RESEARCH PAPER

Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France?

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ABSTRACT

Aim To test how far can macroecological hypotheses relating diversity to environmental factors be extrapolated to functional and phylogenetic diversities, i.e. to the extent to which functional traits and evolutionary backgrounds vary among species in a community or region. We use a spatial partitioning of diversity where regional or γ-diversity is calculated by aggregating information on local communities, local or α-diversity corresponds to diversity in one locality, and turnover or β-diversity corresponds to the average turnover between localities and the region.

Location France.

Methods We used the Rao quadratic entropy decomposition of diversity to calculate local, regional and turnover diversity for each of three diversity facets (taxonomic, phylogenetic and functional) in breeding bird communities of France. Spatial autoregressive models and partial regression analyses were used to analyse the relationships between each diversity facet and environmental gradients (climate and land use).

Results Changes in γ-diversity are driven by changes in both α- and β-diversity. Low levels of human impact generally favour all three facets of regional diversity and heterogeneous landscapes usually harbour higher β-diversity in the three facets of diversity, although functional and phylogenetic turnover show some relationships in the opposite direction. Spatial and environmental factors explain a large percentage of the variation in the three diversity facets (>60%), and this is especially true for phylogenetic diversity. In all cases, spatial structure plays a preponderant role in explaining diversity gradients, suggesting an important role for dispersal limitations in structuring diversity at different spatial scales.

Main conclusions Our results generally support the idea that hypotheses that have previously been applied to taxonomic diversity, both at local and regional scales, can be extended to phylogenetic and functional diversity. Specifically, changes in regional diversity are the result of changes in both local and turnover diversity, some environmental conditions such as human development have a great impact on diversity levels, and heterogeneous landscapes tend to have higher diversity levels. Interestingly, differences between diversity facets could potentially provide further insights into how large- and small-scale ecological processes interact at the onset of macroecological patterns.

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INTRODUCTION

Understanding the mechanisms and processes that shape the distribution of biological diversity along environmental gradients has become a key issue in the study of the potential effects of global change, the identification of vulnerable ecosystems or species, and the proposal of meaningful conservation measures to mitigate the current diversity crisis (Díaz *et al.*, 2007; Kraft *et al.*, 2008; Reiss *et al.*, 2009). Recently, there has been an upsurge in ecological studies pointing to the multi-facetted character of biological diversity, and incorporating phylogenetic and functional diversity (Díaz *et al.*, 2007; Graham & Fine, 2008; Cavender-Bares *et al.*, 2009; Reiss *et al.*, 2009). The interest in doing so is three-fold. First, functional and phylogenetic diversity may be related to a system's resilience to environmental changes. Functional diversity has been defined and measured in different ways, including the extent to which species differ in a set of functional traits (Petchey & Gaston, 2006; Mouchet *et al.*, 2010), or the mean and variance of specific functional traits in a univariate or multi-variate analysis (see Mouchet *et al.*, 2010, for a review). Functional diversity may indeed reflect the ability of a given community to respond effectively to global change allowing the maintenance of functional capacity, including ecosystem services that are of interest to human societies (Díaz *et al.*, 2007; Cadotte *et al.*, 2009; Reiss *et al.*, 2009). Similarly, phylogenetic diversity may reflect the accumulated evolutionary history of a community, and therefore could be related to either the system's capacity to generate new evolutionary solutions in the face of change or to persist despite those changes (Forest *et al.*, 2007; Faith, 2008). Second, the interest in functional and phylogenetic diversity may also be justified simply because conserving as much as possible of all types of biological diversity is of high priority. Moreover, functional and phylogenetic diversity may be closely related to each other due to evolutionary conservatism (Webb *et al.*, 2002), so that protecting phylogenetic diversity would partially cover the need to ensure the maintenance of ecosystem function (Forest *et al.*, 2007; Cadotte *et al.*, 2009; Devictor *et al.*, 2010a). Third, considering functional and phylogenetic components of diversity might help to disentangle neutral versus niche processes in community assembly (Helmus *et al.*, 2007; Kraft *et al.*, 2008; Cavender-Bares *et al.*, 2009).

Beyond this multi-faceted nature of diversity, another level of complexity concerns spatial scale and structure (Loreau, 2000; Crist & Veech, 2006). Biological diversity can be characterized by decomposing regional diversity, also called γ-diversity, into local or α-diversity and turnover or β-diversity (Lande, 1996; Jost, 2007; Ricotta & Szeidl, 2009). Some issues of spatial scale related

to this partitioning have permeated community ecology. For example, it has generally being argued that the 'local scale' is one at which species are interacting, and therefore processes such as competition and random dispersal may be detected, whereas 'regional scales' are those for which there is enough environmental variation that processes such as environmental filtering can be assessed (Loreau, 2000). In general, however, the spatial partitioning of diversity has been applied at multiple spatial scales and is seen as a nested spatial analysis that can help us understand the processes that shape diversity (Loreau, 2000; Crist & Veech, 2006).

