

Research paper

Landscape heterogeneity as a surrogate of biodiversity in mountain systems: What is the most appropriate spatial analytical unit?



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ABSTRACT

The estimated potential of landscape metrics as a surrogate for biodiversity is strongly dependent on the spatial analytical unit used for evaluation. We assessed the relationship between terrestrial vertebrate species richness (total and taxonomic) and structural landscape heterogeneity, testing the impact of using different spatial analytical units in three mountain systems in Spain. Landscape heterogeneity was quantified through an additive partitioning of the Shannon diversity index of landscape classes. Both landscape heterogeneity and species richness were calculated using two spatial analytical unit approaches: eco-geographic vs. arbitrary (i.e., watersheds vs. square windows of different sizes 20 × 20 km, 50 × 50 km, 100 × 100 km). We predicted species richness on the basis of landscape heterogeneity by fitting separate linear models for each spatial analytical unit approach. The main results obtained showed that landscape heterogeneity influenced terrestrial vertebrate species richness. However, the emerging relationships were dependent on the spatial analytical unit approach. The eco-geographic approach showed significant relationships between landscape heterogeneity and total and taxonomic species richness in almost all cases (except mammals). Considering the arbitrary approach, landscape heterogeneity appeared as a predictor of species richness only for mammals and breeding birds and at the coarsest spatial scales. Our results claim for further consideration of eco-geographical spatial analytical unit approaches in biodiversity studies and show that the methods of this study offer a valuable cost-effective framework for biodiversity management and spatial modeling, with potential to be adapted to national and global applications.

1. Introduction

Loss of biodiversity is one of the main impacts of land use change, and is associated with landscape fragmentation and habitat loss over recent decades (Lindenmayer et al., 2002; Herrando et al., 2014). Knowledge of the factors driving biodiversity patterns has become a priority for researchers and conservation practitioners (Morelli et al., 2013). Considerable efforts have been made to develop and improve methods for evaluating components of current biodiversity to enable the identification of priorities for conservation (Priego-Santander et al., 2013). Conservation strategies require the quantification of biodiversity, although time and cost limitations of biodiversity data collection make this a challenging task (Ewers et al., 2005). Thus, the development of biodiversity indicators that reduce the effort of biodiversity estimation, therefore speeding up the decision-making process, has become a priority for conservation biologists (Rossi and van Halder 2010; Laurila-Pant et al., 2015).

There is a large body of literature in which different environmental

variables (e.g., climate, land cover (Kivinen et al., 2007; Mehr et al., 2011), topography (Krömer et al., 2013; Yu et al., 2015), soil properties (Medinski et al., 2010), human population density or habitat diversity (Moreno-Rueda and Pizarro, 2007) have been used to make spatial predictions of species richness. Currently, there is increasing agreement about the consideration of landscape as the most pertinent level for biodiversity management actions (Walz, 2011), since landscape-based evaluations provide a larger-scale perspective of ecological processes than traditional site-based ones (Pino et al., 2000). The use of landscape metrics as a proxy of species richness has become a popular approach (Lindenmayer et al., 2002; Rossi and van Halder, 2010), made easier by the continuous development of remote sensing techniques and Geographic Information Systems (GIS) (Wagner and Fortin, 1987). Amongst the large number of landscape metrics used as biodiversity surrogates, landscape heterogeneity is gaining valuable recognition within conservation strategies (Walz, 2011). It is generally accepted that landscape heterogeneity is positively related to ecological niche diversity (Katayama et al., 2014). Furthermore, landscape heterogeneity plays an

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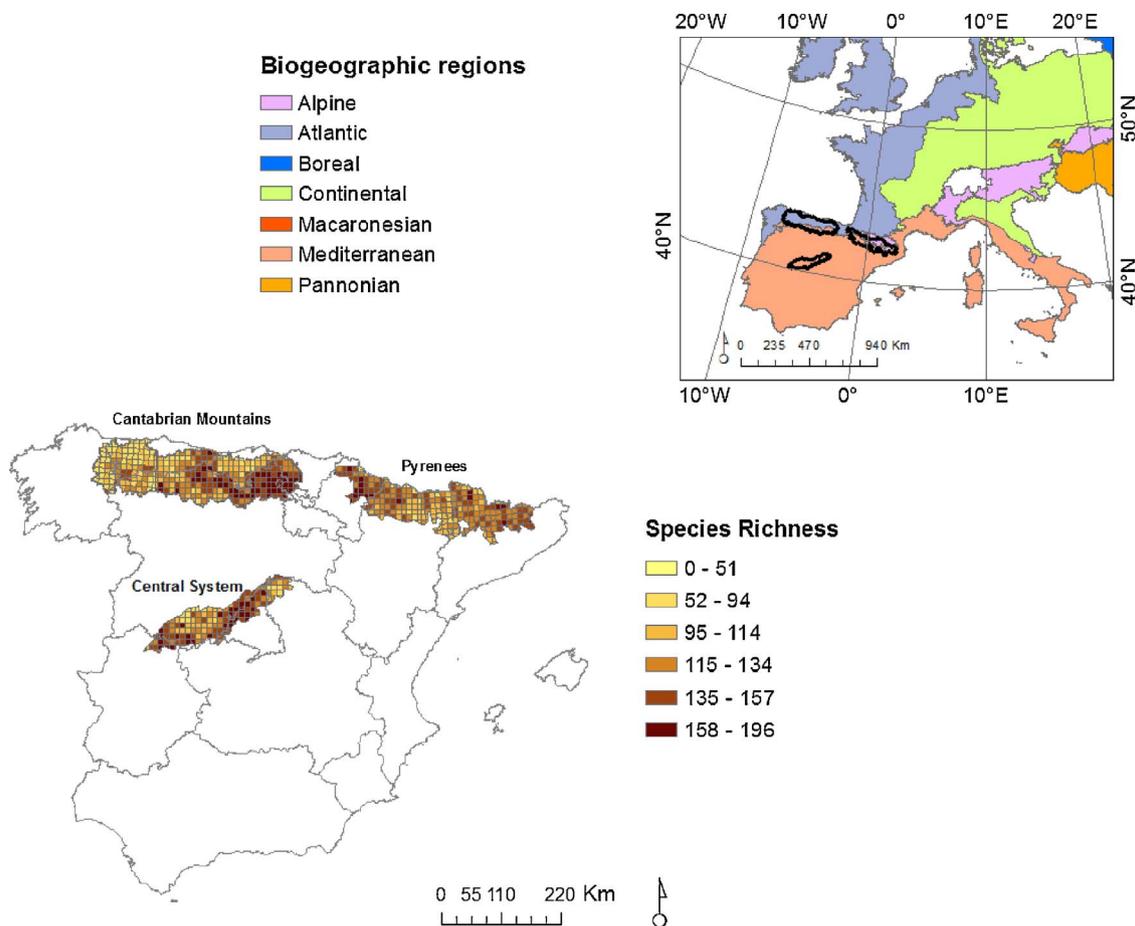


