



The coincidence of people and biodiversity in Europe

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ABSTRACT

A positive correlation between human population density and species richness has been recorded across the tropics. Here I investigate whether this correlation holds true for Europe. Analyses reveal a positive correlation between human population density and plant ($\rho = 0.505$), mammal ($\rho = 0.471$) and reptile and amphibian ($\rho = 0.556$) species richness. The results are largely concordant with those obtained in similar studies for Africa. However, contrary to previous analyses, the correlation found between people and breeding bird species richness ($\rho = 0.186$) was weak. Of three measures of endemism used,

only combined European endemic species richness correlated with human density ($\rho = 0.437$). Richness among combined restricted-range European endemics was not correlated ($\rho = 0.095$) with human density, while richness among all combined restricted-range species was only weakly correlated with human density ($\rho = 0.167$). The results partially support the idea of a correlation between people and biodiversity, although there are some important exceptions. Discussion of possible mechanisms underlying the observed patterns is undertaken.

Key words biodiversity, conservation priorities, endemism, Europe, human population density, species richness.

INTRODUCTION

The processes that generate diversity have been discussed in the literature by researchers with different perspectives (for reviews see, e.g. Huston, 1994; Rosenzweig, 1995; Maurer, 1999; Gaston & Blackburn, 2000). A number of patterns have been identified as well as competing hypotheses to explain them. Teasing apart mechanisms underlying an observed pattern, from indirect factors that correlate with it, is often difficult. For example, recent studies have shown that human population density was positively correlated with terrestrial vertebrate and plant species richness across sub-Saharan Africa (Balmford *et al.*, 2001a,b). These observations coincide with those of Fjeldsø & Rahbek (1998), who noted a tendency for human settlements to be located near the centres of bird endemism in the tropical Andes. Considered altogether these studies imply that areas preferred by humans might coincide with those preferred by many extant species. The mechanisms underlying such pattern of congruence are not fully understood and it is likely that the observed relationship between human density and biodiversity are due to covarying factors, such as climatic stability (e.g. Fjeldsø & Rahbek, 1998), productivity (e.g. Waide *et al.*, 1999), or landscape heterogeneity

(e.g. Atauri & Lucio, 2001; van Rensburg *et al.*, 2002). However, if human density was indeed related directly to biodiversity, then the relationship should reoccur with analyses of data from different parts of the world. In this study, I investigate the extent to which a positive correlation between human population density and plant, mammal, bird, reptile and amphibian species richness occurs across Europe. Local and regional deviations from a broad pattern of covariation between these variables are also explored.

MATERIALS AND METHODS

Species data included 868 960 occurrence records of European higher plants and terrestrial vertebrates. These included 2294 plant species (Jalas & Suominen, 1972–96), 186 mammal species (Mitchell-Jones *et al.*, 1999), 440 breeding bird species (Hagemeijer & Blair, 1997) and 143 amphibian and reptile species (hereafter referred to as herptiles) (Gasc *et al.*, 1997). Terrestrial vertebrates include all extant European species, whereas plants comprise ~20% of the European flora. The grid is based on the *Atlas Florae Europaeae* (Lathi & Lampinen, 1999), with cell boundaries typically following the 50 km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts (for details concerning data conversion see Williams *et al.*, 2000). Human population density surfaces were created in two stages, the first involved generating high-resolution

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estimates across Europe (Openshaw & Turner, 2001), and the second involved aggregating these high-resolution estimates at the coarser resolution of the AFE grid. A more detailed description of the process is described in Araújo *et al.* (2002).

