RESEARCH PAPER

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 showed that stochastic sampling processes predicted a substantial part (over 40%) of the observed variation in species richness, but left considerable variation unexplained. This remaining variation in species richness may be better understood as the result of alternative ecological processes. First, the sampling model explained more variation in species richness when the probability that a species colonises a new locality was assumed to increase with its niche width, suggesting that ecological differences between species matter when it comes to explaining macroecological patterns. Second, extinction risk was 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.

Keywords

Birds, Mediterranean biome, neutral theory, niche-filtering, niche width, sampling, Spain, species richness.

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INTRODUCTION

Species richness is often linked to energy measures, with the more productive or warmer sites typically containing a larger number of species than less productive or colder sites (Brown, 1981; Wright, 1983; 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 & 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 does the number of different species by chance (Fisher *et al.*, 1943; Preston, 1962; Coleman, 1981; Kaspari *et al.*, 2003; Evans *et al.*, 2005a). 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 because of the effect of geographical differences in diversification rates (Rohde, 1992; Cardillo, 1999; Hawkins *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 in 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 developed a simple stochastic metacommunity model to test whether a battery of different stochastic sampling processes could accurately reproduce species richness patterns. The model reproduced different sampling scenarios. In the first scenario, species were sampled with the same probability (equal probability model, EP). In the second one, species were sampled in proportion to the effect of regional densities (mass-effect model, ME). Thirdly, the probability of being sampled was defined as a function of species' niche width (niche-filtering immigration model, NI). The greater the niche width, the greater was the probability of being sampled. Applying this model, we evaluated if we could predict an additional amount of variation in species richness when considering the coupling of sampling effects and the existence of dispersal constraints associated with species niche width (Wiens & Donoghue, 2004). The sampling models were used to generate species richness patterns of forest birds, which were then compared with real patterns from a well-surveyed region from the Mediterranean basin (Estrada *et al.*, 2004).

We next evaluated the possibility that abundance–extinction dynamics were acting in concert with stochastic sampling processes to maintain the species–energy relationship. Under the abundance–extinction hypothesis, we expected an increase in extinction risk in low energy zones (Kaspari *et al.*, 2003; Evans *et al.*, 2005a,b; Carnicer *et al.*, 2007).

Bird and environmental data

We studied species richness patterns of forest birds in Catalonia, a region of over 30,900 km^2 located in north-east Spain. We obtained data on forest bird species abundance at 10×10 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 10×10 km grid system based on a UTM projection covering the region. A total of 309 grid cells (localities, hereafter) were considered in this study. Only forest birds were considered (67 species), following the classification of the *Catalan Breeding Bird Atlas* (Estrada *et al.*, 2004, page 569), including all species that have been found to be breeding in forest habitats in Catalonia (Muntaner *et al.*, 1984; Estrada *et al.*, 2004). A more detailed description of the census techniques implemented is provided in Appendix S1 (see Supplementary Material).

We calculated numbers of colonizations and extinctions in each 10×10 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 10×10 km square. NOAA satellite data and several digital sources were used to obtain NDVI, land cover percentages and climatic data (http://mediambient.gencat.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 (10×10 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 accounted for the two most relevant characteristics of Hubbell's neutral model (2001), i.e. random sampling and dispersal limitation effects (Alonso *et al.*, 2006), but without considering either random extinction dynamics or speciation processes. Thus, it is important to highlight that our model was in no way reproducing Hubbell's neutral theory. Instead, our stochastic sampling model was a much simpler model designed to specifically test the sampling hypothesis. The model shared 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 was empty. The algorithm added one new individual at each step (t)
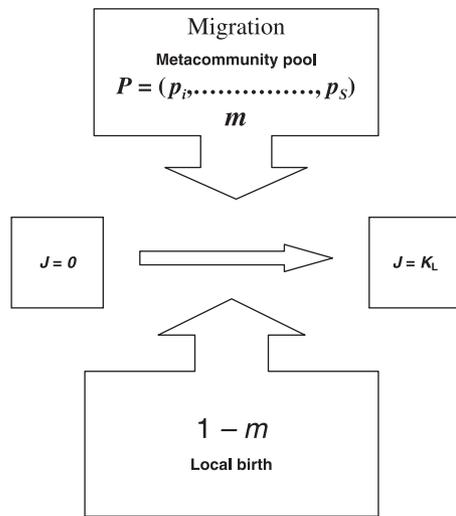
Figure 1 A scheme showing the sampling procedure applied. (P: metacommunity vector of species probabilities; K_L: specific carrying capacity of each locality L; J: community size or total number of individuals in each locality, and m: migration rate).

