + b$ in Fig. 1) ($R^2_{Y|X|adj} = 0.348$, $P = 0.001$). As nearly a third of this contribution could also be predicted by PCNMs (fraction b in Fig. 1), we concluded that a significant proportion of the species composition and environmental data was spatially structured. Environmental features alone explained the largest proportion of beta diversity (approx. 24%), thus strengthening the 'species sorting' paradigm (fraction a in Fig. 1) ($R^2_{Y|X|adj} = 0.237$, $P = 0.001$). The pure spatial control comprised the smallest proportion of the explained beta diversity across the entire gradient (fraction c in Fig. 1) ($R^2_{Y|W|adj} = 0.065$, $P = 0.001$).

The best predictive variables organized along the first axis were sand cover and vegetation heterogeneity,

while vegetation height and the spatial filters were mainly correlated with the second axis. We generated a RDA biplot based on samples, environmental variables and spatial descriptors (Fig. 2 left), which indicated that the dune plots were characterized by the tallest vegetation and an intermediate proportion of sand cover. Beach plots showed a higher proportion of sand cover, while grassland plots were characterized by a higher proportion of vegetation cover (the inverse of sand cover) and the highest values of vegetation heterogeneity. An additional RDA biplot based on species abundances including both spatial and environmental descriptors showed that Passeriformes (represented by numbers 31–58 in the right panel of Fig. 2) were mainly associated with grasslands and dunes, while Charadriiformes (numbers 10–24) were associated with the beach.

Winter

We recorded 68 species (2856 detections) distributed among 25 families in the winter. A total of 21 species were recorded on the beach, 33 in dunes and 45 in grasslands.

According to the alpha criterion of the forward selection procedure, two environmental variables were selected: sand cover and vegetation height (accumulated $R^2_{Y|X|adj} = 0.327$, $P = 0.001$). The P-value for the other variables was higher than 0.05. The same procedure selected five spatial descriptors in decreasing order of importance: PCNM3, PCNM2, PCNM6, PCNM1 and PCNM4 (accumulated $R^2_{Y|X|adj} = 0.153$, $P = 0.001$). However, the $R^2_{Y|X|adj}$ obtained for these five PCNMs was higher than that of the global test ($R^2_{Y|X|adj} = 0.152$), indicating a type I error in the forward selection procedure. For this reason we eliminated the fifth spatial descriptor (PCNM4), decreasing the $R^2_{Y|X|adj}$ to 0.134.

Our model based on spatial and environmental descriptors resulted in a similar pattern to that
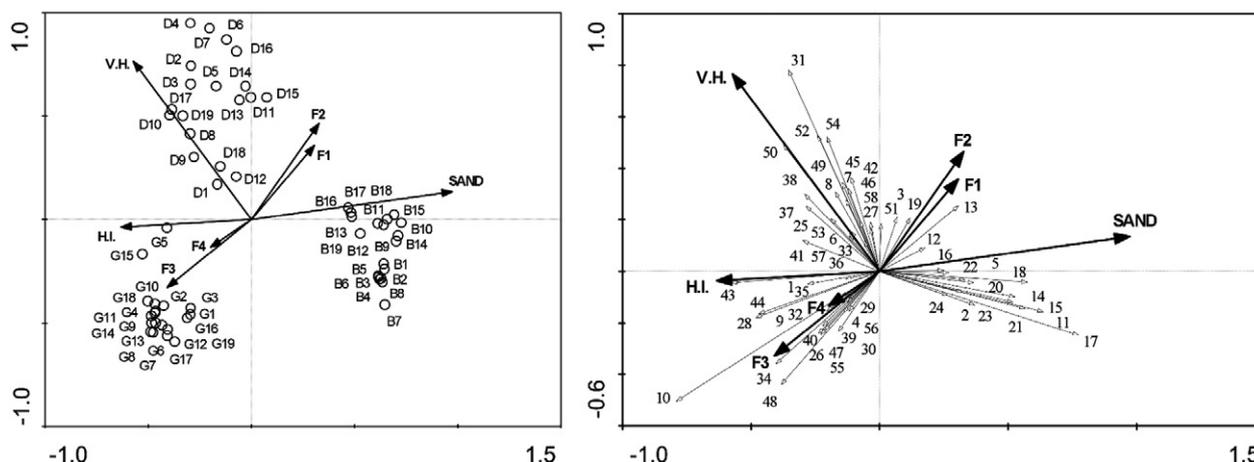
Fig. 2. Redundancy analysis biplot including spatial descriptors and environmental variables representing plots (left) and species (right) in the summer. Bold and head-filled arrows represent variables; unfilled circles represent plots (left); head-unfilled arrows are species (right). Abbreviations correspond to: H.I. = vegetation heterogeneity index; V.H. = vegetation height; SAND = sand cover; F1 to F4 are the four spatial filters (principal coordinates of neighbour matrices) included in the model. G1 to G19 are the 19 grassland plots; D1 to D19 are dune plots; and B1 to B19 are beach plots. 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. *Sterna trudeaui*; 22. *Thalasseus sandvicensis*; 23. *Thalasseus 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 striaticollis*; 34. *Anumbius annumbi*; 35. *Xolmis irupero*; 36. *Machetornis rixosa*; 37. *Pitangus sulphuratus*; 38. *Tyrannus 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*.

