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RESUMO

A região mediterrânica é reconhecida pela sua riqueza e diversidade biológica, sendo um hotspot de biodiversidade (Myers e tal., 2000; Blondel e tal., 2010).

As paisagens na bacia do Mediterrâneo estão actualmente sujeitas a um conjunto de dinâmicas de alterações causadas pelas actividades humana, em que se destacam a intensificação agrícola e florestal e o abandono agrícola (Proença e Pereira, 2010). Estas alterações de paisagem causam alterações aos habitats e afectam as espécies que os habitam (Blondel, 2006; Sirami e tal., 2010; Gonzáles-Megías e tal., 2011). Assim, é fundamental perceber quais as respostas das diferentes espécies a estas alterações de habitat e qual a sua capacidade de adaptação, e como essas respostas se traduzem a diferentes escalas espaciais.

A relação entre o número de espécies que habita uma área e a dimensão dessa área é dos padrões mais estudados em ecologia, sendo designada como a relação espécies-área (Arrhenius, 1921). A relação espécies-área tem sido largamente verificada para vários sistemas naturais, no entanto, num contexto de alteração da paisagem e dos habitats nativos, a relação espécies-área apresenta limitações ao assumir que todo o habitat é uniforme e contínuo. Uma vez que as espécies reagem diferentemente às alterações de habitat (Tews e tal., 2004), é necessário integrar o efeito da área com o efeito de habitat. Aliás, vários estudos têm-se debruçado sobre o efeito que a diversidade de habitats tem sobre a diversidade de espécies (Williamson, 1988; Tjorve, 2002; Desrochers et al. 2011) O modelo da relação espécies-área "countryside, proposto por Pereira e Daily (2006), considera não só a existência de diferentes habitats na paisagem mas também o uso diferencial dos mesmos pelos diferentes grupos de espécies.

Neste contexto, o presente trabalho, tentou responder às seguintes questões: (I) Será a heterogeneidade de habitats um proxy para a diversidade de espécies? (II) É o efeito da área e o efeito da diversidade de habitats na riqueza de espécies, dependente da escala ou dependente nas características de cada grupo de espécies? Para responder a estas questões, utilizou-se a Península Ibérica como caso de estudo e analisaram-se os padrões de diversidade de passeriformes, répteis e anfíbios à escala da grelha de 10x10 Km^2, testando a influência de três classes de variáveis ambientais: uso do solo, variáveis climáticas e topográficas. No caso dos passeriformes, analisou-se diversidade de cada grupo de espécies com afinidades similares para os diferentes habitats, tendo-se para isso procedido à classificação das espécies em cada um destes grupos previamente.

Para responder à questão (I) realizámos uma série de análises. A relação entre os diferentes grupos de espécies e os vários preditores ambientais foi avaliada utilizando análises de correlação (Spearman´s rho). A importância relativa dos diferentes grupos de preditores (climáticos, topográficos e de habitat) na distribuição da riqueza específica foi avaliada com uma abordagem multi-modelo, onde em cada modelo de regressão linear foram considerados várias combinações de preditores (Tabela 2). A relação entre riqueza específica e a estrutura da paisagem (heterogeneidade) para Espanha, foi avaliada através de correlação de Spearman´s e análise visual de boxplots. Para responder à segunda questão (II) comparámos o desempenho do modelo espécies-área *clássico* (eqn 1) com o modelo *countryside*-SAR (eqn 2 e 3) à escala regional. O desempenho dos modelos foi comparado usando o Akaike Information Criterion (AIC) e o Root Mean Squared Error (RMSE). Todas as análises foram efectuadas no programa R (http://www.r-project.org/).

Os mapas da riqueza específica construídos para a Península Ibérica mostram que a distribuição das espécies não é homogénea, e que depende do taxon (Figura 3). Cada taxon respondeu diferentemente às variáveis ambientais testadas (Tabela 3). Todos os grupos de espécies, excepto o grupo de passeriformes com afinidade para habitats agrícolas, reagiram negativamente à presença de áreas agrícolas. Todos os grupos de espécies de passeriformes mostraram uma relação negativa com a presença de floresta exótica. Estes resultados estão em acordo com outros trabalhos que mostraram que muitas espécies tendem a evitar áreas de cultivo intensivo e plantações (Diáz e tal., 1998; Donald e tal., 2001; Benton e tal, 2003).

O clima revelou-se o factor principal na determinação da diversidade das espécies. No entanto, quando as variáveis de habitat são adicionadas aos modelos de regressão com variáveis climáticas, o poder explicativo dos padrões de diversidade melhora significativamente (Tabela 4). Encontrámos também uma relação entre a heterogeneidade da paisagem e a diversidade para vários grupos taxonómicos. A dominância das variáveis climáticas não surpreende dado que a esta escala regional ($10x10km^2$) os modelos de distribuição de espécies têm usado com sucesso apenas variáveis climáticas (Wisz e Guisan 2009), mas diverge de padrões encontrados à escala local, em que a estrutura dos habitats parece ser o factor mais relevante (Atauri e Lucio, 2001; Nogués e Martínez 2004; Moreno e Pizarro, 2007).

A variedade de respostas à heterogeneidade da paisagem, pelos diferentes grupos (Tabela 5, Figura 4), indica que as espécies (i.e., os grupos de espécies), usam a paisagem de diferente modo. A diversidade de espécies num habitat está ligada com a sua capacidade de fornecer as estruturas

necessárias para a sua sobrevivência, zonas de predação, refugio, reprodução, etc. (Keitt e tal, 1997; Mazerolle e Villard, 1999; Atuari e Lucio, 2001; Gil-Tena e tal., 2007; Desroches e tal 2011).

A comparação do modelo clássico espécies-área com o modelo *countryside* demonstra que, numa paisagem multi-habitat à escala regional, o modelo *countryside* é o que melhor explica a riqueza específica de cada um dos grupos de espécies e do total número de espécies (Tabela 6). Para investigar o efeito da escala, os resultados foram comparados com os obtidos a escala local em estudos com plantas e aves, por Proença (2009) e Guilherme (2009), respectivamente. Em ambos os trabalhos constatou-se que o modelo *countryside* explicava melhor os padrões espécies-área à escala da paisagem. À semelhança do encontrado à escala regional, o parâmetro de afinidade para o habitat preferencial apresentou o valor máximo em cada grupo de espécies. No entanto, enquanto na escala local os grupos de espécies apresentaram valores de afinidade significativos para os habitats alternativos, à escala regional apenas as espécies florestais mostraram afinidades baixas para os habitats alternativos.

Palavras-chave: relação espécies-área (SAR), countryside-SAR, heterogeneidade de habitats, diversidade de espécies, modelos multi-habitat

ABSTRACT

The Mediterranean basin is one of the world “hotspots” of biological diversity, being characterized by a long history of human use and landscape modification. Different organisms will respond differently to landscape changes and habitat modification, and the affinity of species for different habitats has to be taken into account when modeling species-area patterns. Here, we studied the effect of area and habitat diversity on the diversity of amphibians, reptiles and passerines at the Iberian Peninsula scale in a grid of 10x10km^2. Passerine species were separated into groups sharing similar habitat affinities. We tested the relationship between species diversity and habitat heterogeneity, assessed the relative importance of habitat predictors, climate and topographic predictors on explaining species diversity, and compared the performance of a multi-habitat species-area model against the performance of the classic species-area relationship. All species groups reacted positively to landscape heterogeneity, and several groups reacted negatively to the area of exotic forests and agricultural area.

Climatic predictors explained most of the species richness distribution, but the fit of models was improved when habitat predictors were added. Species diversity patterns in a multi-habitat landscape were well described by the countryside species-area relationship. The countryside species-area relationship had a better fit both when predicting species-area patterns of species groups and of total species richness. Previous studies had identified the importance of land-use for species diversity at the local scale. Our results suggest that, even at a regional scale, understanding the relationships between land-use and species richness may help to assess species responses to habitat change and to define more efficient conservation measures.

Keywords: Species diversity, habitat heterogeneity, multi-habitat landscapes, species-area relationship (SAR), countryside-SAR

CONTENTS

1. INTRODUCTION

Mediterranean landscapes are widely recognized for their richness and diversity. The Mediterranean region supports up to 25 000 native species, corresponding to 10% of the world´s flowering plants, of which 13 000 are endemic species (Blondel and Aronson, 1999; Médail and Quézel 1999; Cuttelod et al., 2008), constituting one of the world's biodiversity hotspots (Myers et al., 2000; Blondel et al., 20100. The structure and dynamics of Mediterranean landscapes are complex because of their spatial and temporal diversity (Blondel, 2006; Gonzáles-Megías et al., 2011). They are generally characterized by highly heterogeneous and fine-grain mosaic, resulting from natural topographic and climatic variability (Cowling et al., 1996; Luterbacher et al., 2004) and long-term interactions of biotic, abiotic, and anthropogenic processes (Blondel, 2006; Sirami et al., 2010; Blondel et al., 2010).

The Mediterranean Basin has been repeatedly manipulated or 'redesigned' by man over the last millennia, being the stage of diverse landscape dynamics, from the recurrent use of fire and, overexploitation of forest resources, to urban development processes and abandonment of agricultural land (Blondel et al., 2010). The continuous redesign of landscapes and habitats has had profound consequences for the distribution, dynamics, and turnover of species and communities (Blondel, 2006; Sirami et al., 2010; Gonzáles-Megías et al., 2011). Clearing large tracts of forest for pastures and crops may have benefited native species that preferred open habitats and may have caused changes in the composition of natural communities. While these changes created an advantage for species adapted to open land habitats, other species more dependent of forest habitats may have declined due to changes in the landscape and to direct pressure from human activities (Blondel 2006; Desrochers et al. 2011).

