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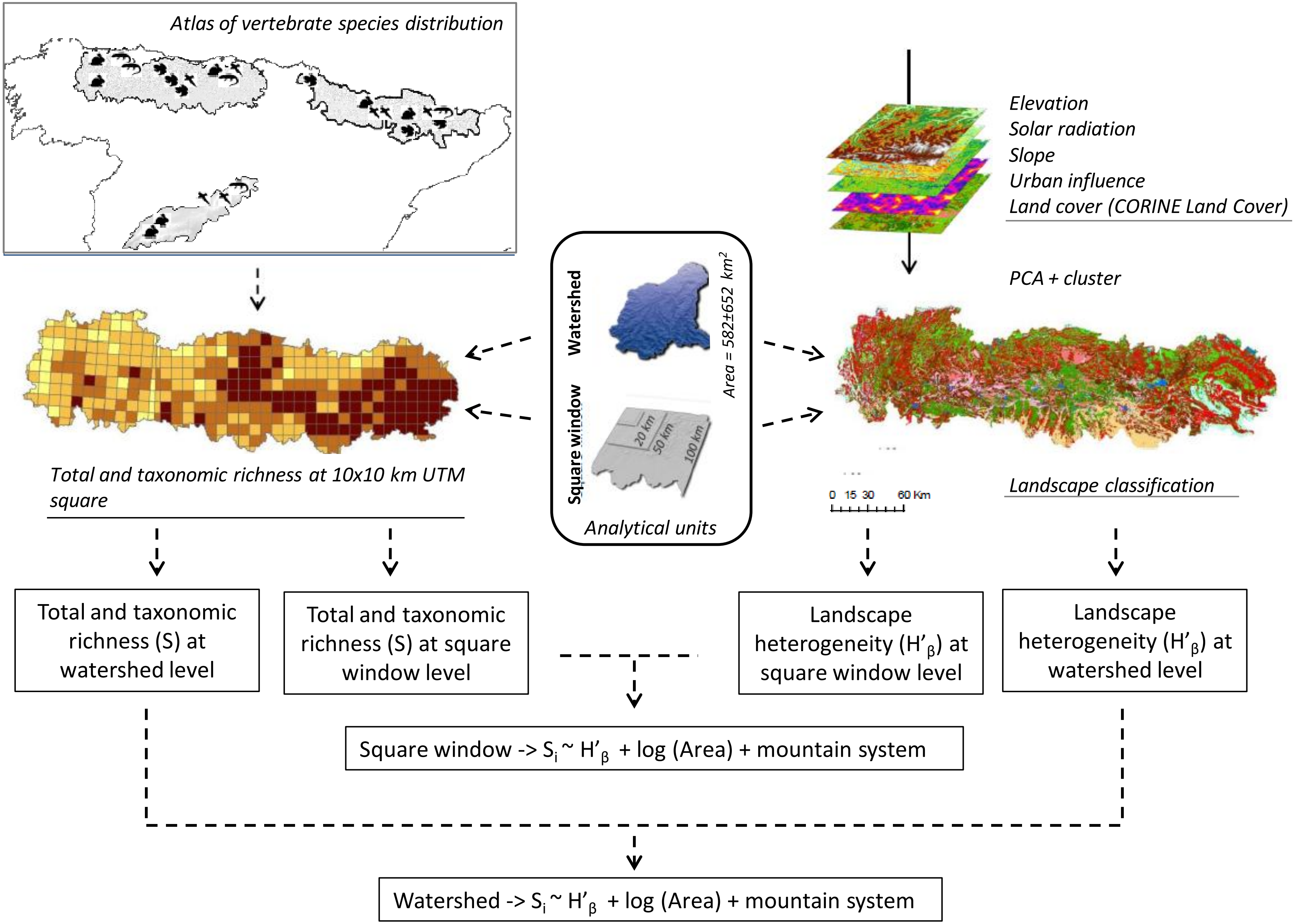
Abstract: The estimated potential of landscape metrics as a surrogate for biodiversity is strongly dependent on the spatial analytical unit used for evaluation. We assessed the relationship between terrestrial vertebrate species richness (total and taxonomic) and structural landscape heterogeneity, testing 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 20x20 km, 50x50 km, 100x100km). 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.

Response to Reviewers: Dear Dr. Petina Lesley Pert, Associate Editor of the journal Ecological Indicators:

We are pleased to submit a revised version of the manuscript ECOLIND-7602R1 "Landscape heterogeneity as a surrogate of biodiversity in mountain systems: what is the most appropriate spatial analytical unit?"

Graphical Abstract(for review)



Atlas of vertebrate species distribution

Elevation
Solar radiation
Slope
Urban influence
Land cover (CORINE Land Cover)

PCA + cluster

Analytical units

Total and taxonomic richness at 10x10 km UTM square

Landscape classification

Total and taxonomic richness (S) at watershed level

Total and taxonomic richness (S) at square window level

Landscape heterogeneity (H'_β) at square window level

Landscape heterogeneity (H'_β) at watershed level

Square window -> $S_i \sim H'_\beta$ + log (Area) + mountain system

Watershed -> $S_i \sim H'_\beta$ + log (Area) + mountain system

Highlights

- Landscape heterogeneity turned to be a good surrogate o terrestrial vertebrate species richness, although conditioned by the selected analytical approach and landscape data.
- The eco-geographic approach offered a good analytical scheme for assessing relationships between landscape heterogeneity and species richness in biodiversity studies
- The size of arbitrary analytical units affects predictive power of landscape heterogeneity, this increasing when increasing the analytical units' size.

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 20x20 km, 50x50 km, 100x100km). 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.

Keywords: habitat diversity; mammals; birds; reptiles; terrestrial vertebrates; watersheds.

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 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 Mc Garigal 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. Atauri 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 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 et al 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 (Figure 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 to 1500 mm in CS and 600 to 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, Echinospartum 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.

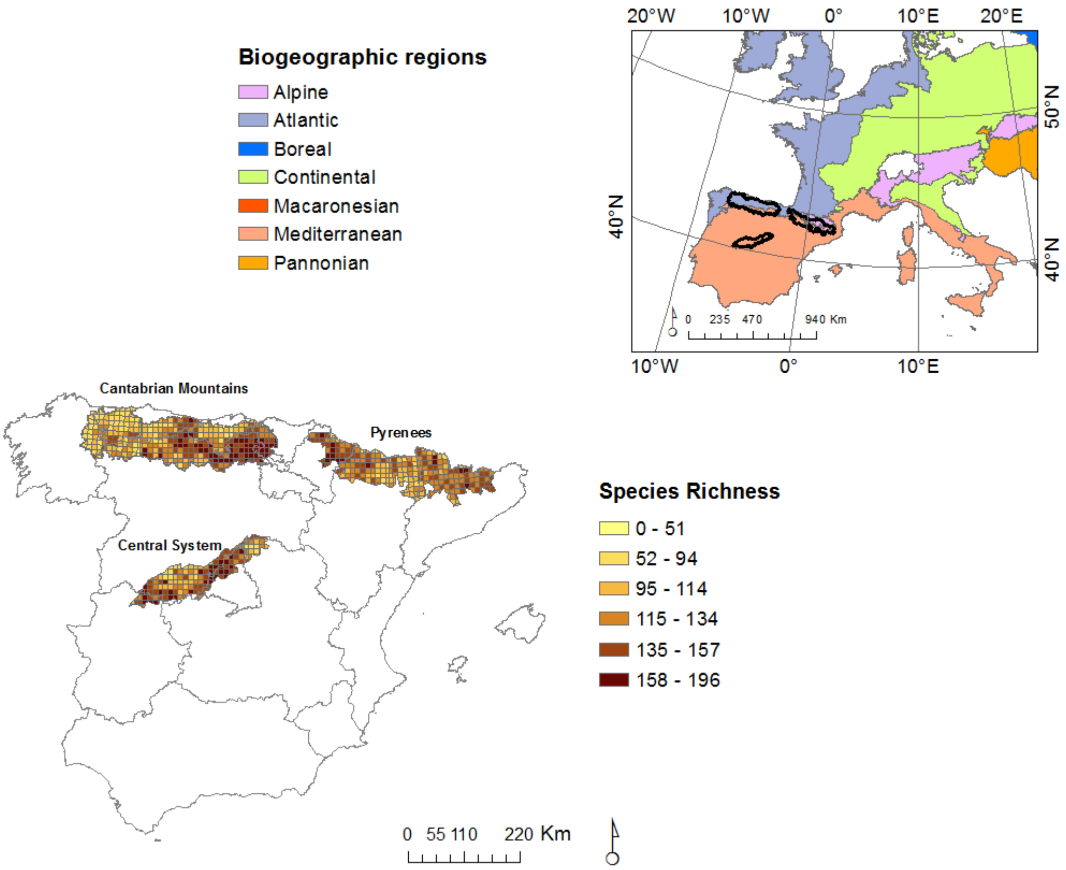

Figure 1. Study area: The Cantabrian Mountains, the Central System and the Spanish Pyrenees. Information on biogeographic regions was obtained from the Spanish Ministry of Agriculture, Food and Environment (http://www.magrama.gob.es/). Additionally, total species richness in the three corresponding mountain 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).

2.2Spatial 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 (Figure 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 10x10 km UTM square (the basic resolution of the analyses, constrained by species data availability). Watersheds covering only one 10x10 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 km^2 (range 102.33-4227.79 km^2).

