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Geographic differences between functional groups in patterns of bird species richness in North America

Jofre Carnicer, Ricardo Díaz-Delgado*

Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Pabellón del Perú. Av, María Luisa s/n, E-41013 Sevilla, Spain

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ABSTRACT

Geographic divergences in patterns of species richness were studied for the terrestrial birds of North America using Breeding Bird Survey (BBS) census data subdivided for guild and migratory groups. Our aim was to study if species richness patterns for North American birds were best viewed as the convergent response of different groups to a common mechanism or as the result of several different processes. We observed opposite geographical patterns of species richness and differences in the variables associated with species richness depending on the guild or migratory status considered. Several ecological variables seem to regulate large-scale patterns of terrestrial bird species richness in North America, mainly temperature-, productivity- and landscape habitat structure-related variables. These variables are diverse and group-specific. For instance, the results supported the productivity hypothesis in migratory and frugivore groups and the winter tolerance hypothesis in residents. Habitat structure was also identified as an important factor driving species richness, total abundance and community body mass variation. Overall, our results indicate that the large-scale patterns of bird species richness are the result of several divergent, group-specific processes, and that understanding diversity gradients requires the identification of the functional ecological groups included.

1. Introduction

Species richness gradients are ultimately generated by speciation, colonization and extinction processes along ecological and historical time scales (Ricklefs and Schluter, 1993; Hubbell, 2001; Evans et al., 2005b; Hawkins et al., 2006; Mittelbach et al., 2007). Some authors have studied the role of speciation, extinction and colonization dynamics in generating species richness gradients (Cardillo, 1999; Evans et al., 2005a,b; Carnicer et al., 2007; Weir and Schluter, 2007, and see supplementary material A1 for a review). This approach has been complemented by a number of studies examining the environmental correlates of species richness gradients which generally have not measured speciation, colonization and extinction rates (Turner et al., 1987; Currie, 1991; Hawkins et al., 2003a,b; Pautasso and Gaston, 2005; Evans et al., 2006; Mönkkönen et al., 2006). These studies have identified productivity as the best predictor of bird species richness at the global scale (Hawkins et al., 2003a,b), suggesting the existence of a common global mechanism associated with energy variation that determines variation in species richness (Brown, 1981; Wright, 1983; Currie et al., 2004; Carnicer et al., 2007). In the particular case of North American breeding birds, positive correlations among species richness, abundance and energy

* *Corresponding author.*
E-mail address: jofrecarnicer@ebd.csic.es (J. Carnicer).
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availability measures (species-energy relationships) have been reported suggesting also the existence of a unique mechanism accounting for most of the species richness variation in that region (Hurlbert and Haskell, 2003; Hurlbert, 2004; Hawkins et al., 2003b; H-Acevedo and Currie, 2003; Hawkins, 2004; Hurlbert, 2004; Pautasso and Gaston, 2005; Evans et al., 2006; Mönkkönen et al., 2006).

However, some results contrast with this unifying and synthetic view, suggesting that several mechanisms might be underlying this general trend. First, the strength of the relationship between bird total abundance and productivity in North American breeding birds has been claimed to be too small to account for the observed changes in species richness (Currie et al., 2004), indicating that an important part of the variation might be associated to other processes not related to species-energy variations. Second, species-energy relationships have been found to vary qualitatively between functional groups in North American birds. For instance, winter species richness and abundance are best predicted by temperature variation (Evans et al., 2006) whereas breeding bird communities respond more strongly to the Normalized Difference vegetation Index (NDVI) (Hurlbert and Haskell, 2003; Hawkins, 2004; Evans et al., 2006). Third, species-energy relationships have been found to be qualitatively different in communities with different habitat structures (Hurlbert, 2004), with strong differences between open and closed habitats. Fourth, different hypotheses might contribute to the generation of species-energy relationships (reviewed in Evans et al., 2005a) and thus the observed patterns might respond to a diverse array of processes.

Overall a question emerges: are species richness patterns for North American birds the convergent response of different groups to a common mechanism or the result of several different processes? If convergence in patterns and processes among functional groups dominates, we should expect that most groups would respond to the same predictor variables when testing a battery of environmental predictors to explain richness variation. Similarly, we should expect that functional groups would present similar geographical patterns in species richness. On the contrary, if pattern and process divergence is on the basis of the observed gradients, different groups should respond to different predictors and present geographically consistent differences.

To assess this question we compiled data from the North American Breeding Bird Survey and explored the existence of divergences among bird groups in patterns of species richness. Birds were grouped by guild and migratory status and patterns of species richness were modelled using biotic and environmental variables. To test for the existence of geographical divergences in patterns of species richness we mapped species richness independently for each group and compared the geographical trends obtained. To explore the existence of process divergence we applied a model selection approach in which we contrasted five distinct hypotheses: the productivity hypothesis, the ambient-energy hypothesis, the winter-tolerance hypothesis, the habitat structure hypothesis and the heterogeneity hypothesis.

The productivity hypothesis (Hutchinson, 1959; Brown, 1981; Wright, 1983; Currie et al., 2004) asserts that productivity is the main variable limiting energy-availability thus determining bird abundance and species richness gradients. For instance, more productive forests have been found to sustain increased abundances of arthropods, higher abundances of insectivore birds and increased nestling success (Blondel et al., 2006; Buler et al., 2007). The more individuals hypothesis (MIH) (Srivastava and Lawton, 1998) is a variant of the productivity hypothesis and states that under the reasonable assumption that an increase in productive energy (NPP) increases the number of individuals that a locality can support (J), we should expect more species in high-energy areas than in poor-energy ones (Kaspari et al., 2003; Evans et al., 2005a, 2006; Mönkkönen et al., 2006). Thus, both the productivity and the more individuals hypotheses predict positive decelerating functions between productivity, community size and species richness (prediction 1, Table 1).

