RESEARCH ARTICLE

Plant and animal diversity in a region of the Southern Alps: the role of environmental and spatial processes

Matteo Dainese · Livio Poldini

Abstract Different organisms respond to landscape configuration and spatial structure in different terms and across different spatial scales. Here, regression models with variation partitioning were applied to determine relative influence of the three groups of variables (climate, land use and environmental heterogeneity) and spatial structure variables on plant, bird, orthopteran and butterfly species richness in a region of the Southern Alps, ranging in elevation from the sea level to 2,780 m. Grassland and forest cover were positively correlated with species richness in both taxonomic groups, whilst species richness decreased with increasing urban elements and arable land. The variation was mainly explained by the shared component between the three groups in plants and between landscape and environmental heterogeneity in birds. The variation was related to independent land use effect in insects. The distribution in species richness was spatially structured for plants, birds and orthopterans, whilst in butterflies, no spatial structure was detected. Plant richness was associated with linear trend variation and broad-scale spatial structure in the northern part of the region, whilst bird richness with broad-scale variation which occurs on the external Alpine ridge. Orthopteran diversity was strongly related to fine-scale spatial structure, generated by dynamic processes or by unmeasured spatially structured abiotic factors. Although the study was carried out in relatively small area, the four taxonomic groups seem to respond to biodiversity drivers in a surprisingly different way. This has considerable implications for conservation planning as it restricts the usefulness of simple indicators in prioritizing areas for conservation purposes.

Keywords Climate · Elevation · Habitat heterogeneity · Human impact · Land use · PCNM · Variation partitioning

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Introduction

Understanding the factors controlling the spatial variability of species distribution and richness is one of the major tasks of biogeography (Huston 1994). Knowledge of the important driving variables is crucial for developing effective in situ conservation policies for sustainable land use (Gaston 2000). Even though the taxonomic dimension of biodiversity comprises a number of components, each operationally defined by a

number of indices, species richness has been used recently as a surrogate for diversity in general (Rosenzweig 1995; Gaston 1998), especially in biogeography and macroecology (Gotelli et al. 2009). Species richness also is an intuitive measure of obvious significance to managers and the public. Moreover, species richness is likely to remain a key variable for land-use planning due to logistic and financial constraints (Mac Nally and Fleishman 2002). Nevertheless, in species richness modeling one must consider that it is not possible to derive any information about the composition of species assemblages (i.e., we only know whether the species present are equitable in numbers or distribution or whether the community is composed of a few abundant species and many rare ones) (Van Dyke 2008; Guisan and Rahbek 2011).

In recent years the evaluation of diversity along elevational gradients has become a popular approach. General diversity patterns along elevational gradients seem likely to result from the combined effects of several complex, and often nonlinear, processes that covary with elevation (Lomolino 2001). Depending on the scale and taxonomic group, the spatial patterns observed in biogeography can be caused by multiple factors.

At macroecological scales, it is widely accepted that distributions of plants and animals are broadly constrained by their physiological tolerances to climatic factors (Woodward 1990). The interaction between energy and water is known to be an important driver of diversity patterns for several taxonomic groups (Hawkins et al. 2003; Whittaker et al. 2007).

Recent advances in biogeography (e.g., Atauri and de Lucio 2001; Thuiller et al. 2004; Luoto et al. 2007) have also revealed the strong impact of landscape configuration on species distributions. More specifically, because humans have transformed most of the Earth's land surface, land use may play a significant role as a driver of biodiversity (e.g., Heikkinen et al. 2004; Marini et al. 2008a, 2011; Yamaura et al. 2011). The assessment of the effects of landscape composition on biodiversity is best achieved when studying simultaneously several taxonomic groups that respond to different spatial scales (Mac Nally et al. 2004; Bossenbroek et al. 2005).

Environmental heterogeneity, typically measured as topographic and habitat complexity, is another factor that determines the patterns of species richness by its influence on species turnover (Kerr and Packer 1997) and/or species diversification rates (Qian and Ricklefs 2000). Structurally complex environments may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Tews et al. 2004; Ruggiero and Hawkins 2008). As elevational gradients might be associated with large variations in topographical, climatic and habitat heterogeneity, this factor should be included in analyses more often (Marini et al. 2011).

Understanding how environmental variables influence the spatial patterns of species diversity requires the use of methods that take into account both spatial autocorrelation in the data sets and collinearity between explanatory variables (Heikkinen et al. 2004). Including the spatial structure in the modelling of species–environment relationships enables us to make better predictions of species occurrence. It also enables us to determine when spatial structure is mainly due to biotic interactions, to an underlying unmeasured environmental factor or to a common spatial structure shared by species data and environmental variables (Borcard et al. 1992).

The availability of extensive taxonomic surveys carried out on defined geographical units and their analysis in relation to environmental information are powerful tools to help us explore this issue at different spatial scales (Marini et al. 2008a). There is actually a need for multiscale and multitaxa approaches taking into account the distinct responses of different species guilds to landscape structure and composition (Grand et al. 2004; Cushman et al. 2008).

Comparative analyses are essential to place our understanding of pattern and process in a more comprehensive framework (Rowe 2009). In particular, the omission of potentially important components such as land use or environmental heterogeneity might influence understanding of the mechanisms underlying the observed species–elevation relationship due to the common statistical dependence between measures of the different processes (Marini et al. 2011). Our study region (Friuli Venezia Giulia Region, NE Italy), occupied by the Alps northwards and by plains southwards, provides a suitable model system to explore the impact of climate, land use and environmental heterogeneity on spatial distribution of plant and animal richness. We used four model communities (plant, bird, orthopteran and butterfly) to address the following questions: (1) What are the main

environmental factors determining species richness of different taxonomic groups? (2) How much does the relative importance of the three sets of variables differ between the taxonomic groups? (3) Does the incorporation of spatial structure improve the explanatory power of the environmental models in explaining the distribution of plant and animal species richness?