These arguments have recently been extended to phylogenetic and functional diversity, with a particular interest in their turnover or β-diversity components (Graham & Fine, 2008; Mouchet *et al.*, 2010). For example, given a strong environmental gradient and strong species sorting along those gradients, we would expect species as well as functional turnover (Mouchet *et al.*, 2010). On the contrary, in the absence of species sorting, we would not expect changes in functional traits, i.e. we do not expect functional turnover, although species turnover can occur (Mouchet *et al.*, 2010).

Despite this recent interest in functional and phylogenetic diversity, until now studies relating environmental gradients to either functional or phylogenetic diversity have focused mainly on variations in one of the diversity components, usually α-diversity. Their results tend to support the ideas that functional and phylogenetic diversity are positively correlated to taxonomic diversity (Forest *et al.*, 2007; Petchey *et al.*, 2007; Faith, 2008) and that lower- or intermediate-elevation areas tend to hold higher diversity in general (Bryant *et al.*, 2008). Less attention has been given, however, to the relationship between the β-diversity component of each facet and environmental or spatial gradients, although they can help understand processes that are behind the maintenance of diversity (Graham & Fine, 2008). For instance, Bryant *et al.* (2008) showed that phylogenetic turnover between sites among microbial and plant communities is positively related to differences in elevation. This suggests that phylogenetic macroecological patterns of variation of α- and β-diversity may be similar to those described for taxonomic diversity. Regarding functional diversity, Flynn *et al.* (2009) demonstrated that land-use intensification decreases the amount of diversity in traits held by bird and mammal communities, suggesting a predominant influence of environmental filters on the functional structure of communities that is not necessarily reflected in their taxonomic structure. To our knowledge, there are currently no studies linking simultaneously all three facets of diversity (taxonomic, functional and phyloge-

netic) to environmental gradients, and incorporating a spatial decomposition of diversity into α, β and γ components.

In this study we simultaneously investigated how a range of environmental factors drive taxonomic, functional and phylogenetic α-, γ- and β-diversity at a regional scale. Our main goal was to understand whether or not functional and phylogenetic diversity responded to environmental gradients in a similar way to taxonomic diversity, and to characterize variations in functional and phylogenetic diversity using a spatial partitioning framework. We tested two general hypotheses that have been widely cited in the literature with respect to taxonomic diversity: (1) changes in γ-diversity are due to either higher β-diversity between heterogeneous sites or to higher α-diversity within sites, or a combination of both (Lande, 1996; Jost, 2007); and (2) particular environmental conditions favour biological diversity more than others. More specifically, regions with higher vegetation productivity, as measured either by a vegetation index or by a combination of temperature and precipitation, should harbour higher diversity, and regions with a mosaic of landscape features or a set of landscape uses that reflect low human impact should also harbour higher diversity than homogeneous or highly developed areas (Hawkins *et al.*, 2003; Rahbek *et al.*, 2007). Here we purposely remain general in scope in order to explore for the first time how widely hypotheses related to taxonomic diversity can be extrapolated to functional and phylogenetic facets of diversity.

To test these predictions we used an extensive database that includes breeding bird surveys over several years in a large variety of environments in France. We used a distance-based approach based on the Rao diversity decomposition (Ricotta & Szeidl, 2009; de Bello *et al.*, 2010). This approach has the major advantage that it can be applied to all three facets of diversity, providing for a common framework for a multi-faceted diversity decomposition (de Bello *et al.*, 2010). We then linked these measures of diversity to environmental gradients using spatial and partial regression analyses, teasing out the environmental effect from its interactions with the spatial structure of the data.

METHODS

Breeding bird survey data

The French Breeding Bird Survey (FBBS) scheme is the coordinated and standardized national monitoring of breeding birds that has been carried out systematically since 2001 in the same plots (Julliard *et al.*, 2006; Devictor *et al.*, 2008). Numerous studies have shown that this database is robust with respect to estimates of species relative abundances of common bird species analysed here (see Devictor *et al.*, 2008, and references therein) making it suitable for analysis of large-scale diversity. In short, 2×2 km surveyed plots were selected at random within a 10-km radius around a volunteer's residence (e.g. one out of 80 possible plots). Each surveyed plot contains 10 point counts scattered across the landscape in different habitat types. Each plot is surveyed by the same observer twice a year during the breeding season (April–June), and at approximately the same dates across

years, by counting all birds during 5 minutes. Overall these plots are scattered across France over a wide variety of environments, land-use types and fragmentation levels (Devictor *et al.*, 2008).

For the purposes of this study data were grouped within each 2×2 km plot by summing the maximum yearly count (obtained during the first or the second sampling session) of each of the 10 points of the plot. The maximum abundance for each species and each plot was used in the rest of the analysis as a measure of the relative abundance of the local species. We selected survey squares that were located in continental France and sampled in at least 2 years, resulting in 1186 grid cells (sampling effort within each plot was therefore of at least 2 years × 2 surveys per year × 10 survey points = 40 surveys/plot). Seabirds, defined as species that breed solely in coastal habitats, are not efficiently captured by this terrestrial monitoring scheme and they were therefore discarded from the analysis. This left 229 species available for the analysis.