One approach to the study of the response of biodiversity to habitat changes is the species-area relationship (SAR), one of ecology´s few laws (Arrhenius, 1921; Brown and Lomolino, 1998). It is given by the following power law:

$$S = c \times A^{z} \tag{1}$$

where S is the number of species in a sampling area of size A, c and z are constants that depend on the taxonomic group and sampling scheme respectively (Crawley and Harral, 2001, Rosenzweig, 1995). The SAR, herein classic SAR, assumes that all habitat is uniform (i.e., that species are randomly distributed within it) and continuous (i.e., unfragmented). However, when landscapes are heterogeneous, as in the case of the Mediterranean region, species will use the landscape in different ways. If landscapes are changed, organisms will respond differently to those changes. Depending on the taxonomic group, the vegetation structure, region and the spatial scale (Tews et al., 2004), some species may disappear locally or even regionally, others may tolerate the changes and adapt, and another ones can even benefit from those changes (Mazerolle and Villard, 1999; Atuari and Lucio, 2001; Pereira and Daily, 2006). Species responses to habitat heterogeneity may vary considerably depending on what is perceived as a habitat by the species studied, per instance, landscape structure that constitute habitat heterogeneity for one group may be perceive as habitat fragmentation by another taxonomic group (Tews et al., 2004).

Overall the application of the *classic* SAR to projecting the response of biodiversity to land-use change assumes that the only mechanism behind the species-area relationship is the increase of area *per se*. However habitat diversity may also explain species richness in a certain area. This relationship has been described, as the habitat hypothesis (Williams, 1964).Whether area or habitat diversity is more important in determining species richness in a particularly region or scale has been subject of debate (MacArthur and Wilson, 1967; Connor and McCoy, 1979; Williamson, 1988; Ricklefs and Lovette, 1999; Rosenzweig, 1995; Tjørve, 2002; Tews et al., 2004; Desrochers et al., 2011). Many authors have suggested that the area *per se* and the habitat diversity hypothesis are not mutually exclusive but complementary (Williamson, 1998; Ricklefs and Lovette, 1999).

With the aim of integrating these two mechanisms, the habitat hypothesis and the area *per se* hypothesis, several models for multi-habitat environments have been proposed (Tjorve 2002; Triantis et al. 2003; Pereira and Daily, 2006; Koh and Ghazoul, 2010). These models consider both, habitat diversity and, habitat size to explain species richness patterns.

Pereira and Daily (2006) proposed the countryside model, which is a multi-habitat model build on the classic SAR that accounts for the existence of different habitats in the landscape and for the differential use of habitats by species. Species are classified in species groups sharing similar habitat affinities. The estimated species richness of each species group is:

$$S_i = c_i \left(\sum_j h_{ij} A_j \right)^z \tag{2}$$

where S_i is the number of species in group i, h_{ij} is the affinity of species group i to habitat j and A_j is the area cover by habitat j. The total number of species in the landscape will then be given by the sum of species in each group:

$$S = \sum_{i=1}^{m} S_i \ , \tag{3}$$

where S is the total number of species in the landscape and m is the number of species groups.

Multi-habitat SAR models may constitute an useful tool to assess species responses to changing landscapes, providing an important contribution to practical conservation efforts. The countryside SAR is particularly suited for this purpose because it integrates the differential use of natural and human-modified habitats by different species groups, and therefore provides more fine-tuned analyses of species responses to habitat change.

The aim of this study was to provide answers to the following questions:

(1) Is landscape heterogeneity (i.e., habitat diversity) a proxy for species diversity?

- We hypothesized that for a fixed area (i) the importance of landscape heterogeneity varies with the taxonomic group and the level of specialization of species for a specific habitat, and (ii) the richness of species groups with more diverse use of habitats will be more associated with habitat diversity than the richness of species groups particularly associated with a habitat and with low affinity for other habitats; hence we predict that landscape heterogeneity will only be a proxy of species diversity if species use several habitats. Previous studies have approached the relationship between habitat heterogeneity and species diversity, yet they were mostly focused on fixed scales and small study areas (Atuari and Lucio., 2001; Tews et al., 2004; Gonzáles-Megías et al., 2011), the effects at coarser scales are still poorly understood,

(2) Is the effect of area and habitat diversity on species richness dependent on the spatial scale or on the characteristics of the species group?

- We hypothesized that (iii) at multi-habitat scales, species richness is better explained by multi-habitat species-area models, namely the countryside model, which considers both the effect of area and the effect of habitat composition on species richness, than by the classic species-area model, which only considers area, and that (iv) the countryside model will better fit species-area data when species groups show a differential use of habitats (i.e., do not use the landscape homogeneously).

2. METHODS

2.1. *Study area*

The Iberian Peninsula was selected as the study area (Fig. 1). The Macaronesic territories (Madeira, Azores and Canary Islands), the Balearic Islands and the Spanish territories located in the Northern Africa were excluded from the analyses. The Iberian Peninsula has an area of 580,456 Km^2 and is located in the Mediterranean Basin in southwestern Europe and includes the countries of Spain and Portugal. It is bordered on the southeast and east by the Mediterranean Sea and on the north, west and southwest by the Atlantic Ocean. The Pyrenees mountains, in the northeast edge of the peninsula, separate it from the rest of Europe.

The Iberian Peninsula intersects two large biogeographic regions: Mediterranean and Atlantic. The Mediterranean region encompasses almost the entire surface of Spain and Portugal and is characterized by warm to hot, dry summers with a lengthy period of drought. The Atlantic region includes territories located along the coastland of northern Portugal and northern Spain, and is characterized by cold winters and lack of a distinct dry season. The elevation ranges from sea level to 3478m, and the mean annual air temperature ranges from values below 2.5 °C in areas of highest altitude, namely the Pyrenees in Spain, to temperatures higher than 17 °C in southeast Spain. Mean annual precipitation shows a large spatial variability, with the highest values above 2,200 mm and usually in mountain areas, and the lowest values being below 300 mm in the southeast of Spain. Monthly average rainfall has a significant seasonality in the southern half of the Peninsula and less variation in the northwest region of the Peninsula (AEMet and IM, 2011).

Vegetation and land-use are conditioned by topographic and climatic variability, varying from semi-desertic flora, grassland, shrubland and steppe-land areas, to evergreen pine forest, Mediterranean oak forests (including dehesas featuring mainly evergreen oaks such as holm oaks, *Quercus ilex*, and cork oaks, *Quercus suber*), deciduous forests and sub-alpine and alpine vegetation. Interconnecting all these habitats we can find vast mosaics of farming areas.

2.2. *Land-cover and Environmental data*

We mapped land-cover for Iberia by combining the Land Cover database COS´90 (IGP, 1990) of Portugal and the database from the Second Spanish National Forest Inventory IFN2 (MARM, 1998). The full COS database and IFN2 land cover legend is available through the Portuguese

