



Universitat Autònoma de Barcelona

Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia

Unitat d'Ecologia



Estación Biológica de Doñana

Species richness, interaction networks, and diversification in bird communities: a synthetic ecological and evolutionary perspective.

PhD Thesis

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Introduction

Species richness gradients have been analyzed during many decades and they have progressively emerged as a central topic in community ecology (Darwin 1859, Wallace 1878, Willis 1922, Dobzhansky 1950, Fisher 1960, Hillebrand 2004, Ricklefs 2004, Mittelbach et al. 2007, among others). Historically, species richness gradients have been analyzed from two main points of view: the ecological and the evolutionary perspective (Ricklefs 2004, 2006b). The ecological perspective assumes that populations are evolutionarily fixed and studies species richness gradients as the result of regional colonization and extinction processes, and ecological interactions (MacArthur and Wilson 1967b, Scheiner and Willig 2005). Contrarily, the evolutionary approach states that species richness gradients are the result of geographic differences in the long-term evolutionary processes of speciation and lineage extinction (Rohde 1978, 1992, Mittelbach et al. 2007). For instance, according to the evolutionary view, tropical regions achieve higher species numbers due to increased diversification rates in low latitude areas (i.e. increased speciation and/or reduced extinction rates). Interestingly enough, recent empirical evidence derived from phylogenetic studies suggests that bird diversification rates are effectively higher in the tropics thus providing empirical support for the evolutionary view (Cardillo 1999, Cardillo et al. 2005, Golberg et al. 2005, Ricklefs 2006a, Jablonski et al. 2006, Weir and Schluter 2007).

In contrast with the evolutionary approach, the ecological approach assumes that populations are evolutionary stable units and focus on the effect of regional colonization-extinction dynamics, local conditions and local interactions in determining species richness gradients (Hutchinson 1959, MacArthur and Wilson 1963, 1967ab, MacArthur and Levins 1967, May 1975, Ricklefs 2006b). The ecological approach highlights that species richness gradients can be generated by ecological mechanisms independently of the evolutionary processes of speciation and lineage extinction that conform the regional pool of available species. For instance, an environmental gradient can cause a species richness gradient by limiting the number of successful colonizations in environmentally severe localities without the participation of any speciation process in the regional pool (Wright 1983, Hanski 1997, Boulinier et al. 1998).

These two contrasting and complementary views, the evolutionary and ecological approaches, are progressively being merged in a unified framework (Ricklefs 2006b, Johnson and Stinchcombe 2007). For instance, Johnson and Stinchcombe have recently proposed that two general hypotheses (H_1 , H_2) are underlying a new synthesis between community ecology and evolutionary biology. On one hand (H_1), evolutionary processes explain present-day community patterns and the ecological dynamics of species interactions. For instance, extinction and colonization processes that generate species richness gradients might be shaped by species' adaptations, history and phylogenetic relationships (Wiens and Donoghue 2004, Wiens and Graham 2005, Kraft et al. 2007). On the other hand (H_2), Johnson and Stinchcombe highlighted that both species interactions and community context strongly influence the direction, rate and outcome of present-day evolutionary processes (Benkman 1999, Thompson 2005). Overall, the emerging synthesis of community ecology and evolutionary ecology highlights that ecological and evolutionary views are profoundly interlinked.

Here we applied an evolutionary and ecological synthetic perspective to the study of the generation and maintenance of species richness in bird communities (Johnson and Stinchcombe 2007). As a first preliminary step, we examined geographical patterns of bird species richness in North America in several functional groups and the associated environmental correlates at the continental scale (Chapter 1). Our results showed that global

large-scale patterns of avian diversity in temperate regions were best viewed as the overlaid response of distinct species groups to diverse ecological factors. These results strongly suggested the convenience of choosing specific functional groups in order to examine specific macroecological evolutionary and ecological hypotheses.

Consequently, in Chapter 2, we next chose forest birds as a study group for the analysis of macroecological patterns, because they are the largest group in Nearctic and Palaeoarctic regions among terrestrial birds, and hold strong species-energy relationships (Mönkkönen et al. 2006). Regional data with colonization and extinction estimates for forest birds were available in Catalonia along an altitudinal gradient (Estrada et al. 2004) providing an exceptional dataset to study the ecological and evolutionary processes behind species richness gradients (Chapters 2 and 3). We examined the altitudinal species richness gradient in Catalonia from an evolutionary and ecological synthetic perspective. First, the role of evolutionary processes in the gradient was assessed studying changes in community phylogenetic structure along the altitudinal gradient. Secondly, the role of ecological processes was examined by studying colonization and extinction dynamics at an ecological time-scale (20 years). These analyses allowed us to examine the role of phylogeny, colonizations, extinctions, community size, productivity, habitat availability, and dispersal limitation in generating bird species richness gradients in Catalonia. However, due to the coarse structure of macroecological data used, the role of local species interactions in such processes remained yet obscure and elusive.

Understanding the role of species interactions in the processes of coexistence and diversification of bird communities thus remained as a big challenge. Since long ago, ecological interactions have been hypothesized to play a role in the maintenance of diversity (Hutchinson 1959, MacArthur and Levins 1967, McPeck 1997, Mittelbach et al. 2007). Therefore, the quantitative study of species interactions was expected to provide insights on the processes that ultimately generate species richness in bird communities (Cattin et al. 2006, Rezende et al. 2007). However, data on species interactions is usually available only for specific local communities. Therefore, a macroecological approach is precluded because the bulk of the studies of community interaction networks are carried out at local scales. Accordingly, we examined the role of species interactions in the generation of species richness in a local Mediterranean bird community for which interaction good-quality data was available (Chapters 4 and 5) (Jordano 1984, 1987). We addressed the two general hypotheses delineated by Johnson and Stinchcombe (2007). First, in chapter 4, we analyzed if evolutionary processes causally affect present-day community interaction patterns and the dynamics of species interactions (H_1). Secondly, in chapter five, we assessed if species interactions and community context might influence the direction, rate and outcome of present-day diversification processes that ultimately generate species richness (H_2). Overall, our results provide strong support for the two hypotheses examined, thus highlighting the idea that evolutionary and ecological processes are effectively profoundly interlinked. On one hand, we show that long-term evolutionary processes effectively modulate present-day community interaction patterns and dynamics (Webb et al. 2002, Cavender-Bares and Wilczek 2003, Johnson and Stinchcombe 2007, Chapter 4). Likewise, we demonstrate that community context can potentially shape bird morphological diversification processes and drive speciation (Thompson 2005, Abrams 2006, Johnson and Stinchcombe 2007, Chapter 5). Overall, Chapters 4 and 5 provide some new empirical and theoretical insights dealing with the processes that generate and maintain local bird diversity from an integrated evolutionary and ecological perspective.

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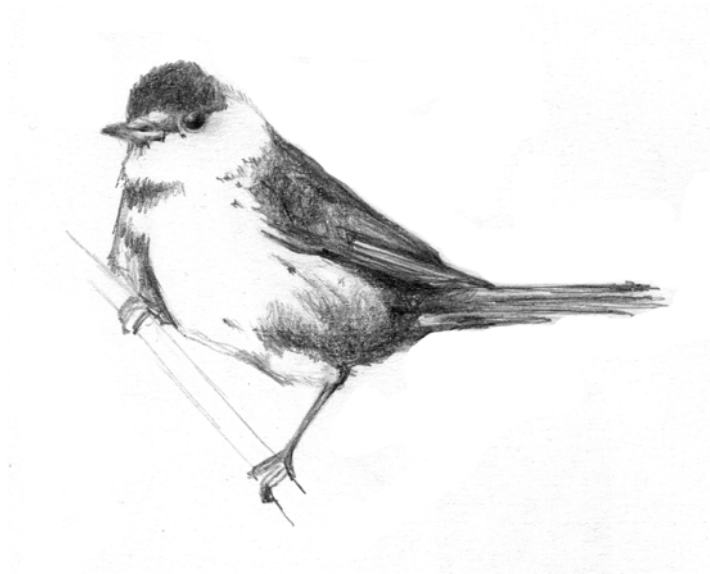
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Part 1

Macroecology. Processes in species richness gradients



CHAPTER 1: Geographic differences between functional groups in patterns of bird species richness in North America

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In review.

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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. 2005a, 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 (Boulinier et al. 1998, Brown et al. 2001, Cardillo 1999, Parody et al. 2001, Evans et al. 2005a, La Sorte and Boecklen 2005ab, Evans et al. 2005a, Cardillo et al. 2005, Ricklefs 2006a, La Sorte 2006, Jablonski et al. 2006, Carnicer et al. 2007, Benton and Emerson 2007, Weir and Schluter 2007, see Supplementary material A1). This view has been complemented by a number of studies examining the environmental correlates of species richness gradients without accounting for specific measures of speciation, colonization and extinction rates (Turner 1987, Currie 1991, Hawkins 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 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). For North American breeding birds, positive correlations among species richness, abundance and energy 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 patterns 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. 2005) 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 not very dissimilar 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. To test for the existence of geographical divergences in patterns of species richness we mapped species richness independently for each functional 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.

Hypotheses	Predictor variables	sign	Predictions (P)	
<i>Productivity (MIH)</i>	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
<i>Ambient energy</i>	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.
<i>Winter tolerance</i>	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
<i>Heterogeneity</i>	pca1het, pca2het	+	P4	Heterogeneity measures will be positively associated with species richness and will be selected in the model selection approach
<i>Habitat structure</i>	pca1hs pca2hs	+/-	P5	Habitat structure variables will be positively associated with species richness and will be selected as predictors in the model approach
			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.

Table 1. Hypotheses tested and their predictions. Predictor variables tested and predicted signs of the correlations with species richness.

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. 2005, Evans et al. 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, Turner et al. 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 Humboldt (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 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 distributed in northern Mexico, USA and part of Canada (Sauer, Hines & Fallon, 2003; Figure 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 (www.pwrc.usgs.gov). Abundance trends were averaged for the 1966-1999 period by applying LOESS-based Nonlinear Semiparametric Route Regression (NSRR) analyses (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).

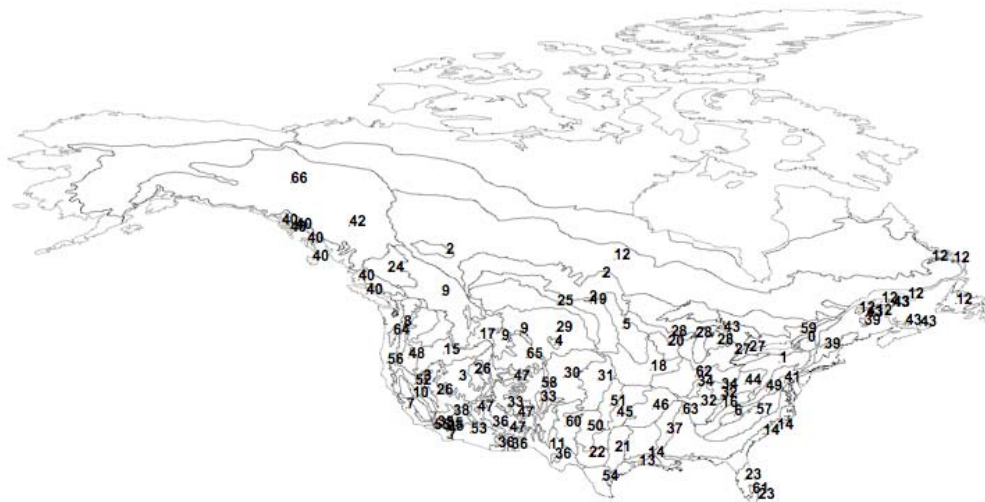


Fig. 1. BBS physiographic strata map. A list of the names of the regions is available in supplementary material A3.

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, savanna), 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, Elliot, Sargatal (1992), Dunning (1993) and the Nature Serve web site (www.natureserve.org/explorer/). Most species were characterized by mixed diets. For each species, we reviewed the existing literature on species diet. The relative fractions of different resources in the diet were studied and species were classified according 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. To our knowledge, this is the first study that examines species richness patterns for dietary guild groups in North America at continental scale, and that describes the relationships between migratory-status trends and guild trends.

2.2 Environmental variables

For each physiographic stratum, we estimated *geographic variables* (baricenter of latitude and longitude); *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, Kaspari et al. 2003, Hawkins et al. 2003ab, 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 temporal 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 generated a GIS system integrating all these 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. Step function on R package (R Development Core Team, 2004) was used selecting 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. To address sampling effects (area and route number effects), we included those measures as independent variables if those variables showed significant coefficients (Frenckleton 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.

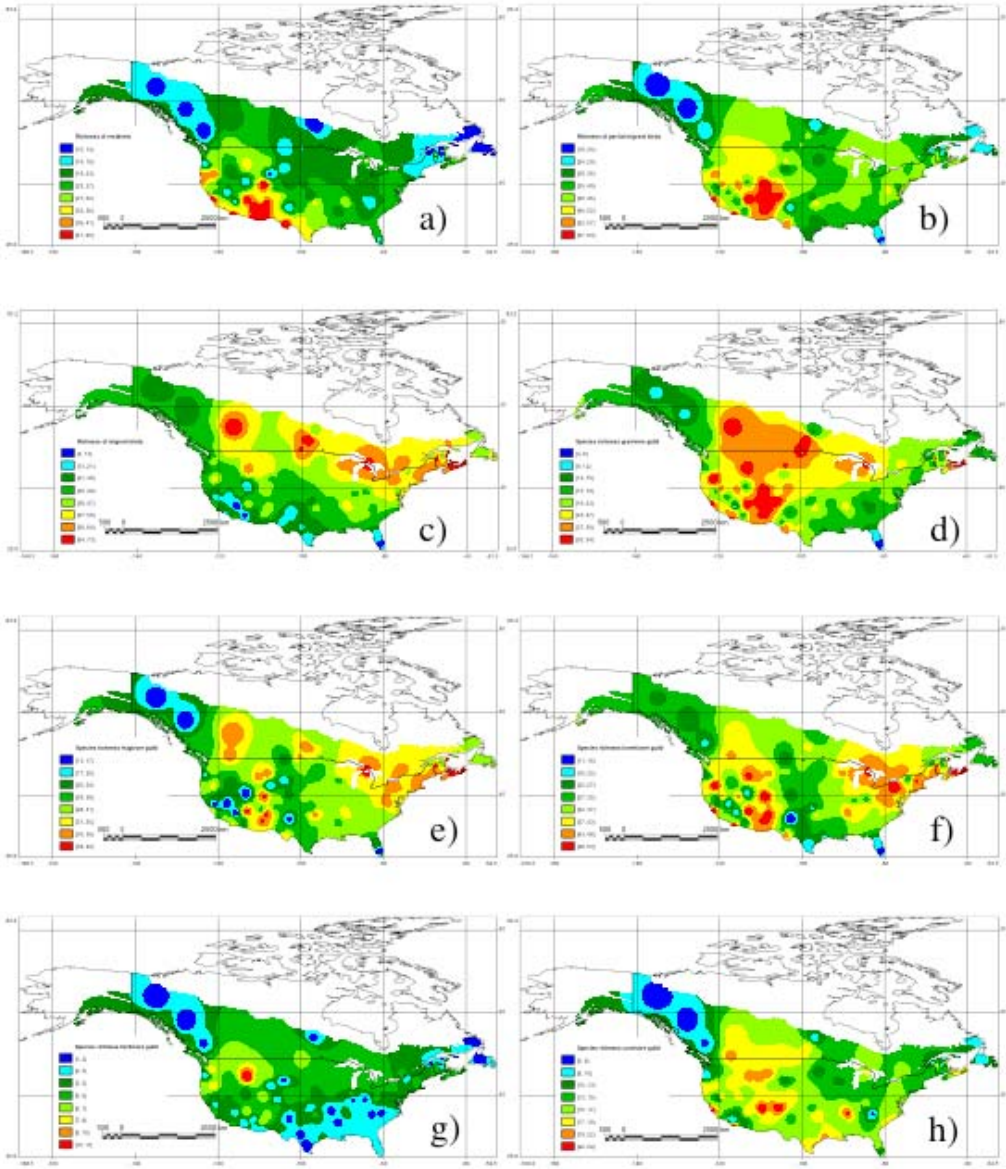
2.4 Mapping species richness and hypothesis testing

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 relationships between environmental variables and species richness for each functional group, testing the correlative support for a set of different hypotheses (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 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.

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 strata. 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.



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 (Fig. 2). 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 fits well also 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 and 3). 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, 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).

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 (table 2, table 5).

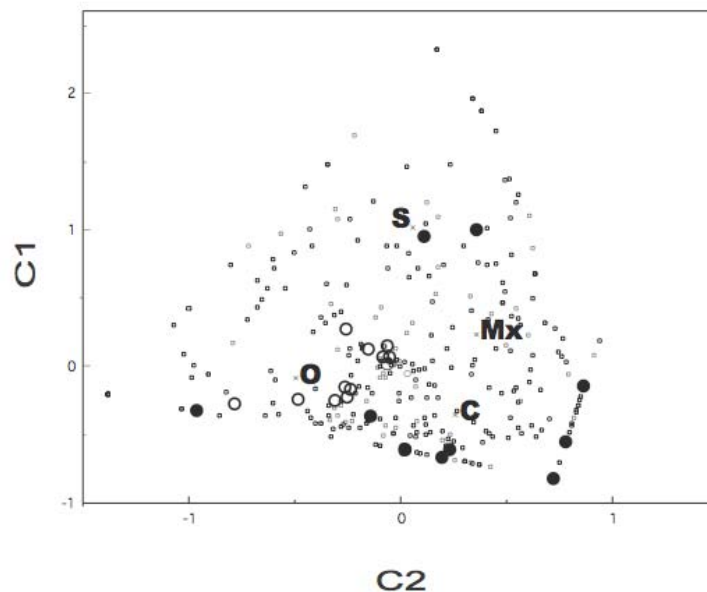


Fig. 3. Correspondence analysis showing the relationships between species regional composition and regional habitat structures (O: open; Cl: closed; Mx: mixed; S:shrubland). Black dots: 15 species with lower continental regional mean population density. White dots: 15 species with higher continental 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 an habitat structure type.

Habitat structure is very important determining the shape and significance of S-J and S-M relationships (table 5). 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 5).

Dep. V.	Independent variables	DF	AIC	R ² adj	p
	Bird variables				
log S	log J - M	64	-344.97	0.59	<.0001
log S _C	-M _C	64	-303.9	0.32	<.0001
log S _F	log J _F - M _F	64	-495.77	0.65	<.0001
log S _G	log J _G - M _G	64	-316.06	0.67	<.0001
log S _I	log J _I - M _I	64	-300.3	0.53	<.0001
log S _R	log J _R - M _R	64	-286.79	0.37	<.0001
log S _{PM}	log J _{PM} - M _{PM}	64	-327.2	0.42	<.0001
log S _{Mi}	log J _{Mi} - M _{Mi}	64	-266.45	0.68	<.0001
	Environmental Variables		Loglik	R ² adj	p
S	- JuneT ⁻ + JNDVI	58	-255.49	0.38	<.0001
S _C	JuneT ⁺ +pca2het	62	-163.05	0.36	<.0001
S _F	JNDVI - JNDVI ²	63	-194.86	0.32	<.0001
S _G	- JuneT ⁻ - Rainfall	61	-371.4	0.54	<.0001
S _I	- JuneT ⁺ + JNDVI	61	-204.29	0.47	<.0001
S _R	DecT ⁺	63	-216.79	0.32	<.0001
S _{PM}	-JuneT ⁻ + DVJuneT ⁻	61	-193.083	0.45	<.0001
S _{Mi}	-JuneT ⁻ + pca2hs	61	-201.62	0.75	<.0001

Table 2. Models forecasting 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).

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: $p=0.01$).

<i>variable</i>		S_G	S_F	S_I	S_C	S_H	S_R	S_{PM}	S_{Mi}
BV	logJ	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. Struct.	% Cropland								0.21°
	% 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**	

<i>variable</i>		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 Dec T		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. Struct.	% Cropland	0.54****	0.43***		0.61****	0.31**	0.5****	0.71****	
	% 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**	

Table 3. 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: ° $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$. Empty spaces indicate non significant correlations.

Table 4 Models forecasting 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	<.0001
2	J _C	pca2hs+JuneT ⁺	2,63	23.44	0.77	<.0001
3	J _F	pca2hs	1,64	-134.68	0.64	<.0001
4	J _G	- pca1hs	1,64	-157.43	0.63	<.0001
5	J _I	JNDVI	1,64	-134.03	0.19	<.001
6	J _R	- pca1hs + pca2hs + DecT ⁺	4,61	-139.51	0.72	<.0001
7	J _{PM}	- pca1hs + pca2hs + JuneT ⁺	3,62	-146.52	0.56	<.0001
8	J _{Mi}	JNDVI – JuneT ⁻ -pca1hs	3,57	-139.1	0.37	<.0001
9	M	DecT ⁻ - pca1hs	2,63	-217.23	0.5	<.0001
10	M _F	JuneT ⁺ - pca2hs	3,62	-157.67	0.45	<.0001
11	M _G	- pca1hs - JNDVI + DecT ⁻	3,57	143.19	0.51	<.0001
12	M _I	JuneT ⁻ -pca1hs – pca2hs	3,57	131.86	0.65	<.0001
13	M _R	-pca1hs + DecT ⁻²	2,63	132.31	0.28	<.0001
14	M _{PM}	DecT ⁻ + DecT ⁻² + pca1hs	4,61	157.24	0.5	<.0001
15	M _{Mi}	-pca1hs – pca2hs	2,63	129.84	0.37	<.0001

Table 5. 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: ° 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	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 J	Open			0.24**	0.31**			0.41***		0.58****
	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*	

Correspondence analysis (figure 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 figure 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, C1).

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), 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 *et al.* 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 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 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 unique 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. 2 c,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 (M_i) presented significantly higher 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. In line with this result, Polo and Carrascal (1999) showed 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 2005 ab, 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). In line with these trends, we found that the percentage of cropland areas is the strongest factor predicting community size variation (J , all birds grouped; r^2 : 0.69, $p < 0.0001$) but it did not predict species richness variation (table 3). 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 functional 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 overlaid response of different groups to diverse ecological factors.

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Supplementary material A1.

Speciation, colonization and extinction rates in the avifauna of North America.

Here we briefly review the existing evidence dealing with the role of speciation, colonization and extinction rates in generating species richness gradients in North America. Two perspectives (the ecological and evolutionary approaches) are analyzed separately (following Ricklefs 2004).

Ecological studies

Currie and collaborators (2004) highlighted that species richness (S) should covary with: 1) the total number of individuals in an area (J), that is the sum of colonizations (c), extinctions (e), birth (b) and deaths (d) [$J = (c + b) - (e + d)$]; and 2) environmental predictors of population densities (ε_i) and area (A).

$$\text{Log } S \propto \text{Log } J \propto \text{Log} [(c+b)-(e+d)] \propto \text{Log} [A (\beta_1 \varepsilon_1 + \dots + \beta_n \varepsilon_n)]$$

In North America, the patterns of geographical variation in species richness (S), total abundances (J), and environmental variables (ε_n) are relatively well known (see Hurlbert and Haskell 2003, Currie et al. 2004, Evans et al. 2006 for a review). However, only a few works have studied the colonization and extinction dynamics associated to abundance variation (J). Brown et al. (2001) and Parody et al. (2001) have shown that equilibrated numbers of extinction and colonization events have maintained proximately steady state values of species richness in a number of localities during decades in North America. In a recent work, Le Sorte and Boecklen (2005a&b) highlighted that the bulk of North American bird species have experienced similar numbers of local colonizations and extinctions during the last 30 years. However, Le Sorte highlighted that some species associated with anthropogenic activities have colonized a great number of localities leading to an increase in species richness in numerous localities and to generalized changes in local densities (Le Sorte and Boecklen 2005 a,b, La Sorte 2006).

Colonization and extinctions are unevenly distributed in the space: areas with low habitat availability and lower abundances are characterized with higher colonization and extinction rates (Boulinier et al. 1998). This uneven distribution has been recently linked with the generation and maintenance of species richness gradients (Carnicer et al. 2007).

Evolutionary studies

Essentially, the evolutionary approach states that species richness gradients are the result of geographic differences in the long-term evolutionary processes of speciation and lineage extinction. According to the evolutionary view, tropical regions achieve higher species numbers due to increased diversification rates (i.e. increased speciation and/or reduced extinction rates). Interestingly enough, available evidence suggests that

diversification rates are effectively higher in the tropics (Cardillo et al. 2005, Golberg et al. 2005, Ricklefs 2006ab, Jablonski et al. 2006, Weir and Schluter 2006). Several reasons have been explored to explain higher diversification rates in the tropics: reduced climate change oscillations (Dyanesius and Jansson 2000), increased geographical area (Rosenweig 1995, Fine and Ree 2006), reduced physiological tolerances and dispersal limitation (Janzen 1967, Ghalambor et al. 2006), stronger temperature effects on evolutionary speed (Rohde 1992, Gillooly et al. 2005) or a predominance of biotic interactions (Mittelbach et al. 2007).

The relative importance of speciation and extinction rates in generating the latitudinal gradient of diversification rates is unknown (Ricklefs 2006a, Benton and Emerson 2007, Mittelbach et al. 2007, Phillimore et al. 2006). Weir and Schluter (2007) recently suggested that both extinction and speciation rates might be higher in temperate regions than in the tropics, leading to an increase in taxonomic turnover rate at northern latitudes. Other studies also supported higher extinction rates in temperate regions but argued that speciation rates might be higher in the tropics (Goldberg et al. 2005). Finally, some studies assume that that speciation rates are higher in the tropics and model extinction rates as a constant fraction of speciation rates (Ricklefs 2006b).

Supplementary material A2

Energy availability at the population and community levels

Energy availability at the population level

Kaspari (2000) described the derivative of energy availability for a single species i as a function of net primary productivity and physiological temperature-linked functions (modified from Kaspari et al. 2000):

$$dE_i/dt = \text{NPP} f_i - i_i = \text{NPP} f_i - N_i (i_0 m_i^{2/3} e^{-E/kT}) \quad (1)$$

where E is energy, NPP is net primary productivity, f is foraging efficiency (dimensionless, varying from 0 to 1) and i are the basal metabolism costs (in $\text{g cm}^{-2} \text{yr}^{-1}$) (McKechnie and Wolf 2004), i_0 is a normalization constant independent of body size, m_i is the body mass of species i , E is the activation energy, k is Boltzmann's constant and T is absolute temperature in K (Brown et al. 2004). f and i are physiological functions dependant on temperature, being usually parabolic or "U shaped" functions in endotherms. According to the ambient energy hypothesis these functions (f , i) might change species' energy budgets with changes in environmental temperature. The term $e^{-E/kT}$ has a constant value given that birds are endotherm animals with a constant body temperature of about 40 °C. Following Peters (1983), temperature effects on metabolic rate (i) in equation 1 are described by:

$$i_i = N_i c (T_b - T_a) = N_i 0.11 m_i^{1/2} (T_b - T_a) \quad \text{if } T_a < T_{lc} \quad (2)$$

where T_{lc} is the lower critical temperature (below which metabolic heat production rises to offset heat loss and stabilize body temperature), T_b is the body temperature, T_a is the ambient temperature, c is the conductance (rate of change in metabolic rate with change in ambient temperature between the lower critical and the ambient temperatures), and i_i is the total bird heat loss (Calder and King 1974, Peters 1983, Meehan et al. 2004). Note that in the case of the winter-tolerance hypothesis $T_a =$ winter temperature.

Energy availability at the community level

At the community level, energy available is fractioned among S species. Energy allocated in each species is divided among the number of individuals of that species (N_i). The amount of energy destined to each individual is proportional to the mean species body mass (m_i). Equation 3 (BSNM equation hereafter) is a simple statement that relates energetically these community attributes. This equation describes the partition of the biomass:

$$B = \sum_i^s b_i = \sum_i^s N_i m_i = J \left(\frac{\sum_j^J m_j}{J} \right) = JM_J \quad (3)$$

where b_i is the biomass represented by each species; N_i is the population density of species i ; m_i is the body mass of species i , S is the number of species in one physiographic strata, m_j is the size of each community individual, and J and M_J are the total number of individuals and the mean body mass of all individuals, respectively. Note that this equation can be extended by substituting m_i by species metabolic rate ($i_i = i_0 m_i^{2/3} e^{-E/kT}$) thus describing bird energy use (Brown *et al.* 2004, McKechnie and Wolf 2004). Equation 3 highlights that the partition of energy at the community level relates species richness with two kinds of community distributions: the distribution of abundances (N_i, J) and the distribution of body sizes (m_i). A general framework relating the distribution of community abundances and species richness has been provided by the neutral theory (Hubbell 2001, Alonso and McKane 2004, Etienne 2005, Etienne and Alonso 2005). To our knowledge, no general framework has been provided relating species richness and body size distributions (but see May 1985, Loehle 2006). The neutral theory predicts reductions in species richness associated to a decrease in both the total number of individuals that a locality holds (that is local community size or J) and in the total number of individuals at the metacommunity level (J_M). For instance, Hubbell (2001, page 90) defined the expected abundance of the species i (under the ergodic model with migration) to be equal to:

$$E\{N_i\} = JP_i$$

where J is equal to the local community size and P_i is the metacommunity relative abundance of the i th species. According with the productivity hypothesis, if energy availability increases the number of individuals that a locality holds (J), we should expect from a neutral perspective that an increased number of species (S) may attain abundances greater than zero.

Supplementary material A3

Names of the regions described in Figure 1

0: Adirondack Mountains; 1: Allegheny Plateau; 2: Aspen Parklands; 3: Basin & Range; 4: Black Hills; 5: Black Prairie; 6: Blue Ridge Mountains; 7: California Foothills; 8: Cascade Mountains; 9: Central Rockies; 10: Central Valley; 11: Chihuahuan desert; 12: Closed Boreal Forest; 13: Coastal Praeries; 14: Coastal flatwoods; 15: Columbia Plateau; 16: Cumberland Transition; 17: Dissected Rockies; 18: Dissected Till Plains; 19: Drift Prairie; 20: Driftless Area; 21: East Texas Praeries; 22: Edwards Plateau; 23: Floridian; 24: Fraser Plateau; 25: Glaciated Missouri Plateau; 26: Great Basin Deserts; 27: Great Lakes Plain; 28: Great Lakes Transition; 29: Great Plains Roughlands; 30: High Plains; 31: High Plains Border, 32: Highland Rim; 33: Intermountain Grasslands; 34: Lexington Plain; 35: Los Angeles Ranges; 36: Mexican Highlands; 37: Mississippi Alluvial Plain, 38: Mojave Desert; 39: Northern New England; 40: Northern Pacific Rainforest; 41: Northern Piedmont; 42: Northern Rockies; 43: Northern Spruce/Hardwoods; 44: Ohio Hills; 45: Osage Plain/Cross Timbers; 46: Ozark/Ouachita Plateau; 47: Pinyon/Juniper Woodlands; 48: Pitt-Klamath Plateau; 49: Ridge & Valley; 50: Rolling Red Plains; 51: Rolling Red Praeries; 52: Sierra Nevada; 53: Sonoran Deserts; 54: South Texas Brushlands; 55: Southern California Grassl; 56: Southern Pacific Rainforest; 57: Southern Piedmont; 58: Southern Rockies; 59: St. Lawrence River Plain; 60: Staked Plains; 61: Subtropical; 62: Till Plains; 63: Upper coastal plain; 64: Willamette Lowlands; 65: Wyoming Basin; 66: Yukon.