The second spatial analytical unit approach (the "arbitrary approach") involved the definition of square windows of different size (20x20 km, 50x50 km, 100x100 km), which were obtained by successive aggregation of the original UTM grid system of 10x10 km. The different sizes made it possible to assess the role of scale on the performance of spatial analytical units. The 20x20 km and 50x50 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 100x100 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 imply 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 20x20 km and 50x50 km window size) and 45% (at 100x100km window size).This resulted in 154 windows of 20x20 km (75 in CM, 28 in SC and 51 in SP), 20 of 50x50 km (10 in CM, 4 in SC and 6 in SP) and 12 of 100x100 km (5 in CM, 3 in SC and 4 in SP).

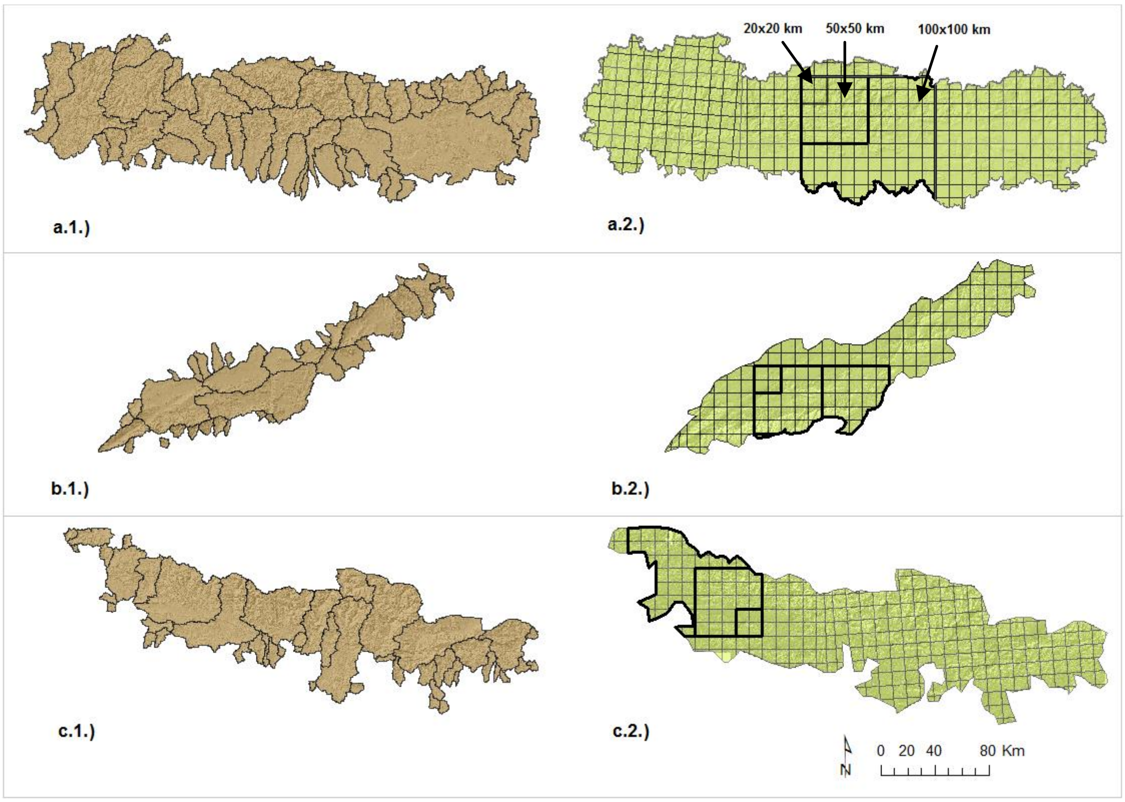

Figure 2. Spatial analytical units: watersheds on the left (a.1 to c.1) *vs.* square windows of different size (20x20 km, 50x50 km and 100x100 km) on the right (a.2 to c.2) in the three mountain systems studied: a) the Cantabrian Mountains; b) the Central System; c) the Spanish Pyrenees.

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 10x10 km (Pleguezuelos et al 2002; Martí and del Moral 2003; Palomo et al 2007).

Species richness was calculated for each 10x10 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 100km^2), both total richness and species richness per taxonomic group for each mountain system (See Figure 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 10x10 km UTM grid system. The 10x10 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 30m; 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 to 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; Tárrega et al 1997; Jost 2006, 2007).

$$H'_{\beta} = \mathrm{H}'_{\gamma} - \frac{\sum_{\mathrm{i=1}}^{\mathrm{N}} \mathrm{H}'_{\alpha_{\mathrm{i}}}}{N} \qquad \text{(Eq. 1)}$$

where H'_{γ} is gamma diversity (i.e., the diversity of landscape classes at each spatial analytical unit) and $\mathrm{H}'_{\alpha_{\mathrm{i}}}$ is alpha diversity (i.e., the diversity of landscape classes at each 10x10 km UTM square within each spatial analytical unit). Both H'_{γ} and $\mathrm{H}'_{\alpha_{\mathrm{i}}}$ were calculated using the Shannon diversity index (Shannon 1948) (Eq. 2),

$$H' = -\sum_{i=1}^{R} p_i \ln p_i \qquad \text{(Eq. 2)}$$

where p_i is the proportion of each landscape class within the spatial analytical unit or the 10x10 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 (Figure 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 (Figure 3).

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 heterogeneigy; 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.

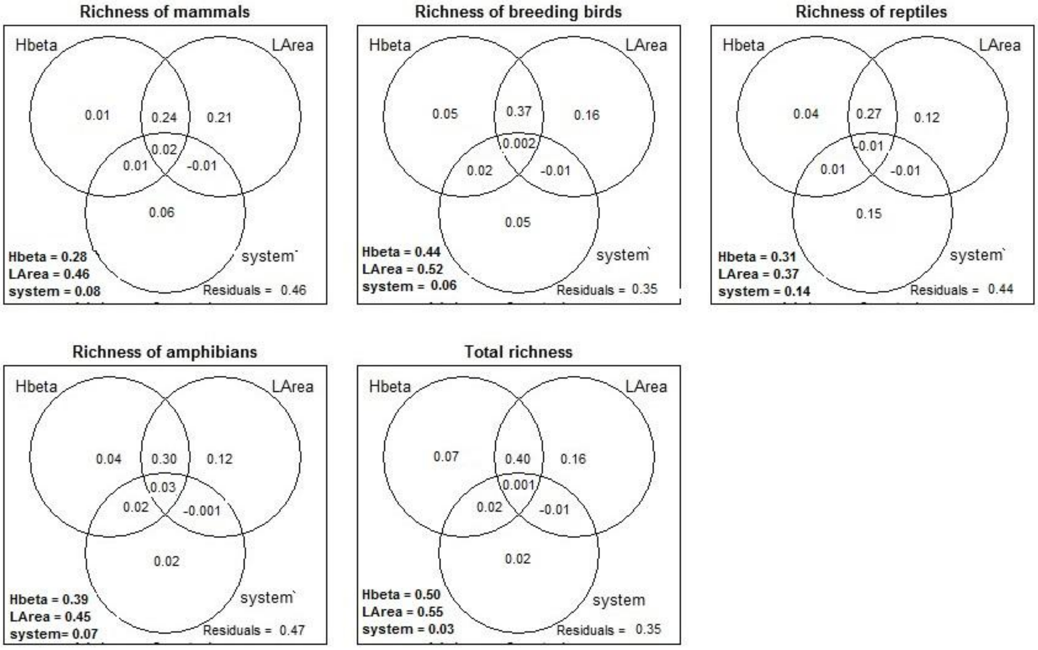

Figure 3. Variance partitioning of species richness in watersheds explained by the pure and combined effect of landscape heterogeneity (Hbeta), logarithm of watershed area (Larea) and mountain system (system). Total variance (pure and combined effect) explained by predictors is in bold. For example, 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) .

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 20x20 km, more than 46 % at 50x50 km and more than 71% at 100x100 km window size. Significant relationships between landscape heterogeneity and species richness were only found for mammals and breeding birds at the largest window size (100x100 km) (Table 2). The percentage of total 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 (Figure 4). The significance of the effect and predictive power of landscape heterogeneity decreased for all taxa for the smallest window sizes (i.e. 50x50 and 20x20 km) (Table 2; Table A4 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 20x20 km window size, these variables mainly explaining total variance of models. At 50x50 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 100x100 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; Figure 4 and Table A5 from the appendix).

Table 2. Anova table including: explained sum of squares (*Sum. Sq.*), *F* value, significance (*Sig.*) and normal coefficients of determination (R^2) of linear models based on square windows of different sizes (20x20 km, 50x50 km and 100x100 km).

	20x20				50x50				100x100			
	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.

