

Spatial variation in bird species abundances: Environmental constraints across southern Neotropical regions

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Abstract

Climate and habitat type are frequently related with the abundance of individual species and have been hypothesized to be primary drivers of the spatial variation in species abundances at the regional scale. Our aim is to evaluate the relative roles of those environmental factors in determining spatial variation in bird species abundance. We surveyed birds and habitat-cover variables and compiled climatic data along a 1700-km latitudinal gradient in the southern Neotropics. To identify the primary environmental variable explaining spatial changes in species abundances we performed simple regressions; a goodness of fit test identified the environmental factor that most frequently acted as the primary predictor. Mantel tests and partial regressions were performed to account for the spatial structure of abundance and environmental factors and collinearity between them. Of the 88 species included, 70% responded primarily to habitat cover and the remaining to climate. Forest cover and annual thermal amplitude were the main habitat-cover and climatic variables, respectively, explaining spatial variation in bird abundances. Our results indicated that the considered environmental factors accounted for latitudinal changes in species abundances; however, habitat cover and climate together explained a higher proportion of the variation than each factor independently of each other. There was a primacy of habitat-cover type over climate to predict spatial changes in bird species abundances across the neotropical biogeographic regions studied, but the underlying causes are likely related with the interaction of both factors.

Zusammenfassung

Klima und Habitattyp sind häufig mit der Abundanz von einzelnen Arten verknüpft, und es wird angenommen, dass sie primäre Steuergrößen der räumlichen Variation der Abundanz von Arten auf der regionalen Skala sind. Unser Ziel war es, die relative Bedeutung dieser Umweltfaktoren für die räumliche Variation der Abundanz von Vogelarten zu bestimmen. Wir erfassten Daten zu den Vögeln und zur Flächendeckung der Habitattypen und stellten Klimadaten für einen 1700-km langen Breitengradienten in der südlichen Neotropis zusammen. Um die primären Umweltvariablen für die Erklärung räumlicher Änderungen in der Abundanz der Arten zu ermitteln, führten wir einfache Regressionen durch. Ein Anpassungstest identifizierte den Umweltfaktor, der am häufigsten als primärer Prädiktor fungierte. Mantel-Tests und partielle Regressionen wurden durchgeführt, um der räumlichen Struktur von Abundanz und Umweltfaktoren und der Kollinearität zwischen ihnen Rechnung zu tragen. Von den 88 untersuchten Arten reagierten 70% primär auf die Habitatbedeckung und der Rest auf das Klima. Bedeckung mit Wald und die jährliche Temperaturamplitude waren die wichtigste Habitat- bzw. Klimavariablen. Unsere

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Ergebnisse zeigten, dass die betrachteten Umweltfaktoren Änderungen der Abundanz der Arten mit der Breite bedingten. Indessen erklärten Habitatbedeckung und Klima zusammen einen höheren Anteil der Variation als jeder der beiden Faktoren für sich. Die Flächendeckung mit Habitaten bestimmte stärker als das Klima Abundanzänderungen der Vogelarten über die untersuchten neotropischen biogeographischen Regionen, aber die zugrundeliegenden Ursachen sind vermutlich mit der Interaktion zwischen den beiden Faktoren verbunden.

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Introduction

The study of broad-scale patterns and processes involved in the distribution of biological diversity has been a central issue in ecology and biogeography, especially since the late 1980s (Brown & Maurer 1989; Gaston & Blackburn 2003). Much attention has been focused on species richness (Rohde 1992; Hawkins 2001; Willig, Kaufman, & Stevens 2003) and more recently on beta (Qian 2009) and functional diversity (Petchey & Gaston 2006). Surprisingly, other biodiversity components such as the abundances of individual species have been more difficult to evaluate. Significant progress has been made in the understanding of the relationship between the number of species and abundance or between abundance and distributional range size (Gaston & Blackburn 2000; Evans, James, & Gaston 2006), but questions related to the main factors driving geographical patterns in the species abundance have been difficult to address due to the lack of broad-scale data (but see Brown 1984; Tellería & Santos 1993; Brown, Mehlman, & Stevens 1995; Flather & Sauer 1996; Blackburn, Gaston, Quinn, & Gregory 1999).