The ambient energy hypothesis (Turner et al., 1987, 1988; Currie, 1991; Lennon et al., 2000) holds that direct temperature effects on animal physiology and energy budgets constrain animal species richness by increased mortality or demographic negative effects (see supplementary material A2 for a more detailed view). The ambient energy hypothesis predicts that temperature measures will perform as the best predictors of species richness variation (prediction 2, Table 1). The winter-tolerance hypothesis (or freezing-tolerance hypothesis), a special case of the ambient energy hypothesis proposed by von Humbold (1808), states that the effect of winter temperatures at high latitudes (Meehan et al., 2004) is the predominant cause for the latitudinal gradient in species richness. According to the winter-tolerance hypothesis, species richness patterns are constrained by the increased physiological costs of low winter temperature values in species energy availability (see supplementary material A2). The winter-tolerance hypothesis predicts that species richness variation will be associated with winter temperature measures (prediction 3, Table 1).

The heterogeneity hypothesis (MacArthur et al., 1966; Pianka, 1966; Davidowitz and Rosenzweig, 1998; Kerr et al., 2001; Lavers and Field, 2006; González-Megías et al., 2007) asserts that the greater the heterogeneity of resources and conditions in a habitat, the greater the number of species that can co-exist in that habitat. This hypothesis predicts a linear relationship between heterogeneity measures and species richness (MacArthur et al., 1966) (prediction 4, Table 1). A secondary prediction, not tested here, is that this relationship should be observed at diverse spatial grains (Davidowitz and Rosenzweig, 1998; González-Megías et al., 2007).

Recently, Hurlbert (2004) highlighted that species-energy relationships differed between localities with different habitat structure. The habitat structure hypothesis states that local communities that differ in habitat structure (i.e. forests versus open fields or scrub areas) are colonized by different sets of species (Tews et al., 2004; Fuller et al., 2005) leading to differences in their species-energy relationships (Hurlbert, 2004). Indeed, differences in habitat structure have been found to be associated with differences in both community body-size distributions (Polo and Carrascal, 1999), abundance distributions (Flather and Sauer, 1996; Hurlbert, 2004) and in species richness (Atauri and de Lucio, 2001), suggesting that different habitat structures are associated with differences in all the components of energy flow (i.e. densities, body mass and

Table 1 – Hypotheses tested and their predictions. Predictor variables tested and predicted signs of the correlations with species richness. JNDVI: June NDVI; J: community size or total number of individuals in a locality; JuneT$^-$: mean June minimum temperature; JuneT$^+$: mean June maximum temperature; DV_JuneT: mean daily variation of June temperatures; DecT$^+$: mean December mean maximum temperature; DecT$^-$: mean December minimum temperature; pca1het: first principal component of PCA with heterogeneity variables; pca2het: second component, pca1hs: first principal component of PCA with habitat structure variables, pca2hs: second component

Hypotheses	Predictor variables	Expected sign	Predictions (P)	
Productivity (MIH)	JNDVI, Rainfall	+	P1	Productivity measures will be positively associated with both species richness and abundance measures; productivity will be selected as a predictor in the model selection approach
	J	+		Community size will be associated with species richness in a positive decelerating function and will be selected in the model selection approach using bird variables
Ambient energy	JuneT$^+$, JuneT$^-$, DV_JuneT	+/−	P2	Summer temperatures will be positively or negatively related with species richness and will be selected in the model selection approach
Winter tolerance	DecT$^+$, DecT$^-$	+	P3	Winter temperatures will be positively correlated with species richness and abundance and will be selected as predictors in the model selection approach
Heterogeneity	pca1het, pca2het	+	P4	Heterogeneity measures will be positively associated with species richness and will be selected in the model selection approach
Habitat structure	pca1hs,	+/−	P5	Habitat structure variables will be positively associated with species richness and will be selected as predictors in the model approach
	pca2hs		P6	Regions with different habitat structure (O = open, Cl = closed, S = shrub, Mx = mixed) will sustain significantly different values of species richness
			P7	Regions with different habitat structure (O, Cl, S, Mx) will sustain significantly different values of total abundance
			P8	Regions with different habitat structure (O, Cl, S, Mx) will sustain significant differences in the shape of body mass distributions (median community body mass, M)
			P9	Species will be associated with habitat structure types (O, Cl, S, Mx) in a correspondence analysis comparing all the regions
	M_i	−	P10	Regions with complex habitat structure (Cl) will sustain increased richness and a greater proportion of smaller species. Therefore, M (median community body mass) will be negatively associated to species richness

species richness). Overall, the habitat structure hypothesis predicts that habitat structure variables will predict species richness variation (prediction 5, Table 1). Furthermore, we expect to find significant differences in species richness (prediction 6), body mass distributions (prediction 7), and density distributions (prediction 8) between regions that strongly differ in their habitat structure. It predicts also that different species will be consistently associated with different habitat structure types (prediction 9). Finally, according to the existing evidence (MacArthur and MacArthur, 1961; Polo and Carrascal, 1999) we should expect that more complex habitats will sustain increased species richness and smaller species, leading to a negative association between community body mass measures and species richness (prediction 10).