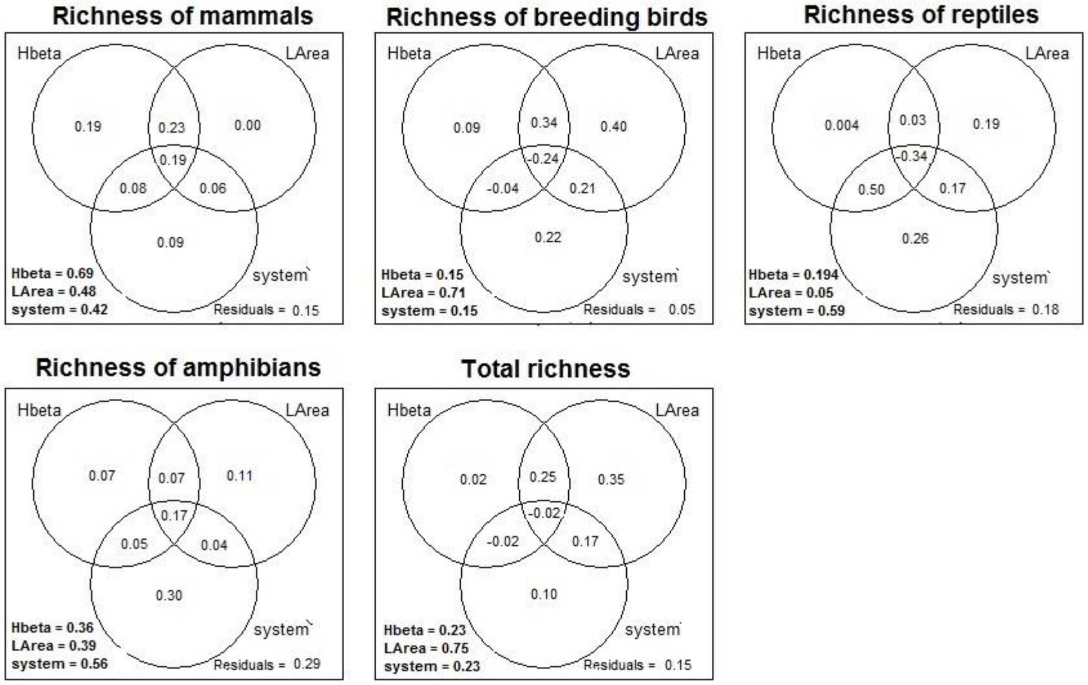

Figure 4. Variance partitioning of species richness explained by pure and combined effects of landscape heterogeneity (Hbeta), logarithm of window area (Larea) and mountain system (system) for windows of 100x100 km (or less if they intersected the limits of the study area). Total variance (pure and combined 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).

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 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 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 100x100 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 x 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., 20x20 and 50x50 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., Shipam 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 (Shipam 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 1992; 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 x 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 (Duflot 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 (Tamm 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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Bibliography

Álvarez-Martínez JM, Suárez-Seoane S, Stoorvogel JJ, Luis Calabuig E (2014) Influence of land use and climate on recent forest expansion: a case study in the Eurosiberian-Mediterranean limit of north-west Spain. J Ecol 102(4):905−919

Amano T, Kusumoto Y, Tokuoka Y, Yamada S, Kim EY, Yamamoto S (2008) Spatial and temporal variations in the use of rice-paddy dominated landscapes by birds in Japan. Biol Cons 141(6):1704−1746

Atauri JA, de Lucio JV (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecol 16(2):147−159

Baattrup-Pedersen A, Andersen HE, Larsen SE, Nygaard B, Ejrnæs R (2012) Predictive modelling of protected habitats in riparian areas from catchment characteristics. Ecol Indic 18:227−235

Baloch MA, Tanik A (2008) Development of an integrated watershed management strategy for resource conservation in Balochistan Province of Pakistan. Desalination 226(1−3): 38−46

Barbaro L, Van Halder I (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32(2):321–333

Bjornstad ON (2013) ncf: spatial nonparametric covariance functions. R package version 1.1-5. Available online at http://CRAN.R-project.org/package=ncf

Blasi C, Zavattero L, Marignani M, Smiraglia D, Copiz R, Rosati L, Del Vico E (2008) The concept of land ecological network and its design using a land unit approach. Pl Biosystmes 142(3):540−549

Cale PG, Hobbs RJ (1994) Landscape heterogeneity indices: problems of scale and applicability, with particular reference to animal habitat description. Pac Conserv Biol, 1(3):183-193

Chambers CL, Cushman SA, Medina-Fitoria A, Martínez-Fonseca J, Chávez-Velásquez M (2016) Influences of scale on bat habitat relationships in a forested landscape in Nicaragua. Landscape Ecol 31(6):1299−1318

Congalton, RG (2001) Accuracy assessment and validation of remotely sensed and other spatial information. Int. J. Wildl. Fire 10(4), 321–328.

Cushman SA; McGarigal K (2008). Landscape metrics, scales of resolution. In von Gadow K, Pukkala T (Eds.) Designing Green Landscapes. Springer, Netherlands.

Dark SJ, Bram D (2007) The modifi able areal unit problem (MAUP) in physical geography. Progr Phys Geog 31(5):471–479

Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol Lett 13(8):1030–1040

Duflot R, Georges R, Ernoult A, Aviron S, Burel F (2014) Landscape heterogeneity as an ecological filter of species traits. Acta Oecol 56:19–26

Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. Ecography 29(4):573-584.

Dungan JL, Perry JN, Dale MRT, Legendre P, Citron-Pousty S, Fortin MJ, Jakomulska A, Miriti M, Rosenberg MS (2002) A balance view of scale in spatial statistical analysis. Ecography 25(5):626−640

Ewers RM, Didham RK, Wratten SD, Tylianakis JM (2005) Remotely sensed landscape heterogeneity as a rapid tool for assessing local biodiversity value in a highly modified New Zeland landscape. Biodivers Conserv 14(6):1469−1485

Farina A (2001) Landscape and their ecological components. Living World 4:435−448

Flick T, Feagan S, Fahrig L (2012) Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada. Agr Ecosyst Environ 156:123−133

García-Llamas P, Calvo L, Álvarez-Martínez JM, Suárez-Seoane S (2016) Using remote sensing products to classify landscape. A multi-spatial resolution approach. Int J Appl Earth Obs 50:95−105

Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York

Gimona A, Messager P, Occhi M (2009) CORINE-based landscape indices weakly correlate with plant species richness in a northern European landscape transect. Landscape Ecol 24(1):53−64

Herrando S, Anton M, Sardà-Palomera F, Bota G, Gregory RD, Brotons L (2014) Indicators of the impact of land use changes using large-scale bird surveys: Land abandonment in a Mediterranean region. Ecol Indic 45:235−244

Jelinski DE, Wu J (1996) The modifiable areal unit problem and implications for landscape ecology. Landsc Ecol 11(3):129–140

Jobbágy EG, Paruelo JM, León RJ (1996) Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia (Argentina). J Veg Sci 7(4):599-608

Johnson AR, Wiens JA, Milne BT, Crist TO (1992) Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecol 7(1):63−75

Jost L (2006) Entropy and diversity. Oikos 113(2): 363−375

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88(10): 2427−2439

Kallimanis AS, Mazaris AD, Tzanopoulos J, Halley JM, Pantis JD, Sgardelis SP (2008) How does habitat diversity affect the species-area relationship? Global Ecol Biogeogr 17(4):532−538

Karadağ AA (2013) Use of watersheds boundaries in the landscape planning. In: Özyabuz M (ed.) Advances in landscape architecture. InTech

Katayama N, Amano T, Naoe S, Yamakita T, Komatsu I, Takagawa S, Sato N, Ueta M, Miyashita T (2014) Lanscape heterogeneity - biodiversity relationships: effect of range size. PLoS ONE 9(3):e93359

Kivinen S, Luoto M, Kuussaari M, Saarinen K (2007) Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes. Agri Ecos Environ 122(4)453−460

Kohn DD, Walsh DM (1994) Plant species richness-the effect of island size and habitat diversity. J Ecol 82:367−377

Krömer T, Acebey A, Kluge J, Kessler M (2013) Effects of altitude and climate in determining elevational plant species richness patterns: a case study from Los Tuxtlas, Mexico. Flora 208(3):197−210

La Sorte FA, Jetz W.(2010) Projected range contractions of montane biodiversity under global warming. Proc R Soc B 277: 3401–3410.

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76:5−13

Lasanta-Martínez T, Vicente-Serrano SM, Cuadrat-Prats JM (2005) Mountain Mediterranean landscape evolution caused by the abandonment of traditional primary activities: a study of the Spanish Central Pyrenees. Appl Geogr 25(1):47−65

Laurila-Pant M, Lehikoinen A, Uusitalo L, Venesjärvi R (2015) How to value biodiversity in environmental management? Ecol Indic 55:1−11

Lee MB, Martin JA (2017) Avian species and functional diversity in agricultural landscapes: does landscape heterogeneity matter? PLoS ONE 12(1):e0170540

Lechner AM, Langford WT, Jones SD, Bekessy SA, Gordon A (2012) Investigating species-environment relationships at multiple scales: differentiating between intrinsic scales and the modifiable areal unit problem. Ecol Complex 11:91−102

Legendre P, Legendre L (2012) Numerical ecology. Elsevier, Amsterdam

Li J, Zhou ZX (2015) Coupled analysis on landscape pattern and hydrological processes in Yanhe watershed of China. Sci Total Environ 505:927−938

Li Y, Chen J, Jiang L, Qiao G (2017) Islands conserve high species richness and areas of endemism of *Hormaphidinae aphids*. Curr Zool 1−10

Lindenmayer DB, Cunningham RB, Donnelly CF, Lesslie R (2002) On the use of landscape surrogates as ecological indicators in fragmented forests. Forest Ecol Manag 159(3):203−216

López-Sáez JA, Abel-Schaad D, Pérez-Díaz S, Blanco-González A, Alba-Sánchez F, Dorado M, Ruiz-Zapata B, Gil-García MJ, Gómez-González C, Franco-Múgica F (2014) Vegetation history, climate and human impact in the Spanish Central System over the last 9000 years. Quater Int 353:98−122

Maiorano L, Amori G, Capula M, Falcucci A, Masi M, Montemaggiori A, Pottier J, Psomas A, Rondinini C, Russo D, Zimmermann NE, Boitani L, Guisan A, (2013) Threats from climate change to terrestrial vertebrate hotspots in Europe. PLoS ONE 8(9) e74989

Martí R, del Moral JC (eds) (2003) Atlas de las aves reproductoras de España. Dirección General de la Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid.

