RESEARCH PAPER

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

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ABSTRACT

Aim To consider the role of local colonization and extinction rates in explaining the generation and maintenance of species richness gradients at the regional scale.

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

Methods We analysed 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 Hubbell's neutral theory of biodiversity and biogeography. 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, which 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 variation in species richness only in low-productivity areas; in high-productivity areas, species richness was uncorrelated with community size and productivity measures.

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

Keywords
Altitudinal gradients, birds, extinction rate, neutral theory, sampling, species richness.

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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 & Graves, 2001; Jetz & 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.*, 2003a), adding support to the

species–energy hypothesis over other hypotheses proposed to explain richness patterns at large spatial scales. However, the question of which processes increase species richness in more productive areas is still a matter of 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 historical and ecological processes (Ricklefs & Schluter, 1993, Wiens & Donoghue, 2004). 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 into 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 present-day gradients. Hawkins *et al.* (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 extra-tropical areas, and the diversification in these zones of more derived clades, adapted to colder and drier niches (e.g. high tropical mountains). Thus, there is a strong historical signal in the present-day latitudinal gradients, but the question of which ecological mechanisms have maintained the shape of the gradient for more than 20 Myr 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 an ecological time-scale we should limit our approach to a study zone with the following attributes. First, it should be a geographical region in which a strong bird species richness gradient is correlated 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, phylogenetic variation should not be collinear with productivity along the gradient. This should permit the interpretation of the results in terms of a purely ecological time-scale. Fourth, there should not be a strong dispersal limitation that precludes immigration of species from the regional pool to any point of the gradient. This will exclude 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 overlap of different trends associated with habitat preferences along the gradient (Fuller *et al.*, 2005).

In a region with the characteristics described above, it should be possible to analyse the effects of colonization and extinction rates on the maintenance of the gradient. Here we use such a system to evaluate two mechanisms — the abundance–extinction hypothesis and the abundance–colonization hypothesis — which 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. Both mechanisms postulate that increased productivity allows the maintenance of a greater number of individuals (community size, or *J* hereafter) in a given locality, but the two hypotheses differ in the role played by the processes of extinction and colonization.

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 (Mönkkönen *et al.*, 1990;

Mönkkönen & 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.

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 colonizations, respectively. However, as predicted by the neutral theory of biodiversity and biogeography (Hubbell, 2001), community size may have direct effects on species richness not associated with the variation in proportions of extinction or colonization. Neutral theory is a sampling theory (Hubbell, 2001; Alonso & McKane, 2004; Etienne, 2005; Etienne & Alonso, 2005; Alonso *et al.*, 2006), which 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, p. 90) defined $E\{N_i\}$, the expected local abundance of 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 meta-community relative abundance of the *i*th species. In a larger local assemblage (larger *J*), a greater number of rare species will be represented ($E\{N_i\} \geq 1$). Thus, in theory, neutral sampling effects are directly associated with local variations in community size.

Here we analyse the 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. Our aim is to evaluate the relative role of direct sampling effects and indirect effects through rates of extinction and colonization in the dynamic processes that shape an altitudinal species richness gradient.

METHODS

Study area

Catalonia is a region located in the north-east of Spain with an area of 31,930 km² and a complex and remarkably varied landscape. Altitudes range from 0 to 3115 m (summit of La Pica d'Estats). The average altitude of the region is around 700 m. Plains are scarce and usually small; upland areas occupy most of the territory (Estrada *et al.*, 2004). Catalonia is a Mediterranean region that matches all the pre-requisites enumerated above 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); Kerr & Ostrovsky, 2003] and community size counts (see Results). Second, rates of colonization and extinction may be calculated by analysing the two surveys carried out along the altitudinal

gradient in the last century (1980–83; Muntaner *et al.*, 1984, 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 species (70%) are distributed along all of 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 lack of large deforested areas that may act as dispersal barriers support 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 geographical trends associated with several habitat functional groups in a single species richness variable (Fuller *et al.*, 2005).