Supplementary material A4

Guild groups used in the study

Broad classification	Detailed classification
<i>Guilds</i> 1. Invertivore (I) 2. Frugivore (F) 3. Granivore (G) 4. Herbivore (H) 5. Carnivore (C)	 1.1. Invertivore (I) 1.2. Invertivore-nectarivore (IN) 2.1. Frugivore-invertivore (FI) 2.2. Frugivore-granivore-invertivore (FGI) 2.3. Frugivore-granivore (FG) 3.1. Granivore (G) 3.2. Granivore-invertivore (GI) 4.1. Herbivore (H) 4.2. Herbivore-frugivore (HF) 4.3. Herbivore-granivore (HG) 5.1. Carnivore (C) 5.2. Carnivore-invertivore (CI)

Supplementary material A5

Contingency table with observed percentages among guild and migratory categories.

Count	R	PM	Mi	
Total %				
Col %				
Row %				
C	23 7,08 22,12 50,00	18 5,54 18,37 39,13	5 1,54 4,07 10,87	46 14,15
F	30 9,23 28,85 35,29	24 7,38 24,49 28,24	31 9,54 25,20 36,47	85 26,15
G	23 7,08 22,12 35,38	24 7,38 24,49 36,92	18 5,54 14,63 27,69	65 20,00
H	13 4,00 12,50 86,67	1 0,31 1,02 6,67	1 0,31 0,81 6,67	15 4,62
I	15 4,62 14,42 13,16	31 9,54 31,63 27,19	68 20,92 55,28 59,65	114 35,08
	104 32,00	98 30,15	123 37,85	325

Supplementary material A6

GIS variables describing sampling, geographic and ecological variables studied. Note that only a subset of the studied variables was used in the modelling approach.

CODE	VARIABLE	DESCRIPTION
	<i>Sampling Effects</i>	
A	Area	km ²
NR	Number of BBS Routes	Number of routes or transects per physiographic strata
	<i>Geographic Factors</i>	
Lat	Mean latitude	Baricenter of latitude
Long	Mean longitude	Baricenter of longitude
	<i>Productivity Factors</i>	
DNDVI	Mean December NDVI	Mean of the NDVI value for 1980-1990 period per km ²
JNDVI	Mean June NDVI	Mean of the NDVI value for 1980-1990 period per km ²
NPP	Net primary productivity	Mean net primary productivity for 2000-2004.
AET	Actual evapotranspiration	Actual evapotranspiration
R	Rainfall	Annual mm of precipitation
	<i>Ambient-energy factors</i>	
JuneT ⁺	Maximum June Temp.	Mean June maximum temperature
JuneT ⁻	Minimum June Temp.	Mean June minimum temperature
DV June T	Mean daily Variation June T	June T ⁺ - June T ⁻
DV Dec T	Mean daily Variation Dec T	Dec T ⁺ - Dec T ⁻
PET	Potential evapotranspiration	Potential evapotranspiration
	<i>Winter-tolerance factors</i>	
DecT ⁺	Maximum Dec. Temp.	Mean December maximum temperature
DecT ⁻	Minimum Dec. Temp.	Mean December minimum temperature
	<i>Heterogeneity factors</i>	
pca1het	First principal component axis	
pca2het	Second principal component axis	
SCV_JNDVI	Spatial JNDVI variation	Variation coefficient between 1km grid pixels in a year
SCV_DNDVI	Spatial DNDVI variation	Variation coefficient between 1km grid pixels in a year

TCV_JNDVI	Annual JNDVI variation	Variation coefficient between years in 1km grid cels
TCV_DNDVI	Annual DNDVI variation	Variation coefficient between years in 1km grid cels
SNDVI	Seasonality in NDVI	(J)NDVI max – (D)NDVI min / (J)NDVI max
Alt	Mean altitude	Calculated using a digital elevation model (1km pixel grid)
CV_Alt	Altitudinal heterogeneity	Variation coefficient of altitude
C_DIV	Cover type diversity	$C_DIV = \sum (p_i \log_2 p_i)$
C_Eq	Equitability in Cover type	$E = \sum (p_i \log_2 p_i) \log_2 N$
C_Het	Cover heterogeneity	Number of cover type / km ²
JTSCV ⁺	June Max. Temp. CV	Spatial variation (CV) of June maximum temperatures
DTSCV ⁺	Dec. Max. Temp. CV	Spatial variation of December maximum temperatures
JTSCV ⁺	June Max. Temp. CV	Spatial variation (CV) of June maximum temperatures
<i>Habitat structure factors</i>		
pca1hs	First principal component axis	
pca2hs	Second principal component axis	
%Forest	Habitat structure	forest area / total region area
%Cropland	Percentage cropland area	Cropland area / total region area
% Deciduous	Percentage of deciduos forest area	Deciduous forest area / total region area
% Needleleaf	Percentage of evergreen needleleaf forest	Evergreen needleleaf forest area / total region area
% Grassland	Percentage of grassland area	Grassland area / total region area
% Shrubland	Percentage of shrubland area	Shrubland area / total region area
% Urban	Percentage of urban area	Urban or built-up area / total region area
% Savanna	Percentage of savanna area	Savanna area / total region area
% Wooded Tundra	Percentage of wooded tundra	Wooded tundra area / total region area

Supplementary material A7. Digital information sources used.

BBS regions

<http://nationalatlas.gov>

www.mbr-pwrc.usgs.gov

NDVI data

<http://daac.gsfc.nasa.gov>

Climate data

<http://www.climatesource.com>

<http://www.ocs.oregonstate.edu/index.html>

Digital elevation model and land uses

<http://edcdaac.usgs.gov/glcc/>

<http://glcf.umiacs.umd.edu/data/landcover/data.shtml>

<http://edc2.usgs.gov/geodata/index.php>

Supplementary material A8

Pairwise correlations among median community body mass (M) and environmental predictor variables.

	<i>Variable</i>	M_G	M_F	M_I	M_C	M_H	M_R	M_{PM}	M_{Mi}
Amb.	JuneT ⁺	0.33**	0.52****	0.54****				0.23*	0.43***
Energy	JuneT- DV JuneT	0.47****	0.37**	0.59****				0.57**** -0.39****	0.25*
Win..T	DecT ⁻	0.48****	0.46****	0.47****			-0.26*	0.33**	0.28*
Prod.	JNDVI Rainfall	-0.33**	-0.44**** -0.39****	-0.36** -0.23°	-0.31**		-0.24*		-0.4*** -0.34**
Hab. Struct.	%Cropland %Forest		-0.46****	0.23° -0.31**			0.29**	0.36**	-0.37**
Het.	pca1het pca2het	-0.35**				-0.34**		-0.54****	
Sampl. effects	NR Area		-0.25*						
GV	Lat Long Alt	-0.37**	-0.45****	-0.51****	0.3** 0.26*	-0.24*		-0.32** -0.43**** -0.43****	-0.34**

CHAPTER 2: Community based processes behind species richness gradients: contrasting abundance-extinction dynamics and sampling effects in low- and high productivity areas

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Abstract

Aim The consideration of the role of local colonization and extinction rates to explain the generation and maintenance of species richness gradients at the regional scale.

Location Catalonia, Spain. Mediterranean biome (oak forests, deciduous forests, shrublands, pinewoods, firwoods, alpine heathlands, crops).

Methods We analyzed the relative importance of direct and indirect effects of community size in explaining species richness gradients. Direct sampling effects of community size on species richness are predicted by the neutral theory (Hubbell 2001). The greater the number of individuals in a locality, the greater the number of species expected by random direct sampling effects. Indirect effects are predicted by the abundance-extinction hypothesis (Kaspari et al. 2003) that states that in more productive sites increased population densities and reduced extinction rates may lead to high species richness. The study system was an altitudinal gradient of forest bird species richness.

Results We found significant support for the existence of both direct and indirect effects of community size in species richness. Thus, both the neutral and the abundance-extinction hypotheses were supported for the altitudinal species richness gradient of forest birds in Catalonia. However, these mechanisms seem to drive species richness variation only at low productivity areas and not in high productivity areas where species richness was uncorrelated with community size and productivity measures.

Main Conclusions Our results support the existence of a geographic mosaic of community based processes behind species richness gradients, with contrasting abundance-extinction dynamics and sampling effects in low- and high productivity areas.

Keywords species richness, bird, extinction rate, sampling, neutral theory, altitudinal gradients.

Introduction

Geographical variation in species richness and its relationship with energy availability is a classic and widely debated topic in ecology (Wallace 1878, Hutchinson 1959, Brown 1981, Wright 1983, Currie 1991, Rosenweig 1995, Waide et al. 1999, Rahbek and Graves 2001, Jetz and Rahbek 2002, Willig et al. 2003, Currie et al. 2004, Evans et al. 2005a). A global linear relationship between productivity measures and species richness has been described for birds (Hawkins et al. 2003), adding support to the species-energy hypothesis over other hypotheses proposed to explain richness patterns at large spatial scales. However, which concrete processes increase species richness in more productive areas is yet an open debate (see Evans et al. 2005a for a review).

Recently, it has been argued that large-scale species richness gradients should be understood as the combined outcome of both historic and ecological processes (Ricklefs and Schluter 1993, Wiens and Donoghue 2004). The consideration of the processes of speciation, dispersal, extinction and colonization in an integrated ecological and historical perspective should provide a more comprehensive view of the generation and maintenance of the species richness gradients (Evans et al. 2005b, Hawkins et al. 2006). Phylogenetic information has also been incorporated to the analyses of global bird species richness gradients and this has provided a way to test the historical effect of differential speciation and extinction of different clades on the contemporary gradients. Hawkins and collaborators (2006) showed that the global bird species richness gradient has a strong phylogenetic signal that might be interpreted as the preferential extinction of basal clades, adapted to wet and warm climates, during the cooling period of the Miocene in extratropical areas and the diversification in these zones of more derived clades, adapted to colder and dryer tropical niches (high tropical mountains). Thus, there is a strong historical signal in the contemporary latitudinal gradients but the question of which ecological mechanisms had maintained the shape of the gradient for more than 20 millions of years remains unsolved. These mechanisms should concern dispersal, colonization and extinction in a temporal perspective.

To study the ecological mechanisms that maintain bird species richness gradients at the ecological time scale we should limit our approach to a study zone matching the following attributes: First, it should be a geographical region characterized by the presence of a marked bird species richness gradient associated with productivity measures. Second, a measure of extinction and colonization rates for each locality should be available. Third, spatial variation in species richness should not be associated with changes in the phylogenetic structure along the gradient. In other words, the gradient should not present a geographic phylogenetic signal associated. This should permit the interpretation of the results in purely ecological time-scale terms. Fourth, there should not be strong dispersal limitations that preclude the arrival of species from the regional pool at any point of the gradient. This will prevent the influence of historical dispersal clines (Hawkins et al. 2006) in the interpretation of current patterns. Fifth, only one habitat functional group should be considered (i.e. forest, wetland or farmland birds), avoiding the mixture of different trends associated to habitat preferences along the gradient (Fuller et al. 2005).

In a region with the characteristics described above it should be possible to analyze the effect of colonization and extinction rates on the maintenance of the gradient. Here we evaluate two mechanisms, the abundance-extinction hypothesis and the abundance-colonization hypothesis, that may contribute to the maintenance of a bird species richness gradient that is associated with productivity measures and community size. The two hypotheses consider colonization and extinction processes on the ecological time scale. These two mechanisms assume that increased productivity allows the maintenance of a greater number of individuals

(community size or J , hereafter) in a given locality, but differ in the role played by the processes of extinction and colonization respectively.

The abundance-colonization hypothesis states that localities with higher community sizes (more productive sites) will be preferentially selected as breeding places (by the effect of heterospecific attraction among forest birds (Mönkönen et al. 1990, Mönkönen and Forsman 2002) or other processes) leading to an increase in colonization rates and species richness. The abundance-extinction hypothesis (Kaspari et al. 2003, Evans et al. 2005a) asserts that localities with higher community sizes (or more productive sites) will support increased population densities, and a reduced proportion of species that become extinguished. Higher productivity and community size areas will support reduced extinction risk and increased species richness, whereas low productivity zones will support a higher proportion of extinction events, and reduced species richness and community sizes.

These two hypotheses address the existence of indirect effects of community size on local species richness through the increase of the proportions of extinctions and colonisations respectively. However, as predicted by the neutral theory (Hubbell 2001), community size may have direct effects on species richness not associated to the variation in extinction or colonization proportions. The neutral theory is a sampling theory (Hubbell 2001, Alonso and McKane 2004, Etienne 2005, Etienne and Alonso 2005, Alonso et al. 2006) and predicts reductions in species richness associated with a decrease in the total number of individuals that a locality holds (that is community size or J). Local community size is an important parameter when considering the sampling effects of the neutral theory. For instance, Hubbell (2001, page 90) defined the expected abundance of the species i (under the ergodic model with migration) to be equal to:

$$E\{N_i\} = JP_i$$

where J is equal to the local community size and P_i is the metacommunity relative abundance of the i th species and $E[N_i]$ is the expected local abundance. Thus, in theory, sampling neutral effects are directly associated with local variation in community size.

Here we analyse species richness gradient of forest birds occurring in Catalonia to test the role of colonization and extinction rates in the maintenance of the species richness gradient testing a set of predictions of the two hypotheses under examination. Our aim is to evaluate the relative role of direct sampling effects and indirect effects through extinction and colonisation rates in the dynamic processes that shape an altitudinal species richness gradient.

Methods

Study area

Catalonia is a region located in the northeast of Spain with an extension of 31.930 km². The relief of Catalonia is the product of different geological formations that conform a complex and remarkably varied landscape. Altitudes range from 0 m to 3115 m (La Pica d'Estats summit). The average altitude of the region is around 700 m, plains are scarce and usually small, and upland areas occupy most of the territory (Estrada *et al.* 2004). Catalonia is a Mediterranean region that matches all the pre-requisites enumerated previously to evaluate the

hypotheses behind species richness gradients. First, the region presents a hump-shaped altitudinal species richness gradient that is well correlated with productivity surrogate measures (Normalized Difference vegetation Index, NDVI hereafter (Kerr and Ostrovsky 2003) and community size counts (see results). Second, colonization and extinction rates are calculable analyzing the two surveys effectuated along the altitudinal gradient in the last century (1980-1983; Muntaner et al. 1984, and 1999-2002; Estrada et al. 2004). Third, the richness gradient is not associated with changes in the phylogenetic structure along the gradient (see below). Fourth, there are no strong dispersal limitations along the gradient, the bulk of the species (70%) are distributed along all the gradient (high- medium- and low altitudinal bands), and the remaining 30% of the species are distributed in at least two of these zones (high and medium altitudinal bands or low and medium altitudinal bands). The regional scale of the study and the inexistence of large deforested areas that may act as dispersal barriers support the examination of the gradient as a single biogeographical unit. Fifth, the study includes a single functional habitat category (forest birds) and thus excludes the noise introduced by the mixture of different geographic trends associated with several habitat functional groups in a single species richness variable (Fuller et al. 2005).

Bird data

Bird species richness at 10x10 km and 1x1 km of grid resolution for birds in Catalonia was obtained from the Catalan Breeding Bird Atlas, a project of the Catalan Institute of Ornithology (see Estrada *et al.* 2004 for detailed information on census procedures used). The Catalan breeding bird atlas project uses a standardized 10x10 km grid system based on a UTM projection covering the region. Presence/absence data were obtained at two different resolutions. First, surveys at each of the 10x10 km squares was conducted in two different time periods t_0 , 1980-83 and t_1 , 1999-2002 (Estrada et al. 2004, and see also Hagemeijer and Blair 1997, Martí and del Moral 2002, Bibby et al. 2000). Second, within each of the 10x10km squares, a sub-sample of five to ten 1x1 km squares were surveyed a total of two hours during the period t_1 (1999-2002). This approach is similar to that used in the British and Swiss ornithological atlases (Gibbons et al. 1993, Schmid et al. 1998, Estrada et al. 2004) and allowed the time controlled and detailed survey of nearly 10% of the total land surface considered in this study (30.900 km², nearly all Catalonia surface) at a lower resolution. In order to reproduce as accurately as possible the environmental heterogeneity of each 10x10 km square, 1x1km squares were selected by the observers to proportionally represent habitat variability within 10x10 km squares. Sampling effort for each 10x10 km square in terms of effective surveying time was estimated from species-sampling time accumulation curves (see Estrada et al. 2004 for detailed results). Total number of individuals in a given square was obtained from 1999-2002 survey data.

We calculated colonization and extinction numbers in each 10x10km grid cell by comparing the number of species occurring in each of the two periods analysed (t_0 , 1980-83 and t_1 , 1999-2002, Estrada *et al.* 2004). Colonisation rate was calculated by estimating the proportion of species in t_1 not detected in t_0 , while extinction rate corresponded to the proportion of species per 10 km square detected in t_0 and not observed later in t_1 . Data for colonization and extinction rates were only available at 10 km of grain size and thus models using these variables were performed only at this grain size.

Altitudinal bands and spatial grain

To explore the geographical variation in abundance-extinction and abundance-colonisation dynamics along the altitudinal gradient we divided the study zone in contiguous altitudinal bands of different amplitude: 1) one band

covering all the range (0-3100 m) and 2) three equal width bands (0-1033, 1033-2066 and 2066-3100 m). A model selection analysis was independently performed for each band. To account for grain effects, analyses were carried at grain sizes of 1x1 km and 10x10 km, when using environmental data. This is recommendable if we consider the existence of important interactions among spatial grain, species richness, productivity and altitude. For instance, productivity is a better predictor of species richness at finer spatial resolutions but elevation range becomes increasingly important for predicting species richness at coarser spatial resolutions (Fraser 1998, Rahbek and Graves 2001, Van Rensburg et al. 2002, Hurlbert and Haskell 2003). The central band (1033-2066m) sustains significantly higher NDVI values (Normalized Difference Vegetation Index) than the other two altitudinal bands (0-1033; 2066-3100m) (Tukey- Kramer test, $p < .0001$).

Phylogenetic structure along the altitudinal gradient

We reviewed the existent phylogenetical information available at the family level for the species present in the area (Sibley and Alquist 1990, Fain and Houde 2004, Barker et al. 2004, Jönsson and Fjeldså 2006). Bird fauna present at each altitudinal band (presence/ absence data) was compared by correspondence analyses using JMP package at the family level. For each species, we calculated the familial root distance (Hawkins et al. 2006), that is the number of nodes separating each species' family from the base of a phylogenetic tree. The tree phylogeny was compiled from Barker et al. 2004 (passerines) and Fain and Houde 2004 (other orders).

Analyses

The abundance-colonisation hypothesis predicts that colonisation rates will be positively and significantly correlated with community size counts (prediction C1, table 1; note that community size refers to the total number of individuals in a grid cell in the 1999-2002 survey). Similarly, the abundance-extinction hypothesis predicts a negative and significant relationship among extinction rates and community size (prediction E1, table 1). The existence of significant associations between those variables is a necessary requirement of the mechanisms examined here.

First, we modelled colonisation and extinction rates as a function of community size (generalized least squares models, Crawley 2002). Our aim was to explore the existence of a significant association between extinction- or colonization rates and community size (fig. 1 A, abundance dependence) and the possible existence of different types of responses (fig. 1 B).

Second, to address the effects of the abundance-extinction and abundance-colonization mechanisms on determining species richness patterns along the altitudinal gradient, we applied a model selection approach to the possible variants of the following model:

$$S = \beta_1 J + \beta_2 (1-E) + \beta_3 C + \beta_4 J*(1-E) + \beta_5 J*C + \beta_6 (1-E)*C + \beta_7 J*(1-E)*C$$

where S is species richness, J is community size, E is extinction rate and C is colonization rate. The abundance-extinction mechanism was supported if the interaction term $J*(1-E)$ acted as a good predictor of the geographical variation of species richness counts (prediction E2, table 1) and was preferentially selected.

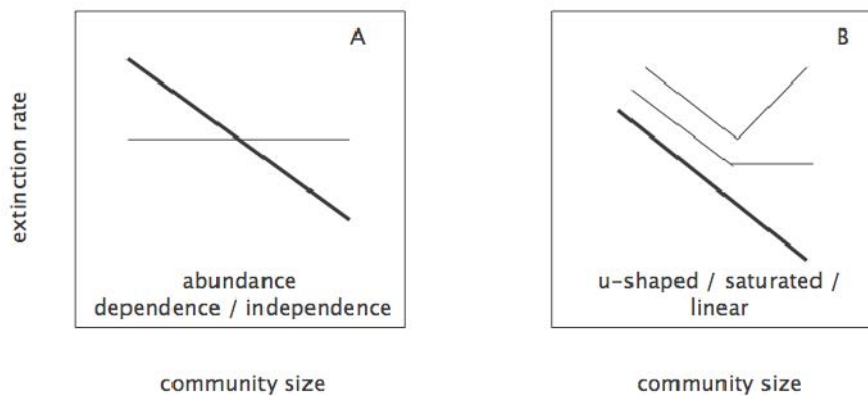


Figure 1. Summary of some of the patterns expected when analyzing extinction-abundance relationships: (a) abundance-dependence (significant association) or independence; (b) types of responses.

The same was valid with the abundance-colonization mechanism with the interaction term $J \cdot C$ (prediction C2, table 1). All the analyses were carried out first for all the gradient and then by subdividing it in three altitudinal bands. Third, we performed a path analysis to deconstruct the causal relationships between community size (J), species richness, extinction rates (E) and colonization rates (C). This enabled us to examine the relative strength of direct community size effects on species richness (predicted by the neutral sampling hypothesis) versus the indirect effects (predicted by the abundance-extinction or colonization hypotheses). The variance explained by each path scales the reliability of each causal model proposed here (Mitchell 1992, Sol et al. 2005) (Predictions E3, C3, N2, table 1).

Finally, we complemented the analysis modelling species richness with environmental data (climate and landscape cover data). Environmental data modelling allowed the evaluation of the association among landscape cover variables, productivity surrogate variables, temperature variables and species richness along the whole altitudinal gradient and grouping by altitudinal bands. Environmental modelling was performed also for community size as a dependent variable. If the mechanisms under examination are operative, we expect that productivity surrogates (NDVI) and forest habitat availability variables will be associated with the variation of species richness. The step function in R package (R Development Core Team, 2004) was used to select models based on the Akaike's Information Criterion (AIC).

Bird and environmental models were spatially corrected by updating base models 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 nonspatial models to obtain values of the spatial covariance parameters (nugget, sill and range) and improve convergence. 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. Effective sampling effort variables derived from species-time curves were included in the models as independent variables.

Hypothesis	Theory (T) and Predictions (P)
<i>Abundance-colonization hypothesis</i>	<p>T: Localities with higher community sizes will show an increased proportion of colonization events and sustain increased species richness for this reason.</p> <p>P C1: Colonization rates are positively and significantly correlated with community size.</p> <p>P C2: When modelling species richness the interaction term J^*C will be a good predictor of species richness variation and will be included a model selection process.</p> <p>P C3: A Path analysis will indicate that indirect effects of community size through colonization rates in species richness are significant.</p>
<i>Abundance-extinction Hypothesis</i>	<p>T: Localities sustaining higher community sizes will show reduced extinction rates and thus increased species richness.</p> <p>P E1 Extinction rates will be negatively and significantly related with community size.</p> <p>P E2 The interaction term $J^*(1-E)$ will perform as a good predictor of species richness variation and will be included in a model selection process.</p> <p>P E3 A path analysis will show that indirect effects of community size through extinction in species richness rates are significant.</p>
<i>Neutral Sampling hypothesis</i>	<p>T: Species richness will be higher in those localities that sustain an increased number of individuals (higher community sizes) by direct neutral sampling effects from the biogeographic pool.</p> <p>P N1: Species richness patterns will be successfully predicted by neutral sampling models that incorporate community size as a key variable.</p> <p>P N2: Path analysis will indicate that direct effects of community size (J) on species richness (S) are significant.</p>

Table 1. Hypotheses and predictions tested.

We obtained environmental data from several digital sources [¹NOAA Satellite; ²Departament de Medi Ambient de la Generalitat de Catalunya (DMAH) <http://mediambient.gencat.net>; ³Universitat Autònoma de Barcelona (UAB) <http://magno.uab.es/atles-climatic/>; ⁴ Institut Cartogràfic de Catalunya (ICC) www.icc.es and ⁵Institut Català d'Ornitologia (ICO) <http://www.ornitologia.org/monitoratge/atles.htm>]. From these digital sources we calculated the climatic variables³ (mean annual temperature, winter and summer temperature, annual rainfall and summer rainfall); geographic variables⁴ (latitude, longitude, altitude, and slope variance); productivity surrogate variables¹ (NDVI, NDVI temporal variation) and landscape cover uses^{1,2} (conifer forest, deciduous forest, fir

forest, oak forest, shrub, wetland, urban, bare ground, irrigated crops, dry fruit crops, irrigated fruit crops, alpine meadows, herbaceous meadows). NDVI data were calculated from NOAA Satellite, using the time series of April-July 2002. This time period corresponded proximately to the bird breeding season. Source data were obtained at 1 km of spatial resolution.

Results

Phylogenetic structure along the altitudinal gradient

The correspondence analysis showed no evidence that altitudinal bands differ in the proportion of species belonging to different taxonomic families, suggesting little phylogenetic effects on species distribution. The unique exceptions were *Oriolus oriolus* (family Oriolidae), which is absent from the 2066-3100m band, and *Remiz pendulinus* (Remizidae), a species restricted to low altitude riparian forests in the 0-1033m band. Altitudinal bands presented very similar familial root distance distributions that do not differ in their mean root distance (Tukey-Kramer test, $p > 0.1$). We concluded that any phylogenetic trend associated to the altitudinal gradient was observed.

Correlations between J, E and C (Predictions E1 and C1)

The region presents a hump-shaped altitudinal species richness gradient that is well correlated with productivity surrogate measures (NDVI) and community size counts (Figure 2).

Altitude band	Grain	Dep. Var.	Ind. Var.	β	DF	AIC	R ² Adj	p
One band	10 km	E ₀₋₂₅₀₀	J	$-4.85 \cdot 10^{-6} \pm 7.93 \cdot 10^{-7}$	307	-297.03	0.13	<.0001
Three bands	10 km	E ₀₋₁₀₃₃	J	$-5.4 \cdot 10^{-6} \pm 8.9 \cdot 10^{-7}$	233	-204.19	0.17	<.0001
		E ₁₀₃₃₋₂₀₆₆	J	-	55	-	-	ns
		E ₂₀₆₆₋₃₁₀₀	J	$-1 \cdot 10^{-5} \pm 2 \cdot 10^{-6}$	15	-1.7	0.6	<.0001

Table 2 Models predicting extinction and colonization rates as a function of community size values. All colonization rates models were non-significant and are not shown.

Colonization rates (C) were not associated with community size measures (J), but the contrary was observed in extinction rates (E) (Figure 3). However, this association varies along the altitudinal gradient. Association among extinction rates and community size was only observed at low-productivity altitudinal bands (0-1033; 2066-3100 bands), and was much stronger at high-altitude zones (2066-3100 band, table 2, Figure 3).

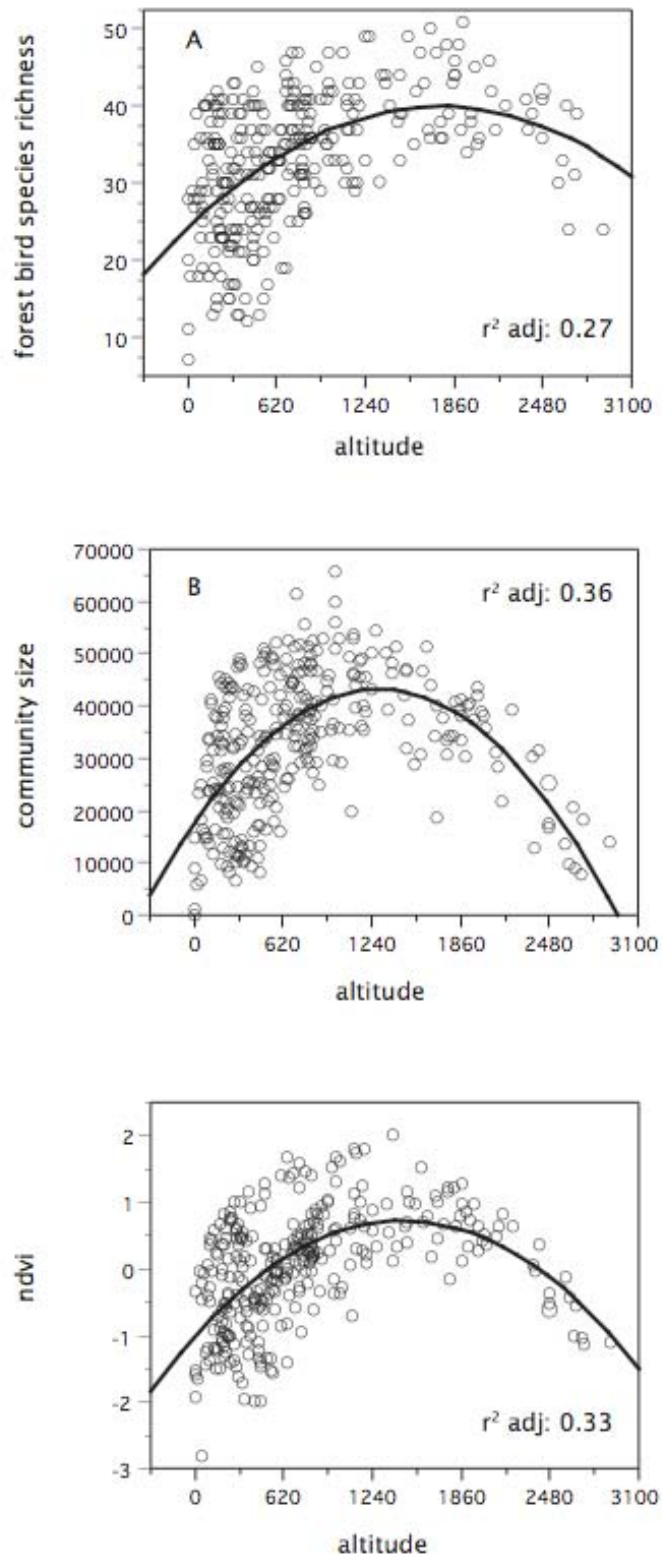


Figure 2 Patterns of the co-variation between altitude and (a) species richness, (b) community size, and (c) NDVI.