Environmental factors play key roles in determining spatial patterns in the abundances of individual species (referred to as species abundance from here on) (Brown 1984; Root 1988a, 1988b). If the environment is spatially structured as a gradient and if species abundance responds to environmental constraints, gradual changes in bird abundance are expected across space. In such a case, abundance will reach a maximum where environmental conditions are optimal for the species and decline as conditions become less suitable (Whittaker 1967; Brown 1984). It was initially thought that optimum conditions occurred at the geographical centre of the distributional range (Brown 1984; Brown et al. 1995), but the generalization of that pattern has been challenged (Sagarin and Gaines 2002; Sagarin et al. 2006). Regardless of the particular statistical model describing the spatial changes of species abundance, most species tend to be abundant in some sites and rare in others across their geographical range (Murray & Lepschi 2004). Even when “bands of abundance” occur across the range (Gaston 1990), there is no consensus about the cause of such patterns (Gaston 1990; McGill & Collins 2003). Our work is among the few exploring environmental correlates with species abundances; in this approach, we contrast two broad environmental factors (climate and habitat type) to explain spatial changes in bird abundances over a wide geographical area.

Abiotic factors such as climate strongly affect the distribution and abundance of species (MacArthur 1972; Brown et al. 1995). Climate may influence the abundance of individual species through physiological limitations to extreme conditions and/or resource production and availability (e.g., Redpath et al. 2002). For example, there is evidence that temperature affects species abundances and distributions in the Palaearctic (Lennon, Greenwood, & Turner 2000), and that bird abundances respond to humidity gradients in the boreal forest (Willson & Comet 1996). Here, we explore the role of climatic factors in determining spatial changes of species abundance through several regions/biomes extending from subtropical to cold climates in the Neotropics.

The spatial arrangement of habitat types determines landscape patterns over regions (Forman 1995), influencing the distribution of biological diversity across space. It has been documented that habitat-cover patterns have a strong influence on the abundance of species of many taxa (Atauri & de Lucio 2001; Cleary et al. 2005; Michel, Burel, & Butet 2006). A mix of habitat types offers a variety of resources in the landscape, and individual species may respond positively or negatively to the availability of any particular habitat type depending on whether their requirements are fulfilled. Previous studies have shown that bird species responded to both quality and quantity of habitat types (e.g., Flather & Sauer 1996; Drapeau et al. 2000). Thus, in our study we considered an area covered by different habitat types in the landscape as a relevant element influencing bird abundance across a region.

Our goal is to explore climatic and habitat-cover constraints to explain latitudinal variation of species abundances. We ask what environmental factor primarily determines spatial variation in population sizes over large geographical scales. Our approach is to examine the relative influence of both climatic and habitat cover constraints on the abundance of 88 bird species along a latitudinal gradient covering five ecoregions in South America, and then combine data to identify the main factor explaining spatial changes in bird abundance across all species.

Materials and methods

Study area

The study covered approximately 1700 km (from 27°39' S 62°25' W to 41°16' S 68°43' W), through five



Fig. 1. Location of the 22 transects surveyed in central Argentina (black dots). Five ecoregions were crossed (white areas). Other regions of Argentina were not surveyed (black areas).

phytogeographical regions (Cabrera 1971) in central Argentina: Chaco, Espinal, Pampeana, Monte and Patagonia (Fig. 1). In the Chaco region, the climate is warm and dry; mean annual temperature ranges from 20 to 23 °C and rainfall varies between 500 and 1200 mm (from W to E with most rain falling in summer). The original xerophilous forest was dominated by *Schinopsis* trees, and it is currently converted into savannas or steppes due to prescribed fires and wood extraction. Espinal climate is warm, wet in the north and dry in the west; annual rainfall varies between 340 and 1170 mm and mean annual temperature between 15 and 20 °C. The savanna and xerophilous forest are lower in high than in Chaco and dominated by *Prosopis* spp.: the region has also been largely modified by human activities. Climate in the Pampean region is temperate-warm; mean annual temperature ranges between 13 and 17 °C, with rainfall occurring year round (600–1100 mm). Grasses of the Poaceae dominate the plant community. The natural grasslands suffered a fast and intense degradation due to agriculture during the 20th century (Soriano 1991). In the Monte region the climate is cool and dry, and vegetation is dominated by *Larrea* shrubs 1–2 m

in height. Mean annual temperature varies between 13 and 17.5 °C, and annual rainfall between 80 and 250 mm. The climate in Patagonia is cold and dry with snow and freezing temperatures occurring almost year round, at least in the south. Mean annual temperature in northern Patagonia is 13.4 °C and precipitation varies between 100 and 270 mm. The Patagonian steppe is dominated by grasses of the genus *Stipa*.