2. Materials and methods

2.1. *Species richness and community variables*

Data on breeding bird abundances from the Breeding Bird Survey (BBS) were obtained for 67 contiguous physiographic strata (i.e. regions characterized by different vegetation types) distributed in northern Mexico, USA and part of Canada (Sauer et al., 2003; Fig. 1). The Breeding Bird Surveys are conducted during the peak of the nesting season (May–June). Each route is 39.4 km long, with a total of fifty observer stops located at 0.8 km intervals along the route. Bird abundances were measured in individuals/route. Physiographic strata for the BBS were developed by modifying existing vegetation and soil distribution maps (Robbins et al., 1986). Our regional approach allowed us to compare regions that were characterized by consistent differences in their habitat structure at the regional scale. Regional population averages derived from survey data were provided by the Patuxent Wildlife Research Center (http://www.pwrc.usgs.gov). Abundance trends were averaged for the 1966–1999 (James et al., 1996; Link and Sauer, 1997). Species richness was calculated as the cumulated number of species for all routes considered within each physiographic stratum (Cam et al., 2002). Landscape structure of each physiographic stratum was studied analyzing the percentages of land cover types in each region. Regions were grouped in four main habitat structure types: open habitat structure (O: cropland, grassland, savannah), closed habitat structure (Cl: deciduous, needleleaf forests, woodlands); shrubland habitat structure (S: shrubland) and mixed habitat structure (regions that were composed by a mixture of the former categories). Data on bird body sizes, migration behaviour and diet were obtained from del Hoyo et al. (1992), Dunning (1993) and the Nature Serve web site (http://www.natureserve.org/explorer/). Most species were characterized by mixed diets. For each species, we reviewed the existing literature on its diet. The relative fractions of different resources in the diet were studied and species were classified according

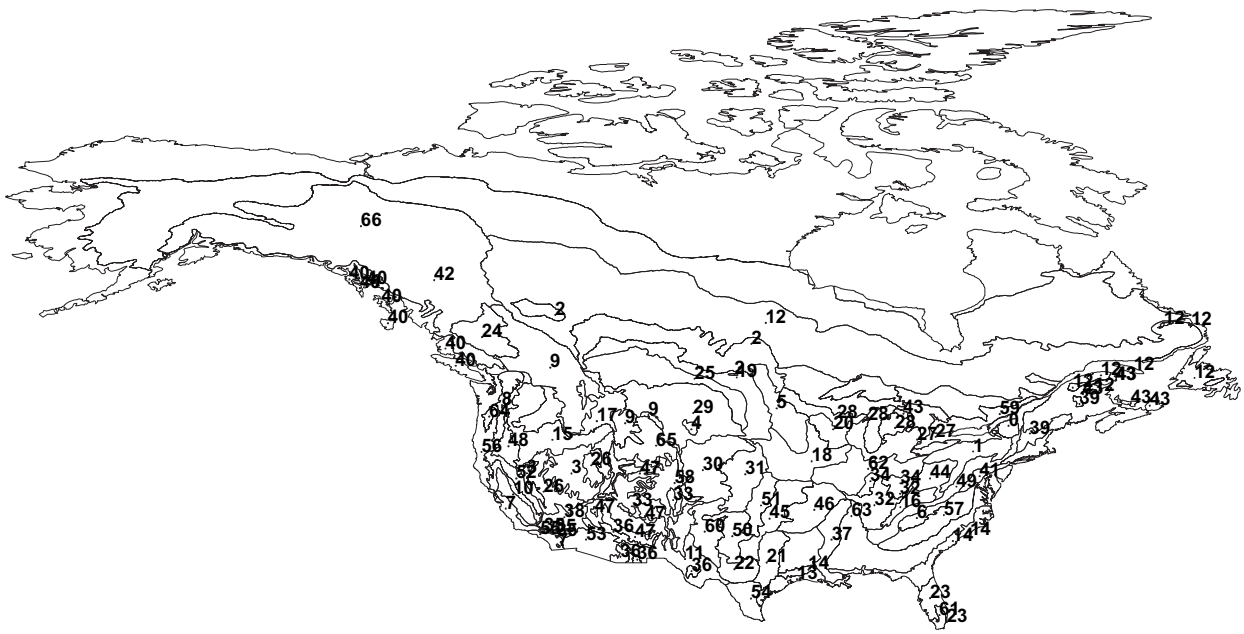

Fig. 1 – BBS physiographic strata map. A list of the names of the regions is available in supplementary material A3.

to the major fraction. We explored several classifications, from more detailed to more broad migratory and guild groups (see supplementary material A4 for a description). Results obtained for the more precise guild classification are not shown, but were consistent with the main results presented here for dietary groups. Guild and residency-status categories were found to be not independent attributes (supplementary Table A5, Chi square likelihood ratio test; $\chi^2 = 69.18$; $p < 0.0001$). Invertivore species were mainly concentrated in the migratory group (Mi), carnivore and granivore in resident (R) and partially migratory species (PM); herbivores were resident species, and the frugivore guild was a mixture of resident, partially migratory and migratory species.

2.2. *Environmental variables*

For each physiographic stratum, we estimated *geographic variables* (baricenter of latitude and longitude; where baricenter refers to the central geometrical point of the polygon or region); *productivity variables* (June NDVI (JNDVI), December NDVI (DNDVI), and rainfall) (Hurlbert and Haskell, 2003; Hawkins et al., 2003b; Hurlbert, 2004; Evans et al., 2006); *ambient-energy variables* (June maximum and minimum temperatures [JuneT$^+$, JuneT$^-$], daily variation in June temperatures [DV JuneT] and *winter-tolerance variables* (December maximum and minimum temperatures [DecT$^+$, DecT$^-$]) (Kaspari et al., 2000, 2003; Hawkins et al., 2003a,b; Meehan et al., 2004; Evans et al., 2006). *Heterogeneity variables* (listed in supplementary material A6) were summarized by means of PCA analysis (Kerr and Packer, 1997; Kaspari et al., 2003; Hawkins et al., 2003a; Hurlbert and Haskell, 2003). The first PCA axis (pca1het) accounted for 28% of the variance and ranged from high NDVI spatial variation to high variation in altitude and temperature, describing the longitudinal increase of heterogeneity associated with the Rocky Mountains system. The second axis (pca2het) ranged from NDVI interannual variation to spatial variation in winter temperature and heterogeneity in cover type and accounted for 19% of total variation. *Habitat structure variables* (percentage of area occupied by habitat types) were also summarized by means of PCA analysis (Kerr et al., 2001; Hawkins et al., 2003b; Tews et al., 2004; Fuller et al., 2005; Mönkkönen et al., 2006). The first axis (pca1hs) ranged from open to forested cover types and was interpreted as a measure of complexity of vegetation structure. The second axis (pca2hs) ranged from shrubland/grassland to cropland/forested areas, representing the longitudinal transition in habitat structure from the Rocky Mountains system to the coasts. Pca1hs and pca2hs accounted for 60% of variation.