Environmental data

The environmental variables considered (Table 1) cover a wide variety of climatic and land-use predictors that may reflect both differences in productivity (vegetation productivity index, temperature and precipitation) as well as differences in human impacts (land use, fragmentation and landscape diversity). All environmental data were processed using a geographic information system and were resampled to an equal area grid of 2-km resolution using focal statistics within ArcGIS 9.2 when necessary. All variables were standardized to have a mean of 0 and variance of 1 before being included in the analysis.

Unit of analysis: 50-km windows

We calculated α-, γ- and β-diversity within 50-km windows (Fig. 1), which allowed us to compare regions with different environmental and heterogeneity characteristics standardizing sampling effort and spatial extent. In this analysis, a circle with a radius of 50-km was centred on each 2-km plot (so that all plots are the centre of one 50-km window). We randomly selected nine additional plots, meaning that each window included 10 survey plots (Fig. 1). The mean number of plots within each window was 21 ± 10, so that on average 11 plots from each window were excluded from the analysis by this procedure. Windows that did not include at least 10 survey plots were discarded from the rest of the analysis, resulting in a total of 1037 windows. The 10 selected survey plots were subsequently used to calculate the three facets of diversity, as well as the mean and coefficient of variation (standard deviation/mean) of environmental conditions. Notice that windows are overlapping and that some plots included in one window will be included in neighbouring ones. We take this into account by including a spatial autocorrelation modelling in the analysis (see 'Statistical Analysis' section). We also considered other window sizes (using 25, 50, 100, 150 and 200 km windows with 5, 10, 20, 30 and 40 plots), and found that 50-km represented a good compromise

Table 1 Environmental variables used, listed by category.

Variable name	Description	Source and resolution
Climatic variables		
Mean temperature	Climate data were available as monthly averages, minimum and	Aurelhy (Benichou and Le Breton, 1987),
Temperature range	maximum values over a period of 30 years. We calculated yearly	monthly, 1-km
Maximum temperature	mean, maximum, minimum and range values from these data	
Minimum temperature		
Mean rainfall		
Rainfall range		
Maximum rainfall		
Minimum rainfall		
Mean altitude	Mean and range of altitude within the surveyed 2-km plots as	USGS SRTM data (http://srtm.usgs.gov/), 90 m
Altitudinal range	calculated from the raw 90 m grid	
Landscape variables		
% Development	We reclassified the original land-use category in larger groups, and	CORINE land-cover vector data (Bossard *et al.*,
% Artificial green	calculated the percentage of each category within the 2-km	2000), derived from 25-m resolution satellite data
% Annual agriculture	plots. For example, 'development' includes urban and industrial	
% Perennial agriculture	areas, 'artificial green' includes green urban areas, sports and	
% Mixed agricultural	leisure facilities, 'mixed agricultural' includes annual crops	
% Scrub	associated with perennial crops, complex cultivation patterns,	
% Meadows	and agricultural areas associated with natural vegetation	
% Forests		
FRAGM	Number of patches of each land-use category in a 2-km plot,	CORINE land-cover vector data (Bossard *et al.*,
	calculated from CORINE land-cover data. A patch is any	2000), derived from 25-m resolution satellite data
	continuous land surface with a single land use type	
EVI	Enhanced vegetation index, a remotely sensed measure of	Downloaded from MODIS
	vegetation productivity. The data for the summers from 2000 to	(http://modis.gsfc.nasa.gov/) at 250-m resolution
	2005 were downloaded, and then an average, maximum,	
	minimum and standard deviation values were calculated for	
	each grid cell across all years	
Landscape diversity	Calculated by applying the Simpson index of diversity on the	CORINE land-cover vector data (Bossard *et al.*,
	percentage of different land-use categories within each	2000), derived from 25-m resolution satellite data
	2-km plot.	

USGS, United States Geological Survey; SRTM, Shuttle Radar Topography Mission
Data that were originally at different resolutions were resampled to 2-km resolution by using focal statistics within ArcGIS 9.2 before extracting their values for every 2-km plot for which bird survey data were available. For each 50-km window, the mean and coefficient of variation (standard deviation divided by the mean) were calculated by considering the same plots considered in the calculation of diversity (see Fig. 1).

between including too few local sites or including too wide an extent representing a large proportion of the study area within each window.

Measures of diversity

We used the Rao partitioning of diversity, which allowed us to use the same theoretical framework for all three types of diversity (Jost, 2007; Ricotta & Szeidl, 2009; de Bello *et al.*, 2010). The starting point for this calculation is having a phylogenetic or functional tree which represents the phylogenetic or functional relationships between species (see Appendices S1 and S2, respectively, in the Supporting Information). In these trees, closely related species or species that are very similar with respect to the functional traits considered are placed next to each other, yielding a small phylogenetic or functional distance with respect to species that are more dissimilar or have a more ancient relation-

ship. Both phylogenetic and functional distances were extracted from these trees and standardized to have a maximum value of 1 in order to facilitate comparisons between the three facets (de Bello *et al.*, 2010).