Fig. 1. Study area: The Cantabrian Mountains, the Central System and the Spanish Pyrenees. Information on biogeographic regions was obtained from the Spanish Ministry of Agriculture, Food and Environment (<http://www.magrama.gob.es/>).

important role in population dynamics, as it may control dispersal rates, movement patterns or foraging strategies (Johnson et al., 1992), which suggests some connection between landscape heterogeneity and species richness. Nevertheless, the estimation of biodiversity from landscape metrics is often affected by the methods employed to observe, analyse and process landscape patterns (Walz, 2011). Since landscape metrics, including landscape heterogeneity, describe geometric and spatial properties of landscape (Gimona et al., 2009), the ecological response emerging from landscape analyses might be conditioned by the shape (i.e., delineated boundaries; Moser et al., 2007; Cushman and McGarigal, 2008) or size (i.e., spatial scale) of the analytical unit used for landscape quantification (Weibull et al., 2000; Plexida et al., 2014; Ye et al., 2015).

The landscape is a continuum, but for practical reasons it must be split into spatial analytical units providing a frame for landscape metrics quantification. This is often rather arbitrary (Verberk et al., 2006; Walz, 2011). Difficulties arise as differently delineated spatial analytical units might provide different statistical relationships for the same ecological process, making the interpretation and applicability of landscape metrics estimations challenging (Saura and Martínez-Millán, 2001). Most studies addressing landscape heterogeneity as a surrogate of species richness (e.g. Aauri and de Lucio, 2001; Moreno-Rueda and Pizarro, 2007; Schindler et al., 2013) are based on a systematic partition of the landscape using arbitrarily defined spatial analytical units, such as UTM grids or circular buffers. However, the use of spatial analytical units with eco-geographic meaning could also provide a useful approach when predicting biodiversity, as displayed by Priego-Santander et al. (2013). This study showed the potential of landscape heterogeneity as a predictor of plant richness on the basis of land units

defined from geomorphology, geology, relief, climate, soil and land cover features. Watersheds are increasingly being used in environmental modelling and management, as they represent integrated socio-ecological (Mayer et al., 2014), geomorphological (Montgomery et al., 1995) and multifunctional (Karadağ, 2013) units with potential application for analyses at multiple scales (Tinker et al., 1998). For example, watersheds have been considered as operational spatial units to assess the relationship between soil erosion and regional landscape change (Li and Zhou, 2015), to identify and manage natural resources (Baloch and Tanik, 2008) and to analyse land cover change (Mendoza et al., 2011; Álvarez-Martínez et al., 2014). However, the application of eco-geographical units, including watersheds, as spatial analytical units in biodiversity modelling is under-evaluated. There is a clear need to explore the role of eco-geographical spatial analytical unit approaches as an alternative to traditional arbitrary ones in biodiversity studies.

Similarly, the influence of the size of the spatial analytical unit on the detection of relationships between landscape heterogeneity and species richness has been highlighted in different studies (e.g. Tews et al., 2004; Morelli et al., 2013; Schindler et al., 2013). Relationships emerging from the use of a particular spatial analytical-unit size are not necessarily consistent across different sizes. This is a consequence of the operational scale at which organisms interact with their environment (Tews et al., 2004). Taxa with a higher mobility and a strong demand for space are expected to be more influenced by larger landscape surface areas than smaller or sedentary species (Suárez-Seoane and Baudry, 2002; Schindler et al., 2013). Thus, multiscale analyses are required to detect the scale at which ecological phenomena leave their biological signal (Lechner et al., 2012).

