

Habitat heterogeneity drives bird species richness, nestedness and habitat selection by individual species in fluvial wetlands of the Paraná River, Argentina

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Abstract We assessed the relationship between habitat heterogeneity and bird species richness and composition within wetlands of the floodplain of the Middle Paraná River, Argentina. Given the high habitat heterogeneity in these wetland systems, we sought to determine whether (i) there was a positive relationship between bird species richness and habitat heterogeneity; (ii) whether bird species richness was associated with certain types of individual habitat types; (iii) whether there was a pattern of species nestedness and turnover between sites as a function of habitat heterogeneity and composition, respectively; and (iv) whether individual species exhibited associations with habitat heterogeneity. Point counts were used to survey birds at 60 sites. We estimated the area of eight habitat types found within a 200-m radius from the centre of each site and calculated number and Pielou's evenness of habitat types. These indices, together with area proportion of each habitat type, were used as explanatory factors of bird species richness in linear regression models. Habitat heterogeneity *per se* rather than area of individual habitat types was a more important predictor of species richness in these fluvial wetlands. Sites with more habitat types supported more bird species. Results showed that individual bird species were associated with different habitat types and, therefore, sites that contained more habitat types contained more species. Number of habitat types accounted for species nestedness between sites whereas composition of habitat types accounted for species turnover between sites. Results suggest that selection of heterogeneous sites by individual species could help explain the positive heterogeneity–species richness relationship. Our findings highlight the importance of habitat heterogeneity *per se* resulting from flood disturbances in maintaining bird richness in fluvial systems.

Key words: floodplain, nestedness, riparian corridor, species turnover.

INTRODUCTION

Natural riparian systems are habitats of critical conservation concern worldwide as they support a diverse array of species that are distinct from those of upland systems (Sabo *et al.* 2005). This is a result of a set of properties, among which the habitat heterogeneity (i.e. number of different habitats) of riparian systems is one of the most important (Robinson *et al.* 2002; Ward *et al.* 1999). Topographic variation and connectivity with dynamic flows of water result in a heterogeneous floodplain with a shifting fine-grained mosaic of habitat types.

This spatial heterogeneity within floodplain systems is often invoked to explain the high number of species present in fluvial habitats (Gregory *et al.* 1991; Naiman *et al.* 1993; Ward *et al.* 1999). However, although it is widely thought that heterogeneous habitats should maintain more species than homogeneous ones, the extent and generality of positive heterogeneity–richness relationships

are still debated because of the existence of non-significant, negative and hump-shaped patterns observed in some studies of heterogeneity and richness (Stein *et al.* 2014). In general, the extent of variation in species richness among sites within riparian corridors that support different levels of spatial heterogeneity has not been extensively studied. Yet, a better understanding of this relationship is important in terms of conservation and management, especially for understanding which conditions help explain the coexistence of a high number of species.

The premise of a positive relationship between habitat heterogeneity and species richness (positive HR relationships hereafter) is based on classical niche theory (Allouche *et al.* 2012; Laanisto *et al.* 2013). It is widely accepted that for a given area, heterogeneous habitats provide more niches than homogenous habitats and, therefore, can support more speciose communities (Rosenzweig 1995). If different species are associated with different habitats, sites that contain more habitat types likely will contain more species (i.e. niche-based hypothesis). Also, sites that contain fewer habitat types

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will contain only a subset of the species from sites with larger numbers of types, leading to a pattern of nestedness in the composition of communities (i.e. nested habitat hypothesis, Hylander *et al.* 2005). Similarly, according to niche-based hypothesis, it can be expected that differences in the composition of habitat types (i.e. the set of habitat types that are present on a site) drive species turnover between sites (e.g. if a habitat type is present on two sites, these sites also share species associated with it). In this context, the level of similarity in relative areas of different habitat types within a site (e.g. evenness of the area of habitat types per site) could also be an important variable because the small size of some types of habitats in heterogeneous sites (i.e. low evenness of the area of habitat types in heterogeneous sites) may limit its use as a habitat by species (Haslem & Bennett 2008). Thus, although a site may contain different types of habitats, that site may not necessarily contain a high number of species if many of those habitat types are small in area.

A second hypothesis to explain the positive HR relationship proposes that it may be due, in part, simply to the increased likelihood that a more heterogeneous site will contain a key habitat type (Davidar *et al.* 2001). Habitat types which maintain the highest species richness have been termed 'keystone habitats' (Davidar *et al.* 2001) and their presence or area can be a better predictor of species richness at a particular site than habitat heterogeneity *per se*.

Both hypotheses (niche-based and keystone-habitat hypotheses) suggest that individual species may not be responding to habitat heterogeneity *per se*, but rather to the presence of specifically suitable habitat types (Rice *et al.* 1983). However, habitat heterogeneity is also an important factor contributing to habitat selection by individual species (Cousin & Phillips 2008). Because individual species require a variety of resources to complete their life cycle, a more heterogeneous site with different habitat types that offer different resources could be required by certain species (Dunning *et al.* 1992), leading to higher overall richness in heterogeneous sites. Conversely, homogeneous sites could be preferred by species associated with individual habitat types because for a given area, the area of a particular habitat type decreases as heterogeneity increases (Allouche *et al.* 2012). Thus, while a single habitat type can provide necessary resources for a single species which requires homogeneous sites of that particular type, other species may require a set of different habitat types so they will be associated positively with habitat heterogeneity.

The importance of habitat heterogeneity to avian ecology was proposed over half a century ago (MacArthur & MacArthur 1961); many subsequent studies have demonstrated positive correlations between species richness and number and area of habitat types (e.g. Davidar *et al.* 2001; Codesido *et al.* 2013; Tews *et al.* 2004 and

references therein). In riparian landscapes, different species may be associated with different types of habitats (Ronchi-Virgolini *et al.* 2008; Weller 1999). Given their mobility, however, birds can use a myriad of habitat types inside riparian systems (Sullivan *et al.* 2007; Weller 1999). Therefore, individual species may respond to habitat heterogeneity *per se* and not to the presence – absence of certain individual habitat types. In this case, selection of more heterogeneous sites by individual species could help explain the existence of a positive HR relationship in riparian systems.

In this study, we evaluated the relationship between bird species richness and habitat heterogeneity (number of habitat types), habitat evenness (the relative areas of different habitat types) and composition (set of habitat types per site) at a local scale (i.e. 0.13 km²) along the floodplain of the Middle Paraná riparian corridor in Argentina. More specifically, our objectives were to determine whether: (i) there was a positive relationship between bird species richness and habitat heterogeneity; (ii) whether bird species richness was associated with certain types of individual habitat types; (iii) whether there was a pattern of species nestedness and turnover between sites as a function of habitat heterogeneity and composition, respectively; and (iv) whether individual species exhibited associations with habitat heterogeneity.