Alpha diversity is calculated by weighting each species phylogenetic or functional distances by their relative abundances:

$$\alpha_{Rao} = \sum d_{ij} p_i p_j$$

where d_{ij} is the phylogenetic or functional distance between two species, and p_i and p_j are species relative abundance. Note that the same formula is used to calculate taxonomic diversity with all species considered equivalent (distance between different species = 1, distance between individuals of the same species = 0). In the particular case of taxonomic diversity, the Rao index becomes equivalent to the Simpson diversity index. Gamma diversity is calculated using the same formula by pooling up all the information corresponding to local communities (Ricotta &
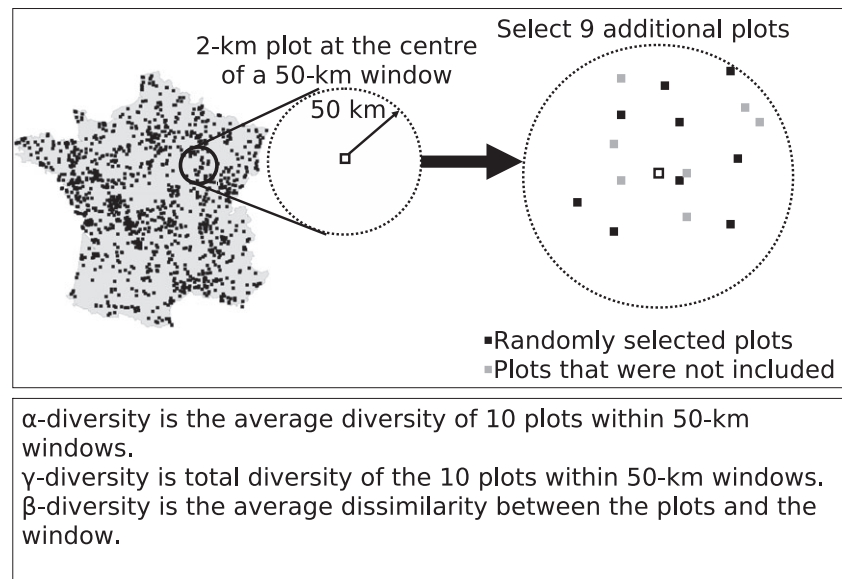
Figure 1 Calculation of α-, β- and γ-diversity. First, a 50-km circle was defined around each survey plot. This is what we call a 50-km window. Within this window, we randomly selected an additional nine plots. In this manner, all windows contain 10 plots which were used in the calculations of diversity and environmental conditions.

Szeidl, 2009). Notice that here β-diversity is the average difference between regional (window-level) and local (plot-level) communities, rather than the turnover between pairs of plots.

We further applied a correction proposed by Jost (2007) in the context of taxonomic diversity, and recently extended to functional and phylogenetic diversity measures (Ricotta & Szeidl, 2009; de Bello *et al.*, 2010). These corrections are based on equivalent numbers (de Bello *et al.*, 2010):

$$\alpha_{corrected} = 1/(1 - \alpha_{Rao}),$$

$$\gamma_{corrected} = 1/(1 - \gamma_{Rao}),$$

$$\beta_{corrected} = \gamma_{corrected} - \alpha_{corrected}.$$

Under this framework, local and regional diversity vary between 1 and the total number of species within the community or within the region, respectively, whereas β is the average difference between local and regional diversity. Here we further expressed β as a percentage of regional diversity (de Bello *et al.*, 2010).

Statistical analyses

Relationship between α-, β- and γ-diversity

We used linear regressions between α, β and γ components to investigate the relationship between regional diversity and both turnover and local diversities.

Relationships between γ- and β-diversity and the environment

First, we used a spatial simultaneous autoregressive modelling technique (SAR; *spdep* library in R v2.8.1) (Haining, 2003; Kissling & Carl, 2008), with each γ-diversity measure (taxonomic, functional or phylogenetic) as the response variable and

mean environmental conditions as predictors, in order to take into account spatial autocorrelation. In this type of autoregressive model, called a spatial error model, a spatial error term is added as a predictor, which is a function of the spatial neighbourhood of the response variable. This assumes that the spatially autocorrelated component is not fully explained by the environmental predictors considered or that it is emerges directly from the response variable (Kissling & Carl, 2008). The visualization of the spatial correlogram was used to determine the maximal distance for the spatial neighbourhood matrix. Several maximal distances were tested around the visual estimate, and two weight functions were tested as spatial weights ($1/x$ and $1/x^2$) for each response variable, choosing the one that produced the lower Akaike information criterion (AIC) value in a spatial regression with no other predictors (see Kissling & Carl, 2008). Maximum distance was always around 200 km and the weight function was always $1/x^2$.

Second, we used a simultaneous autoregressive model (SAR) as above to test whether more heterogeneous windows harbour greater β-diversity. In these regressions, β-diversity was the response variable and environmental heterogeneity, as measured by the coefficient of variation of the environmental variables, were the predictors.