and stopped when all the individuals were added (up to 10 million individuals, corresponding to all the localities together). New individuals could have two distinct origins: local birth or immigration from the regional pool. During each time step (t):
(1) A new individual was added, but was randomly defined as immigrant (with probability m) or as local birth (with probability $1 - m$).
(2) In case of immigration, the individual was assigned to a species according to the probabilities of the metacommunity vector P. This vector described the probability of immigration of each species from the regional pool.
(3) In case of local birth, the new individual was assigned randomly among the species already present at the locality.
The performance of the model is summarized in Fig. 1. The carrying capacity of the community (K_L) was equal to the total number of individuals estimated at each locality (Estrada *et al.*, 2004; Herrando *et al.*, 2007). The metacommunity was defined as the regional collection of local communities (i.e. each 10×10 km cell). Only immigrant individuals, $i(t)$, could add new species to the local community, and hence increase local species richness, in the community. Species richness increased when the sampled individual was not already present in a locality; local births, $b(t)$, increased community size without contributing to species richness counts. Our model assumed 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 of the two processes (i and b) was determined by the migration rate (m), which stated the probability of local colonization. This parameter might be considered analogous to Hubbell's m (Hubbell, 2001 and see Volkov *et al.*, 2003; McKane *et al.*, 2004 and He, 2005 for analytical solutions) but was expected to achieve lower values than those reached in neutral models because our model did not simulate small populations that colonize a locality and become extinct

after one or a 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 was 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 had enough dispersal capabilities to reach any square within the study region at each time step and, therefore, immigration was not limited by distance.

Once the local community reached 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 remained fixed. The species richness estimated when the local community reached the carrying capacity was then used to test to what extent sampling expectations corresponded 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 described the probability for each species to be sampled from the regional pool ($p_1, p_2 ... p_S$). We performed the sampling simulations with four different types of P vectors, as described in Table 1. Each P vector tested for a specific hypothesis. The different P vectors were 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 & 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 generated 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 best accounted for variation in local species richness (Fig. 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 & Michener, 1958; Gower & Legendre, 1986). Similarly, we tested other similarity measures available in the software package R (R Development

Table 1 Vectors used to determine the probability of each species being sampled from the regional metacommunity pool.

CODE	Hypotheses	Pool vector (P) and theory
EP	Equal immigration probability	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 changes in numbers of individuals in a given locality (J_L) without incorporating metacommunity mass-effects.
ME	Mass-effect	Probability of being sampled is equal to the relative population abundance of each species in Catalonia. Species richness and composition in a locality will depend on the abundances of the species at the metacommunity level.
NI	Niche-filtering immigration	Probability of a species dispersing 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	Mass-effect and Niche-filtering immigration	This model combines the two previous models. 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.

S, Species richness.

Core Team 2004). The results obtained did not qualitatively differ from those obtained using the Sokal–Michener distance and are not shown.

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 & Donoghue, 2004; Wiens & 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 by applying a metacommunity vector *P* of regional abundances.

Recently, Wiens & 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 & Donoghue, 2004; Wiens & Graham, 2005).