Methods

Study region

The study area was the Friuli Venezia Giulia Region (north-east Italy), an area of 7,845 km^2 (WGS84: N 45°34.5′–46°38.3′, E 12°18.1′–13°55.1′) on the southern border of the European Alps. About 43% of the territory is occupied by mountains, 38% by plains and the remaining 19% by hills. The Adriatic coast extends for ca. 150 km, from the mouth of the Tagliamento mouth (west) to the Slovenian border (east). The elevation range varies from sea level to 2,780 m a.s.l. The local climates vary from sub-Mediterranean conditions in the south-east part to continental conditions in the inner valley. Precipitation differences were mainly related to orographic effects. Moving northwards, the highest precipitation occurred on the external Alpine ridge, where the humid air coming from the sea was forced to rise over the mountain range. The average annual rainfall varies from ca. 1,000 mm year^{-1} along the Adriatic coast to ca. 3,000 mm year^{-1} of Julian Prealps. The annual mean temperature is ca. 8.7°C, and varies from ca. −1.5°C in the Alps to ca. 14.1°C along the Adriatic coast.

Data on taxa distribution

Information on the distribution of plants was extracted from the floristic atlas of the Friuli Venezia Giulia Region (Poldini 2002). The region was subdivided into a regular grid of 81 cells or operational geographic units (OGUs, basic area: ¼ of a sheet of the IGM map of Italy—1:50.000) each spanning 11 km × 13 km (Appendix A in supplementary material). Information on the distribution of birds was extracted from the checklist and distribution of the Friuli Venezia Giulia fauna database (AA.VV. 1991) and elaborated by Bressan (2005). Finally, information on the

distribution of Orthoptera (Ensifera and Caelifera) and diurnal Lepidoptera (Hesperioidea and Papilionoidea), hereafter labelled as butterflies, were obtained from the checklist and distribution of the Italian fauna database (Ruffo and Stoch 2007). Only native species were considered in the subsequent analysis. To give same reference scale between the taxa, orthopteran, butterfly and bird species richness were estimated to the scale of the floristic atlas (81 cells of 11 km × 13 km). Grid cells at the border of the region were considered if >50% of their area lies within the region. This resulted in valid information of species occurrences for 57 grid cells (Appendix A in supplementary material).

Environmental variables

Climate

Annual precipitation (PREC) was considered as an indicator of water availability, and annual mean temperature (TEM) as a measure of available energy. The data were retrieved from continuous raster-based climatic maps with a resolution of 100 m × 100 m (1991–2008) which were provided by the Meteorological Observatory of Friuli Venezia Giulia (OS-MER). A drought index was also quantified by computing the ratio between annual mean potential evapotranspiration (PET) and annual precipitation, where a value below 1 indicates a positive water balance and a value above 1 indicates a negative water balance. PET was computed using the formula described in Holland (1978) [PET = (1.2 × 1,010) exp (−4,620/T_K), where T_K is the annual mean temperature in kelvin]. The formula estimates the potential amount of water which could be evapotranspired in 1 year under optimal conditions of soil moisture and vegetation conditions.

Land use

The habitat classification was derived from a vector-based CORINE biotope map (1:50.000) of the region (Servizio Valutazione Impatto Ambientale—Direzione Centrale Ambiente e Lavori Pubblici, Trieste, Italy). The vector-based data were converted to a raster model with a cell size of 25 m × 25 m. Then, the proportion of the habitat classes within each cell

was calculated using FRAGSTATS (version 3.3; McGarigal et al. 2002). The European Nature Information System (EUNIS) Habitat Classification, a standard classification of European habitats developed by the European Environment Agency (http://eunis.eea.europa.eu/habitats.jsp), was adopted. CORINE biotope types were transferred to the EUNIS Habitats Classification based on the classification scheme of Lapresa et al. (2004). In total, 26 habitat classes were used (Table 1). The EUNIS habitats were grouped into four main land use classes: (1) water habitats (WAT), (2) grassland habitats (GRA), (3) forest habitats (FOR) and (4) man-made habitats (MAN, urban elements + agricultural land cover). In order to identify which habitat type accounted for the greatest variation in species richness, a separate forward selection within each of the four land use groups was performed (Appendix B in supplementary material). In subsequent analyses, land use classes (WAT, GRA, FOR and MAN) have been assembled using forward selected habitats (e.g., in plant model, E1, E2 and E4.4 habitat cover were summed into grassland land use class).

Environmental heterogeneity

To provide measures of environmental heterogeneity within each cell, two indices were derived as follows. Habitat diversity (HAB-D) was quantified using the modified Shannon diversity index proposed by Jost (2006) [$\exp(-\Sigma p_i \ln p_i)$], where p_i is the relative cover of each land-use class within the cell. HAB-D was calculated using the 26 habitats described above. Topographic roughness was calculated using the standard deviation of elevation within each cell (ELE-SD). Information on elevation was derived from a digital elevation model (DEM) with a resolution of 10 m × 10 m.

Spatial variables

Principal coordinates of neighbour matrices (PCNM) was used for detecting and quantifying spatial patterns in species data across a wide range of scales (see Borcard and Legendre 2002; Borcard et al. 2004 for details). The PCNM method is actually a special case of a wider family of methods that are now called MEM (Moran's eigenvector maps; Dray et al. 2006). This approach is based on a principal coordinate analysis of a truncated geographical distance matrix among sampling locations. The method creates a set of explanatory spatial variables (i.e., PCNM variables) that have structures at all scales encompassed by the data matrix, and determines to which of these variables the response data (univariate or multivariate) are statistically responding.

The geographical centroids of each grid cell were used as input spatial relationships. The PCNM method was performed as follows: (1) A matrix of Euclidean distance among the geographic coordinates of grid cells was constructed. (2) Each matrix was then truncated at the distance between nearest neighbors (smallest distance that keeps all sites connected into a single network). (3) The truncated matrix was then analyzed by principal coordinate analysis (PCoA). The eigenvectors that model positive spatial correlation (Moran's I larger than expected value of Moran's I) were retained and represent the spatial structure in the dataset. The eigenvectors associated with the higher eigenvalues represent broader-scale variations, while eigenvectors derived from the smaller eigenvalues represent finer-scale variations. PCNM variables were created using the R package "PCNM" (Legendre et al. 2010).