METHODS

Study system

Our study system includes the middle section of Paraná River (Fig. 1). The Middle Paraná River represents an extensive floodplain – river system that forms a 600-km north–south riparian corridor (Nestler *et al.* 2007). This corridor begins at the confluence of the Paraguay and Paraná rivers (27° 17'S–58° 38'W) and extends to the beginning of the Paraná River Delta (32° 04'S–60° 38'W, Nestler *et al.* 2007). This part of the river is included in the Paraná Flooded Savanna ecoregion (Olson *et al.* 2001). Climate is subtropical – humid in the northern parts, where average annual temperature is 21 °C (annual range: 19.9–21.8 °C) and average annual rainfall is 1100 mm (annual range: 614.8–2076.5 mm, Cáceres 1980), shifting to temperate – humid in the south (Iriondo & Pairea 2007), where average annual temperatures are around 19 °C (annual range: 17.7–19.7 °C) and average annual rainfall is 900 mm (annual range: 611.2–1602.4 mm, Rojas & Saluso 1987). Along its route, Middle Paraná River traverses mainly the Humid Chaco and Espinal ecoregions that differ in climate, soil type, flora and structural characteristics of vegetation (Olson *et al.* 2001, Fig. 1).

Bird counts

We use data from a bird monitoring programme through which birds were sampled in four locations along the Middle Paraná

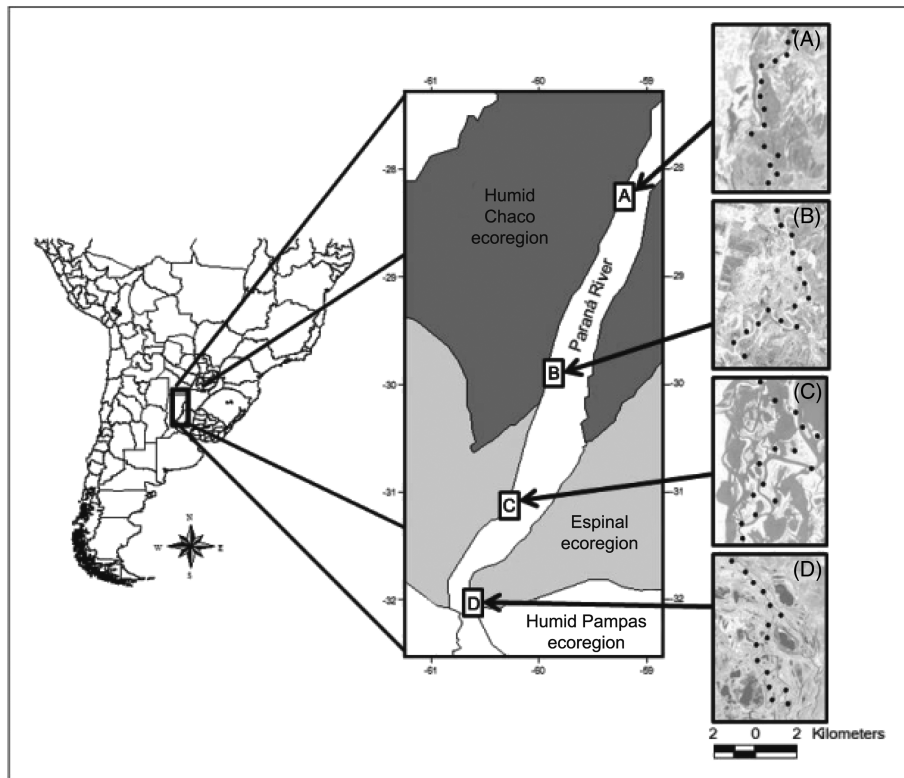


Fig. 1. Location of Middle Paraná River in the southern cone of South America showing four study localities (A, B, C, D) and distribution of sites.

River (Fig. 1). Within each location, birds were sampled at 15 sites 16 times roughly every 45 days during two years (2011–2013; four counts per season, two seasons per year). Sites were systematically located in a north–south direction, predominantly along waterways to ensure accessibility under different hydrological conditions of the river. Sites were separated by at least 800 m to represent independent landscapes. Sites were located along the sides (relative to the course of Paraná River) of the floodplain in shrub swamps and marshes. These environments are dominated by shrubs and herbaceous plants that can tolerate hydric soils because of permanent (water bodies) or periodic (intermediate areas) presence of water, according to the topographic relief and the influence of the hydrological pulse (Sabattini & Lallana 2007). Water bodies and their edges are dominated by herbaceous plants (e.g. *Panicum elephantipes*, *Sagittaria montevidensis*) and shrubs (e.g. *Solanum glaucophyllum*, *Sesbania virgata*). Various floating plants (e.g. *Eichhornia* spp., *Pistia stratiotes* and *Salvinia* spp.) were present in more open water areas. Intermediate areas were dominated by *Panicum prionitis*. Scattered woody individuals of such species as *Acacia caven*, *Sapium haematospermum* and *Albizia inundata* also were present.

The distribution of sites was determined using a systematic sampling method (Gregory *et al.* 2004). Navigable waterways located predominantly in a north–south direction were selected to represent the side of the floodplain within each locality. The location of the first site in each locality was determined by the

availability of boat ramps and navigable rivers to allow access to the selected waterways because we required motorboats to move from site to site. However, bird counts were conducted on *terra firme*. The first site at each locality was located on the bank of the selected waterways at the same latitude as the boat ramp, for logistical considerations. From that site we located the remaining sites at about 800-m intervals along the river. In some cases, however, there were no accessible places to establish a sampling site (e.g. where stream banks were covered with dense riparian forests) and in these cases, we increased the distances between sites until suitable places were encountered.

We established a point count at each site for bird sampling. All birds seen and heard within a radius of 100 m from the centre of each site were recorded during a 10-min sampling period (Ralph *et al.* 1996). We used a relatively large radius because counts were conducted in open areas with good visibility. We used range-finders for distance determinations. Probabilities of detecting species could vary among sites, depending on habitat, time of day and other factors. Bird counts began at sunrise and continued for 4 h, a period of greater stability in terms of detecting birds (Robbins 1981). Further, we alternated (northwards versus southwards) the order in which sites were sampled to avoid possible effects of time of day (Verner & Milne 1989). Also, we selected only shrub swamps and marshes, so visibility was good in all cases. Moreover, we repeated the surveys (16 visits per site, four visits per season), increasing the probability

of detecting species present at a given site (Gu & Swihart 2004). Counts were performed by the same observer (REL) in all cases.

Bird data were combined (i.e. average species richness and abundance across all counts) among the 16 repeated visits per site to calculate response variables used in data analysis (Table 1).

Habitat metrics

Topographic relief within floodplains produces different patterns of connectivity with dynamic flows of water and results in a shifting mosaic of habitat types with distinct structural characteristics of vegetation (Ward *et al.* 2002). Consequently, we used primarily structural characteristics to classify these habitats by vegetation type or other types of land cover when vegetation was absent. Some of the vegetation types also showed differences in floristic composition (e.g. grasslands are composed of *P. prionitis*) and thus, we did not differentiate structural and floristic influences on bird species but only report overall habitat heterogeneity effects. Types of habitats were adapted from previous studies in the area (e.g. Quiroga *et al.* 2013) and were: (i) open water; (ii) floating macrophytes (e.g. *Eichhornia* spp., *P. stratiotes* and *Salvinia* spp.); (iii) emergent macrophytes (e.g. *P. elephantipes*, *S. montevidensis*); (iv) shrublands (e.g. *S. glaucophyllum*, *S. virgata*); (v) grazed

pastures; (vi) beach; (vii) grasslands, dominated by *P. prionitis*; and (ix) trees.

