

Geographic patterns of vertebrate diversity and identification of relevant areas for conservation in Europe

M. J. T. Assunção-Albuquerque,
J. M. Rey Benayas, M. Á. Rodríguez
& F. S. Albuquerque

Assunção-Albuquerque, M. J. T., Rey Benayas, J. M. Rodríguez, M. Á. & Albuquerque, F. S., 2012. Geographic patterns of vertebrate diversity and identification of relevant areas for conservation in Europe. *Animal Biodiversity and Conservation*, 35.1: 1–11.

Abstract

Geographic patterns of vertebrate diversity and identification of relevant areas for conservation in Europe.— The 'EU Council conclusions on biodiversity post-2010' re-enforced Europe's commitment to halt biodiversity loss by 2020. Identifying areas of high-value for biodiversity conservation is an important issue to meet this target. We investigated the geographic pattern of terrestrial vertebrate diversity status in Europe by assessing the species richness, rarity, vulnerability (according to IUCN criteria), and a combined index of the three former for the amphibians, reptiles, bird and mammals of this region. We also correlated the value of all indices with climate and human influence variables. Overall, clear geographic gradients of species diversity were found. The combined biodiversity index indicated that high-value biodiversity areas were mostly located in the Mediterranean basin and the highest vulnerability was found in the Iberian peninsula for most taxa. Across all indexes, the proportion of variance explained by climate and human influence factors was moderate to low. The results obtained in this study have the potential to provide valuable support for nature conservation policies in Europe and, consequently, might contribute to mitigate biodiversity decline in this region.

Key words: High-value biodiversity areas, Human influence, Richness, Rarity, Vulnerability.

Resumen

Patrones geográficos de diversidad de vertebrados e identificación de áreas relevantes para su conservación en Europa.— Las conclusiones del 'Consejo de la UE sobre la biodiversidad post-2010' reforzaron el compromiso europeo de detener la pérdida de la misma para el año 2020. La identificación de áreas de alto valor para la conservación de la biodiversidad resulta importante para alcanzar esta meta. En el presente estudio investigamos la distribución geográfica del estatus de la diversidad de vertebrados en Europa evaluando la riqueza de especies, rareza, vulnerabilidad (según criterios de la UICN) y un índice combinado de los tres anteriores para anfibios, reptiles, aves y mamíferos de esta región. Además, se correlacionó el valor de estos cuatro índices con variables climáticas e influencia humana. En general, se identificaron gradientes geográficos claros de diversidad de las especies. El índice combinado de biodiversidad indicó que, para la mayoría de los taxones, las áreas de alto valor de biodiversidad se encuentran principalmente en la cuenca mediterránea y la mayor vulnerabilidad en la península Ibérica. La proporción de variación explicada por el clima y la influencia humana fue de moderada a baja para todos los índices. Los resultados de este estudio tienen el potencial de proporcionar un valioso soporte científico para las políticas europeas de conservación de la naturaleza y, consecuentemente, pueden contribuir a mitigar la pérdida de biodiversidad en esta región.

Palabras clave: Áreas de alto valor de biodiversidad, Influencia humana, Riqueza, Rareza, Vulnerabilidad.

(Received: 13 XI 11; Conditional acceptance: 1 II 12; Final acceptance: 1 III 12)

M. J. T. Assunção-Albuquerque, J. M. Rey Benayas & M. Á. Rodríguez, Dept. of Ecology, Univ. of Alcalá, 28871 Alcalá de Henares, Madrid, España (Spain).— F. S. Albuquerque, Grupo de Ecología Terrestre, Centro Andaluz de Medio Ambiente, Univ. Granada–Junta de Andalucía, Av. del Mediterráneo s/n., 18006 Granada, España (Spain).

Corresponding author: M. J. T. Assunção-Albuquerque. E-mail: mariajose.teixeira@edu.uah.es

Introduction

Assessing broad geographical patterns of species distribution is crucial to identify areas with highest species richness, rarity or vulnerability that are relevant for species conservation (Davies et al., 2006; Kati et al., 2004; Mittermeier, 2005; Myers et al., 2000; Orme et al., 2005). Myers (1988) used the term 'hotspots' to refer to those areas with relevant biodiversity characteristics that are threatened with destruction. These areas usually harbour high species richness and a high number of endemic species (Myers et al., 2000). The identification of biodiversity hotspots has been mostly based on the amount of biodiversity per land unit area (Veech, 2000), although some efforts have also considered the distribution of biodiversity threats (Balmford et al., 2000; Fleishman et al., 2006; Rey Benayas & de la Montaña, 2003; Sierra et al., 2002).

Metrics that take biodiversity and the risk of species loss into account in a particular region are important for conservation efforts and allow the identification of areas that need urgent protection (Didier et al., 2010; Margules & Pressey, 2000; Rey Benayas & de la Montaña, 2003). Identifying factors that affect species threats in a particular area may provide the bases for protection and inspire prevention measures to mitigate such threats and thus extinction risk. The relationships between human factors and biodiversity are important to assess such risk of extinction as human pressures are often related to large changes in biological diversity. However, the literature shows contradictory results. Previous studies report that human influence may affect species' spatial distribution both negatively and positively (Young et al., 2005). On the one hand, human factors, such as human activities (Araújo et al., 2002; Cincotta et al., 2000; Clergeau et al., 2006; Donald et al., 2001) and, in particular, the alteration of habitats (Kiesecker et al., 2001; Peres et al., 2010) are major causes of biodiversity loss (Brooks et al., 2002; Cardillo et al., 2004; Gaston, 2006; McKee et al., 2003; McKinney, 2001; Singh, 2002; Van Rensburg et al., 2004). On the other hand, several studies have even shown a positive relationship between human density and biodiversity, indicating that species-rich areas and human settlements often co-occur (Albuquerque & Rueda, 2010; Luck, 2007; Maffi, 2005; Sutherland 2003). However, this might be a purely correlative effect in many instances, particularly for species that are associated with farming and human habitation such as aphids (Pautasso & Powel, 2009) or ants (Schlick-Steiner et al., 2008) that may behave as invasive pests causing an absolute loss of diversity by displacing other species.