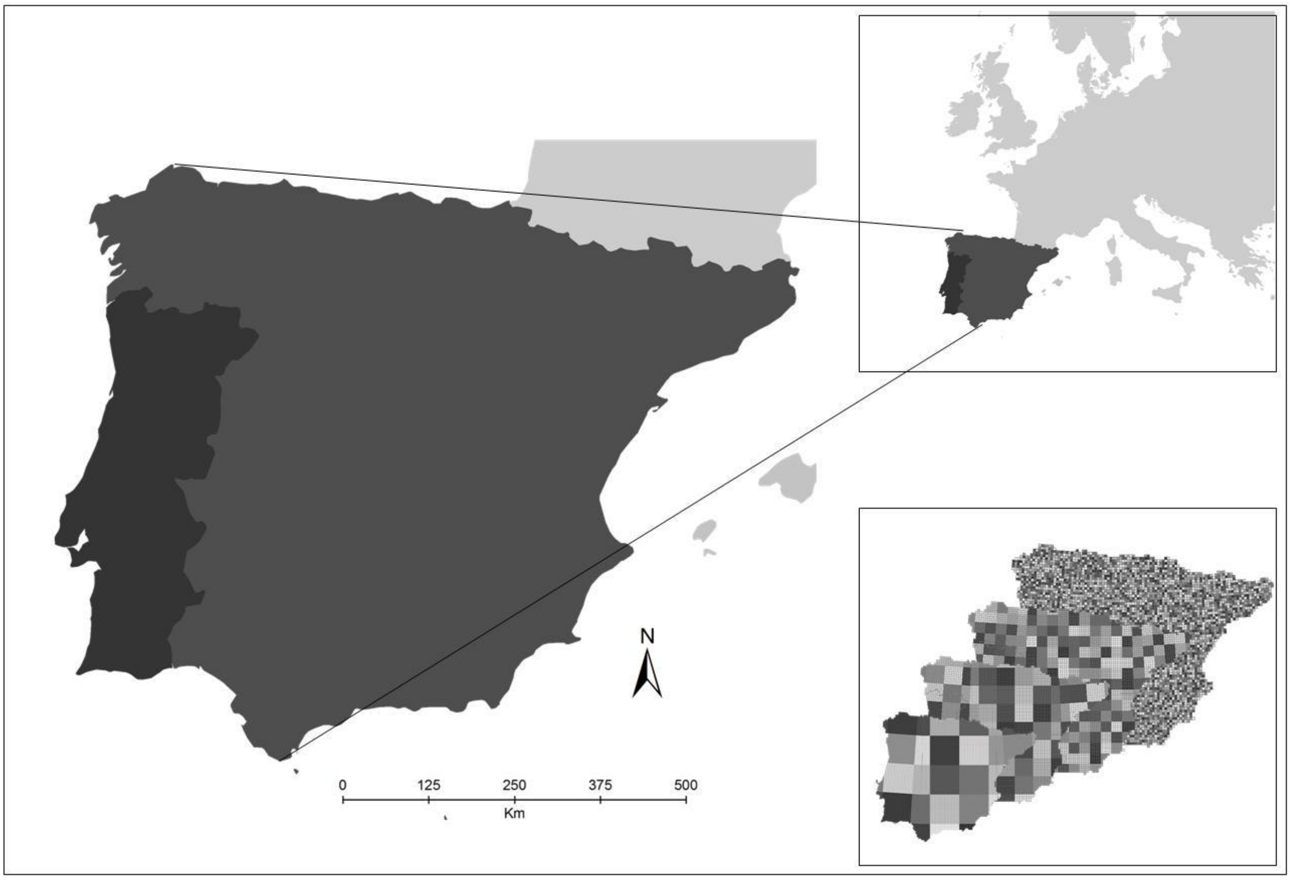


Fig. 1. Geographic location of the Iberian Peninsula (top right and central map).The bottom right figure represents the different UTM scales considered in our work (from right to left): 5885 cells 10 x 10Km, 261 cells 50 x 50Km, 90 cells 100 x 100Km and 29 cells 200 x 200Km.

Geographical Institute and Spanish Ministry of Environment web sites (respectively, http://www.igeo.pt/instituto/cegig/got/3_Docs/Files/Nery_2007ed_FontesPrimariasCLCCOS.pdf and http://www.marm.es/es/biodiversidad/servicios/banco-de-datos-biodiversidad/explicaciones_y_m%C3%A9todos_tcm7-171562.pdf). Land-cover classes were grouped into four main categories: agricultural land, uncultivated land, forest and exotic forest (Fig.2; see Table 1 for more details). Water bodies, rocky areas, human-dominated areas (e.g., urban fabric, quarries, green urban areas, etc.) and unclassified land cover were excluded from the analyses.

We intersected the land-cover map with the UTM 10x10 grid, and selected only with grid cells that had more than 25% cover in any of the four classes above, resulting in a final set of 5885 cells of 10 Km x 10 Km (cells dropped from the analysis include gap cells in the original land-cover products, cells in urban areas, and cells along the edge of the peninsula). The presence and the percentage cover of each habitat in each cell was calculated using ArcGIS 9.3 (ESRI, 2009). For some analysis, the 10 Km x 10 Km cells were aggregated into larger cells of 50 x 50 Km^2, 100 x 100 Km^2 and 200 x 200 Km^2.

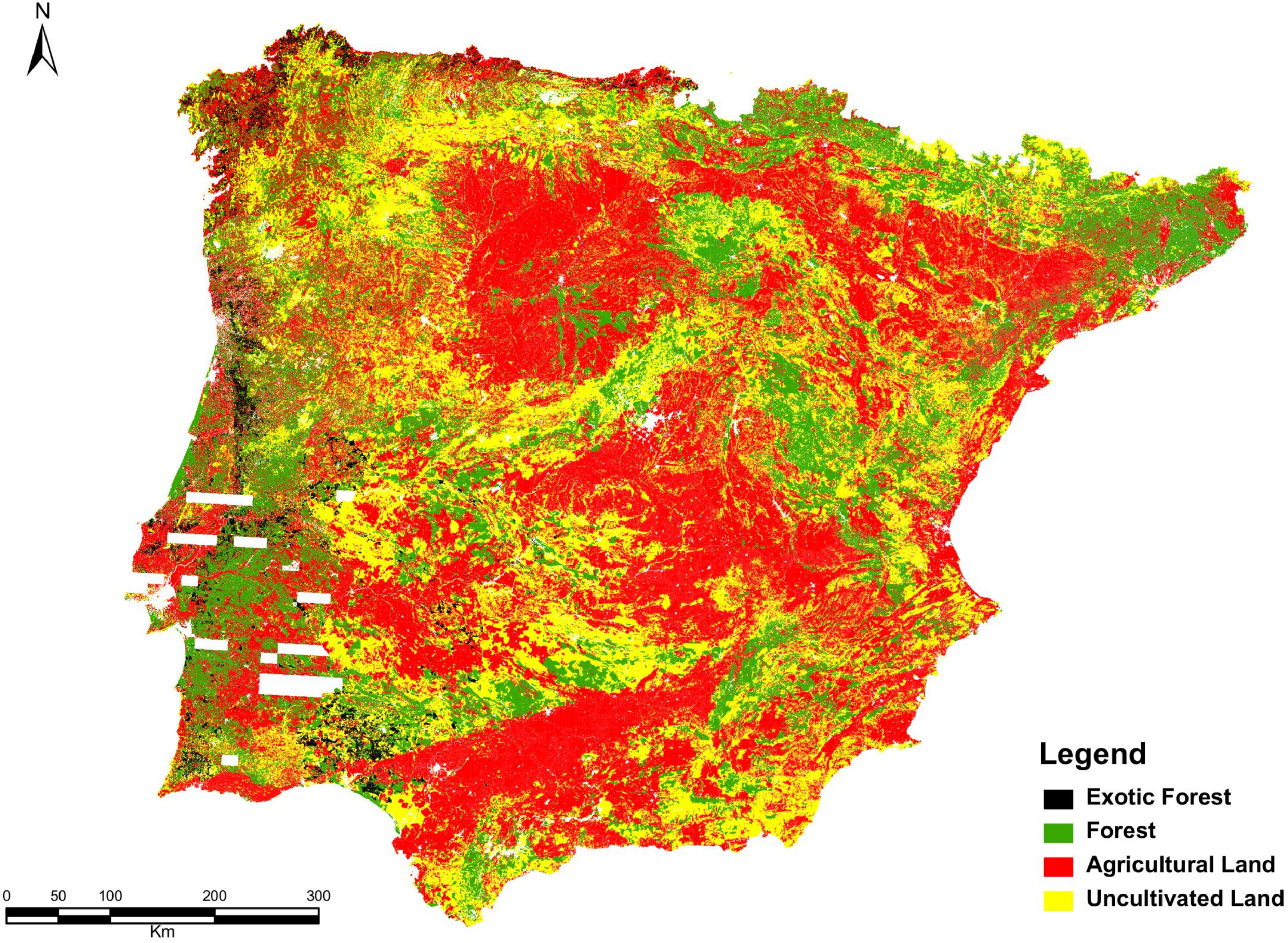
Climatic variables were obtained from the Climatic Research Unit (CRU) TS 1.2 dataset (Mitchell et al. 2003). Information on average monthly temperature, DTR (i.e., Diurnal temperature range) and annual precipitation were extracted and resampled on a 10x10 km^2 cell size. Elevation, aspect and slope data came from the United States Geological Survey HYDRO 1k digital terrain model (USGS, 2000).

In order to avoid multicolinearity, all predictors were previously tested for pairwise correlations using Spearman´s rank correlation coefficient. Predictors with correlation higher than 0.7 were removed from the analysis (Elith et al., 2006, Wisz and Guisan, 2009).

Table 1
The land-use classification used in the study.

Aggregated land use category	**Original land use category for Portugal**	**Original land use category for Spain**
Agriculture land (AG)	Arable land, annual crops, permanent crops, heterogeneous agricultural areas, olive grove, vineyard, orchard, other shrubs, permanent grassland, agro-forestry areas (where agriculture area dominate).	Agriculture land
Uncultivated land (UL)	Poor rangeland, low shrub, sclerophyllous vegetation, high shrub and degraded or transition forest, uncovered areas with little or no vegetation, abandoned olive grove, recently burned areas.	Land with scrub species and / or natural grassland or weak human intervention, pasture or grass mixed with brush, scrub and/or herbaceous vegetation associations, open spaces with little or no vegetation.
Forest (F)	*Quercus ilex, Quercus suber, Quercus sp. , Castanea sativa, Pinus pinea, Pinus pinaster,* other brodleaf and coniferous species.	*Quercus sp, Olea european, Fagus sylvatica, Myrica faya, Castanea sativa, Populous nigra, Juniperus thurifera, Abies alba, Pinus sp,* mixed pine species, mixed hardwood species,mixed oak species, other coniferous and broadleaf species.
Exotic forest (EF)	*Eucalyptus sp.*	*Eucalyptus sp*.

Fig.2. Landcover map of Iberian Peninsula


N
Legend
Exotic Forest
Forest
Agricultural Land
Uncultivated Land
0
50
100
200
300
Km

2.3. *Species distribution*

We collected presence/absence data on the distribution of 399 vertebrate species from Spanish and Portuguese distribution atlases based on UTM cells of 10 x 10 Km: 306 common breeding birds (Equipa Atlas 2008; Loureiro et al 2008), 59 reptiles and 34 amphibians (Pleguezuelos et al. 2002; Martí and Moral 2003).

We selected 82 passerine species among the breeding birds database due to their high diversity and presence in most ecological niches, which makes them a good model to explore species responses to landscape changes (Polo and Carrascal, 2001). Habitat preferences of passerine species living in the Iberian Peninsula (i.e., excluding islands) were obtained from literature (Pleguezuelos et al., 2002; Martí and Moral, 2003; Equipa Atlas, 2008; Catry et al., 2010) and from expert knowledge. Species were then divided in three groups according to those preferences: agricultural land species, uncultivated land species, and forest species. Only species present in a least 10 study units (i.e., UTM 10 x 10 Km cell) were used in the analysis.