In comparison with other systems, the higher environmental

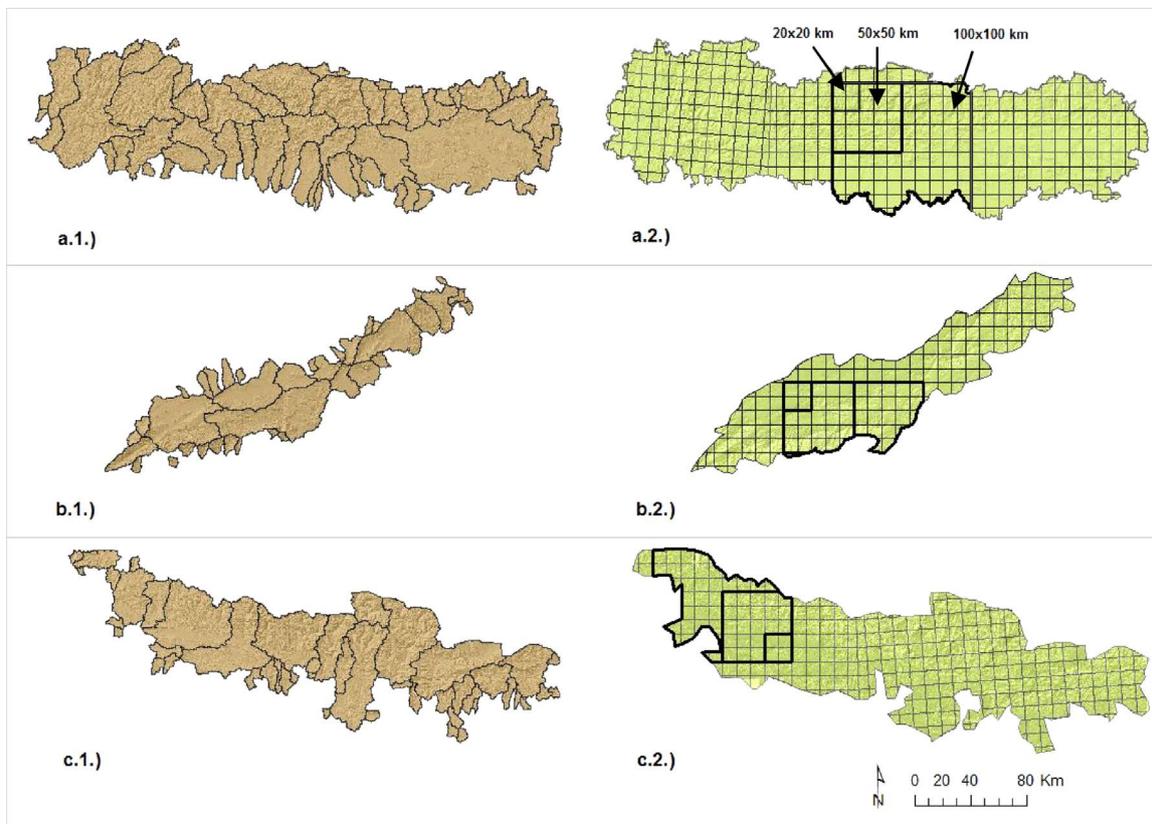


Fig. 2. Spatial analytical units: watersheds on the left (a.1 to c.1) vs. square windows of different size (20×20 km, 50×50 km and 100×100 km) on the right (a.2 to c.2) in the three mountain systems studied: a) the Cantabrian Mountains; b) the Central System; c) the Spanish Pyrenees.

variability found in mountains provides a large diversity of habitats, and therefore landscape heterogeneity (Jobbágy et al., 1996), which allows for higher species richness (Dufour et al., 2006). In fact, mountains have been largely recognized as important sources of biodiversity worldwide (La Sorte and Jetz, 2010). Meanwhile, they are highly prone to biodiversity loss due to their susceptibility to human and natural disturbances (Martinelli, 2007). Therefore, the need to explore potential biodiversity predictors, such as landscape heterogeneity, becomes particularly relevant in mountain systems.

The main goal of this study was to evaluate the potential of landscape heterogeneity as an indicator of species richness, assessing the effect of different methodological choices on the detection of significant ecological relationships. Specifically, we assessed the impact of using analytical units of different shape and size, i.e. following an eco-geographic (watersheds) versus an arbitrary (square windows of different size) spatial analytical approach, to quantify species richness and landscape heterogeneity. As a study case, we evaluated the effect of the different choices on the relationship between landscape heterogeneity and species richness of vertebrates (total and per taxonomic group) in three mountain systems with different biogeographical influences in Spain.

2. Material and methods

2.1. Study area

The study area includes three mountain ranges located across Spain (Fig. 1): the Cantabrian Mountains (CM), the Central System (CS) and the Spanish Pyrenees (SP). CM represent the transition between Atlantic and Mediterranean regions, CS is a typical example of the Mediterranean area and SP are located at the transition between the Mediterranean, Atlantic and Alpine regions (Rivas-Martínez et al., 1987). All of them present a great diversity of climatic conditions. Annual rainfall

ranges from 700 to 2400 mm in CM, 500–1500 mm in CS and 600–1400 mm in SP. Mean annual temperature ranges from -2.5 to 22.5 °C in all cases. These mountain systems are of particular interest as they are partially or totally included in the Mediterranean Basin, often considered as a biodiversity hotspot (Myers et al., 2000; Maiorano et al., 2013), and they house a wide variety of ecosystems, habitats and endemic species. In particular, CM and SP represent the southern limit of a wide range of species of Euro-Siberian origin and the northern-most distribution of species of Iberian and Ibero-African origin (Martínez-Rica and Recoder, 1990; Morán-Ordóñez, 2012), while CS has been recognized as a migratory route and speciation centre (López-Sáez et al., 2014).

In CM, where altitude ranges from sea level up to 2650 m a.s.l., dominant land covers are crop fields, in lowlands, and natural formations, such as heathlands, scrublands and deciduous forests (dominated by *Fagus sylvatica*, *Betula pubescens*, *Quercus petraea* and *Q. robur*, on northern slopes or by *Q. pyrenaica* and *Q. ilex*, on southern slopes), in mid-highlands (Morán-Ordóñez et al., 2011). Natural grasslands mainly cover areas at the highest altitudes. In CS, altitude ranges from 280 to 2592 m a.s.l. The landscape is dominated by forests of *Q. pyrenaica*, *Q. ilex* and *Q. suber* (especially in the western sector) and *Pinus sylvestris* and *P. nigra* eastwards (López-Sáez et al., 2014). Shrublands and heathlands of *Cytisus oromediterraneus*, *Echinopartum ibericum*, *E. barnadesii* or *Erica australis* constitute the main features of the landscape above 1600 m a.s.l. (Rivas-Martínez et al., 1987), while grasslands dominate in the areas at the highest altitudes (López-Sáez et al., 2014). In SP, the altitude ranges from 100 to 3404 m a.s.l. The landscape mosaic is mainly dominated by natural formations such as *Quercus pubescens* and *Q. ilex* and *Pinus sylvestris* and *Fagus sylvatica* forests, covering, respectively, sunny and shaded slopes, while *P. uncinata* forests appear above 1800 m a.s.l. (Lasanta-Martínez et al., 2005; Roura-Pascual et al., 2005), along with scrublands and natural grasslands. Crop fields can be found in valley bottoms.

Additionally, total species richness in the three corresponding mountain systems. Information on species richness was obtained from the official database of vertebrates of Spain (Ministry of Agriculture, Food and Environment 2012; www.magrama.gob.es).

2.2. Spatial analytical unit approaches

To assess the influence of the spatial analytical unit chosen to evaluate the relationship between landscape heterogeneity and species richness, we considered two different approaches that consisted of splitting the study area according to either geographic-ecological or arbitrary criteria (Fig. 2). The first approach (the “eco-geographic approach”) involved the delineation of a set of watersheds that were derived from a Digital Elevation Model (DEM) at 25 m resolution (www.ign.es) using ArcGIS 10.2 (ESRI, 2014), for each mountain system. Only watersheds of the highest order (i.e., fourth order) were considered, since those of lower order were smaller than the 10 × 10 km UTM square (the basic resolution of the analyses, constrained by species data availability). Watersheds covering only one 10 × 10 km UTM square were also excluded from the analyses since they did not allow for landscape heterogeneity quantification. As a result, we selected 76 watersheds for further analyses (39 in CM, 13 in SC and 24 in SP); mean area size was 582 ± 652 km² (range 102.33–4227.79 km²).