Martinelli G (2007) Mountain biodiversity in Brazil. Rev Bras Botânica 30(4):587–597

Martínez-Rica JP, Recoder PM (1990) Biogeographic features of the Pyrenean range. Mt Res Dev 10(3):235−240

Mawangi PK (2010) The influence of landscape heterogeneity on amphibian species richness in Malaga province, Spain. Master dissertation, International Institute for Geo-Information Science and Earth Observation, Enschede

Maxell BA (2009) State-wide assessment of status, predicted distribution, and landscape-level habitat suitability of amphibians and reptiles in Montana. Dissertation, University of Montana, Missoula

Mayer A, Winkler R, Fry L (2014) Classification of watersheds into integrated social and biophysical indicators with clustering analysis. Ecol Indic 45:340−349

Mazía CN, Chaneton EJ, Kitzberger T (2006) Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. J Arid Environ 67(2):177−194

Medinski TV, Mills AJ, Esler KJ, Schmiedel U, Jürgens N (2010) Do soil properties constrain species richness? Insights from boundary line analysis across several biomes in south western Africa. J Arid Environ 74(9):1052−1060

Mehr M, Brandl R, Hothorn T, Dziock F, Förster B, Müller J (2011) Land use is more important than climate for species richness and composition of bat assemblages on a regional scale. Mamm Biol (DNLM) 76(4):451−460

Mendoza ME, López Granados E, Geneletti D, Pérez-Salicrup DR, Salinas V (2011) Analysing land cover and land use change processes at watershed level: a multitemporal study in the Lake Cuitzeo Watershed, Mexico (1975-2003). Appl Geogr 31(1):237−250

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on species? Landscape Ecol 31(6):1177−1194

Ministry of Agriculture, Food and Environment (2012) Base de datos de los vertebrados de España. Ministerio de Medio Ambiente, Madrid

Montgomery DR, Grant GE, Sullivan K (1995) Watershed analysis as a framework for implementing ecosystem management. JAWRA 31(3):369−386

Morán-Ordóñez A, Suárez-Seoane S, Calvo L, De Luis E (2011) Using predictive models as a spatially explicit support tool for managing cultural landscapes. Appl Geogr 31(2):839−848

Morán-Ordóñez A (2012) Spatio-temporal modelling of services provided by the diversity of shrub and heath communities in the Cantabrian Mountains (NW Spain). Effect of socio-economic changes at different scales. Dissertation, University of León

Morelli F, Pruscini F, Santolini R, Perna P, Benedetti Y, Sisti D (2013) Landscape heterogeneity metrics as indicators of bird diversity: determining the optimal spatial scales in different landscapes. Ecol Ind 34:372−379

Moreno-Rueda G, Pizarro M (2007) The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. Acta Ecol 32(1):50−58

Morillo C, Gómez-Campo C (2000) Conservation in Spain, 1980–2000. Biol Conser 95(2):165–174

Moser B, Jaeger JAG, Tappeiner U, Tasser E, Eiselt B (2007) Modification of the effective mesh size for measuring landscape fragmentation to solve the boundary problem. Landscape Ecol 22(3):447–459

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nimon KF, Oswald FL (2013) Understanding the results of multiple linear regression: beyond standardized regression coefficients. Organ Res Meth 16(4):650–674

Nogués-Bravo D, Martínez-Rica JP (2004) Factors controlling the spatial species richness pattern of four groups of terrestrial vertebrates in an area between two different biogeographic regions in northern Spain. J Biogeogr 31(4):629−640

Nouri H, Anderson S, Sutton P, Beecham S, Nagler P, Jarchow CJ, Roberts RA (2017) NDVI, scale invariance and the modifiable areal unit problem: an assessment of vegetation in the Adelaide Parklands. Sci Total Environ 584−585:11−18

Oindo BO, Skidmore AK, de Salvo P (2003) Mapping habitat and biological diversity in the Maasai Mara ecosystem. Int J Remote Sensing 24(5):1053−1069

Oliver T, Roy DB, Hill JK, Brereton T, Thomas CD (2010) Heterogeneous landscapes promote population stability. Ecol Lett 13(4):473−484

Palomo LJ, Gisbert J, Blanco JC (2007) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid, 588 pp

Perović D, Gámez-Virués S, Börschig C, Klein AM, Krauss J, Steckel J, Rothenwöhrer C, Erasmi S, Tscharntke T, Westphal C (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. J Appl Ecol 52(2):505–513

Pino J, Rodà F, Ribas J, Pons X (2000) Landscape structure and birds species richness: implications for conservation in rural areas between natural parks. Lands Urban Plan 49(1−2):35−48

Pleguezuelos JM, Márquez R, Lizana M (eds) (2002) Atlas y libro rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación de Herpetología Española, Madrid

Plexida SG, Sfougaris AI, Ispikoudis IP, Papanastasis VP (2014) Selecting landscape metrics as indicators of spatial heterogeneity-A comparison among Greek landscapes. Int J Appl Earth Obs 26:26−35

Priego-Santander ÁG, Campos M, Bocco G, Ramírez-Sánchez LG (2013) Relationship between landscape heterogeneity and plant species richness on the Mexican Pacific coast. Appl Geogr 40:171−178

R Development Core Team (2014) R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. Available online at http://www.R-project.org/

Ray-Mukherjee J, Nimon K, Mukherjee S, Morris DW, Slotow R, Hamer M (2014) Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. Methods Ecol Evol 5(4):320-328

Rempel RS, Kaukinen D, Carr AP (2012) Patch Analyst and Patch Grid. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario

Rivas-Martínez S, Gandullo JM, Serrada R, Allué JL, Montero JL, González JL (1987) Memoria del mapa de series de vegetación de España. Ministerio de Agricultura, Pesca y Alimentación, ICONA Serie Técnica, Madrid

Rossi JP, van Halder I (2010) Towards indicators of butterfly biodiversity based on a multiscale landscape description. Ecol Ind 10(2):452−458

Roura-Pascual N, Pons P, Etienne M, Lambert B (2005) Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. Mt Res Dev 25(3):252−261

Saura S, Martínez-Millán J (2001) Sensitivity of landscape pattern metrics to map spatial extent. Photogramm Eng Remote Sens 67(9):1027−1036

Schindler S, von Wehrden H, Poirazidis K, Wrbka T, Kati V (2013) Multiscale performance of landscape metrics as indicators of species richness of plants, insects and vertebrates. Ecol Ind 31:41−48

Seoane J (2014) ¿Modelos mixtos (lineales)? Una introducción para el usuario temeroso. Etologuía 24

Shannon CE (1948) A Mathematical Theory of Communication. Bell System Tech J 27:379−423, 623−656

Shao G, Wu J (2008) On the accuracy of landscape pattern analysis using remote sensing data. Landscape Ecol 23(5):505−511

Shipman PA, Fox SF, Thill RE, Phelps JP, Leslie DM (2004) Reptile communities under diverse forest management in the Ouachita Mountains, Arkansas. In: Guldin JM (Ed.) Ouachita and Ozark Mountains Symposium: Ecosystem Management Research, Hot Springs, Arkansas, October 26–28, 1999. General Technical Report Nº SRS-74. Southern Research Station, USDA Forest Service, Asheville, NC, pp. 174–182

Suárez-Seoane S, Baudry J (2002) Scale dependence of spatial patterns and cartography on the detection of landscape change: relationships with species' perception. Ecography 25(4):499-511

Tamma K, Marathe A, Ramakrishnan U (2016) Past influences present: mammalian species from different biogeographic pools sort environmentally in the Indian subcontinent. Front Biogeogr 8(1):e26262

Tarrega R, Luis-Calabuig E, Alonso I (1997) Space-time heterogeneity in the recovery after experimental burning and cutting in the *Cytisus laurifolius* shrubland. Plant Ecol 129(2):179−187

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31(1):79−92

Tinker DB, Resor CA, Beauvais GP, Kipfmueller KF, Fernandes CI, Baker WL (1998) Watershed analysis of forest fragmentation by clearcuts and roads in a Wyoming forest. Landscape Ecol 13(3):149−165

Triantis KA, Mylonas M, Lika K, Vardinoyannis K (2003) A model for the species–area-habitat relationship. J Biogeogr 30(1):19−27

Verberk WCEP, van Duinen GA, Brock AMT, Leuven RSEW, Siepel H, Verdonschot PFM, van der Velder G, Esselink H (2006) Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. J Nat Conserv 14(2):78−90

Wagner HH, Fortin MJ (2005) Spatial analysis of landscapes: concepts and statistics. Ecology 86(8):1975−1987

Walz U (2011) Landscape structure, landscape metrics and biodiversity. Living Rev Landscape Res 5(3):1-35

Washington Forest Practice Board (WFPB) (1992) Standard methodology for conducting watershed analysis. Washington forest act board manual, version 1.0, 13 pp

Washington Forest Practice Board (WFPB) (1992) Standard methodology for conducting watershed analysis. Washington forest act board manual, version 2.0, 85 p

Weibull AC, Bengtsson J, Nohlgren E (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. Ecography 23(6):743−750

Wong D (2009) The modifiable areal unit problem (MAUP). In Fotheringham AS, Rogerson PA. The SAGE handbook of spatial analysis. Los Angeles, Sage, pp 105–124