The present study joins previous conservation biogeography efforts to identify critical areas to protect European vertebrate diversity (Araújo & Pearson, 2005; Jelaska et al., 2010); it aimed to document geographic patterns of species richness, rarity, vulnerability, and a combined index of the three former measures at the 50-km grain resolution for each major taxa. We also analyzed relationships between human

influence and these biodiversity indices, highlighting key areas for vertebrate conservation. Our analysis provides insights into how to address anthropogenically-derived conservation issues.

Material and methods

Distribution data

Distribution data from atlas maps for amphibian, reptile, bird, and mammal species in Europe were obtained from Gasc et al. (1997); Hagemeyer & Blair (1997) and Mitchell–Jones et al. (1999). These maps were digitalized and processed in Arc GIS 9.3 in a grid comprising 2,194 UTM cells of 50 x 50 km each. All islands, except Great Britain, and cells with less than 50% land cover were excluded from the analyses. Preliminary data analyses identified some cells with abnormally low amphibian and reptile richness compared with nearby cells. We identified these cells as outliers and they were excluded from analysis.

Criteria for identifying areas of high-value diversity

We followed Rey Benayas & de la Montaña (2003) to identify areas of high-value diversity of the various taxonomic groups. The following biodiversity criteria were assessed in all cells: a) species richness, b) rarity, c) vulnerability, and d) a combined index of biodiversity that integrates the three former criteria.

Rarity (R) was computed for each cell r as:

$$R = \sum_{i=1}^s (1/n_{ri}) / S_r$$

where n is the number of cells in which species i is present, and S_r is the cell's species richness.

For vulnerability (V), we first ranked the five threat categories defined by the International Union for Nature Conservation (IUCN, 2006) as: (1) non-threatened, (2) insufficiently known, (3) rare, (4) undetermined or vulnerable, and (5) endangered, and then computed the index for each cell as:

$$V = \sum_{i=1}^s (v_{ri}) / S_r$$

where v_{ri} is the vulnerability rank of species i , and S_r is the richness of cell r . Initially, we also computed this index using the similar categories defined by the European Nature Information System (EUNIS, 2005) but obtained similar results (not shown) which led us to omit this index from the study.

Then, we calculated the combined index of biodiversity (C), which jointly evaluates the species richness, rarity and vulnerability for each cell:

$$C = \sum_{i=1}^s (1/n_{ri}) v_{ri}$$

in which species richness is implicit in the expression $\sum_{i=1}^s$, rarity is represented by $1/n_{ri}$, and vulnerability by v_{ri} .

Finally, we calculated a standardized biodiversity index (SBI) by dividing the combined index of biodiversity of each taxonomic group in every cell by its

mean across all cells. Next, we summed the four standardized combined indices. The *SBI* formula is:

$$SBI = \sum_{j=1}^4 1 / m_j \sum_{i=1}^{jS} (1 / n_{ji}) V_{ji}$$

where m_j refers to the mean combined index of biodiversity of the taxonomic group j across cells.

Climate and human influence variables

We generated 21 variables to explain geographic patterns of vertebrate richness, rarity and vulnerability. These comprised the 19 climate variables of the WorldClim database (annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter and mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter; Hijmans et al., 2005), and two surrogates of human influence, namely, human population density and a habitat fragmentation index. Human density was obtained from the Gridded Population of the World [urban mapping project, version 3 produced by the Center for International Earth Science Information Network (CIESIN) and available at: <http://sedac.ciesin.columbia.edu/gpw/> (last accessed February 2012)]. The habitat fragmentation index measures the fragmentation of land by urbanization, transport infrastructure and agriculture. It calculates how many natural complexes are found within each cell and the compactness of these complexes (average size of complex in a cell versus total area of complexes in the cell). This index was produced by the European Environment Agency and is available at <http://www.eea.europa.eu/data-and-maps/figures/fragmentation-by-urbanisation-infrastructure-and-agriculture> (last accessed February 2012).

Data analysis

Initially, relationships among the four biodiversity variables (species richness, rarity, vulnerability and the combined index of biodiversity) within taxonomic groups were examined by means of Spearman rank correlation using Bonferroni correction for multiple comparisons. We also performed a principal component analysis (PCA) including all biodiversity variables (species richness, rarity, vulnerability, and the combined index of biodiversity) for each taxonomic group as well as the combined biodiversity index to highlight relationships among multiple and highly correlated variables. Additionally, relationships of each biodiversity index with climate and human influence variables were investigated by means of a redundancy analysis-based variation partitioning (Borcard et al., 1992; Legendre & Legendre, 1998;

Péres–Neto et al., 2006). This analysis provides a synthetic view of the relationships by partitioning the variation of a response variable in the study area (*i.e.* a biodiversity index of a particular vertebrate group) into components independently and jointly explained by groups of explanatory variables (*i.e.* climate variables and human factors in this study). Finally, we also took into account the results of Whittaker et al. (2007) who found that relationships of amphibian, bird, and mammal (but not reptile) species richness with solar radiation (a measure of the amount of energy available in the environment) shifted from positive in northern Europe to negative in the south of this region, and that the line separating these two zones was different for each group. Thus, we repeated the above-mentioned analyses separately for each of these regions and species groups. All analyses were performed in R (R Development Core Team, 2009) using the 'vegan' package (Oksanen et al., 2009).