Bird data

Bird species richness data for Catalonia were obtained from the Catalan Breeding Bird Atlas, a project of the Catalan Institute of Ornithology (see Estrada *et al.*, 2004, for detailed information on the census procedures used). The Catalan Breeding Bird Atlas project used a standardized 10×10 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 10×10 km squares were conducted in two different time periods: t_0, 1980–83 and t_1, 1999–2002 (Estrada *et al.*, 2004; see also Hagemeijer & Blair, 1997; Bibby *et al.*, 2000; Martí & del Moral, 2002). Second, within each of the 10×10 km squares, a subsample of five to ten 1×1 km squares were surveyed for a total of 2 h 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 a time-controlled, detailed survey of nearly 10% of the total land surface considered in this study (30,900 km^2, nearly all of Catalonia's area) at a lower resolution. In order to reproduce as accurately as possible the environmental heterogeneity of each 10×10 km square, 1×1 km squares were selected by the observers to proportionally represent habitat variability within 10×10 km squares. Sampling effort for each 10×10 km square in terms of effective surveying time was estimated from species-sampling time accumulation curves (see Estrada *et al.*, 2004, for detailed results). The total number of individuals in a given square was obtained from 1999–2002 survey data.

We calculated colonization and extinction numbers in each 10×10 km 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). The colonization rate was calculated by estimating the proportion of species in t_1 not detected in t_0, while the extinction rate corresponded to the proportion of species per 10 km square detected in t_0 but not observed later in t_1. Data for colonization and extinction rates were only available at 10 km 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–colonization dynamics along the altitudinal gradient, we divided the study zone into contiguous altitudinal bands of different amplitude: (1) one band covering all the range (0–3100 m); and (2) three bands of equal width (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 1×1 km and 10×10 km when using environmental data. This is recommended if we consider the existence of important interactions between 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 & Graves, 2001; van Rensburg *et al.*, 2002; Hurlbert & Haskell, 2003). The central band (1033–2066 m) sustains significantly higher NDVI values than the other two altitudinal bands (0–1033 and 2066–3100m) (Tukey–Kramer test, $P < 0.0001$).

Phylogenetic structure along the altitudinal gradient

We reviewed the existing phylogenetic information available at the family level for the species present in the area (Sibley & Alquist, 1990; Fain & Houde, 2004; Barker *et al.,* 2004; Jønsson & Fjeldså, 2006). Bird fauna present at each altitudinal band (presence/absence data) were compared by correspondence analyses using the JMP package at the family level (http://www.jmp.com/). 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) for passerines and Fain & Houde (2004) for other orders.

Analyses

The abundance–colonization hypothesis predicts that colonization 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 correlation between 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 colonization and extinction rates as a function of community size (generalized least squares models; Crawley, 2002). Our aim was to test for an association between extinction or colonization rates and community size (Fig. 1a, abundance dependence) and to examine the shape of the relationship (Fig. 1b).

Second, to address the effects of the abundance–extinction and abundance–colonization mechanisms on determining species richness patterns along the altitudinal gradient, we

Table 1 Hypotheses and predictions tested.

| Hypothesis	Theory (T) and predictions (P)
Abundance–colonization hypothesis	T: Localities with higher community sizes will show an increased proportion of colonization events and sustain increased species richness for this reason
	P C1: Colonization rates are positively and significantly correlated with community size
	P C2: When modelling species richness, the interaction term $J*C$ will be a good predictor of species richness variation and will be included in a model selection process
	P C3: A path analysis will indicate that indirect effects of community size through colonization rates in species richness are significant
Abundance–extinction hypothesis	T: Localities sustaining higher community sizes will show reduced extinction rates and thus increased species richness
	P E1: Extinction rates will be negatively and significantly related to community size
	P E2: The interaction term $J*(1 − E)$ will be a good predictor of species richness variation and will be included in a model selection process
	P E3: A path analysis will show that indirect effects of community size through extinction in species richness rates are significant
Neutral sampling hypothesis	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 N1: Species richness patterns will be successfully predicted by neutral sampling models that incorporate community size as a key variable
	P N2: Path analysis will indicate that direct effects of community size (J) on species richness (S) are significant
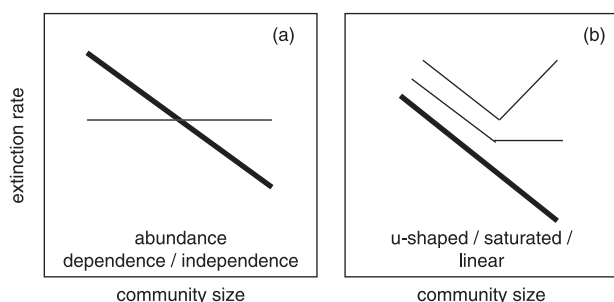
Figure 1 Summary of some of the patterns expected when analyzing extinction–abundance relationships: (a) abundance dependence (significant association) or independence; (b) types of responses.