Bird surveys

Terrestrial birds were surveyed along 22 line transects at least 100 km apart in the north-south direction (Fig. 1). Each transect was 25-km long and located on a non-paved road. We surveyed one transect a day from north to south. We used the point count technique (Bibby, Jones, & Mardsen 1998). Along each transect, we made 5-min observation stops every 1 km, for a total of 26 observation stops per transect (578 for the entire gradient). All birds seen or heard using habitats located adjacent to the road were recorded. The 1 km separation between observation points prevented double counting. Surveys were conducted by the same two observers, from sunrise to 4 h after sunrise during the spring. To avoid double counting at each observation point, observers were positioned back-to-back to cover the complementary 180°, and alerted each other when a bird flew across the road; a third person recorded the species of each individual bird detected by observers. To obtain a comparative measure of abundance for each species among sites, we used a standard method for counting the number of individuals of each species at each observation point. Study biomes were basically open habitats (shrublands, grasslands, cropfields, and degraded dry forest). The radius was not fixed previous to the surveys; instead, we checked the maximum detection distance (150 m) at northern transects in the dry forest (even if basically open, it was the closest habitat type) and maintained that distance for all surveys. Thus, the species detection radius was assumed to be the same for all observation points and the encounter rates (i.e., number of individuals per transect) were directly comparable for a species between transects (Bibby et al. 1998). Then, for each species we obtained a relative measure of abundance based on the encounter rate, estimated as the numbers of individuals recorded per transect.

Environmental variables

Four climatic variables and five habitat-cover classes were generated for the analysis (Table 1). The climate variables were derived from the 10' (~20 km) spatial resolution, available in the WorldClim database (<http://www.worldclim.org>) (Hijmans, Cameron, Parra, Jones, & Jarvis 2005). Habitat-cover was surveyed while driving along the 22 line transects. We recorded the distance covered by each habitat type along both sides of the road in each transect and then calculated the percentage occupied by each type (Filloy & Bellocq 2007).

Table 1. Environmental variables considered in the study to explain spatial variation in terrestrial bird abundances.

Factor	Variable
Climate	Mean annual temperature
	Annual thermal amplitude ^a
	Annual precipitation
	Rain seasonality ^b
Habitat cover	Forest
	Shrubland
	Pastures and grassland
	Cultivated fields
	Steppe

^aCalculated as (mean maximum temp. of the warmest month – mean minimum temp. of the coldest month).

^bCalculated as ((summer rainfall – winter rainfall)).

Data analysis

We examined the relationship between spatial changes in bird species abundances and environmental variables following Field et al. (2009). We analyzed each species separately, and then combined the results to identify the factor (climate or habitat type) explaining spatial changes in bird abundance across all species. Simple linear and non-linear regressions were performed between abundance and environmental variables to identify the variable most strongly related to individual species abundance, evaluated by coefficients of determination (r^2). We calculated the proportion of cases in which either the climatic or the habitat-cover factor better explained species abundance (“primacy” *sensu* Field et al. 2009), and examined the difference by performing a Goodness of Fit test (with 1:1 as the null model). As habitat cover and climate are expected to have a degree of covariation along the gradient, we performed partial regressions between the two factors to account for the variation in bird abundance shared by them and the proportion of variation that was explained independently by those factors. We used the SAM statistical package (Rangel, Diniz-Filho, & Bini 2010). We extracted the proportion of variation in species abundances that was accounted independently by each factor and the proportion of variation shared by them. Those proportions were compared by a Kruskal–Wallis test (= KW-test) and multiple post hoc comparisons as described by Conover (1999), using the InfoStat software (Di Rienzo et al. 2011).