Results

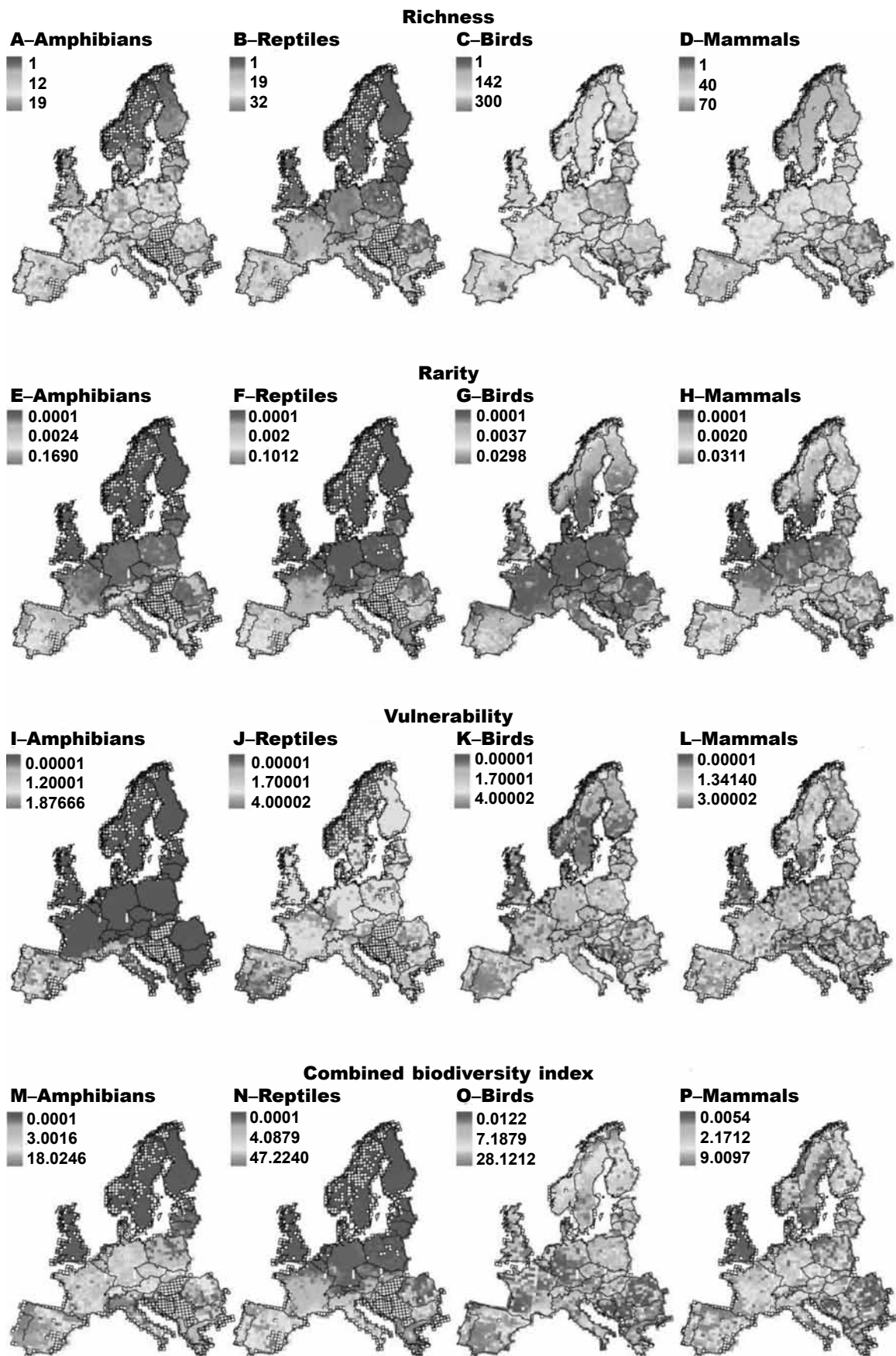
Geographical patterns of vertebrate diversity

There are 817 terrestrial vertebrate species in our study area, of which 52 are amphibians, 108 reptiles, 515 birds, and 142 mammals. Except for birds, which showed higher species richness in central European regions, there was a tendency of the richness of the other three vertebrate groups to increase southwards, with picks of highest richness values occurring in central Europe for amphibians and mammals, and in Mediterranean areas (Iberian peninsula and Greece) for reptiles (figs. 1A–1D). The overall geographic pattern of rarity (*R*) was similar for the four taxonomic groups, with rarity generally increasing southwards, although for birds and mammals it also showed secondary peaks in the north (Norway, Sweden and Finland; figs. 1E–1H).

Higher values of the vulnerability index (*V*) based on the IUCN threat categories for amphibians were recorded in north-eastern Portugal and west-central Spain; for reptiles in France and Germany primarily, and Norway, Sweden and Romania secondarily; and for birds and mammals across the Iberian Peninsula, Poland, Ukraine and Romania, with mammals also picking in north-eastern Europe (figs. 1I–1L).

Amphibians and reptiles showed a clear north-to-south gradient of increasing values of the combined index of biodiversity (*C*), mammals did the same albeit, with a more patchy distribution, and birds showed no clear trend, with high values occurring in localized areas of southern (Iberian and Greek peninsulas), central (*e.g.* Great Britain and Hungary) and northern (Norway, Sweden and Finland) Europe (figs. 1M–1P).

Highest values of the standardized biodiversity index (*SBI*) that integrates all biodiversity criteria for the four taxonomic groups were mainly observed in the Mediterranean basin, especially in Portugal, Spain, Greece and Bulgaria, with a secondary peak in Northern Europe (fig. 2).



Relationships among biodiversity criteria

Correlation analyses between species richness, rarity, vulnerability, and the combined biodiversity index within each vertebrate group indicated that almost all these biodiversity estimates were significantly and positively correlated (table 1). The combined biodiversity index was positively correlated with all estimates and especially with rarity for all groups.