While the coefficients of variation of the different environmental predictors were not highly correlated (all Pearson $R < 0.6$), some means were highly correlated (Pearson $R > 0.8$). In a first step, we chose from any pair of variables that were highly correlated the one predictor that represented best mean conditions. For example, mean and maximum temperature being highly correlated, we only kept mean temperature for further analysis. We then eliminated in a backward stepwise fashion the least significant variables first, until all variables in the model were significant (Crawley, 2007). Model residuals were then checked for normality and for potential remaining spatial autocorrelation using Moran's *I*. We then used partial regression analysis (Legendre & Legendre, 1998) to tease out the relative

	Taxonomic	Phylogenetic	Functional
Intercept	27.17 ± 0.45***	2.30 ± 0.02***	1.79 ± 0.02***
Mean rainfall	−1.82 ± 0.31***		
Rainfall range	1.34 ± 0.38***		−0.02 ± 0.01**
Mean temperature	−1.60 ± 0.33***	0.05 ± 0.00***	0.05 ± 0.01***
% Annual agriculture	−0.97 ± 0.19***	0.02 ± 0.00***	0.01 ± 0.00**
% Perennial agriculture	−1.13 ± 0.20***	0.02 ± 0.00***	−0.01 ± 0.00**
% Mixed	−1.11 ± 0.18***		0.01 ± 0.00**
% Meadows	−0.70 ± 0.18***	0.02 ± 0.00***	0.02 ± 0.00***
% Development	−2.34 ± 0.17***	−0.01 ± 0.00**	−0.01 ± 0.00***
% Scrub	−0.63 ± 0.20**	0.01 ± 0.00***	
Mean EVI	−1.00 ± 0.26***		−0.02 ± 0.01***
Landscape diversity	1.04 ± 0.14***		
Taxonomic γ-diversity		0.01 ± 0.00***	0.01 ± 0.00***
Model R^2	0.66	0.85	0.62

Table 2 Results from simultaneous autoregressive (SAR) models relating γ-diversity to mean environmental conditions.

EVI, enhanced vegetation index, a vegetation productivity index derived from satellite data (see Table 1). Results represent the coefficient estimates ± 1 standard deviation for regressions where each facet of diversity (taxonomic, phylogenetic or functional γ-diversity) is the response variable. Asterisks show the level of significance for each variable: ***$P < 0.001$; **$0.001 < P < 0.01$.

effect of spatial structure and environmental gradients (see Appendix S3 for details). We used R v. 2.8.1 (R Development Core Team, 2005) for all analyses.

As noted in a different study, the three facets of diversity were significantly correlated (see Fig. 2 in Devictor *et al.*, 2010a). We discuss the extent and consequences of these spatial congruencies between diversity facets in a different paper (Devictor *et al.*, 2010a), but took them into account here by incorporating taxonomic diversity as a predictor in all regressions involving functional and phylogenetic diversity.

RESULTS

Relationship between α-, β- and γ-diversity

A regression analysis revealed that an increase in any facet of γ-diversity was in fact coupled with an increase in both α- and β-diversity (Fig. 2). In other words, whenever there was a change in regional diversity there was a corresponding change in both local and turnover diversity. For the three facets of diversity, changes in α-diversity explained a larger proportion of the changes in γ-diversity than variations in β-diversity (Fig. 2).

Relationships between γ- and β-diversity and the environment

Overall the total percentage of variance explained in γ-diversity varied from 62% for functional γ-diversity to 85% for phylogenetic γ-diversity (Table 2). In all three cases, the relative contribution of the environment in explaining diversity variations was small compared with the contribution of the spatial structure and its interaction with the environmental variables (Fig. 3a).

Taxonomic γ-diversity was higher in regions with high landscape diversity and rainfall range but low mean rainfall and temperature and low development levels (Table 2). High phylo-
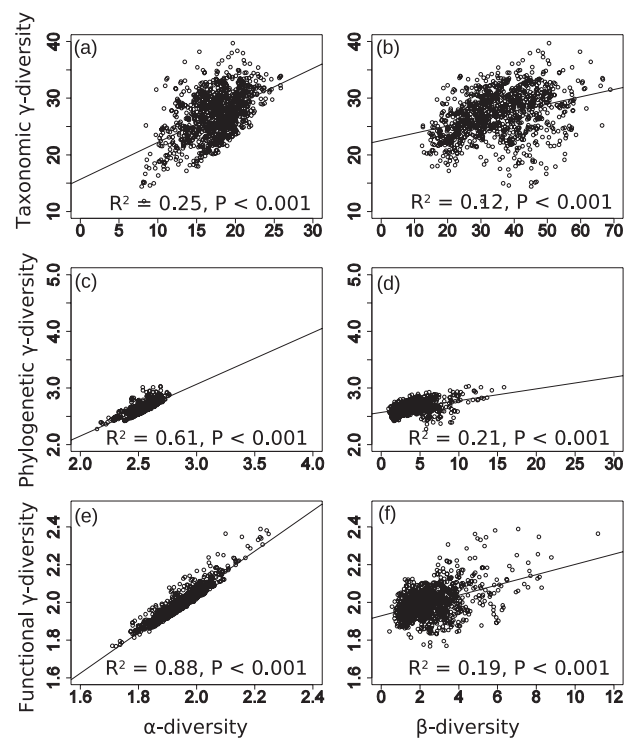