We used GIS to integrate all the information for the study area. Digital information sources are provided in supplementary material A7.

2.3. *Statistical methods*

We analysed the pairwise correlations among all variables studied (Lennon et al., 2000). Models were corrected spatially by updating the model with geographical coordinates and accounting for spatial covariance using spherical, gaussian, or exponential theoretical covariance functions in which covariance parameters are specified (Crawley, 2002). We plotted a semivariogram of non-spatial models to obtain values of the spatial covariance parameters (nugget, sill and range) and improve convergence. Models were compared and the most parsimonious was selected based on Akaike's Information Criterion (lower AIC values). Adequacy of spatially-corrected models was checked by inspection of the sample variogram for the normalized residuals. Constancy in the variance was checked by plotting normalized values against fitted values. We used step function on R package (R Development Core Team, 2004) to select models based on the Akaike's Information

Criterion (AIC). Pairwise correlations among predictor variables used were analyzed. We rejected those models including two or more strong collinear variables (see supplementary material A8). To address sampling effects (area and route number effects), we included those measures as independent variables if those variables showed significant coefficients (Frenkleton, 2002). Following Moran (2003), we did not apply the sequential Bonferroni test or similar corrections for Type I errors and report pairwise correlations results including exact *p*-values.

2.4. *Mapping species richness and hypothesis testing*

To study the differences in geographic trends, species richness was independently mapped in each functional group. Additionally, geographical variation was studied modelling species richness as a function of latitude and longitude.

We analyzed the correlations between environmental variables and species richness for each functional group, testing the correlative support for all the hypotheses examined (predictions 1, 2, 3, 4 & 5, Table 1). We adopted a model selection approach (sensu Johnson and Omland, 2004) to identify a best single model, thus lending support to one particular hypothesis. Models included productivity-related variables (rainfall, NDVI), ambient-energy variables (summer temperatures, temperature daily variation), winter-tolerance variables (winter temperatures), habitat structure variables (landscape types summarized by principal component analyses) and explicit measures of habitat heterogeneity (heterogeneity measures summarized by principal component analyses). Quadratic effects of temperature and productivity variables were incorporated, given the existence of hump-shaped relationships with these variables for birds in North America (Hawkins et al., 2003b).

Additionally, we analyzed the existence of significant associations between body mass distributions (median body mass) and species richness variation (S–M relationship; prediction 10, Table 1). We examined the associations between the total number of individuals (J) and species richness (S–J relationships; prediction 1). To evaluate the more individuals hypothesis, we assessed the prediction that species richness (S) is a positive function of increased community size (J, i.e. the total number of individuals) on a log–log scale (Preston, 1962; May, 1978; Evans et al., 2006; Mönkkönen et al., 2006). S–J and S–M relationships were analyzed separately by each functional group.

The effect of habitat structure in S–J and S–M relationships was analyzed by grouping according to open and closed habitat structure regions. To evaluate the role of habitat structure in determining variation in total abundance (J) and body mass distributions (M) (predictions 7 & 8) we used a model selection approach for community size and median community body mass as the dependent variables and with environmental variables as predictors. According to the habitat structure hypothesis habitat structure variables should be selected as predictors.

We evaluated the existence of significant differences in species richness, body size distributions and density distributions (habitat structure hypothesis; predictions 6, 7 & 8) between regions with different habitat structures (O: open, Cl: closed, S: shrubland, Mx: mixed) performing Tukey–Kramer tests. Finally, we performed a correspondence analysis in order to evaluate the existence of associations between regional species composition and regional habitat structure types (prediction 9).

3. Results

3.1. *Geographically divergent patterns*

Bird species richness presents a complex geographic pattern that emerges as a mixture of the trends for the residency-status and guild-type groupings. Subdividing by groups the pattern is simplified, and geographically divergent patterns appear. We observe strong opposite geographic richness gradients: a significant latitudinal increase of migratory species richness (S_{Mi}), a significant decrease of resident and carnivore species richness with latitude (S_R, S_C), a significant increase of granivore and partial migratory richness with altitude (S_G, S_{PM}), and a significant reduction of frugivore and migratory species richness with longitude (S_F, S_{Mi}). Migratory species are dominant at northern areas (up to 40° latitude, they represent >45% of the species present; residents, <25%) while residents are the dominant group at southern parts (under 30° latitude, resident include >35% of the species, and migrants <25%).

The overall latitudinal richness pattern is better described by a polynomial second-degree function with a maximum at 40–50° of latitude. A second order function also fits well for the species richness trends of partially migratory, migratory, granivore, herbivore, invertivore, frugivore and carnivore groups, but each guild presents a distinct response (Fig. 2). The carnivore and resident groups have higher species richness, densities and biomass at southern latitudes, showing a linear reduction with latitude. Some guilds and migrant groups show negative correlations for the percentage of total species represented by each group. Thus, over the latitudinal gradient, the percentage of migratory and invertivore species increases with latitude but the percentage of carnivore and resident species decreases. Along the longitude gradient, the frugivore guild is dominant at eastern longitudes and is strongly reduced and replaced in the western regions by an increased dominance of granivore species (Fig. 2).