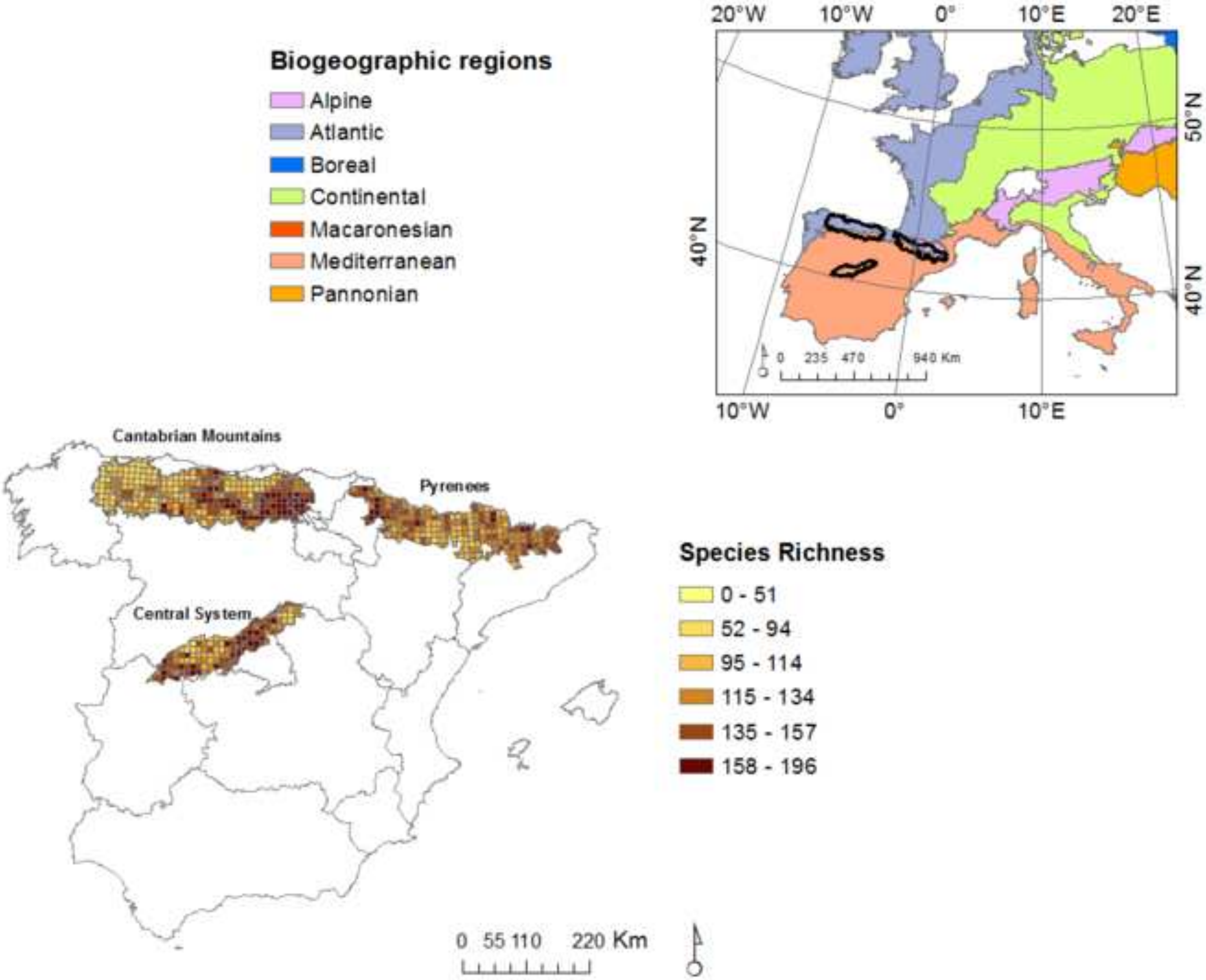
Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecol 19(2):125−138

Ye X, Wang T, Skidmore AK, Fortin D, Bastille-Rousseau G, Parrott L (2015) A wavelet-based approach to evaluate the roles of structural and functional landscape heterogeneity in animal space use at multiple scales. Ecography 38(7):740–750

Yu F, Wang T, Groen TA, Skidmore AK, Yang X, Geng Y, Ma K (2015) Multi-scale comparison of topographic complexity indices in relation to plant species richness. Ecol Complex 22:93−101

Zhang Y, Zhang S, Ma K, Fu B, Anand M (2014) Woody species diversity in forest plantations in a mountainous region of Beijing, China: effects of sampling scale and species selection. PloS ONE 9(12):e115038

Figure1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Alpine
Atlantic
Boreal
Continental
Macaronesian
Mediterranean
Pannonian
20°W
10°W
0°
10°E
20°E
50°N
40°N
40°N
0 235 470 940 Km
10°W
0°
10°E
Cantabrian Mountains
Pyrenees
Central System
Species Richness
0 - 51
52 - 94
95 - 114
115 - 134
135 - 157
158 - 196
0 55 110 220 Km

Figure2

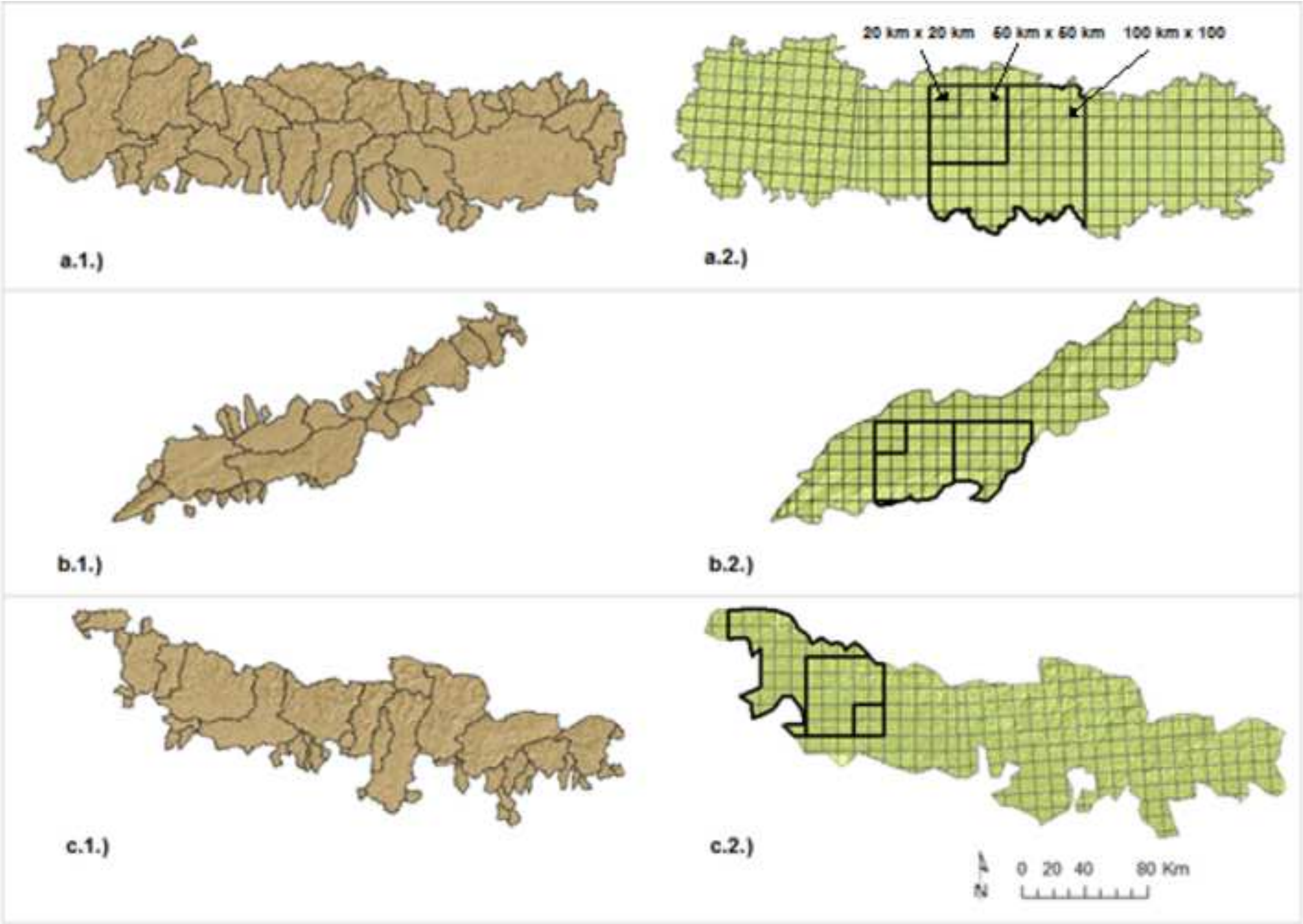
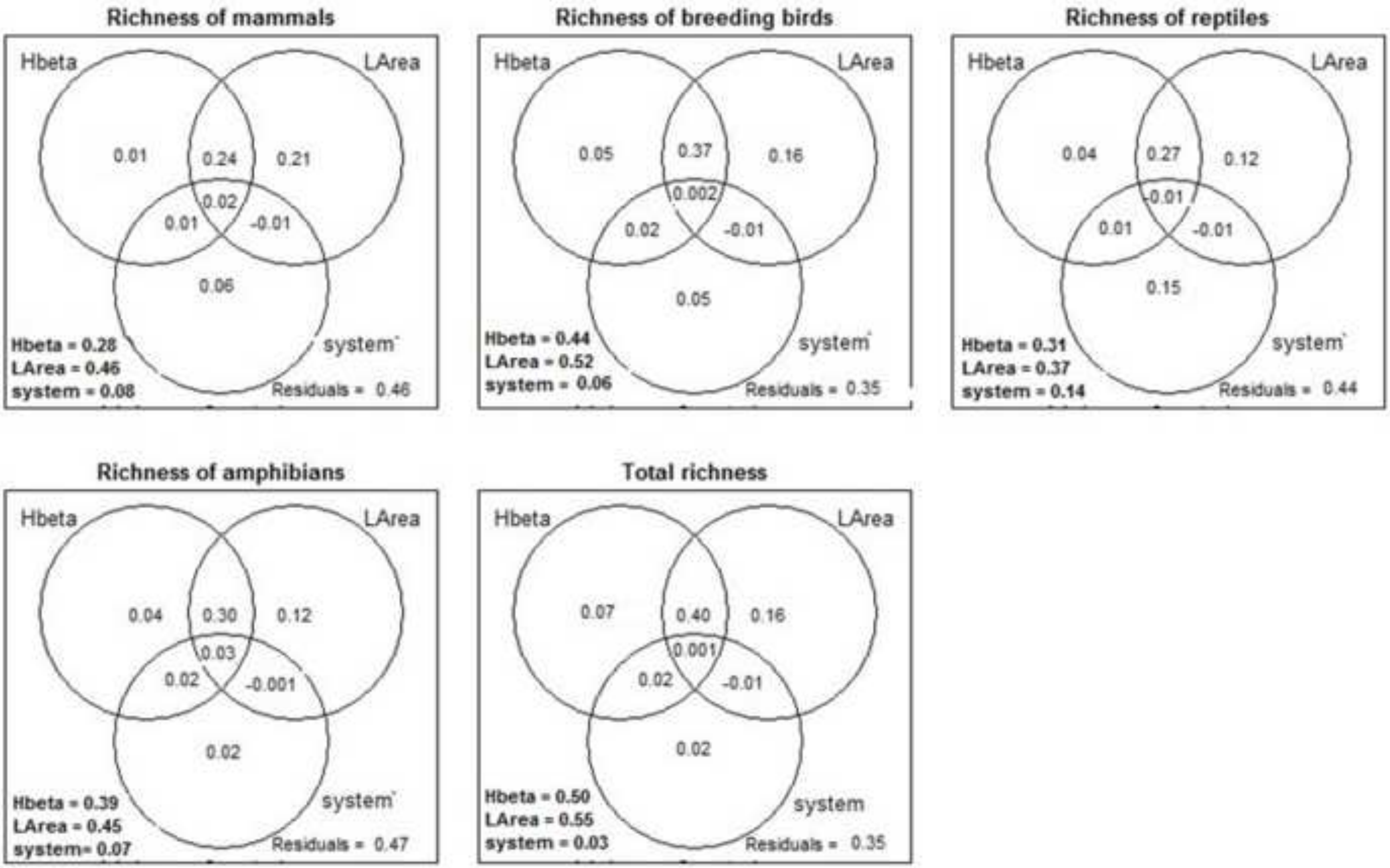