The two first axes of the PCA performed on all biodiversity criteria absorbed 36.8% and 18.1% of the variation, respectively. The visual inspection of this graph revealed association of rarity, the combined index and the standardized biodiversity index on one side, and of vulnerability and species richness on the other side (fig. 3). Taxonomic groups were spread throughout the PCA bi-plot; however, it is noticeable the fact that the bird diversity criteria are relatively independent from those of all remaining taxa (fig. 3).

Variation of vertebrate diversity explained by climate and human influence

The proportion of variation explained by climate and human influence variables was highest for richness, especially for amphibians (41%) and reptiles (42%) (table 2). Rarity, vulnerability and combined biodiversity indexes were, in general, less associated with climate and human influence variables. In all cases, climate contributed more than human influences to explain these biodiversity variables. This was also reflected in the results of the variation partitioning analyses conducted separately for north and south Europe for amphibians, birds and mammals, although more variation was explained by the models for the north (table 2).

Discussion

This study identified high-value diversity areas for amphibians, reptiles, birds, and mammals in Europe by documenting the geographic distribution of five biodiversity criteria and analysing their relationships with climate and human influence factors. For most groups (amphibians, reptiles and mammals) we observed a general north-to-south gradient of increasing richness, whereas for birds, the patterns were more complex and richness picked at central European regions. Still, climate was more important than human

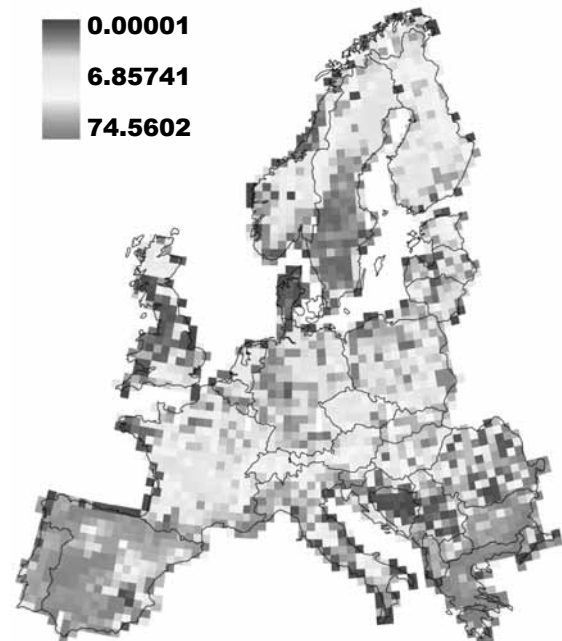


Fig. 2. Geographical patterns of the standardized biodiversity index (SBI) in Europe, which integrates all biodiversity criteria for the four vertebrate groups.

Fig. 2. Patrones geográficos del índice de biodiversidad estandarizado (SBI) en Europa, que integra todos los criterios de diversidad para los cuatro grupos de vertebrados.

influences in driving the patterns in all cases. Similar richness gradients and relationships with climate have been reported by previous studies for these taxa across Europe (Araújo & Pearson, 2005; Carrascal & Díaz, 2003; Nogués-Bravo & Martínez-Rica, 2004; Olalla-Tárraga et al, 2006; Qian & Xiao, 2012; Rodríguez et al, 2005; Rojas et al., 2001).

We also found a strong and positive correlation between rarity and the combined index of biodiversity for all groups, which highlights rarity as a key criterion to identify high-value biodiversity areas over broad geographical extents. This supports

Fig. 1. Geographical pattern of species richness (A–D), rarity (E–H), vulnerability (I–L), and combined biodiversity index (M–P) for amphibians, reptiles, birds, and mammals in Europe based on UTM grid cells with a grain of 50 x 50 km. White cells lack reliable data (see the text).

Fig. 1. Patrón geográfico de la riqueza de especies (A–D), su rareza (E–H), su vulnerabilidad (I–L) y el índice de biodiversidad combinada (M–P) para anfibios, reptiles, aves y mamíferos en Europa, basándose en celdas de una cuadrícula de coordenadas UTM de 50 x 50 km. Las celdas blancas carecen de datos fiables (véase el texto).

Table 1. Spearman rank correlation coefficients between criteria used to identify areas of high-value diversity within taxonomic groups in Europe. Coefficients in bold are significant at $p < 0.05$ after applying Bonferroni corrections for multiple comparisons: S. Richness; R. Rarity; V. Vulnerability; C. Combined index.

Tabla 1. Coeficientes de correlación de rango de Spearman entre los criterios utilizados en la identificación de las áreas de gran valor en cuanto a diversidad de los grupos taxonómicos de Europa. Los coeficientes en negrita son significativos para $p < 0,05$ tras aplicar las correcciones de Bonferroni para comparaciones múltiples: S. Riqueza; R. Rareza; V. Vulnerabilidad; C. Índice combinado.

	Amphibians (n = 1,674)			Reptiles (n = 1,648)			Birds (n = 2,144)			Mammals (n = 1,875)		
	S	R	V	S	R	V	S	R	V	S	R	V
Amphibians												
S	0.25											
V	0.68	0.34										
C	0.28	0.81	0.31									
Reptiles												
S				0.65								
V				0.49	0.25							
C				0.57	0.92	0.14						
Birds												
S							0.03					
V							0.54	0.26				
C							0.25	0.73	0.26			
Mammals												
S										0.22		
V										0.69	0.51	
C										0.52	0.69	0.45

previous claims pointing out that rarity is likely to be more effective than richness to identify priority areas for conservation (Williams et al., 1996). This result is important, since richness is the conservation criterion that is used by decision makers most often (Médail & Quézel, 1997; Reyers et al., 2000; Rodrigues et al., 2004).