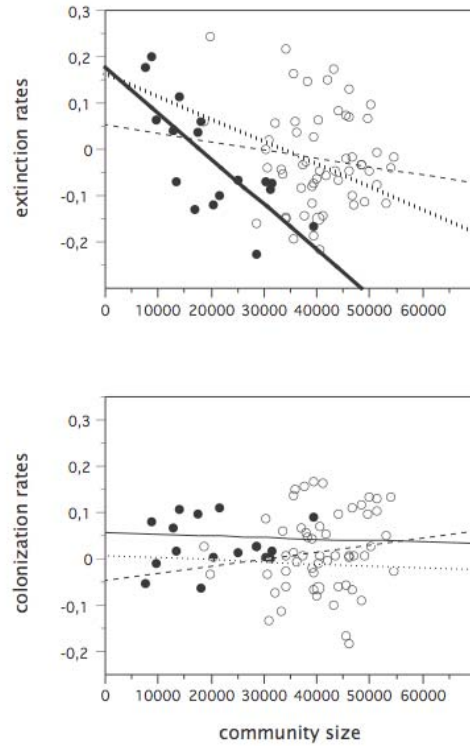


Figure 3 Extinction-abundance and colonization-abundance relationships for the three altitudinal bands (0-1033 m: dotted line; 1033-2066 m: dashed line, white dots; 2066-3100 m: black line, black dots). Significant associations (abundance dependence) are indicated with thicker lines. Only black and dotted lines in the extinction plot represent significant fits.

Band	Dep. Var.	Indep. Var	DF	β values	AIC	R^2 adjusted	p
0-1033	S	$J^*(1-E)$ (1-E)	232	$4 \cdot 10^{-4}$ 6.16	769.89	0.63	<.0001
1033-2066	S	(1-E)	55	29.15	184.06	0.28	<.0001
2066-3100	S	$J^*(1-E)$	15	$4.8 \cdot 10^{-4}$	50.97	0.50	<.0001
All bands	S	$J^*(1-E)$ (1 - E)	306	$4.3 \cdot 10^{-4}$ 9.51	1086.74	0.54	<.0001

Table 3. Results of the model selection approach using colonization, extinction rates and community size variables and their interactions

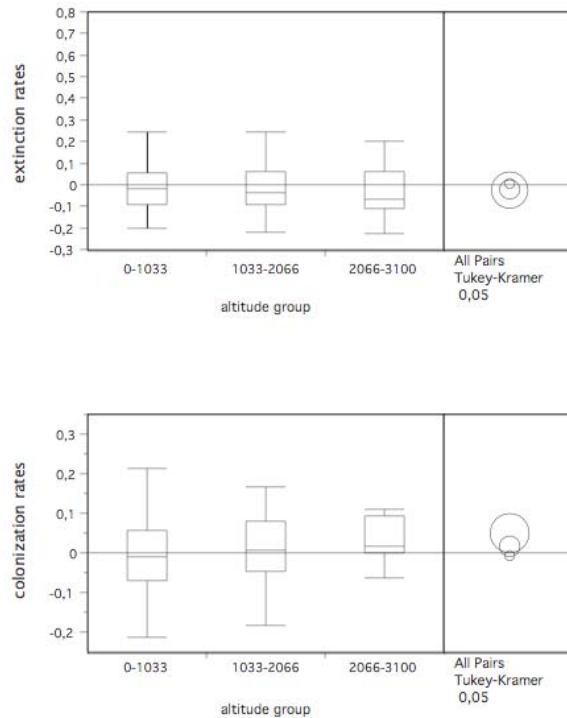


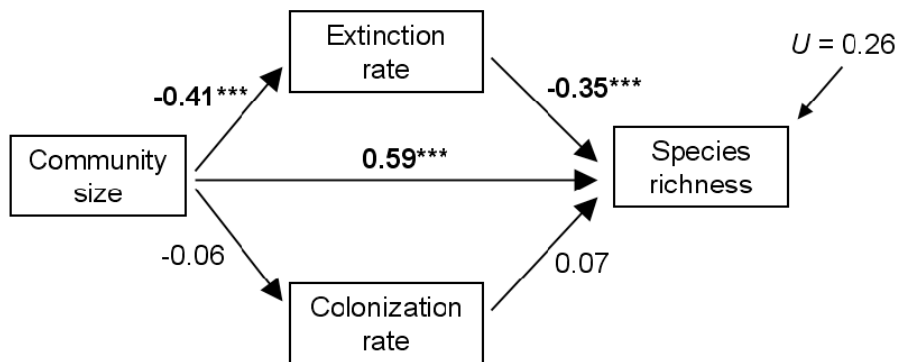
Figure 4 Results of the Tukey-Kramer tests comparing mean extinction and colonization rates for three altitudinal bands. You can compare each pair of group means visually by examining how the comparison circles intersect. The outside angle of intersection tells you whether group means are significantly different. Circles for means that are significantly different either do not intersect or intersect slightly so that the outside angle of intersection is less than 90 degrees. If the circles intersect by an angle of more than 90 degrees or if they are nested, the means are not significantly different.

The relationships between community size and extinction rates appeared to be linear (Figure 1 B, types of responses). Altitudinal bands differ in the range of community size values shown (Tukey-Kramer test, $p < 0.0001$) but not in the mean of extinction rate values. We concluded that there is empirical support for the extinction-abundance hypothesis only at the low productivity altitudinal bands (prediction E1, table 1). No significant differences were observed in mean extinction rates along the altitudinal gradient (Tukey-Kramer test, $p = 0.11$; Figure 4). On the contrary, colonization rates increased with altitude (r^2 adjusted: 0.11, $p < 0.0001$) and the lower altitudinal band (0-1033 m) presented significantly lower colonization rates (Tukey-Kramer test, $p < 0.0001$).

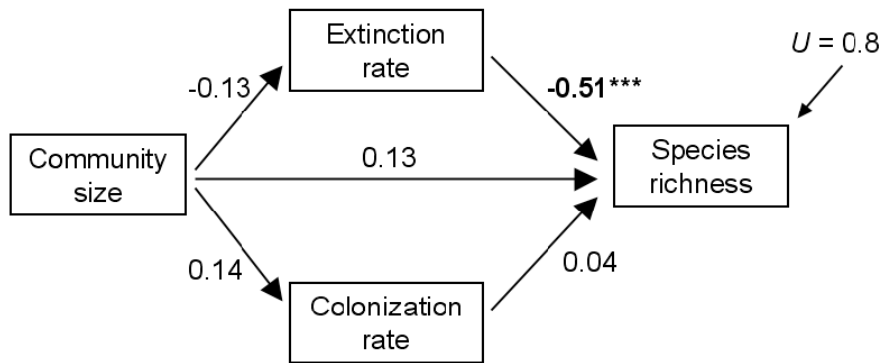
Model selection (Predictions E2 and C2)

The interaction term $J^*(1-E)$ was selected in the modelling process at the low-productivity altitudinal bands (0-1033 & 2066-3100 m) giving support to the abundance-extinction hypothesis on these areas (Prediction E2, table 3)

A. Altitude 0-1033m



B. Altitude 1033-2066



C. Altitude 2066-3100

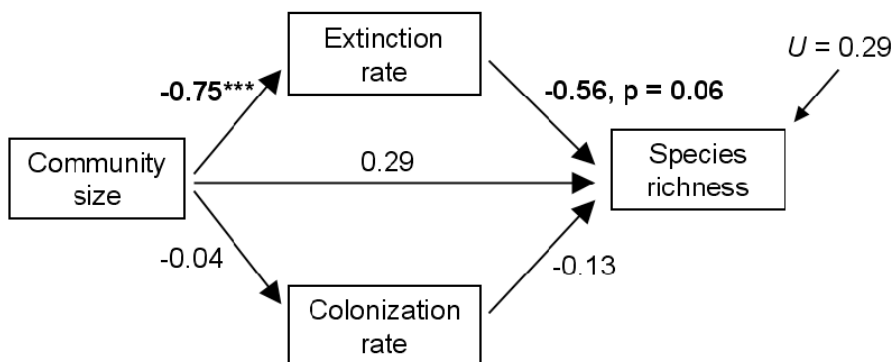


Figure 5. Path diagram of expected causal effects of extinction rate, colonization rate and community size on avian species richness. Bold arrows with asterisks indicate path coefficients that are significant at $p < 0.001$. The variance in species richness unexplained by the model is referred to as U.

Path analysis (Predictions N2, E3 and C3)

Indirect effects of community size through extinction rates on species richness were significant and supported by the path analysis only in low NDVI regions (Prediction E3), supporting the abundance-extinction hypothesis on these areas (figure 5). On the other hand, direct effects were supported only at the lowest altitude region (0-1033) (Prediction N2). In that region, direct sampling effects seem to explain the bulk of the species richness variation. Direct effects of community size in the high altitude band were marginally non-significant, but this might be attributed to a type II error due to the low sample size (N=17). Interestingly, at the higher NDVI band (1033-2066 m) species richness was not correlated with community size measures, whereas the contrary happened at the low NDVI bands (0-1033; 2066-3100 m).

Environmental modelling

Species richness model fit varied significantly along the altitudinal gradient and different variables were selected depending on the altitudinal band considered. The models explained a lower amount of variation in the high-productivity band (table 4). Within this band (1033-2066 m), species richness was only weakly associated with productivity and forest habitat availability measures (% of forested area) or with any other predictor variable. On the other hand, at low-energy zones (0-1033; 2066-3100 m bands), productivity and forest habitat availability measures were positively and strongly associated with species richness and selected as predictor variables. Temperature was only selected as a predictor of species richness at the coarser grain size (10 km), and showed distinct associations depending on the altitudinal band considered.

Community size was positively associated with habitat availability measures (percentage of forest cover types) and productivity surrogate measures (NDVI) and negatively related to open space areas (irrigated croplands, alpine meadows). The models explained a lower amount of variation in the high-productivity band, in line with the trend observed in the species richness models.

Alt band width	Grain	Dep Var	Independent variables	DF	AIC	R ² Adj	p
All gradient	1 km	S ₀₋₃₁₀₀	NDVI+Conifer-Herbaceous meadow	3073	9641	0.39	<.0001
	10 km	S ₀₋₃₁₀₀	Conifer+NDVI-Irrigated Crop	305	1879.45	0.64	<.0001
		J ₀₋₃₁₀₀	Conifer+NDVI-Irrigated-Crop-Temp ² +Temp	303	6058.44	0.81	<.0001
Three bands	1 km	S ₀₋₁₀₃₃	NDVI+Conifer-Herbaceous meadow	2502	7733.61	0.42	<.0001
		S ₁₀₃₃₋₂₀₆₆	NDVI-Shrub-Alpinemeadow+HolmOak	445	2549.42	0.11	<.0001
		S ₂₀₆₆₋₃₁₀₀	Conifer+Shrub+NDVI ²	117	677.66	0.62	<.0001
	10 km	S ₀₋₁₀₃₃	Rainfall+Conifer-Temperature	230	1436.79	0.66	<.0001
		S ₁₀₃₃₋₂₀₆₆	-Temperature ²	54	373.48	0.19	<.002
		S ₂₀₆₆₋₃₁₀₀	Temperature-Herbaceous meadow	14	112.54	0.58	<.003
		J ₀₋₁₀₃₃	Conifer-Temperature+Rainfall-Irr.Crop	230	4635.61	0.85	<.0001
		J ₁₀₃₃₋₂₀₆₆	-Scrub+Temperature-Temperature ² +Conifer	52	1106.69	0.61	<.0001
		J ₂₀₆₆₋₃₁₀₀	Conifer-Alpine meadow	13	284.42	0.87	<.0001

Table 4. Results of the model selection approach using environmental variables. NDVI: Normalized difference vegetation index; Irr. Crop: percentage of irrigate cropland surface, Conifer: percentage of surface occupied by conifer forests, Temp: mean annual temperature, Alp. Meadow: percentage of surface occupied by alpine meadows, Shrub: percentage of shrubland cover.

Discussion

The species-richness relationship of forest birds in Catalonia shows a clear altitudinal geographic structure, with matching altitudinal hump-shaped patterns in productivity surrogates (NDVI), community size and species richness variables. However, the pattern and strength of the associations among these three variables varies along the altitudinal gradient. NDVI and community size were strongly associated with species richness only at the extremes of the gradient (low productivity altitudinal bands). In these areas variation of species richness can be explained by direct sampling effects associated to community size variation, as predicted by the neutral theory (Hubbell 2001). However, our results suggest that indirect effects of community size in the extinction rates may contribute to explain the number of species that a locality holds. Thus, our results support two specific mechanisms that might be underlying the pattern and are in line with the abundance-extinction hypothesis and the sampling hypothesis.

We found no support favourable to the abundance-colonisation hypothesis. This is not an unexpected tendency. Indeed, Evans et al. (2005b) refused empirically the idea that species-energy relationships are a consequence of higher colonization rates in high-energy areas (abundance-colonisation hypothesis). Our results provide additional support to their main conclusions. Furthermore, Evans (2005b) showed that colonisation rates in some functional groups might vary significantly with energy availability, but showing a negative response (contrary to the predictions of the abundance-colonisation hypothesis). In other functional groups, Evans did not find any significant relationship between colonisation rates and energy availability, coinciding with the patterns described in our study. The divergence in the spatial dynamics of colonisation and extinction rates is not surprising specially if one considers the results of recent work on the topic (Gaston and Blackburn 2002, Evans et al. 2005b). For instance, Gaston and Blackburn (2002) showed that both variables are differently associated with population size, body size, natal and breeding dispersal, and range size (see also Paradis et al. 1998).

A number of the mechanisms proposed to generate the species-energy relationship assume a positive association between community size and species richness (Evans et al. 2005a). We should then conclude that these mechanisms may be driving species richness variation only in low-productivity areas, where the association between community size and species richness is significant, and thus qualitatively different processes may be determining species-richness variation at high-productivity regions (Kerr and Packer 1997, and see Lavers and Field 2006). This is consistent with the observed decrease in species richness predictability at the high-productivity altitudinal band when modelling with environmental data.

Environmental models for the whole gradient suggest that productivity and habitat availability are the main causes determining richness variation in the whole gradient (Wright 1983, Hawkins et al. 2003b, Lavers and Field 2006). However, the analyses conducted by altitudinal bands suggest that the current dynamics among high- and low-productivity regions consistently differ. Species richness variation is tightly constrained by community size and productivity surrogates only in low-energy regions. High-energy regions present a great amount of species richness variance that is not explained by community size and NDVI variation.

Furthermore, our results suggest that local variation in extinction rates in low NDVI areas might contribute to explain a part of the geographical variation in species richness. This suggests the existence of a geographic mosaic on the association among extinction rates and community size, indicating that processes determining abundance-extinction relationships and species richness variation vary geographically in a qualitative way.

The idea of the existence of geographic mosaics in the processes governing richness is not a completely novel idea. Kerr and Packer (1997), in a study of the environmental variables associated with species richness variation in the mammals of North America concluded that “the species-energy hypothesis applies to North American mammals only over a limited geographical area in which climatic energy levels are low, rather than on continental scale as was previously been accepted” (Kerr and Packer 1998). Similarly, at the global or continental scale, the idea of the existence of geographic shifts in the variables associated with species richness gradients has been extensively debated, and empirical support was found in favour of the water-energy dynamics hypothesis (O’Brien, 1998; Whittaker and Field 2000; Hawkins et al. 2003b).

Our results are in line with the historical phylogenetic signal that indicates that numerous extinction processes in basal clades (adapted to warm and humid climates) might have occurred in extratropical regions during the cooling period of the Miocene, that was accompanied with strong reductions in ecosystem productivity and habitat availability (Hawkins et al. 2006). The patterns reported here suggest that the abundance-extinction hypothesis is a plausible mechanism that might explain the maintenance of the latitudinal species richness gradient in an historical time scale. Our results showed that this mechanism operates at the ecological time-scale (20 years).

The observation of a negative association between extinction rates and community size is one of the predictions of the abundance-extinction mechanism. However, an increased extinction risk in low-energy areas may be also motivated by more specific mechanisms than the abundance-extinction hypothesis proposed here. First, a greater abundance of resources in high-energy areas may reduce species niche breath and lead to an increase in co-occurrence rates and species richness by decreasing extinction rates (niche breath hypothesis) (Evans et al. 2005a). Second, if higher energy availability increase recovery rates from disturbance (dynamic equilibrium hypothesis) this may also lead to lower extinction rates in high-energy areas (Huston 1979, Evans et al. 2005a). Third, if increased energy enhances the availability of rare resources in high-energy areas this may also reduce the extinction rate in niche specialists (niche position hypothesis) (Evans et al. 2005a). Finally, if high-energy availability increases consumption rates and leads to a reduction in prey populations, this can reduce extinction rates of prey species in high energy-areas (consumer pressure hypothesis) (Paine 1966, Janzen 1970, Evans et al. 2005a). All these mechanisms may be seen as variants of the abundance-extinction hypothesis, but their diagnostic predictions are not evaluated here.

Overall, our work shows that the mechanisms regulating species richness gradients vary geographically, causing spatial mosaics in the processes that determine species richness variation. For instance, low and high productivity regions seem to differ in both the existence of a significant abundance-extinction and species richness-community size relationships. The extinction-abundance hypothesis and other mechanisms associated with community size might be acting at different rates depending on the specific ecological conditions of each locality thus leading to a geographical mosaic on the processes that conform species richness gradients. We conclude that current gradients in species richness may be the product of a variety of different processes. Among these processes, an important part of the variation in species richness might be the result of qualitative changes in community dynamics related to low productivity and low community size and the associated increases in extinction risk (Evans et al. 2005b). We conclude that the abundance-extinction mechanism operates at the ecological-time scale and might be an active mechanism maintaining species richness gradients.

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CHAPTER 3: Random sampling, abundance-extinction dynamics and niche-filtering immigration constraints explain the generation of species richness gradients

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Abstract

Aim The paradigm that species' patterns of distribution, abundance and coexistence are the result of adaptations of the species to their niches has recently been challenged by evidence that similar patterns may be generated by simple random processes. We argue here that a better understanding of macroecological patterns requires an integration of both ecological and neutral stochastic approaches. We demonstrate the utility of such an integrative approach by testing the sampling hypothesis in a species-energy relationship of forest bird species.

Location A Mediterranean biome in Catalonia, Spain.

Methods To test the sampling hypothesis we designed a metacommunity model that reproduces the stochastic sampling from a regional pool to predict local species richness variation. Four conceptually different sampling procedures were evaluated.

Results We show that stochastic sampling processes predict a substantial part (over 40%) of the observed variation in species richness, but leave considerable variation unexplained. This remaining variation in species richness is better understood as result of alternative ecological processes. First, the sampling model explains more variation in species richness when the probability that a species colonises a new locality is assumed to increase with its niche width, suggesting that ecological differences between species matter when it comes to explain macroecological patterns. Second, extinction risk is significantly lower for species inhabiting high-energy regions, suggesting that abundance-extinction processes play a significant role in shaping species richness patterns.

Main conclusions We conclude that species-energy relationships may not simply be understood as a result of either ecological or random sampling processes, but more likely as a combination of both.

Introduction

Species richness is often linked to energy measures, with the more productive or warm sites typically containing a larger number of species than less productive or colder sites (Brown 1981, Wright 1983, Turner et al. 1987, Lennon et al. 2000, Currie et al. 2004). Such associations are referred to as species-energy relationships, and are generally held to result from high-productivity regions being able to provide more resources for individuals and hence sustain larger population sizes (reviewed in Evans et al. 2005a). While there are well-supported mechanisms that link the availability of resources to the abundance or biomass of organisms, it is less obvious how or why this should necessarily equate to higher species diversity (Clarke and Gaston 2006). Some authors believe that the association between community size (i.e. the total number of individuals present in a locality) and species richness could simply result from simple random sampling processes: as community size increases, so it does the number of different species by chance (Fisher *et al.* 1943, Preston 1962, Coleman *et al.* 1981, 1982, Srivastava and Lawton 1998, Kaspari *et al.* 2003, Evans *et al.* 2005a, Scheiner and Willig 2005). According to the sampling hypothesis, more productive areas should contain more species than less-productive areas even though individuals are randomly sampled from a regional pool. However, other processes might cause the association between community size and species richness. For instance, the abundance-extinction hypothesis argues that an increase in abundance should lead to higher diversity because larger populations buffer species against extinction (MacArthur and Wilson 1967, Lande 1993). Similarly, more productive regions characterized with greater community sizes might hold an increased number of species simply by the effect of geographical differences in diversification rates (Rohde 1992, Cardillo 1999, Ricklefs 2007, Hawkins *et al.* 2007, Mittelbach *et al.* 2007).

Here we performed a test of the sampling hypothesis in the Catalan avifauna developing a simple metacommunity model and contrasting theoretical and empirical patterns. We test if different stochastic sampling processes can accurately predict observed geographical variability in patterns of species richness. We evaluate several sampling scenarios in which species differ on their dispersal ability according to their niche width or their regional population abundance.

Methods

To validate the random sampling hypothesis, it is necessary to reproduce the stochastic sampling from a regional pool to predict local species richness variation. We develop a simple stochastic metacommunity model to test whether a battery of different stochastic sampling processes can accurately reproduce species richness patterns. The model reproduces different sampling scenarios. In the first scenario, species are sampled with the same probability (equal probability model, EP). In the second one, species are sampled accounting for the effect of regional densities (mass-effect model, ME). Thirdly, the probability of being sampled is defined as a function of species' niche width (niche-filtering immigration model, NI). The greater the niche width, the greater is the probability of being sampled. Applying this model, we evaluated if we can predict an additional amount of variation in species richness considering the coupled effect of sampling effects and the existence of dispersal constraints associated with species niche width (Wiens and Donoghue 2004). The sampling models are used to generate species richness patterns of forest birds, which are then compared with real patterns from a well-surveyed region from the Mediterranean basin (Estrada et al. 2004).

We next evaluate the possibility that abundance-extinction dynamics were acting in concert with stochastic sampling processes to maintain the species-energy relationship. According to the abundance-extinction hypothesis, we should expect an increase in extinction risk in low energy zones (Kaspari et al. 2003, Evans *et al.* 2005a, Evans *et al.* 2005b, Carnicer et al. 2007). This prediction was evaluated and, in addition, we conducted a path analysis to deconstruct the causal relationships among species richness, community size, direct sampling effects, extinction rate and colonisation rate (Carnicer et al. 2007).

Bird and environmental data

We studied species richness patterns of forest birds in Catalonia, a region of over 30.900 km² located in NE Spain. We obtained data on forest bird species data at 10x10 km grid resolution from the Catalan Breeding Bird Atlas (www.ornitologia.org/monitoratge/atlesa.htm), a project of the Catalan Institute of Ornithology (Estrada *et al.* 2004). The Catalan breeding bird atlas summarizes the distribution of birds in the region in two different periods of time: 1975-1983 and 1999-2002. It uses a standardized 10x10 km grid system based on a UTM projection covering the region. 309 grids (localities, hereafter) were considered in this study. 67 species of forest birds were considered, following the classification of the Catalan Breeding Bird Atlas (Estrada et al. 2004, page 569), that includes all species that have been found to be breeding in forest habitats in Catalonia (Muntaner et al. 1983, Cramp and Perrins 1994, Estrada et al. 2004). A more detailed description of census techniques implemented is provided in Appendix A.

We calculated colonization and extinction numbers in each 10x10 km square by comparing the number of species breeding there in each of the two periods analyzed (t_0 , 1975-83 and t_1 , 1999-2002, Estrada *et al.* 2004). Colonization rate was calculated by estimating the proportion of species in t_1 not detected in t_0 , while extinction rate corresponded to the proportion of species per 10 km square breeding in t_0 and not observed later in t_1 . The estimates of extinction and colonization rates were then corrected for the differences in sampling effort between 1980-83 and 1999-2002 in each grid cell (see Estrada et al. 2004 for details). Finally, the residuals of this relationship were then used as an unbiased measure of extinction and colonization rates.

To validate the assumption that species richness is linked to energy measures, we gathered information on NDVI (Normalized Difference Vegetation Index), land cover percentages and climatic data for each 10 x 10 km square. NOAA satellite data and several digital sources were used to obtain NDVI, land cover percentages and climatic data (<http://mediambient.genct.net>, <http://magno.uab.es/atles-climatic/>, <http://www.icc.es>). A more detailed description of the variables and sources is provided in Carnicer et al. (2007).

A metacommunity sampling model

We first generated a simple algorithm that simulates the random increase in the number of individuals in the 309 studied localities (10x10 km cells corresponding to the spatial units defined for field bird surveys, where a given locality is noted by using subscript ' L ') from zero individuals ($J_L=0$) to the carrying capacity ($J_L=K_L$) by random sampling from a metacommunity pool. Our metacommunity sampling model accounts for the two most relevant characteristics of Hubbell's neutral model (2001), i.e. random sampling and dispersal limitation effects (Etienne 2005, Alonso et al. 2006), but without considering neither random extinction dynamics nor speciation processes. Thus, it is important to highlight that our model is not reproducing at all Hubbell's neutral theory. Instead, our stochastic sampling model is a much more simpler model designed to specifically test the sampling hypothesis.

The model shares some of the Hubbell's model attributes, but the results obtained are not to be interpreted as a test of the neutral theory.

At the initial stage of the algorithm, each local community is empty. The algorithm adds one new individual at each step (t) and stops when all the individuals are added (up to 10 million individuals, corresponding to all the localities together). New individuals can have two distinct origins: local birth or immigration from the regional pool. During each time step (t):

- (1) A new individual is added, but is randomly defined as immigrant (with probability m) or as local birth (with probability $1-m$).
- (2) In case of immigration, the individual is assigned to a species according to the probabilities of the metacommunity vector P . This vector describes the probability of immigration of each species from the regional pool.
- (3) In case of local birth, the new individual is assigned randomly among the species already present at the locality.

The performance of the model is summarized in figure 1.

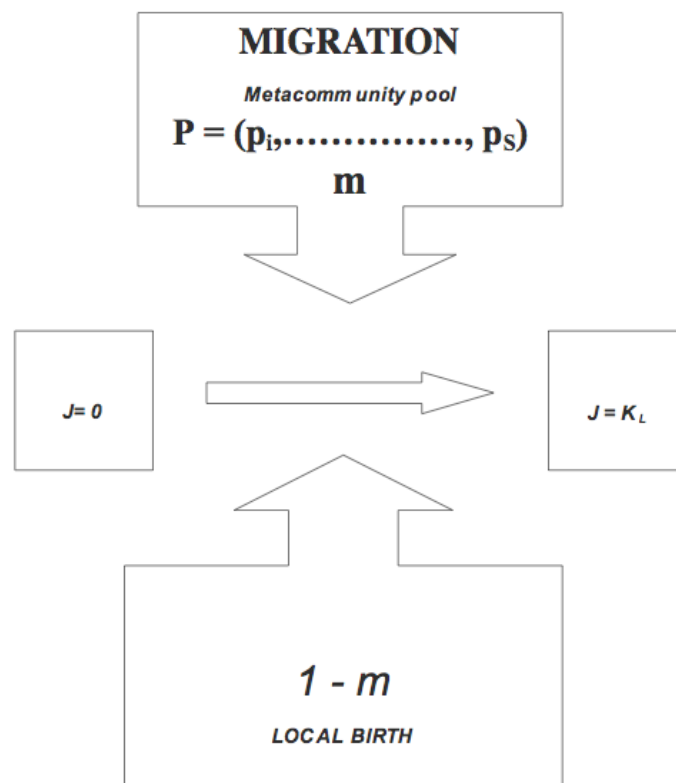


Figure 1 A scheme showing the sampling procedure applied.

The carrying capacity of the community (K_L) is equal to the total number of individuals estimated at each locality (Estrada et al. 2004, Herrando et al. 2007). The metacommunity is defined as the regional collection of local communities (i.e. each 10x10 km cell). Only immigrant individuals, $i(t)$, can add new species to the local

community, and hence increase local species richness, in the community. Species richness increases when the sampled individual is not already present in a locality; local births, $b(t)$, increase community size without contributing to species richness counts. Our model assumes a constant ratio between i and b when a local community is growing from $J_L = 0$ to the carrying capacity K_L . The ratio among the two processes (i and b) is determined by the migration rate (m), which states the probability of local colonization. This parameter might be considered analogous to Hubbell's m (Hubbell 2001 and see Volkov et al. 2003, Alonso 2003, McKane et al. 2004 and He 2005 for analytical solutions) but is expected to achieve lower values than those reached in neutral models because our model does not simulate small populations that colonize a locality and become extinct after one or few generations (abundance-extinction dynamics). Small populations that become extinct might be expected to be an important fraction of the colonization cases, especially in localities with low community sizes (Hanski 1997, Hubbell 2001, Adler et al. 2007, Carnicer et al. 2007). The expected number of births and immigrants in a locality is equal to $E\{b\} = (1 - m) J_L$, and $E\{i\} = m J_L$. Given the spatial scale at which the model was developed, we assumed that individuals have enough dispersal capabilities to reach any square within the study region at each time step and therefore, immigration is not limited by distance.

CODE	Hypotheses	Pool vector and theory
EP	<i>Equal Immigration Probability</i>	All species have the same probability of being sampled into a locality. P vector is a uniform distribution with probability equal to $1/S$. This hypothesis accounts for the variation in species richness caused by local changes in J_L without incorporating metacommunity mass-effects.
ME	<i>Mass-effect</i>	Probability of being sampled is equal to the relative frequency of population abundance of each species in Catalonia. Species richness and composition in a locality will depend of their community size and the abundances of the species at the metacommunity level.
NI	<i>Niche-filtering immigration</i>	Probability of a species to disperse is equal to a measure of niche amplitude of habitat preferences. This model assumes that species immigrate in a different manner, with the existence of habitat generalist and habitat restrictive species, and that those differences are important explaining spatial variation in species richness.
ME*NI	<i>Mass-effect & Niche-filtering immigration</i>	This model combines the two previous ones. The probability of being sampled in the community is equal to multiplication of the vectors ME and NI. Thus, this models accounts for the interaction among mass-effects and niche-dispersal cues.

Table 1. Vectors used determining species probability of being sampled from the regional metacommunity pool.

Once the local community reaches the carrying capacity (K_L), the incorporation of new individuals by both immigration and reproduction stops, and thus the total number of individuals, local composition and abundances remain fixed. The species richness estimated when the local community reaches the carrying capacity is then used to test to what extent sampling expectations correspond to avian species richness estimated during field surveys. The local communities were built by sampling the individuals from a regional

metacommunity pool composed by all Catalan forest bird species. To perform the sampling, we defined a vector of probabilities (P) that describes the probability for each species to be sampled from the regional pool (p_1, p_2, \dots, p_S). We performed the sampling simulations with four different types of P vectors, as described in Table 1.