3.2. *Hypothesis testing*

Analysing species richness according to groups defined by migratory habit or guild type leads to stronger predictors of species richness and clearer geographical gradients (Table 2). The analysis of pairwise correlations indicates that species richness of migratory (S_{Mi}), frugivores (S_F), and invertivores (S_I) is best correlated with June NDVI, minimum June temperatures and forest cover percentage (following predictions 1, 2 and 5); while resident species richness (S_R) is correlated with high winter temperatures (prediction 3). The partially migratory (S_{PM}) and granivore species richness (S_G) is positively correlated with June temperature daily variation, altitude and negatively related to rainfall. The overall richness pattern (S) is dominated by the effect of the partially migratory,

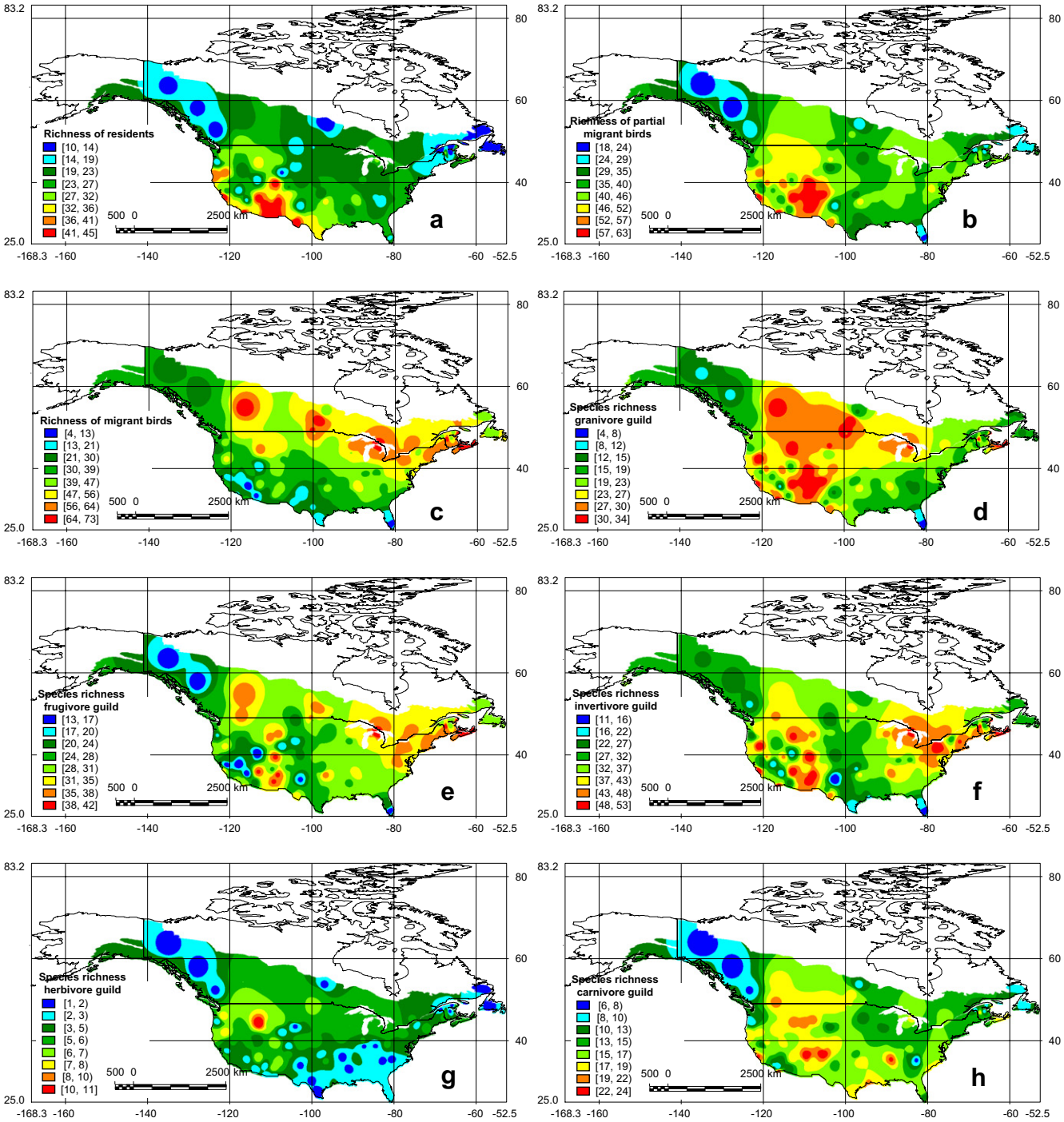

Fig. 2 – Species richness distribution maps by guilds and migration groups. Maps have been produced by spatial interpolation with an inverse distance interpolator over the points centred on every physiographic stratum. Therefore, the spatial interpolation fits data values in each location and changes across the space as a function of the closest point. (a): resident, (b): partially migratory, (c): migratory, (d): granivore, (e): frugivore, (f): invertivore, (g): herbivore, (h): carnivore. Red colour indicates maximum species richness values.

migratory, frugivore and invertivore groups, because they are the richest groups.

In the model selection approach (Table 2) we have found support for a predominance of winter effects (DecT) on resident species richness (prediction 3), and support for productivity effects on frugivore and invertivore groups (prediction 1). Summer temperatures were selected in carnivores, invertivores, partial migratory and migratory groups (prediction 2). Habitat structure measures were selected only in migratory species (prediction 5).