The proportion of area covered by each habitat type within 200-m radius (range-finders were used to determine distance) of the centre of each site was estimated through direct field observations. A relatively small 200-m radius was used because our objective was assessing the influence of local- and fine-grained habitat heterogeneity on bird species richness and composition. Beyond 200 m the presence of riparian forests interrupts the continuity of shrub swamps and marshes in many of the sites. We estimated only proportion of area because we considered that this level of precision was sufficient for our objectives (i.e. it is unlikely that small variations in the size of the area occupied by different habitat types are associated with changes in the presence and/or abundance of birds). We used this information to calculate measures of habitat composition, heterogeneity and evenness (Table 1).

Number and area proportion of habitat types per site varied during the 16 surveys as a result of varying hydrological conditions that could lead to drying out of the lagoons, waterlogging of beaches and changes in vegetation dynamics (e.g. changes in the surface covered by floating vegetation). Therefore, habitat measures were averaged across 16 repeated visits to obtain unique values for each site (Table 1). These unique values per site of habitat measures varied among the 60 sites (Fig. S1, S2 and S3).

Table 1. Response, explanatory and co-variables used in data analysis

| Variable (<i>n</i> = 60 sites) | Calculation | Measure of |
|--|--|---|
| <i>Response variables (100 m radius-sites)</i> | | |
| Species richness per site | Average of species richness among the 16 visits per site | Bird species richness |
| Relative abundances of species per site | Relative abundances calculated as the average of species' abundances among the 16 visits per site | Bird relative abundances |
| | Species combined in a matrix of relative abundances × 60 sites for multivariate analysis | Bird species composition |
| Presence-absence of species per site | Presence-absence of species per site. Presence (1) was defined as the detection of the species in at least one of 16 visits to each site | Bird species presence-absence |
| Dissimilarity of species composition between sites | Dissimilarity matrix of bird species composition based on Bray Curtis index between 60 sites | Variation in bird composition |
| Species turnover between sites | Dissimilarity matrix based on component of species' turnover of Sorensen index (= Simpson index) between 60 sites | Turnover of bird species |
| Nestedness of species between sites | Dissimilarity matrix based on component of species' nestedness of Sorensen index between 60 sites. | Nestedness of bird species |
| <i>Explanatory variables (200 m radius-sites)</i> | | |
| Relative areas of habitat types per site | Average of relative area of habitat types among the 16 visits per site. Eight habitat types combined in a matrix of area of habitat types × 60 sites for multivariate analysis | Area of habitat types Composition of habitat types |
| Number of habitat types per site | Average of the number of habitat types among the 16 visits per site | Habitat heterogeneity |
| Evenness of the relative areas of habitat types per site | Average of Pielou's evenness index, based on the relative area of each habitat type, among the 16 visits per site | Similarity of the habitat types in their relative areas |
| <i>Covariates</i> | | |
| Total bird abundance per site | Average of total bird abundance among the 16 visits per site. | Bird total abundance |
| Localities | Categorical variable with four levels: localities A, B, C and D. | Spatial structure |
| Euclidean distances between sites | Distance matrix based on Euclidean distances calculated from latitude and longitude of the sites | Spatial structure |

Analyses

Relationship between habitat heterogeneity and bird species richness

Histograms of individual variables and scatterplots between predictor (number and evenness of habitat types, relative areas of the eight habitat types per site, localities, total abundance) and response (species richness) variables (Table 1) were used primarily to check the shape of the relationship between variables, collinearity between explanatory variables, the normality of the response variable, the existence of outliers and if sampling effort was balanced for the range of values reached by the explanatory variables. Based on this exploratory data analysis, we used linear models with normal error distribution to assess the influence of habitat heterogeneity measures and area of each habitat type on bird species richness. Linear models were used because the response variable, bird species richness, was continuous (average among 16 visits, Table 1) and because we found good fits in the residual plots (Quinn & Keough 2002). Generalized variance inflation factor (GVIF) implemented with the *car* package (Fox & Weisberg 2011) in R (R Core Team 2015) was used to assess multicollinearity between predictor variables; because GVIF values were < 4 , all predictors were included in the models (Fox 2002). Graphical analysis and statistical tests of Moran's I autocorrelation index implemented by package *ape* (Paradis *et al.* 2004) in R (R Core Team 2015) showed that no autocorrelation remained in the residuals.

We ran separate linear models to examine the relationships between bird species richness and habitat characteristics during breeding (October–February surveys) and non-breeding (March–August surveys) seasons; bird and habitat data were averaged among the eight surveys (four counts per season during two years) for analyses by season. We combined the data from all 16 surveys in a two-year model (Table 1). Total abundance of birds (i.e. average of total bird abundance among the 16 visits per site) and localities were included in the models as factors to control for the effects of these variables on species richness. Statistical significance ($P < 0.05$) of individual variables was assessed by *F*-test for nested models. Hierarchical partitioning analysis was used to compare the effects among predictors. Hierarchical partitioning allows one to determine the independent effects of each predictor variable (i.e. because of that variable alone) excluding effects from the combined action of that variable with other predictor variables. The method considers all possible regression models, and measures the increase in model fit associated with each predictor variable as the average of additional explanatory power gained in all models where that variable appears (Mac Nally 2000). Covariates (total abundance of birds and localities) were always kept in the models. Hierarchical partitioning analysis was implemented by package *relaimpo* (Grömping 2006) in R (R Core Team 2015).

Relationship between habitat heterogeneity and bird composition

Non-metric multidimensional scaling (NMDS) was used to explore the relationship between habitat types and the bird community. Prior to ordination, the bird community was reduced to 95 species by removing those species with less than 10% of occurrences across 60 sites (i.e. 5 or fewer sites). The NMDS ordination was created using the 'metaMDS' function in the *vegan* package (Oksanen *et al.* 2015) for R (R Core Team 2015). The matrix of bird relative abundances (Table 1) was relativized through Wisconsin double standardization where species are first standardized by maxima and then sites by site totals (Oksanen 2011). The bird dissimilarity matrix was based on the Bray–Curtis index. The ordination was evaluated by the coefficient of determination based on stress (R^2 , Oksanen 2011). To describe the relationship of the bird ordination to the changes in area and number of habitat types, we overlaid those variables on the NMDS plot by 'envfit' analysis of the *vegan* package (Oksanen *et al.* 2015). The 'Envfit' function fits vectors of habitat variables onto an ordination such that projections of points onto vectors have maximum correlation. Goodness-of-fit of habitat vectors was assessed by the squared correlation coefficient (R^2). Significance of goodness-of-fit was assessed by permutations (999, Oksanen 2011).