2.4. *Data analysis*

We mapped the species richness of amphibians, reptiles and passerine birds and of agricultural land passerine species, uncultivated land passerine species and forest passerine species (Fig. 3). We used the Spearman´s rho to test the association between single environmental variables (described in Table 2) and the richness of each taxa. The relative importance of the different environmental factors was assessed through multi-model selection. Three types of models were tested (Table 2): (1) models with only one type of environmental predictors (i.e., climatic, topographic and habitat), (2) models with two types of predictors (i.e., climatic plus topographic, climatic plus habitat and topographic plus habitat), and (3) all predictors together. For all models the dependent variable was species richness. Models were compared using the Akaike´s Information Criterion:

$$AIC = -2\, ln\, (L_m) + 2p$$

where L_m is the maximum likelihood of the model, p is the number of free parameters of the model (Sakamoto et al. 1986).

We test the effect of habitat heterogeneity on species richness using Spearman´s rho and with visual analyses of boxplots. Due to the original structure of the landcover datasets, only data from

Spain presented the conditions for this analysis. Landscape heterogeneity was defined as the number of landcover types in a 10 Km x 10 Km cell.

We assessed the fit of the classic SAR and the countryside SAR to the species richness in each group, from the 10x10km^2 scale to the entire Iberia, using the intermediate cell sizes 50 x 50 Km^2, 100 x 100 Km^2 and 200 x 200 Km^2. The models were fit to data by non-linear regression (Rosenzweig, 1995), choosing the fit with the lowest SSE (i.e., Sum of Squares error). Parameters *c* and *z* were estimated for both models, and affinities h_{ij} were estimated for countryside-SARs. Models were compared using the Akaike´s Information Criterion (Sakamoto et al. 1986) and the Root Mean Square Error (RMSE):

$$RMSE = \sqrt{\frac{SEE}{n-k}}$$

RMSE is a measure of fit that gives the standard deviation of the model prediction error, where *n* is the number o data points and *k* is the number of parameters in the model. When comparing two models, the one with the lowest value of RMSE and/or AIC is considered to have the best fit to data (Sakamoto et al. 1986). Visual analyses of residuals plots were also carried.

Statistical analyses were performed using the R statistical software system (http://www.r-project.org/). SARs were fit using the *nls* function from the *stats* package in R.

Table 2

Models used to test the role of environmental variables in species richness. Predictors were grouped into 3 environmental categories to reflect ecological meaning.

Competing models		Predictors	Type of Aggregation
M_C	Climatic Predictors	**Dmt.jul** (average daily temperature of July)	Weighted mean of subpixels (ºC)
		Dtr.jul (diurnal temperature range of July)	Weighted mean of subpixels (ºC)
		Pre.ann (annual precipitation)	Weighted mean of subpixels (mm)
M_T	Topographic Predictors	**Alt.mea** (mean Elevation)	mean of subpixels (m)
		Asp.N (north aspect)	sum of subpixels (%)
		Asp.S (south aspect)	sum of subpixels (%)
		Asp.E (east aspect)	sum of subpixels (%)
		Asp.W (eest aspect)	sum of subpixels (%)
M_H	Habitat Predictors	**Agr.sum** (proportion of Agricultural land)	sum of subpixels (%)
		Unc.sum (proportion of Uncultivated land)	sum of subpixels (%)
		For.sum (proportion of Forest)	sum of subpixels (%)
		Exo.sum (proportion of Exotic forest)	sum of subpixels (%)
M_{CT}	Climatic Predictors	**Dmt.jul; Dtr.jul; Pre.ann**	
	Topographic Predictors	**Alt.mea; Asp.N; Asp.S; Asp.e; Asp.W**	
M_{CH}	Climatic Predictors	**Dmt.jul; Dtr.jul; Pre.ann**	
	Habitat Predictors	**Agr.sum; Unc.sum; For.sum; Exo.sum; nºhabitats; Hetre.hab**	
M_{TH}	Topographic Predictors	**Alt.mea; Asp.N; Asp.S; Asp.e; Asp.W**	
	Habitat Predictors	**Agr.sum; Unc.sum; For.sum; Exo.sum; nºhabitats; Hetre.hab**	
M_{CTH}	Climatic Predictors	**Dmt.jul; Dtr.jul; Pre.ann**	
	Topographic Predictors	**Alt.mea; Asp.N; Asp.S; Asp.e; Asp.W**	
	Habitat Predictors	**Agr.sum; Unc.sum; For.sum; Exo.sum; nºhabitats; Hetre.hab**	

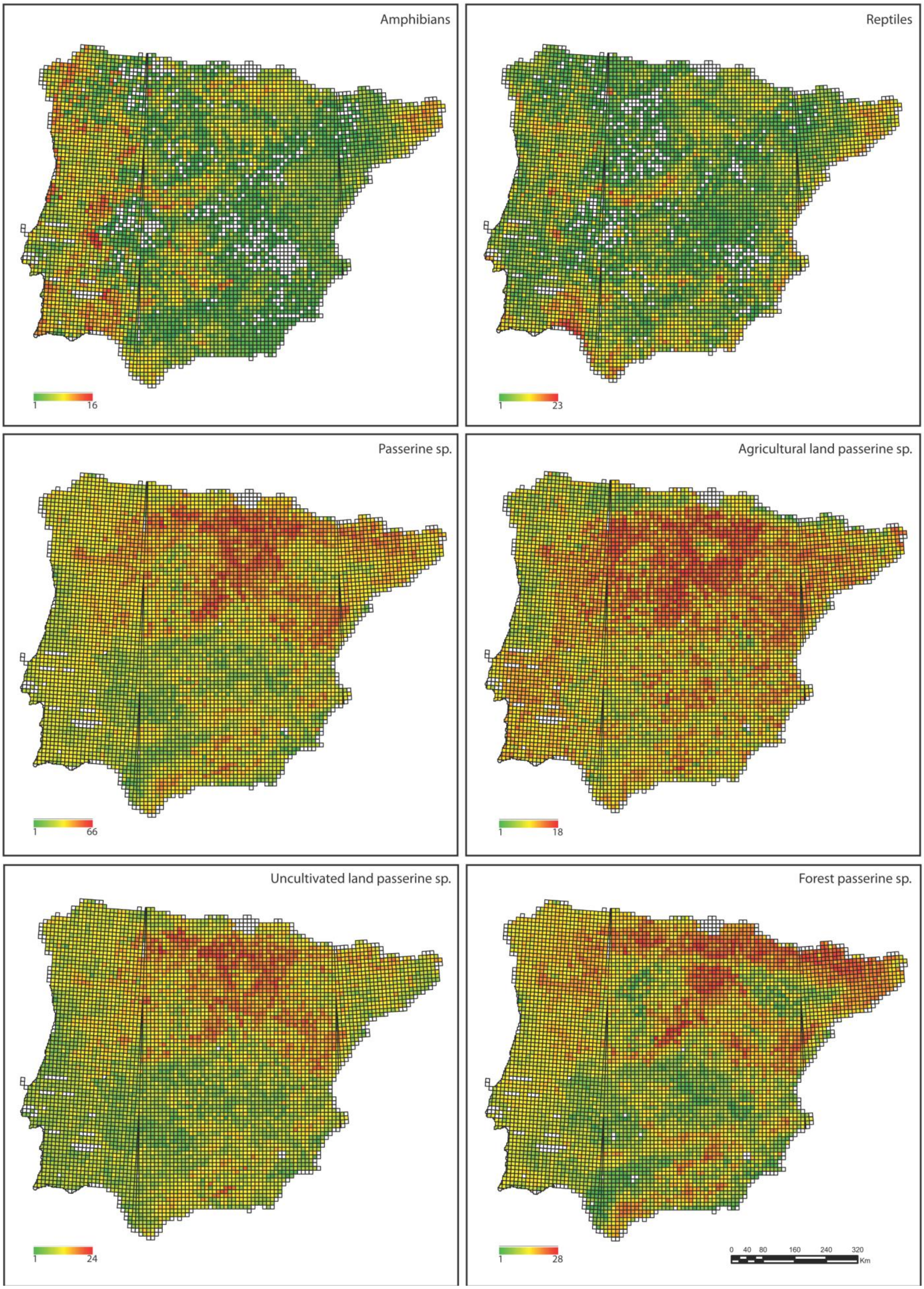


Fig. 3. Species richness maps. (a) amphibians; (b) reptiles; (c) all passerine birds; (d) agriculture land passerine sp.; (e) uncultivated land passerine sp; (f) forest passerine sp.

3. RESULTS

Passerine species were divided according to their habitat affinities. The group of forest species was the richest with 32 species (39.0%), followed by the uncultivated land group with 31 species (37.8%), and the agricultural land group with 19 species (23,2%). We excluded from the analysis the species associated with wetlands and coastal habitats (e.g., Acrocephalus scirpaceus), the species specially associated with urban habitats (e.g., *Passer domesticus*) and three ubiquitous species. The complete species list is presented in Appendix I.

The distribution of species in the Iberian Peninsula is not homogeneous (Fig. 3). While particular areas are consistently associated with high richness of species for the different taxa (amphibians, reptiles, passerines, and passerine species groups), the particular pattern of richness is somehow taxon specific. The areas with higher number of amphibians species are concentrated in the western portion of the Mediterranean biogeographic region across Galicia, and in the Central mountain range (Fig.3). The areas of high species richness for reptiles are mainly located in the southern part of Spain and the central region of Iberia (i.e., Central mountain range and Extremadura). Considering all passerine species, species seems to be concentrated in particular regions, mainly high/moderate altitude areas across the northern part of the Iberian Peninsula (Fig.3).