reported for summer, explaining about 35% of the avian beta diversity in winter ($R^2_{Y|X,W|adj}$ = 0.346, P = 0.001) (Fig. 1 right). Nearly 33% of the beta diversity was explained by environmental variables (fraction $a + b$ in the right panel of Fig. 1) ($R^2_{Y|X|adj}$ = 0.327, P = 0.001). Again, nearly a third of the explained beta diversity resulted from the shared effects of environmental and spatial variables (fraction b in Fig. 1). Similarly to summer, environmental features per se explained approximately 21% of the beta diversity (fraction a in Fig. 1) ($R^2_{Y|X|adj}$ = 0.211, P = 0.001). Spatial descriptors alone explained less than 2% of the avian beta diversity across the entire gradient (fraction c in Fig. 1) ($R^2_{Y|W|adj}$ = 0.018, P = 0.001).

The best predictor of species composition in the winter was the proportion of sand cover. Similarly to the summer, vegetation height and the spatial filters added information along the second ordination axis. The RDA biplot based on samples, environmental variables and spatial descriptors (Fig. 3 left) revealed a very similar pattern to that found for summer, forming three different groups of samples according to the different environmental features contained within it. The RDA biplot based on species abundances, spatial descriptors and environmental variables showed that Anseriformes (numbers 2–6 in the right panel of

Fig. 3) were mainly associated with grasslands, Passeriformes were associated with grasslands and dunes (numbers 35–68 in Fig. 3), and Charadriiformes were again typically correlated with the beach (numbers 17–30).

Variation partitioning within habitat types

Summer

No environmental variable was selected for any habitat type in summer, resulting in the non-significance of the environmental component. Five PCNMs were generated for the beach, but only the first was retained after the forward selection procedure ($R^2_{Y|X|adj}$ = 0.221, P = 0.001). Thus, the total amount of explained beta diversity (22%) on the beach was completely defined by space. Seven PCNMs were generated for dunes, but only four were retained (PCNM2; PCNM4; PCNM3; PCNM1; accumulated $R^2_{Y|X|adj}$ = 0.212, P = 0.001). Accordingly, the pure spatial control explained about 21% of beta diversity on dunes. Two PCNMs were generated for grasslands, but only one was retained (PCNM1; $R^2_{Y|X|adj}$ = 0.074,
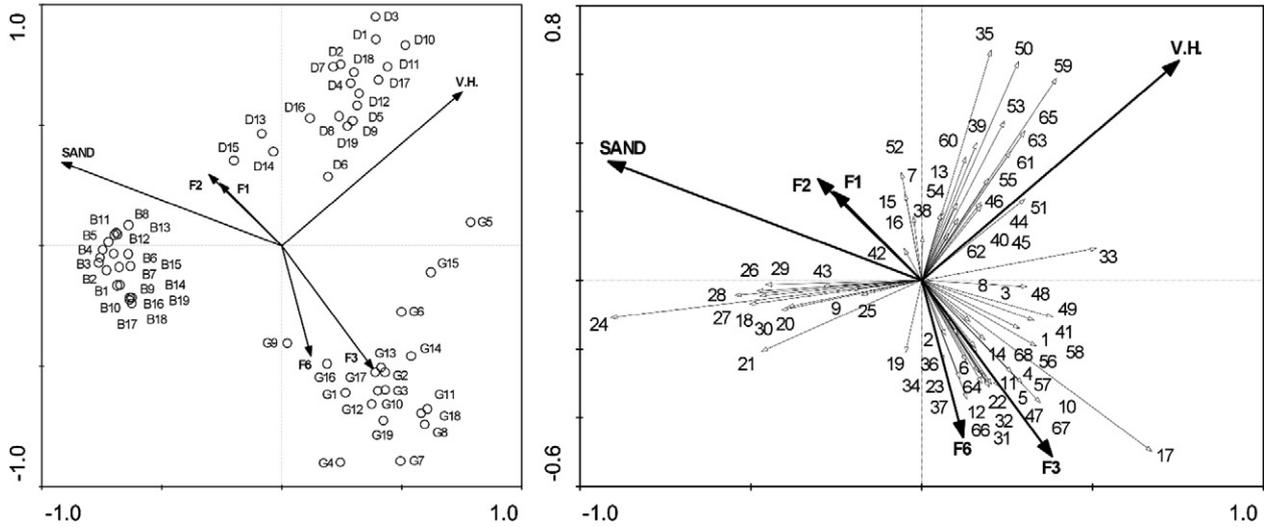
Fig. 3. Redundancy analysis biplot including spatial descriptors and environmental variables representing plots (left) and species (right) in the winter. Bold and head-filled arrows represent variables; unfilled circles represent plots (left); head-unfilled arrows are species (right). Abbreviations correspond to: V.H. = vegetation height; SAND = sand cover; F1 to F6 are the four spatial filters (principal coordinates of neighbour matrices) included in the model. G1 to G19 are the 19 grassland plots; D1 to D19 are dune plots; B1 to B19 are beach plots. 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. *Sterna 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*.