The second spatial analytical unit approach (the “arbitrary approach”) involved the definition of square windows of different size (20 × 20 km, 50 × 50 km, 100 × 100 km), which were obtained by successive aggregation of the original UTM grid system of 10 × 10 km. The different sizes made it possible to assess the role of scale on the performance of spatial analytical units. The 20 × 20 km and 50 × 50 km window sizes were chosen as proximal sizes to the mean ± SD watershed area. Furthermore, conservation planning in Spain is often conducted at a regional or sub-regional scale, thus we selected the 100 × 100 km window size as a proximal size to a sub-regional spatial scale. The need of adapting square windows to the biogeographic limits of the mountain systems implied that coverage was not complete for some windows located across the borders of the study area. Incomplete windows are usually excluded from the analyses (Li et al., 2017) in order to avoid potential bias on species richness and landscape heterogeneity. However, aiming to include as much as possible of the area of the mountain systems, we only excluded from further analyses windows with a coverage lower than 75% (at 20 × 20 km and 50 × 50 km window size) and 45% (at 100 × 100 km window size). This resulted in 154 windows of 20 × 20 km (75 in CM, 28 in SC and 51 in SP), 20 of 50 × 50 km (10 in CM, 4 in SC and 6 in SP) and 12 of 100 × 100 km (5 in CM, 3 in SC and 4 in SP).

2.3. Vertebrate species data

Distribution of terrestrial vertebrate species was obtained from the official database of vertebrates of Spain (Ministry of Agriculture, Food and Environment, 2012; www.magrama.gob.es), which combines field records gathered by volunteers with information from published sources. The data consist of species presence and absence locations for the period 1980–2007, collected on the basis of direct observations and indirect methods (pellets, tracks, bed sites) and assembled in a regular UTM grid system of 10 × 10 km (Pleguezuelos et al., 2002; Martí and del Moral, 2003; Palomo et al., 2007).

Species richness was calculated for each 10 × 10 km UTM square as: (i) “total richness” or total number of species; and (ii) “taxonomic richness” or the number of species per taxonomic group (mammals, breeding birds, reptiles and amphibians). Similarly, we calculated the relative value of species richness (number of species per 100 km²), both total richness and species richness per taxonomic group for each mountain system (See Fig. 1 and Table A1 from the appendix). Only squares with at least 75% coverage of their area included within the

limits of each mountain system were considered for analyses, resulting in a set of 624 squares. Based on these squares, total and species richness per taxonomic group were also computed for both watersheds and square windows of different size, by aggregating the original information from the 10 × 10 km UTM grid system. The 10 × 10 km squares intersecting boundaries between watersheds were fully considered as part of the watershed if they overlapped at least 50% with the watershed area.

2.4. Estimators of landscape heterogeneity

Landscape heterogeneity was calculated on the basis of a landscape classification elaborated by integrating variables accounting for topography, urban influence and land cover. Land cover was obtained from the categorical map CORINE Land Cover 2006 (derived from LANDSAT at 30 m; <http://land.copernicus.eu/pan-european/corine-land-cover>), which had previously been converted into independent continuous variables by calculating the proportion covered by each class. Topographic variables consisted of elevation, solar radiation and slope. They were derived from a Digital Elevation Model (DEM) (25 m spatial resolution), obtained from the Spanish Geographic Institute (www.ign.es) and resampled at the resolution of the land cover variables (i.e. 30 m), by applying the nearest neighbor method. Urban influence was measured as the Euclidean distance from each 30 m pixel to the nearest settlement, using input data downloaded from the Spanish Geographic Institute site (www.ign.es) at 1:25000 and 1:200000 spatial resolution. Landscape classification consisted of running a Principal Component Analysis (PCA) over the pool of variables, followed by an ISODATA unsupervised classification accomplished by using the Iso Cluster unsupervised classification function in ArcGis 10.2 (ESRI, 2014); this aggregated pixels into coherent classes. The number of classes was defined aiming to represent at best the ecological framework of the study area according to our expert knowledge. To do this, classes resulting from the classification process were characterized by using thematic information related to topography, urban influence and land cover and when necessary, they were combined or reclassified. The classification process led to 11 landscape classes in the CM, 13 in the CS and 8 in the SP (Figure A1 and Table A2 from the appendix). The overall accuracy of classifications and user’s and producer’s accuracy per class were evaluated through confusion error matrices (Congalton, 2001) by using thematic information related to topography, urban influence, land cover and ortho-photographs (years 2006–2009, scale 1:5000 to 1:10000). Overall accuracy was 88% for the CM and the SP and 84% for the CS (Table A3 from appendix). See García-Llamas et al. (2016) for more technical details on the landscape classification method.

Landscape heterogeneity was estimated as beta diversity (H'_β ; Eq. (1)) for each spatial analytical unit (watershed or regular window) using an additive model based on the comparison of both alpha and gamma diversity (Lande 1996; Tarrega et al., 1997; Jost 2006, 2007).

$$H'_\beta = H'_\gamma - \frac{\sum_{i=1}^N H'_{\alpha_i}}{N} \quad (1)$$

where H'_γ is gamma diversity (i.e., the diversity of landscape classes at each spatial analytical unit) and H'_{α_i} is alpha diversity (i.e., the diversity of landscape classes at each 10 × 10 km UTM square within each spatial analytical unit). Both H'_γ and H'_{α_i} were calculated using the Shannon diversity index (Shannon, 1948) (Eq. (2)),

$$H' = -\sum_{i=1}^R p_i \ln p_i \quad (2)$$

where p_i is the proportion of each landscape class within the spatial analytical unit or the 10 × 10 km UTM square, respectively.

All analyses were done in ArcGIS 10.2 (ESRI, 2014) and by using the Patch Analyst extension (Rempel et al., 2012).

2.5. Statistical analyses

To analyse the relationship between landscape heterogeneity and absolute richness (total and species richness per taxonomic group) of terrestrial vertebrates, separate linear models were fitted for each of the considered spatial analytical unit approaches (eco-geographic approach vs. arbitrary approach). In the particular case of mammals and amphibians, richness data were transformed for normality by using the log (x) function.