Pairwise Spearman rank correlation coefficients were calculated for human population density and species richness, using SPSS version 10 (Norusis, 1999). Correlations were also calculated between human density and endemic species richness. Three measures of endemism were used: (a) European endemic species richness, which is a count of the number of all species per grid cell whose distributions are restricted to the mapped area of Europe (i.e. 794 plants, 10 birds, eight mammals and 70 herptiles, accounting for 29% of the species overall) (see Williams *et al.*, 2000); (b) narrow European endemic species richness, which is a count of the number of European endemic species per grid cell among the 25% most restricted species; (c) restricted-range species richness, which is a count of the number of all species per grid cell among the 25% most restricted species, regardless of whether they extended elsewhere. This third measure is, strictly speaking, not a measure of endemism but was used to allow direct comparison with the 'endemism' measure of Balmford *et al.* (2001a). The use of thresholds, such as the rarest quartile or 25% species, to identifying centres of endemism has become increasingly popular (e.g. ICBP, 1992; Williams *et al.*, 1996), despite criticism of their arbitrariness (for a review see Gaston, 1994). Nevertheless, alternative continuous measures of endemism do not avoid arbitrariness. They simply transfer it from the choice of threshold to the choice of the formula used to weight species range size. Hence, rather than using a single measure of endemism it becomes appropriate to compare different approaches to its measurement. The frequency distributions of all three measures of endemism and human population scores were highly peaked (high kurtosis) and skewed to the right (high positive skewness) (Table 1). They were transformed to $\ln(\text{variable} + 1)$ to achieve approximate normality. This would not be necessary, because Spearman rank correlation is a non-parametric method and does not require data to be normally distributed. Indeed, transformation does not affect the correlation coefficient, because it is based on the rank order of values rather than on their original value. Nevertheless, transformation of values was carried out to ensure visual comparability with the scatter diagrams of the relationship between human density and species richness presented by Balmford *et al.* (2001a,b).

Spatial deviations from an overall relationship between human population density and species richness are investigated with the two-colour overlay technique described by

Table 1 Skewness and kurtosis among species and human population data ($N = 2434$)

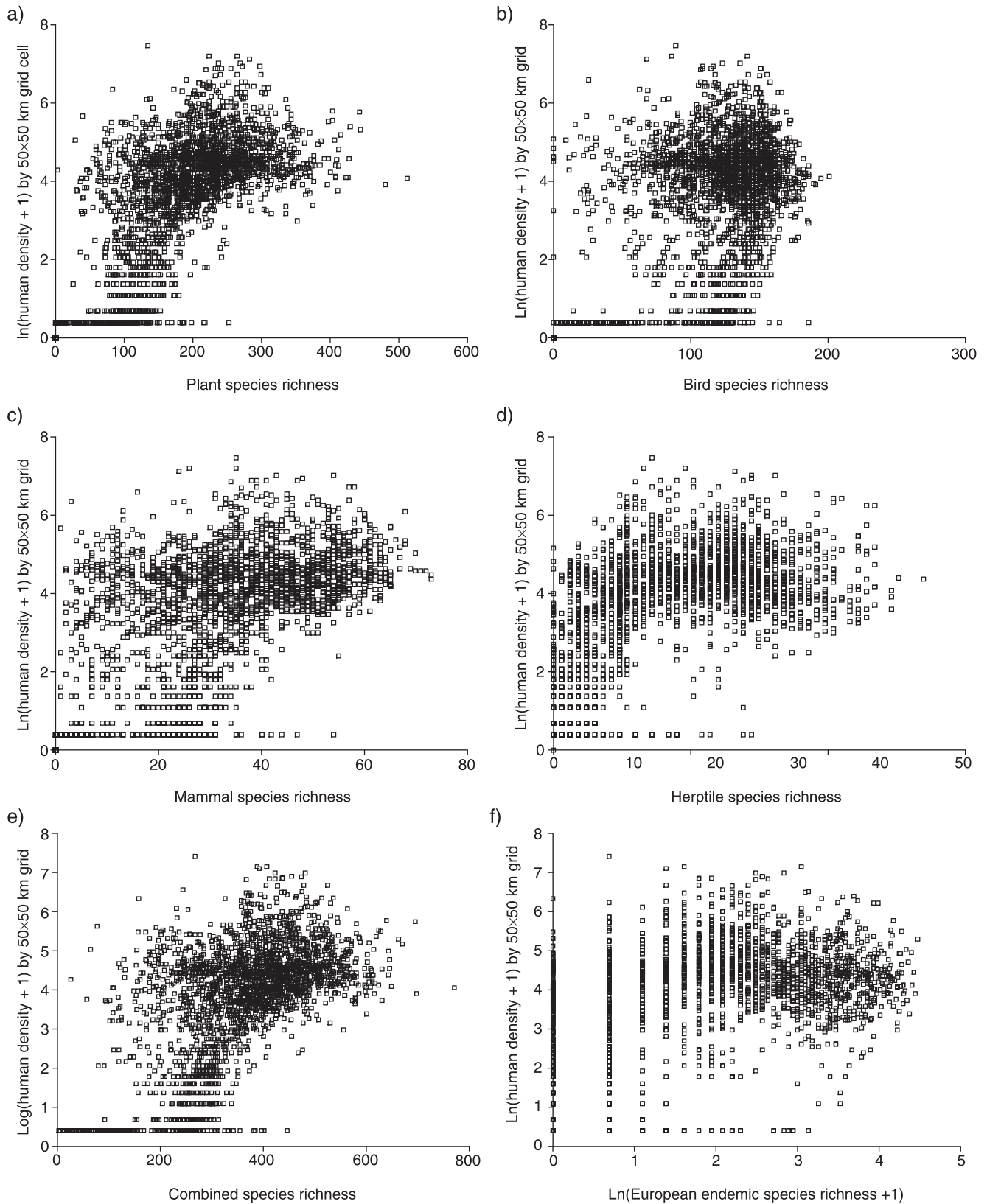
	Skewness	Kurtosis
Plant species richness	0.23	-0.16
Bird species richness	-1.08	0.98
Mammal species richness	-0.08	-0.74
Herptile species richness	0.27	-0.91
All species richness	-0.29	0.00
All species richness, lower 25% range	4.85	32.36
European endemic species richness	1.79	3.06
European endemic species richness, lower 25% range	7.22	71.46
Human population density	4.50	31.26