Data analysis

The R language v2.10.1 (R Development Core Team 2009) was used for all statistical analyses. To avoid multicollinearity among the predictors of the same environmental category the following methods were used (Appendix C in supplementary material): (i) bivariate regressions were performed to evaluate the explanatory power of each predictor for the species richness of the four taxonomical groups; (ii) correlations between the predictors of the same environmental category were examined to evaluate the degree of collinearity; (iii) in the case of collinearity among the predictors (Pearson correlations $r > 0.60$), only the best individual predictor was kept in its model. Climatic variables were significantly correlated with each other, so DRO in plant model, PREC in bird model and TEM in orthopteran and butterfly models were used as the best predictors for the climate group. FOR and MAN were strongly correlated in plant model, so FOR was omitted from land-use variables. Again FOR was strongly correlated with GRA and

Table 1 Descriptive statistics and abbreviations of the explanatory variables calculated for each of the 57 cells in Friuli Venezia-Giulia Region, and used in the analyses

Variable names and explanation		Unit	Mean	Min	Max
Climate					
PREC	Annual precipitation	mm	1551	976	2465
TEM	Annual mean temperature	°C	10.18	4.75	13.68
DRO	Drought index (PET/Precipitation)	–	0.70	0.33	1.23
Land use					
Water habitats (WAT)					
C1	Surface standing waters	%	0.36	0.00	2.01
C2	Surface running waters	%	0.23	0.00	2.01
C3	Littoral zone of inland surface waterbodies	%	1.42	0.00	8.60
D2	Valley mires, poor fens and transition mires	%	0.03	0.00	0.53
Grassland habitats (GRA)					
E1	Dry grasslands	%	1.71	0.00	21.73
E2	Mesic grasslands	%	1.70	0.00	8.78
E4.3	Acid alpine and subalpine grassland	%	0.70	0.00	10.36
E4.4	Calcareous alpine and subalpine grassland	%	2.03	0.00	12.38
E4.5	Alpine and subalpine enriched grassland	%	0.15	0.00	1.86
Forest habitats (FOR)					
F2	Arctic, alpine and subalpine scrub	%	4.91	0.00	31.88
F3	Temperate and mediterranean-montane scrub	%	1.22	0.01	7.28
F9	Riverine and fen scrubs	%	0.12	0.00	1.47
G1.1	Riparian and gallery woodland	%	0.63	0.00	3.40
G1.4	Broadleaved swamp woodland not on acid peat	%	0.08	0.00	1.05
G1.6	[*Fagus*] woodland	%	15.20	0.00	55.24
G1.7	Thermophilous deciduous woodland	%	5.40	0.00	30.68
G1.8	Acidophilous [*Quercus*]-dominated woodland	%	2.27	0.00	27.32
G1.A	Meso- and eutrophic [*Quercus*] and related woodland	%	1.78	0.00	20.71
G3.1	[*Abies*] and [*Picea*] woodland	%	8.23	0.00	55.17
G3.2	Alpine [*Larix*] − [*Pinus cembra*] woodland	%	1.72	0.00	12.23
G3.5	[*Pinus nigra*] woodland	%	4.00	0.00	23.83
Man-made habitats (MAN agricultural + urban elements)					
FB	Shrub plantations	%	1.93	0.00	20.02
G1.D	Fruit and nut tree orchards	%	0.19	0.00	1.44
I1	Arable land and market gardens	%	32.27	0.00	89.66
I2	Cultivated areas of gardens and parks	%	0.16	0.00	1.40
J	Constructed, industrial and other artificial habitats	%	6.46	0.00	30.26
Environmental heterogeneity					
HAB-D	Habitat diversity [exp(Shannon index)]	–	5.60	1.50	10.52
ELE-SD	Topographic roughness (SD of elevation)	m	210.07	0.68	472.86

MAN in orthopteran model, so FOR was omitted from land-use variables. Quadratic terms were added to the models to detect nonlinear relationships. To avoid a high degree of collinearity among the terms, each of the predictors were centred and then squared (Quinn and Keough 2002).

After that, further analyses were carried out:

1. A separate forward selection was performed within each of the three sets of explanatory variables (climate, land use and environmental heterogeneity) to select significant predictors ($P < 0.05$ after 999 random permutations) which accounted for the greatest variation in plant, bird, orthopteran and butterfly species richness. The problems of the classical forward selection were minimized by applying the double-step procedure proposed by Blanchet et al. (2008). This procedure corrects for the overestimation of the proportion of explained variance by using two stopping criteria: (1) 0.05 significance level, and (2) adjusted-R^2 (adj-R^2) of the global model. Thus, one runs a multiple regression with all explanatory variables included and uses the adj-R^2 of this model as another stopping criterion. Only these selected variables were used in subsequent analyses. Forward selection was performed using the R package 'packfor' (Dray et al. 2007). One cell was excluded as an outlier (Cook's distance > 1.5). Afterwards, multiple regression models were generated including the previous forward selected variables and used their standardized regression coefficients to rank their relative influences on taxonomic richness, since these relationships depend on the influence of the other variables. Sometimes these partial coefficients have widely different values, and even signs opposite to those of the simple linear regression models. Standardized regression coefficients were calculated multiply the regression coefficient of unstandardized variables by the ratio between the standard deviation of the respective independent variable and the standard deviation of the dependent variable (Quinn and Keough 2002).

2. Variation partitioning (VP) was applied to determine the relative influence of climate, land use and environmental heterogeneity. The variation in species richness was decomposed using a series of (partial) regression analyses implemented in the 'vegan' package for R (Oksanen et al. 2008). The total explained variation (TVE) in species richness was decomposed into seven components: the pure effect of climate (C), land cover (L), and environmental heterogeneity (H); three first-order joint components (C∩L, C∩H and L∩H); and the joint component among the three groups (C∩L∩H). The variation explained in each model was reported as the adjusted R^2 (R^2_{adj}), which takes the number of predictor

variables and sample size into account to prevent the inflation of R^2 values (Peres-Neto et al. 2006). When a negative R^2_{adj} was obtained, we interpreted it as a zero value (Peres-Neto et al. 2006), which means that not all fractions of one VP always add up to a perfect 100%.