3.1. *Correlation between species and environmental predictors*

Table 3 shows the correlation of species richness of amphibians, reptiles and the different passerine groups, with each environmental predictor. The richness of amphibians is negatively related with the area of agricultural land (rho=-0.28, p<0.001) and positively related with native and exotic forest (rho=0.34 and rho=0.32, p<0.001). In addition, amphibian diversity presents a slightly negative correlation with altitude and with daily temperature fluctuations, and a positive correlation with precipitation. The richness of reptiles shows a similar pattern to that of amphibians regarding the preference of habitats: it is positively correlated with native forest area (rho=0.23, p<0.001), and negatively correlated with agricultural areas (rho=-0.26, p<0.001). Regarding climatic and topography predictors, reptiles exhibit the same patterns as amphibians.

Passerine species richness increased with altitude (rho=0.21-0.48, p<0.001), and decreased with mean daily temperature in July.. In relation to land use predictors, the richness of passerine affinity groups showed a correlation with the area of their preferred habitat (e.g., forest species occur more in areas of forest, rho=0.58, p<0.001, and agriculture species are richer in areas of agriculture land, rho=0.12, p<0.001). Furthermore, we detected that, exotic forest correlated negatively with all bird species groups and that, all taxa, except for agricultural passerine species, correlated negatively with area of agriculture land, with forest showing the larger negative correlation (rho=-0.51, p<0.001).

Table 3
Values of correlation (rho) between taxa richness and climatic, topographic and habitat predictors (* P < 0.05, ** P < 0.01, *** P < 0.001).See Table 2 for predictors legend.

	Amphibians	Reptiles	Passerine birds	Agriculture passerine sp.	Uncultivated land passerine sp.	Forest passerine sp.
Dmt.jul	-0.13***	0.01	-0.56***	-0.09	-0.51***	-0.64***
Dtr.jul	**-0.25*****	**-0.24*****	**-0.10*****	0.15***	-0.03	-0.26***
Pre.ann	**0.41*****	**0.21*****	**0.26*****	-0.20***	0.13***	0.50***
Alt.mea	**-0.17*****	-0.12***	**0.48*****	**0.21*****	**0.48*****	**0.43*****
Asp.N	-0.04***	-0.01	0.05***	0.01**	0.06***	0.03
Asp.S	0.04*	-0.04*	-0.03***	-0.06***	-0.05	0.02
Asp.E	0.06***	0.12***	0.07***	0.05***	0.04	0.08***
Asp.W	-0.02*	-0.06***	-0.06***	-0.05	-0.04**	-0.06***
Agr.sum	**-0.28*****	**-0.26*****	**-0.29*****	0.12***	**-0.13*****	**-0.51*****
Unc.sum	0.01	0.13***	0.21***	0.02***	0.21***	0.24***
For.sum	**0.34*****	**0.23*****	0.36***	-0.01***	0.13***	0.58***
Exo.sum	0.32***	0.08***	**-0.27*****	**-0.26*****	**-0.33*****	**-0.11****

3.2. *Multiple regressions between species and sets of environmental predictors*

Considering the first set of models (M_C, M_T, M_H), amphibians responded equally to climate and topographic predictors (r^2=0.18, p<0.001) (Table 4), while reptiles responded more to topography (r^2=0.14, p<0.001). Nevertheless, in both cases the variance explained by the predictors is low. All groups of passerines reacted primarily to climate predictors (r^2=0.21-0.40, p<0.001).

When the set of predictors were tested in pairs (M_{TC}, M_{CH}, M_{TH}), the amphibians responded best to the combination of climatic and habitat predictors (r^2=0.25, p<0.001), while reptiles responded equally to all three combinations of predictors (r^2=0.18, p<0.001). Total passerine diversity had the highest fit to the combination of climatic and habitat predictors (r^2=0.41, p<0.001). Forest species richness was also better explained by the combination of climatic and habitat variables, but the richness of agricultural land species were best explain by the model combining climatic and topographic predictors (r^2=0.26 and r^2=0.39, <0.001).

The model that included all three sets of predictors (M_{CTH}) was the model that explained the most variance in all cases (i.e., had lower AIC´s), although the r^2 values are very similar, in some cases even equal, to the best models combining two sets of predictors. .

Overall climate predictors explained most of the variance, while habitat predictors contributed to improve the fit of the models.

3.3. *Correlation between species and heterogeneity*

All groups showed a positive correlation with landscape heterogeneity, that is, with the increase in the number of land uses (Fig. 4; Table 5). Passerine forest species showed the highest correlation (*r*= 0.44, *p*<0.001), while agricultural land species had the weakest response to landscape heterogeneity (*r*=0.06, *p*<0.001).

Table 5
Correlations between richness and habitat heterogeneity, in a 10 Km x 10 Km cells. (P < 0.001***).

	rho
Amphibians	0.34***
Reptiles	0.22***
Passerine birds	0.35***
Agric. passerine sp.	0.06***
Uncul. land passerine sp.	0.27***
Forest passerine sp.	0.44***

Table 4

Multiple r^2 values, considering as independent variables the different sets of predictors, individually and jointly, for each group of species considered as a dependent variable (in all cases $P < 0.001$).

	Clim. (**M$_1$**)		Topo. (**M$_2$**)		Habit. (**M$_3$**)		Clim. & Topo. (**M$_4$**)		Clim. & Habit. (**M$_5$**)		Topo. & Habit. (**M$_6$**)		Clim. & Topo. & Habit. (**M$_7$**)	
	r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC	r^2	AIC
Amphibians	0.18	29795	0.06	30663	0.18	29835	0.2	29727	0.25	29348	0.2	29713	0.26	29283
Reptiles	0.11	33360	0.14	33183	0.08	33573	0.18	32927	0.18	32873	0.18	32921	0.21	32678
Passerine Birds	0.37	40602	0.23	41763	0.13	42423	0.39	40388	0.41	40229	0.28	41392	0.42	40056
Agric. passerine sp.	0.21	26750	0.15	27167	0.04	27877	0.26	26416	0.21	26727	0.16	27104	0.26	26383
Uncul. land passerine sp.	0.37	29543	0.22	30848	0.07	31879	0.39	29411	0.38	29485	0.22	30852	0.39	29358
Forest passerine sp.	0.4	32889	0.32	33665	0.34	33522	0.46	32302	0.55	31225	0.48	32125	0.57	30934

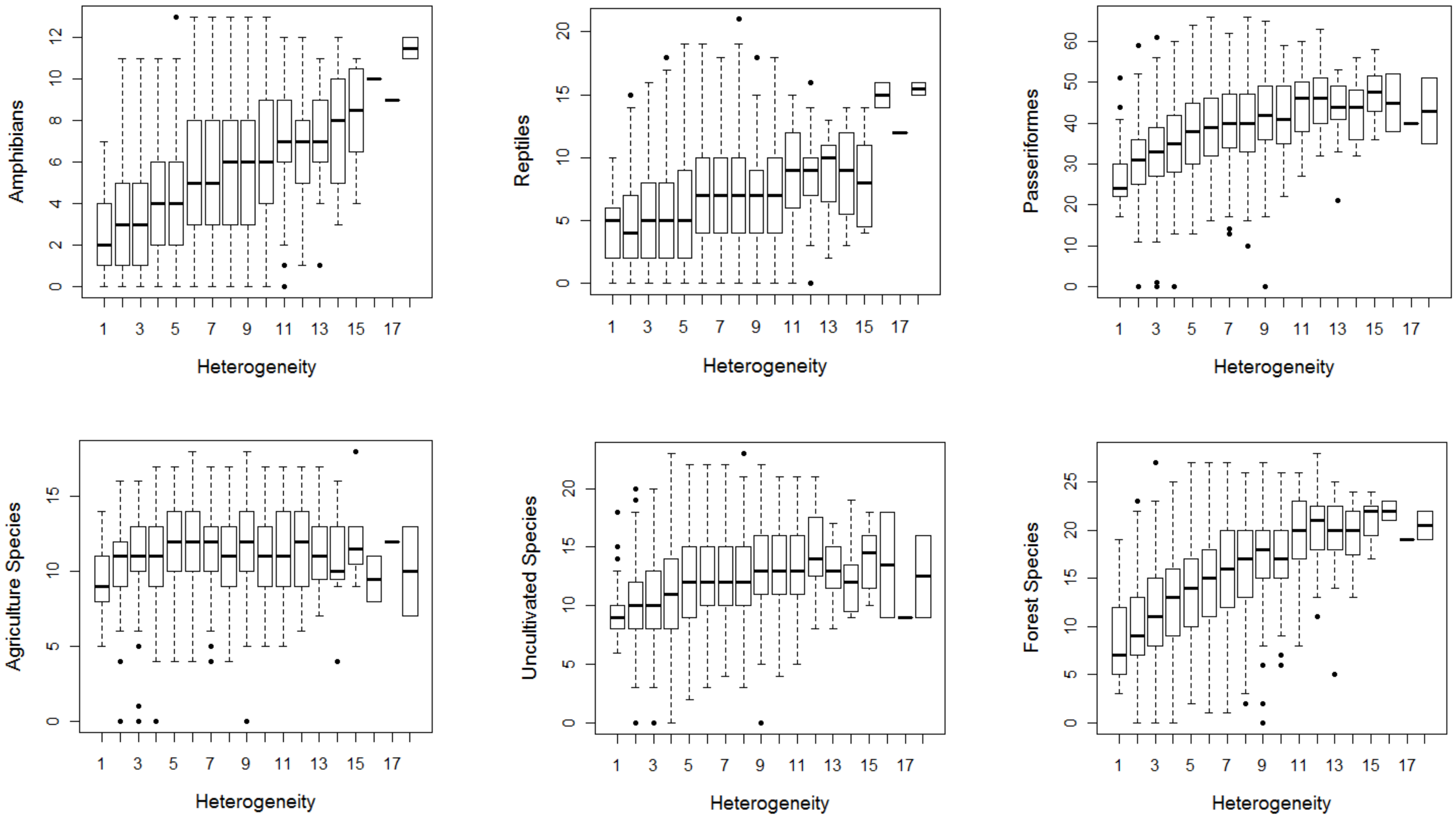


Fig. 4. Relationship between the richness of the taxa and landscape heterogeneity (estimated as number of landcover types per cell) for the 3970 10 x 10 Km cells covering Spain. (a) Reptiles (b) Amphibians (c) Passeriformes (d) Passerine Forest species (e) Passerine Agriculture species (f) Passerine Uncultivated species).