Table 2 – Models predicting species richness (S) for all species pooled and by migrant categories (subscripts for S indicate: R, resident; PM, partial migrant; Mi, migrant) and guild groups (C, carnivore; F, frugivore; G, granivore; I, invertivore)

Dep. V.	Independent variables	DF	AIC	r^2 adj	p
Bird variables					
log S	$\log J - M$	64	−344.97	0.59	<0.0001
$\log S_C$	$-M_C$	64	−303.9	0.32	<0.0001
$\log S_F$	$\log J_F - M_F$	64	−495.77	0.65	<0.0001
$\log S_G$	$\log J_G - M_G$	64	−316.06	0.67	<0.0001
$\log S_I$	$\log J_I - M_I$	64	−300.3	0.53	<0.0001
$\log S_R$	$\log J_R - M_R$	64	−286.79	0.37	<0.0001
$\log S_{PM}$	$\log J_{PM} - M_{PM}$	64	−327.2	0.42	<0.0001
$\log S_{Mi}$	$\log J_{Mi} - M_{Mi}$	64	−266.45	0.68	<0.0001
Environmental variables			Loglik	r^2 adj	p
S	$-\text{JuneT}^- + \text{JNDVI}$	58	−255.49	0.38	<0.0001
S_C	$\text{JuneT}^+ + \text{pca2het}$	62	−163.05	0.36	<0.0001
S_F	$\text{JNDVI} - \text{JNDVI}^2$	63	−194.86	0.32	<0.0001
S_G	$-\text{JuneT}^- - \text{Rainfall}$	61	−371.4	0.54	<0.0001
S_I	$-\text{JuneT}^- + \text{JNDVI}$	61	−204.29	0.47	<0.0001
S_R	DecT^+	63	−216.79	0.32	<0.0001
S_{PM}	$-\text{JuneT}^- + \text{DVJuneT}^-$	61	−193.083	0.45	<0.0001
S_{Mi}	$-\text{JuneT}^- + \text{pca2hs}$	61	−201.62	0.75	<0.0001

The productivity hypothesis is supported only in frugivore, invertivore and migratory groups. In these three groups species richness is correlated with JNDVI and community size (the summed number of individuals) following the predictions of the MIH (prediction 1). Community size and median body mass are the best bird community measures predicting richness in most bird groups (Tables 2 and 3).

Habitat structure is very important determining the shape and significance of *S–J* and *S–M* relationships (Table 3). In open habitat and cropland regions, a few dominant species reach the highest continental densities, and community size is a poor predictor of species richness. In these open habitat communities an increase of community size arises from a few species that are two orders of magnitude more abundant than the others and thus is not accompanied with a general increase in species richness. Once we correct for the effect of maximum densities, by taking the residuals from a plot between community size and maximum densities, some of the S–J relationships in open habitats became significant (Table 3).

Habitat structure variables (pca1hs, pcahs2) were selected in most groups as predictors of the variation in community abundances and body size distributions (Table 4). Open regions sustained significant higher community sizes in most groups (prediction 8; Tukey–Kramer tests; carnivores: $p = 0.0047$; granivores: $p = 0.0001$; herbivores: $p = 0.0007$; residents: $p = 0.0029$; partial migratory: $p = 0.0001$) and significantly bigger species in shrubland and open habitat regions (prediction 7; median community body size Tukey–Kramer tests; frugivores; $p = 0.0001$; granivores; $p = 0.042$; invertivores; $p = 0.0007$; residents: $p = 0.037$; partial migratory: $p = 0.033$; migratory: $p = 0.0015$). Significant habitat structure effects in species richness were detected only in migratory, frugivore and invertivore groups and were much weaker. Species richness was significantly higher in closed habitats in these three groups (prediction 6; Tukey–Kramer tests; frugivores; $p = 0.01$; invertivores; $p = 0.02$; migratory: $p = 0.01$).

Correspondence analysis (Fig. 3) indicated the existence of species that were associated with habitat structure types (prediction 9) but also the existence of generalist species that were distributed in all kinds of regions. Interestingly enough, the most abundant species (white dots in Fig. 3) were habitat generalists or open habitat species whereas those species reaching the lowest densities (black dots) were specialized in one habitat structure (more frequently in forest habitat structure, Cl).

4. Discussion

The study of species-energy relationships has failed to propose a unified mechanism linking energy availability, productivity, temperature, abundance, body mass and species richness. The results of this study indicate that this is a reasonable failure for several reasons, at least in North American birds. First, several ecological factors regulate large scale patterns of terrestrial bird species richness in North America, mainly temperature-, productivity- and landscape habitat structure-related factors. Second, those factors are diverse and group-specific. The divergence of mechanisms implicated in regulating species richness among guilds or migratory groups is reflected in the opposite geographic gradients of species richness when comparing groups. The most impressive opposite gradients are the latitudinal increase of migrant species richness (MacArthur, 1959; Herrera, 1978; Lennon et al., 2000),

Table 3 – Models comparing the effect of landscape habitat structure on: 1) log S–log J relationships; 2) log S–log J relationships correcting for the effect of maximum densities; 3) correlation strength of log species richness and median community body size. Significant p values: $^{\circ}p < 0.1$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{****}p < 0.0001$. Empty spaces indicate non-significant correlations

	Habitat structure	Log S All	G	F	I	C	H	R	PM	Mi
Log J	Open		0.23^{**}					0.34^{**}		
	Closed	0.56^{****}	0.24^{**}	0.6^{****}	0.3^{**}	0.28^{**}	0.3^{**}	0.31^{**}	0.53^{****}	0.37^{***}
Residual	Open			**0.24^{**}**	**0.31^{**}**			0.41^{***}		**0.58^{****}**
J	Closed	0.59^{****}	0.31^{**}	0.51^{****}	0.3^{**}	0.34^{**}	0.3^{**}	0.36^{***}	0.61^{****}	0.51^{****}
M	Open	**-0.72^{****}**	**-0.61^{****}**	**-0.76^{****}**	**-0.53^{****}**			**-0.43^{***}**	**-0.32^{**}**	-0.13^{*}
	Closed	-0.16^{*}				-0.16^{*}			-0.21^{*}	