Indeed, Wiens & 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 on an 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 make more accurate predictions of species richness than the other sampling models. In our metacommunity sampling model this prediction was tested by 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:

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

where *i* was the species, f_{ij} was the species normalized preference for habitat *j*, f_{il} was the species normalized preference for habitat *l*, and d_{jl} was the distance between habitats *j* and *l*. A more detailed mathematical description is provided in Appendix S2. 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
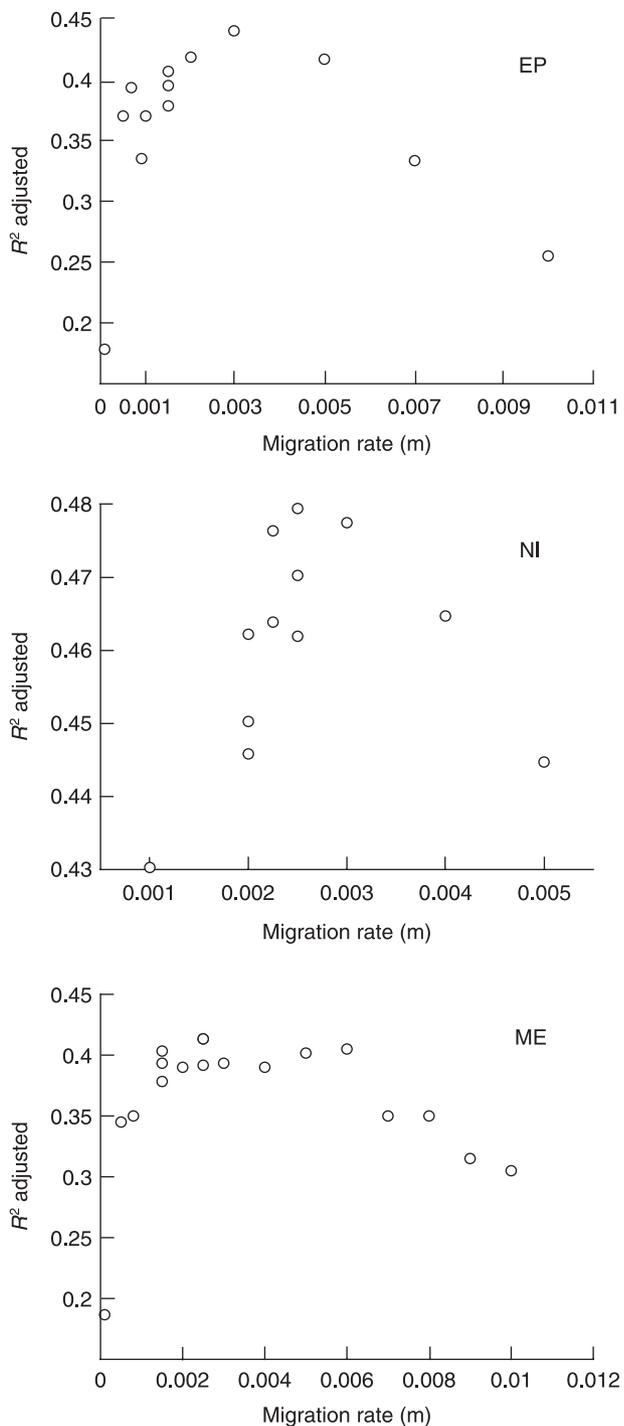
Figure 2 Plot of illustrative simulations showing the stochastic variability of the explained variance (R^2) of species richness by the sampling models (EP: equal probability hypothesis; NI: niche-filtering immigration hypothesis; and ME: mass-effect hypothesis) as a function of migration rate (m). Two scales of variation are showed: figures EP & ME show the variation of R^2 for the whole ranges of m values analyzed; figure NI shows the variation of R^2 for small increases in m beside the optimal rate.

operated, we expected that the niche sampling model would better predict local species richness variation and local composition than the equal probability and mass-effect models. 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 & Patterson, 1993). Thus, species characterized with lower pool abundances will only be 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. Accordingly, the number of localities that a species *i* occupies (R_i) should be described by the 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 *et al.* (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 & Patterson, 1993) (http://www.fieldmuseum.org/ research_Collections/zoology/nested.htm; see Appendix S3 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 each 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,b). 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 the abundance–extinction hypothesis holds, a path analysis should indicate that indirect effect of community size through extinction rate is significant when explaining species richness variation.