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. The abundance–colonization mechanism was supported if the interaction term $J*C$ was significant (prediction C2, Table 1). All the analyses were carried out first for the entire gradient, and then by subdividing it into three altitudinal bands.

Third, we performed a path analysis to deconstruct the causal relationships between community size (J), species richness (S),

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 abundance–colonization hypotheses). The variance explained by each path reflects the influence of each of the mechanisms proposed here (Mitchell, 1992; Sol *et al.*, 2005) (predictions E3, C3, N2, Table 1).

Finally, we complemented the analysis by modelling species richness with environmental data (climate and landscape cover data). Environmental data modelling allowed the evaluation of the association with landscape cover variables, productivity surrogate variables, temperature variables and species richness along the whole altitudinal gradient and within altitudinal bands. Environmental modelling was also performed 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 the R statistical package (R Development Core Team, 2004) was used to select models based on the Akaike information criterion (AIC). All models were corrected for spatial autocorrelation 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 semi-variogram of non-spatial models to obtain values of the spatial covariance parameters (nugget, sill and range) and improve convergence. The 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–

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time curves were included in the models as independent variables.

We obtained environmental data from several digital sources: (1) NOAA satellite; (2) Departament de Medi Ambient de la Generalitat de Catalunya (DMAH) (http://mediambient. gencat.net); (3) Universitat Autònoma de Barcelona (UAB) (http://magno.uab.es/atles-climatic/); (4) Institut Cartogràfic de Catalunya (ICC) (http://www.icc.es/); and (5) Institut Català d'Ornitologia (ICO) (http://www.ornitologia.org/monitoratge/ atles.htm). From these digital sources we calculated climatic variables (from 3; mean annual temperature, winter and summer temperature, annual rainfall and summer rainfall), geographical variables (from 4; latitude, longitude, altitude, and slope variance), productivity surrogate variables (from 1; NDVI, NDVI temporal variation) and landscape cover uses (from 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 the NOAA satellite, using the time series of April–July 2002. This time period corresponded approximately 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 few phylogenetic effects on species distribution. The unique exceptions were *Oriolus oriolus* (family Oriolidae), which is absent from the 2066–3100 m band, and *Remiz pendulinus* (Remizidae), a species restricted to low-altitude riparian forests in the 0–1033 m 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 with 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 (Fig. 2).