Finally, both bird abundances and environmental variables were expected to be spatially autocorrelated because of the survey design across a latitudinal gradient (Legendre 1993). To account for autocorrelation, we first analyzed the spatial structure of the environmental factors. Three dissimilarity matrices were constructed each based on climatic variables, habitat-cover variables or geographic coordinates. The Gower index was used to quantify environmental dissimilarities between pairs of transects, and the Euclidean coefficient to quantify geographic distances (Legendre &

Legendre 1998). Thus, we performed Mantel tests between sets of variables (climatic, habitat-cover) and the geographic distance matrix (Legendre & Legendre 1998). We also performed partial regressions between bird abundances and the respective primary variable to account for the influence of the spatial component (Borcard, Legendre, & Drapeau 1992). We extracted the proportion of variation in species abundances that was accounted for by the primary variable independently of space, shared by the primary variable and space (i.e., spatially structured primary variable), and explained only by space (i.e., spatial structure from unknown causes). We compared those proportions by performing a KW-test and post hoc comparisons.

Results

We tested the response of bird abundance for 88 species (from 30 families). Simple regressions showed that the abundance of 62 out of the 88 species (70%) responded primarily to a habitat-cover variable, whereas the remaining 26 species (30%) responded primarily to a climate variable (Appendix A). The primacy of the habitat-cover factor differed significantly from that of the climatic factor ($\chi_1^2 = 14.73$, $p < 0.001$).

Best responses to habitat-cover variables were all positive whereas best responses to climate variables were positive, negative or unimodal (Fig. 2). Forest cover was the primary variable explaining spatial changes in the abundance of 44% of the species that responded primarily to habitat cover (27 species), whereas steppe, agriculture, shrubland or grassland cover were primary variables for approximately 14% of the species (Fig. 2A). Annual thermal amplitude was the primary variable for half of the species that responded mainly to a climate variable, whereas mean temperature and annual rainfalls were primary variables for 27% and 23% of the species, respectively (Fig. 2B). The KW-test and post hoc comparisons performed on the proportions of variation obtained from partial regressions revealed that the proportion of variation that was shared by both factors was higher than that explained independently by each one (Fig. 3A). The abundance of most species was better explained simultaneously by both factors than separately by each one.

Mantel tests revealed both a climate and a habitat-cover gradient across latitude in the southern Neotropics ($r_{Spearman} = 0.20$, $p < 0.02$ and $r_{Spearman} = 0.19$, $p < 0.02$, respectively); differences in both climate and habitat-cover variables increased as distance between transects increased. The KW-test and post hoc comparisons revealed that the proportion of variation accounted for by spatially structured primary variables was higher than that explained by the primary variables when partialling out spatially structured environmental effects, which was higher than the proportion of variation explained by spatially structured unknown causes (Fig. 3B).