Species richness was considered in the models as the dependent variable and landscape heterogeneity (H_{β}) as the predictor. For the arbitrary approach, in order to avoid potential bias due to the incomplete coverage of some windows across borders of mountain systems, we included the logarithm of the area of the square window (i.e. proportion of the square window included within the study area) as an additional predictor in models. For the eco-geographical approach, we included the logarithm of the watershed area as an additional predictor of landscape heterogeneity in order to partial-out the confounding effect of the different areas of individual watersheds (which is expected to affect both species richness and landscape heterogeneity *per se*). To control for intrinsic differences in species richness between the three study areas, “mountain system” was also included in both approaches as a predictor (Gelman and Hill, 2006; Seoane, 2014). In all cases, we checked model residuals to assess the appropriateness of the model and confirmed the absence of spatial autocorrelation by computing correlograms. Data analyses were carried out with the R 3.1.2 statistical programme (R Development Core Team, 2014) using the ‘lm’ function (R Development Core Team, 2014). Correlograms were computed with the ‘correlog’ function in the ‘ncf’ R package (Bjornstad, 2013).

In addition, the relative effect of the explanatory variables in each model was also assessed by commonality analysis (Legendre and Legendre, 2012; Ray-Mukherjee et al. 2014). This method, based on the normal R^2 of partial and complete regression models, apportions the variation of the response (species richness) in several fractions: the pure effect of the singular predictors, the shared effect of each pair, triplet or any subset of predictors and the shared effect of the total set of predictors. For this, we used the ‘commonalityCoefficients’ function in the R package ‘Yhat’ (Nimon and Oswald, 2013).

3. Results

Landscape heterogeneity exerted a positive effect on species richness in all the fitted models. The magnitude and significance of its effects, however, varied according to the spatial analytical unit approach and the taxonomic group (Tables 1 and 2; Tables A4 and A5 from appendix). For the case of the eco-geographic approach, models accounted for more than 53% of the variance of species richness (Table 1). Landscape heterogeneity was a significant predictor of species richness in all cases, except in mammals. It explained between 28% (mammals) and 50% (all taxa together) of the variance of species richness, although between 26% and 40% of this variation was shared with the logarithm of watershed area (Fig. 3). Indeed, the logarithm of watershed area had a significant effect on species richness in all taxa considered, explaining between 37% (reptiles) and 55% (total richness) of the variance of species richness. The mountain system had a significant effect in all cases, except for both amphibians and for total species richness (Table 1). It explained between 3% (total richness) and 14% (reptiles) of the total variance (Fig. 3).

The performance of the arbitrary approach was poorer than the eco-geographical one, with a clear influence of windows size on the significance of relationships. Models accounted for more than 24% of the variance of species richness at 20 × 20 km, more than 46% at 50 × 50 km and more than 71% at 100 × 100 km window size. Significant relationships between landscape heterogeneity and species richness were only found for mammals and breeding birds at the largest window size (100 × 100 km) (Table 2). The percentage of total

Table 1

Anova table including: the explained sum of squares (*Sum. Sq.*), *F* value, significance (*Sig.*) and normal coefficients of determination (R^2) of regression linear models achieved when working with watersheds as spatial analytical units and landscape heterogeneity.

	Sum Sq	F value	Sig.	R^2
Mammal richness				0.54
H_{β}	0.09	0.86	n.s.	
log(A)	3.54	32.13	***	
Mountain system	0.95	4.29	*	
Breeding bird richness				0.65
H_{β}	1555.90	9.53	**	
log(A)	5167.20	31.64	***	
Mountain system	1782.90	5.46	**	
Reptile richness				0.56
H_{β}	92.12	5.90	*	
log(A)	301.07	19.28	***	
Mountain system	366.81	11.75	***	
Amphibian richness				0.53
H_{β}	33.83	6.55	*	
log(A)	96.45	18.68	***	
Mountain system	14.77	1.43	n.s.	
Total richness				0.65
H_{β}	7214.00	12.76	***	
log(A)	17726.00	31.35	***	
Mountain system	1694.00	1.50	n.s.	

H_{β} landscape heterogeneity; log(A) logarithm of watershed area; ***significance at level < 0.001; **significance at level 0.01; *significance at level 0.05; n.s. no significance.

variation explained by landscape heterogeneity was between 69% (mammals) and 15% (breeding birds), although between 42% and 10% of this variance was shared with the logarithm of the area of the square window, and between 27% and –28% with the mountain system (Fig. 4). The significance of the effect and predictive power of landscape heterogeneity decreased for all taxa for the smallest window sizes (i.e. 50 × 50 and 20 × 20 km) (Table 2; Table A5 and Figures A2 and A3 from the appendix).

Further, we found an influence of the mountain system and the logarithm of the area of the square windows, depending on the window size and taxonomic group. Mountain system and area had a significant effect on total richness and richness of all taxonomic groups, at 20 × 20 km window size, these variables mainly explaining total variance of models. At 50 × 50 km, only mountain system significantly influenced results, this accounting for most species richness total variance (Table 2, Table A5 and Figures A2 and A3 from the appendix). At 100 × 100 km, the mountain system and the area significantly influenced breeding birds, reptiles and total species richness (only the area in this case). The mountain system accounted for between 15% (breeding birds) and 59% (reptiles) and the area between 5% (reptiles) and 75% (total richness) of the total variance of models (Table 2; Fig. 4 and Table A5 from the appendix).

4. Discussion

Landscape heterogeneity has been largely recognized as a cost-effective instrument to predict biodiversity (Ewers et al., 2005), especially in large areas. However, as we demonstrated in this study, the predictive power of this indicator depends on the spatial analytical unit approach. Thus, the selection of an appropriate analytical framework for assessing landscape heterogeneity-species richness relationships requires careful consideration in view of a practical implementation. In this sense, our study advocates the need to incorporate eco-geographically relevant spatial analytical units, based on linkages between physical and biological resources and processes (Montgomery et al. 1995), rather than arbitrarily delineated ones (typical of traditional approaches) within the framework of biodiversity studies.