Components of species nestedness and turnover of Sorensen index (Baselga 2010) were used to calculate two pair-wise bird dissimilarity matrices and to assess the influence by a Partial Mantel test of habitat heterogeneity (i.e. number of habitat types) and habitat-type composition (i.e. matrix of relative area of habitat types, Table 1) on these two components. Pair-wise dissimilarity matrices were calculated between all 60 sites. Decomposition of Sorensen index into components of species nestedness and turnover was implemented by package *betapart* (Baselga and Orme 2012) in R (R Core Team 2015). Dissimilarity matrices of habitat-type composition and habitat-type number were calculated using Euclidean distances and were used alternatively as control matrices in the analysis. A matrix of Euclidean latitudinal and longitudinal distances was included to account for spatial pattern in the analysis. The significance of the Mantel coefficient ($H_0: r = 0$) was assessed through 999 permutations. Partial Mantel analysis was implemented by package *ecodist* (Goslee & Urban 2007) in R (R Core Team 2015).

Relationships between habitat heterogeneity and individual species

To assess the relationship between individual species and habitat heterogeneity (i.e. number of habitat types), we used linear and generalized linear models implemented by *stats* package in R (R Core Team 2015). Linear models were used to analyse relative abundances of species that had a high frequency of occurrence across the 60 sites and for species that showed a good fit (assessed by residual plots) to these models. Generalized

linear models with binomial distribution were used to assess presence–absence of species with 10 or more occurrences across 60 sites but that did not show a good fit by linear models (e.g. high proportion of zeros). Generalized linear models for 17 of the species showed significant lack-of-fit according to at least one of Pearson's chi-square or Hosmer–Lemeshow goodness-of-fit tests and were excluded from the analysis. Locality was included as a covariate. Statistical significance ($P < 0.05$) of habitat type number was assessed by F (linear models) and likelihood ratio (generalized linear models) tests for nested models; marginally significant results ($0.05 < P < 0.1$) also were indicated. Hierarchical partitioning analysis implemented by *hier.part* package (Walsh & Mac Nally 2013) in R (R Core Team 2015) was used to assess the relative importance of habitat type number in the models. Hierarchical partitioning for the linear and generalized linear models was implemented using R^2 and log-likelihood as the goodness-of-fit measure, respectively. Global fit and relative importance of habitat type number in generalized linear models was expressed by McFadden's pseudo- R^2 (Veall & Zimmermann 1996). The 'null' model used in the calculation of McFadden's pseudo- R^2 was a generalized linear model fitted without variables. Therefore, the McFadden's pseudo- R^2 of each generalized linear model reflects the additional variability explained (expressed as log-likelihood and obtained by hierarchical partitioning) by the global model (habitat type number and localities) and individually by the habitat type number.

RESULTS

General results

We recorded 12 738 individuals representing 162 bird species. Species richness per site ranged from 2.7 to 8.4 species (mean \pm SD = 5.3 ± 1.2). The number of habitat types per site ranged from 2.13 to 4.38 (mean \pm SD = 3.20 ± 0.89) and evenness of relative areas of habitat types ranged from 0.51 to 0.95 (mean \pm SD = 0.84 ± 0.07). Habitat types that had the highest and lowest average of total areas among the 60 sites were open water (mean \pm SD = $22.2 \pm 14.6\%$) and beaches (mean \pm SD = $2.0 \pm 2.5\%$), respectively.

Relationship between habitat heterogeneity and bird species richness

Bird species richness was positively associated with number of habitat types per site over the entire two-year period as well as in the non-breeding and breeding seasons separately (Table 2, Fig. 2). Bird species richness was not associated with evenness and area proportion of habitat types (Table 2). Although in the two-year period bird species richness was negatively associated with proportion of open water and grasslands, and positively associated with proportion of shrublands, the

Table 2. Multiple regression models to account for variation in bird species richness as a function of habitat heterogeneity (number of habitat types), evenness of the area of habitat types and areas of habitat types in non-breeding and breeding seasons and for all samples averaged among 16 visits per site across two years (2011–2013)

| | Non-breeding | | Breeding | | Two years | |
|-------------------------------|---------------------------------|----------|---------------------------------|---------|---------------------------------|----------|
| | β | P | β | P | β | P |
| <i>Habitat heterogeneity</i> | | | | | | |
| Number of habitat types | 0.76 ± 0.20 | <0.001** | 0.88 ± 0.34 | 0.013** | 0.84 ± 0.22 | <0.001** |
| Evenness | -0.13 ± 0.16 | 0.399 | 0.24 ± 0.23 | 0.289 | 0.07 ± 0.15 | 0.662 |
| <i>Areas of habitat types</i> | | | | | | |
| Open water | -0.22 ± 0.15 | 0.154 | -0.35 ± 0.28 | 0.207 | -0.33 ± 0.17 | 0.056* |
| Floating macrophytes | 0.14 ± 0.17 | 0.412 | -0.29 ± 0.27 | 0.287 | -0.06 ± 0.17 | 0.715 |
| Emergent macrophytes | -0.19 ± 0.15 | 0.217 | 0.13 ± 0.24 | 0.601 | 0.02 ± 0.15 | 0.882 |
| Shrublands | 0.23 ± 0.17 | 0.182 | 0.28 ± 0.30 | 0.347 | 0.34 ± 0.18 | 0.068* |
| Grazed pastures | -0.09 ± 0.18 | 0.622 | -0.03 ± 0.28 | 0.925 | 0.02 ± 0.17 | 0.899 |
| Beach | 0.25 ± 0.15 | 0.103 | 0.01 ± 0.20 | 0.950 | 0.18 ± 0.15 | 0.230 |
| Grasslands | -0.26 ± 0.17 | 0.146 | -0.34 ± 0.27 | 0.218 | -0.36 ± 0.18 | 0.052* |
| Trees | -0.27 ± 0.19 | 0.175 | -0.07 ± 0.30 | 0.819 | -0.19 ± 0.20 | 0.350 |
| <i>Controlled variables</i> | | | | | | |
| Bird abundance | 0.34 ± 0.16 | 0.037 | 0.24 ± 0.22 | 0.275 | 0.2 ± 0.14 | 0.096 |
| Locality | B: 0.18 ± 0.40 | 0.437 | B: -0.84 ± 0.58 | 0.007 | B: -0.23 ± 0.38 | 0.016 |
| | C: 0.02 ± 0.43 | | C: -1.26 ± 0.65 | | C: -0.50 ± 0.42 | |
| | D: -0.48 ± 0.47 | | D: -2.38 ± 0.68 | | D: -1.36 ± 0.45 | |
| | | | | | | |
| R^2 adjusted | 0.44 | | 0.31 | | 0.43 | |
| Global significance | $F_{14,45} = 4.2$; $P < 0.001$ | | $F_{14,45} = 3.9$; $P < 0.001$ | | $F_{14,45} = 4.1$; $P < 0.001$ | |

For each model we report regression coefficients \pm standard errors ($\beta \pm$ SE) and P -values (P) of individual variables, and coefficient of multiple determination adjusted (R^2) and significance of global models. Significant ($P < 0.05$) and marginally significant ($0.1 < P > 0.05$) values are indicated with two **and one *asterisks, respectively.