Each P vector tests for a specific hypothesis. The different P vectors are analogous to different values of P in Hubbell's model (Hubbell 2001, ergodic model with immigration, chapter four).

Setting model parameters

Local species richness was expected to vary with changes in migration rate (Hubbell 2001, Mouquet and Loreau 2003, Cadotte 2006). Consequently, simulations were performed for a range of migration rate values (m), allowing us to evaluate the percentage of variation in species richness explained by each value. We only considered the range of m values that generate realistic predictions, and we rejected m values that underestimated or overestimated species richness when compared with real data in a plot. The optimal m value (referred as to m_o) was defined as the value that better accounted for variation in local species richness (figure 2). Once the optimum migration rate (m_o) was estimated, species richness for a locality was estimated as the mean of 10 iterations of the sample algorithm. An optimal m value (m_o) was separately obtained for each metacommunity vector used (P).

To evaluate the performance of the simulations derived from the model, we compared real species richness counts against the values predicted by the model by means of linear regressions. Additionally, we evaluated the power of the model in predicting local species composition. We applied a measure of similarity (the Sokal-Michener distance) to compare observed and predicted species composition at each locality (Sokal and Michener 1958, Gower and Legendre 1986).

Sampling hypotheses tested

The use of different metacommunity P vectors allowed us to contrast the hypotheses that species behave as a similar sampling units (equal probability of immigration hypothesis, Table 1), that species are sampled proportionally to their regional abundances (mass-effect hypothesis), and the hypothesis that species differ in their likelihood to enter into the local community due to differences in species' traits that affect colonization probability (niche-filtering immigration hypothesis) (Wiens and Donoghue 2004, Wiens and Graham 2005).

If we assume that all species have the same probability of being sampled (equal probability hypothesis), then the model basically describes a sampling effect that is independent of the metacommunity distribution. In this case variation of species richness mostly depends on local community size variation (J) and migration rate (m). However, most neutral models assume that the probability of being sampled is proportional to the abundance in the regional pool of a species (mass-effect hypothesis) (Hubbell 2001, Gravel et al. 2006). This possibility was simulated applying a metacommunity vector P of regional abundances.

Recently, Wiens and Donoghue (2004) argued that species might present phylogenetically conserved differences in the habitat conditions in which they can successfully persist. Such differences can determine the habitats in which the species may spread (Wiens and Donoghue 2004, Wiens and Graham 2005). Indeed, Wiens and Donoghue (2004) stressed that species' niches might be phylogenetically conserved over long evolutionary timescales and determine the success of the diverse dispersal and colonisation processes that generate species

richness gradients in the ecological time scale. Accordingly, we should expect that species characterized by wider niches (i.e. positive preferences for a higher number of habitats) will have a greater probability of success in immigrating and successfully colonizing new localities, whereas species with a narrow niche of habitat preferences will be more prone to be excluded. Overall, the niche-filtering immigration hypothesis states that the species' habitat niche width and their success in immigrating into new localities are positively related. Therefore, it predicts that a sampling model that accounts for species niche width differences will forecast to a greater extent local species richness variation than the other sampling models. In our metacommunity sampling model this prediction can be tested setting the species' probability of being sampled (P) proportional to a measure of the species niche width. Niche width for a species i (A_i) was calculated using:

$$A_i = \frac{\sum_j^h \sum_l^h f_{ij} f_{il} d_{jl}^2}{\sum_j^h \sum_l^h f_{ij} f_{il}}$$

where i is the species, f_{ij} is the species normalized preference for habitat j , f_{il} is the species normalized preference for habitat l , and d_{jl} is the distance between habitats j and l . A more detailed mathematical description is provided in Appendix B. The calculation of niche width measures allowed us to test for the reliability of immigration constraints associated to niche width in the generation of species richness gradients. If niche constraints operated, we would expect that the niche sampling model better predicts local species richness variation and local composition than the equal probability and mass-effect models (Chase 2005). We develop in the next section a simple method to quantify the relative importance of niche constraints and mass-effect sampling effects.

A test for discriminating among mass-effects and niche immigration assembly

If species are sampled proportionally to their regional abundance (mass-effect hypothesis), we should expect the distribution of species across localities to show a nested structure (Atmar and Patterson 1993). Thus, species characterized with lower pool abundances will be only sampled in localities with high community size whereas very abundant species will be sampled in most of the localities. In other words, if localities differ greatly in their community size values (J_L) and species richness counts (S_L), then a matrix of n localities (rows) that compares species composition (columns) should present a nested structure. According to that, the number of localities that a species i occupy (R_i) should be described by species' metacommunity abundances, following the linear model:

$$R_i = a + \beta_2 M_i$$

where M_i is a measure of the abundance of species i in the metacommunity, β_2 is the coefficient of regression and a the intercept. Note that the model variables are logarithmically transformed following Bell (2006). However, if niche immigration constraints operate, we expect that niche width measures explain at least a part of the variation in local composition. Then, local composition should be better predicted by a model that integrates metacommunity neutral mass-effects and niche constraints on immigration rates:

$$R_i = a + \beta_1 A_i + \beta_2 M_i$$

where A_i is a measure of species i niche width. This model should perform better and explain a greater amount of variation when compared to a neutral one that only incorporates the mass-effects of immigration from the metacommunity. In order to discriminate among mass-effects and niche-immigration limitation effects when explaining local species composition, we estimated and compared both models for our study region. To evaluate if our presence-absence matrix was effectively nested, as predicted, we used the Nestedness Temperature Calculator Program (Atmar and Patterson 1993; [http:// www.fieldmuseum.org/](http://www.fieldmuseum.org/); see Appendix C for more details). Considering that abundant and rare species differentially contribute to species-energy relationships (Evans et al. 2005c), the analyses were carried also grouping by high-density species and low-density species. Grouping was effectuated as follows: species were ranked according to their metacommunity densities and divided into two groups that contained 50% of the species.

Testing the abundance-extinction hypothesis

An increase in extinction risk in low energy zones is a prediction shared in some of the alternative mechanisms proposed to account for variation in species richness (Kaspari et al. 2003, Evans *et al.* 2005a, Evans *et al.* 2005b). The abundance-extinction hypothesis makes two diagnostic predictions. First, it predicts the existence of a negative association among energy measures and extinction rates. Second, if abundance-extinction hypothesis holds, a path analysis should indicate that indirect effects of community size through extinction rate are significant when explaining species richness variation.

To evaluate the first prediction we calculated the number of colonization and extinction numbers that have occurred in each locality between the period 1980s and 2000s, and relate the rate of extinctions observed to the energy available in the locality (temperature, NDVI and J). We repeated these calculations with the proportions of colonisations and extinctions (following Evans *et al.* 2005b).

To test the second prediction, we conducted a path analysis to deconstruct the causal relationships among species richness and community size, extinction rate and colonisation rate. Path analysis allows the partition of the correlations in a set of variables according to a specific model about their causal relationships (Li 1975, Grace 2006). To evaluate the relative importance of each link in the path diagram, we calculated the path coefficients as standardized partial regression coefficients of a multiple regression model. The value of any compound path was estimated as the product of its path coefficients, allowing for the comparison of direct and indirect effects. The residual error term (U) of each response variable in the model reflects unexplained variance (the effect of unmeasured variables) plus measurement error, and it is quantified as the square root of one minus the coefficient of determination.

Our hypothesised causal model was defined by the three paths linking community size, extinction rate and colonisation rate to species richness (see the results section for the specific path diagram proposed). A significant direct effect of community size on species richness is expected under a random sampling process, whereas an indirect effect of community size on species richness via decreased extinction rates is expected under the abundance-extinction hypothesis (Carnicer et al. 2007). The coexistence of neutral sampling and abundance-extinction dynamics would be supported by both significant direct and indirect effects in the diagram.

Model selection

We modelled extinction and colonization rates as a function of energy measures to test the predictions of the abundance-extinction hypothesis. We also modelled the number of localities occupied by a species (R_i) as a function of metacommunity regional abundance (M_i) and habitat niche amplitude measures (A_i) testing for the existence of niche constraints on dispersal and mass-effect processes.

The step function in R package (R Development Core Team, 2004) was used to select models based on the Akaike's Information Criterion (AIC). 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, Evans et al. 2005b). Exponential covariance functions performed better than spherical and Gaussian in all the cases examined. We plotted a semivariogram of nonspatial models to obtain values of the spatial covariance parameters (nugget, sill and range) and improve convergence. Models were compared and the most parsimonious one was selected. 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. Detailed examples and discussion of all these modelling procedures can be found in Crawley (2002).

Results

Species-energy relationship

Forest bird species richness was positively associated with surrogates of productivity measures in Catalonia [rainfall (hump-shaped relationship; R^2_{adj} : 0.47; $p < 0.0001$), NDVI (positive linear relationship, R^2_{adj} : 0.24; $p < 0.0001$), and with total number of individuals (positive decelerating function, R^2_{adj} : 0.44; $p < 0.0001$), conforming a typical species-energy relationship. NDVI and percentage of forested area were the best predictors of community size variation (NDVI R^2_{adj} : 0.36; $p < 0.0001$; forested area, R^2_{adj} : 0.41; $p < 0.0001$). Both predictors explained independent portions of the variability in community size (NDVI & forested area, R^2_{adj} : 0.59; $p < 0.0001$).

Sampling model results

Optimal migration rates obtained were: 0.0015 (EP); 0.0015 (ME); 0.0025 (NI, niche-filtering immigration model) and 0.003 (ME*NI). Our sampling models that did not account for niche width differences [equal probability model (EP) & mass-effect model (ME)] explained around 40% of the variation in species richness (Figure 2&3), but they left unexplained a substantial fraction of the variation in species richness. We therefore analysed whether this remaining variation could be understood in terms of niche width constraints on dispersal, applying the niche-filtering immigration model (NI). Indeed, the niche-filtering immigration hypothesis (NI) explained a significantly greater amount of variation when compared to the other models (EP&ME) (figure 3). This result was robust, and was also observed after setting the three models to the EP&ME optimal rate (m : 0.0015).

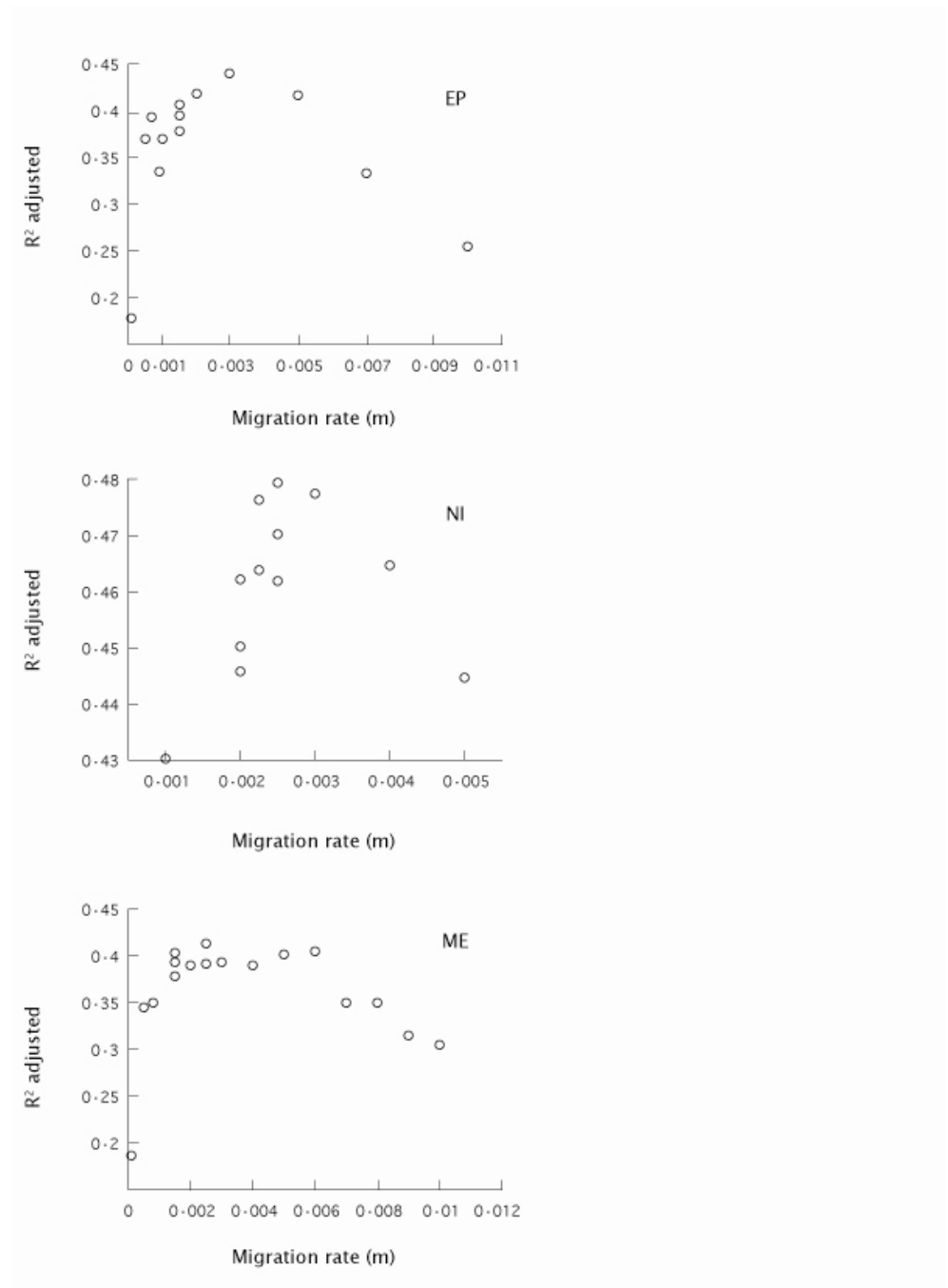


Figure 2. Plot of illustrative simulations showing the stochastic variability of the explained variance (R^2) of species richness by the sampling models (EP: equal probability hypothesis; NI: niche-filtering immigration hypothesis; and ME: mass-effect hypothesis) as a function of migration rate (m).

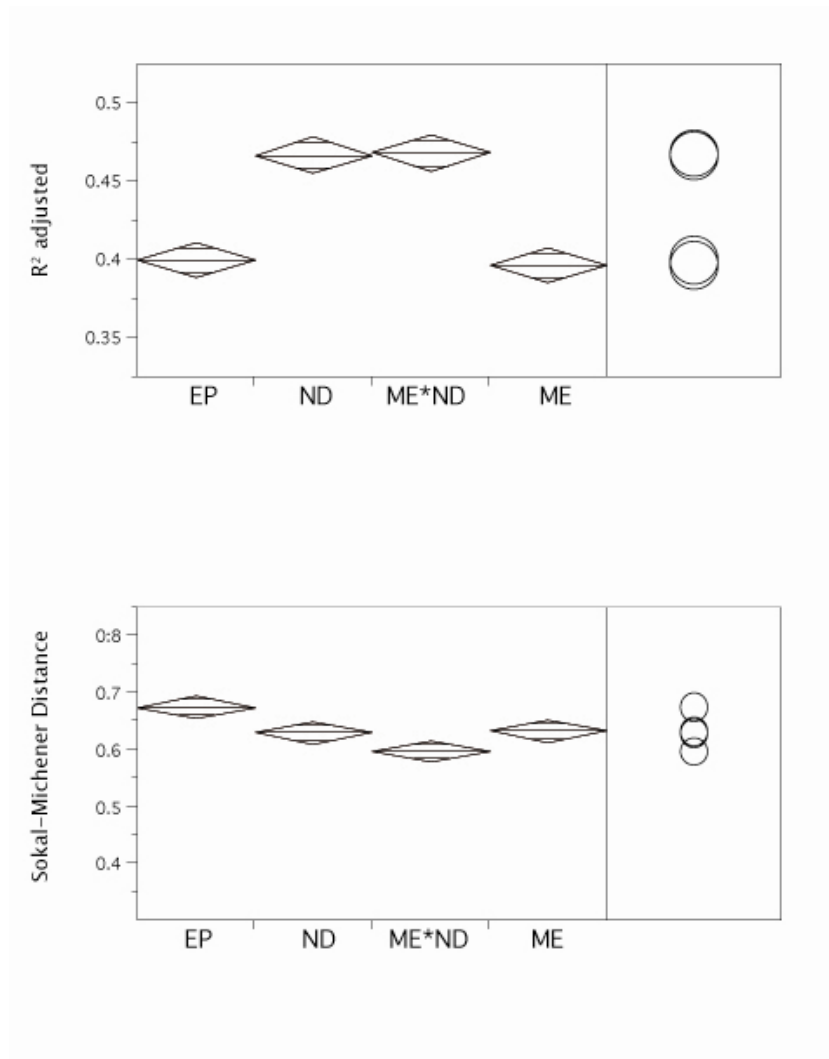


Figure 3. Percentage of variation predicted (R^2) and Sokal-Michener Distance obtained by each sampling model. Larger Sokal-Michener distances imply less accuracy in forecasting local composition. Circles on the right side represent the results of the Tukey-Kramer test allowing the quantitative assessment of differences between models.

The niche-filtering (NI) and the mass-effect model (ME) predicted to a greater extent the specific local composition when compared with equal probability model (EP). The differences in local composition predictability were not significant between the niche-immigration (NI) and the mass-effect model (ME). However, the pool measures of regional abundance and niche width were not significantly correlated (R^2 adj: 0.036; $p=0.076$), and thus both models seem to explain an independent part of the variation (see below for a specific test on their independence). The best performance of the sampling procedure was obtained accounting for the interaction of mass-effects and niche-filtering constraints (ME*NI model). However, the results of the interaction model (ME*NI) and the niche-filtering (NI) did not differ significantly (Figure 3). Thus, we found empirical support favourable to the three cases analyzed here: the existence of local sampling effects not related to metacommunity composition (EP), the existence of mass-effects from the metacommunity and the existence of niche-filtering constraints on the generation of species-richness gradients.

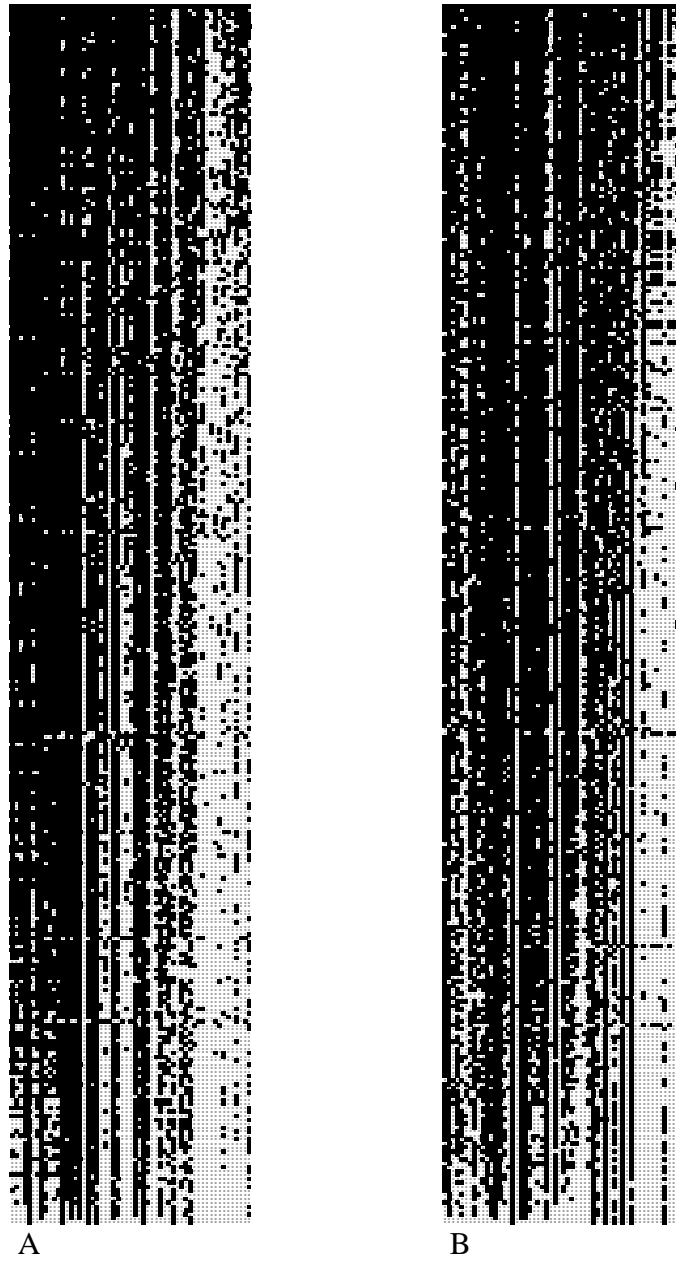
Niche-filtering immigration and mass-effects test

When grouping all the communities into a species vs localities matrix, we observed a significantly nested structure (Nestedness temperature calculator, $p < 0.0001$; Atmar and Patterson 1993). A nested structure was obtained ordering species by regional abundances or niche width measures (see supplementary figure A1), suggesting that both variables may explain the nested pattern. Nestedness observed in niche-ranked and abundance-ranked matrices was similar and highly significant. Matrix temperatures obtained were 18.29° for the niche-ranked matrix ($p < 7.5 \cdot 10^{-22}$) and 19.76° for the abundance-ranked matrix ($p < 2.3 \cdot 10^{-22}$).

The modelling of the number of localities that a species occupies (R_i) demonstrated that both variables account for an independent part of the variation (table 2). Furthermore, models showed that the effect of niche-filtering immigration was more important in low-density species whereas mass-effects were more important for high-abundance species. These results advocate for the coexistence of mass-effects and niche-filtering constraints on the generation of species richness gradients.

Dependent Variable	Independent variable	DF	AIC	Model fit R^2 Adj.
<i>All species</i>				
R_A	A	56	506.67	0.32
R_M	M	56	494.37	0.44
R_{A+H}	A + M	55	475.87	0.61
<i>Low density species</i>				
R_A	A	26	243.42	0.35
R_M	M	26	250.10	0.18
R_{M+A}	A + M	25	239.24	0.46
<i>High density species</i>				
R_A	A	27	245.84	0.26
R_M	M	27	244.83	0.28
R_{A+M}	A + M	26	241.10	0.39

Table 2. Models predicting the variation of the number of localities (R_i) occupied by a species i . A: niche width measures, M: metacommunity density measures.



Additional Figure A1. Presence-absence matrix of local community occupation (rows) by bird species (columns). The matrix, with 309 communities (rows) has been ranked by their species richness. Species (columns) were ranked by: A metacommunity densities; B: niche amplitude measures.

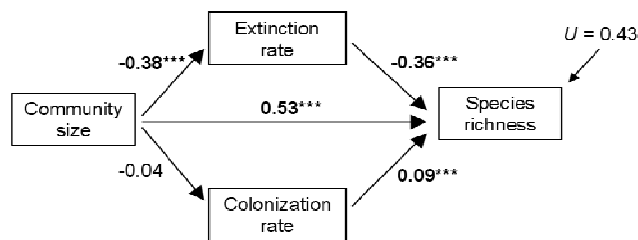


Figure 4. Results of the path analysis. Path coefficients are indicated. U describes the proportion of variance that is not explained by the model. ***: $p < 0.0001$.

The abundance-extinction hypothesis

The abundance-extinction hypothesis may also contribute to explain an additional part of the variation in species richness. The two predictions of the abundance-extinction hypothesis were strongly supported. First, extinction numbers and rates were significantly related to productivity and community size measures (NDVI and J, Table 3), when spatial autocorrelation was controlled for. Second, a path analysis supports the view that community size affects species richness not only directly, but also indirectly through its influence on extinction rates (Fig. 4).

The indirect path explained a relatively small (14%) but significant fraction of the correlation between community size and species richness under the proposed model, whereas direct effects accounted for 53% of that correlation. The existence of an indirect effect of community size on species richness via colonization rate was not supported by the path analysis. The model left 43% of the variance unexplained, but explained more variation than the sampling models, that do not take into account abundance-extinction dynamics.

Discussion

General hypotheses dealing with diversity gradients have often invoked colonization-extinction dynamics at the regional scale to explain the observed link between productivity, community size and species richness (MacArthur and Wilson 1967, Wright 1983, Hubbell 2001, Rangel and Diniz-Filho 2005, Scheiner and Willig 2005, Carnicer et al. 2007). For instance, in the abundance-extinction hypothesis, larger population sizes are thought to contribute to maintain species richness by reducing the chances that species become locally extinct (Newton 1995, Boulinier et al. 1998, Carnicer et al. 2007). Similarly, other ecologists have recently noted that an association between community size and species richness can also be generated by regional sampling processes: as the number of individuals present in a locality increases, so it does the number of different species by random (Blackburn and Gaston 2001, Kaspari et al. 2003, Evans et al. 2005a, Schwilk and Ackerly 2005). Our empirical results suggest that both explanations may be correct, showing that variation in species richness along energy gradients are possibly shaped by a mixture of sampling and abundance-extinction effects (Carnicer et al. 2007).

Clarke and Gaston (2006) recently highlighted that the mechanisms that link high local productivity, bird population sizes and species richness continue to be obscure. A primary explanation for this lack of a general empirically supported mechanism might be the existence of diverse species-specific responses that ultimately determine local presence in more productive regions (Newton 1995). In line with these assertions, our results suggest that regional sampling dynamics are effectively shaped by species-specific responses. Indeed, abundant and generalist species occupy both low- and high-productivity areas, whereas species with narrow niches tend to be restricted to high-productivity areas (see also Brändle et al. 2002, Evans et al. 2006).

Dep. Var.	Indep. Var.	Test	β	AIC	R ² Adj.
Colonization number	NDVI	GLS	0.86±0.23	1656.7	0.038
		Spatial	ns	1611.7****	
	Temperature	GLS	ns		
		Spatial	ns		
	<i>J</i>	GLS	8e ⁻⁴ ±1.5e ⁻⁵	1661.41	0.083
		Spatial	5.4e ⁻⁵ ±2.1e ⁻⁵	1621.27****	
Extinction Number	NDVI	GLS	-0.47±0.18	1500.1	0.018
		Spatial	-0.56±0.22	1494**	
	Temperature	GLS	ns		
		Spatial	ns		
	<i>J</i>	GLS	-3.8e ⁻⁵ ±1.2e ⁻⁵	1515.61	0.03
		Spatial	-5.8e ⁻⁵ ±1.5e ⁻⁵	1505.48****	
Colonization proportion	NDVI	GLS	ns		
		Spatial	ns		
	Temperature	GLS	ns		
		Spatial	ns		
	<i>J</i>	GLS	ns		
		Spatial	ns		
Extinction proportion	NDVI	GLS	-0.05±0.01	-288.72	0.07
		Spatial	-0.052±0.012	-297.82**	
	Temperature	GLS	0.0001±2e ⁻⁵	-271.64	0.06
		Spatial	0.00013±0.5 e ⁻⁵	-281.58****	
	<i>J</i>	GLS	-4.e ⁻⁵ ±6.3e ⁻⁷	-287.7	0.13
		Spatial	-4.85e ⁻⁶ ±7.93e ⁻⁷	-297.03**	

Table 3. Non-spatial (GLS) and spatial corrected (Spatial) models predicting extinction and colonization numbers as a function of NDVI, temperature and total number of individuals (*J*). Differences in sampling effort among censuses in each locality were incorporated in the models as independent variables. Asterisks indicate statistically significant differences between the AIC values of spatially and non-spatially corrected models (e.g., **** p<0.0001).

A review of the existing evidence in the literature suggests that such species-specific responses to productivity gradients might be promoted by diverse factors such as habitat selection (Grinnell 1917, Lack 1933, James 1971, Rotenberry and Wiens 1980, Hutto 1985, Böhning-Gaese et al. 2001, Martin 2001, Fuller et al. 2005, Blondel et al. 2006), resource availability (Martin 1987, Newton 1998, Gregory and Gaston 2000, Martin 2001, Blondel et al. 2006), life-story traits (Böhning-Gaese 2001, Sol et al. 2005) and dispersal and migratory behaviour (Newton 1995, Flather and Sauer 1996, Paradis et al. 1998, Böhning-Gaese et al. 1998, Böhning-Gaese 2001, Mettke-Hoffmann and Gwinner 2004, Böhning-Gaese et al. 2006).

We next briefly discuss the interpretation of our results in the context of the neutral theory (Hubbell 2001). The unified neutral theory of biodiversity is a stochastic sampling theory (Hubbell 2001, Volkov et al. 2003, Alonso and McKane 2004, Etienne 2005, Etienne and Alonso 2005, Alonso et al. 2006) and defines a regional pool, called the metacommunity, from which local communities are sampled (Hubbell 2001, Liebold et al. 2004). Alonso (2006) and others (e.g. Etienne 2005) have recently argued that sampling and dispersal limitation are two of the key elements that would explain the success of the neutral models in mimicking real patterns of species-abundance distributions. Our metacommunity sampling model supports this view. On one hand, the Equal probability model (EP) explained considerable variation (up to 40%) of the species richness of forest birds, despite not taking into account neither variation in species metacommunity densities, nor local variation in migration rates or speciation and extinction dynamics. On the other hand, the predictive power of the model improves when considering that the probability of successful colonization by a species in a locality increases with its abundance in the metacommunity. The observation of a significant nested pattern in species ranges across localities provides additional support for this mass-effect hypothesis. Rich localities were composed by those species that were present in poor localities and an additional amount of species characterized low metacommunity densities, conforming a nested geographical structure. Thus, as proposed by the neutral theory (Hubbell 2001, Volkov et al. 2003, McGill 2003), our results suggest that bird communities are dispersal-limited and sampling structured.

However, unlike the neutral theory, which models species as ecologically equivalent (Hubbell 2001 and see Volkov et al. 2003, Hubbell 2006, Adler et al. 2007), our results suggest that species identity matters when accounting for the dispersal processes that generate species richness gradients. Although the proposed sampling neutral model leads to realistic predictions, the incorporation of niche constraints on immigration clearly improves the variance explained by the model. In addition, the nested geographical structure of species richness across regions was in part related to an overrepresentation of habitat specialists in species-rich localities. This finding emphasizes the need to incorporate information on species-specific traits into neutral sampling models if we are to improve our ability to model local species composition.