Williams & Gaston (1998) and available in WORLDMAP software (Williams, 1999). If human population density were correlated linearly with species richness, then maps overlaying the two variables would be black and white; areas with the highest human population density would be the most species-rich (white), while areas with lowest human density would be the most species-poor (black). Perfectly covarying scores, with intermediate values, would be shown in different shades of grey. Because the correlation is not perfect, residuals (i.e. spatial trends in deviations from overall pattern) are shown in blue and green on the map. Here, blue represents excesses of human population density over species richness; and green represents excesses of species richness over human population density.

RESULTS

Spearman's rank correlation analyses reveal that, across Europe, human population density is generally higher in areas of high plant ($\rho = 0.593$, Fig. 1a), mammal ($\rho = 0.471$, Fig. 1c), and herptile ($\rho = 0.556$, Fig. 1d) species richness, and vice versa. Human population density is correlated only weakly with breeding bird species richness ($\rho = 0.186$, Fig. 1b). When taking all species combined, the correlation between richness and human density is high ($\rho = 0.546$), but is reduced when only vertebrates are considered together ($\rho = 0.380$). The correlation between human density and endemism varies with the measure used. European endemic species richness correlates with human density ($\rho = 0.437$), but richness among the most restricted-range European endemics does not ($\rho = 0.095$). Similarly, richness among all restricted-range species is only weakly correlated with people ($\rho = 0.167$).

Fig. 1 Correlation between human population density (number of people within each 50×50 km grid cell) and: (a) plant species richness; (b) bird species richness; (c) mammal species richness; (d) herptile species richness; (e) combined richness for all groups of species; (f) combined richness among European endemic species; (g) combined richness among narrow European endemic species; and (h) combined richness among restricted-range species. Each point represents a 50×50 km grid cell.