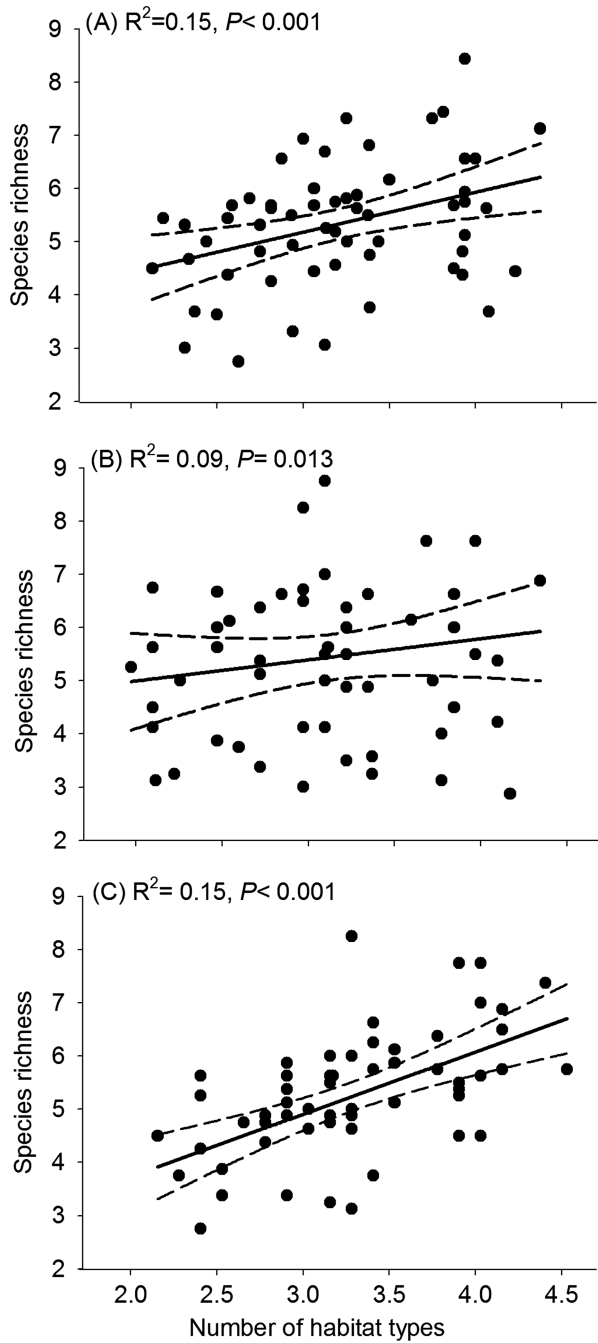


Fig. 2. Bird species number as a function of number of habitat types in the non-breeding (A), breeding (B) and two-year (C) datasets. Regression line (continuous line) and 95% confidence intervals (dashed lines) are shown.

relationships were marginally significant (Table 2). Hierarchical partitioning showed that the number of habitat types accounted for a substantially greater component of variance in species richness than did area of individual habitat types (Fig. 3). Although the number of habitat types accounted for a relatively low percentage of variance in the breeding period (Fig. 2b), it was still of

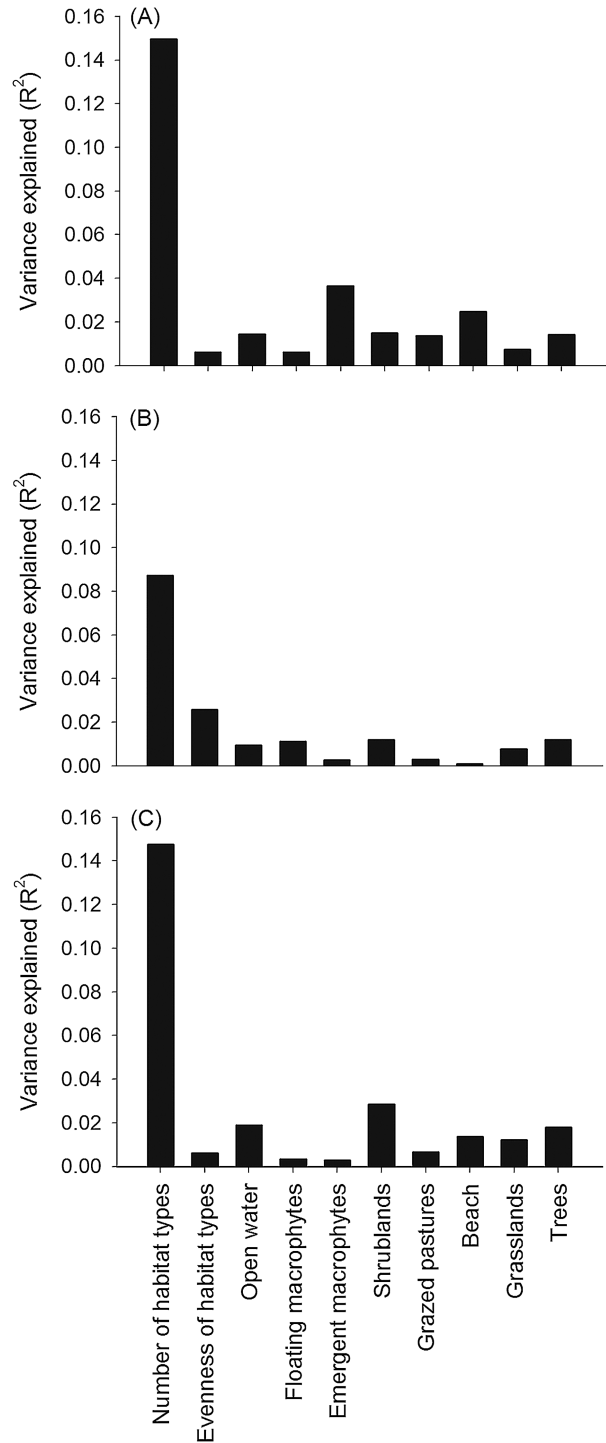


Fig. 3. Independent effects obtained by hierarchical partitioning of variance of number, evenness and area of individual habitat types on bird species richness in the non-breeding (A) and breeding (B) two-year (C) datasets.

greater importance than the variance accounted for by the area of individual habitat types (Fig. 3b). Although bird species richness showed a marginally significant

relationship with open water, grasslands and shrublands in the two-year period, these habitat types accounted for a relatively low percentage of variance in this model (Fig. 3c).

Relationship between habitat heterogeneity and bird composition

NMDS showed that individual species were associated with area of individual (e.g. grasslands) and combinations (e.g. open water-emergent macrophytes, open water-beaches) of habitat types (Fig. 4). Also, habitat type number was associated with changes in bird composition among sites (Fig. 4).

Pair-wise species nestedness and turnover of bird composition between sites varied between 0.00–0.31 and 0.14–0.81, respectively. The number of habitat types accounted for variation in species nestedness between sites (Mantel: $r = 0.12$, $P = 0.008$) but was not associated with turnover of species (Mantel: $r = -0.01$, $P = 0.755$). In contrast, composition of habitat types accounted for variation in turnover of species between sites (Mantel: $r = 0.25$, $P = 0.001$) but was not associated with species nestedness (Mantel: $r = -0.09$, $P = 0.143$).