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Appendix

A. Bird data

Presence/absence data was obtained at two different resolutions. First, surveys at each of the 10x10 km squares were conducted (Estrada et al. 2004, and see also Hagemeyer and Blair 1997, Martí and del Moral 2002, Bibby et al. 2000). Second, within each of the 10x10km squares, a sub-sample of ten 1x1 km squares were surveyed a total of two hours in the 1999-2002 survey (Estrada et al. 2004). This approach is similar to that used in the British and Swiss ornithological atlases (Gibbons et al. 1993, Schmid et al. 1998, Estrada et al. 2004) and allowed the time controlled and detailed survey of nearly 10% of the total land surface considered in this study (30.900 km², nearly all Catalonia surface) at a finer resolution. In order to reproduce as accurately as possible the environmental heterogeneity of each 10x10 km square, 1x1 km squares were selected by the observers to proportionally represent habitat variability within 10x10 km squares. Population abundances in a given 10x10 km square and species richness values were obtained from 1999-2002 survey data, using three different methodologies: 1) For the bulk of the forest bird species (31 out of 67 species) absolute population abundance data (pairs/km²) was obtained from transect counts conducted in a sub-sample of the 1x1 km grid cells (Järvinen and Väisänen 1975). Each observer recorded all individuals of all bird species detected, sighted or heard on 1km long walked itineraries (further details in Herrando et al. 2007; and Estrada et al. 2004). These absolute estimates of bird population abundance at 1x1 km grid cell were then related to relative measures of density obtained at 1x1 km by means of habitat modelling (independent from transect estimates) (Guisan and Zimmermann 2000, Brotons et al. 2007, Herrando et al. 2007). This was done by applying an exponential Poisson model between absolute population abundance (pairs/km², dependent variable) and relative estimates of population abundance (probability of presence, independent variable). Absolute population abundance measures were finally obtained at 10x10 km grid cell by averaging information of all 1x1 km cells in each 10x10 km cell. This approach is similar to those developed in other surveys (Gibbons et al. 1993, Harrisson et al. 1997, Hustings and Veerger, 2002); 2) For 8 species subjected to specific monitoring censuses due to their scarcity, their population abundances were estimated by direct counts using different censuses techniques (see Brotons et al. 2007); 3) For the rest of the species (28 out of 67) population abundance estimates were derived from rough and approximate counts made by individual observers at 10x10 km grid cells. We applied the geometric mean methodology used in Hagemeyer and Blair (1997) to obtain total population abundance estimates. Although these estimates of population abundance are likely to be less accurate than those obtained by the other previous methods, the method yielded estimations that were very close to them (for n=31 species for which abundances with methods 1 and 3 were available; $r^2 = 0.73$; $p > 0.0001$; Herrando et al. 2007). Thus, differences in the method used to estimate population abundance of the species are unlikely to affect the conclusions.

B. Niche width calculation

We obtained a measure of niche width (habitat amplitude) using the following procedure. First, habitat preferences by a species *i* for each habitat *j* was obtained calculating an index of habitat selection (Estrada et al. 2004):

$$p_{ij} = \left[\frac{p_{range}}{p_{cat}} \right] - 1$$

where p_{range} is the proportion of surface of habitat j in the sampled 1x1km squares in which the species i is present and p_{cat} is the proportion of surface occupied by habitat j in all sampled 1x1 km squares in Catalonia. 22 habitat categories were used, following the forest and land cover maps of Catalonia (<http://www.creaf.uab.es/mcsc/index.htm>). We defined a matrix P with s rows (species) and h columns (habitats) containing all p_{ij} values. A second matrix F was calculated setting all negative preferences equal to zero and normalizing p_{ij} values. Normalization was applied by dividing the maximum p_{ij} value that was obtained for each species. F matrix values varied between 0 and 1 (i.e. minimum or maximum preference). A third matrix R ($h \times h$) was calculated, in which r_{jl} corresponded to the Pearson correlation coefficient between habitats j and l (columns in the matrix P). Note that the Pearson correlation coefficient varies among -1 and $+1$. Matrix R then was used to calculate a matrix D of Pearson distances, where d_{jl} was equal to $1 - r_{jl}$. This matrix of Pearson distances from species habitat selection preferences was calculated to assess to what extent pairs of habitats are regarded as similar resources. Therefore, habitats related with high r_{jl} values were perceived by species as similar ecological habitats and selected in a similar way. Finally, niche width for a species i (A_i) was calculated using equation 1 and matrices F and D.

C. Nestedness

Nestedness is measured by system temperature (T), a measure of the number of deviations of unexpected presences and absences in the observed matrix above and below a calculated boundary threshold of a perfectly nested matrix. For all unexpected presences or absences, an averaged normalized measure of global distance to the boundary is calculated.

Temperatures can take values between 0° and 100° , with $T=0^\circ$ representing a perfectly nested matrix.

Part 2

Interaction patterns. Adaptation, coexistence and diversification



CHAPTER 4: The temporal structure of interaction networks: assessing the relative role of ecological and evolutionary processes

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Abstract

Ecological networks patterns are due to a diverse array of ecological processes that operate at different temporal scales. Here we analyzed if the coupled effect of local abundance variation, seasonally phenotypic plastic responses and species evolutionary adaptations might act in concert to shape network patterns. We studied the temporal variation in three interaction bird properties (number of interactions per species, interaction strength and asymmetry) in a temporal sequence of 28 networks spanning two years in a Mediterranean bird community. Three main hypotheses dealing with the temporal variation of networks properties were tested, that respectively examine the effect of abundance, switching behaviour between alternative resources and morphological traits in determining consumer interaction patterns. Our results demonstrate that temporal variation in consumer interaction patterns is explained by short-term variation in resource and bird abundances and seasonal dietary switches between alternative resources (fruits and insects). Moreover, differences on beak morphology are clearly associated with differences in switching behaviour between resources, suggesting an important role of foraging adaptations in determining network patterns. Therefore, we argue that adaptations on beak shape might determine generalist and specialist feeding behaviours and thus the whole network architecture. Finally, we provide a preliminary framework to interpret phylogenetic signal in plant-animal networks. Indeed, we show that the strength of the phylogenetic signal in networks depend on the relative importance of abundance, behavioural and morphological variables. We show that these variables strongly differ in their phylogenetic conservatism. Consequently, we suggest that moderate and significant phylogenetic signals should be commonly observed in networks.

Introduction

Ecological networks are characterized by a low number of strong interactions and a much greater number of weak interactions (Jordano 1987, Paine 1992, McCann et al. 1998). Interactions tend to be asymmetric, in both the number of links per species and the strength of the interaction (Jordano 1987, Jordano et al. 2003, Vázquez and Aizen 2004, Bascompte et al. 2006). More generally, networks are characterized by a few species that concentrate most of the interactions and usually exert a strong influence in most of the species (Jordano 1987b, Bascompte et al. 2003). However, and in spite of the importance of the issue, which are the underlying mechanisms that generate such asymmetric relationships in the number and strength of interactions between species in ecological networks is yet an unresolved debate (Thompson 2005, Lewinsohn et al. 2006, Jordano et al. 2006, Stang et al. 2006, Bascompte et al. 2007, Vázquez et al. 2007).

Network patterns are the result of a diverse array of ecological and evolutionary processes that operate along a wide range of temporal scales (Johnson and Stinchcombe 2007). On one hand, at short ecological time-scales, communities vary in species composition due to processes of birth, death, migration, and dispersal, among others. All these processes cause abundance and composition variation and might alter the type, number and strength of interactions observed (Jordano 1984, Herrera 1984, Jordano 1985, Jordano 1994, Vázquez et al. 2007). Similarly, at short ecological time-scales species might respond to changes in the environmental conditions by phenotypic plastic responses (Agrawal 2001, Price et al. 2003). For instance, consumer species may seasonally switch the resources used, thus modifying the interactions exerted and causing variation in network properties at short-time scales (Jordano 1984, Rooney et al. 2006). On the other hand, at much longer time scales, species evolve or coevolve in a set of morphological and behavioural traits (adaptations) that might determine the species with whom they interact (Thompson 2005). Such evolutionary processes may imply the generation of geographical mosaics of selection, coevolutionary hot-spots, and trait remixing processes (Thompson 2005, Gomulkiewicz et al. 2007). All these processes may require a considerable number of generations and thus are thought to operate at longer temporal scales (Johnson and Stinchcombe 2007).

Here we studied the temporal variation in three network properties of consumer bird species (number of interactions per species, interaction strength and asymmetry) in a temporal sequence of 28 networks spanning two years. The mutualistic plant-animal network analyzed was composed by 24 birds and 15 plants that produce fleshy fruits and is located in a Mediterranean shrub community in the south of Spain (Jordano 1984). Three main hypotheses dealing with the temporal variation of consumer interaction properties were tested (table 1). The three hypotheses examine the effect of bird abundance, behaviour and morphology in determining network patterns.

The abundance hypothesis (Jordano 1987b, Vázquez and Aizen 2004, Vázquez et al. 2007) states that short-term variation in local population abundance is the principal factor that determines the variation in the number and strength of interactions in ecological networks. It predicts that the greater the abundance of a species, the greater will be both the number of interactions established and the interaction strength produced in the rest of the species (Vázquez et al. 2005, Stang et al. 2006, Vázquez et al. 2007).

The switching behaviour hypothesis states that consumer species will show increased number of interactions and higher interaction strengths in the resource-channel that use preferentially during an elapse of time (Murdoch 1969, Berthold 1976, Abrams 2006, Rooney et al. 2006).

	Hypotheses	Indep. Var.	Theory (T) and predictions (P)	Expected phylogenetic conservatism (K)
H₁	Consumer Abundance	N_m	T: Differences in local consumer and resource population abundance produce asymmetrical relationships in plant-animal interactions.	Non significant or low
	Resource Abundance	R_1 R_2		
	Consumer abundance & Resource abundance	$N_m * R_1$ $N_m * R_2$	P: Variation in bird population abundance, resource abundance, or their interaction will significantly predict bird interaction properties (k_m , IS_m and A_m).	
H₂	Switching behaviour	$\%R_1$ $\%R_2$	<p>T: Species seasonally switch the percentage of diet destined to different alternative resource-channels (R_1: fruits; R_2: invertebrates). Differences in the quantitative use of the channels shape asymmetrical relationships in plant-animal interactions.</p> <p>P: The seasonal variation in the percentage of fruits in the diet will significantly predict bird interaction properties (k_m, IS_m and A_m).</p>	Mid or high
H₃	Species trait	Sp	<p>T: Bird species differ in life-story and morphological traits that are products of their unique evolutionary histories. Such differences between species determine specific interaction patterns and produce asymmetrical relationships.</p> <p>P: Interspecific differences in bird morphological traits will be associated with differences between species in bird interaction properties (k_m, IS_m and A_m) by direct or indirect causal paths (figure 1).</p> <p>P: Bird species identity (Sp) will consistently predict differences in bird interaction properties (k_m, IS_m and A_m).</p>	High

Table 1. Hypotheses and predictions tested. N_m bird abundance, R_1 fruit abundance, R_2 invertebrate abundance, $\%R_1$ percentage of fruits in the diet, $\%R_2$ percentage of invertebrates in the diet, Sp species identity.

Resource channels (Rooney et al. 2006) are composed by two or more sets of species that are usually unrelated at high taxonomic levels (i.e. fungi versus bacteria, invertebrates versus fleshy fruits), that show specific turnover rates (production:biomass ratios), and share common top-consumer species (Rooney et al 2006). In our study system, top-consumers are bird species that alternate between two resource-channels: fruits (R_1) and invertebrates (R_2) (Jordano 1984, 1985, 1987a).

The species trait hypothesis states that evolutionary processes had produced unique morphological, behavioural and life-story traits that determine the type, number and strength of the interactions exerted by species (Thompson 2005, Stang et al. 2006, Björklund 2006). The species trait hypothesis predicts the existence of a limited set of morphological, behavioural or life-story traits that explain interspecific differences observed between species in the number and strength of interactions (Stang et al. 2006). Similarly, according to the species trait hypothesis, the identity of a species (used as a proxy of their unique evolutionary history) is expected to be a fundamental variable explaining the temporal variation in the type, number and strength in the interactions exerted. If adaptation strongly determines network patterns, we predict that species would maintain consistently a different number and strength of interaction along the whole temporal sequence examined here (two years), irrespective of temporal changes in abundance or species behaviour.

Overall, our main aim here is to contrast the abundance, the switching behaviour and the species trait hypotheses, evaluate if these three mechanisms are active and assess their relative importance.

Methods

Study site

Field work was conducted in "Hato Ratón", an area located at the northeast border of the Doñana National Park, Huelva province, SW Spain (Jordano 1984). The study period extended from early 1981 throughout April 1983, encompassing two consecutive fruiting seasons. The study site is a medium to high (2,5-5 m) dense sclerophyllous shrubland growing on sandy soils at 13 m of elevation. Vegetation was dominated by tall shrubs and treelets of *Pistacia lentiscus* (Anacardiaceae), *Olea europaea* var. *sylvestris* (Oleaceae), *Phyllirea angustifolia* (Oleaceae) and *Rhamnus lycioides* (Rhamnaceae). The shrubland is characteristic in having a great cover and diversity of plants producing fleshy fruits (72,2% cover, n=21 species), but is dominated by *P. lentiscus* (33,4 %cover).

Data

Quantitative data about the interactions between birds and fleshy-fruited plants were derived from faecal samples of birds captured in mist-nets (Jordano 1984). A total of 6-10 mist-nets were operated weekly, 2 days per week. The nets were opened from dawn to dusk and checked at hourly intervals. The relative importance of animal prey (mostly arthropods) and vegetable remains (mostly fruits) in bird faeces was assessed. The percent volume occupied by each fraction (to the nearest 10%) was estimated visually. These measures were used as an estimate of the relative resource-channel use (fruits, % R_1 , and invertebrates, % R_2). Faecal samples were mostly composed by fruits and invertebrates. Flowers or other resources were very scarce and occupy negligible fractions of the samples. Thus, for all the samples, % $R_1 \cong 100 - \%R_2$. Both seeds and pulp remains in the faeces

were identified, the latter by microscopic inspection of the pericarp tissue. The analyses were carried out from June to November, covering a total of 28 periods of 15 days in 1981-1983. This led to a temporal sequence of 28 networks, with 13 and 15 networks per year respectively. Bird abundance data was obtained performing weekly counts along a permanent 1-km-length transect following the procedure of Emlen (1981). Variation in fruit production was estimated by transect counts of the total number of ripe fruits per unit area that were checked every 15 days in 15 replicate plots 30 m x 1.5 m (Jordano 1984). Relative variation in invertebrate abundance was calculated using adhesive traps that were set hanging from vegetation and on the ground (Jordano 1984); these traps were monitored weekly. Bird morphological measures used (wing, tail, body size, gape width, tarsus, culmen) were obtained from birds captured in the mist-nets using standard procedures (Jordano 1984, Jordano 1987a).

Network properties measured

The three hypotheses were examined on three network properties in consumer bird species (the number of interactions per species or degree, interaction strength and asymmetry). Therefore, we restricted our analysis to consumer bird species in the mutualistic plant-animal network (fruits and birds). This restriction allowed us to focus on hypotheses based on bird natural history. Arthropod-bird interactions were not included in the analyses because taxonomic resolution was much lower (order level) and produced coarse and very imprecise networks. Pajek software was used to calculate species degree and interaction strength for each bird (de Nooy et al. 2005; <http://vlado.fmf.uni-lj.si/pub/networks/pajek/>). Bird species degree (k_m) was defined as the number of interactions of a focal bird species m with other plant species in each temporal sequence. Interaction strength (IS_{mn} , hereafter) was estimated as the total number of fruits described for a plant-animal interaction during two weeks. This is justified considering that interaction frequency has been claimed to perform as a good surrogate of interaction strength (Vázquez et al. 2005, Vázquez et al. 2007). Interaction strength for a bird species m (IS_m) was calculated as the sum of all the interactions strengths with n interacting plants ($IS_m = \sum IS_{mn}$) (Bascompte et al. 2006). Following Vázquez and collaborators (2007), we defined asymmetry (A_m) as a species-level property that evaluates the relative difference between the effect of a focal species on their interacting species and the effect of these interacting species on the focal species. A detailed mathematical description is provided in Vázquez et al. (2007). Asymmetry values range between -1 and 1 . Positive values indicate that the focal species effects on their interacting species is quantitatively more important than the reciprocal effect exerted by the interaction partners on the focal species (Vázquez et al. 2007). Negative values indicate the reversed situation, in which the influence of interacting species on the focal species is more important than the effect of focal species on them. 0 values indicate that the interactive relationships are symmetrical (Vázquez et al. 2007). Asymmetry values along the temporal sequence for each species were calculated using a MatLab code that is available upon request to the authors. Complementarily, we measured other network traits: maximum and minimum interaction strength for each species and period time, core, and centrality. A description of this network measures is provided in de Nooy et al. (2005).

Temporal trends in network structure, switching and abundances

We studied the temporal variation of three variables: plant-bird interactions (1), bird switching behaviour between invertebrates and fruits (2), and bird abundance (3). First, we analyzed faecal samples collected along two years and obtained a temporal sequence of the variation of plant-bird interactions. This sequence was graphed using Pajek software (de Nooy et al. 2005). Secondly, faecal samples were used to assess the proportion of fruits and invertebrates used by each species along the temporal sequence (switching behaviour). We regressed the percentage of resource in the diet ($\%R_1$, $\%R_2$) against the ratio of both resources in the environment (R_1/R_2). These analyses allowed the evaluation of switching behavioural responses in relation to the changes in the relative proportion of resources in the environment for each species. Thirdly, census data were used to estimate the temporal variation in bird abundances.

Hypothesis testing

To assess the relative support for each of the hypotheses examined, we modelled bird interaction properties as a function of the variables associated with each hypothesis (table 1). The abundance hypothesis predicts that bird interaction properties (k_m , IS_m , A_m) would be positively related with the temporal variation of bird abundance (N_m) and/or resource abundance (R_1 , R_2). If both bird and resource abundance increase the probability of interaction, an increased number and stronger interactions should be observed when both birds and resources are very abundant. This was tested introducing the interactions $N_m * R_1$ and $N_m * R_2$ in the models. The switching behaviour hypothesis predicted a positive and significant association between the temporal variation in the percentage of fruits used in the diet ($\%R_1$) and network properties measured (k_m , IS_m , A_m). Finally, the species trait hypothesis predicts that species identity (Sp) will be associated with significantly different values of network properties (k_m , IS_m , A_m) along all the temporal sequence. We used generalized linear mixed models with node identity (Sp), percentage of fruits in the diet ($\%R_1$), bird abundance (N_m), fruit abundance (R_1), invertivore abundance (R_2) and the interactions ($N_m * R_1$; $N_m * R_2$) as independent variables (table 1) (Wolfinger and O'Connell 1993). Time period (15 days periods) and year were introduced in the models as random variables (table 1). We used the Glimmix procedure of SAS 9.1.3 and JMP 5 to perform the analyses.

Testing for the independence of the hypotheses

The hypotheses examined (abundance, switching behaviour and species trait) are likely to be not independent. Indeed, life-story and morphological traits are known to affect both bird abundance and resource choice behaviour (Böhning-Gaese and Oberrath 1999, 2001, Stang 2006). To assess if morphological traits were effectively associated with bird abundance and interspecific differences in switching behaviour (fig. 1), we applied two different approaches. First, we modelled the percentage of fruits in the diet ($\%R_{1m}$) and abundance (N_m) as a function of 9 morphological traits (body mass, wing, tail, tarsus, culmen1, culmen2, wide, height, gape width). Specifically, traits were measured in 2028 birds captured in the mist-nets during along the whole study period. These models allowed us to evaluate if abundance variation and switching behaviour were associated with interspecific differences in these morphological traits.

Secondly, we conducted a path analysis to assess the existence of significant direct and indirect effects of morphological traits on the percentage of fruits in the diet ($\%R_{1m}$), bird abundance (N_m) and bird interaction

properties (k_m , IS_m , A_m) (Fig. 1). Phylogenetic contrasts were applied to estimate the influence of phylogenetic conservatism in the path coefficients (Midford et al 2002).

Testing for phylogenetic conservatism in the variables used

The coupled effect of population abundance variation, switching adaptive behaviour and morphological traits might determine to some extent bird interaction patterns (Jordano 1987, Jordano et al. 2003, Stang et al. 2006, Vázquez et al. 2007). Interestingly enough, abundance, behavioural and morphological variables are expected to differ in the degree of phylogenetic signal showed. For instance, local bird abundances have been found to exhibit low or no significant phylogenetic signal (Cofre et al. 2007), and behavioural traits usually exhibit less phylogenetic signal than morphological traits (Wcislo 1989, Blomberg et al. 2003). Thus network properties might rely on a set of variables or specific traits that evolve at different rates and strongly differ in their phylogenetic conservatism (Böhning-Gaese and Oberrath 1999, Blomberg et al. 2003, Cattin et al. 2004, Cofre et al. 2007). Overall, we point that the phylogenetic signal observed in network properties should be quite variable depending on the relative importance of abundance, behavioural and morphological traits implied (Fig. 1, table 1). Therefore, phylogenetic signal in networks should be expected to reach intermediate K values between those observed for abundance (low or non significant) and morphological traits (high).

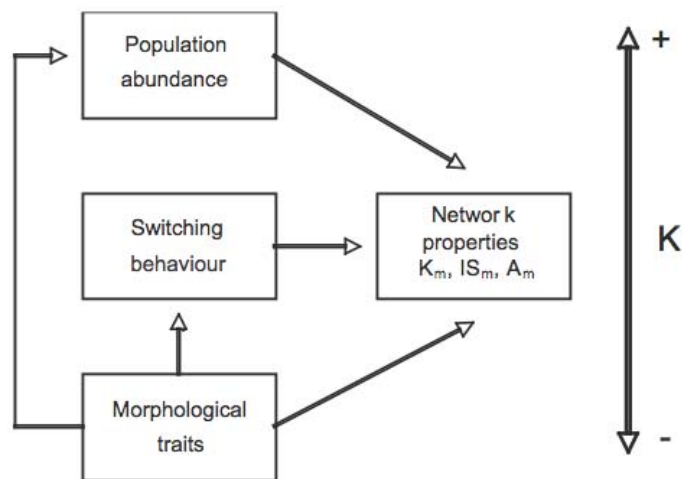


Figure 1 An illustrative scheme of the hypothesised causal relationships among abundance, behavioural and morphological traits, network properties and phylogenetic conservatism (measured by the statistic K).

To assess the degree of phylogenetic conservatism in bird consumer interaction properties (k_m , IS_m , A_m) we applied a randomization test for phylogenetic signal to de variables under study (degree, interaction strength and asymmetry) (Blomberg et al. 2003). The means of the values in k_m , IS_m , A_m for all the temporal sequence were used for each species. We used the MatLab program PHYSIG.m to calculate the statistic K (Blomberg et al. 2003). A K less than one implies that species resemble each other less than expected under Brownian motion evolution along the candidate tree. A K greater than one implies that close relatives are more similar than expected under Brownian motion evolution, and thus indicates strong phylogenetic conservatism (Blomberg et al. 2003). K values obtained for the dependent variables studied (k_m , IS_m , A_m) were compared to those observed

for bird abundance (N_m), switching behaviour ($\%R_1$) and nine morphological traits (body size, wing, tail, height, tarsus, culmen 1, culmen 2, gape width and intestine length). These comparisons allowed us to assess the relative phylogenetic conservatism of network traits relative to abundance, behaviour and morphological traits.

Results

Temporal trends in abundance, resource switching and network interactions

The two resource-channels (fruits and invertebrates) varied asynchronously with contrasting peaks. Fruits presented a maximum of production in autumn, whereas invertebrate production maximum was in spring, with a secondary peak in autumn (Fig. 2a). Bird species abundance varied temporally, by the effect of autumn and spring passes, migration of wintering and breeding species, and variation in local resident abundance. Overall, bird abundances were greater in autumn and winter, matching the temporal pattern of fruit abundance (Fig. 2b). The bulk of the species presented seasonal shifts in the proportion of fruits ($\%R_1$) and invertebrates ($\%R_2$) in the diet. Switching behaviour was observed in 14 out of 24 species. We could differentiate three basic types of switching behaviour: *fast switchers* (Fig. 2c), *slow switchers* (Fig. 2d) and *invertebrate specialists* (Fig. 2e). Fast switchers were species that increased very rapidly the proportion of fruits in the diet with relatively small increases in the ratio of fruits/invertebrates in the environment. Slow switchers demanded a much greater asymmetry in the ratio of fruits/invertebrates to start switching to the fruit resource channel (Fig. 3). When finally switched, they switched to a less extent, thus conserving a relatively high proportion of invertebrates in the diet. Finally, invertebrate specialists were those species that were insensible to the changes in the environmental ratio of fruits/invertebrates and maintained consistently an invertivorous diet coupled with the occasional ingestion of some fruits. 10 out of 20 species species behaved as fast switchers (*Erithacus rubecula*, *Phoenicurus phoenicurus*, *Sylvia atricapilla*, *S. borin*, *S. cantillans*, *S. communis*, *S. hortensis*, *S. melanocephala*, *Turdus merula* and *T. philomelos*), 4 species behaved as slow switchers (*Luscinia megarhynchos*, *S. undata*, *Muscicapa striata*, and *Ficedula hypoleuca*), and 5 as invertivore specialists (*Hippolais polyglotta*, *Phylloscopus collybita*, *P. bonelli*, *P. trochilus*, *Regulus ignicapillus*). Finally, for 6 species interaction data was too scarce to evaluate any temporal tendency in resource-channel use (*Parus caeruleus*, *P. major*, *P. cristatus*, *Phoenicurus ochruros*, *Saxicola torquata*, and *Turdus iliacus*).

The temporal structure of plant-bird interactions is showed in figures 4 and 5. The total number of interactions was higher during the fruit peak periods (September-November), matching the trends of fruit resource variation and bird abundance (Fig. 2a,b).

Figure 2 Temporal trends observed in the studied variables. **a.** Variation in fruit and insect abundance (R_1 , R_2) **b.** Bird density. **c.** Proportion of fruits in the diet in fast switchers. **d.** Proportion of fruits in the diet in slow switchers. **e.** Proportion of fruits in the diet in invertivore specialists. Switching curves were fitted using the cubic spline method using JMP package (version 5). This method uses a set of third-degree polynomials spliced together such that the resulting curve is continuous and smooth at the splices (knot points). The estimation is done by minimizing an objective function composed by a combination of the sum of squares error and a penalty for curvature integrated over the curve extent. Change lambda values (λ) were fitted to $\lambda=100$ for all curves showed.

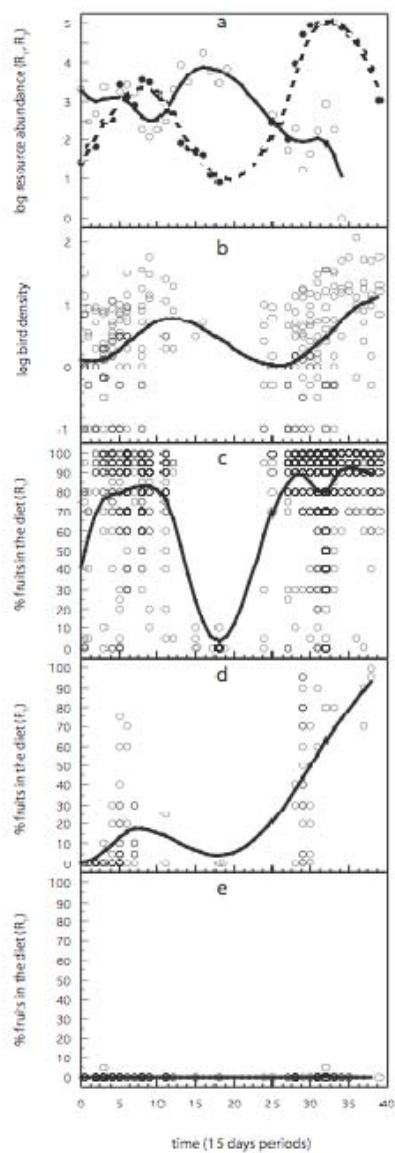


Figure 3 Switching behaviour trends observed. The figure distinguishes between fast switchers (white dots, solid lines), slow switchers (black dots, dashed lines) and invertebrate specialists (dark squares, pointed lines). R_1 : fruits; R_2 : invertebrates.

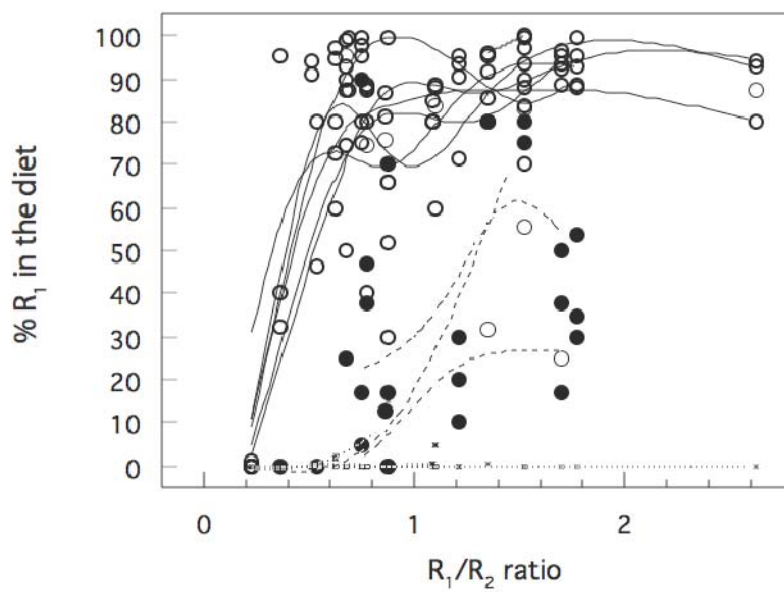


Figure 4 Temporal changes in network structure in 1981-82. For illustrative purposes, bird nodes were scaled to daily energetic requirement in a logarithmic scale (kJ/day) using scaling regression techniques (Nagy 1987). Plant nodes were scaled to the logarithm of fruit energy production (kJ/15 days) using specific estimates of fruit energy content (kJ/species of fruit) and fruit crop estimates (Jordano 1984).