$P = 0.043$). Thus, the pure spatial model explained about 7% of beta diversity on grasslands.

Winter

Similarly to summer, the pure environmental component was not significant in explaining beta diversity patterns within habitat types in winter. However, the environmental variable 'vegetation height' was selected as a predictor of species distribution in the dunes. This variable was spatially structured, resulting in approximately 4% of the shared effects between space and environment affecting species distribution in the dunes.

Only one PCNM was retained for further analyses on the beach ($R^2_{Y|X|adj} = 0.054$, $P = 0.029$). Thus, the pure spatial component, which explained around 5% of beta diversity on the beach, was the only significant fraction in our model. For dunes, only PCNM1 and PCNM3 were selected; together, these spatial descrip-

tors explained around 8% of beta diversity in the dunes ($R^2_{Y|X|adj} = 0.079$, $P = 0.019$). For grasslands, two PCNMs were generated and retained for posterior analyses ($R^2_{Y|X|adj} = 0.072$, $P = 0.009$). The total amount of explained beta diversity in the grasslands was approximately 7% and was completely defined by space.

DISCUSSION

Our results represent the first step in a better comprehension of avian metacommunities in Brazilian temperate coastal ecosystems. In our study system, strong environmental heterogeneity occurs within a few kilometres across the gradient formed by the sandy beach, coastal dunes and grasslands, with important consequences for avian species distribution. We first showed that, irrespective of the season considered, the local effects of environmental variables on avian species composition were the main driver of beta diversity

across the entire ecological gradient. These results supported our first hypothesis, strengthening the species sorting perspective, which predicts that in a scenario of high dispersal rates, environmental habitat filtering is the main process determining the variation in species composition across ecological gradients (Leibold *et al.* 2004).

We suggest that the absence of important barriers to avian dispersal on the southern Brazilian coastal plain allows birds to track changes in environmental conditions across the well-marked ecological gradient, as also reported by Holyoak *et al.* (2005) for other organism groups inhabiting different ecosystems. As a group, birds are very mobile organisms, with many species performing long-distance migrations (Elphick & Lovejoy 2007), especially Charadriiformes, which fly from the Arctic to southern South America in order to select foraging sites based on very specific environmental conditions (Vooren & Chiaradia 1990; Blanco *et al.* 2006).

Second, we showed that the shared effects of spatial and environmental factors across the coastal gradient explained nearly a third of the variation in species composition in both seasons, representing the fraction of environmental variables and species abundance data that was spatially structured, which agrees with our second prediction. While the neutral model, patch dynamics and mass effects frameworks predict autocorrelation in species composition, the species sorting perspective is the only type of metacommunity model that disregards this premise, unless the environmental gradient is also autocorrelated in space (Leibold *et al.* 2004). The pattern observed in this study may result from the negative impacts on vegetation structure across the gradient from the beach through dunes to grasslands. For instance, negative physical and chemical effects of salinity and wave impact on plant establishment are expected across coastal ecosystems (e.g. Oosting 1945), and the vegetation structure directly and indirectly affects bird distribution and abundance (MacArthur & MacArthur 1961; Meynard & Quinn 2008). Therefore, features of the study system and avian ecology lead us to suggest that species sorting is the main mechanism affecting the community assembly in this context.