Relationships between habitat heterogeneity and individual species

Species-specific analyses showed that of the 53 species considered in the analysis, 14 showed a significant (9 species) or marginally significant (5 species) positive relationship with habitat heterogeneity; one species, *Poospiza nigrorufa*, had a marginally significant negative relationship (Table 3). NMDS showed that species with a positive relationship were associated with different combinations of habitat types (Fig. 4). For example, *Ardea cocoi*, *Butorides striata* and *Fluvicola albiventer* were associated with combinations of open water, emergent macrophytes and shrublands in the sites; *Tringa melanotos*, *Tringa solitaria*, *Phimosus infuscatus*, *Charadrius collaris* and *Amazonetta brasiliensis* were associated with combinations of open water, beaches and grazed pastures in the sites. *P. nigrorufa*, a species negatively associated with the number of habitat types, was associated principally with shrublands and emergent macrophytes (Fig. 4).

DISCUSSION

Relationship between habitat heterogeneity and bird species richness

Recent studies have suggested that the shape of the relationship between habitat heterogeneity and species richness (HR relationship hereafter) is unclear and that it is not necessarily linear and/or positive but could vary

under different conditions (Allouche *et al.* 2012; Laanisto *et al.* 2013). In fact, most relationships are specific to the habitat type, the taxonomic group and the spatial scale of the study. Consequently, the extent and generality of positive HR relationships are still debated (Stein *et al.* 2014) and illustrate the value of studies that assess the relationship in different contexts. In this study, we documented a positive HR relationship in fluvial wetlands of the Middle Paraná riparian corridor. Fine-grained habitat heterogeneity *per se* within sites of 0.13 km² rather than individual habitat types of the floodplain was a more important predictor of species richness.

This positive HR relationship held during non-breeding and breeding seasons and in a model that included the mean species richness averaged across 2 years demonstrated the generality of the relationship. However, the proportion of explained variability in bird species richness was low in all three models, especially in the breeding season model, suggesting that while habitat heterogeneity influences bird species richness along the floodplain, other variables that were not considered in this study (e.g. productivity, river hydrology) can also be important. The classification of habitat types used can be a good indicator of habitat availability for birds as different wetland species are associated with different habitat types (Ronchi-Virgolini *et al.* 2008) and because individual species could select sites with specific composition of habitat types (e.g. Riffell *et al.* 2001). However, other classifications and other scales are also possible and may improve the fit of the models if they are included because the selection of habitats by species can occur hierarchically from large (regions, landscapes, lagoon complexes) to smaller (individual lagoons, microhabitat within lagoons) scales (Weller 1999).

Relatively few studies have addressed the HR relationship in wetlands and floodplains (Naiman *et al.* 2005; González-Gajardo *et al.* 2009; see reviews in Tews *et al.* 2004; Tamme *et al.* 2010; Stein *et al.* 2014), despite the great habitat heterogeneity typical of these systems. In general, studies in wetlands that have examined the influence of habitat heterogeneity on bird species richness have found a positive relationship (Sillen & Solbreck 1977; Henderson & Harper 1992; Celada & Bogliani 1993; Saab 1999; González-Gajardo *et al.* 2009), although exceptions have also been reported (Craig & Beal 1992; Fairbairn & Dinsmore 2001; De Stefano *et al.* 2012).

Area or presence-absence of certain habitat types can account for spatial variation in species richness, and even become more important than measures of habitat heterogeneity (e.g. Davidar *et al.* 2001). Although the areas of individual types of habitat were also included in the models, hierarchical analysis showed that these areas were of lower importance than habitat heterogeneity in accounting for bird species richness.

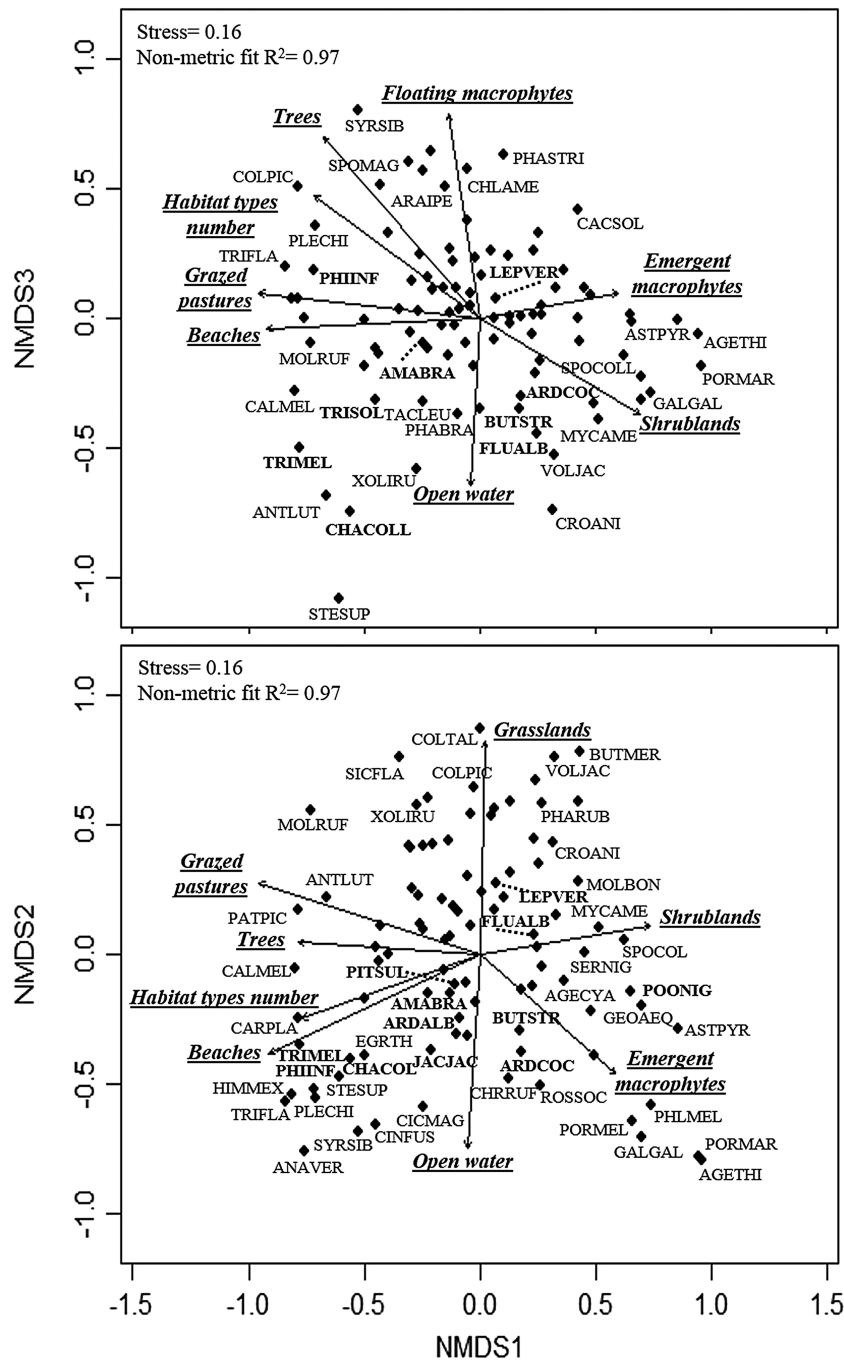


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of bird composition among the 60 sites. Number and area of habitat types were fit onto ordination result. Only habitat variables with P (obtained by 999 permutations) < 0.05 are shown. Species are indicated with points and 3 + 3-letter abbreviations (e.g. *Anas versicolor*: ANAVER, see Table S1 for all species abbreviated names). Species in bold showed a significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.1$) relationship with habitat type number (see results).