In general, for the four biodiversity criteria analysed, the proportion of variation explained by climate and human influence factors was moderate to low, suggesting that other factors might be important for the described geographical pattern of vertebrate diversity in Europe. Thus, the patterns found for amphibians and reptiles may be related to the lower dispersal capacity of these groups compared to that exhibited by other vertebrates, as species with low dispersal rates need a longer time to colonize sites away from their origin (Aragón et al., 2010; Araújo & Pearson, 2005), which in turn might be associated with their higher levels of endemism (Williams et al., 2000). In agreement, Araújo & Pearson (2005) reported low levels of equilibrium (*i.e.* the time

needed to reach saturated communities) between the distribution of reptile and amphibian species in Europe and current climate, whereas they found that major ice-age refugia (Iberia, Italy and the Balkans) were key determinants of the current distributions of these species across this region (see also Whittaker et al., 2007). The contrasted geographical patterns found for bird richness in Europe (see fig. 1C), and the relatively independent location of this taxon with respect to all other taxa in the ordination of biodiversity criteria (see figure 3), may be related with the location of speciation centres, dispersal capacity and environmental preferences of the species of this taxon (Covas & Blondel, 1998). Also, bird and mammals appear to have been under a strong selective pressure by human disturbance in the northern hemisphere since the last glaciation, which may have also played a relevant role in driving the diversity patterns of these groups (Nogués-Bravo & Matrinez-Rica, 2004; Walther et al., 2002). Previous results have indicated that areas with high species rarity and vulnerability are usually associated with

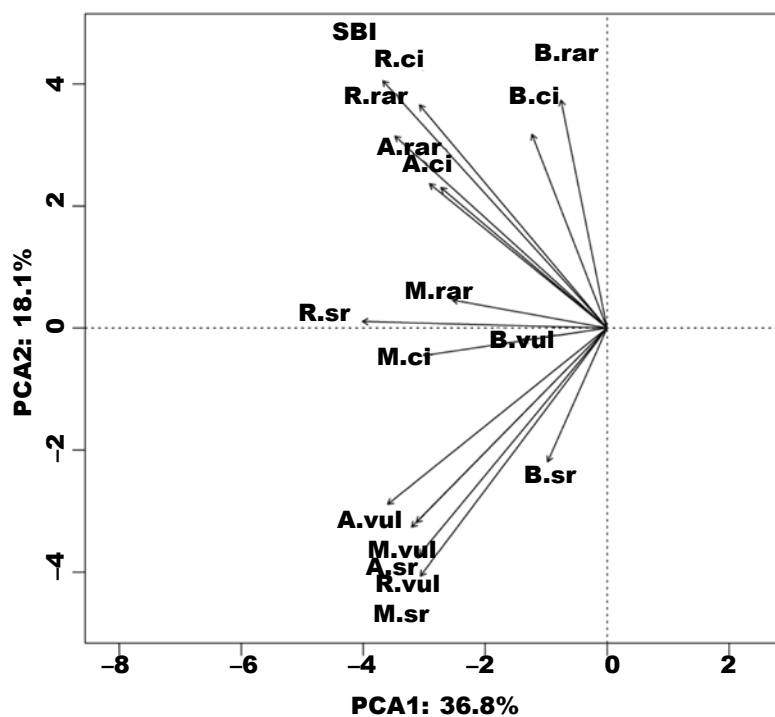


Fig. 3. Principal component analysis of vertebrate diversity criteria in Europe. Labels are the following: A.sr. Amphibian species richness; A.rar. Amphibian rarity; A.vul. Amphibian vulnerability; A.ci. Amphibian combined index; R.sr. Reptile species richness; R.rar. Reptile rarity; R.vul. Reptile vulnerability; R.ci. Reptile combined index; B.sr. Bird species richness; B.rar. Bird rarity; B.vul. Bird vulnerability; B.ci. Bird combined index; M.sr. Mammal species richness; M.rar. Mammal rarity; M.vul. Mammal vulnerability; M.ci. Mammal combined index; SBI. Standardized biodiversity index.

Fig. 3. Análisis de componentes principales de los criterios de la diversidad de vertebrados en Europa. Las etiquetas son las siguientes: A.sr. Riqueza de especies de anfibios; A.rar. Rareza de anfibios; A.vul. Vulnerabilidad de anfibios; A.ci. Índice combinado de anfibios; R.sr. Riqueza de especies de reptiles; R.rar. Rareza de reptiles; R.vul. Vulnerabilidad de reptiles; R.ci. Índice combinado de reptiles; B.sr. Riqueza de especies de aves; B.rar. Rareza de aves; B.vul. Vulnerabilidad de aves; B.ci. Índice combinado de aves; M.sr. Riqueza de especies de mamíferos; M.rar. Rareza de mamíferos; M.vul. Vulnerabilidad de mamíferos; M.ci. Índice combinado de mamíferos; SBI. Índice estandarizado de biodiversidad.

low habitat variety, forest loss, human impacts and climate change (Carrascal & Palomino, 2006; Mainka & Howard, 2010; Nuñez et al., 2010; Vié et al., 2009), in agreement with theory and empirical evidence that relate population declines with disturbance and habitat homogenization (Echeverría et al., 2004; Rey Benayas et al., 1999). However, our results show a weak association between rarity and vulnerability of these taxa with climate and human influence variables. This difference may be related to the coarser grain used in this study, in agreement with suggestions that the relationship between the ecological characteristics of a given species and its rarity and vulnerability value are scale-dependent (Murray & Lepschi, 2004). Even though our results suggest relatively minor effects of climate and hu-

man influence variables on vertebrate rarity and vulnerability, it should be noted that these results were obtained for a particular geographical extent (Europe) and grain (cells of 50 km²), and we cannot discard a stronger role of human influence at smaller scales (e.g. see Derraik & Phillips, 2010; Nuñez et al., 2010; Rowley et al., 2010). Additionally, the IUCN Red List clearly shows that many vertebrate species are under threat of extinction mainly as a direct or indirect result of human activities and climate change (Vié et al., 2009).