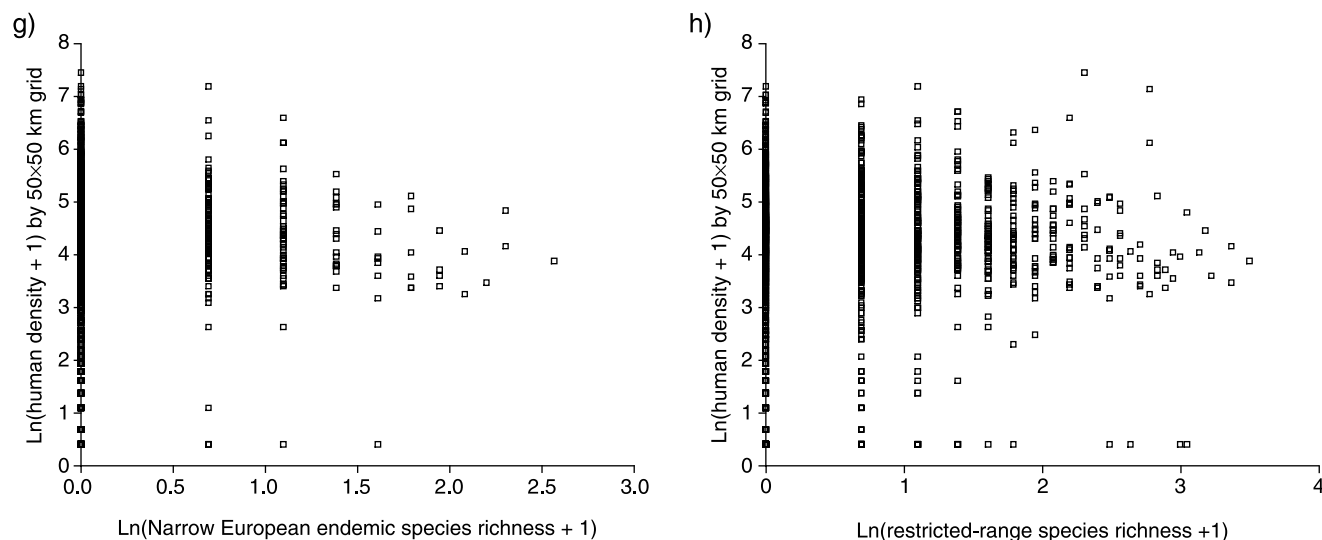


Fig. 1 continued.

Spatial deviations from broad patterns of covariation between human population density and species richness are shown in Fig. 2. Perfectly covarying scores are shown in shades of black and white, while departures from a linear relationship between the human density and species richness are shown in green and blue. Blue areas have an excess of people over species richness and are located in the most densely populated areas of Britain, central Europe, the most industrialized areas of northern Italy, north-west of the Iberian Peninsula and the Balkans. Green areas have an excess of species richness relative to human population density and are located in Scandinavia, southern France, the Alps, some areas in the Iberian Peninsula and the Balkans. England has strong departures of people over species richness (blue), while the central and southern parts of France have departures of species richness over people (green). Similarly, the Iberian Peninsula deviates from a broader trend by having increasing scores of herptile species richness relative to human density. Scandinavia deviates from broader trends by having increasing scores of bird species richness relative to human population density.

DISCUSSION

The results of this study provide only partial support for the idea that areas with high human population density coincide with areas of high species richness. A correlation was found between human population density and species richness among plants, mammals and herptiles, although only a weak correlation was found between people and breeding bird species richness. Given that the first three groups account for 86% of the species and 67% of the records, it is unsurprising that richness among the combined set of all species also shows

relatively strong correlation with human density. In this study, human density was either not or only weakly correlated to species richness among narrow endemics.

There are some striking similarities of pattern between analyses in this study and those conducted for Africa by Balmford *et al.* (2001a,b) (Table 2). For example, the correlation found for mammal species richness and people in Africa is $\rho = 0.43$ (Balmford *et al.*, 2001a), while the correlation in Europe is $\rho = 0.47$. Among the major six taxonomic orders of European terrestrial mammals (i.e. Artiodactyla, Carnivora, Chiroptera, Insectivora, Lagomorpha and Rodentia), only species richness among carnivores does not correlate with local human population density ($\rho = 0.05$). Balmford and colleagues did not have information for all herptiles in Africa, which precludes a direct comparison between the two studies. However, when comparing the correlations obtained for the subgroups of African herptiles available for Africa (i.e. snakes and amphibians), there are again some similarities. The correlation between people and snakes in Africa was $\rho = 0.43$, while in Europe it was $\rho = 0.46$. Among amphibians the coincidence between the two studies is weaker (Table 2), although Balmford and colleagues noted this was the most poorly sampled group in their analysis and there was a positive relationship between sampling intensity and the relationship between people and species richness. Hence they would expect the correlation between people and amphibian species richness to be underestimated. Because there is no indication of sampling intensity among the vertebrate groups studied in Europe I cannot perform such a comparison.