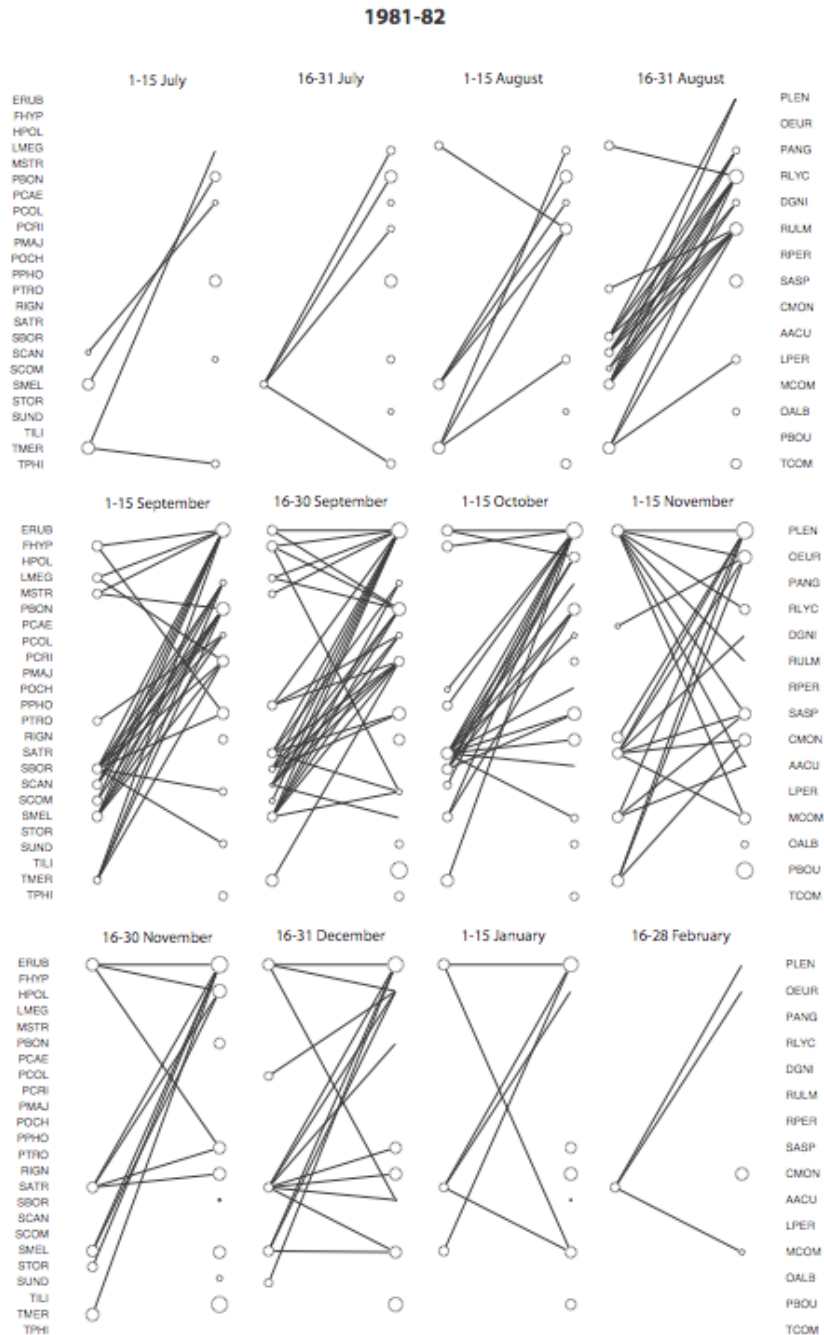
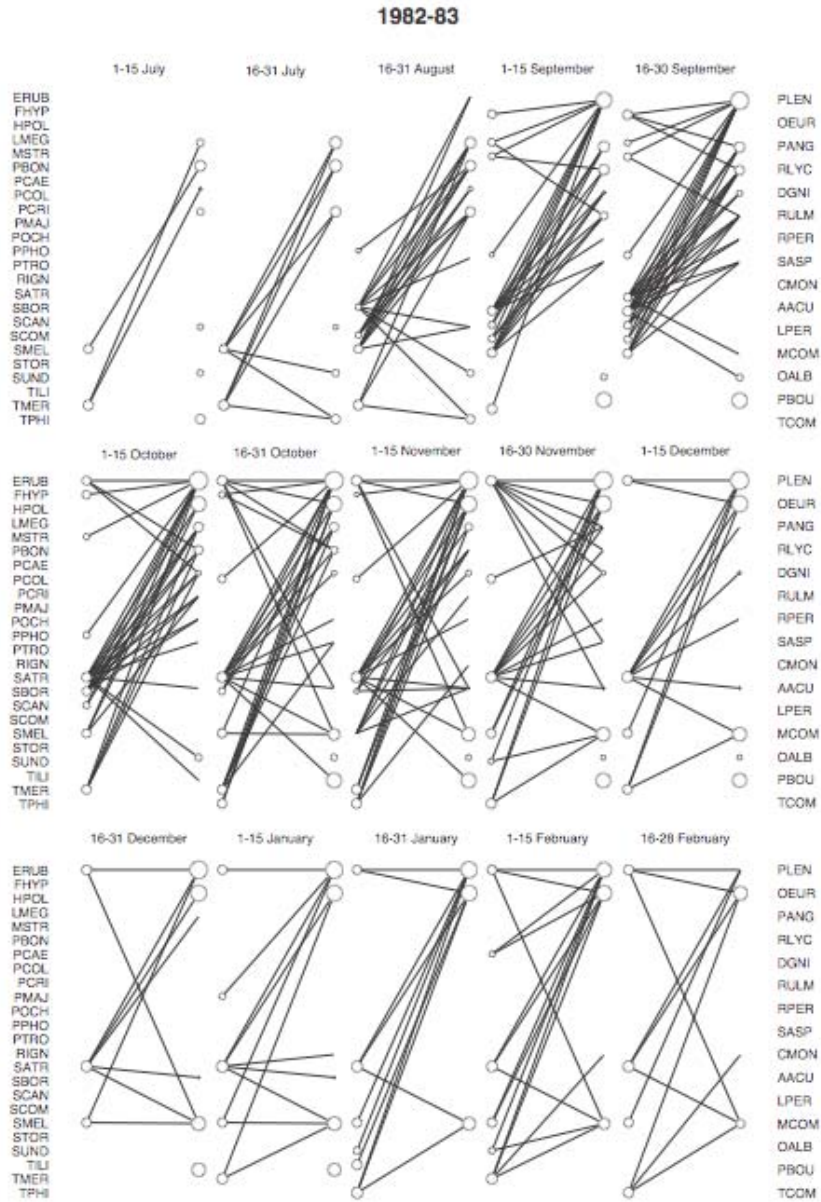


Figure 5 Temporal changes in network structure in 1982-83.



Variables	k_m			IS_m			A_m		
	$R^2_{adj}=0.65$			$R^2_{adj}=0.64$			$R^2_{adj}=0.71$		
	SS	F	P	SS	F	P	SS	F	P
Sp	147.13	4.14	<0.0001	93070.8	4.47	<0.0001	5.996	3.954	<0.0001
$\%R_1$	12.55	6.36	0.013	2625.1	2.27	0.1356	0.824	9.787	0.002
N_m	12.92	6.55	0.012	51376.2	44.47	<0.0001	0.555	6.597	0.012
R_1	2.60	1.31	0.254	4953.3	4.28	0.041	0.195	2.316	0.13
R_2	0.55	0.28	0.597	524.21	0.45	0.5024	0.011	0.129	0.720
$N_m * R_1$	17.13	8.69	0.0042	16515.3	14.2	0.0003	0.054	0.646	0.423
$N_m * R_2$	13.45	6.82	0.010	31073.6	26.9	<0.0001	0.043	0.519	0.473

Table 2 Effect tests for the independent variables. Dependent variables are the number of interactions or degree (k_m), interaction strength (IS_m) and asymmetry (A_m). The total percentage of variance explained (R^2_{adj} , $p < 0.0001$) is also provided for the three models (k_m , IS_m , A_m).

Hypothesis testing

The three hypotheses examined were empirically supported. However, a different pattern of response was observed for species degree and interaction strength patterns. Indeed, abundance variables were the best predictors for interaction strength patterns, but explained a lesser amount of variation in qualitative network patterns (degree) (Table 2). The interaction among resource and bird abundance was strongly significant for degree and interaction strength, indicating that both consumer and resource abundances contribute to increase the probability of interaction. The models explained between 64-71% of the variation in network properties (Table 2). When species identity (Sp) was included in the models, both the abundance and the switching behaviour hypothesis remained significant, but the variance explained by the switching behaviour hypothesis was strongly reduced.

Testing for hypotheses independence

Models explaining the variation of bird abundances (N_m) and the percentage of fruits in the diet ($\%R_1$) using morphological traits performed much better in the case of the percentage of frugivory in the diet than with abundance (Table 3). Indeed, morphological traits explained only 6% of the variation in bird abundances ($p < 0.05$) but explained 43% of the variation between species in the percentage of fruits in the diet ($p < 0.0001$). Beak morphology traits (gape width and culmen length) were strongly associated with the percentage of fruits in the diet (Table 3).

In line with these results, path analyses indicated that beak morphology traits affected indirectly network properties through their effect on switching behaviour ($\%R_1$). Interestingly enough, when phylogenetic contrasts were applied, the effect of beak morphological traits on switching behaviour was totally reduced, indicating strong phylogenetic conservatism in this causal path (fig. 6). Thus, our results suggest that switching behaviour is associated with foraging morphological traits, being gape width the character more strongly associated with this behaviour.

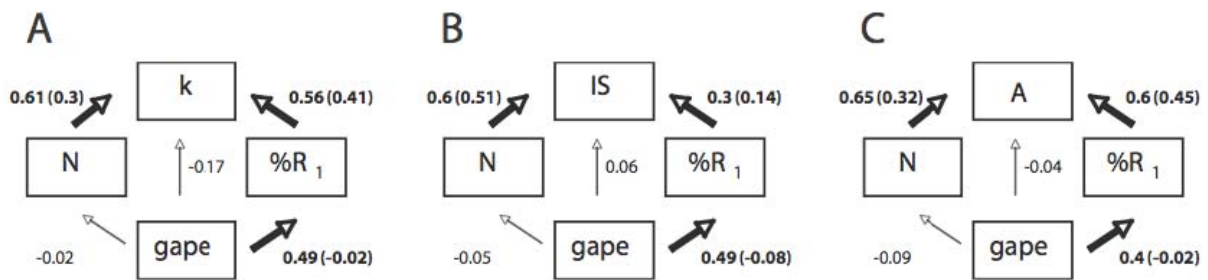


Figure 6. Path diagram of expected causal effects of gape width (gape), bird population density (N_m) and switching behaviour ($\%R_1$) on three network properties (**A**: degree (k_m); **B**: interaction strength (IS_m); **C**: asymmetry (A_m)). Bold arrows and numbers indicate path coefficients that are significant at $p < 0.05$. Values inside parenthesis are path coefficients corrected by phylogenetic contrasts.

Dependent Var.	%R ₁ Percentage of fruits in the diet			
R ² adj	0.43****			
Effect	SS	F	P	Sign
Body mass	6314.42	7.12	0.0087	+
Wing	8646.83	9.75	0.0023	-
Tail	4846.22	5.46	0.0210	+
Tarsus	12.66	0.014	0.9050	+
Culmen1	9782.02	11.028	0.0012	-
Culmen2	127.77	0.144	0.7049	+
Wide	11.70	0.013	0.9088	+
Height	139.48	0.157	0.6924	-
Gape width	14401.91	16.23	0.0001	+

Table 3. Model predicting the variation in the proportion of fruits in the diet. 9 bird morphological variables were used as independent variables. Test effects for each morphological variable are provided. **** $p < 0.0001$

Testing for phylogenetic conservatism

The three bird interaction properties examined (k_m , IS_m , A_m) showed a significant phylogenetic signal (Table 4). Contrarily, other network measures (centrality and minimum interaction strength) did not show a significant phylogenetic effect. As was expected, morphological traits were characterized with the stronger phylogenetic signals and abundance was not significantly associated with phylogeny. Interestingly enough, we found intermediate K values for all network properties examined. Indeed, network K values were weaker than K values for morphological traits, similar to K values observed for behavioural traits and greater than K values observed for species abundance (fig. 7).

Figure 7 Comparison of the values of the statistic K in network properties (degree, interaction strength, asymmetry, maximum interaction strength, minimum interaction strength, centrality and core, white dots) and K values for abundance, behavioural and morphological traits (N_m , % R_1 , gape width, body size, intestine length, height, wing, tail, tarsus and culmen, black dots). A Tukey Kramer test is provided comparing the mean phylogenetic signal in network properties versus morphological traits ($p < 0.0001$).

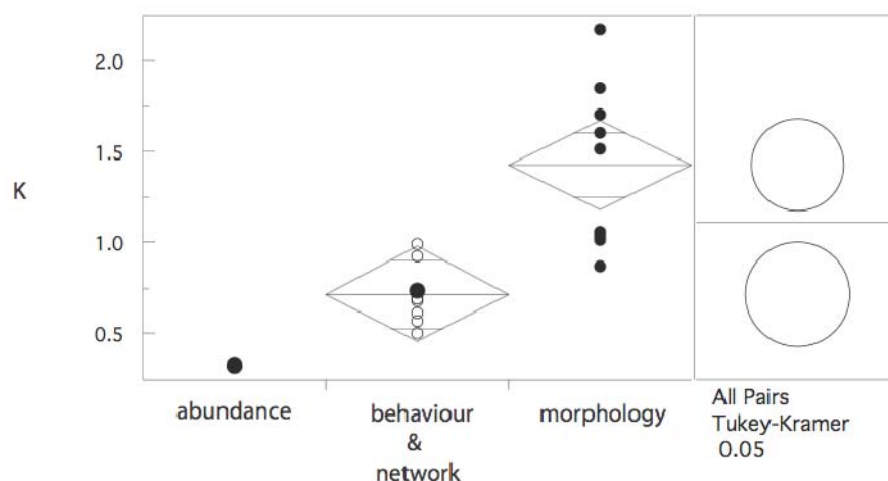


Table 4. Values and significance of the statistic K for the variables under study.

Variable	K	P
Network		
Degree	0.929	0.005
Interaction Strength (IS)	0.993	0.023
Maximum IS	0.7	0.019
Minimum IS	0.51	ns (0.081)
Asymmetry	0.681	0.01
Core	0.62	0.027
Centrality	0.57	ns (0.076)
Abundance & Behaviour		
Bird abundance	0.330	ns (0.523)
Mean percentage of fruits	0.743	0.003
Morphological		
Gape width	1.850	<0.001
Body size	2.171	<0.001
Intestine length	1.52	<0.001
Height	1.71	<0.001
Wing	1.61	<0.001
Tail	0.87	<0.001
Tarsus	1.02	<0.001
Culmen 1	1.04	<0.001
Culmen 2	1.06	0.002

Discussion

Our results suggest that ecological networks patterns are due to a diverse array of ecological processes that may operate at different temporal time-scales (Hastings 2004). The coupled effect of local abundance variation, phenotypic plastic responses (switching behaviour) and species evolutionary adaptive processes might be shaping network patterns. We showed that both species abundance and switching behaviour vary at an ecological time-scale and determine bird interaction patterns. Our results supported also the existence of adaptations in foraging traits that shape the architecture of network patterns (Stang et al. 2006). However, the importance of morphological constraints differed in the case of species abundance and switching behaviour hypotheses. Morphological traits were weakly related with interspecific differences in bird abundance but strongly related to the percentage of fruits in the diet and the ability of switch among invertebrates and fruits. Thus, switching behaviour varies seasonally at an ecological time-scale but it depends on foraging morphological traits (beak shape) that might evolve at much more slower temporal rates.

These findings are consistent with the existing literature that suggests an important role of bird beak shape in: setting the type and number of interactions established by birds (Jordano 1987a&b, Benkman 1999, Böhning-Gaese et al. 2003); promoting diet diversification and speciation processes (Abzhanov et al. 2004, Wu et al. 2004, Fitzpatrick et al. 2005, Phillimore et al. 2006, Grant and Grant 2006) and that highlight a possible role of beak shape in driving the evolution of bird behaviour (Podos 2001).

Our results provide a preliminary framework to interpret consumer specialization and generalization patterns in bird-fleshy fruiting plants networks. First, three main types of specialization-generalization behaviours were found in birds: fast switchers (generalists), slow switchers (circumstantial generalists) and invertebrate specialists. Only fast switchers play a significant role shaping the architecture of plant-bird network in terms of degree and interaction strength. Thus, bird species characterized with a low number of plant-bird interactions and weak interactions strengths were invertebrate eaters that only feed on fruits when they were extremely abundant (slow switchers) or invertebrate eaters that only occasionally rely in fruits (invertebrate specialists). Interestingly enough, these findings are consistent with the predictions of optimal foraging theory. Optimal foraging theory (Charvov 1976, Stephens and Krebs 1986, Berec et al. 2003) predicts that species with higher handling times (smaller gape widths) would only use to the less profitable prey (fruits) when the rate of encounter with the more profitable prey (insects) falls below a critical value (i.e. when fruits are very abundant and insects are scarce) (Berec et al. 2003, Berthold 1976). Thus, switching in invertivore species should be more prone to occur in the autumn fruiting peak, when fruits are abundant and invertebrates scarce. This is consistent with the trends described for slow switching species. We suggest that optimal foraging theory might be applied to understand and predict bird specialization-generalization network patterns (Beckerman et al. 2006).

The patterns shown highlight that bird interaction strength patterns are strongly associated with abundance variation. Indeed, abundance was found to be the best predictor of interaction strength variation. The interaction of resource and consumer abundance was highly significant, suggesting that the coupled phenomena of high consumer and resource abundances increases the probability of interaction. Abundance was weakly related with the variation in morphological traits and no phylogenetic signal was observed in bird abundance. All these evidence imply that bird interaction strength patterns might be much less constrained by evolutionary constraints. This assertion is strongly supported by recent findings of Rezende et al. (2007), who reviewed 36

plant-pollinator and 23 plant-frugivore mutualistic networks and found that the amount of phylogenetic signal for interaction strength was significantly lower than for estimates of species degree. Overall, we suggest that switching behaviour and morphological constraints play a greater role in determining the type and number of interactions exerted by bird species whereas abundance variation plays a more active role in determining bird interaction strength patterns.

Our results also provide some new insights to the question of what determines the strength of phylogenetic signal in network patterns. We showed that bird interaction properties depend on species abundance, behavioural and morphological traits. All these types of properties strongly differ in their phylogenetic conservatism (Blomberg et al. 2003). Therefore, the strength of phylogenetic signal observed in network patterns might be explained by the relative importance of abundance, behavioural and morphological variables and should usually take intermediate K values. Accordingly, we should expect that interaction strength patterns would be characterized by weaker phylogenetic signals because they are more influenced by abundance variation. Empirical evidence available supports this assertion (Rezende et al. 2007).

Overall, we point that network patterns are determined by short-term variation in abundance and seasonal variation in resource switching behaviour. Nevertheless, acting at slower temporal rates of variation, the adaptive processes shaping foraging morphological traits seems to play also a very important role in defining global network architecture. Evolutionary adaptive processes acting on beak morphology and other traits may establish the ability of bird species to switch to fruits and the relative percentage of fruits in the diet for each species (Jordano 1987, Thompson 2005, Abzhanov et al. 2004, Wu et al. 2004) and thus shape degree patterns. Therefore, adaptive processes acting on bird foraging traits possibly defined the roles of bird generalist and specialist species and the whole network architecture (Stang et al. 2006).

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CHAPTER 5: Switching behavior and diversification: empirical community-wide evidence matches theoretical predictions

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In review

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Abstract

A primary goal for ecologists is the identification of the structures and processes that generate diversity in natural communities. Theory shows that behavioral switching between two alternative resources can increase diversity, both by enhancing species coexistence and increasing lineage diversification in mathematical models. However, an empirical demonstration of the community-wide patterns of switching predicted by this theory is still lacking. Here we evaluate the nature of switching behavior between two alternative resource channels, invertebrates and fruits, in a Mediterranean scrubland bird community. We also examine morphological differences in a trait related to the use of these channels. Our results are the first community-wide empirical evidence showing that different patterns of resource switching that correlate with morphological differences characterize a group of potentially competing species. These patterns are consistent with theoretical predictions, suggesting a possible role of switching behavior in promoting avian coexistence and diversification.

The impact of adaptive behavior on species diversity in natural communities has periodically received attention from both ecologists and evolutionary biologists. A positive role of adaptive behaviors in allowing coexistence and/or promoting morphological diversification of competing species has been demonstrated in several models over the years (1–7). Switching behavior is the ability of consumers to adaptively increase the consumption of one resource at the expense of decreased consumption of an alternative resource. Behavioral switching has been shown to enhance the possibility for coexistence of consumer species (4–7). A second potential diversity-enhancing impact of switching behavior is its role in generating new species and promoting morphological diversification. While such a role has been suggested several times (8–10), a rigorous theoretical formalization of such an impact was lacking until recently (6–7). However, two recent models have explored the role of adaptive foraging behavior in the evolution and diversification of foraging morphological traits (6–7). These models examine evolution in the context of a system that initially has a single lineage of consumers exploiting two resource types, with a trade-off in their abilities to use both based on the evolution of a morphological foraging trait. Rueffler et al. (6) showed that adaptive diet choice based on energy content and handling time could allow evolution of two coexisting morphological types when only one type can exist in the absence of behavior. Abrams (7) demonstrated that behavioral switching between two food types in a variable environment promote evolutionary diversification of a morphological trait that is related to the relative use of the food types. Different morphological traits cause the competing consumers to exhibit different temporal patterns of resource switching, and the resulting temporal resource segregation allows coexistence. Switching expanded the conditions for evolution of multiple morphological types compared to an analogous model that lacked switching behavior (11), acting as a behavioral driver of morphological diversification in foraging traits. Switching behavior guided natural selection on morphological traits because only resources that are consumed contribute to the direction of the selection experienced (6, 10).

Interestingly, Rooney and collaborators (3) have recently shown that two groups of alternative resources are exploited selectively by top consumers in a number of terrestrial and marine food webs (12). Thus, the prerequisites for evolutionary diversification by foraging adaptive behavior (6, 7) are effectively present in many systems. In spite of their potential generalized key role in diversification processes, there is as yet little empirical evidence of the relationship of switching behavior to trophic morphology in diverse natural communities. Furthermore, empirical evaluations of switching behavior have usually focussed in one or few species (13), and community-wide evaluations of the relative importance of switching have been precluded due to the lack of precise data. Hence, we lack evidence for the predicted pattern of differential switching behavior of morphologically different types in a multi-species community.

Here we evaluated the existence, ecological basis, and morphological correlates of switching behavior in a scrubland bird community located in Southern Spain during two years (14–15). The community was composed of 20 passerine bird species that were found to use invertebrates and/or fleshy fruits as resources throughout the year. Species might act as generalists and adaptively adjust their relative use of two resources (invertebrates and fruits) in response to the marked seasonality of these resources. Alternatively, bird species might be specialists in one of the two resource channels without switching. The two resources were found to vary asynchronously with

contrasting seasonal peaks (Fig. 1), a characteristic feature of Mediterranean scrubland habitats.

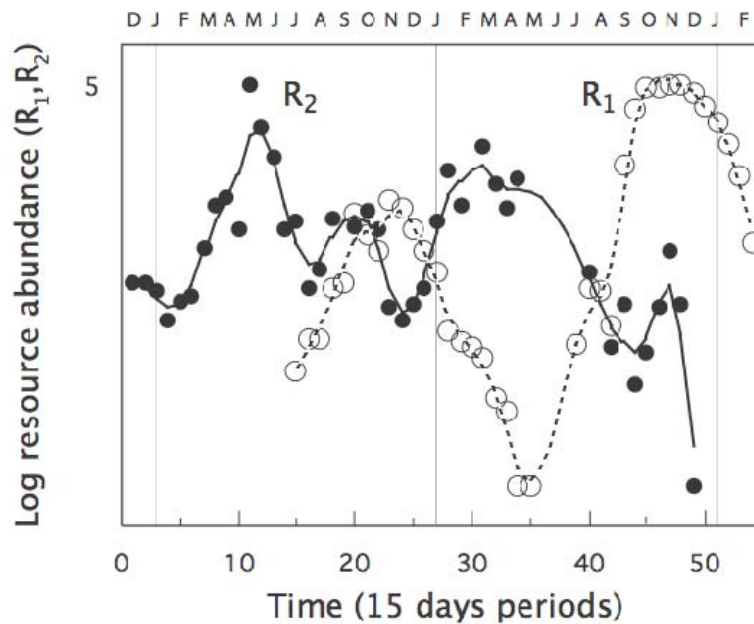
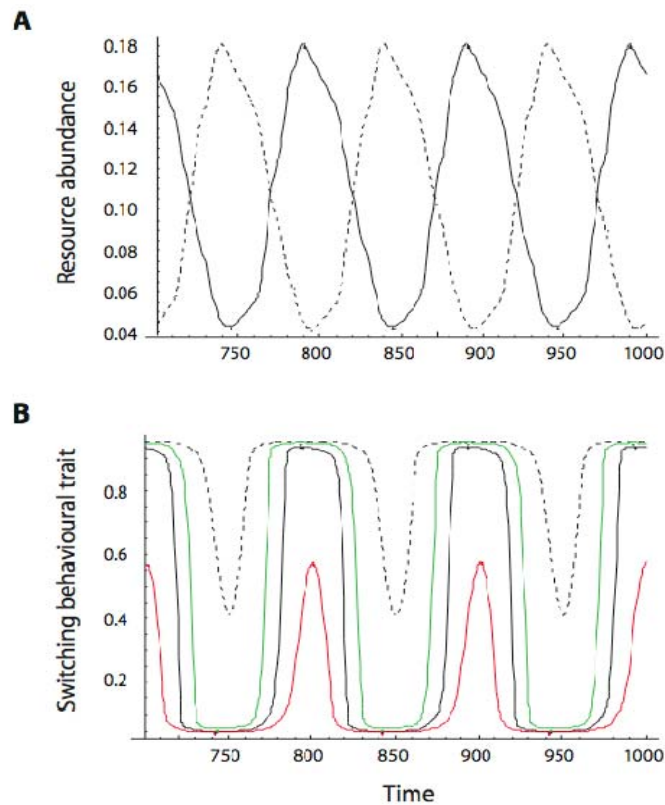


Fig. 1. Temporal variation in the availability of fruits (R_1) and invertebrates (R_2) in the study area. Production of fruits is measured in kJ/ha and invertebrate production is measured in relative abundance units (number of invertebrates/ sample surface unit).

For each bird species, temporal changes in the proportions of invertebrates and fruits in the diet were evaluated during two years using fecal samples from periodical censuses (14–15). The existence of strong temporal switching events in the proportions of both resources in response to resource fluctuation was evaluated. The observed patterns in switching behavior were compared with theoretical predictions derived from a model presented by Abrams (7, 16). The model of consumer-resource dynamics incorporates switching behavior and morphological evolution in a foraging trait (e.g. bill shape) by means of two variables. The maximum consumption rate of particular resource by a given consumer was assumed to be the product of the consumer's behavioral and morphological trait variables. Figure 2 provides an example of the dynamics of the behavioral traits as a function of resource densities in a set of four species whose morphological traits have attained an evolutionary equilibrium. More specialized species exhibit less change in relative consumption when their preferred resource decreases, and that change takes longer to occur than it does for more generalist species.

Fig. 2. Theoretical expected behavioral dynamics of the evolutionary stable coalition for four generalist species derived from Abrams' model. The parameters used are $I_1=0.25$, $I_2=0.25$, $E_1=0.15$, $E_2=0.15$, $C_{1max}=5$, $C_{2max}=5$, $h=1$, $b=0.1$, $d=0.03$, $\nu_x=0.005$, $\nu_z=20$, $\varepsilon_x=0.001$, $\varepsilon_z=0.000001$, $q_1=100$, $q_2=100$, $L=50$, $\gamma_1=0.8$, $\gamma_2=0.8$, $n=0.75$, $m=1$. **(A)** Resource abundance variation (R_1 , R_2) when resource input rates are described by sinusoidal functions. Resource 1 is denoted by the solid line and resource 2 by the dashed line. There are very low amplitude fluctuations in the four consumer populations (not shown) as a result of the resource cycles. **(B)** Switching behavior (z_i) observed in four generalist species that coexist. The evolutionarily stable phenotypes in this model are: $x_1=0.152$ (red line), 0.328 (solid black line), 0.573 (green line) and 0.845 (dashed black line). This represents a spectrum of increasing specialization on resource 1, with $x_1=0.845$ being the most specialized on resource 1. The evolutionary rate is low enough that these values are effectively constant.



To determine whether observed seasonal changes in diet composition were consistent with the theoretical predictions of the Abrams model (7), we tested five main predictions derived from the model with empirical data. Specifically, we used the most numerous genus *Sylvia* (7 species out of 20 passerine species recorded in the area) to test predictions about the expected relationships between morphology and switching for species in a single evolutionary lineage (17). The five predictions studied were as follows. First, switching was expected in all the species that behaved as generalists, i.e., that consumed the two resources. Specifically, switching requires that for each generalist species, the proportion of a resource in the diet will increase more rapidly than the

proportion in the environment (prediction 1). Second, species were expected to differ in the averaged proportion of both resources in the diet [$MR^*_{ij} = \text{mean } R^*_{ij}$; where MR^*_{ij} is the averaged proportion of resource j used by species i , and R^*_{ij} is the proportion of resource j used by species i in each sample (18)] (prediction 2). Third, the difference in the averaged proportion of resource j used by species i (MR^*_{ij}) should be correlated with specific values of a morphological foraging trait related to the relative ability to utilize the two resource types (prediction 3). Fourth, the proportion of resource use (R^*_{ij}) should be correlated with the variation in resource abundance (R_1, R_2) (prediction 4). Finally, species are expected to differ qualitatively in their response to an increase in the proportion of a resource in the environment. As one resource (e.g., fruits) first becomes more abundant, the generalist switching species that are most similar to a fruit specialist, both morphologically and in terms of average diet, should switch first, and the species most similar to the opposite specialist (more insectivorous species, with a lower proportion of fruits in the diet) should switch later (prediction 5).

We found that switching behavior is a common strategy. The bulk of the species (14 out of 20) were generalists that switched between invertebrates and fruits following the resource peaks, suggesting that switching behavior might be a pervasive and widespread phenomenon, at least in Mediterranean bird communities (Fig. 3). Switching behavior was observed in all the groups in the studied community (residents, autumn- and spring-passage migrants, breeding and wintering species), suggesting that switching is a common strategy in most bird functional migratory groups. Among the species that did not switch, 5 were specialized in eating only invertebrates, whereas only one was a non-switching generalist that ate both seeds and fruits (Table S1 and fig. S1). All *Sylvia* warblers exhibited switching behavior.