Table 4 – Models predicting community size (J) and community median body size (M) for all species pooled and by migrant categories (subscripts for S indicate: R, resident; PM, partial migrant; Mi, migrant) and guild groups (C, carnivore; F, frugivore; G, granivore; I, invertivore)

Model	Dep. V.	Independent variables	DF	Loglik	*r* squared adjusted	*p*
1	J	−pca1hs + pca2hs	2,63	−408.59	0.57	<0.0000
2	J_C	pca2hs + JuneT$^+$	2,63	23.44	0.77	<0.0000
3	J_F	pca2hs	1,64	−134.68	0.64	<0.0000
4	J_G	−pca1hs	1,64	−157.43	0.63	<0.0000
5	J_I	JNDVI	1,64	−134.03	0.19	<0.001
6	J_R	−pca1hs + pca2hs + DecT$^+$	4,61	−139.51	0.72	<0.0000
7	J_{PM}	−pca1hs + pca2hs + JuneT$^+$	3,62	−146.52	0.56	<0.0000
8	J_{Mi}	JNDVI − JuneT$^-$ − pca1hs	3,57	−139.1	0.37	<0.0000
9	M	DecT$^-$ − pca1hs	2,63	−217.23	0.5	<0.0001
10	M_F	JuneT$^+$ − pca2hs	3,62	−157.67	0.45	<0.0001
11	M_G	−pca1hs − JNDVI + DecT$^-$	3,57	143.19	0.51	<0.0001
12	M_I	JuneT$^-$ − pca1hs − pca2hs	3,57	131.86	0.65	<0.0001
13	M_R	−pca1hs + DecT^{-2}	2,63	132.31	0.28	<0.0001
14	M_{PM}	DecT$^-$ + DecT^{-2} + pca1hs	4,61	157.24	0.5	<0.0001
15	M_{Mi}	−pca1hs − pca2hs	2,63	129.84	0.37	<0.0001

compared with the observed decline for residents (Hinsley et al., 1998; Newton, 1995; Lennon et al., 2000) and the concurrent longitudinal decrease in frugivore and migrant richness and increased granivore richness in western mountain areas. Global large-scale patterns of avian diversity are thus best viewed as the overlaid response of different groups to diverse ecological factors.

The finding that temperature-related mechanisms might be more important in resident species is in line with previous results of other authors (Forsman and Monkkonen, 2003; Meehan et al., 2004; Evans et al., 2006). Summer temperature variables were selected in most of the groups, suggesting an important role of the more general ambient-energy hypothesis. However, other studies have shown that productivity variables are stronger predictors than summer temperatures when carrying the analysis at finer spatial grains (Hurlbert and Haskell, 2003; Carnicer et al., 2007) and thus this result possibly is an effect of the coarse spatial grain of this study.

We found JNDVI to be the only good predictor of species richness in frugivore, invertivore and migratory species for the Nearctic region. This is in line with previous results that showed that summer NDVI is a stronger predictor in migratory assemblages (Hurlbert and Haskell, 2003; Evans et al., 2006). Furthermore, our results coincide with recent findings that supported the productivity hypothesis in invertivore and frugivore migratory species at the local and regional scale (Buler et al., 2007).

Landscape heterogeneity effects are not detected at the large scale, although several studies assert their importance determining richness patterns (Kerr and Packer, 1997; Lennon et al., 2000; Pino et al., 2000; Atauri and de Lucio, 2001; Van Rensburg et al., 2002). Our results match those of previous tests of the heterogeneity hypothesis in North America that failed to find significant effects in other taxonomic groups (Davidowitz and Rosenzweig, 1998, but see Kerr et al., 2001). The exception could be found in the partially migratory and granivore groups. We found granivore and partially migratory species richness to increase abruptly left to the 100° meridian (Fig. 2c,d), which is the starting point of a rapid longitudinal decrease in annual precipitation and rapid increase in temperature variation and altitudinal heterogeneity. In line with these results, rainfall and altitude have been described as important factors limiting bird distributions on western areas (Root, 1988).

Our results showed that habitat structure variables should be considered in the macroecological analyses dealing with bird abundances, body mass, species richness and species composition patterns (Flather and Sauer, 1996; Hurlbert, 2004; Buler et al., 2007). Habitat structure effects on species richness were detected in migratory, frugivore and invertivore groups. The migratory group (Mi) presented significantly higher

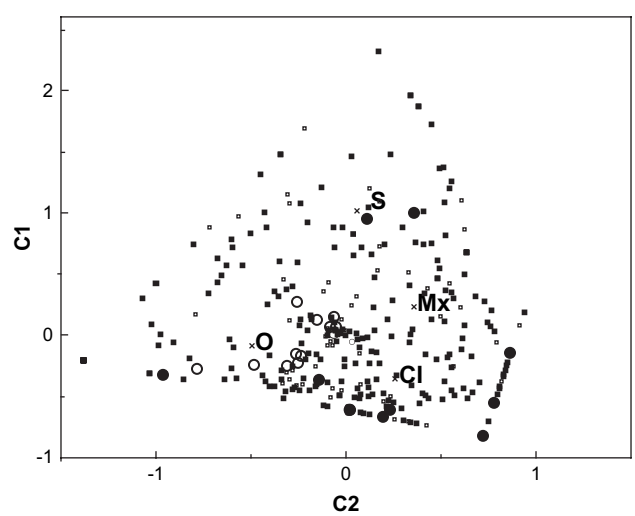

Fig. 3 – Correspondence analysis showing the relationships between species regional composition and regional habitat structures (O: open; Cl: closed; Mx: mixed; S: shrubland). Black dots: 15 species with lower continental regional mean population density. White dots: 15 species with higher continental mean population density. Squares: other bird species. Species situated near the centre of the figure are habitat structure generalists. Species situated in the edges are restricted to a habitat structure type.