3. The forward selection procedure described above was performed to select PCNM variables. Due to a significant liner trend from southwest to northeast which was observed in plant and orthopteran species richness, the response variables were detrended (species richness were regressed on the X–Y coordinates and the residuals were retained as response variables) before forward selection. A trend indicates the presence of a spatial structure at a scale broader than the sampling extent and this makes these variables non stationary. It may also obscure other structures in the dataset that could be more optimally modelled by PCNM variables (Borcard et al. 2004). Forward selection was repeated for each taxon individually, so that a different number of PCNM variables were selected (plants = 9; birds = 7; orthopterans = 7; butterflies = 0). After that, environmental (climate, land use and environmental heterogeneity) and spatial (PCNM variables and X–Y coordinates in presence of linear trend) variables were used in VP to quantify the unique and joint fractions of variation explained by these matrices. For the environmental information the previous forward selected variables were used. The response data were not detrended prior to VP, but rather linear trend was tested and incorporated it in the partitioning procedure if it was significant. In order to access the relative importance of spatially structured environmental variation and spatial effects alone, at different scales, a further VP was performed. Forward selected PCNM variables were divided into two groups: broad scale (PCNM between 1 and 7) and fine scale (PCNM between 12 and 21). The groups have been formed by drawing maps of the significant PCNM variables and selecting them according to the scale of the patterns they represent (Borcard et al. 2011). The choices however are arbitrary: there is no general rule defining what is broad or fine scale (Borcard et al. 2011). For plants and orthopterans, linear trend (X–Y coordinates) was considered as source of variation like PCNM variables.

Finally, a further forward regression was used (as above) to determine the main habitat variables related to PCNM vectors at broad and fine scale. For a

graphical interpretation of the spatial filters, each vector was plotted in an ordination diagram with fitted smooth surfaces using thinplate splines in general additive models in function 'ordisurf', in the 'vegan' package (Oksanen et al. 2008).

Results

The total number of species found in the study area is 2,289 plants, 177 birds, 135 orthopterans and 134 butterflies. The number of species richness recorded in individual cell ranged from 358 to 1,074 for plants, from 6 to 101 for birds, from 1 to 90 for orthopterans and from 1 to 90 for butterflies. Species richness showed a hump-shaped relationship with elevation in plants, birds and butterflies, while a positive linear relationship in orthopterans (Fig. 1).

Environmental models

In the climate model, plant richness was negative related to DRO, while bird richness was positively related to PREC (Table 2; Fig. 2). Orthopteran showed a negative relationship with TEM, while

butterfly richness showed instead a hump-shaped relationship. The explained variation ranged between 6.2 and 49.4%.

The richness of the four taxonomical groups was associated with several land use variables (explained variation range between 23.0 and 62.5%) (Table 2). The plant model included only the linear term of MAN. The bird model included the MAN (linear and quadratic terms) and the linear term of FOR. The orthopteran model included only the linear term of GRA, while the butterfly model included the GRA (linear and quadratic terms) and the linear term of FOR. Plant richness showed a linear negative relationship with MAN, while bird richness a nonlinear negative relationship (Fig. 2). Orthopteran richness showed a linear positive relationship with GRA, whilst bird and butterfly richness with FOR (Fig. 2).

With regard to the environmental heterogeneity model, only plants and birds showed a significant relationship (explained variation range between 40.6 and 56.1%), mainly with HAB-D (Table 2).

Land use variables had the strongest standardized coefficients in plant and insect models, suggesting that plant was mainly driven by MAN, whilst orthopteran and butterfly species richness by GRA (Fig. 3). In the

Fig. 1 Scatterplots of a plant, b bird, c orthopteran, and d butterfly species richness per cell versus elevation in the 57 cells (11 km × 13 km). Trends are shown by fitting linear or quadratic functions when significant (F-test, $P < 0.05$)
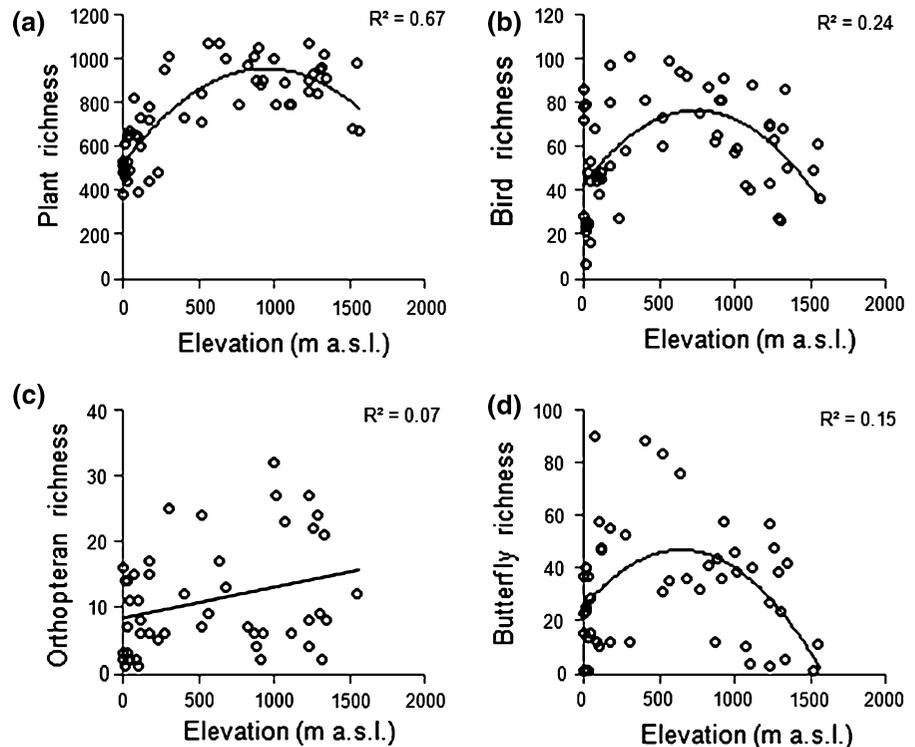
Table 2 Summary of the relationships between species richness and the selected predictors for climate, land use, and environmental heterogeneity variables

	Climate		Landscape		Heterogenity	
	Adj-R^2		Adj-R^2		Adj-R^2	
Plant	49.4	DRO (−)	62.5	MAN (−)	56.1	HAB-D (+)
						ELE-H (+)
Bird	17.3	PRE (+)	39.7	FOR (+)	40.6	HAB-D (+)
				MAN (+)		
				MAN^2 (−)		
Orthopteran	6.2	TEM (−)	23.0	GRA (+)	–	n.s
Butterfly	11.0	TEM (−)	24.2	GRA (+)	–	n.s
		TEM^2 (−)		GRA^2 (−)		
				FOR (+)		