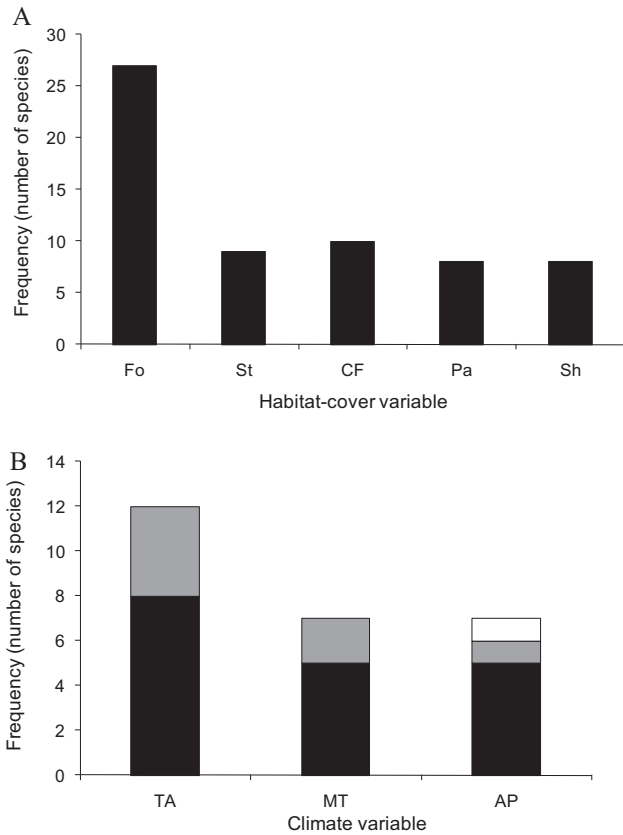


Fig. 2. Frequency of species showing primary responses to (A) habitat-cover and (B) climate variables. Shaded sections of columns indicate response types (black for positive, grey for negative and white for unimodal responses). Fo, forest; St, steppe; CF, cultivated fields; Pa, pastures and grasslands; Sh, shrublands; TA, thermal amplitude; MT, mean temperature; AP, annual precipitation.

Discussion

Our findings indicate the primacy of habitat-cover variables over climate variables in explaining spatial changes in bird species abundances at the mesoscale. Species responses to habitat cover type and climate have long been studied independently (Root 1988a; Tellería & Santos 1993; Fahrig 2001). By analyzing climate and habitat simultaneously, our results suggest that spatial variations in bird species abundances along a latitudinal gradient are mostly determined by the interaction between climate and habitat cover. A small portion of variation in bird abundance was explained by each factor independently of the other. Thus, at the study scale, site suitability should be investigated and understood by taking into account both factors together.

The single approach may enlighten about the nature of the relationship of bird abundance with each environmental dimension considered in the analysis. Our study showed that bird abundance can be primarily predicted by habitat-cover variables in the southern Neotropics. It is possible that most species increased their abundances in response to increasing availability of suitable habitat. For some species,

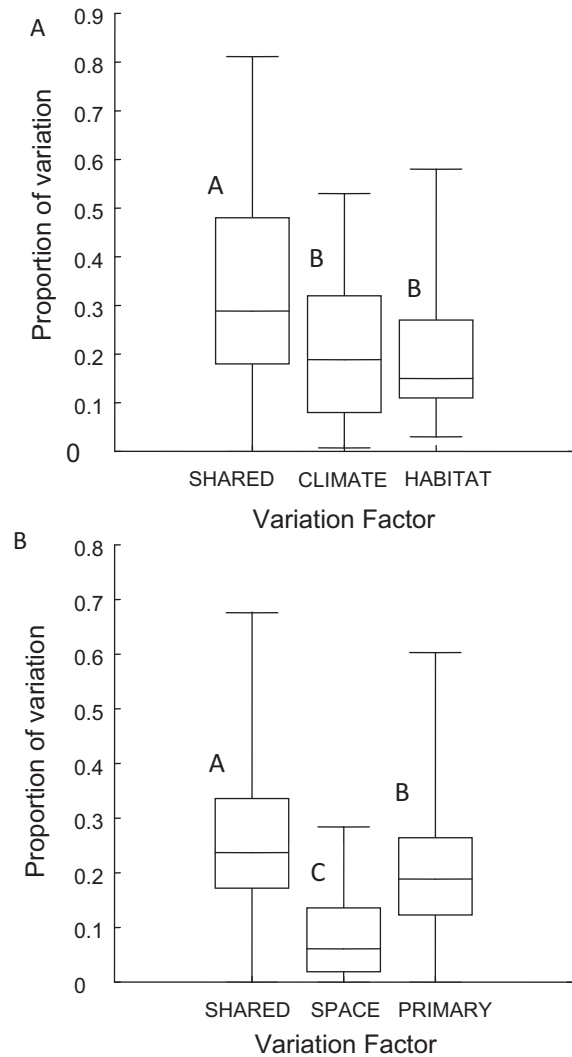


Fig. 3. KW-tests and post hoc comparisons of proportion of variation in bird abundances explained for (A) climate independently of habitat cover, shared by habitat cover and climate, and habitat cover independently of climate and (B) primary variable independently of spatially structured unmeasured causes, spatially structured primary variable (“shared”) and spatially structured unmeasured causes independently of primary variable. Different letters indicate significant differences among factors ($p < 0.0001$). Centre line: Median; box: 25–75% Quantil; whisker: 1–99% Quantil.

however, latitudinal trends in bird abundances would be determined by the climatic context mediated mainly by thermal seasonality (i.e., annual thermal amplitude). Environmental factors included here were themselves spatially autocorrelated showing a strong spatial structure which displayed similar environmental conditions between close sites, enhancing the differences as distance between sites increased. Those factors, spatially structured as a gradient, accounted for the observed latitudinal changes in species abundances.