The eco-geographic spatial analytical unit approach, based on the

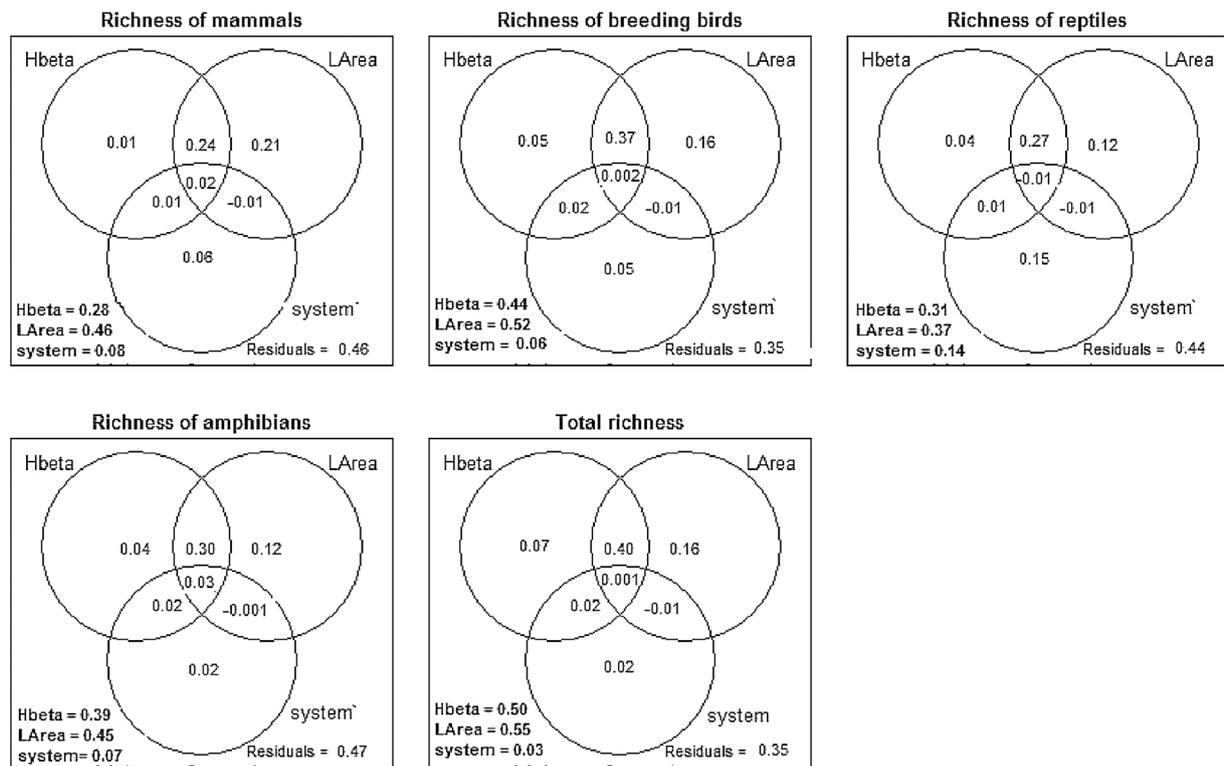


Fig. 3. Variance partitioning of species richness in watersheds explained by the pure and combined effect of landscape heterogeneity (Hbeta), logarithm of watershed area (Larea) and mountain system (system). Total variance (pure and combined effect) explained by predictors is in bold. For example, for richness of mammals total variance of Hbeta = 0.01 (pure effect) + (0.24 + 0.02 + 0.01; shared effect) = 0.28. Negative effects arise from the presence of suppression among predictors due to correlation among variables (Ray-Mukherjee et al. 2014).

use of watersheds, enabled the detection of significant relationships between landscape heterogeneity and species richness for almost all taxonomic groups. Generally, species richness depends on the presence of ‘keystone structures’ (i.e., distinct spatial landscape structures providing resources, shelter or goods crucial for species; Tews et al., 2004), which are the result of interaction between biotic and abiotic features

(e.g. climate, soil type, watering, human perturbations; Blasi et al., 2008) and influence the use of territory by animals (Mazía et al., 2006). In this context, watersheds may better reflect these keystone structures than arbitrary spatial analytical units, as they represent areas where climate, hydrology, geomorphology and land use history interact in predictable and repetitive ways, determining the composition and

Table 2

Anova table including: explained sum of squares (Sum. Sq.), F value, significance (Sig.) and normal coefficients of determination (R²) of linear models when working with square windows of different sizes (20 × 20 km, 50 × 50 km and 100 × 100 km) as spatial analytical units.

	20 × 20				50 × 50				100 × 100			
	Sum Sq	F value	Sig.	R ²	Sum Sq	F value	Sig.	R ²	Sum Sq	F value	Sig.	R ²
Mammal richness				0.24				0.46				0.83
H _β	0.16	1.54	n.s.		0.004	0.53	n.s.		0.02	7.38	*	
log(A)	2.08	20.18	***		0.001	0.21	n.s.		0.00	0.001	n.s.	
Mountain system	2.17	10.53	***		0.05	2.72	n.s.		0.01	1.86	n.s.	
Breeding bird richness				0.35				0.47				0.95
H _β	98.50	0.47	n.s.		40.49	0.76	n.s.		163.01	11.14	*	
log(A)	11924.9	56.55	***		142.63	2.68	n.s.		754.46	51.59	***	
Mountain system	3291.1	7.80	***		325.67	3.05	n.s.		410.50	14.04	**	
Reptile richness				0.35				0.85				0.82
H _β	52.77	3.36	n.s.		0.37	0.14	n.s.		0.35	0.16	n.s.	
log(A)	234.07	14.92	***		2.09	0.76	n.s.		16.63	7.40	*	
Mountain system	922.96	2941	***		221.53	40.44	***		22.78	5.07	*	
Amphibian richness				0.27				0.64				0.71
H _β	24.83	3.36	n.s.		15.55	4.42	n.s.		2.79	1.70	n.s.	
log(A)	107.20	7.24	**		4.72	1.98	n.s.		0.45	0.27	n.s.	
Mountain system	139.34	18.83	***		29.21	6.12	*		11.86	3.61	n.s.	
Total richness				0.38				0.60				0.85
H _β	1675.00	2.96	n.s.		190.22	1.99	n.s.		115.82	0.91	n.s.	0
log(A)	37761.00	66.83	***		157.27	1.65	n.s.		2156.07	16.85	**	
Mountain system	5970.00	5.28	**		902.48	4.73	*		584.81	2.28	n.s.	

H_β landscape heterogeneity; ***significance at level < 0.001; **significance at level 0.01; *significance at level 0.05; n.s. no significance.