Tests of the variables were performed within each taxa (plant, bird, orthopteran and butterfly) and environmental group, separately

In each analysis, linear terms as well as curvilinear terms for each predictor were included to test for nonlinear relations. Each of the predictors were centred and then squared. Only terms significant at $P < 0.05$ were included. (+) or (−) indicate direction of the effect. One cell was excluded as an outlier (Cook's distance > 1.5). See Table 1 for variable definition

bird model, HAB-D and MAN had the strongest standardized coefficients. Climate variables had also important effects on plant, bird and butterfly species richness, but they were substantially lower than those of land use variables. While ELE-SD was positively related with plant species richness in the simple regression model (Appendix C in supplementary material) or forward selection model (Table 2), the multiple regression model yielded a negative relationship (Fig. 3).

The VP of the plant model indicated that the pure effects of the three groups were small (<10%) and that almost all of the variation was explained by the shared component between the three groups (48%) (Fig. 4a). The VP of the bird model showed that almost all of the variation was related to the shared component (35%) between landscape and environmental heterogeneity (20%) and between the three groups (15%) (Fig. 4b). The VP of the orthopteran (Fig. 4c) and the butterfly (Fig. 4d) models indicated that almost all of the variation was related to pure land use effect (15 and 19% respectively), with additional impacts of the shared component with climate (summing to 5–8%).

Spatial models

Forward selection of the spatial variables included 9 PCNMs in the plants spatial model, 8 PCNMs in birds, 7 PCNMs in orthopterans, while no significant

PCNMs were selected in the butterflies' model. At broad-scale, PCNMs were mainly related to arable land and mixed woodland and scrub in plants, to deciduous and mixed woodland and scrub in birds, and to mixed woodland in orthopterans (Fig. 5; Appendix D in supplementary material). At fine-scale, PCNMs were mainly related to man-made habitats in plants, to water habitats in birds, while no significant variables were selected in orthopterans' model.

Variation partitioning revealed that ca. 20–30% of variation in plant, bird and orthopteran models was due to pure spatial components (Fig. 4). No significant spatial structure was found in the butterfly model (Fig. 4). In the case of the plant model the largest part of the variation in species richness was explained by the share component between environmental and spatial attributes (64%). The spatial structure variation, either alone or in conjunction with environment, was primarily due to linear trend variation (49%) and broad-scale variation (23%), whilst fine-scale variation had lower importance (8%) (Fig. 4a). Both spatial components, pure (24%) and joint with the environment (27%), reach a comparatively substantial value in bird model, as well as the pure environmental variables (20%). The influence of space resulted mainly from broad-scale variation (45%) (Fig. 4b). The VP of orthopteran models indicated that most of the variation was related to spatial components, i.e. a relatively large proportion was a pure spatial effect

Fig. 2 Scatterplots of the best individual predictor (original value—uncentred data) in each environmental group (climate, land use and environmental heterogeneity) for **a** plant, **b** bird, **c** orthopteran, and **d** butterfly species richness. Trends are shown by fitting linear and quadratic functions when significant (F-test, $P < 0.05$). The plots were One cell was excluded as an outlier (Cook's distance > 1.5)
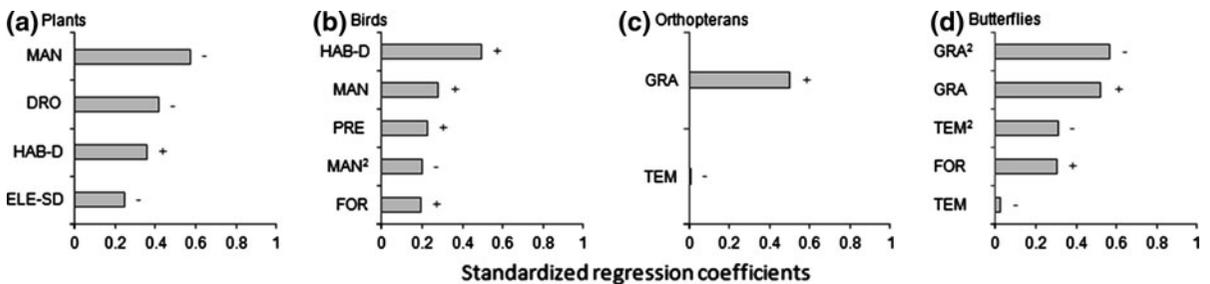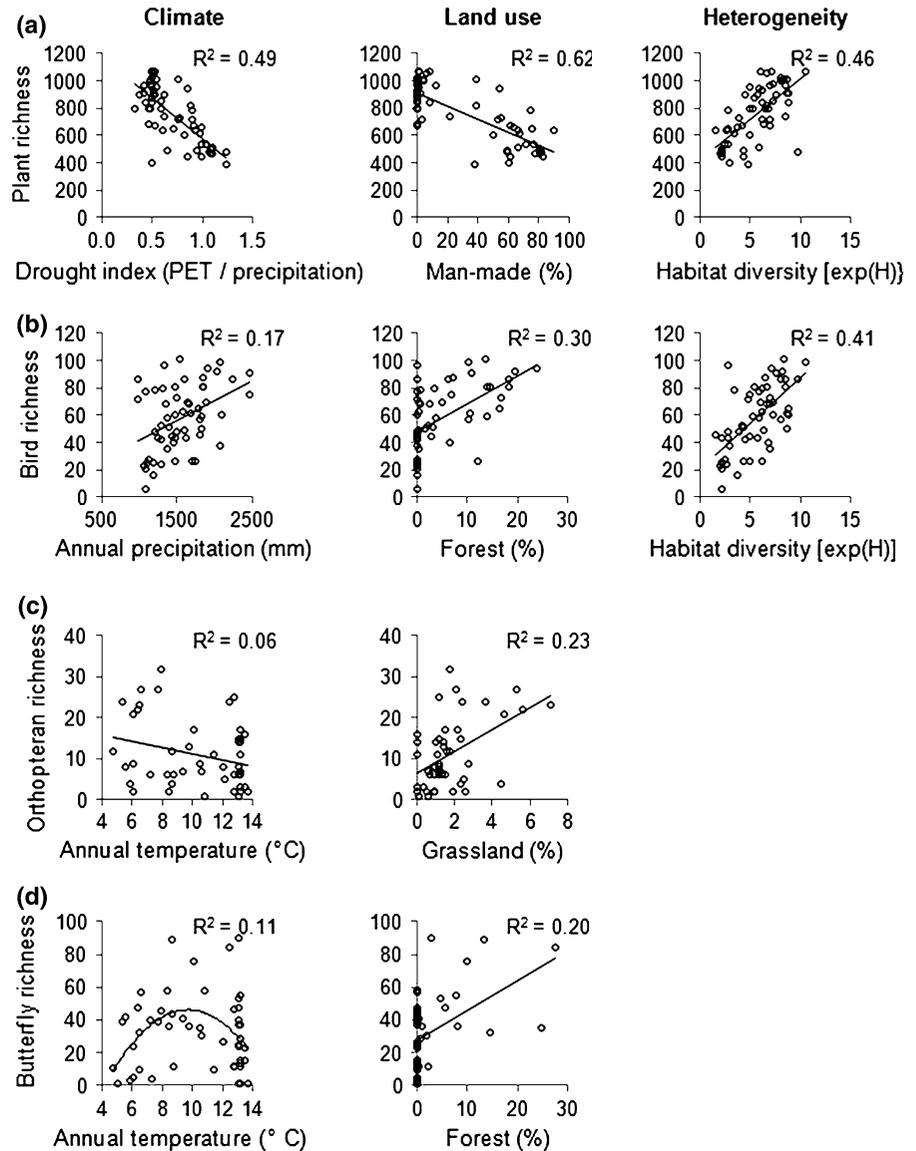