3.4. *Species-area-relationships*

The countryside SAR model had a better fit (i.e., lower RMSE and AIC values) than the classic SAR models, when explaining diversity patterns of species groups and of total number of species (Table 6). SARs of all species groups had z-values ($0.10 < z < 0.16$) characteristic of mainland species-area-curves (Fig 5; Rosenzweig 1995, Crawley & Harral 2001). The affinities of agricultural, uncultivated, and forest species, as estimated by countryside-SAR, had maximum values in the respective preferred habitat (h=1). Species groups of open habitats (i.e., agriculture and uncultivated species) show moderate affinity to others habitats. The forest groups present low ($h< 0.01$) and very low ($h< 0.00001$) affinity for uncultivated and agriculture land, respectively.

Table 6

Multi-habitat species-area relationships of species groups and total species using the classic model (SAR) and the countryside model (C.SAR). A total of 6225 points, including all scales, were used in the analysis. Parameters h_{AL}, h_{UL}, and h_F represent the affinity of the species groups for agriculture land, uncultivated land and forest respectively. The countryside species-area relationship for total species is expressed by the sum of species-area relationships of species groups. RMSE and AIC are measure to compare the fitness of the models.

	c	z	h_{AL}	h_{UL}	h_F	RMSE	AIC
Agricultural Land species							
SAR	1.78	0.100	--	--	--	2.50	29178
CSAR	1.88	0.100	1	0.59	0.31	2.48	29118
Uncultivated Land species							
SAR	0.57	0.164	--	--	--	3.65	33945
CSAR	0.68	0.160	0.20	1	0.37	3.59	33739
Forest species							
SAR	1.06	0.141	--	--	--	5.01	37896
CSAR	1.92	0.125	0.51×10^{-6}	0.65×10^{-2}	1	3.91	34813
Total species							
SAR	3.00	0.137	--	--	--	9.27	45592
CSAR		$S_{total}=S_{agriculture\ land} + S_{uncultivated\ land} + S_{forest}$				8.40	

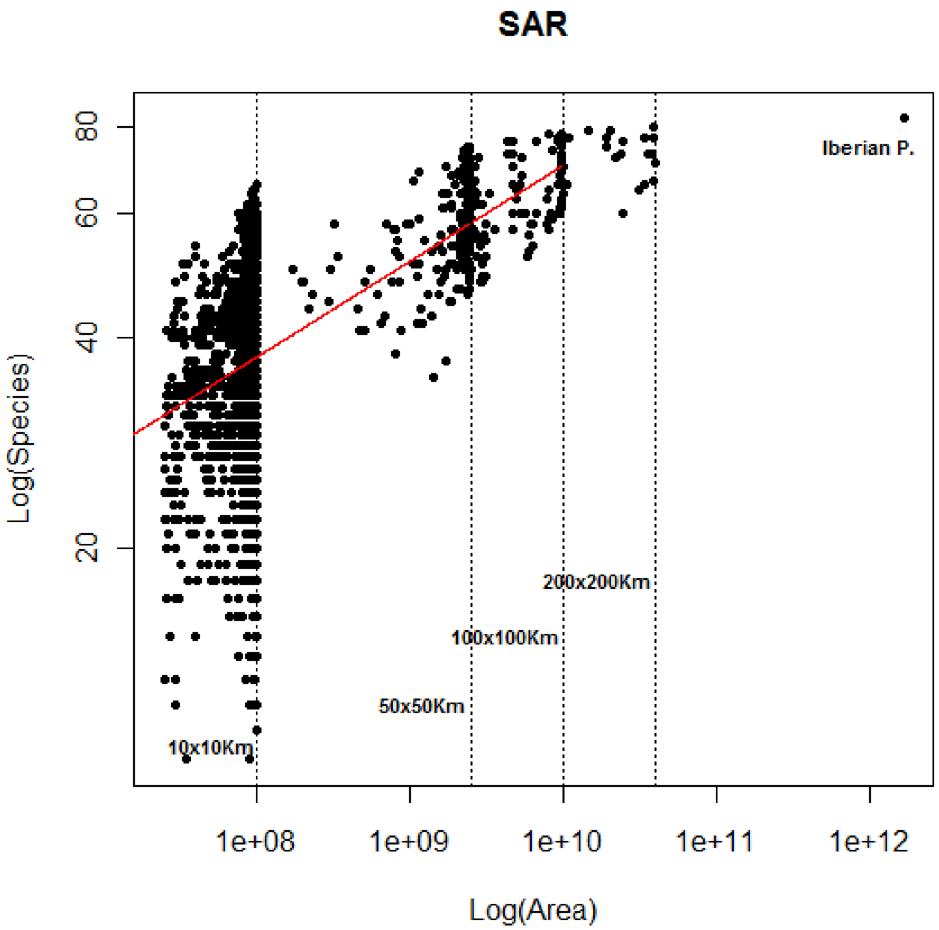


Fig. 5. Plot in the Log-Log space of observed species-area relationship (SAR). Plot parameters are shown in Table 6.

4. DISCUSSION

4.1. *Landscape heterogeneity as a determinant of species diversity.*

Several studies have found habitat structure to be the most important determinant of species richness at the local scale (Atauri and Lucio, 2001; Nogués and Martínez 2004; Moreno and Pizarro, 2007). Our results suggest that at the regional scale climate is the principal determinant of species richness, although habitat still plays a role in most species groups. This suggests that the relative importance of climate and habitat structure in controlling species richness varies with scale (Rahbek and Graves, 2001; van Rensburg et al., 2002; Hurlbert and Haskell, 2003).

The diversity of the different taxonomic groups exhibited a positive response to habitat heterogeneity, although of different intensities.

The variety of responses of taxa to landscape heterogeneity may be related to the scale at which these groups perceive the landscape. Species use structural characteristics of the habitat that occur on a specific scale, reflecting important habitat requirements such as escape from predation, foraging or reproduction requirements (Keitt et al, 1997; Mazerolle and Villard, 1999; Atuari and Lucio, 2001; Gil-Tena et al., 2007; Desroches et al 2011). Thus, the presence or quality of these specific structures in a given area can be determinant for increasing species diversity of certain taxa. The high correlation of amphibians with habitat heterogeneity can be indicator of the presence of these "keystone structures", since most of the landuse classes used in this analyses were forest habitats, where amphibians are more likely to occupy water bodies (Guerry and Hunter Jr., 2002; Herrmann et al., 2004). The structure of the database used in this study may have also influenced the results, since the landcover information was more detailed towards forest habitats due to its original use in the context of the Spanish forest inventory. The strong response of forest birds to habitat heterogeneity is likely explained by their specialization to the different forest types. This bias in the database may also explain the low response of agricultural passerines and uncultivated land passerine to habitat heterogeneity: from a list of 58 habitats only 2 habitats represent the diversity of open land areas (see Appendix II). Although, is well know that some specific agricultural practices, like intensive agriculture, reduce the heterogeneity of the landscape (Benton et al, 2003), studies have highlight the capacity of agricultural species to use different agricultural habitats (Benton et al, 2003; Báldi and Batáry, 2011), and surrounding habitats (i.e., forest, open areas, urban areas, etc.) (Herzon and O´Hara, 2007).

Almost all species groups showed a positive response to forest area and a negative response with agricultural area, suggesting that even in the context of a region with a long history of human use, some species seem to avoid human-dominated habitats. Forest bird species seems to be particularly susceptible to the structure of the their habitat (Diáz et al., 1998;Trzcinski et al., 1999).. Changes in agricultural practices throughout the last century let to an increase of homogeneous patches (Krebs et al, 2001), mainly due to agriculture intensification and forestry policies, creating unsuitable habitats for birds breeding (Diáz et al., 1998; Donald et al., 2001; Benton et al, 2003).

In summary, although climate is shown as the main factor affecting the richness of species groups studied in the Iberian Peninsula, habitat heterogeneity and habitat structure can be determinant. Species diversity increases with the number of landcover classes, perhaps because a greater number of landcover classes (habitats) is capable of satisfying the needs of different species (Atuari and Lucio, 2001; Tews et al., 2004; Desrochers et al., 2010).

4.2. *Effect of area and habitat diversity on species richness*

We evaluated the performance of the countryside SAR, at the regional scale, against the performance of the classic SAR when predicting species-area patterns in a multi-habitat landscapes. Species richness of each of the species groups and the total number of species were best described using the countryside SAR.