species richness in closed habitats and significantly smaller-sized body mass distributions in closed habitats. Further, habitat structure variables were selected on the model selection approach for this group. In line with these results, migratory birds have been found to be more sensitive to landscape structure than either partial migratory or residents, being more abundant in landscapes with a greater proportion of forest and fewer edge habitats (Flather and Sauer, 1996; Buler et al., 2007). Constraints imposed by habitat structure on species body-sizes and densities could lead to an increase of species richness in closed habitats. Forested habitat structure is associated with a reduction in median body size of breeding bird species (M_i) in most of the groups. In our study, descriptors of reduced community body mass structure (low M_i values) are associated with increased richness in all groups, being M_i a good predictor of species richness. This might be explained by the findings of Polo and Carrascal (1999), showing that species that forage in pliable and slender substrata are lighter and occupy mainly forested zones, while species that forage on the ground are mainly open-country species and are heavier.

However, habitat structure effects seem to be more important in determining the shape of community abundance and body mass distributions than determining richness patterns. Most groups presented significantly higher values of community size and median community body mass in open regions, but this was not translated into significant differences in species richness. The differences in population density between open and closed habitats were of 1–3 orders of magnitude and thus were not attributable to sampling or detectability biases. Instead, it seems more reasonable to think that global changes in land uses associated with the intensification of the agriculture have promoted the emergency of species tightly associated with croplands and humanized lands that develop huge abundances (La Sorte and Boecklen, 2005a,b; La Sorte, 2006; La Sorte and McKinney, 2007).

We suggest that the effects of global change in land use should be considered when interpreting macroecological patterns for North American birds at the continental scale (La Sorte, 2006). For instance, we found that the percentage of cropland areas is the strongest factor predicting community

Table 5 – Pairwise *r* values among ecological group richness and bird variables (BV), environmental variables (EV) and geographical variables (GV). S_G: granivore species richness; S_F: frugivore; S_I: invertivore; S_C: carnivore; S_H: herbivore; S_R: resident; S_{PM}: partial migrant; S_{Mi}: migrant; J: community size; M_i: regional median body size. Significant *p* values: $^{\circ}p < 0.1$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{****}p < 0.0001$. Empty spaces indicate non-significant correlations

	Variable	S_G	S_F	S_I	S_C	S_H	S_R	S_{PM}	S_{Mi}
BV	log *J*	**0.38****	**0.59******	**0.51******	**0.27***	**0.34****	**0.48******	**0.34****	**0.76******
	M_i	**−0.45******	**−0.61******	**−0.47******	**−0.31****	**−0.33****	**−0.42*****	**−0.43*****	**−0.47******
EV									
Amb.	JuneT^{+}			−0.23*	0.35**		0.29*		−0.36**
Energy	JuneT−	−0.58****		−0.46***		−0.53****		−0.49****	−0.42***
	DV JuneT	**0.6******			**0.41*****	0.4**	0.25*	**0.61******	
Win.T	DecT^{-}	−0.29*			0.25^{*+}		**0.47******		−0.57****
Prod.	JNDVI		**0.51******	**0.41*****					**0.46******
	Rainfall	**−0.41*****			−0.31**			−0.32**	
Hab.	%Cropland								0.21°
Struct.	%Forest	−0.31**	0.29*	0.26*	−0.25*				0.33**
Het.	pca1het	0.39**						0.40***	
	pca2het				0.35**				
Sampl. effects	NR	0.45***	0.25*	0.28*	0.36**	0.31**		0.29*	0.43***
	Area						−0.22°		0.29**
GV	Lat						−0.47****		0.47****
	Long		−0.49****	−0.21°					−0.44****
	Alt	0.29*						0.27**	
	Variable	J_G	J_F	J_I	J_C	J_H	J_R	J_{PM}	J_{Mi}
Amb.	JuneT^{+}	0.44***			0.33**	0.57****	0.54****	0.42***	
Energy	JuneT^{-}		0.35**		0.57****	0.47****	**0.63******	0.31**	−0.31**
	DV JuneT	0.32**	−0.33**		−0.45***				
	DV DecT		0.25*			0.27*	0.23°		
Win.T	DecT^{-}				0.34**	0.41***	**0.56******		−0.3**
Prod.	JNDVI	−0.21°	**0.55******	**0.33****	0.28*				**0.38*****
	Rainfall	**−0.52******	0.23°					−0.29*	
Hab.	%Cropland	**0.54******	0.43***		**0.61******	0.31**	0.5****	0.71****	
Struct.	%Forest	**−0.66******				−0.48****	−0.3*	−0.39***	
Het.	pca1het		−0.53****	−0.26*	−0.61***		−0.44***	−0.28*	
	pca2het				0.25*				
Sampl. effects	NR		−0.26*		−0.26*		−0.37**		
	Area		−0.24*		−0.26*		−0.39***	−0.24*	0.28**
GV	Lat					−0.47****	−0.57****		0.31**
	Long		−0.6****				−0.29*	−0.4***	
	Alt		−0.51****				−0.45****	−0.36**	

size variation (J, all birds grouped; r^2: 0.69, $p < 0.0001$) but it did not predict species richness variation (Table 5). In cropland-grassland areas, we found significantly higher values of J caused by the presence of some abundant species that attain huge densities in a low-richness, humanized environment. Indeed, our correspondence analysis showed the existence of high-density species that behave as habitat generalists and are widespread, but tend to be more common in open habitat regions.

Overall, our study highlights that migratory and guild groups differ in patterns and processes that determine species richness variation. Our results suggest that global large-scale patterns of avian diversity are thus best viewed as the combined response of different groups to diverse ecological factors.

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Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.actao.2007.12.001.

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