Colonization rates (*C*) were not associated with community size measures (*J*), but the contrary was observed in extinction rates (*E*) (Fig. 3). However, this association varied along the altitudinal gradient. An association between extinction rates and community size was only observed in the low-productivity altitudinal bands (0–1033 and 2066–3100 bands), and was strongest in the high-altitude zones (2066–3100 band; Table 2 & Fig. 3). These significant relationships appeared to be linear (Fig. 1b, types of responses). Altitudinal bands differed 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
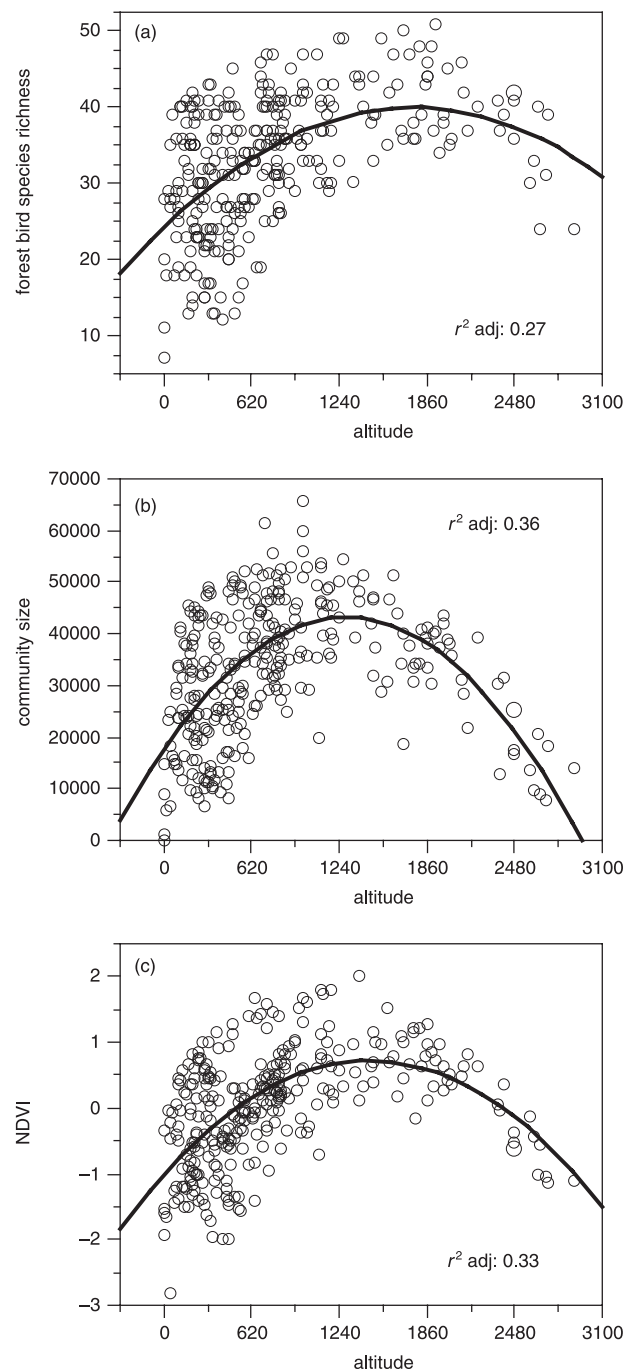

Figure 2 Patterns of the co-variation between altitude and (a) species richness, (b) community size and (c) NDVI.

there is empirical support for the extinction–abundance hypothesis only for 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, $P = 0.11$; Fig. 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, $P < 0.0001$).

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.

Altitude band width	Grain	Dependent variable	Independent variable	β	DF	AIC	R^2 adj.	P
One band	10 km	E_{0-2500}	J	$-4.85 \times 10^{-6} \pm 7.93 \times 10^{-7}$	307	−297.03	0.13	< 0.0001
Three bands	10 km	E_{0-1033}	J	$-5.4 \times 10^{-6} \pm 8.9 \times 10^{-7}$	233	−204.19	0.17	< 0.0001
		$E_{1033-2066}$	J	—	55	—	—	n.s.
		$E_{2066-3100}$	J	$-1 \times 10^{-5} \pm 2 \times 10^{-6}$	15	−1.7	0.6	< 0.0001