Figure3


Richness of mammals

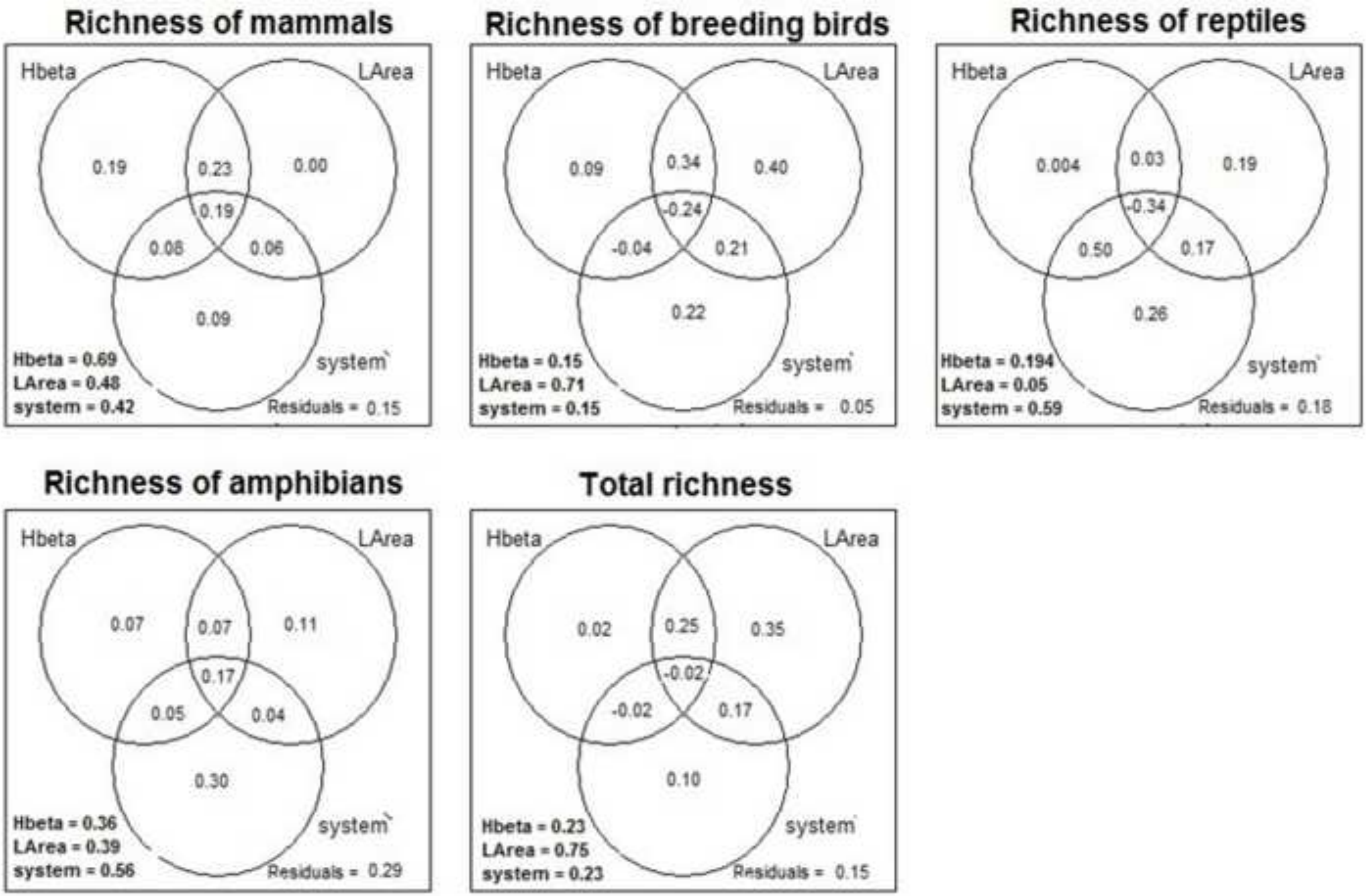
Richness of breeding birds

Richness of reptiles

Richness of amphibians

Total richness

Figure4



Richness of mammals

Richness of breeding birds

Richness of reptiles

Richness of amphibians

Total richness

Table A1. Absolute (S_a; number of species) and relative (S_r; number of species per 100 km^2) values of species richness: total and taxonomic (mammals, breeding birds, reptiles and amphibians) richness for each mountain system (Cantabrian Mountains, Central System and the Spanish Pyrenees).

	Cantabrian Mountains		Central System		Spanish Pyrenees	
	S_a	S_r	S_a	S_r	S_a	S_r
Mammals	88	0.27	85	0.07	64	0.29
Breeding birds	198	0.62	188	0.10	166	0.74
Reptiles	29	0.09	30	0.23	20	0.09
Amphibians	19	0.06	17	0.13	15	0.07
Total species	334	1.06	320	0.20	265	1.18

Figure A1. Landscape classifications based on CORINE, for a.1) the Cantabrian Mountains; b.1) the Central System; c.1) the Spanish Pyrenees.