The species–area relationship has been applied in the conservation context to predict species richness declines as natural area is converted to human dominated land covers (Sala et al., 2005; Desrochers et al, 2011). This approach is based on the assumption that the transformed landscape is completely uninhabitable. Yet in many situations habitat change does not translate into loss of inhabitable habitat. The conversion of natural cover could introduce new habitat types and allow generalist species to occur (Desrochers et al, 2011). Furthermore, the progressive conversion of small amounts of natural area can lead to a habitat that is more heterogeneous, which could lead to an increase in species richness at the local scale.

Species will not use only their preferred habitat, but instead use alternative habitats when needed,. Still, the benefits that species accrue from the different habitats may not be detected in small scale studies (Jones, 2011). For instance, the relationship between several agricultural birds species and arable land depends on the proportion of arable land in a given region (Gates and Donald, 2001).

This scale dependence is important and, as most intensive studies are conducted in very local areas, extrapolations have to be made with caution.

In order to investigate the effect of scale, we compared our results with the studies performed by Proença (2009), and by Guilherme (2009) with plants and birds, respectively, in a mountain parish in northern Portugal. Both studies found that the species richness of species groups and of total species were best described using the countryside SAR. In addition, in both studies, all groups of species also showed a higher affinity for their preferred habitat. In contrast with our results, all species groups at the local scale had very low affinities for the alternative habitats, especially in the case of plants. At the regional scale, only forest species had very low affinity to the alternative habitats, which may be result of their specialist use of habitats. Forest species appear to be more dependent of their preferred habitat and less able to use alternative habitats independent of the scale. On the other hand, agricultural species showed relatively high affinity to non-agricultural habitats. Many studies have highlighted the importance of these habitats in maintaining agriculture biodiversity, by providing nesting and foraging habitats (Hinsley and Bellamy, 2000; Herzon and O´Hara, 2007). These facts suggest that, at larger scales, we are more likely to find non-forest habitat specialist outside their preferred habitats.

The results presented in this study confirm the countryside SAR as an improved model, with easy empirical application, to assess species-area patterns in a multi-habitat landscapes. In the last decade there have been other attempts to create a multi-habitat species-area model. Tjorve (2002) proposed a framework to build species-area models by combining specie-area curves for different habitat.,He explored the effect of the size and number of habitats, but he did not explore the way that different species may perceive the different habitats. The choros model proposed by Triantis et al. (2003), combines the total effect of area and habitat diversity to determine the regional species richness. The variable area is replaced by the variable choros, which arises as the result of the multiplication of the number of different habitats in an area by the size of that area. Yet, like Tjorve´s model, this model does not consider the possibility of differential use of habitats by different species. The countryside SAR considers the differential use of habitats by different species groups, and accounts for the area and number of habitats, and so it is more appropriate for applications when projections of biodiversity responses to land-use changes are needed.

CONSERVATION IMPLICATIONS

Our results indicate that the distribution of vertebrate species richness in Iberian Peninsula is related to different factors depending on the taxonomic class considered. Areas that have high value to some taxon may be inadequate for others (Rey-Benayas and Montanã, 2003). A better understanding of the relationships between different environmental and geographic factors and species richness may help determine the most effective locations to establish new conservation areas or to allocate funds.

The countryside-SAR provided a new model to understand fauna distribution on the Iberian Peninsula. Multi-habitat models are nowadays essential tools to assess species responses to changing landscapes.

Conservation strategies for sustaining biodiversity must consider that species richness and ecological processes are controlled by parameters operating at a wide array of scales

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REFERENCES

AEMet, State Meteorological Agency and IM, Institute of Meteorology, 2011. Iberian Climate Atlas: Air Temperature and Precipitation (1971-2000). Ministerio de Medio Ambiente, Medio Rural y Marino,Madrid.

Arrhenius, O.1921. Species and Area. Journal of Ecology 9, 95-99.

Atauri, J.A., de Lucio, J.V., 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecology 16, 147–159.

Báldi, A., Batáry, P., 2011. Spatial heterogeneity and farmland birds: different perspectives in Western and Eastern Europe. Ibis 153, 875-876.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182-188.

Blondel, J., 2006. The “Design” of Mediterranean Landscapes: A Millennial Story of Humans and Ecological Systems during the Historic Period. Human Ecology 34, 713-729.

Blondel, J., Aronson, J., 1999. Biology and wildlife of the Mediterranean region. Oxford University Press, USA.

Blondel, J., Aronson, J., Bodiou, J.-Y., 2010. The Mediterranean region: biological diversity in space and time. Oxford University Press.

Brown, J.H., Lomolino, M.V., 1998. Biogeography. Sinauer Associates Sunderland.

Catry, P., Costa, H., Elias, G., Matias, R., 2010. Aves de Portugal. Orinitologia do Território Continental. Assírio & Alvim, Lisboa.

Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species-area relationship. The American Naturalist 113, 791–833.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Kalin Arroyo, M., Arianoutsou, M., 1996. Plant diversity in Mediterranean-climate regions. Trends in Ecology & Evolution 11, 362–366.

Crawley, M.J., Harral, J.E., 2001. Scale dependence in plant biodiversity. Science 291, 864.

Cuttelod, A., García, N., Malak, D.A., Temple, H., Katariya, V., 2009. The Mediterranean: a biodiversity hotspot under threat. Wildlife in a Changing World–An Analysis of the 2008 IUCN Red List of Threatened Species 89.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture, Ecosystems & Environment 98, 321-329.

Desrochers, R.E., Kerr, J.T., Currie, D.J., n.d. How, and how much, natural cover loss increases species richness. Global Ecology and Biogeography.

Díaz, M., Carbonell, R., Santos, T., Tellería, J., 1998. Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects. Journal of Applied Ecology 35, 562–574.

Donal, P.F., Gree, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc Biol Sci 268, 25-29.

Elith, J., Graham*, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., others, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Equipa Atlas, 2008. Atlas das Aves Nidificantes em Portugal (1999-2005). Instituto da Conservação da Natureza e da Biodiversidade, Sociedade Portuguesa para o Estudo das Aves, Parque Natural da Madeira e Secretaria Regional do Ambiente e do Mar. Assírio & Alvim, Lisboa.

ESRI, 2009. ArcGIS. Environmental Systems Resource Institute, Redlands,CA.

Gil-Tena, A., Saura, S., Brotons, L., 2007. Effects of forest composition and structure on bird species richness in a Mediterranean context: implications for forest ecosystem management. Forest ecology and Management 242, 470–476.

González-Megías, A., Gómez, J.M., Sánchez-Piñero, F., Maio. Spatio-temporal change in the relationship between habitat heterogeneity and species diversity. Acta Oecologica 37, 179-186.

Guerry, A.D., Hunter Jr., M.L., 2002. Amphibian Distributions in a Landscape of Forests and Agriculture: an Examination of Landscape Composition and Configuration. Conservation Biology 16, 745-754.

Guilherme, J.L., 2009. Modeling bird diversity in a multi-habitat mountain landscape undergoing agricultural abandonment. Tese de Mestrado. Universidade de Lisboa Faculdade de Ciências, Lisboa.

Hazeu, G.W., Metzger, M.J., Mücher, C.A., Perez-Soba, M., Renetzeder, C., Andersen, E., n.d. European environmental stratifications and typologies: An overview. Agriculture, Ecosystems & Environment In Press, Corrected Proof.

Herrmann, H.L., Babbitt, K.J., Baber, M.J., Congalton, R.G., 2005. Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape. Biological Conservation 123, 139-149.

Herzon, I., O'Hara, R.B., 2007. Effects of landscape complexity on farmland birds in the Baltic States. Agriculture, Ecosystems & Environment 118, 297-306.

Hinsley, S., Bellamy, P., 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. Journal of Environmental Management 60, 33–49.

Hurlbert, A.H., Haskell, J.P., 2003. The effect of energy and seasonality on avian species richness and community composition. The American Naturalist 161, 83–97.

IGP, 1990. Carta de Ocupação do Solo – COS 90. Portuguese Geographic Institute (IGP). Retrieved April 10, 2008, from http://www.igeo.pt/produtos/CEGIG/COS.htm (in Portuguese).

Jones, J.P.G., 2011. Monitoring species abundance and distribution at the landscape scale. Journal of Applied Ecology 48, 9–13.

Keitt, T.H., Urban, D.L., Milne, B.T., 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology 1, 4.

Koh, L.P.I.N., Ghazoul, J., 2010. A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. Conservation Biology 24, 994–1001.

Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second silent spring? NATURE-LONDON- 611–612.

Loureiro, A., Ferrand de Almeida, N., Carretero, M.A., Paulo, O.S., 2008. Atlas dos Anfíbios e Répteis de Portugal. Instituto da Conservação da Natureza e da Biodiversidade, Lisboa, 257 pp.

Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M., Wanner, H., 2004. European Seasonal and Annual Temperature Variability, Trends, and Extremes Since 1500. Science 303, 1499 -1503.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton Univ Pr.

MARM, Ministerio de Medio Ambiente, Medio Rural y Marino, 1998. IFN2- II Inventario Forestal Nacional (1986 – 1996). Dirección General de Medio Natural y Política, Madrid.

Martí, R., Moral, J.C. (Eds.), 2003. Atlas de las Aves Reproductoras de España. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología. Madrid, Spain.

Mazerolle, M.J., Villard, M., 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6, 117–124.

Médail, F., Quezél, P., 1999. Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. Conservation Biology 13, 1510–1513.

Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M., New, M., 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). Tyndall Centre for Climate Change Research Working Paper 55, 25.