For example, an increase in the area of shrublands on sites also increased species richness. Shrubs can attract a significant number of species of passerines (e.g. based on NMDS results: *P. nigrorufa*, *Asthenes phyrroleuca*, *Geothlypis aequinoctialis*, *Volatinia jacarina*) and thereby

increase overall species richness. Conversely, species richness decreased with an increase in the area of open water and grasslands, suggesting that relatively few species would be associated exclusively with these types of habitat.

Table 3. Species-specific responses of birds to variation in habitat heterogeneity (i.e. number of habitat types) across 60 sites along the Middle Paraná riparian corridor

| Species | Frequency of occurrence | Model type | Global R^2 | Number of habitat types effect | | |
|----------------------------------|-------------------------|------------|--------------|--------------------------------|----------|-------|
| | | | | $\beta \pm SE$ | P | R^2 |
| <i>Amazonetta brasiliensis</i> | 36 (0.60) | GLM | 0.24 | 1.17 ± 0.51 | 0.022** | 0.09 |
| <i>Anas versicolor</i> | 20 (0.33) | GLM | 0.14 | 0.20 ± 0.45 | 0.650 | <0.01 |
| <i>Ciconia maguari</i> | 16 (0.27) | GLM | 0.05 | 0.43 ± 0.40 | 0.273 | 0.01 |
| <i>Phalacrocorax brasilianus</i> | 23 (0.38) | GLM | 0.07 | 0.55 ± 0.36 | 0.116 | 0.02 |
| <i>Ardea cocoi</i> | 37 (0.62) | GLM | 0.27 | 1.44 ± 0.44 | 0.005** | 0.10 |
| <i>Ardea alba</i> | 37 (0.62) | GLM | 0.15 | 0.94 ± 0.43 | 0.020** | 0.08 |
| <i>Butorides striata</i> | 19 (0.32) | GLM | 0.25 | 1.15 ± 0.50 | 0.010** | 0.07 |
| <i>Plegadis chihi</i> | 27 (0.45) | GLM | 0.39 | -0.02 ± 0.40 | 0.952 | 0.05 |
| <i>Phimosus infuscatus</i> | 19 (0.32) | GLM | 0.24 | 1.01 ± 0.44 | 0.013** | 0.12 |
| <i>Aramus guaranauna</i> | 46 (0.77) | GLM | 0.08 | 0.47 ± 0.39 | 0.208 | 0.03 |
| <i>Aramides ipecaha</i> | 18 (0.30) | GLM | 0.28 | 0.16 ± 0.42 | 0.695 | 0.02 |
| <i>Porphyrio martinicus</i> | 10 (0.17) | GLM | 0.50 | -0.44 ± 0.76 | 0.549 | 0.05 |
| <i>Vanellus chilensis</i> | 48 (0.80) | LM | 0.18 | 0.07 ± 0.07 | 0.367 | 0.06 |
| <i>Charadrius collaris</i> | 16 (0.27) | GLM | 0.10 | 0.71 ± 0.42 | 0.073* | 0.04 |
| <i>Tringa flavipes</i> | 22 (0.37) | GLM | 0.34 | 0.20 ± 0.45 | 0.653 | 0.05 |
| <i>Tringa solitaria</i> | 17 (0.28) | GLM | 0.11 | 0.61 ± 0.38 | 0.092* | 0.03 |
| <i>Tringa melanotos</i> | 16 (0.27) | GLM | 0.29 | 0.86 ± 0.51 | 0.073* | 0.07 |
| <i>Jacana jacana</i> | 59 (0.98) | LM | 0.31 | 0.67 ± 0.15 | <0.001** | 0.13 |
| <i>Crotophaga ani</i> | 11 (0.18) | GLM | 0.42 | 0.06 ± 0.44 | 0.900 | <0.01 |
| <i>Megasceryle torquata</i> | 10 (0.17) | GLM | 0.09 | 0.75 ± 0.50 | 0.108 | 0.06 |
| <i>Leptotila verreauxi</i> | 15 (0.25) | GLM | 0.17 | 1.09 ± 0.55 | 0.013** | 0.07 |
| <i>Columbina picui</i> | 30 (0.50) | GLM | 0.44 | 0.47 ± 0.51 | 0.338 | <0.01 |
| <i>Colaptes melanochloros</i> | 16 (0.27) | GLM | 0.19 | -0.24 ± 0.36 | 0.500 | <0.01 |
| <i>Myopsitta monachus</i> | 26 (0.43) | GLM | 0.19 | 0.58 ± 0.39 | 0.121 | 0.03 |
| <i>Furnarius rufus</i> | 48 (0.80) | LM | 0.58 | 0.05 ± 0.04 | 0.185 | 0.13 |
| <i>Phacellodomus ruber</i> | 31 (0.52) | GLM | 0.31 | 0.56 ± 0.46 | 0.201 | <0.01 |
| <i>Certhiaxis cinnamomeus</i> | 47 (0.78) | LM | 0.21 | -0.04 ± 0.05 | 0.412 | 0.02 |
| <i>Asthenes pyrrholeuca</i> | 15 (0.25) | GLM | 0.22 | -0.55 ± 0.54 | 0.301 | 0.06 |
| <i>Cinclodes fuscus</i> | 12 (0.20) | GLM | 0.11 | 0.53 ± 0.48 | 0.256 | 0.04 |
| <i>Pitangus sulphuratus</i> | 59 (0.98) | LM | 0.25 | 0.13 ± 0.03 | 0.001** | 0.22 |
| <i>Hymenops perspicillatus</i> | 52 (0.87) | LM | 0.23 | -0.02 ± 0.02 | 0.433 | 0.04 |
| <i>Satrapa icterophrys</i> | 14 (0.23) | GLM | 0.07 | 0.75 ± 0.42 | 0.064* | 0.05 |
| <i>Tyrannus melancholicus</i> | 29 (0.48) | GLM | 0.34 | 0.40 ± 0.44 | 0.354 | <0.01 |
| <i>Fluvicola albiventer</i> | 26 (0.43) | GLM | 0.34 | 1.00 ± 0.43 | 0.012** | 0.05 |
| <i>Xolmis irupero</i> | 15 (0.25) | GLM | 0.43 | 0.35 ± 0.40 | 0.370 | <0.01 |
| <i>Progne tapera</i> | 22 (0.37) | GLM | 0.15 | 0.32 ± 0.36 | 0.368 | 0.01 |
| <i>Tachycineta leucorrhoa</i> | 12 (0.20) | GLM | 0.05 | 0.41 ± 0.41 | 0.320 | 0.02 |
| <i>Poliophtila dumicola</i> | 13 (0.22) | GLM | 0.12 | 0.66 ± 0.55 | 0.212 | 0.06 |
| <i>Turdus amaurochalinus</i> | 19 (0.32) | GLM | 0.20 | 0.11 ± 0.35 | 0.752 | <0.01 |
| <i>Paroaria capitata</i> | 56 (0.93) | LM | 0.03 | 0.07 ± 0.06 | 0.228 | 0.01 |
| <i>Paroaria coronata</i> | 44 (0.73) | GLM | 0.31 | 1.09 ± 0.68 | 0.091* | 0.07 |
| <i>Poospiza migrorufa</i> | 14 (0.23) | GLM | 0.16 | -1.08 ± 0.59 | 0.052* | 0.06 |
| <i>Sicalis luteola</i> | 11 (0.18) | GLM | 0.23 | -0.18 ± 0.39 | 0.646 | <0.01 |
| <i>Sporophila collaris</i> | 30 (0.50) | GLM | 0.22 | -0.36 ± 0.36 | 0.310 | 0.05 |
| <i>Saltator caeruleus</i> | 41 (0.68) | LM | 0.28 | 0.01 ± 0.04 | 0.773 | <0.01 |
| <i>Saltator aurantiorostris</i> | 12 (0.20) | GLM | 0.15 | -0.12 ± 0.38 | 0.748 | <0.01 |
| <i>Zonotrichia capensis</i> | 50 (0.83) | LM | 0.09 | -0.02 ± 0.04 | 0.641 | 0.01 |
| <i>Agelasticus cyanopus</i> | 53 (0.88) | LM | 0.33 | -0.04 ± 0.05 | 0.461 | <0.01 |
| <i>Geothlypis aequinoctialis</i> | 24 (0.40) | GLM | 0.33 | -0.40 ± 0.37 | 0.266 | 0.08 |
| <i>Chrysomus ruficapillus</i> | 43 (0.72) | LM | 0.14 | 0.01 ± 0.23 | 0.953 | <0.01 |
| <i>Agelaioides badius</i> | 33 (0.55) | GLM | 0.30 | 0.21 ± 0.39 | 0.593 | <0.01 |
| <i>Molothrus bonariensis</i> | 20 (0.33) | GLM | 0.15 | -0.75 ± 0.50 | 0.121 | 0.05 |
| <i>Molothrus rufoaxillaris</i> | 11 (0.18) | GLM | 0.11 | -0.12 ± 0.44 | 0.789 | <0.01 |