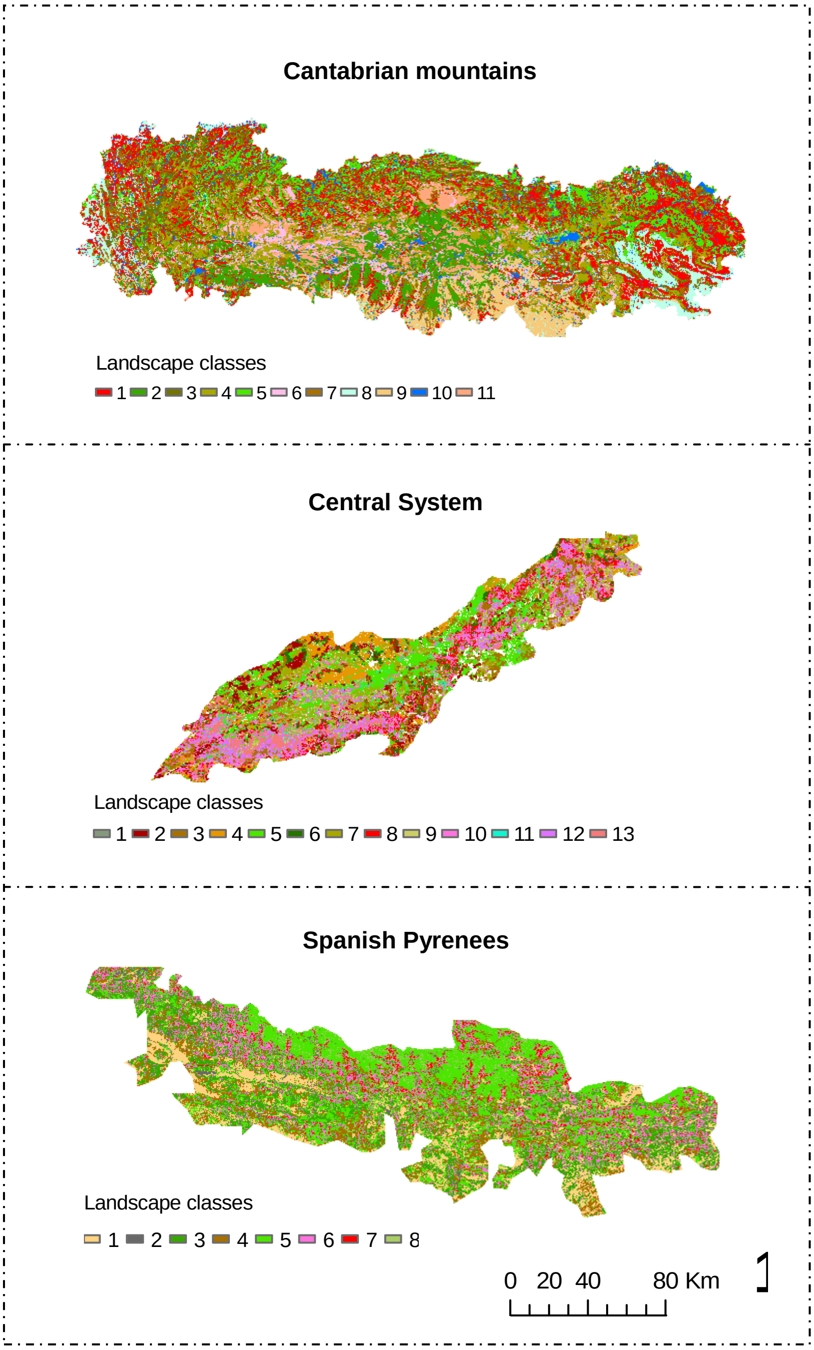


Table A2. Description of landscape classes obtained from a set of variables accounting for topography, urban influence and land cover (CORINE).

Class	Description
	Cantabrian Mountains
1	Forests covering coastal and middle-mountain areas at an average altitude of 688.16 ± 299.69 m.a.s.l., in areas with moderate to steep slope (mean value 20.73º ± 10.72º) and at mid-distance to settlements (mean value 3.65 ± 4.05 km)
2	Forests covering central mountains and piedmont areas at an average altitude of 1267.14 ± 240.47 m.a.s.l. with moderate slope (mean value 17.56 9 ± 9.77º), those being at mid-distance to settlements (mean distance 2.67 ± 2.48 km)
3	Transitional to woodlands with low urban influence (mean distance to settlements 5.24 ± 4.92 km), covering mainly Atlantic and Sub-Atlantic mountains located at low altitudes (mean value 624 ± 213.42 m.a.s.l.), with moderate to steep slope (mean value 24.08º ± 9.86º)
4	Transitional woodlands from central and southern areas of the Cantabrian Mountains, with relatively low urban influence (mean distance to settlements 3.9 ± 4.11 km), those being located at an average altitude of 1207.40 ± 290.56 m.a.s.l., in areas with moderate slope (mean value 18.05º ± 10.30º)
5	Pastures from mid-low Atlantic mountains and coastal areas (mean altitude 520.22 ± 263.10 m.a.s.l.), with moderate slope (mean value 15.87º ± 9.68º) and at mid-distance to settlements (mean value 3.66 ± 4.69 km)
6	Pastures covering bottom valleys and hillsides of the central Cantabrian Mountains, lying at an average altitude of 1216.65 ± 290.14 m.a.s.l., in areas with moderate slope (mean value 16.22º ± 10.51º) at mid-distance to settlements (average distance 2.8 ± 3.54 km)
7	Shrub-herbaceous associations lying at an average altitude of 816.66 ± 378.43 m.a.s.l., in hillsides with moderate slope (mean value 19.27º ± 10.88º) and at mid-distance to settlements (mean distance 3.63 ± 3.83 km)
8	Croplands from depressions and coastal plains (average slope 8.84º ± 8.18º), lying at the lowest altitudes (mean value 605.05 ± 241.81 m.a.s.l.) and those being close to settlements (mean distance 1.64 ± 1.80 km)
9	Croplands (non-irrigated arable lands) from paramos and countryside (mean slope 5.70º ± 5.79º) lying at an average altitude of 977.27 ± 99.30 m.a.s.l. and those being the closest class to settlements (mean distance 1.26 ± 0.99 km)
10	Water surfaces and artificial surfaces lying at an average altitude of 654.15 ± 393.13 m.a.s.l., in areas with moderate slope (mean slope 14.58º ± 11.05º) and at mid-distance to settlements (mean value 2.56 ± 3.54 km)
11	Rocks and areas with little or no vegetation covering the highest altitudinal ranges (mean value 1352.71± 485.47 m.a.s.l.), in areas with steep slope (mean value 25.94º ±12.54º), those being far from settlements (mean distance 4 ± 3.58 km)

Table A2. (cont.)

	Central System
1	Forests covering lowlands and bottom valleys (mean slope 5.28º ± 2.47º), at an average altitude of 1131.37±253.73 m.a.s.l. and at mid-distance to settlements (mean value 2.63 ± 1.38 km)
2	Forests lying at an average altitude of 1226.79 ± 305.41 m.a.s.l. on hillsides with moderate slope (mean value13.32º ± 3º) and at mid-distance to settlements (mean value 28.55 ± 15.36 km)
3	Forests lying at an average altitude of 1223.95 ± 336.03 m.a.s.l., on hillsides with moderate to steep slope (mean value 22.60º ± 6.25º) and at a mid-distance to settlements (mean value 28.62 ± 15.68 km)
4	Transitional to woodlands covering lowlands (mean altitude 1252.28 ± 275.44 m.a.s.l.) and areas with slight slope (mean value 5.31º ± 2.37º), those being at mid-distance to settlements (mean value 2.50 ± 14.51 km)
5	Transitional to woodlands covering middle-hillsides (mean altitude 1352.24 ± 332.77 m.a.s.l.) with moderate slope (mean value 12.80º ± 2.79º), those being at mid-distance to settlements (mean value 2.86 ± 1.66 km)
6	Transitional to woodlands covering the highest altitudes (mean value 1436.55 ± 339.83 m.a.s.l.) with moderate to steep slope (mean value 24.69º ± 6.04º), those being at mid-distance to settlements (mean value 3.55 ± 1.84 km)
7	Pastures covering valley bottoms (mean altitude 1181.78 ± 246.51 m.a.s.l.) and hillsides with a slight slope (mean value 5.16º ± 3.22º) and at mid-distance to settlements (mean 2.29 ± 1.70 km)
8	Pastures covering middle mountain areas (mean value 1348.88 ± 314.95 m.a.s.l.) with moderate slope (mean value 14.62º ± 3.25º) and at mid-distance to settlement (mean value 2.60 ± 1.72 km)
9	Shrub-herbaceous associations located at low altitudinal ranges (mean value 1177.51 ± 301.89 m.a.s.l.) on hillsides with moderate slope (mean value 13.17º ± 8.63º) and at mid-distance to settlements (mean value 2.75 ± 1.64 km)
10	Croplands (herbaceous) covering valley bottoms and plains (mean slope 5.01º ± 4.70º) at an average altitude of 1028.33 ± 201.01 m.a.s.l., those being close to settlements (mean value 1.46 ± 0.9 km)
11	Woody croplands covering valley bottoms and plains (mean slope 6.75º ± 5.40º) at an average altitudinal range of 962.96 ± 233.65 m.a.s.l., those being close to settlements (mean value 2.06 ± 1.34 km)
12	Water surfaces and artificial surfaces located at an average altitude of 1002.28 ± 229.45 m.a.s.l., in areas of slight slope (mean value 4.87º ± 4.22º), those being close to settlements (mean value 1.31 ± 1.25 km)
13	Rocks and areas with little or no vegetation covering the highest altitudes (mean value 1481.65 ± 371.04 m.s.a.l.), in areas with moderate to steep slope (20.08º ± 10.21º) at mid-distance to settlements (mean distance 3.54 ± 2.17 km)
	Spanish Pyrenees
1	Forests lying at an average altitude of 1000.49 ± 323.21 m.a.s.l., covering hillsides with moderate slope (mean value 14.28º ± 5.29º) at mid-distance to settlements (mean distance 2.95 ± 1.74 km)
2	Forests lying at an average altitude of 1163.56 ± 368.78 m.a.s.l., covering hillsides with steep slope (mean value 27.97º ± 3.57º), those being at mid-distance to settlements (mean value 2.97 ± 1.77 km)
3	Forests lying at an average altitude of 1313.67 ± 397.56 m.a.s.l., in areas with very steep slope (mean value 39.39º ± 4.23º), those being at mid-distance to settlements (mean value 2.98 ± 1.83 km)
4	Mosaic of grasslands, rocks and areas with little or no vegetation and transitional to woodlands, covering the highest altitudinal rages (mean value 1547.19 ± 623.41 m.a.s.l.), in areas with moderate slopes (mean value 20.09º ± 9.55º) and at mid-distance to settlements (mean value 3.69 ± 2.61 km)
5	Mosaic of grasslands, rocks and areas with little or no vegetation, covering the highest altitudinal ranges (mean value 1588.50 ± 653.16 m.a.s.l.), in areas with very steep slopes (mean value 44.02º ± 9.07º) and relatively far from settlements (mean value 3.83 ± 2.64 km)
6	Shrub-herbaceous associations lying at an average altitude of 1080.83 ± 414.27 m.a.s.l., covering hillsides with moderate slope (mean value 19.17º ± 9.36º) and at mid-distance to settlements (mean value 2.53 ± 1.58 km)
7	Croplands covering valley bottoms lying at the lowest altitudinal ranges (mean value 775.08 ± 219.38 m.a.s.l.) in areas with slight slope (mean value 10.56º ± 8.04º), those being close to settlements (mean value 1.89 ± 1.51 km)
8	Water surfaces and artificial surfaces lying at an average altitude of 803.85 ± 395.78 m.a.s.l., in areas with moderate slope (mean value 14.21º ± 10.07º), those being close to settlements (mean distance 2.05 ± 1.91 km)

Table A3. Overall accuracy of landscape classifications and user's and producer's accuracy per class, obtained from topography, urban influence and CORINE (as a proxy of land cover) data.