Moller, A.P., Soler, J.J., Vivaldi, M.M., 2010. Spatial heterogeneity in distribution and ecology of Western Palearctic birds. Ecology 91, 2769–2782.

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 Oecologica 32, 50-58.

Moreno-Rueda, G., Pizarro, M., 2009. Relative influence of habitat heterogeneity, climate, human disturbance, and spatial structure on vertebrate species richness in Spain. Ecological research 24, 335–344.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Nogués-Bravo, D., Martínez-Rica, J.P., 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. Journal of Biogeography 31, 629-640.

O'Connor, R.J., Shrubb, M., Watson, D., 1990. Farming & birds. Cambridge Univ Pr.

Öckinger, E., Smith, H.G., 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149, 526-534.

Patrick, D.A., Harper, E.B., Hunter Jr, M.L., Calhoun, A.J.K., 2008. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. Ecology 89, 2563–2574.

Pereira, H.M., Daily, G.C., 2006. Modeling biodiversity dynamics in countryside landscapes. Ecology 87, 1877–1885.

Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), 2004. Atlas y Libro Rojo de los Anfibios y Reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, Spain.

Polo, V., Carrascal, L.M., 1999. Shaping the body mass distribution of Passeriformes: habitat use and body mass are evolutionarily and ecologically related. Journal of Animal Ecology 68, 324-337.

Proença, V., 2009. Galicio-Portuguese oak forest of *Quercus robur* and *Quercus pyrenaica*: biodiversity patterns and forest response to fire. Tese de Doutoramento. Universidade de Lisboa Faculdade de Ciências, Lisboa.

Proença, V., Pereira, H.M. 2010. Appendix 2:Meditterranean Forest. *In* Biodiversity Scenarios: projections of the 21st century change in biodiversity and associated ecosystem services. Leadley, P.W., Pereira, H.M., Alkemade, J., Fernandez-Manjarrés, Proença, V. Scharlemann, J.P.W., Walpole (eds). 60-67

Proença, V.M., Pereira, H.M., Guilherme, J., Vicente, L., 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. Acta Oecologica 36, 219–226.

Rahbek, C., Graves, G.R., 2001. Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Sciences 98, 4534.

Ricklefs, R.E., Lovette, I.J., 1999. The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology 68, 1142–1160.

Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge Univ Pr.

Sakamoto, Y., Ishiguro, M. , Kitagawa, G., 1986. Akaike Information Criterion statistics. KTK Scientific Publishers, Tokyo.

Sala, O., Vuuren, V., Pereira, H., Lodge, D., Alder, J., Cumming, G., Dobson, A., Wolters, V., Xenopoulos, M., Carpenter, S., Pingali, P., Bennett, E., Zurek, M., 2005. Chapter 10: Biodiversity across scenarios, in: Ecosystems and Human Well-being: Scenarios, Volume 2. Island Press, Washington, DC.

Sirami, C., Nespoulous, A., Cheylan, J.P., Marty, P., Hvenegaard, G.T., Geniez, P., Schatz, B., Martin, J.L., 2010. Long-term anthropogenic and ecological dynamics of a Mediterranean landscape: Impacts on multiple taxa. Landscape and Urban Planning 96, 214–223.f

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31, 79–92.

Tjõrve, E., 2002. Habitat size and number in multi-habitat landscapes: a model approach based on species-area curves. Ecography 25, 17–24.

Triantis, K.A., Mylonas, M., Lika, K., Vardinoyannis, K., 2003. A model for the species–area–habitat relationship. Journal of Biogeography 30, 19–27.

USGS , United States Geological Survey, 2000. HYDRO1k elevation derivative database (Europe). Distributed by the Land Processes Distributed Active Archive Center (LPDAAC), at the USGS EROS Data Center. (available online at http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30/hydro)

Van Rensburg, B., Chown, S., Gaston, K., 2002. Sp ecies richness, environmental correlates, and spatial scale: a test using South African birds. The American Naturalist 159, 566–577.

Williams, C.B., 1964. Patterns in the balance of nature and related problems of quantitative ecology. Patterns in the balance of nature and related problems of quantitative ecology.

Williamson, M., 1988. Relationship of species number to area, distance and other variables. Analytical Biogeography. Chapman & Hall, London.

Wisz, M., Guisan, A., 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC ecology 9, 8.

APPENDICES

APPENDIX I

List of passerine species considered in the analysis. Abbreviations: Classification by affinity group (AL-agriculture land; UL-uncultivated land; F-Forest) and country were they occur (PT-Portugal; SP-Spain). Species were assigned to their group according with the literature and expert opinion.

Species	Species code	Region	Affinity group
Aegithalos caudatus	AEGCAU	PT/SP	F
Alauda arvensis	ALAARV	PT/SP	UL
Anthus campSPtris	ANTCAM	PT/SP	AL
Anthus spinoletta	ANTSPI	PT/SP	AL
Anthus trivialis	ANTTRI	PT/SP	F
Calandrella brachydactyla	CALBRA	PT/SP	UL
Carduelis cannabina	CARCAN	PT/SP	UL
Carduelis carduelis	CARCAR	PT/SP	AL
Carduelis chloris	CARCHL	PT/SP	AL
Certhia familiaris	CERFAM	PT/SP	F
Cercotrichas galactotes	CERGAL	SP	F
Cettia cetti	CETCET	PT/SP	UL
Chersophilus duponti	CHEDUP	SP	UL
Cisticola juncidis	CISJUN	PT/SP	UL
Corvus corax	CORCOR	PT/SP	UL
Corvus monedula	CORMON	PT/SP	AL
Cyanopica cyana	CYACYA	PT/SP	F
Emberiza calandra	EMBCAL	PT/SP	AL
Emberiza cia	EMBCIA	PT/SP	UL
Emberiza cirlus	EMBCIR	PT/SP	AL
Emberiza citrinella	EMBCIT	PT/SP	UL
Emberiza hortulana	EMBHOR	PT/SP	UL
Erithacus rubecula	ERIRUB	PT/SP	F
Ficedula hypoleuca	FICHYP	SP	F
Fringilla coelebs	FRICOE	PT/SP	F
Galerida cristata	GALCRI	PT/SP	AL
Galerida theklae	GALTHE	PT/SP	UL
Garrulus glandarius	GARGLA	PT/SP	F
Hippolais pallida	HIPPAL	PT/SP	UL
Hippolais polyglotta	HIPPOL	PT/SP	UL
Lanius collurio	LANCOL	PT/SP	AL
Lanius excubitor	LANEXC	PT/SP	AL
Lanius senator	LANSEN	PT/SP	AL
Locustella naevia	LOCNAE	SP	AL
Loxia curvirostra	LOXCUR	PT/SP	F
Lullula arborea	LULARB	PT/SP	AL
Luscinia megarhynchos	LUSMEG	PT/SP	F
Luscinia svecica	LUSSVE	PT/SP	UL
Melanocorypha calandra	MELCAL	PT/SP	UL
Monticola saxatilis	MONSAX	PT/SP	UL
Monticola solitarius	MONSOL	PT/SP	UL
Motacilla alba	MOTALB	PT/SP	AL
Motacilla cinerea	MOTCIN	PT/SP	UL
Motacilla flava	MOTFLA	PT/SP	AL
Muscicapa striata	MUSSTR	PT/SP	F
Oenanthe hispanica	OENHIS	PT/SP	AL
Oenanthe leucura	OENLEU	PT/SP	UL
Oenanthe oenanthe	OENOEN	PT/SP	UL

Appendix I (continued)

Species	Species code	Region	Affinity group
Oriolus oriolus	ORIORI	PT/SP	F
Parus ater	PARATE	PT/SP	F
Parus caeruleus	PARCAE	PT/SP	F
Parus cristatus	PARCRI	PT/SP	F
Parus major	PARMAJ	PT/SP	F
Parus palustris	PARPAL	SP	F
Passer montanus	PASMON	PT/SP	AL
Petronia petronia	PETPET	PT/SP	UL
Phoenicurus phoenicurus	PHOPHO	PT/SP	F
Phylloscopus bonelli	PHYBON	PT/SP	F
Phylloscopus collybita	PHYCOL	PT/SP	F
Phylloscopus ibericus	PHYIBE	PT/SP	F
Pica pica	PICPIC	PT/SP	F
Prunella collaris	PRUCOL	SP	UL
Prunella modularis	PRUMOD	PT/SP	UL
Pyrrhocorax graculus	PYRGRA	SP	UL
Pyrrhula pyrrhula	PYRPYR	PT/SP	UL
Pyrrhocorax pyrrhocorax	PYRRHO	PT/SP	F
Regulus ignicapilla	REGIGN	PT/SP	F
Regulus regulus	REGREG	PT/SP	F
Remiz pendulinus	REMPEN	PT/SP	UL
Saxicola rubetra	SAXRUB	PT/SP	UL
Saxicola torquatus	SAXTOR	PT/SP	UL
Serinus citrinella	SERCIT	SP	F
Serinus serinus	SERSER	PT/SP	AL
Sitta europaea	SITEUR	PT/SP	F
Sturnus unicolor	STUUNI	PT/SP	AL
Sylvia cantillans	SYLCAN	PT/SP	F
Sylvia communis	SYLCOM	PT/SP	UL
Sylvia conspicillata	SYLCON	PT/SP	UL
Sylvia hortensis	SYLHOR	PT/SP	F
Sylvia melanocephala	SYLMEL	PT/SP	F
Sylvia undata	SYLUND	PT/SP	UL
Turdus merula	TURMER	PT/SP	F
Turdus philomelos	TURPHI	PT/SP	F
Turdus torquatus	TURTOR	PT/SP	F