To evaluate the first prediction, we calculated the numbers of colonizations and extinctions that have occurred in each locality between the two time periods (1980s and 2000s), and related 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 (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 reflected unexplained variance (the effect of unmeasured variables) plus measurement error, and it was 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 was expected under a random sampling process, whereas an indirect effect of community size on species richness via decreased extinction rates was 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 the R software 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 were specified (Crawley, 2002; Evans *et al.*, 2005b). Exponential covariance functions performed better than spherical and Gaussian in all the cases examined. We plotted a semi-variogram 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 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; $P < 0.0001$)), consistent with 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 and forested area, R^2_{adj}: 0.59; $P < 0.0001$).

Sampling models 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) and mass-effect model (ME)) explained around 40% of the variation in species richness (Fig. 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 and ME) (Fig. 3). This result was robust, and was also observed after setting the three models to the EP and ME optimal rate (m: 0.0015).

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; $P = 0.076$),
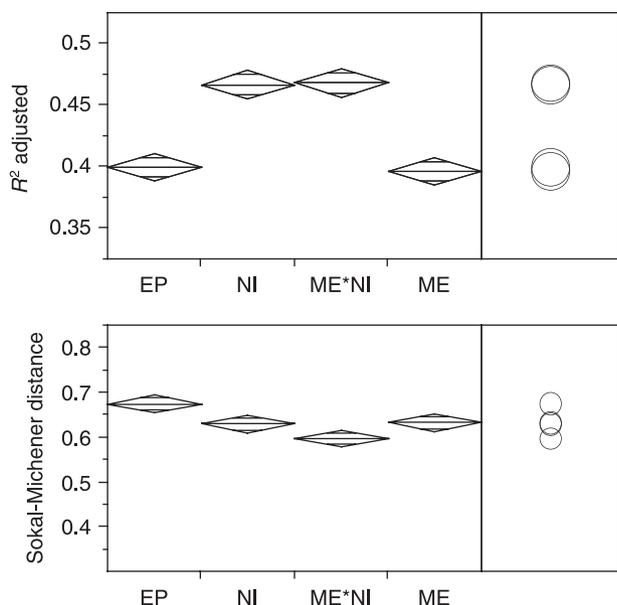
Figure 3 Percentage of variation predicted (R^2) and Sokal-Michener Distance obtained by each sampling model (EP: equal probability hypothesis; NI: niche-filtering immigration hypothesis; and ME: mass-effect hypothesis). Larger Sokal-Michener distances imply less accuracy in forecasting local composition. Circles on the right side represent the results of the Tukey–Kramer test allowing the quantitative assessment of differences between models. The line across each diamond represents the group mean. The vertical span of each diamond represents the 95% confidence interval for each group.

and thus both models seemed 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 (Fig. 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 & Patterson, 1993). A nested structure was obtained ordering species by regional abundances or niche width measures (see Appendix S4), 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 ($P < 7.5\ 10^{-22}$) and 19.76° for the abundance-ranked matrix ($P < 2.3\ 10^{-22}$).

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.

Dependent variable	Independent variable	d.f.	AIC	Model fit R^2_{adj}
All species				
R_A	A	56	506.67	0.32
R_M	M	56	494.37	0.44
R_{A+M}	A + M	55	475.87	0.61
Low density species				
R_A	A	26	243.42	0.35
R_M	M	26	250.10	0.18
R_{A+M}	A + M	25	239.24	0.46
High density species				
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

AIC, Akaike's Information Criterion.

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.