Absolute and relative (in parentheses) frequencies, coefficient of multiple determination (Global R^2) of the models and beta coefficients \pm standard errors ($\beta \pm SE$), P -values and coefficient of determination (obtained by hierarchical partitioning) of habitat type number effect are shown. Species that did not show good fit by linear models (LM) were analysed by binomial (presence-absence) generalized models (GLM). McFadden's pseudo- R^2 was used for GLMs. Significant ($P < 0.05$) and marginally significant ($0.05 > P > 0.1$) values are indicated with two **and one *asterisks, respectively.

Processes underlying to the positive habitat heterogeneity–bird species richness relationship

In our study, at least two processes might explain the positive HR relationship. The first process can be related to the fact that different bird species are associated with different habitat types (i.e. niche-based hypothesis). Numerous lines of evidence suggest that individual species are associated with individual habitat types in wetlands (Weller 1999; Ronchi-Virgolini *et al.* 2008). In our study, NMDS analysis revealed associations of individual species with certain habitat types. Accordingly, the number of habitat types accounted for species nestedness between sites (i.e. sites with fewer habitat types supported a subset of the species present in sites with more habitat types) and composition of habitat types accounted for species turnover between sites (i.e. differences between sites in the identity of bird species was related to the habitat types present). Therefore, sites that contained more habitat types contained more bird species while sites with less habitat types held only a subset of those species, supporting the nested-habitat hypothesis.

Selection of heterogeneous sites by individual bird species may be a second process that helps explain the positive HR relationship in our study. Certain species might not be associated with a particular habitat type, but rather to sites containing more habitat types. This may be particularly true in floodplain landscapes, where there are a large number of habitat types on small scales relative to the home range of bird species. Other studies have shown associations of individual bird species to habitat heterogeneity in wetlands and river landscapes (Saab 1999; Fairbairn & Dinsmore 2001; Riffell *et al.* 2001). In our study, a set of 14 species was more frequent and/or abundant in heterogeneous sites suggesting that these species are associated with heterogeneous habitats. Most of these species were waterfowl (nine species) or birds that use the beaches as feeding sites (seven species; e.g. *Ardea* spp., *B. striata*, *P. infuscatus*, *Tringa* spp.). Combinations of habitat types can provide more resources, different types of resources and/or make those resources available to birds. For example, based on NMDS results, beaches-grazed pastures, open water and trees can provide feeding sites, food and roosting-refuge places, respectively, to *P. infuscatus*. Shrublands, emergent macrophytes and open water can provide feeding sites, protection and food to *B. striata* and *A. cocoi*. Therefore, habitat heterogeneity may provide more suitable habitats for a number of species of floodplain systems (Gregory *et al.* 1991). However, the low fit value of the models ($R^2 < 0.13$ in all cases) may indicate that the types of habitats present in heterogeneous sites, in addition to their number, may also be important for these species (i.e. heterogeneous sites that do not contain the types of habitats used by birds are not habitats

used by the species associated positively with habitat heterogeneity). Other causes related to the low fit value of the models may be related to the fact that some species do not occupy all patches of suitable habitat ('unsaturation'), to stochastic fluctuations such as chance colonization, and that other unmeasured variables (e.g. productivity) can also define habitat selection (Titeux *et al.* 2004).

Conversely, only one of the analysed species, *P. nigrorufa*, had a negative association with habitat heterogeneity. This species is associated with riparian shrublands (Stotz 1996), as indicated in our data analysis by the NMDS. Therefore, the results suggest that *P. nigrorufa* is associated with homogeneous sites on the floodplain that are dominated by shrublands.

General conclusions

Productivity, disturbance and spatial heterogeneity are considered key factors controlling local patterns of species richness (Naiman *et al.* 2005). Studying riparian wetlands, Pollock *et al.* (1998) found that topographic heterogeneity within a site increased plant diversity through effects on flood frequency. Thus, these authors integrated spatial heterogeneity and disturbances to explain the diversity of plants. In floodplain systems, habitat heterogeneity is a result of spatial variation in disturbances caused by floods (Ward *et al.* 1999). Thus, our results also agree with the more general idea that spatial variation in disturbances can increase the species richness of organisms through its positive effects on heterogeneity.

In conclusion, this study provided evidence that spatial habitat heterogeneity *per se* rather than individual habitat types has a positive effect on bird species richness in fluvial wetlands. Thus, while the composition of habitat types can influence species turnover, habitat heterogeneity can have a positive influence on bird species richness, generating patterns of nestedness between assemblages along fluvial wetlands.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site:

Figure S1. Frequency of habitat types per site.

Figure S2. Pielou's evenness of the relative areas of habitat types.

Figure S3. The relative proportion of habitat types among the 60 sites studied.

Table S1. Abbreviations used for bird species names.