This study identified the Mediterranean basin as one of the richest, rarest and most vulnerable areas of Europe in terms of vertebrate diversity, and supports the tenet that Mediterranean basin biodiversity is under strong threat (see fig. 1M–1P).

Table 2. Proportional amounts of the variation of species richness (S), rarity (R), vulnerability (V) and combined index of biodiversity (C) of four vertebrate groups explained independently or in concert (Sh, shared 'effects') by climate (Cl) and human (Hm) influence variables, and unexplained variation (Un) in each case. For amphibians, birds and mammals, results are reported for the entire western European region, as well as for the northern and southern areas for which Whittaker et al. (2007) found contrasted relationships between species richness and climate (see Methods).

Tabla 2. Cantidades proporcionales de la variación de la riqueza de especies (S), su rareza (R), su vulnerabilidad (V) y el índice combinado de biodiversidad en cuatro grupos de vertebrados, explicadas independientemente (C) o en concierto (Sh, 'efectos' compartidos) debidas a las variables del clima (Cl) y la influencia humana (Hm) o a una variación inexplicable (Un), en cada caso. En el caso de anfibios, reptiles, aves y mamíferos los resultados provienen de toda la región europea occidental, así como de las áreas septentrionales y meridionales, para las cuales Whittaker et al. (2007) hallaron relaciones contrastadas entre la riqueza de especies y el clima (véase Métodos).

	Amphibians				Reptiles				Birds				Mammals			
	Cl	Sh	Hm	Un	Cl	Sh	Hm	Un	Cl	Sh	Hm	Un	Cl	Sh	Hm	Un
Europe																
S	0.26	0.13	0.02	0.59	0.39	0.03	0.00	0.58	0.25	0.00	0.01	0.74	0.33	0.03	0.00	0.64
R	0.09	0.01	0.00	0.90	0.23	0.00	0.00	0.77	0.16	0.02	0.01	0.81	0.19	0.04	0.00	0.77
V	0.16	0.03	0.01	0.80	0.12	0.02	0.01	0.85	0.09	0.02	0.02	0.87	0.16	0.09	0.02	0.73
C	0.13	0.01	0.00	0.86	0.18	0.01	0.00	0.81	0.14	0.00	0.01	0.85	0.17	0.00	0.00	0.83
Northern areas																
S	0.35	0.32	0.02	0.31	–	–	–	–	–	0.01	0.00	0.65	0.39	0.09	0.01	0.51
R	0.32	0.09	0.00	0.59	–	–	–	–	–	0.07	0.00	0.86	0.11	0.40	0.02	0.47
V	0.20	0.02	0.00	0.78	–	–	–	–	–	0.02	0.02	0.83	0.16	0.15	0.02	0.67
C	0.37	0.33	0.02	0.28	–	–	–	–	–	0.04	0.01	0.88	0.22	0.05	0.00	0.73
Southern areas																
S	0.23	0.00	0.01	0.76	–	–	–	–	–	0.02	0.01	0.69	0.35	0.01	0.01	0.63
R	0.06	0.00	0.00	0.94	–	–	–	–	–	0.00	0.01	0.59	0.13	0.02	0.00	0.85
V	0.18	0.03	0.03	0.76	–	–	–	–	–	0.04	0.01	0.88	0.14	0.08	0.00	0.78
C	0.13	0.02	0.00	0.85	–	–	–	–	–	0.00	0.00	0.75	0.06	0.03	0.00	0.91

This agrees with the findings of Myers et al. (2000), who recognized the Mediterranean as one of the 25 Global Biodiversity Hotspots. These threats are often attributed to human disturbance, natural disasters, habitat loss and degradation, pollution, or invasive alien species (Vié et al., 2009). However, human influence factors explained a small proportion of the variance of each of the four biodiversity criteria that we investigated. Further research might establish to what extent detection of human influence on diversity patterns are dependent on grain in studies conducted in large areas. Irrespectively, our data allow us to conclude that using a range of biodiversity criteria is necessary to accurately identify high-value diversity areas on a large geographic scale.

Knowing the spatial distribution of species richness, rarity and vulnerability is necessary to mitigate

biodiversity decline and accomplish the goal of the EU Council on biodiversity post-2010 to re-enforce Europe's commitment to halt biodiversity loss by 2020. The results of this study may be relevant to policy makers to target critical areas in order to strengthen conservation.

Acknowledgments

This research was supported by the Spanish Ministry of Science and Education (grants CGL2010–18312 to JMRB and CGL2010–22119 to MAR) and the Madrid Government REMEDINAL project (S2009AMB–1783). M. J. T. Assunção–Albuquerque was supported by the Brazilian Ministry of Education, through CAPES (Coordenação de Aperfeiçoamento de Pessoal de

Nivel Superior) Doctorate scholarship and FSA was supported by BIOTREE-net –project funded by BBVA Foundation. We thank M. A. Olalla-Tárraga for his friendly review on a former version of this manuscript.