Figure 2 Relationship between γ-diversity and α- and β-diversity at the window level. Graphs (a) and (b) represent taxonomic diversity; (c) and (d) represent phylogenetic diversity; and (e) and (f) represent functional diversity. The left-hand side represents α-versus γ-diversity, while the right-hand side represents β- versus γ-diversity.

genetic and functional diversity were found in areas of high mean temperatures and a high percentage of annual agriculture, as well as in areas with a high percentage of meadows and low levels of development (Table 2). Functional and phylogenetic
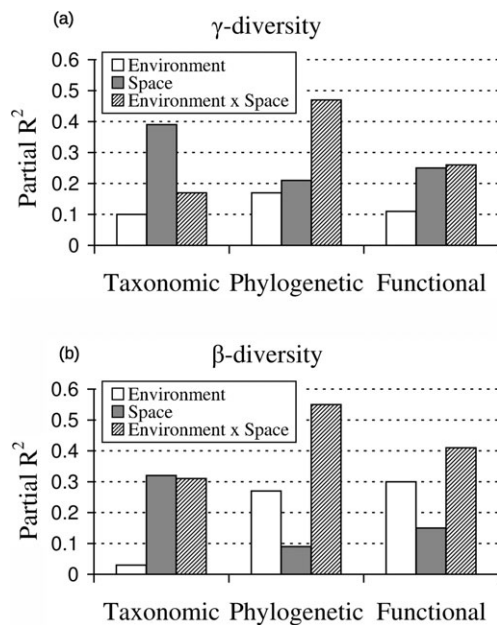
Figure 3 Partial R^2 values resulting from simultaneous autoregressive (SAR) models where diversity is the response variable and environmental conditions are the predictors: (a) γ-diversity as a function of mean environmental conditions; (b) β-diversity as a function of environmental coefficient of variation in environmental conditions. Notice that the partial R^2 value represents the part of variation on the response variable that is explained by the predictor once the effect of the other predictors has been taken into account. For example, we can say that 10% of the variation on taxonomic γ-diversity is explained by the environment once the effect of spatial structure has been removed.

diversity differed in the response they presented to other environmental gradients. For example, while higher phylogenetic diversity was found in sites with a higher percentage of perennial agriculture, the opposite was true for functional diversity (Table 2).

The percentage of variance explained by the coefficient of variation of environmental predictors in β-diversity varied from 66% for taxonomic β-diversity to 91% for phylogenetic β-diversity (Table 3). However, the environmental gradients per se had a weak influence on β-diversity once the effects of the spatial structure were taken into account, especially for taxonomic β-diversity (Fig. 3b). The spatial structure and its interaction with these environmental factors together explained more of the variation in β-diversity than the environmental component by itself (Fig. 3b). Taxonomic β-diversity was positively related to the coefficient of variation of all significant environmental variables considered, such as mean altitude and mean temperature, except for temporal variations in the enhanced vegetation index (EVI; Table 3). On the other hand, phylogenetic and functional β-diversity showed both positive and negative relationships (Table 3). For example, phylogenetic β-diversity showed a positive relationship to the coefficient of variation of mean altitude, fragmentation and EVI, while

showing a negative relationship to variations in rainfall range and mean temperature, percentage of meadows and percentage of scrub, and temporal variations in EVI (Table 3). Functional β-diversity responds in the same direction as phylogenetic β-diversity for the variables that are represented in both regressions, but seems less sensitive to the land-use variables included in the analysis (Table 3).

DISCUSSION

Our results generally support the idea that hypotheses previously applied to taxonomic diversity, both at local and regional scales, can be extended to phylogenetic and functional diversity. More specifically, changes in regional diversity are the result of changes in both local and turnover diversity, some environmental conditions such as human development greatly impact diversity levels for all three facets of diversity, and heterogeneous landscapes tend to have higher diversity levels, although functional and phylogenetic diversity present some exceptions to this pattern that we will discuss below. More interestingly, differences between the three facets of diversity can help us reveal the mechanisms that lie behind macroecological patterns at different spatial scales.

The importance of environmental gradients for determining taxonomic diversity has been widely documented, and it has been linked to energetic constraints at large scales (Hawkins *et al.*, 2003) as well as to environmental filtering at the community level (Leibold *et al.*, 2004; Cottenie, 2005; Tuomisto & Ruokolainen, 2006). Phylogenetic and functional aspects of diversity have recently been emphasized in the literature (Graham & Fine, 2008; Prinzing *et al.*, 2008; Cavender-Bares *et al.*, 2009). These studies usually focus on distinguishing trait conservatism and converging selection, and competition-based versus environmental filtering community assembly (Graham & Fine, 2008; Prinzing *et al.*, 2008; Cavender-Bares *et al.*, 2009). For example, competition is expected to increase trait diversity within local communities creating trait over-dispersion at the local level, as well as phylogenetic over-dispersion if those traits are phylogenetically conserved (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). Environmental filtering is expected to limit community members to those that are pre-adapted, and thus functionally similar, creating a spatial structure that can be explained solely by the spatial structure of environmental gradients (Cottenie, 2005; Legendre *et al.*, 2005; Tuomisto & Ruokolainen, 2006), as well as some phylogenetic clustering at the regional level if niche conservatism is strong (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). In all cases, what these studies suggest is that incorporating phylogenetic and functional aspects into ecological patterns should allow us to draw stronger conclusions regarding the mechanisms that have generated such diversity (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009).