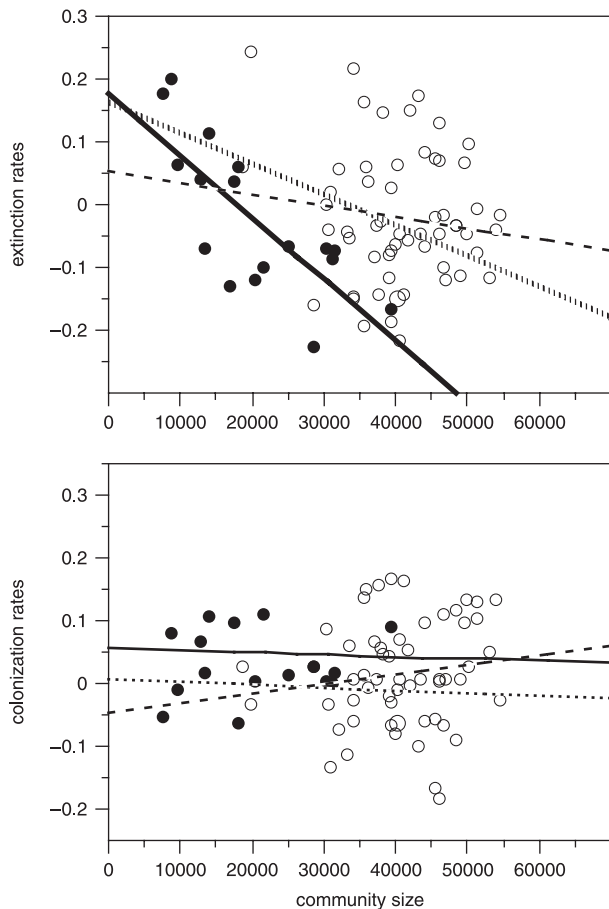DF, error degrees of freedom; AIC, Akaike information criterion.

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.

Figure 4 Results of the Tukey–Kramer tests comparing mean extinction and colonization rates for three altitudinal bands. Each pair of group means may be compared visually by examining how the comparison circles intersect. The outside angle of intersection indicates 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°. If the circles intersect by an angle of more than 90°, or if they are nested, the means are not significantly different.

Model selection (predictions E2 and C2)

The interaction term $J^*(1 - E)$ was selected in the modelling process for the low-productivity altitudinal bands (0–1033 and 2066–3100 m) giving support to the abundance–extinction hypothesis on these areas (prediction E2, Table 3).
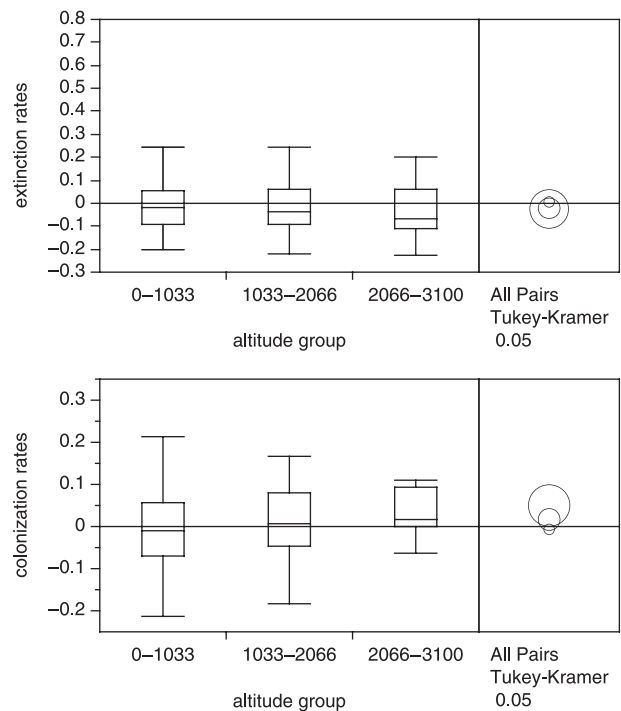
Path analysis (predictions N2, E3 and C3)

Indirect effects of community size on species richness through extinction rates were significant and supported by the path analysis only for low-NDVI regions (prediction E3), supporting the abundance–extinction hypothesis in these areas (Fig. 5). On the other hand, direct effects were supported only at the lowest-altitude region (0–1033 m) (prediction N2). In that region, direct sampling effects seem to explain the bulk of the variation in species richness. The direct effects of community size in the