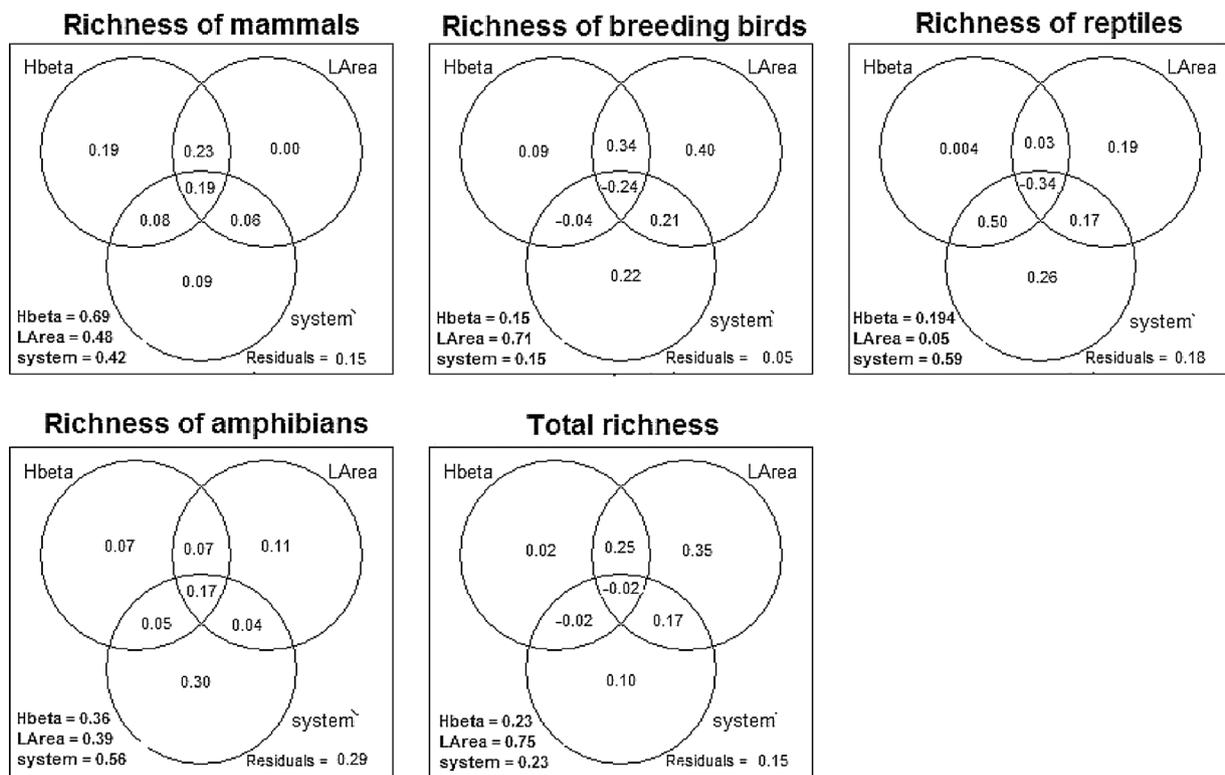


Fig. 4. Variance partitioning of species richness explained by pure and combined effects of landscape heterogeneity (Hbeta), logarithm of window area (Larea) and mountain system (system) for windows of 100 × 100 km (or less if they intersected the limits of the study area). Total variance (pure and combined effect) explained by predictors is in bold. For example, for richness of mammals total variance of Hbeta = 0.19 (pure effect) + (0.23 + 0.19 + 0.08; combined effect) = 0.69. Negative effects arise from the presence of suppression among predictors due to correlation among variables (Ray-Mukherjee et al. 2014).

structure of landscapes and their biotic communities (Karadağ, 2013). In fact, for example, watershed characteristics have been employed to effectively predict the existence of protected habitats (Baattrup-Pedersen et al., 2012).

Although watersheds might offer a good sampling scheme to analyze the relationships between landscape heterogeneity and species richness, variance partitioning analyses showed that the predictive capacity of the landscape heterogeneity was mainly associated with the watershed area. Two of the major mechanisms of increased species richness are the increase in both area (spatial analytical unit size) and variety of habitat types (here expressed as landscape heterogeneity) (Kohn and Walsh, 1994). Both mechanisms are mutually complementary, thus one can act as a surrogate of the effect of the other, making it difficult to discern their direct effect on species richness patterns (Triantis et al., 2003). Consequently, although both area and landscape heterogeneity partially contributed to explaining species richness separately, their large combined effect on species richness means that these two variables should be considered in conjunction (Kallimanis et al., 2008) when working with eco-geographic spatial analytical units, in conservation planning.

Despite being widely accepted in landscape analysis (e.g. Nogués-Bravo and Martínez-Rica, 2004; Flick et al., 2012) the arbitrary spatial analytical unit approach, based on the use of square windows, revealed some limitations with regards to modelling landscape heterogeneity-species richness relationships. Only two taxonomic groups (i.e. mammals and breeding birds) showed significant statistical effects of landscape heterogeneity. Further, the size of the spatial analytical unit also largely influenced the predictive capacity of landscape heterogeneity, as demonstrated in other studies (Morelli et al., 2013; Schindler et al., 2013; Chambers et al., 2016). In our particular case we only found significant relationships between landscape heterogeneity and species richness at the 100 × 100 km window size. Such an outcome might be related to the fact that species attributes (e.g. mobility or dispersal

capacity) widely rule the effect of landscape heterogeneity (Barbaro and Van Halder, 2009; Perović et al., 2015) and the spatial scale (i.e. size of the spatial analytical unit) at which this effect emerges (Miguet et al., 2016). Consequently, it would be expected that the spatial scale at which landscape heterogeneity exerts its effect would be larger for taxa with greater mobility or demand for space (e.g. mammals or birds) than for less mobile ones (e.g. reptiles or amphibians), because they interact with the landscape over a larger spatial extent (Schindler et al., 2013; Miguet et al., 2016). As a result, the lack of explanation of mammal richness within watersheds might suggest that the watersheds in this study are not large enough to efficiently capture the effect of landscape heterogeneity over species richness of this taxon. These results emphasise the need to consider the spatial scale appropriate for both the subject of study and the ecological question posed (Wu, 2004), i.e., it might be associated with the scale at which organisms perceive the landscape.