References

- Albuquerque F. S., Rueda, M., 2010. Forest loss and fragmentation effects on woody plant species richness in Great Britain. *Forest Ecology and Management*, 260: 472–479.
- Aragón, P., Rodríguez, M. Á., Olalla-Tárraga, M. Á. & Lobo, J. M., 2010. Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms. *Animal Conservation*, 13: 363–373.
- Araújo, M. B. & Pearson, R. G., 2005. Equilibrium of species' distributions with climate. *Ecography*, 28: 693–695.
- Araújo, M. B., Williams, P. H. & Turner, A., 2002b. A sequential approach to minimize threats within selected conservation areas. *Biodiversity and Conservation*, 11: 1011–1024.
- Balmford, A., Gaston, K. J., Rodrigues, A. L. & James, A. N., 2000. Integrating costs of conservation into international priority setting. *Conservation Biology*, 14: 597–605.
- Borcard, D., Legendre, P. & Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045–1055.
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C., 2002. Habitat Loss and Extinction in the hotspots of Biodiversity. *Conservation Biology*, 16: 909–923.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., Mace, G. M., 2004. Human Population Density and Extinction Risk in the World's Carnivores. *PLoS Biology*, 2: 0909–0914.
- Carrascal, L. M. & Díaz, L., 2003. Asociación entre distribución continental y regional. Análisis con la avifauna forestal y de medios arbolados de la Península Ibérica. *Graellsia*, 59: 179–207.
- Carrascal, L. M. & Palomino, D., 2006. Rareza, estatus de conservación y sus determinantes ecológicos. Revisión de su aplicación a escala regional. *Graellsia*, 62: 523–538.
- CIESIN, 2007. Center for International Earth Science Information Network., 2000. Gridded population of the world, version 2. <http://sedac.ciesin.columbia.edu/plue/gpw>.
- Cincotta, R. P., Wisniewski, J. & Engelmann, R., 2000. Human Population in the biodiversity hotspots. *Letters to Nature*, 404: 990–992.
- Clergeau, P., Croci, S., Jokimaki, J., Kaisanlahti-Jokimaki, M. L. & Dinetti, M., 2006. Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation*, 127: 336–344.
- Covas, R. & Blondel, J., 1998. Biogeography and history of the Mediterranean bird fauna. *Ibis*, 140: 395–407.
- Davies, R. G., Orme, C. D. L., Olson, V., Thomas, G. H., Ross, S. G., Ding, T.-S., Rasmussen, P. C., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Owens, I. P. F. & Gaston, K. J., 2006. Human impacts and the global distribution of extinction risk. *Proceedings of the Royal Society of London, Series B* 273: 2127–2133.
- Derraik, J. G. B. & Phillips S., 2010. Online trade poses a threat to biosecurity in New Zealand. *Biological Invasions*, 12: 1477–1480.
- Didier, K. A., Wilkie, D., Douglas-Hamilton, I., Frank, L., Georgiadis N., Graham, M., Ihwagi, F., King, A., Cotterill, A., Rubenstein D. & Woodroffe, R., 2010. Conservation planning on a budget: a 'resource light' method for mapping priorities at a landscape scale? *Biodiversity and Conservation*, 18: 1979–2000.
- Donald, P. F., Green, R. E. & Heath, M. F., 2001. Agricultural intensification and collapse of Europe's farmland bird populations. *Proceedings of the Royal Society London, B* 268: 25–29.
- Echeverría, C., Lara, A., Newton, A., Rey Benayas, J. M. & Coomes, D. 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape in southern Chile. *Global Ecology and Biogeography*, 16: 426–439.
- EUNIS, 2005. European Nature Information System. <http://eunis.eea.europa.eu>.
- Fleishman, E., Noon, B. R. & Noss, R. F., 2006. Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators*, 6: 543–553.
- Gasc, J. P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J. P., Maurin, H., Oliveira, M. E., Sofianidou, T. S., Veith, M. & Zuiderwijk, A. (Eds), 1997. Atlas of amphibians and reptiles in Europe. Collection Patrimoine Naturels 29, Societas Europaea Herpetologica, Muséum National d'Histoire Naturelle & Service du Patrimoine Naturel, Paris.
- Gaston, K. J., 2006. Biodiversity and extinction: Macroecological patterns and people. *Progress in Physical Geography*, 30: 258–269.
- Hagemeijer, W. J. M. & Blair, M. J., 1997. *The EBCC atlas of European breeding birds, their distribution and abundance*. Published for European Bird Census Council. Poyser, London.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965–1978.
- IUCN, 2006. Red list of the threatened species. <http://www.redlist.org>.
- Jelaska, S. D., Nikolić, T., Serić Jelaska, L., Kusan, V., Peternel, H., Guzvica, G., Major, Z., 2010. Terrestrial Biodiversity Analyses in Dalmatia (Croatia): A Complementary Approach Using Diversity and Rarity. *Environmental Management*, 45: 616–625.
- Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D. & Lebrun, P., 2004. hotspots, complementarity or