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

Altitude band (m)	Dependent variable	Independent variables	DF	β values	AIC	R^2 adj.	P
0–1033	S	$J*(1-E)(1-E)$	232	4×10^{-4} 6.16	769.89	0.63	< 0.0001
1033–2066	S	$(1-E)$	55	29.15	184.06	0.28	< 0.0001
2066–3100	S	$J*(1-E)$	15	4.8×10^{-4}	50.97	0.50	< 0.0001
All bands	S	$J*(1-E)(1-E)$	306	4.3×10^{-4} 9.51	1086.74	0.54	< 0.0001

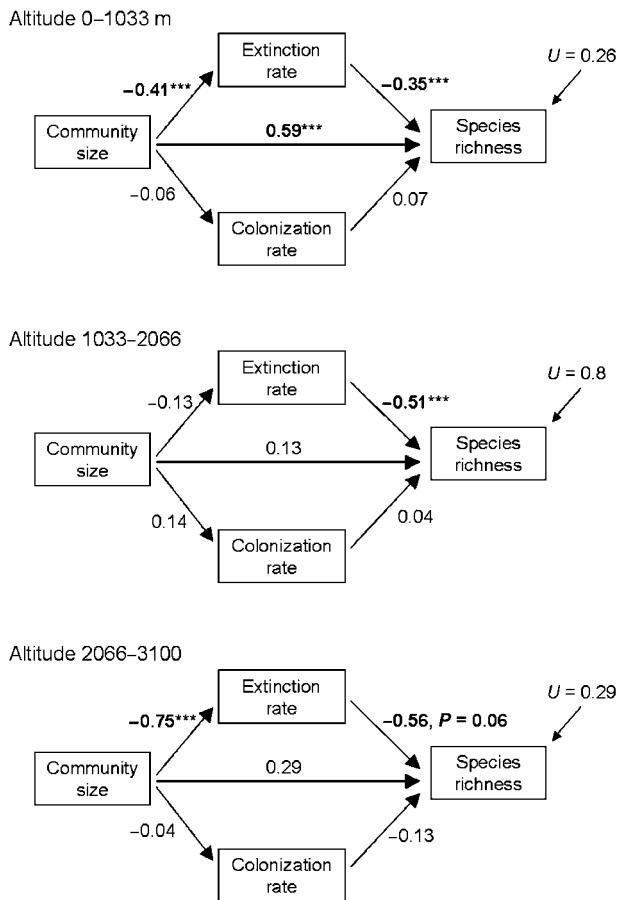DF, error degrees of freedom; AIC, Akaike information criterion.

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 the level $P < 0.001$. The variance in species richness unexplained by the model is referred to as U.

Environmental modelling

The 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 measures of forest habitat availability (% of forested area) or with any other predictor variable. On the other hand, in low-productivity zones (0–1033 and 2066–3100 m bands), species richness was strongly associated with productivity and measures of forest habitat availability.

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 areas of open space (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.

DISCUSSION

The species richness relationship of forest birds in Catalonia shows a clear altitudinal geographical structure, with matching hump-shaped altitudinal 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 with variation in community size, as predicted by the neutral theory (Hubbell, 2001). However, our results suggest that indirect effects of community size on the extinction rate may contribute to explaining 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.

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, for the higher-NDVI band (1033–2066 m), species richness was not correlated with community size measures, whereas the contrary happened for the low-NDVI bands (0–1033 and 2066–3100 m).

Table 4 Results of the model selection approach using environmental variables.