Using spatial autoregressive models, we explained more than 60% of the variation on all facets of γ- and β-diversity (Tables 2 & 3), a rather high percentage compared with previous studies linking diversity to environmental gradients (Ruokolainen &

	Taxonomic	Phylogenetic	Functional
Intercept	34.61 ± 1.20***	−1.79 ± 0.17***	−1.28 ± 0.15***
Mean altitude	0.72 ± 0.37*	0.19 ± 0.04***	0.16 ± 0.03***
Rainfall range		−0.10 ± 0.03***	−0.05 ± 0.02*
Mean temperature	1.50 ± 0.43***	−0.16 ± 0.04***	−0.15 ± 0.04***
% Mixed	0.62 ± 0.28*		
% Meadows		−0.09 ± 0.02***	
% Scrub		−0.04 ± 0.02*	
FRAGM		0.06 ± 0.03*	0.05 ± 0.02*
Mean EVI	2.34 ± 0.35***	0.19 ± 0.04***	0.12 ± 0.03***
Standard deviation in EVI	−0.97 ± 0.29***	−0.12 ± 0.03***	−0.06 ± 0.02**
Landscape diversity	1.31 ± 0.31***	0.11 ± 0.04**	0.07 ± 0.03*
Taxonomic β-diversity		0.16 ± 0.00***	0.11 ± 0.00***
Model R^2	0.66	0.91	0.86

Table 3 Results from a simultaneous autoregressive (SAR) model relating β-diversity to the coefficient of variation (standard deviation divided by the mean) of environmental conditions within 50-km windows.

Results represent the coefficient estimates ± 1 standard deviation for regressions where each facet of diversity (taxonomic, phylogenetic or functional β-diversity) is the response variable. EVI, enhanced vegetation index; FRAGM, number of patches of each land use category (see Table 1).
Asterisks show the level of significance for each variable: ***$P < 0.001$; **$0.001 < P < 0.01$; *$0.01 < P < 0.05$.

Tuomisto, 2002; Tuomisto *et al.*, 2003; Gaston *et al.*, 2007). For both γ- and β-diversity, the spatial structure of the data played a preponderant role. Part of this spatial structure may arise from the fact that our analysis windows are overlapping. However, notice that an average of 11 plots was left out of the analysis within each window, meaning that neighbouring windows do not necessarily include the same plots. Moreover, environmental gradients would be highly correlated to diversity in the cases where a large overlap occurs, producing a pattern opposite to that which we observe.

The importance of the spatial component can arise in at least three other ways. First, the environmental gradients are themselves spatially structured (Legendre & Legendre, 1998; Haining, 2003). Therefore, it is unsurprising that the interactions between the environment and spatial autocorrelation explain such a large portion of variance, both in γ- and β-diversity, while environmental gradients on their own explain a small proportion of variance in diversity (Fig. 3). This interaction might well reflect the impossibility of separating environmental filtering from other processes that would generate the same type of spatial structure (Legendre *et al.*, 2005). Second, spatial structure could have originated with environmental gradients that were not considered in the analysis (Haining, 2003). This would result in a larger role for spatial structure per se (assuming that this missing environmental gradient is spatially autocorrelated) and a smaller role for the environment × space interaction. Third, dispersal can also generate spatially structured patterns (Cottenie, 2005; Kissling & Carl, 2008), and birds are known to be good dispersers due to their ability to fly (Paradis *et al.*, 1998). This makes it difficult to distinguish between assembly theories related to dispersal (lottery competition and mass-effects) and those related to environmental filtering (Leibold *et al.*, 2004). Taken together, our results suggest that dispersal plays a significant role in structuring bird communities. However, the role of

environmental filtering is more difficult to assess. For example, although the environmental gradients considered only explain about 10% of the variation in taxonomic diversity, the interaction between environmental gradients and spatial structure explains an additional 17% (Fig. 3a). This means that we are not able to tell whether that interaction term can be attributed to processes directly linked to environmental filters or to dispersal effects that just happen in a spatially autocorrelated environmental gradient. This ambiguity is particularly important for phylogenetic diversity, for which the interaction environment × spatial structure by itself explains 47% of the variation in γ-diversity.