Fig. 3 Standardized partial regression coefficients of forward select variables for **a** plant, **b** bird, **c** orthopteran, and **d** butterfly species richness. For each taxa, a multiple regression model was performed including all the forward selected variables together (see Table 2). The models are shown, ranked in decreasing standardized regression coefficients. The direction of the relationship is indicated by (+) or (−)
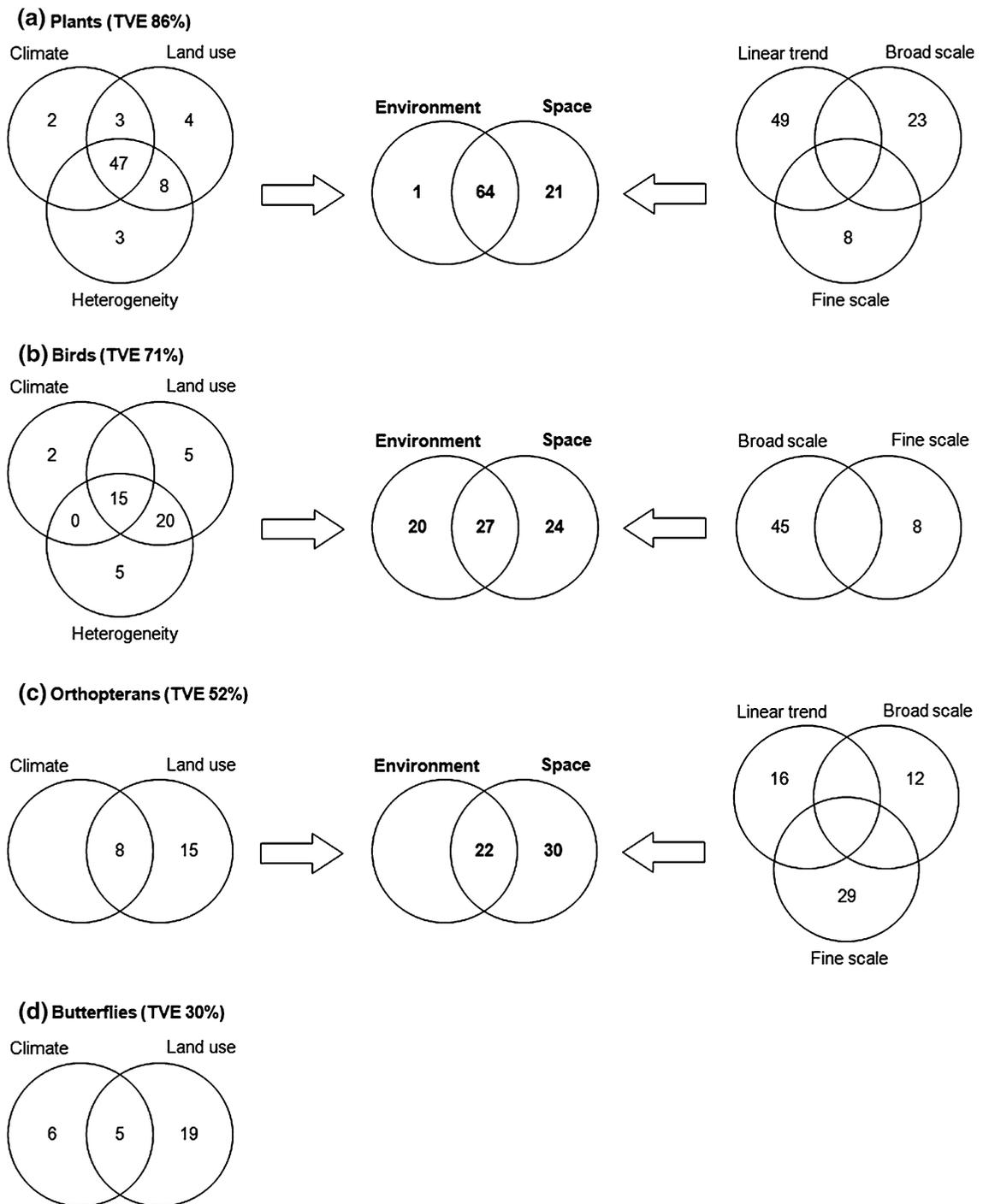
Fig. 4 Variation partitioning of **a** plant, **b** bird, **c** orthopteran, and **d** butterfly species richness into environment and space (adjusted R^2 in %). The partition of the environmental fraction is provided, showing the relative contribution of the climate, land use and environmental heterogeneity components. The partition of the spatial fraction is also provided, showing the relative contribution of the linear trend (X–Y coordinates), broad-scale (PCNM between 1 and 7) and fine-scale (PCNM between 12 and 21) components. Negative or null fractions are not shown
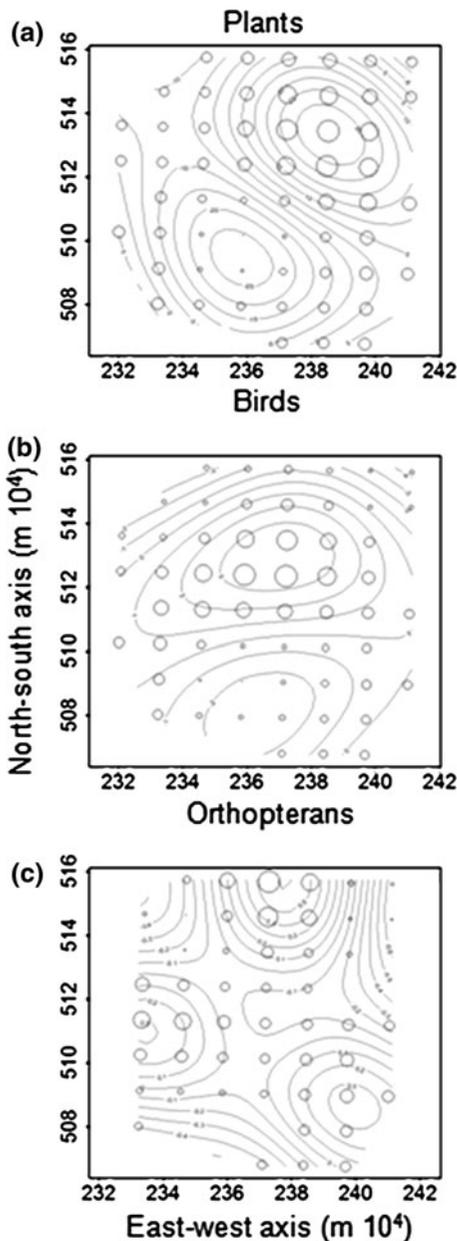
Fig. 5 Broad-scale spatial structure of species richness, with fitted smooth surfaces using thinplate splines in general additive models (GAM). The size of the symbols is associated with detrended values, from negative (*small symbols*) to strongly positive values (*larger symbols*). Spatial models are calculated from detrended species richness (corresponding to the residual variation after regression on X–Y coordinates), using the PCNM variables associated to broader-scale variations: **a** plant (PCNM 1, 3, 5, 6, 7), **b** bird (PCNM 3, 4, 5, 6, 7), and **c** orthopteran (PCNM 6, 8). Splines represent a smooth fitted surface of estimated detrended species richness for each site