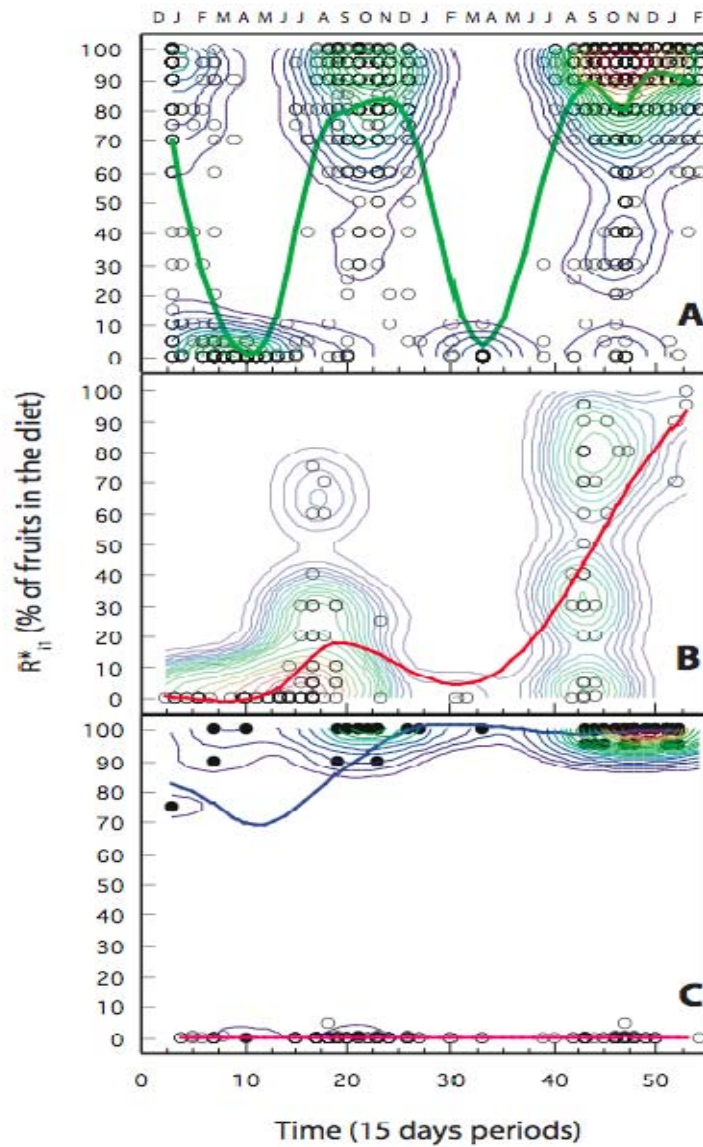


Fig. 3. Observed foraging behaviors. Spline fits describing switching trends are showed. Each dot represents a fecal sample. Species are grouped by switching behavior types: **(A)** Species that respond rapidly to a relative small increase in the availability of fruits (fast switchers, green line). **(B)** Species that showed delayed switching (slow switchers, red line). **(C)** Specialist species in fruits (black dots, blue line) and invertebrates (white dots, pink line). A smooth surface showing the density of data points is provided (except for invertebrate specialists in which all points are in line). Red contour lines indicate maximum point density.

Table S1. Community species. S = species that showed switching between R_1 and R_2 (fruits and invertebrates); S* = species that showed delayed switching behavior; F = species mostly using fruits and seeds; I = species that consumed mostly invertebrates. Number of fecal samples examined for each species is indicated inside brackets.

Specialists

CCHL	<i>Carduelis chloris</i>	(F) [74]
HPOL	<i>Hippolais polyglotta</i>	(I) [34]
PCOL	<i>Phylloscopus collybita</i>	(I) [84]
PTRO	<i>Phylloscopus trochilus</i>	(I) [25]
PBON	<i>Phylloscopus bonelli</i>	(I) [8]
RIGN	<i>Regulus ignicapillus</i>	(I) [8]

Slow Switchers

FHYP	<i>Ficedula hypoleuca</i>	(S*) [50]
LMEG	<i>Luscinia megarhynchos</i>	(S*) [48]
MSTR	<i>Muscicapa striata</i>	(S*) [15]
SUND	<i>Sylvia undata</i>	(S*) [12]

Fast Switchers

PPHO	<i>Phoenicurus phoenicurus</i>	(S) [14]
ERUB	<i>Erithacus rubecula</i>	(S) [291]
SATR	<i>Sylvia atricapilla</i>	(S) [643]
SBOR	<i>Sylvia borin</i>	(S) [183]
SCAN	<i>Sylvia cantillans</i>	(S) [27]
SCOM	<i>Sylvia communis</i>	(S) [12]
SHOR	<i>Sylvia hortensis</i>	(S) [5]
SMEL	<i>Sylvia melanocephala</i>	(S) [238]
TMER	<i>Turdus merula</i>	(S) [77]
TPHI	<i>Turdus philomelos</i>	(S) [14]

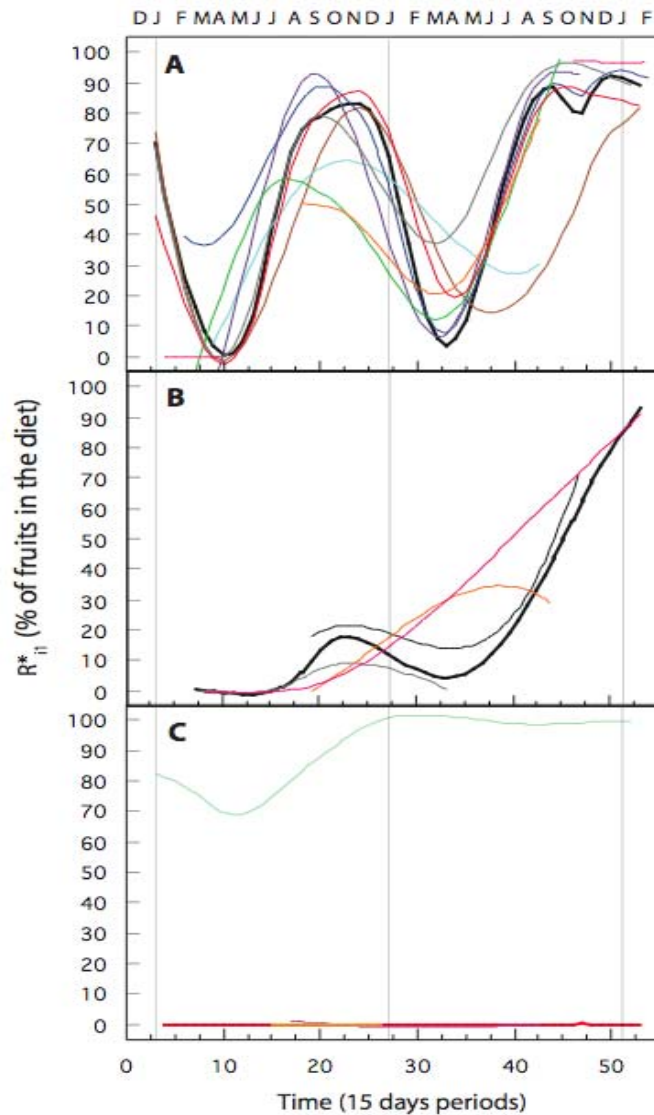


Figure S1: Switching trends for the studied species. (A) Species that switch rapidly due to a small increase in the proportion of fruits (Fast switchers): *Erithacus rubecula* (orange), *Phoenicurus phoenicurus* (light blue), *Sylvia atricapilla* (dark blue), *S. borin* (violet), *S. communis* (orange), *S. melanocephala* (red), *S. cantillans* (green), *Turdus merula* (grey), *T.philomelos* (pink). (B) Species that behaved as delayed switchers (Slow switchers): *Ficedula hypoleuca* (black), *Luscinia megarhynchos* (grey), *Sylvia undata* (pink) and *Muscicapa striata* (orange). (C) Species that behaved as specialists. Seeds and Fruits: *Carduelis chloris* (green); Invertebrates: *Phylloscopus collybita* (red), *P. bonelli* (pink), *P. trochilus* (blue), *Regulus ignicapillus* (yellow), *Hippolais polyglotta* (orange).

Two main types of switching patterns were discernable. Some species rapidly increased the proportion of fruits in the diet following a relatively small increase in the relative ratio of fruits/insects in the environment. Other species switched more slowly and to a lesser extent, and appeared to need much larger fruit/insect resource abundance ratios in the environment to start switching (Fig. 4B).

Interestingly, we also found strong empirical support for the other four predictions outlined. First, species were found to differ consistently in MR^*_{i1} , the averaged proportion of resource 1 used (prediction 2, Tukey-Kramer test, $p < 0.0001$, fig. S2). Second, we analyzed several morphological traits in a single evolutionary lineage, the species-rich genus *Sylvia* (14–15, 17). As expected, we were able to find a foraging trait (x_i = gape width) that was associated with specific differences in the proportion of the two resources used (Fig. 4C, Table S2) following the predictions of the model (prediction 3). Third, the temporal variation in the proportion of resources used (R^*_{ij}) was found to be a function of the variation in resource abundance (R_1, R_2) (prediction 4, Table S2). Finally, *Sylvia* species characterized by a higher averaged proportion of fruits in the diet (MR^*_{i1}) and higher values in the morphological trait (x_i ; gape width; Fig. 4C) switched first in response to the increase in the relative ratio of fruits/insects in the environment as was expected (prediction 5). On the other hand, *Sylvia* species characterized by a higher proportion of insects in the diet and a smaller gape width switched later (Fig. 4C, fig. S1).

Our results provide the first empirical community-wide evaluation of switching behavior in natural communities. We showed that switching behavior is a pervasive and widespread phenomenon in Mediterranean bird communities characterized with strong resource fluctuations. The observed differential switching constitutes a new pattern in community dynamics that has not previously been described. Given that switching has been theoretically associated with diversification processes (7), our empirical findings should encourage community-wide evaluations of switching responses in other systems characterized with sustained resource fluctuations. Interestingly, tropical habitats with sustained resource fluctuations (i.e. forest canopies, ecotones and altitudinal gradients (20–21)) have been also identified as important centres of morphological and behavioral diversification in birds (22–25). Further, existing evidence states that a number of Palaearctic and Nearctic bird species are derived from tropical ancestors specifically adapted to resources that fluctuate seasonally (19, 22–25). Observational data from vertebrate communities cannot establish whether a particular ecological mechanism is involved in speciation, or whether that mechanism is essential for coexistence. However, the close match between theoretical predictions and the data presented here does provide suggestive evidence for a role of switching behavior in the processes of ecological speciation and morphological diversification in birds (26). While it is likely that many mechanisms play a role in bird coexistence (27, 28), theory demonstrates that the patterns of switching observed in the community we studied should at least contribute to coexistence (4, 7, 11, Supplementary text S1).

Table S2. Variables associated with the proportion of resources in the diet. Test effects of a least squares regression model of the variation in the proportion of resource 1 used (R_1^* : fruits) as a function of fruit productivity (R_1), invertebrate productivity (R_2), species (Sp), species gape width (x_i) and year (y).

Dependent variable	Independent variables	Fit	Sum of squares	F	P
<i>All the species</i>					
R_{i1}^*	R_1	$R^2 = 0.47$	645245.0	137.79	0.0001
	R_2	$p < 0.0001$	42326.0	90.39	0.0001
	Sp	DF=17, 1061	274405.2	45.08	0.0001
	x_i		5362.1	11.45	0.0007
	y		64309.2	137.79	0.0001
<i>Sylvia genus</i>					
R_{i1}^*	R_1	$R^2 = 0.36$	74970.6	213.5	0.0001
	R_2	$P < 0.0001$	19893	56.7	0.0001
	Sp	DF=10, 756	21741.1	10.3	0.0001
	x_i		5631.2	16.0	0.0001
	y		38705	110.2	0.0001

Fig. 4. Switching behavior and morphological correlates. **(A)** Observed switching behavior in fast switchers (green line) and slow switchers (red line). Black line indicates temporal variation in fruit production (R_1); black-dashed lines indicate variation in invertebrate production (R_2). **(B)** Observed switching compared to the relative increase in the ratio of fruits/(invertebrates+fruits) in the environment. Rapidly switching species (green, white dots) and slowly switching species (red, black dots) are compared. **(C)** Observed relationship between a foraging morphological trait (x_i : gape width) and the averaged proportion of fruits used (MR^*_{i1}) in the genus *Sylvia*.

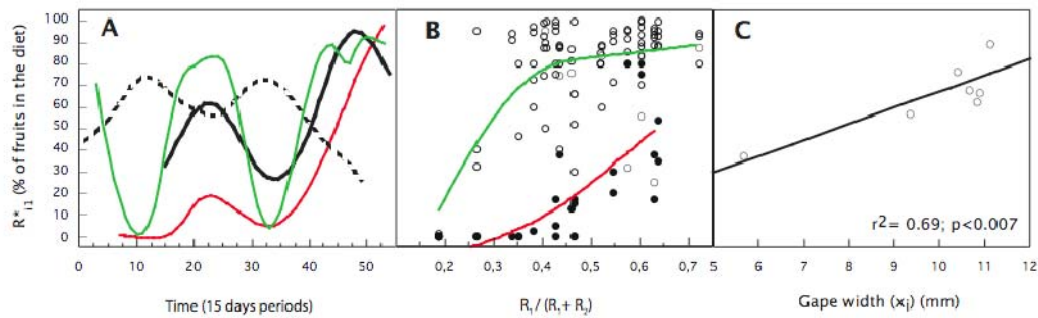
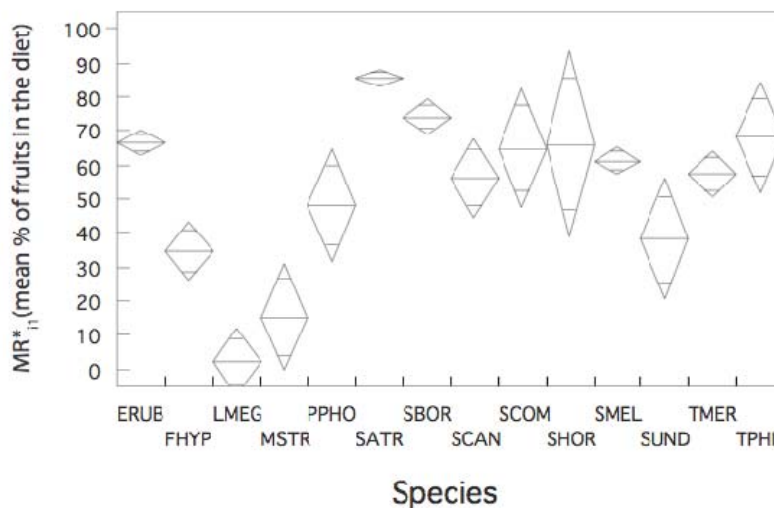


Figure S2: Specific differences in the averaged proportion of fruits in the diet (MR^*_{i1}) (I_6) between switching species. A description of species codes is provided in Table S1. Significant interspecific differences in the values of MR^*_{i1} were statistically supported (Tukey-Kramer test; $p < 0.0001$).



Our study also provides the first evidence for the association between the temporal pattern of switching behavior and a morphological trait. A wider gape width is associated with the rate and extent of switching to seasonally abundant fruit resources (Table S2, fig. S3). In line with our results, both diversification in beak shape and feeding generalization have recently been associated with avian diversification processes (29–31). Moreover, the genetic and development paths for beak shape diversification have also been identified and related to avian diversification processes (32–33). Overall, our data and simulations highlight the need to consider the switching responses of consumers in understanding the organization of bird communities with non-constant resource availabilities. Such community-wide evaluations of switching responses in other tropical and temperate systems may also shed light on the patterns of morphological diversification observed in those communities. Our results argue that experimental testing of the role of switching behavior in promoting morphological diversification is a promising new research line in evolutionary ecology.

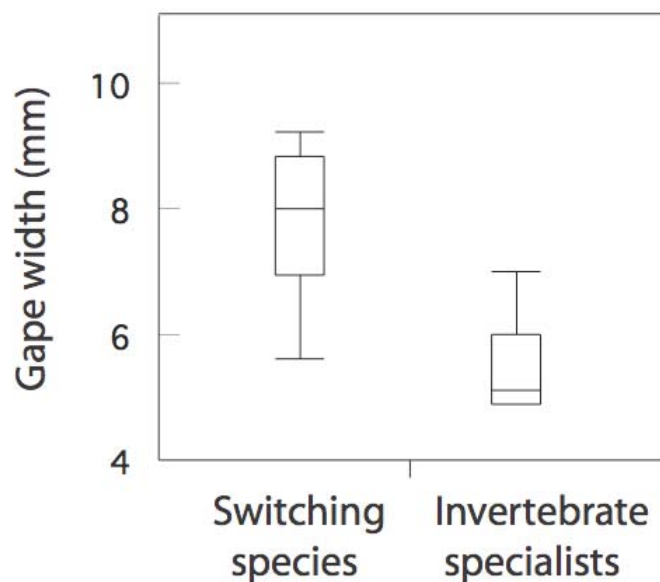


Figure S3. Differences in gape width between switching and non-switching birds. Significant differences were statistically supported (Tukey-Kramer test; $p < 0.0001$).

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Supporting Material for

Switching behavior: empirical community-wide evidence matches theoretical predictions

Jofre Carnicer,* Peter A. Abrams, Pedro Jordano

Materials and Methods

Figs. S4 to S5

Supplementary text S1

References

SUPPORTING MATERIAL

Materials and Methods

Model. Abrams' model (*SI*) simulates the population dynamics of two resources (R_1, R_2), several consumer lineages (N_i), and the dynamic evolution of a foraging morphological trait (x_i) and a switching behavioural trait (z_i) for each consumer lineage:

$$\frac{dR_1}{dt} = I_1 \left\{ 1 + \gamma_1 \sin \left[\frac{2\pi(t + L_1)}{q_1} \right] - E_1 R_1 \right\} - \sum_{i=1}^{i_{\max}} \frac{F_1(z_i) C_1(x_i) N_i R_1}{1 + h [F_1(z_i) C_1(x_i) R_1 + F_2(z_i) C_2(x_i) R_2]}$$

$$\frac{dR_2}{dt} = I_2 \left\{ 1 + \gamma_2 \sin \left[\frac{2\pi(t + L_2)}{q_2} \right] - E_2 R_2 \right\} - \sum_{i=1}^{i_{\max}} \frac{F_2(z_i) C_2(x_i) N_i R_2}{1 + h [F_1(z_i) C_1(x_i) R_1 + F_2(z_i) C_2(x_i) R_2]}$$

$$\frac{dN_i}{dt} = N_i \left\{ b \frac{F_1(z_i) C_1(x_i) R_1 + F_2(z_i) C_2(x_i) R_2}{1 + h [F_1(z_i) C_1(x_i) R_1 + F_2(z_i) C_2(x_i) R_2]} - d \right\} \equiv N_i W_i$$

$$\frac{dx_i}{dt} = \nu_x \left(\frac{\partial W_i}{\partial x_i} \right) + \frac{\varepsilon_x}{x_i^2} - \frac{\varepsilon_x}{(1 - x_i)^2}$$

$$\frac{dz_i}{dt} = \nu_z \left(\frac{\partial W_i}{\partial z_i} \right) + \frac{\varepsilon_z}{z_i^2} - \frac{\varepsilon_z}{(1 - z_i)^2}$$

$$C_{1_i} = C_{1_{\max}} x_i^n$$

$$C_{2_i} = C_{2_{\max}} (1 - x_i)^n$$

$$F_{1_i} = 2^m z_i^m$$

$$F_{2_i} = 2^m (1 - z_i)^m$$

where I_j is the mean input rate of resource j that varies sinusoidally between a maximum of $I_j (1 + \gamma_j)$ and a minimum of $I_j (1 - \gamma_j)$ with a time period of q_j time units, L_1 and L_2 are the lag parameters that determine the relative phase of the variation in growth of the two resources, E_j is the exit rate constant that determines the rate of loss of resource j , C_j are the maximal consumer consume capture rates of resource j per unit density, F_j is the behavioural modification of each of the maximum rates, h is the per-item handling time, b is the conversion efficiency for both resources and all the lineages, d is the per capita death rate for all the lineages, W_i is the

fitness or rate of growth of lineage i , v_x is a constant of proportionality that reflects the additive genetic variance for the trait x_i within the lineage i , v_z is a behavioural constant two orders of magnitude larger than v_x , ε_x and ε_z are two constants that push z_i and x_i away from the limiting values of 0 and 1 if they are close to those values (see reference 2 for a detailed description and discussion).

Peter Abrams' model of consumer-resource dynamics incorporates switching behaviour and morphological evolution in a foraging trait. Switching behaviour is incorporated by means of a specific behavioural choice variable z_i , with $0 < z_i < 1$, where 0 represents maximum specialization of species i on invertebrates, whereas 1 represents maximum specialization on fruits. Similarly, the model simulates the evolution of a morphological trait x_i that produces an analogous trade-off in the consumer's ability to forage on the two alternative resources. Species could be morphologically adapted to prey on resource 1 ($x_i = 1$) or to prey on resource 2 ($x_i = 0$), or could be intermediate. Similarly, species can exhibit behavioural specialization on one resource ($z_i = 0; 1$), a fixed generalist strategy (constant, but intermediate value of z_i), or different degrees of behavioural switching between the two resources (generalists with temporally varying values of z_i). During the simulations, the values of z_i and x_i change in a direction that increases consumer fitness for the current resource densities, with behavioural traits changing much more rapidly. Behavioural evolutionary rate is assumed to be two orders of magnitude faster than the rate of morphological evolution (the two rates differ by a factor of 400).

We have carried out a number of simulations using different parameter values and considering cases with evolution of the morphological trait (x_i) and with several species having x_i values fixed at their evolutionary equilibrium determined by the full model. A robust result is that evolution produces specialists and one or more generalist type, and that the different patterns of switching produced by the different species lead to temporal resource partitioning. An example is provided in Fig. 2.

Data. Temporal changes in the proportion of fruits and invertebrates in the diet were derived from periodical fecal samples of birds captured in mist-nets (S2-S3). A total of 6-10 mist-nets were operated weekly, 2 days per week. The nets were opened from dawn to dusk and checked at hourly intervals. Resource data was logarithmically transformed. The relative ratio between R_1 and R_2 was calculated normalizing fruit and invertebrate abundance (i.e. setting maximum abundance=1). The percent volume in the fecal samples of species i occupied by invertebrates and fruits ($R_{i1}^* \approx 1 - R_{i2}^*$) was estimated (S2-S3). An averaged value was obtained every 15 days for each species. Variation in fruit production was estimated by transect counts of the total number of ripe fruits per unit area that were checked every 15 days (S2-S3). Relative variation in invertebrate abundance was calculated using adhesive traps that were set hanging from vegetation and on the ground (S2-S3). These traps were monitored weekly. Bird abundances were estimated by performing weekly counts following the procedure of Emlen (S4). Bird morphological measures used were obtained from birds captured in the mist-nets using standard procedures (S2-S3). Least square regression models were applied assessing normality assumptions and logarithmically transforming resource variables. Switching curves were fitted using the cubic spline method using JMP package (version 5). This method uses a set of third-degree polynomials spliced together such that the resulting curve is continuous and smooth at the splices (knot points). The estimation is done by minimizing an objective function composed by a combination of the sum of squares error and a penalty

for curvature integrated over the curve extent. Change lambda values (λ) were fitted to $\lambda=100$ for all curves showed (otherwise indicated). Curves obtained for other λ values ($\lambda= 0.1-1000$; not showed) were qualitatively similar.

Supplementary text S1

Switching and population persistence

Local bird communities are usually unsaturated (S5) and built as samples of regional pools through colonization, extinction and migration processes (S6–S7). Our empirical results show that switching among fluctuating resources enables population persistence at the local level. Locally, switching behavior might combine with other factors to enable the persistence of populations at the local scale (S1, S8). For instance, coexistence has been shown to be favoured by the asynchronous variation in the abundance of resources using theoretical simulations (S8–S9). Similarly, the observed differences in morphological foraging traits suggest the existence of trade-offs in the ability of the consumer species to capture resource types. Such trade-offs have been theoretically shown to facilitate species coexistence (S9–S11). Finally, our results suggest that the presence of switching behavior might itself be under strong natural selection. According to these expectations, Berthold (S12) demonstrated the continued existence of switching behavior in captured blackcaps, *Sylvia atricapilla*, that were provided with constant availability of fruits and invertebrates and maintained in controlled conditions during several years. This suggests that the ability to switch between resources might be a phenotypic plastic response that could be genetically assimilated to some extent in a number of species (sensu Price et al. (S13)), and that the costs of the behavior are not so great that it would be rapidly lost in the absence of fluctuations in the relative abundances of different foods. Of course, in the system studied here, annual fluctuations are always present (greater abundance of invertebrates in spring and greater abundance of fruits in autumn)(S2–S3).

Supplementary text S2

Comparison of model predictions and observed demographical changes during the study period.

Real demographic dynamics differed from model predictions in that were strongly influenced by immigration of autumn- and spring-passage migrants, breeding and wintering species. Thus, demographical changes observed were much more complex than predicted by the model (Figure S4&S5).

Figure S4. Model predictions. Species were expected to show seasonal oscillations coinciding with resource peaks.

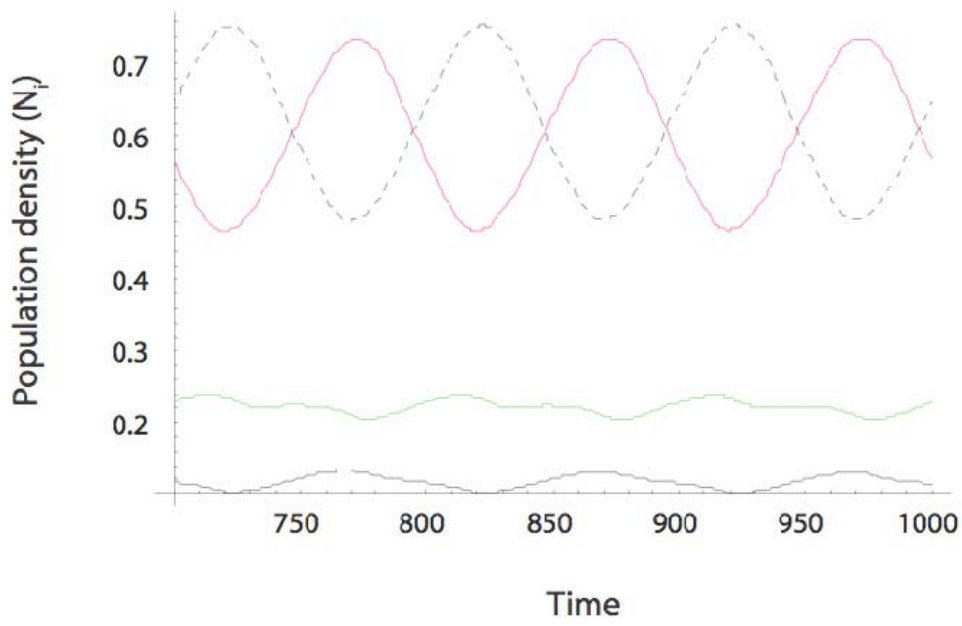
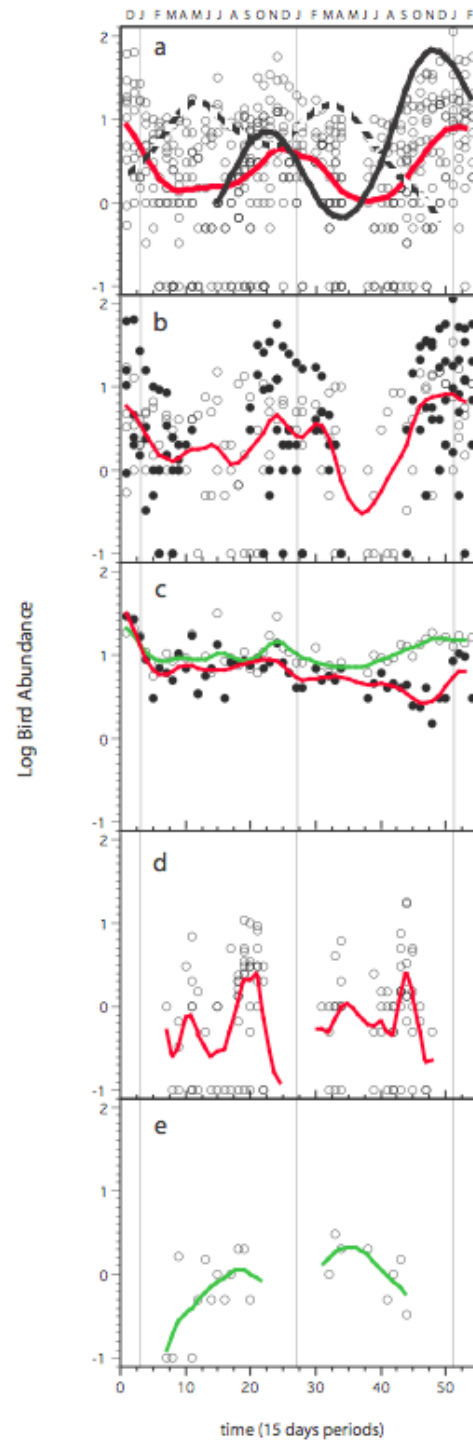


Figure S5. Observed demographic trends in Hato Ratón. Population densities were much higher in November-December and minimum in June, matching the temporal peaks of fruit abundance. **a.** Spline fit for all bird species grouped ($\lambda=100$). The graph shows fruit abundance peaks (black line), invertebrate abundance peaks (black dashed line) and bird population trends for all species grouped (red line). **b.** Most of the resident (white dots) and wintering species (black dots) showed seasonal fluctuations in the number of individuals that coincided with fruiting peaks (residents: *S. undata*, *C. chloris*; wintering: *E. rubecula*, *P. collybita*, *R. ignicapillus*, *S. atricapilla*, *T. philomelos*, *T. iliacus*). Note that many wintering species stay in the zone long periods of time, from late summer to early spring, and are absent only for 3-4 months each year (the breeding period). Some populations have both resident and wintering individuals. **c.** Few resident species showed much smaller temporal fluctuations in abundance (*T. merula* (red line, black dots, $\lambda=10$) and *S. melanocephala* (green line, white dots, $\lambda=10$). **d.** Spring- and autumn-passage migrants showed contrasted seasonal peaks in April and September (*S. communis*, *S. cantillans*, *S. borin*, *F. hypoleuca*, *M. striata*, *H. polyglotta*, *P. phoenicurus*, *P. bonelli*, *P. trochilus*; $\lambda=1$). **e.** One species was only present only during the breeding period (*L. megarhynchos*, $\lambda=10$).

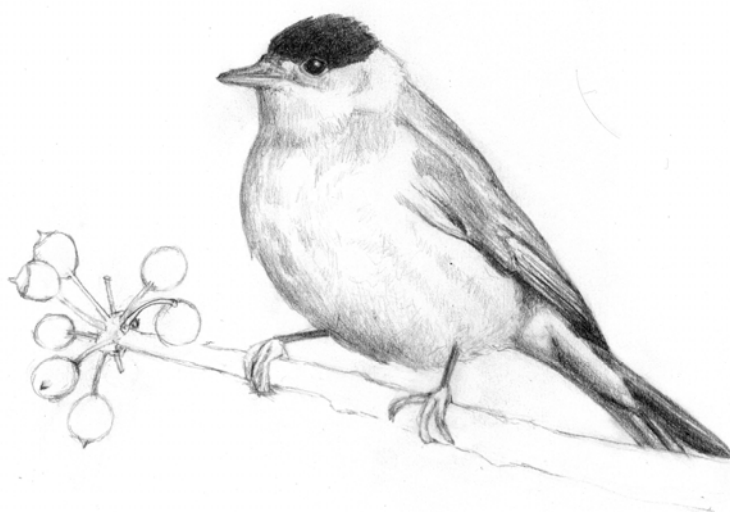
Figure S5



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Part 3
General Discussion



CHAPTER 6: Towards an integrated evolutionary and ecological view of bird species richness gradients

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Unpublished manuscript

Abstract

Historically, species richness gradients have been interpreted as the result of either community ecology processes (colonization and extinction events, environmental filtering, and local interactions) or alternatively as the result of macroevolutionary processes (speciation and lineage extinction). Taking bird species richness gradients as a study case, here we explore how these contrasting perspectives are being progressively merged in a new synthetic perspective. Recent empirical and theoretical advances strongly suggest that the coupled consideration of ecological and evolutionary processes within a unified framework is a necessary step towards a better understanding of the processes behind species richness gradients. Future prospects and research lines to achieve this goal are discussed.