Altitude band width	Grain	Dependent variable	Independent variables	DF	AIC	R^2 adj.	P
All gradient	1 km	S_{0-3100}	NDVI + Conifer − Herb.Meadow	3073	9641	0.39	< 0.0001
	10 km	S_{0-3100}	Conifer + NDVI − Irr.Crop	305	1879.45	0.64	< 0.0001
		J_{0-3100}	Conifer + NDVI − Irr.Crop − (Temp)^2 + Temp	303	6058.44	0.81	< 0.0001
Three bands	1 km	S_{0-1033}	NDVI + Conifer − Herb.Meadow	2502	7733.61	0.42	< 0.0001
		$S_{1033-2066}$	NDVI − Shrub − Alp.Meadow + Holm oak	445	2549.42	0.11	< 0.0001
		$S_{2066-3100}$	Conifer + Shrub + (NDVI)^2	117	677.66	0.62	< 0.0001
	10 km	S_{0-1033}	Rainfall + Conifer − Temp	230	1436.79	0.66	< 0.0001
		$S_{1033-2066}$	− (Temp)^2	54	373.48	0.19	< 0.002
		$S_{2066-3100}$	Temp − Herb.Meadow	14	112.54	0.58	< 0.003
		J_{0-1033}	Conifer − Temp + Rainfall − Irr.Crop	230	4635.61	0.85	< 0.0001
		$J_{1033-2066}$	−Shrub + Temp − (Temp)^2 + Conifer	52	1106.69	0.61	< 0.0001
		$J_{2066-3100}$	Conifer −Alp.Meadow	13	284.42	0.87	< 0.0001

DF, error degrees of freedom; AIC, Akaike information criterion; S_i, species richness at altitudinal band *i*; J_i, community size at altitudinal band *i*; NDVI, normalized difference vegetation index; Irr.Crop, percentage of irrigated cropland surface; Conifer, percentage of surface occupied by conifer forests; Temp, mean annual temperature; Alp.Meadow, percentage of surface occupied by alpine meadows; Herb. Meadow; percentage of surface occupied by herbaceous meadows; Shrub, percentage of shrubland cover.

We found no support in favour of the abundance–colonization hypothesis. This was not unexpected. Evans *et al.* (2005b) similarly found no evidence that species–energy relationships are a consequence of higher colonization rates in high-energy areas (abundance–colonization hypothesis). Our results are consistent with their main conclusions. Furthermore, Evans *et al.* (2005b) showed that colonization rates in some functional groups might vary significantly with energy availability, but negatively, in contrast to the predictions of the abundance–colonization hypothesis. In other functional groups, Evans *et al.* (2005b) found no relationship between colonization rates and energy availability, coinciding with the patterns described in our study. The divergence in the spatial dynamics of colonization and extinction rates is not surprising, especially if one considers the results of recent work on the topic (Gaston & Blackburn, 2002; Evans *et al.*, 2005b). For instance, Gaston & Blackburn (2002) showed that both variables are associated differently 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). Our results suggest that these mechanisms may be driving variation in species richness only in low-productivity areas, where the association between community size and species richness is significant, and thus qualitatively different processes may be determining variation in species richness in high-productivity regions (Kerr & Packer, 1997; and see Lavers & Field, 2006). This is consistent with the observed decrease in the predictability of species richness for 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 factors determining variation in richness over the whole gradient (Wright, 1983; Hawkins *et al.*, 2003b; Lavers & Field, 2006). However,

the analyses conducted within altitudinal bands suggest that the dynamics in high- and low-productivity regions differ. Variation in species richness is tightly constrained by community size and productivity surrogates only in low-energy regions. Richness is poorly related to community size and NDVI variation in high-productivity regions.

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

The idea of the existence of geographical mosaics in the processes governing richness is not a completely novel idea. Kerr & Packer (1997), in a study of the environmental variables associated with variation in species richness 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 & Packer, 1997). Similarly, at the global or continental scale the idea of the existence of geographical 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 & 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 extra-tropical regions during the cooling period of the Miocene, which was accompanied by 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 on an historical time-scale. Our results showed that this mechanism operates at an 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 risk of extinction in low-energy areas may also be due to more specific mechanisms than the abundance–extinction hypothesis proposed here. First, a greater abundance of resources in high-energy areas may reduce the breadth of species niches and lead to an increase in co-occurrence rates and species richness by decreasing extinction rates (niche breadth hypothesis) (Evans *et al.*, 2005a). Second, if higher energy availability increases 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 variation in species richness. For instance, low- and high-productivity regions seem to differ in both the existence of 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 of the processes that shape 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 risk of extinction (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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