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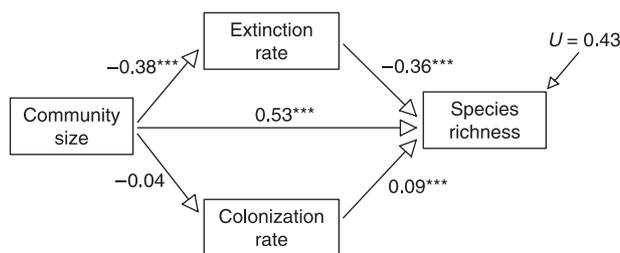
Figure 4 Results of the path analysis. Path coefficients are indicated. U describes the proportion of variance that is not explained by the model. ***$P < 0.0001$.

Table 3 Non-spatial generalized least squares (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. All models are significant at $P < 0.05$; $n = 309$. Confidence intervals around slope estimates show $P = 95\%$.

Dependent Variable	Independent variable	Test	β	AIC	Model fit R^2_{adj}
Colonization number	NDVI	GLS	0.9 ± 0.2	1657	0.038
		Spatial	ns	1612	
	Temperature	GLS	ns		
		Spatial	ns		
	J	GLS	$0.8 \times 10^{-3} \pm 1.5 \times 10^{-5}$	1661	0.083
		Spatial	$5.4 \times 10^{-5} \pm 2.1 \times 10^{-5}$	1621	
Extinction Number	NDVI	GLS	-0.5 ± 0.2	1500	0.018
		Spatial	-0.6 ± 0.2	1494	
	Temperature	GLS	ns		
		Spatial	ns		
	J	GLS	$-3.8 \times 10^{-5} \pm 1.2 \times 10^{-5}$	1516	0.03
		Spatial	$-5.8 \times 10^{-5} \pm 1.5 \times 10^{-5}$	1506	
Colonization Proportion	NDVI	GLS	ns		
		Spatial	ns		
	Temperature	GLS	ns		
		Spatial	ns		
	J	GLS	ns		
		Spatial	ns		
Extinction proportion	NDVI	GLS	$-0.5 \times 10^{-1} \pm 0.1 \times 10^{-1}$	−289	0.07
		Spatial	$-0.5 \times 10^{-1} \pm 0.1 \times 10^{-1}$	−298	
	Temperature	GLS	$0.1 \times 10^{-3} \pm 0.2 \times 10^{-4}$	−272	0.06
		Spatial	$0.1 \times 10^{-3} \pm 0.5 \times 10^{-5}$	−282	
	J	GLS	$-0.4 \times 10^{-4} \pm 0.6 \times 10^{-6}$	−288	0.13
		Spatial	$-0.5 \times 10^{-5} \pm 0.8 \times 10^{-6}$	−297	

AIC = Akaike's Information Criterion, NDVI = Normalized Difference Vegetation Index.

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, which 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 & Wilson, 1967; Wright, 1983; Hubbell, 2001; Rangel & Diniz-Filho 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 to does the number of different species by random (Blackburn & Gaston,

2001; Kaspari *et al.*, 2003; Evans *et al.*, 2005a; Schwilk & 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 & 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 Evans *et al.*, 2006). 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 (Lack, 1933; Böhning-Gaese & Oberrath, 2001; Martin, 2001; Blondel *et al.*, 2006), resource availability (Martin, 1987; Newton, 1998; Gregory & Gaston, 2000; Martin, 2001; Blondel *et al.*, 2006), life-history traits (Böhning-Gaese & Oberrath 1999, 2001; Sol *et al.* 2005)

and dispersal and migratory behaviour (Newton 1995; Flather & Sauer, 1996; Böhning-Gaese *et al.*, 1998; Böhning-Gaese & Oberrath, 1999, 2001; Mettke-Hofmann & 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 & McKane, 2004; Etienne & 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 *et al.* (2006) 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 variation in species metacommunity densities, 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 plus an additional number of species characterized by low metacommunity densities, conforming to a nested geographical structure. Thus, as proposed by the neutral theory (Hubbell, 2001; Volkov *et al.*, 2003), our results suggest that bird communities are dispersal-limited and structured by sampling constraints.

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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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Bird data.

Appendix S2 Niche width calculation.

Appendix S3 Nestedness.

Appendix S4 Presence–absence matrix of local community occupation by bird species.

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