Spatial descriptors alone were much less important in explaining beta diversity across the coastal gradient, which supports our third hypothesis. Considering the high mobility of most bird species and their sensitivity to subtle changes in environmental conditions, it is not surprising that environmental control played an important role in affecting avian beta diversity across the ecological gradient studied. However, unlike most altitudinal gradients, which encompass strong abiotic variation within a few kilometres, resulting in high turnover rates in avian species composition (e.g. Young *et al.* 1998; Blake & Loiselle 2000), this pattern is less

common across horizontal gradients such as our study system. In other words, it is necessary to cover large distances in order to find substantial environmental variation in terrestrial ecosystems arranged along horizontal gradients (e.g. Meynard & Quinn 2008; Driscoll & Lindenmayer 2009; Apellaniz *et al.* 2012). This, in turn, increases the likelihood of detecting stochastic dynamics affecting species distributions. This appears to be a reasonable answer to why neutral dynamics predominates over large flat areas of tropical forest (Hubbell 2001). In our study system, which encompasses three very distinct subsystems, large changes in environmental conditions occur on a relatively fine spatial scale across the horizontal coastal gradient, resulting in high turnover of species composition and a weak spatial signal.

We also showed that, by using the same metacommunity approach within each habitat type along the gradient, the pure environmental causes of beta diversity became non-significant. Moreover, the role of spatial effects on species distribution increased within each habitat type. Taken together, these results corroborate our fourth and fifth hypotheses, respectively. We suggest that the loss of strong environmental heterogeneity within each habitat type weakened the role of species sorting, although we have no data to further support this idea. However, we emphasize that subtler environmental variations that were not assessed in our study, such as floristic variation and changes in prey availability within each habitat, could have led to different results by increasing the total amount of explained variation.

Declerck *et al.* (2011) used a hierarchical sampling design to study Andean cladoceran metacommunities across multiple spatial scales, and found different results. They reported strong environmental control at the smallest spatial scale, whereas neutral processes were more common at the largest spatial scale. Probably these contrasting results are due to the strong environmental heterogeneity included in our study as the spatial scale was broadened from within habitat to the entire gradient, a relationship that was not found by Declerck *et al.* (2011) in their study system. Moreover, whereas birds are active dispersers and are highly mobile, cladocerans are passive dispersers. Thus, it was suggested by Declerck *et al.* (2011) that the physical barriers imposed by the Andes Mountains resulted in the increasing dominance of neutral dynamics as the spatial scale was broadened in their study area.

Importantly, space may be hiding some latent environmental variables that were not adequately assessed in our study (Diniz-Filho & Bini 2005), which may have potentially inflated the pure spatial component on the smaller scale. For instance, human activities in summer are concentrated in the northern part of the beach near the Cassino seaside resort, and this concentration may well explain why some birds could be

avoiding this area, even when favourable habitat is available. Continual human activities may be detrimental to sensitive birds, as is the case for many shorebird species (International Wader Study Group 2003; Steidl & Polweel 2006).

Finally, the large amount of unexplained variance in species composition in our study system may be a result of non-habitat-related phenomena, such as nest predation, agonistic interactions, intraspecific attraction and food limitation (Morales & 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.

In this contribution, we highlighted the importance of local environmental variables and of different habitats across the coastal gradient in driving avian beta diversity. We also demonstrated that more than one metacommunity process might act within a region, depending on the spatial scale and/or the environmental heterogeneity considered. We encourage additional studies in similar coastal areas, including functional and evolutionary aspects of metacommunity dynamics, in order to gain new insights about the assembly processes of ecological communities. Furthermore, studies in the same area focusing on less mobile organisms such as reptiles, amphibians, zooplankton, macroinvertebrate and fish communities inhabiting ephemeral ponds in dunes and grasslands are of interest to assess to what extent our results will remain valid. Finally, we warn that human activity on beaches, wind power installations in grasslands and civil construction will pose increasing challenges to the conservation of biological diversity in temperate ecosystems, as these activities involve losses of natural habitat features and create barriers to animal dispersal across the landscape.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of species recorded in the study area.