	Class	User's accuracy (%)	Producer's accuracy (%)	Overall accuracy (%)
Cantabrian Mountains	1	93.33	88.89	88.33
	2	85.29	78.38	
	3	83.33	68.97	
	4	86.49	96.97	
	5	100.00	91.18	
	6	94.12	94.12	
	7	96.15	100.00	
	8	89.47	85.00	
	9	85.00	89.47	
	10	50.00	100.00	
	11	93.33	100.00	
Central System	1	50.00	100.00	84.39
	2	90.00	81.81	
	3	100.00	84.62	
	4	92.30	80.00	
	5	69.23	75.00	
	6	77.78	80.00	
	7	88.00	91.66	
	8	100.00	37.05	
	9	92.30	100.00	
	10	100.00	84.62	
	11	100.00	100.00	
	12	100.00	100.00	
	13	88.00	91.67	
Spanish Pyrenees	1	85.29	87.87	88.00
	2	95.23	66.67	
	3	85.00	71.51	
	4	80.49	97.05	
	5	100.00	66.67	
	6	100.00	100.00	
	7	89.47	100.00	
	8	50.00	100.00	

Table A4. Estimate, standard error (*Std. error*) and significance (*Sig.*) of regression linear models, achieved when working with watersheds as spatial analytical units and landscape heterogeneity calculated from landscape classifications. The intercept represents the Cantabrian Mountains.

	Estimate	Std. Error	Sig.
Mammal richness			
Intercept	2.03	0.26	***
H_β	0.43	0.47	n.s.
log(A)	0.23	0.05	***
Central System	-0.08	0.11	n.s.
Spanish Pyrenees	-0.26	0.09	**
Breeding bird richness			
Intercept	37.18	9.93	***
H_β	56.66	18.36	**
log(A)	11.18	1.99	***
Central System	12.74	4.23	*
Spanish Pyrenees	7.20	3.47	**
Reptile richness			
Intercept	-6.73	2.93	*
H_β	13.49	5.55	*
log(A)	2.56	0.58	***
Central System	4.64	1.30	***
Spanish Pyrenees	4.31	1.05	***
Amphibian richness			
Intercept	-0.22	1.69	n.s.
H_β	8.21	3.21	*
log(A)	1.45	0.34	***
Central System	-0.27	0.61	n.s.
Spanish Pyrenees	-1.04	0.75	n.s.
Total richness			
Intercept	34.41	19.06	n.s.
H_β	120.18	33.65	***
log(A)	20.89	3.73	***
Central System	13.09	5.98	n.s.
Spanish Pyrenees	5.98	13.09	n.s.

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

Table A5. Estimate, standard error (*Std. error*) and significance (*Sig.*) of regression linear models, achieved when working with regular squared windows as spatial analytical units and landscape heterogeneity calculated from landscape classifications. The intercept represents the Cantabrian Mountains.

	20x20 km			50x50km			100x100km		
	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.
Mammal richness									
Intercept	1.98	0.40	***	3.71	0.88	***	3.52	0.31	***
H_{β}	0.22	0.17	n.s.	0.23	0.32	n.s.	1.50	0.55	*
log(A)	0.31	0.07	***	0.06	0.12	n.s.	0.001	0.05	n.s.
Central System	-0.14	0.07	n.s.	-0.08	0.06	n.s.	0.16	0.1	n.s.
Spanish Pyrenees	-0.26	0.06	***	-0.14	0.07	*	0.21	0.10	n.s.
Breeding bird richness									
Intercept	-31.34	18.11	n.s.	20.76	68.22	n.s.	-81.54	23.43	*
H_{β}	5.40	7.90	n.s.	21.58	24.77	n.s.	114.42	34.47	*
log(A)	23.16	3.08	***	15.28	9.34	n.s.	20.90	2.91	***
Central System	5.42	2.64	*	9.84	4.32	*	36.14	7.05	**
Spanish Pyrenees	12.57	3.26	***	-1.54	5.10	n.s.	29.14	7.07	**
Reptile richness									
Intercept	-9.99	4.94	*	28.08	15.46	n.s.	-4.32	8.39	n.s.
H_{β}	3.95	2.15	n.s.	2.07	5.61	n.s.	-5.22	13.18	n.s.
log(A)	3.24	0.84	***	-1.85	2.11	n.s.	3.04	1.12	*
Central System	6.27	0.89	***	8.49	0.98	***	5.32	2.59	n.s.
Spanish Pyrenees	3.69	0.72	***	5.44	1.16	***	2.03	2.58	n.s.
Amphibian richness									
Intercept	-7.97	3.59	*	29.11	14.57	n.s.	3.22	7.16	n.s.
H_{β}	5.96	3.25	n.s.	11.10	5.28	n.s.	14.70	11.26	n.s.
log(A)	2.65	0.61	***	-2.79	1.99	n.s.	0.50	0.95	n.s.
Central System	2.04	0.63	**	0.05	0.91	**	2.82	2.21	n.s.
Spanish Pyrenees	-0.63	0.51	n.s.	3.10	1.13	n.s.	0.25	2.20	n.s.
Total richness									
Intercept	-75.40	29.65	*	100.99	91.30	n.s.	-75.24	63.26	n.s.
H_{β}	22.26	12.93	n.s.	46.79	33.15	n.s.	94.61	99.46	n.s.
log(A)	41.21	5.04	***	16.05	12.51	n.s.	34.56	8.42	**
Central System	14.61	5.34	**	14.71	5.79	*	29.82	0.72	n.s.
Spanish Pyrenees	-3.40	4.32	n.s.	-6.62	6.83	n.s.	13.98	1.52	n.s.

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

Figure A2. Variance partitioning among pure and combined effects of landscape heterogeneity (Hbeta), logarithm of watershed area (Larea) and mountain system (system), as explanatory variables explaining species richness of mammals, breeding birds, reptiles and amphibians and total species richness, based on squared windows of 20x20 km as spatial units of analysis. Total effect of predictors (shared and pure) is in bold.

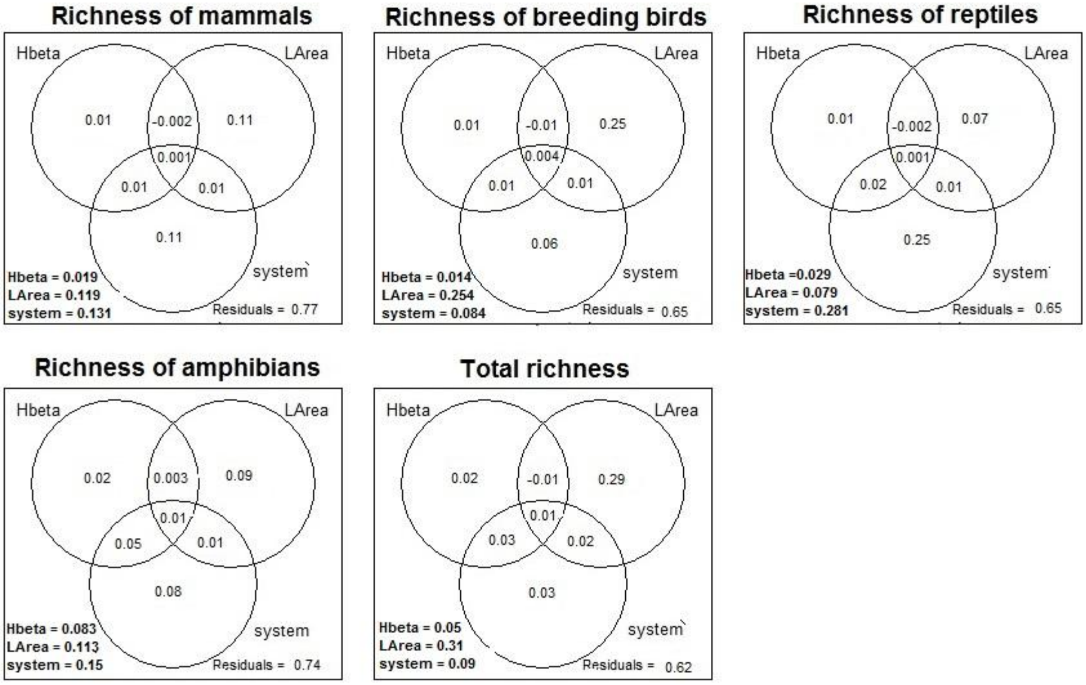


Figure A3. Variance partitioning among pure and combined effects of landscape heterogeneity (Hbeta), logarithm of watershed area (Larea) and mountain system (system), as explanatory variables explaining species richness of mammals, breeding birds, reptiles and amphibians and total species richness, based on squared windows of 50x50 km as spatial units of analysis. Total effect of predictors (shared and pure) is in bold.