Habitat-cover type seemed to influence bird species abundances. Almost all habitat-cover variables considered here partially explain latitudinal changes in species abundances.

Most habitat-cover types, as we classified them, represented common ecosystems in each ecological region. Similar to Zurita and Bellocq (2012) in subtropical forests, our results indicate that the abundance of bird species responded to the percentage cover of the remaining original (or less degraded) biomes. Moreover, our findings also suggest that the individual effects of both habitat cover and climatic conditions on bird abundance are difficult to separate, as they overlap in the explanation of abundance variation. Both habitat cover (seminatural and human-created habitats) and climate are experiencing regional and global transformations due to large-scale human environmental impacts. Furthermore, the spatial distribution in the abundance of species responding primarily to habitat-cover variables may also be affected by climatic change, as it would lead to changes in the availability of different habitat types. That finding has profound conservation implications as bird species could be drastically affected by land management associated with habitat loss and conversion, and it should be considered in land use planning.

We found that bird abundance also changed across latitude as a function of the annual thermal amplitude. Previous studies have found that climate explained spatial changes in bird abundance in temperate systems from the Palearctic and Nearctic at both the regional (Emlen et al. 1986; Tellería & Santos 1993; Storch, Konvicka, Benes, Martinková, & Gaston 2003) and continental (Root 1988b; Forsman & Monkkönen 2003) scales. In our study, the relationships between thermal amplitude and bird abundance differed among species: while some species increased their abundances as thermal amplitude increased, other species showed the opposite pattern. The responses to changes in climatic conditions could reflect either physiological or resource limitations. Yet, the mechanism driving population size of a given species may vary across its geographical range. Redpath et al. (2002), for example, found that the spatial pattern of abundance of the hen harrier *Circus cyaneus* was explained by temperature across the entire geographic range, but the response reflected ecological limitations for species at an extreme of the range (e.g., resource availability, reproductive rate) and physiological limitations at the opposite extreme (e.g., thermal regulation). Previous studies indicate that birds would most likely respond to seasonal differences in temperature through resource availability (Emlen et al. 1986). Ricklefs (1980) proposed that seasonality rather than the absolute level of resources had a strong influence on bird reproductive traits such as clutch size or adult mortality, which directly affect population numbers.

Our findings can be interpreted by invoking the niche-based hypothesis proposed by Brown et al. (1995) who emphasized the role of environmental variables in limiting species abundances. The hypothesis was developed based on Hutchinson's multidimensional niche concept, assuming that each species' ecological niche consists of multiple factors or dimensions. In that context, it is expected that while multiple independent environmental factors may act as niche dimensions, the magnitude of their relative effects on species

abundances might differ. Moreover, those differences may be attributed to differences in the spatial scale at which the factors act. In our study, suitable habitats likely occupy relatively restricted extensions over the regions compared with broader extensions of favourable climatic conditions. Thus, the effects of climate on bird abundances will be obscured by changes in habitat-cover variables.

As a consequence of the primacy of habitat cover in determining changes in bird abundances, most species increased their abundance from south to north, responding positively to increasing cover of forest habitats (i.e., increasing habitat complexity). Habitat complexity/heterogeneity is a key determinant of species richness because it promotes species co-occurrence (Kerr & Packer 1997). Thus, individual responses would collectively lead to increasing species numbers from high to low latitudes. According to McGill and Collins (2003), the spatial structure of abundance across species geographical ranges ultimately explains several macroecological patterns such as range size-abundance correlations or species-area relationships. If the responses we found were driven by niche-based processes, then the species-by-species approach taken in this study would provide a conceptual link between the niche-based hypothesis (Brown et al. 1995) and the latitudinal diversity gradient (Hawkins 2001; Willig et al. 2003). The identification of that link implies a meaningful progress in our understanding of the causes of species distributions.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2013.02.007>.

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