The arbitrariness of the spatial analytical unit influences both the size and shape of the selected spatial analytical units. Any change in these settings will provide a different description of the area of analysis, which is linked to the modifiable areal unit problem (MAUP); and which might affect results of statistical models (Dungan et al., 2002; Dark and Bram, 2007; Nouri et al., 2017). We tried to minimize the usual bias associated to the scale problem of the MAUP (inflated correlation at higher levels of aggregation; Wong, 2009), by estimating both the response (species richness) and the explanatory variables (landscape heterogeneity) as cumulative figures obtained from the 10 × 10 km raw data, rather than as averages or any other measure of central tendency of smaller units. However, contrary to our results with watershed units, for arbitrary windows with a size close to the mean ± SD watershed area (i.e., 20 × 20 km and 50 × 50 km window), no significant effects of landscape heterogeneity on vertebrate species richness were detected. This inconsistency when changing boundary delineation could be the result of the different description of

the region leading to different analytical results, which is related to the zoning problem of the MAUP (Jelinski and Wu, 1996). Further, when boundaries of spatial analytical units are arbitrarily set, they could not reflect the spatial structure of the environmental and biological components of the landscape (Wagner and Fortin, 2005). Thus, arbitrary boundaries may mask relationships between landscape heterogeneity and species richness. As an example, amphibians are usually favored by landscape heterogeneity, as they use a complex landscape matrix of terrestrial and aquatic habitats during different stages of their life cycles (Mawangi, 2010). Further, different species of amphibians could require different aquatic environments from the headwater to the lower reaches. However, arbitrary spatial analytical units might not necessarily encompass both terrestrial and aquatic habitat patches, or all aquatic environments. Consequently, watershed might be a proper landscape approach to include amphibians breeding, foraging and overwintering habitat patches (Maxell, 2009). In the case of reptiles, some studies (e.g., Shipman et al., 2004) have highlighted the importance of preserving watershed-level heterogeneous landscape conditions for preserving their diversity. In fact, the physiography of watersheds (i.e. slope, elevation or naturally-occurring aquatic habitats) determines the diversity of canopy covers and aquatic habitats that ultimately influence the variation of humidity and soil mixture, on which reptiles are highly dependent (Shipman et al. 2004). Therefore, analyzing watersheds, rather than arbitrary spatial analytical units, might give ground for a better understanding of landscape heterogeneity-reptile richness relationships.

Results on the performance of eco-geographical and arbitrary spatial analytical unit approaches have important implications from a practical perspective. Developing an eco-geographical approach based on watersheds is not a new approximation in analysis and conservation management. For example, the unit plan used by the U.S. Forest service until the mid-1970s was based on watershed delineation (Montgomery et al., 1995). Also in the mid-nineties, ecosystem management based on watershed analysis was implemented in the Pacific Northwest federal lands and, on a volunteer basis, on forested watersheds in Washington (WFPB 1992a, 1992b, 1993). In the case of Spain, conservation management is generally addressed independently by different regional autonomous administrations (Morillo and Gómez-Campo, 2000), except for some protected areas (i.e. national parks covering different regions) for which collaborative networks do exist. Consequently, management actions have usually been carried out according to varying arbitrary management units at regional or sub-regional scale, such as administrative boundaries. As our results show, the performance of arbitrary units could not be considered satisfactory. Even for the larger unit size considered (100 × 100 km window), richness for some taxa (and total richness also) appeared unrelated to landscape heterogeneity so, at least with the sizes considered in our study, the arbitrary approach could not be considered an appropriate approximation to a sub-regional scale of management on the ground. On the contrary, our results showed that watersheds, i.e., eco-geographical rather than regular windows, or political or administrative boundaries, might provide a more rational basis for the management of biodiversity, based on potential indicators such as landscape heterogeneity. Thereby, this study revealed the major importance of adopting a trans-bordering and inter-regional management framework that advocates continuous and integrated engagement of all entities involved in decision-making.

Notwithstanding the important role of landscape heterogeneity as an indicator of species richness, caution is urged as high landscape heterogeneity might lead to fragmentation and, may thus have negative effects on biodiversity (Dufлот et al., 2014). Further, it should be noted that the detected relationships between landscape heterogeneity and species richness depend on the landscape metrics used for analyses (Cale and Hobbs, 1994). Although there is no consensus regarding the most appropriate and informative index for landscape heterogeneity, the Shannon diversity index has been successfully used in several studies (e.g. Pino et al., 2000; Oindo et al., 2003; Priego-Santander et al.,

2013; Lee and Martin, 2017), along with other metrics such as patch richness, Simpson's diversity index or Simpson's evenness (Schindler et al., 2013). We are unaware of the use of a beta-diversity metric in landscape analyses, but its performance in our study gives ground for further consideration in this field. Further, we claim for the convenience of using a landscape classification adapted to the study site (i.e. the mountain system), thus allowing the ecological meaning and reliability of landscape classification to be increased and therefore, the reliability of landscape indices (Shao and Wu, 2008). Additionally, the influence of landscape heterogeneity on species richness may depend not only on the spatial analytical unit approach or the used landscape metrics, but also on the study site considered (Amano et al., 2008; Oliver et al., 2010). In this context, the study site might condition the existing pool of species, due to differences in historical land-uses (Devictor et al. 2010), environmental conditions and biogeographical history (Tamma et al., 2016). Therefore, differences in the existing pool of species might determine disparities in the emerging ecological response among study sites. This might stem from the different ways in which species perceive the landscape (Farina, 2001). In this sense, our analyses were performed in mountain areas, where high abiotic heterogeneity (i.e. climate or topography) would increase heterogeneity on the landscape scale, hence resulting in higher site species richness compared to flat areas (Jobbágy et al., 1996). In mountain regions, the watershed is a basic eco-geographic unit that has been used for ecological management (Zhang et al., 2014). However, as watersheds integrate biotic and abiotic processes determining landscape (Karadağ, 2013), we could expect the use of watersheds to also be useful for species richness modeling from landscape heterogeneity, in more homogeneous topographic areas.

5. Conclusions

Our study has shown how landscape heterogeneity, measured by a beta-diversity metric, could predict terrestrial vertebrate richness in mountain systems, although conditioned by the spatial analytical unit approach used for evaluation. This study indicates the high potential of eco-geographical spatial analytical unit approaches, based on watersheds, in biodiversity studies. The arbitrary spatial analytical units approach reflects how limiting it could be to apply spatial analytical units unrelated to the phenomena under study. In connection with this, we corroborate the effect of the size of arbitrary spatial analytical units on predictive power of landscape heterogeneity, which is generally better at larger sizes. These findings have important practical implications as they underline the need to consider landscape heterogeneity in biodiversity conservation strategies. Furthermore, this study offers a valuable cost-effective framework for environmental management and spatial modeling, with potential to be adapted for national and global applications. Simultaneously, it makes visible important methodological issues that may affect biodiversity estimations and that should be considered in decision-making.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.10.026>.

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