- representativeness? Designing optimal small-scale reserves for biodiversity conservation. *Biological Conservation*, 120: 471–480.
- Kiesecker, J. M., Blaustein, A. R. & Belden, L. K., 2001. Complex causes of amphibian population declines. *Nature*, 410: 681–684.
- Legendre, P. & Legendre, L., 1998. *Numerical Ecology*, 2nd English edn. Amsterdam: Elsevier Science BV.
- Luck, G. W., 2007. A review of the relationships between human population density and biodiversity. *Biological Reviews*, 82: 607–645.
- Maffi, L., 2005. Linguistic, cultural, and biological diversity. *Annual Review of Anthropology*, 34: 599–617.
- Mainka, S. A. & Howard, G. W., 2010. Climate change and invasive species: double jeopardy. *Integrative Zoology*, 5: 101–111.
- Margules, C. R. & Pressey, R. L., 2000. Systematic conservation planning. *Nature*, 405: 243–253.
- McKee, J. K., Sciulli, P. W., Foose, C. D. & Waite, T. A., 2003. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, 115: 161–164.
- McKinney, M. L., 2001. Role of human population size in raising bird and mammal threat among nations. *Animal Conservation*, 4: 45–57.
- Medail, F. & Quézel, P., 1997. Hot–Spots analysis for Conservation of plant biodiversity in the Mediterranean Basin. *Annales Missouri Botanical Garden*, 84: 112–127.
- Mitchell–Jones, A. J., Amori, G., Bodganowicz, W., Krystufek, B., Reijnders, P. J. H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralík, V. & Zima, J., 1999. *The Atlas of European mammals*. Academic Press, London.
- Mittermeier, R. A., 2005. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Cemex, Conservation International and Agrupación Sierra Madre, Monterrey, Mexico.
- Murray, B. R. & Lepschi, B. J., 2004. Are locally rare species abundant elsewhere in their geographical range? *Austral Ecology*, 29: 287–293.
- Myers, N., 1988. Threatened biotas: hotspots in tropical forests. *Environmentalist*, 8: 178–208.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kents, 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: 629–641.
- Nuñeza, O. M., Ates, F. B. & Alicante, A. A., 2010. Distribution of endemic and threatened herpetofauna in Mt. Malindang, Mindanao, Philippines. *Biodiversity and Conservation*, 19: 503–518.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H., 2009. *vegan*: community ecology package. Rpackage version 1.15–4. <http://CRAN.R-project.org/package=vegan>.
- Olalla–Tárraga, M. A., Rodríguez, M. A. & Hawkins, B. A., 2006. Broad-scale body size patterns in squamate reptiles of Europe and North America. *Journal of Biogeography*, 33: 781–793.
- Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Oslon, V. A., Webster, A. J., Ding, T., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J. & Owens, I. P. F., 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436: 1016–1019.
- Pautasso, M. & Powell, G., 2009. Aphid biodiversity is positively correlated with human population in European countries. *Oecologia*, 160: 839–846.
- Peres, C. A., Gardner, T. A., Barlow, J., Zuanon, J., Michalski, F., Lees, A. C., Vieira, I. C. G., Moreira, F. M. S. & Feeley, K. J., 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. *Biological Conservation*, 143: 2314–2327.
- Peres–Neto, P. R., Legendre, P., Dray, S. & Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, 87:2614–2625.
- Qian, H. & Xiao, M., 2012. Global patterns of the beta diversity–energy relationship in terrestrial vertebrates. *Acta Oecologica*, 39: 67–71.
- R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3–900051–07–0. <http://www.R-project.org>.
- Rey Benayas, J. M., Scheiner, M., García S., Colomer, M., & Levassor, C., 1999. Commonness and rarity: theory and application of a new model to Mediterranean montane grasslands. *Conservation Ecology*, 3(1): 5 (on line).
- Rey Benayas, J. M. & De la Montaña, E., 2003. Identifying areas of high-value vertebrate diversity for strengthening conservation. *Biological Conservation*, 114: 357–370.
- Reyers, B., Van Jaarsveld, A. S. & Krüger, M., 2000. Complementarity as a biodiversity indicator strategy. *The Royal Society*, 267: 505–513.
- Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D., Da Fonseca, G. A., Gaston, K. J., Hoffmann, M., Long, J.S., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., Watts, M. E. & Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. *Nature*, 428: 640–643.
- Rodríguez, M. Á., Belmontes, J. A. & Hawkins, B. A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. *Acta Oecologica*, 28: 65–70.
- Rojas, A. B., Cotilla, I., Real, R. & Palomo, L. J., 2001. Determinación de las áreas probables de distribución de los mamíferos terrestres en la provincia de Málaga. *Galemys*, 13: 217–229.
- Rowley, J., Brown, R., Bain, R., Kusriani, M., Inger, R., Stuart, B., Wogan, G., Thy, N., Chan–ard, T., Trung, C. T., Diesmos, A., Iskandar, D. T., Lau, M., Ming, L. T., Makchai, S., Truong, N. Q. & Phimmachak, S., 2010. Impending conservation crisis for Southeast

- Asian amphibians. *Biology Letters*, 6: 336–338.
- Schlick–Steiner, B. C., Steiner, F. M. & Pautasso, M., 2008. Ants and people: a test of two mechanisms potentially responsible for the large–scale human population–biodiversity correlation for Formicidae in Europe. *Journal of Biogeography*, 35: 2195–2206.
- Sierra, R., Campos, F. & Chamberlin, J., 2002. Assessing biodiversity conservation priorities: ecosystem risk and representativeness in continental Ecuador. *Landscape and Urban Planning*, 59: 95–110
- Singh, J. S., 2002. The biodiversity crisis: A multifaceted review. *Current Science*, 82: 638–647.
- Sutherland, W. J., 2003. Parallel extinction risk and global distribution of languages and species. *Nature*, 423: 276–279.
- Van Rensburg, B. J., Erasmus, B. F. N., Van Jaarsveld, A. S., Gaston, K. J. & Chown, S. L., 2004: Conservation during times of change: correlations between birds, climate and people in South Africa. *South African Journal of Science*, 100: 266–72.
- Veech, J. A., 2000. Choice of Species–Area Function Affects Identification of Hotspots. *Conservation Biology*, 14: 140–147.
- Vié, J.–C., Hilton–Taylor, C. & Stuart, S. N. (Eds.), 2009. *Wildlife in a Changing World–An Analysis of the 2008 IUCN Red List of Threatened Species*. Gland, Switzerland: IUCN.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.–M., Hoegh–Guldberg, O. & Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, 416: 389–395.
- Whittaker, R. J., Nogués–Bravo, D. & Araújo, M. B., 2007. Geographical gradients of species richness: a test of the water–energy conjecture of Hawkins et al. (2003) using European data for five taxa. *Global Ecology and Biogeography*, 16: 76–89.
- Williams, P. H., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R., 1996. A Comparison of Richness Hotspots, Rarity Hotspots and Complementary Areas for Conserving Diversity of British Birds. *Conservation Biology*, 10: 155–174.
- Williams, P. H., Humphries, C., Araújo, M. B., Lampinen, R., Hagemeyer, W., Gasc, J.–P. & Mitchell–Jones, T., 2000. Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian Journal of Entomology*, 2: 21–46.
- Young, J., Watt, A., Nowicki, P., Alard, D., Clitherow, J., Henle, K., Johnson, R., Laczko, E., Mccracken, D., Matouch, S., Niemela, J. & Richards, C., 2005. Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe. *Biodiversity and Conservation*, 14: 1641–1661.
-