In general, we found that a higher turnover in taxonomic diversity was associated with more heterogeneous landscapes, whereas functional and phylogenetic turnover could be associated with the opposite patterns (Table 3). The fact that turnover is not always associated with more heterogeneous landscapes is certainly puzzling from the theoretical perspective, but it has been found in previous studies. Gaston *et al.* (2007), for example, showed that bird taxonomic β-diversity at a global scale was negatively associated with landscape diversity, temperature and normalized difference vegetation index (NDVI) roughness, while it had a bell-shaped relationship to altitudinal roughness. In this context, the most interesting question here is why do phylogenetic and functional diversity respond differently to environmental heterogeneity. For the three facets, turnover seems to increase with variations in mean altitude, mean EVI and landscape diversity, while decreasing with variations in temporal deviations in EVI. This seems to indicate that turnover is higher in landscapes where EVI is spatially heterogeneous but temporally homogeneous. All these variables are therefore congruent with the hypothesis that more heterogeneous regions harbour more diversity in general. The fact that the percentage of development at the regional level negatively affects the three

facets of γ-diversity (Table 2) also suggests that the level of human impact in the landscape is playing a key role in determining all three facets of diversity. However, results also suggest that phylogenetic and functional turnover are higher in heterogeneous landscapes in terms of mean altitude, fragmentation and EVI, but in homogeneous landscapes in terms of rainfall range and mean temperature (Table 3). This suggests a topographic effect, where even regions with homogeneous climate but rough terrain can produce high phylogenetic and functional turnover. The fact that these responses are different from those observed in taxonomic β-diversity calls for further attention. One possible explanation is that topographic dispersal limitations are affecting particular functional groups, and are therefore expressed more evidently in functional and phylogenetic β-diversity (assuming ecological conservatism).

Finally, we explained a greater proportion of variance in phylogenetic γ- and β-diversity than what we did for functional diversity (see total R^2 in Tables 2 & 3). We can think of at least three reasons why this may be so. First, we could have missed some of the relevant environmental gradients that determine functional diversity but had a better selection of environmental gradients that affect phylogenetic diversity. Although this is possible, our models explained a large proportion of the variation in both types of diversity, and variable selection was carried out in the same way in both cases. Secondly, we could have made a poor choice for the life-history traits used to measure functional diversity. Functional traits used here have been widely advocated as representing a variety of life-history characteristics that are relevant for classing birds into functional groups (Petchey & Gaston, 2006; Sekercioglu, 2006; Cumming & Child, 2009). However, this classification is largely based on their Eltonian niche, i.e. the way species act on ecosystem processes through trophic interactions. An alternative would be to define functional groups based on the Grinnellian niche of species which determines the environmental variables that species can cope with (Devictor et al., 2010b). This latter niche would require other traits related to physiological limits and climate tolerance, and variations among species that are potentially embodied in phylogenetic relationships (Cadotte et al., 2009). Finally, a third alternative is that phylogenetic diversity is simply a more integrative surrogate than functional diversity when using any subset of life-history traits. Indeed, we may argue that the most direct way to reveal the strength of environmental filtering on functional diversity would be to look at those traits that are involved in local adaptations to environmental conditions. If we had complete knowledge about which traits are involved in such adaptations and if we could gather that information for all species involved, it would be logical to expect functional diversity to be a better indicator of community assembly processes than phylogenetic diversity (Díaz et al., 2007; Prinzing et al., 2008). However, we are often limited in the choice of trait characteristics that can be measured easily and are available for large-scale analyses (Petchey & Gaston, 2006; Petchey et al., 2007; Cumming & Child, 2009), and we often lack knowledge about which traits reflect efficient local adaptations. Therefore, the opposite argument, e.g. that phylogenetic diversity is a more integrative measure of functional diversity, can also be made (Cadotte et al., 2009).

The Rao quadratic entropy used here has the advantage of weighting species functional or phylogenetic distances by their relative abundances (Ricotta & Szeidl, 2009; de Bello et al., 2010; Mouchet et al., 2010). Phylogenetic and functional changes are therefore weighted not only by species compositions but also by how abundant the different species are. This might be highly relevant in cases where dominant species (in terms of relative abundance) also perform important ecosystem functions or come from a highly 'original' evolutionary branch. For example, the mass ratio hypothesis, which assumes that ecosystem function is mainly driven by dominant species, can only be tested by using abundance-weighted functional diversity indices (Díaz et al., 2007). On the other hand, carrying out the same analysis with presence–absence data reveals even stronger correlations between the three facets of diversity (see Devictor et al., 2010a), suggesting that abundance can greatly influence the overall functional or phylogenetic structure of communities but that the relative distributions of the three facets of diversity remain robust to the index used.

We have shown here that the Rao decomposition of diversity can be used to analyse the three facets of diversity under a common framework at different spatial scales (Pavoine & Dolédec, 2005; de Bello et al., 2010). To our knowledge this is the first time such an approach has been implemented on the three facets of diversity to study their relationships to the environmental gradients. We believe that this approach will help the understanding of diversity–environment relationships that are fundamental for linking ecological patterns to theory and to propose sound management actions in the face of global change. The multi-faceted spatial decomposition of diversity exemplified here represents a promising tool that can be generalized to study macroecological patterns integrating different spatial scales and different facets of diversity in many other systems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Phylogenetic ultrametric tree.
Appendix S2 Functional ultrametric tree.
Appendix S3 Details about partial regressions.

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BIOSKETCH

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