(30%), with substantial additional impacts (22%) of spatially structured environmental component. In this instance, spatial structure was primarily due to fine-scale variation (29%) (Fig. 4c).

Discussion

Elevation gradients in species richness

The relationship between elevation and species richness reflects the expected hump-shaped pattern found in several other studies (see Rahbek 2005 for thorough review), except for the orthopteran model. Species richness and elevation often show complex relationships, which are dependent on the taxonomic group and gradient considered (Rahbek 1995). The overall pattern could not be attributed to a single universal explanation but rather to a combination of natural and anthropogenic factors that influence species richness. The relationship between plant richness and elevation shows a peak in richness occurring between ca. 800 and 1,100 m. The greatest species richness is concentrated in weakly disturbed cells with high environmental heterogeneity, dominated by grassland and forest (*Fagus* woodland and *Picea* woodland). Regarding bird and butterfly, the relationship shows a peak in richness occurring at a lower altitude ca. 600 and 800 m. The greatest number of these species is concentrated in warmer and more urbanized sites, dominated by thermophilous forest, dry and mesic grassland. In contrast to the most frequently observed patterns in species richness along elevational gradients (hump-shaped and monotonically decreasing; see Rahbek 2005), orthopteran shows a monotonic increase in richness with elevation. Changing habitat features along the elevation gradient probably determine the richness distribution; in fact grassland habitats show a positive relationship with elevation (Appendix A in supplementary material). This coincides with the dependence of most grasshopper species to open grasslands (Steck et al. 2007). An additional explanation to this relationship is that the influence of range size distribution on species richness patterns is related to the spatial scale or grain at which different taxa perceive the environment, according to their body size and/or dispersal capabilities (see Rahbek 2005).

Climate

The results show that water-energy dynamics generate important underlying gradients that determine species richness, as observed by several studies (Hawkins et al. 2003; McCain 2007; Whittaker et al. 2007; Marini et al. 2008a, 2011; Ruggiero and Hawkins 2008). However, the variation partitioning indicates that the independent explanatory power of climate variables is low, but its influence is almost completely shared with land use and environmental heterogeneity. This overlap does not imply that the pure effect of climate was unimportant in shaping the overall plant richness, only that its effect was not separable when considering the whole gradient (Marini et al. 2011).

Along elevation gradients, richness should be reduced by low energy availability at high elevations and the interplay of low water availability and high energy at low elevations (McCain 2007; Marini et al. 2011). Our findings are consistent with this explanation and highlight especially the role of water availability on plant and bird species richness patterns (i.e., the highest species richness occurred in the elevational zone where water availability is maximized). Clearly, water and energy regimes are essential to the physiology of plants and directly influence distribution and species richness (O'Brien 1993; Hawkins et al. 2003; Krömer et al. 2005); but for animal richness patterns, the question of interest becomes the relative importance of direct (physiological) and indirect (resource) effects of water and temperature on species richness patterns (Hawkins et al. 2003).

With regard to orthopteran we found instead a weak negative relationship between species richness and temperature. This pattern might be partially related to the co-variation between elevation and grassland cover, as seen above.

Land use

Land use accounts for a higher proportion of the total variance in orthopteran and butterfly species richness models. Grassland cover, followed by forest cover, has the strongest influence on these taxa. This result is in agreement with several studies, which show that grassland and forest are suitable land-cover types for many species, due to the large internal heterogeneity of these habitats, which is likely to support more ecological groups (Kivinen et al. 2006; Marini et al. 2008a).