Introduction

Species richness gradients are possibly among the most widely discussed patterns in ecology (Darwin 1859, Wallace 1878, Willis 1922, Dobzhansky 1950, Fisher 1960, Hillebrand 2004, Ricklefs 2004, Mittelbach et al. 2007). Historically, species richness gradients have been independently analyzed from two main disciplines: community ecology and evolutionary biology (Ricklefs 2004, 2006b). Community ecology studies have usually ignored the evolutionary changes occurring within populations and focused instead on mechanisms based on present-day colonization and extinction dynamics, dispersal and local interactions (Hutchinson 1959, MacArthur and Wilson 1963, MacArthur and Levins 1967, Brown 1981, Hawkins et al. 2003, Evans et al. 2005, Chapters 1-3). In contrast, evolutionary ecological studies have interpreted species richness gradients as the result of geographic differences in the long-term evolutionary processes of diversification (i.e. clade speciation and extinction) (Rohde 1992, Cardillo 2005, Weir and Schluter 2007). Albeit some studies effectively demonstrate that some regional bird species richness gradients can be generated without the participation of geographic differences in diversification rates (Chapters 2 and 3), other studies have recently demonstrated that diversification rates vary geographically supporting an evolutionary origin of large-scale bird species richness gradients (Cardillo et al. 2005, Golberg et al. 2005, Ricklefs 2006a, Jablonski et al. 2006, Weir and Schluter 2007, Hawkins et al. 2007). Thus, available scientific evidence suggests that both the ecological and evolutionary perspectives are essentially correct and empirically supported.

Fortunately, these two contrasting and complementary views underlying species richness gradients are progressively being merged in a unitary framework (Ricklefs 2006b, Johnson and Stinchcombe 2007). The main rationale under this effort is to highlight that ecological and evolutionary processes that generate and maintain species richness gradients are effectively interlinked. For instance, some variables can promote species richness gradients through both ecological and evolutionary paths. Indeed, community size (i.e. the total number of bird individuals in a given surface area) has been shown to act as a strong driver of species richness gradients through sampling ecological mechanisms (Chapter 2). Similarly, community size is also expected to determine speciation and lineage extinction rates in the unified neutral theory of biodiversity (Hubbell 2001, and see Losos and Schluter 2000 for an empirical test). Thus, community size can simultaneously promote species richness through both ecological and evolutionary mechanisms, revealing an interlink between ecological and evolutionary processes (BOX 1).

Similarly, phylogenetically conserved traits affecting dispersal capacity (Böhning-Gaese et al. 2006) and niche breadth of birds (Brändle et al. 2002) might shape species richness gradients through both ecological and evolutionary paths (Wiens and Donoghue 2004, Wiens and Graham 2005). Indeed, the effect of such adaptive traits is two-fold: ecologically, they determine differences in species colonizing ability that shape present-day gradients (Chapter 3); evolutionarily, they determine long-term diversification dynamics that ultimately conform the regional pool of available species (Phillimore et al. 2006). For instance, existing empirical evidence states that bird clades with increased dispersal abilities are more prone to expand their ranges and diversify (Böhning-Gaese et al. 2006, Phillimore et al. 2006, 2007).

BOX 1: Neutral theory and species richness gradients

Hubbell's model (2001) has provided a unified framework for biodiversity and biogeography that might be successfully applied to the analysis of species richness gradients from both an ecological (Chapters 2 and 3) and an evolutionary perspective (Etienne et al. 2007). Beyond the debate of neutral equivalence of species, the neutral theory provides a good framework for the analysis of species richness gradients for many reasons: 1) uses an individual-level modeling approach, 2) includes dispersal limitation and sampling effects from a regional metacommunity, 3) simulates population colonization and extinction dynamics, 4) highlights community size as a fundamental parameter in the regulation of biodiversity under zero-sum rules, 5) simulates lineage speciation and extinction processes, 6) recognizes population size as the critical parameter controlling the expected time to extinction. Hubbell's model makes some predictions dealing with ecological and evolutionary mechanisms that can generate or maintain species richness gradients. We briefly describe these predictions and contrast the existing evidence available:

P1. Local sampling effects associated to local community size variation.

Neutral theory predicts an increase of species richness with local community size (J_L) by random sampling effects from the metacommunity. Recent empirical evidence supports that this mechanism is effectively generating bird species richness gradients in some regions (Chapters 2 and 3).

P2. Local extinction-abundance dynamics.

Neutral theory identifies local population size as the main driver of local extinction. In line with this assertion, local abundance-extinction dynamics have been found to shape bird species richness gradients (Boulinier et al. 1998, Chapters 2 and 3).

P3. Regional abundance-speciation dynamics.

In Hubbell's model, lineage speciation and extinction rates are controlled by the size of the metacommunity J_M and per capita speciation rate (v). Therefore, lineage probability of speciation and extinction is dictated by species' current relative abundance: common species are more often the progenitors of new species. Interestingly enough, Hubbell's model includes mass-effects on species dispersal, that is, common species at the regional level will have higher probability to disperse and colonize a new locality. Thus, species with higher probability of dispersal also have higher probability of speciation. In line with these general assertions, dispersal ability and range size have been found to be primary determinants of bird diversification rates (Böhning-Gaese et al. 2006, Phillimore et al. 2006, 2007), giving some support to the possible existence abundance-speciation relationships. Neutral models in which speciation is independent of abundance generate less realistic species-abundance distributions (Etienne et al. 2007).

P4. Regional abundance-extinction dynamics.

Under Hubbell's model, lineage extinction rates are lower in larger metacommunities (higher J_M). The reason is that a species i starting with N_i individuals in a larger metacommunity has potentially more states of abundance that it can pass through before extinction occurs. Therefore, the probability of lineage extinction is much higher in low abundance species. Abundance-extinction dynamics have been described in local communities (Boulinier et al. 1998, Chapters 2 and 3), but empirical tests of abundance-lineage extinction dynamics at a regional scale are still lacking.

P5. Steady-state diversification dynamics.

Hubbell's model predicts that under zero-sum rule, lineage extinction rate will increase until it equals lineage speciation rate, thus achieving a steady-state in diversification rate. However, some authors have argued that we lack evidence of such steady-states in diversification rates along the history of diversification of life (Benton and Emerson 2007). Furthermore, Hubbell stated that the number of species arising per unit of time is a function of the total number of individuals of the community, not the number of preexisting species. In Hubbell's model increased diversity is incidentally correlated with lower speciation rates and higher extinction rates. This contradicts recent findings of Emerson and Kolm (2005), who proposed that increased regional diversity might effectively increase diversification rates (but see Cadena et al. 2005).

Overall, it seems that ecological and evolutionary processes that generate bird species richness gradients are effectively interlinked by a number of causal paths. We next review which concrete ecological and evolutionary mechanisms shape bird species richness gradients and their possible interrelationships. We show that both ecological and evolutionary mechanisms can independently generate species richness gradients, but that there are several mutual influences between both, suggesting the convenience of an evolutionary integrated perspective.

Ecological mechanisms

Bird species richness gradients can be easily generated by ecological mechanisms if two coupled phenomena occur. First, there is a geographical gradient in one environmental variable (e.g. productivity, habitat availability). Secondly, this environmental variable causes in turn a geographical gradient in the number of individuals that localities hold (Scheiner and Willig 2005, Chapters 1-3). Given these two conditions, bird species richness gradients can be generated and maintained by three non-exclusive mechanisms: random sampling, abundance-extinction dynamics and niche filtering (Chapter 2 and 3, table 1). Indeed, localities with larger community sizes (i.e. increased total number of bird individuals) are expected to hold an increased number of species by random sampling from the regional pool (Coleman et al. 1982, Hubbell 2001, Chapter 2). Secondly, localities with reduced community sizes experience increased turnover rates and greater extinction rates, and these processes contribute to shape species richness gradients in birds (Boulinier et al. 1998, Chapter 2).

Scale	Ecological Processes	Theory	References
Regional	· Random Sampling	· Localities with increased number of individuals will sustain increased number of species by random sampling effects from the regional pool.	(Chapters 1-3)
	· Abundance-extinction dynamics	· Localities with reduced community sizes will experience greater turnover rates and reduced species richness.	(Chapters 2&3)
	· Niche Filtering	· Colonization and dispersal dynamics will be mediated by phylogenetic conserved traits in niche breadth and dispersal abilities	(Chapters 2&3)
Local	· Local interactions	· Interaction between species, resources and environmental conditions limit local population persistence and define local composition.	(Chapters 4&5)

Table 1. A list of some ecological mechanisms that can potentially shape species richness gradients.

Finally, colonization and extinction events are mediated by species adaptations in habitat selection behavior, dispersal and niche breath (Brändle et al. 2002, Wiens and Donoghe 2004, Sol et al. 2005a, Chapter 3). The available empirical evidence strongly supports that these three ecological mechanisms (i.e. sampling, abundance-extinction dynamics and niche filtering) are effectively acting without any strong influence of regional diversification rates in maintaining the shape of the some species richness gradients (Boulinier et al. 1998, Chapters 2 and 3). However, regional colonization and extinction dynamics possibly rely on species traits that are the result of long-term evolutionary processes (e.g. niche breath, Chapter 3), suggesting the need for an evolutionary integrated perspective.

Scale	Evolutionary Processes	Theory
Regional	<ul style="list-style-type: none"> · Geographic mosaics of selection and speciation rates · Geographic mosaics in extinction rates · Diversification area · Diversification time · Historical dispersal clines · Range expansion, isolation and allopatric diversification 	<ul style="list-style-type: none"> · Geographic differences in selection and speciation rates between areas can potentially origin regional clines in species richness. · Increased lineage extinction rates due to climate and vegetation shifts create gradients in species richness. · Larger habitat areas in the tropics allowed for increased total diversification rates and higher species richness. · Higher diversification time in the tropics allowed for increased total diversification rates. · Historical dispersal clines from centers of diversification yield to species richness clines with maximum values near the origin point. · Topographic barriers can promote species richness gradients if widespread species become isolated by mountain chains or other geographical barriers and diversify by independent evolutionary paths.
Local	<ul style="list-style-type: none"> · Community context · Uneven spatio-temporal distribution of resources · Phenotypically plastic responses 	<ul style="list-style-type: none"> · Geographical gradients of local interactions, such as competition, parasitism, predation or mutualism, can promote divergent selection, influence extinction and diversification rates and shape species richness gradients. · Uneven spatiotemporal distribution of resources promotes the emergence of different evolutionary foraging behavioral strategies, the emergence of migratory behaviour and might potentially drive diversification processes thus shaping species richness gradients. · Phenotypically plastic responses drive local selection pressures and diversification processes.

Table 2. A non-exhaustive list of some evolutionary mechanisms that can potentially conform species richness gradients.

Evolutionary mechanisms

Species richness gradients can be generated by evolutionary mechanisms by the effect of geographical gradients in at least five different variables: speciation rates (Cardillo 1999, Fjeldsa and Rahbek 2006, Weir 2006, Ricklefs 2006, Weir and Schluter 2007), lineage extinction rates (Hawkins 2007, Wiens 2007, Chapter 2), geographical area suitable for speciation (Rosenweig 1995, Fine and Ree 2006), time to diversify (Stephens and Wiens 2003, Fine and Ree 2006, Benton and Emerson 2007, Hawkins et al. 2007) and historical dispersal clines (Hawkins et al. 2006, 2007, Roy and Golberg 2007, Wiens 2007) (Table 2). A latitudinal gradient of increasing diversification rates with decreasing latitude has been empirically described in birds and other groups (Cardillo 1999, Ricklefs 2006, Wright et al. 2006, Weir and Schluter 2007, Wiens 2007). However, the relative importance of lineage extinction rates, speciation rates, area, time and dispersal movements in generating species richness gradients is not well understood yet (Weir 2006, Hawkins et al. 2007, Wiens 2007). The most parsimonious interpretation of existing evidence suggests that all these processes are effectively contributing to the generation of the latitudinal gradient in species richness of birds (Golberg et al. 2005, Fjeldsa and Rahbek 2006, Hawkins et al. 2007, Wiens 2007, Roy and Golberg 2007).

Further work is needed in several areas to achieve a more precise evolutionary perspective of the generation of bird species richness gradients. This new perspective should consider: 1) the evolutionary sequence of traits associated with the diversification of each bird clade (Webb et al. 2002, Donoghue 2005, Benton and Emerson 2007), 2) the history of biogeographical movements of bird clades and biomes, and their association with shifts in diversification rates (Ericson et al. 2003, Moore and Donoghue 2007, Wiens 2007) 3) the role of community context in bird behavioral and morphological diversification (Thomson 2005, Abrams 2006, Johnson and Stinchcombe 2007, Chapter 5) 4) The role of phylogeny in structuring local and regional communities along species richness gradients (Webb et al. 2002, Rezende et al. 2007, Heard and Cox 2007). We next review briefly each of these main points, analyzing existing evidence and future prospects.

1. Sequences of adaptive characters along bird phylogenies

Molecular phylogenetic studies suggest that diversification processes and adaptive radiations frequently imply the progressive acquisition of a set of characters (often called key innovations) that in combination facilitate diversification (Heard and Hauser 1995, Webb et al. 2002, Ree 2005, Vitt and Pianka 2005, Paradis 2005, Donoghue 2005, Ackerly et al. 2006). Streelman and Danley (2003) recently highlighted that vertebrate radiations usually follow similar trajectories, diverging first in characters associated with habitat selection, then in foraging morphology and finally in communication or sexually related traits. The general model pointed out by Streelman and Danley has some empirical support in some bird clades. Indeed, morphological shifts in bird characters associated with habitat use can usually be traced to the most internal nodes of the phylogeny in a number of clades (Diamond 1986, Price 1998, Richman 2007, Ricklefs 2007). Similarly, Ackerly and colleagues (2006) recently suggested that small-scale components of the niche that differ among co-occurring species (such microhabitat use) usually diverge early in the phylogeny during adaptive radiations. Subsequent diversifications in some bird phylogenies are then based on traits associated with foraging behavior and resource tracking movements, such as beak shape, body size and wing length (Price 1998, Remsen 2003, Burns et al. 2003, Ricklefs 2007, BOX 2). However, this general scheme of diversification likely applies only to some bird

clades and should be observed with caution for three main reasons. First, phylogenetic effects on bird traits are quite variable at different phylogenetic levels (Böhning-Gaese and Oberrath 1999), suggesting the likely existence of a myriad of exceptions to any general sequence of traits in bird phylogenies. Secondly, some studies document the possibility of rapid evolution in morphological traits associated with habitat and resource use suggesting again that trait sequences might easily differ between clades (Smith et al. 1997, Böhning-Gaese et al. 2003). Thirdly, trait sequences implied in diversification possibly are much more complex than the evolutionary hypothetical sequences outlined until now (e.g. Price 1998). For instance, apart from foraging and habitat use traits, a considerable number of supplementary traits have been found to be involved in bird speciation processes (BOX 2).

BOX 2: A list of some bird adaptive traits associated with speciation	
Habitat selection traits	Morphological traits associated with habitat use differ among some bird clades during the initial splits of the phylogeny (Diamond 1986, Price 1998, Ricklefs 2007).
Size and Foraging traits	After this initial divergence in habitat use-related traits, subsequent diversifications are usually based on body size and/or traits associated with foraging behaviour (Price 1998).
Dispersal traits	Traits that enhance dispersal, colonization and migration can have long-term effects on the diversification dynamics of clades (Böhning-Gaese et al. 1998, Irwin and Irwin 2006, Phillimore et al. 2007). For instance, the number of bird subspecies covaries with migratory habits and geographical range size (Belliere et al. 2000, Phillimore et al. 2007). Traits associated with enhanced dispersal and migratory ability possibly evolved from local-area feeding strategies such as seasonal resource tracking and altitudinal movements (Levey and Stiles 1992, Mettke-Hofmann and Gwinner 2004, Chapter 5). Subsequently, such behaviors could potentially have facilitated colonization, range expansion and allopatric diversification processes in a number of bird clades (Irwin and Irwin 2006, Phillimore et al. 2006, Böhning-Gaese et al. 2006).
Mate choice traits	Geographical divergence in characters involved in mate choice, such as song, plumage, and behavioural displays likely play also an important role in avian speciation (Møller and Cuervo 1998, Edwards et al. 2005), albeit some authors have suggested that the role is secondary when compared with other factors such as dispersal, range size or feeding generalization (Price 1998, Phillimore et al. 2006). Gradual divergence of song in allopatric populations may result in reproductive isolation upon secondary contact and speciation (Grant and Grant 1997, Irwin 2000, Irwin et al. 2000, 2001, Edwards et al. 2005, Irwin et al. 2005). Songs have been found to diverge as a result of habitat-dependent selection or indirectly as a consequence of morphological adaptations (Slabbekoorn and Smith 2000, Podos 2001, Patten et al. 2004, Seddon 2005). In some specific clades, song can act as a key-character determining diversification dynamics. Indeed, song learning and sexual imprinting explain the sympatric diversification of brood parasitic indigobirds (Sorenson et al. 2003).
Cognitive traits	A larger relative brain size has been found to enhance bird cognitive skills thus promoting feeding generalization and enabling the use of new resources (Lefebvre et al. 1997). This increase in phenotypic plasticity in big-brained birds can increase diversification rates by two causal paths. On one side increased relative brain size has been found to allow birds to shift to new adaptive zones thus promoting morphological diversification (Wyles et al. 1983, Sol et al. 2005b, Sol and Price 2007). Secondly, big-brained individuals might more easily spread to new locations increasing opportunities for allopatric speciation and reducing extinction risk (Sol et al. 2002, Sol et al. 2005a, Sol and Price 2007).

Overall, a considerable number of traits have been associated with bird diversification processes and in some clades can be ordered sequentially providing some initial evolutionary hypotheses. However, more detailed ecomorphological and phylogenetic analyses are yet required to derive a general quantitative perspective of the sequential order of traits implied in each clade and their relative importance (Ree 2005, Paradis 2005, Phillimore et al. 2007).

2. History of biogeographical movements of bird clades and biomes

The geographical spread of clades might promote the emergence of two or more reproductively isolated populations from a former species (Schluter 2001). Albeit ecological speciation might occur in allopatry or in sympatry, empirical evidence suggests that most bird speciation events effectively occur in allopatry (Mayr 1963, Smith et al. 1997, Coyne and Price 2000, Via 2001, Barraclough and Vogler 2000, Sorenson et al. 2003). Therefore, the consideration of bird historical diversification centers and clade historical dispersal clines are essential for the understanding of the historical generation global and regional bird species richness gradients (e.g. Ericson et al. 2003, Hawkins et al. 2007, Roy and Golberg 2007). Episodes of biogeographic movement are in some cases associated with clear shifts in the diversification rates of clades (Moore and Donoghue 2007). For example, empirical evidence supports that colonization of mountain chains strongly increased diversification rates in birds and other taxons (Weir 2006, Fjeldsa and Rahbek 2006, Hughes and Eastwood 2006, Johansson et al. 2007, Moore and Donoghue 2007, Price 2007). Jablonski (2006) proposed a general verbal model of global diversification (the “Out of the Tropics” model) in which the bulk of the clades preferentially originate in the tropics and only some of them expand towards the poles leading to secondary diversification processes there. This general scheme matches the observed phylogenetic trends in bird species richness gradients at a global scale (Hawkins et al. 2007), albeit many exceptions are likely to be expected in a number of clades (Ericson et al. 2003, Wiens 2007). Similarly, in Passerida clade a longitudinal gradient in species richness from their centers of diversification in South East Asia has been described, presumably reflecting both an historical dispersal cline and a time-for-speciation effect (Hawkins et al. 2007). For instance, Richman (1996) showed that *Phylloscopus* warblers spread by multiple invasions from mainland Asia, with only limited subsequent speciation and little associated morphological diversification. Overall, an increased number of phylogeographical studies are yet required to achieve a more comprehensive and detailed view of the history of bird clade migrations and their role in the generation of geographical gradients in species richness (Avice 2000, Ericson et al. 2003, Hawkins 2007, Roy and Golberg 2007).

3. Community context, morphological divergence and speciation

Community context, that is, the geographical variation in community composition and species interactions can influence the outcome of bird speciation and morphological diversification processes (McPeck 1996, Thompson 2005, Abrams 2006, Johnson and Stinchcombe 2007, Chapters 4 and 5). Therefore, a necessary step in order to fully understand the generation bird species richness gradients is to elucidate which specific community contexts allowed increased bird diversification rates in some areas (Chapter 5). Empirical studies assert that spatial and temporal variation in community context effectively cause geographical mosaics of selection in birds, leading to morphological divergence and speciation (Thompson 2005). For instance, geographical differences in local

community composition, such as the presence or absence of resource competitors, have been found to promote the emergence of morphologically distinct populations in crossbills (Benkman, Holimon and Smith 2001, Parchman and Benkman 2002, Benkman 2003). These studies show that direct interactions among two community species (e.g. lodgepole pines and squirrels) can indirectly alter the nature of selection experienced by birds, and thus highlight the importance of community context in explaining morphological diversification and speciation processes.

Another aspect of community context that can facilitate morphological diversification is the uneven spatial and temporal distribution of bird resources (Price 2007). For instance, fruits are predominantly confined to upper vegetation layers (Levey 1988, Loiselle 1988, Loiselle and Blake 1991) and invertebrate types and abundances strongly differ among adjacent vegetation types (Johnson et al. 2005, Blondel et al. 2006). Similarly, seasonality in resource variation is higher at upper vegetation layers but is usually less marked in the ground and understory levels (Blondel 1969, Poulin and Lefebvre 1996). Empirical and theoretical evidence suggests that this uneven distribution of resources might promote ecological speciation through the evolutionary emergence of different feeding behavioral strategies with contrasting morphological traits (Feinsinger and Swam 1982, Smith et al. 1997, Abrams 2006, Chapter 5).

Finally, different community contexts can also directly induce changes on bird morphology through phenotypic plastic responses (Agrawal 2001, Price et al. 2003, Sol and Price 2007). Phenotypic plastic responses might act as drivers of morphological diversification, because determine the direction of selective pressures experienced by populations. Some phenotypic plastic responses, such as resource switching behavior, have been found to be pervasive and widespread in bird communities (Chapters 4 and 5). Different behavioral plastic responses are associated with morphological differences between bird species, providing some support for a role of phenotypic plasticity in bird morphological diversification and speciation (Chapter 5).

Overall, to effectively assess importance of community context in driving diversification processes new research should be conducted in several areas: 1) the study of the spatial and temporal variation of community context (i.e. bird-resource interaction networks) along geographical gradients in species richness (Olesen and Jordano 2002), 2) the quantitative study of resource spatial and temporal distribution along species richness gradients (Johnson et al. 2005, Novotny et al. 2007), and 3) the comparative examination of bird phenotypic plastic responses along species richness gradients (Chapter 5).

4. Community phylogenetics and species richness gradients

A spatially nested analysis of community phylogenetic structures along species richness gradients might provide important cues about the ecological and evolutionary mechanisms that are causing the species richness gradients (Webb et al. 2002, Heard and Cox 2007). For birds, simple phylogenetic analyses have already been conducted at the global scale. Indeed, Hawkins et al. (2007) showed that the global bird species richness gradient has a strong phylogenetic signal that might be interpreted as the preferential extinction of basal clades adapted to warm climates during the cooling period of the Miocene in extra-tropical areas, and the diversification in these zones of more derived clades, adapted to colder and dryer niches (e.g. high tropical mountains) (Hawkins et al. 2007). On the other hand, more complex phylogenetic analyses have been conducted in taxonomically or geographically restricted bird groups. These studies have provided information about a number of ecological and

evolutionary processes that effectively shape species richness gradients. For instance, recent phylogenetic studies have been applied to estimate: 1) latitudinal divergences in diversification rates (Cardillo 1999, Barraclough and Nee 2001, Weir 2006, Weir and Schluter 2007), 2) temporal variation in bird immigration and extinction rates in archipelagos (Ricklefs and Bermingham 2001, Ricklefs and Bermingham 2004), 3) modes of geographical speciation (Barraclough and Vogler 2000), 4) the emergence of hybrid zones (Hewitt 2001, Swenson and Howard 2005), 5) differences in rates of diversification among clades (Barraclough and Nee 2001, Cavender-Bares and Wilczek 2003, Phillimore et al. 2007, Wiens 2007), 6) the role of trait evolution and assembly rules in structuring communities (Cavender-Bares and Wilczek 2003, Ackerly et al. 2006, Silvertown et al. 2006, Lovette and Hochachka 2006, Kraft et al. 2007). Overall, community phylogenetics is progressively emerging as an indispensable tool to analyze a number of ecological and evolutionary processes that ultimately shape species richness gradients.

BOX 3: Future goals in species richness gradients research

- The application of more sophisticated phylogenetic methods will progressively increase our knowledge of both the ecological and evolutionary mechanisms implied in the genesis and maintenance of species richness gradients at the local, regional and global scales. New phylogenetic procedures are available to perform hierarchic analyses of species richness gradients (Heard and Cox 2007), discern the effect of local competition and niche conservatism effects (Lovette and Hochachka 2006), model trait evolution along phylogenies (Ree et al. 2005, Ree 2005, Paradis 2005), describe hybrid zones and phylogeographic breaks (Hewitt 2001, Saetre et al. 2001, Swenson and Howard 2005), or estimate the relative role of speciation and extinction rates in shaping diversification rates (Lovette 2005, Weir 2006, Weir and Schluter 2007).
- More detailed empirical macroecological studies describing present-day colonization-extinction dynamics are being progressively developed providing cues to understand which ecological mechanisms maintain species richness gradients (Chapter 2 and 3).
- More detailed and extensive empirical studies addressing the spatial and temporal variation of bird resources at different scales will improve our current understanding of bird species distributions, migration causes and evolutionary diversification dynamics in bird communities (Johnson et al. 2005, Novotny et al. 2007, Price 2007).
- Similarly, community-wide studies of bird phenotypic plastic responses and geographic mosaics in adaptive traits might provide new insights in the comprehension of community diversification dynamics (Chapter 5, Thompson 2005).
- Clade specific studies dealing with the sequential evolution of morphological, behavioural and sexual traits along phylogeny and their relationship with diversification rates will improve our current understanding of adaptive radiations and speciation (Böhning-Gaese et al. 2003, Wiens 2007).
- A number of new theoretical models are providing insights on several processes that conform species richness gradients: dispersal limitation, niche filtering, abundance-extinction dynamics and sampling effects (Hubbell 2001, Rangel and Diniz-Filho 2005, Hugueny et al. 2007, Kadmon and Allouche 2007, Chapter 3), speciation modes and abundance distributions (Dieckmann and Doebeli 1999, Hubbell 2001, Etienne et al. 2007), clade dispersal clines and centers of diversification (Roy and Golberg 2007) or diversification dynamics (Abrams 2006, Chapter 5).
- Some pioneering works have identified the genes and developmental paths of traits implied in bird speciation processes. These genes and metabolic paths are possibly shared by most of the bird species and might become a powerful tool for the study of the genetic architecture of morphological diversification along phylogenies (Wu et al. 2004, Abzahov et al. 2004, Fitzpatrick et al. 2005).

Conclusions and prospects

We have shown that bird species richness gradients can be produced by ecological mechanisms such as regional extinction-colonization dynamics from a regional evolutionary stable pool and do not necessarily require the existence of a geographical gradient in diversification rates. In contrast, other gradients are effectively based in long-term geographical differences in diversification rates. Nevertheless, we showed that both the evolutionary and ecological perspectives are strongly empirically supported and interlinked through a number of evolutionary and ecological causal paths. BOX 3 outlines some future research lines that might improve our current comprehension of bird species richness gradients from an integrated ecological and evolutionary perspective. These promising lines are very diverse and heterogeneous, and integrate both the ecological and evolutionary approaches. For instance, they include the application of new phylogenetic techniques, neutral and niche modelling approaches, adaptive behaviour and speciation models, the empirical assessment of bird resource distributions, the study of community contexts favourable to speciation and coexistence, the description of present-day extinction-colonization dynamics, and the identification of genes and development paths implied in bird speciation, among others. Hopefully, the development of these diverse approaches will progressively consolidate the emerging evolutionary and ecological synthesis of bird species richness gradients.

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CONCLUSIONS

1. Large-scale patterns of bird species richness are the result of several divergent, group-specific processes. Therefore, understanding diversity gradients requires the identification of the functional ecological groups included.
2. A geographic mosaic of community-based processes can shape bird species richness gradients, with contrasting abundance-extinction dynamics and sampling effects in low- and high productivity areas. We found significant support for the existence of both sampling and abundance-extinction effects of community size in species richness gradients. However, these mechanisms seem to drive species richness variation only at low productivity areas and not in high productivity areas where species richness was uncorrelated with community size and productivity measures.
3. Species-energy relationships are produced by a combination of abundance-extinction, niche-filtering and random sampling mechanisms. We demonstrated that stochastic sampling models can predict a substantial part of the observed variation in species richness gradients. However, metacommunity random sampling models explain more variation in species richness when the probability that a species colonises a new locality is assumed to increase with its niche width. This suggests the existence of niche-filtering processes in the assembly of local assemblages. Similarly, extinction risk is significantly lower for species inhabiting high-energy regions, suggesting that abundance-extinction processes play a significant role in shaping species richness patterns.
4. Local abundance variation, seasonally-driven switching behaviour responses and interspecific differences in morphological traits define the architecture of bird interaction patterns in plant-animal mutualistic networks.
5. Switching behavior is a pervasive and widespread phenomenon in Mediterranean bird communities characterized with strong resource fluctuations. Theory demonstrates that the patterns of switching observed in the community we studied should at least contribute to coexistence. Similarly, they provide suggestive evidence for a role of switching behavior in the processes of ecological speciation and morphological diversification in birds.
6. The coupled consideration of ecological and evolutionary processes in a unified framework is a necessary step towards a better understanding of species richness gradients, interaction networks and diversification processes. Both ecological and evolutionary mechanisms can independently generate species richness gradients, but both perspectives are interlinked by several mechanisms, suggesting the convenience of an evolutionary integrated perspective. We empirically demonstrated that regional bird species richness gradients can be maintained by ecological mechanisms without the participation of geographic clines in diversification rates. However, other empirical studies effectively assert that global

bird species richness gradients are based on the existence of geographic differences in diversification rates. We conclude that both the ecological and evolutionary perspectives are empirically supported and interlinked by a number of causal paths.