The amount of man-made habitats is the best predictor of plant species richness, explaining a large proportion of variation, although its influence is almost completely shared with climate and environmental heterogeneity. Man-made habitat cover also contributes substantially to the bird richness model. An increase of urban elements and arable land shows a decreasing of species richness, although the shape of the relationships is different among taxonomical groups. In plants, species richness decreases linearly with an increase of man-made habitat cover, but nonlinearly in birds where species richness shows no response to man-made habitats up to intermediate cover, but declines rapidly when man-made habitat cover exceeds 40%. Although urbanization, along with agricultural intensification, is one of the most important threats to biodiversity (Matson et al. 1997; Tilman et al. 2001; McKinney 2002; Ricketts and Imhoff 2003; Firbank et al. 2008), the presence of intermediate levels of human disturbance seems to promote bird richness, as reported in previous studies (Chace and Walsh 2006; McKinney 2008). However, our results confirm the decline of species richness in lowland where human settlements and agricultural land are mainly concentrated. As demonstrated by several studies (Donald et al. 2001; Steck et al. 2007; Marini et al. 2008b; McKinney 2008), in temperate European countries, changes in land-use practices associated with urbanization and agricultural intensification have led to a structural transformation of the rural landscape. These changes of local habitat quality and landscape structure threaten the survival of plant and animal species that depend on semi-natural habitats (Tscharntke et al. 2005).

Environmental heterogeneity

Environmental heterogeneity is positively correlated with plant and bird species richness; though explaining a large proportion of variation, its influence is almost completely shared with climate and/or land use. The importance of environmental heterogeneity has recently been highlighted for several taxonomic groups in studies of elevational gradients (Ruggiero and Hawkins 2008; Rowe 2009; Marini et al. 2011).

Our results support the heterogeneity hypothesis for birds and plants, which predicts an increase of richness with the increasing complexity of environmental conditions (Shmida and Wilson 1985), while in insect

diversity no relationship has been shown. An increase in the number of habitat types or greater structural complexity in vegetation can provide more resources than a more uniform environment and may therefore support a greater number of species (Huston 1994). The different response to environmental heterogeneity by different groups of species shows the importance of the scale on which these groups of species perceive the landscape (Atauri and De Lucio 2001). In their review, Tews et al. (2004) stressed that the spatial scale on which measurements are made is crucial. Therefore, they state that: (i) based on the species group, the spatial scale determines the type of structural variable that has to be chosen as different scales require different appropriate variables; (ii) the effect of habitat heterogeneity relative to the structural variable measured may vary depending on the spatial scale. For example, Brose (2003) showed that effects of habitat heterogeneity for ground beetle assemblages were positive on the micro- and meso-scale while they were non-significant on a macro-scale.

Noteworthy the change in sign observed for topographic roughness in plant richness models. A possible explanation for the observed change in sign may be due to the collinearity among the variables. Severe collinearity can have important effects on the estimated regression coefficients, even changing their sign (Quinn and Keough 2002).

Role of spatial patterns

The incorporation of spatial structure provides additional explanatory power in plant, bird and orthopteran models (21, 24 and 30% respectively), when spatial variables are included in the models. For plants, the largest part of variation in species richness is explained by the joint effect between environmental variables and spatial structure (64%). Plant species richness is positively associated with broad-scale spatial structure in the northern part of the region (Fig. 4a), in addition to the liner trend from southwest to northeast. However, this spatial trend is already explained by the variables included in the environmental models: broad-scale PCNM variables are mainly related to cover of *Picea* woodland, arable land, alpine grassland and scrub (Appendix D in supplementary material). Marini et al. (2008a) reported the same results found in our study, where clear spatial trends in plant species richness

distribution were observed, but these strongly overlapped with the environmental factors.

In the bird model, the selected spatial variables explain a significant fraction of the diversity variation at our study site, suggesting that bird diversity is spatially structured (Legendre 1993). The highest bird richness occurs mainly on the external Alpine ridge (Fig. 4b; Appendix A in supplementary material). The results suggest that bird richness is primarily controlled by a broad-scale environmental gradient, but that within the confines of this gradient the finer scale patchiness could be due to other spatial processes. Among them, broad-scale variables are more important than the small-scale ones. Much of the broad-scale variability is related to deciduous and thermophilous forest cover. The detected fine-scale spatial variability is more likely to be related to the littoral zone of inland surface waterbodies.

Orthopteran diversity is strongly related to pure spatial variation, displaying mainly fine-scale spatial structure. No environmental influence could be related to the fine-scale pattern. Fine-scale spatial patterns portray spatial autocorrelation, generated by dynamic processes regulating species richness (e.g., dispersal, biotic interactions) or by unmeasured, spatially structured abiotic factors (Borcard et al. 2004).

With regard to the butterfly model, the absence of spatial structure could mislead and suggest that neutral mechanisms (i.e., biotic processes such as dispersal, growth, mortality, interspecific competition, or predation), which underlie the metapopulation theory (Hanski 1999) and the neutral theory of biodiversity (Hubbell 2001), play a negligible role in determining species richness distribution. Instead, the absence of spatial structure in the butterfly model in our study may be due to the spatial scale at which we analyzed the data. Probably, the coarse resolutions of our species distribution models are unable to capture the spatial component that determines butterfly species richness distribution (Rahbek 2005).

Conclusions

Our results showed a significant effect of environment and spatial structure on species richness. The study revealed that the observed diversity patterns cannot be attributed to a single universal explanation, but rather to a combination of environmental and spatial processes. As diversity patterns have proven to be highly

complex, the omission of potentially important components might influence understanding of the mechanisms underlying these patterns. Although the study was carried out in relatively small area, the four taxonomic groups seem to respond to biodiversity drivers in a surprisingly different way. This has considerable implications for conservation planning as it restricts the usefulness of simple indicators in prioritizing areas for conservation purposes. Moreover, it highlights the importance to generate complex and multi-scale approaches for understanding mechanisms that generate and maintain diversity in different taxonomic groups, allowing us to adequately address their conservation needs.

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