A similar coincidence between the two continent-wide analyses is also recorded for vascular plants. Plant species richness and human density is $\rho = 0.56$ in Africa (Balmford

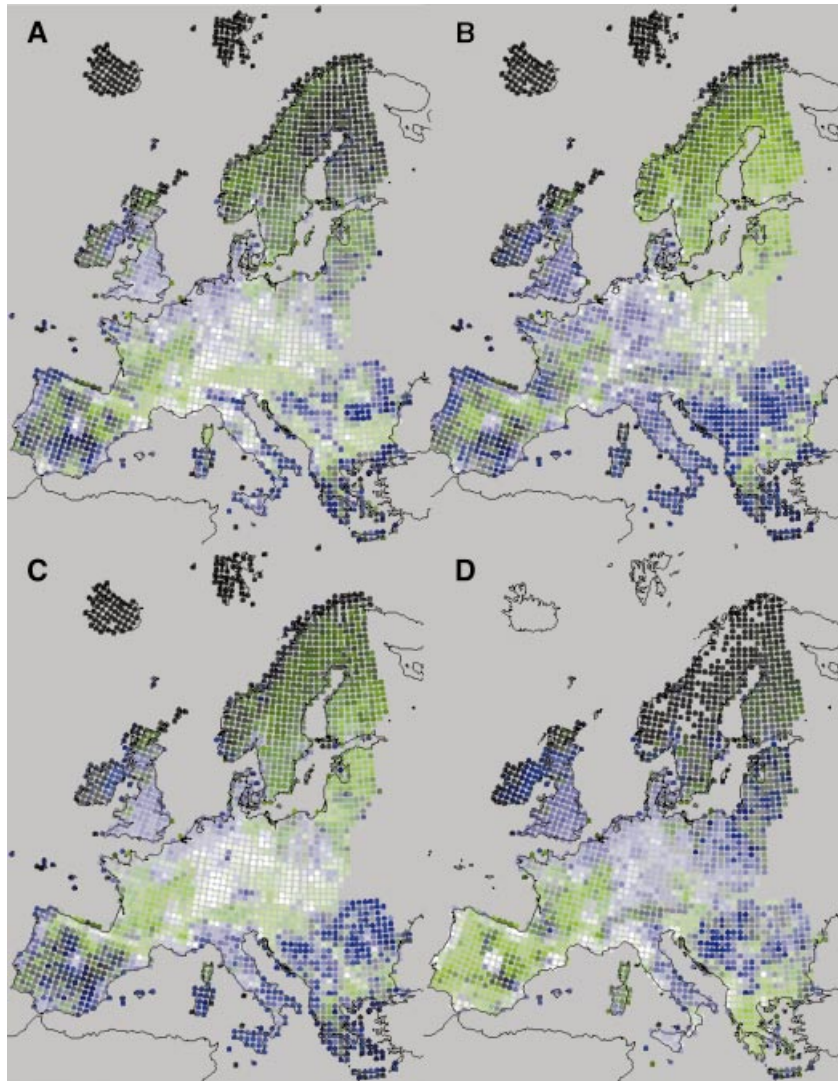


Fig. 2 Overlay between human population density and species richness for (a) plants; (b) birds; (c) mammals; and (d) herptiles among UTM 50×50 km grid cells in Europe. Scores show the regional differences in the overall variation between human density and species richness. Scores are divided into 10 colour-scale classes, where increasing intensities of blue represent increasing scores of human population density and increasing intensities of green represent increasing scores of species richness. Black grid cells show low scores for both human density and species richness; white shows high scores for both measures; and shades of grey show linearly covarying scores for both.

Table 2 Spearman rank correlation (ρ) between $\log(n + 1)$ people human density and species richness in Europe and in the African studies conducted by Balmford *et al.* (2001a,b)

	Europe	Africa
Plants	0.51	0.56
Birds	0.19	0.59
Mammals	0.47	0.43
Snakes	0.46	0.43
Amphibians	0.61	0.35

et al., 2000b), while in Europe it is $\rho = 0.51$. It should be noted, however, that these results might not be entirely comparable. Plant data available for this study represent ~20% of the European flora, whereas the subset of the African flora analysed by Balmford *et al.* (2001b) represents only ~7%. Most importantly, the data used here are biased towards particularly well-represented groups in western and central Europe (e.g. Salicaceae, Caryophyllaceae) and this coincides with some of the most densely populated areas. Important families in the Mediterranean region are missing. Examples include families such as Caprifoliaceae, Cistaceae, Compositae,

Ericaceae, Gramineae, Labiatae, Leguminosae, Oleaceae, and Rhamnaceae, among others. It is possible that analysis of a more complete dataset of European plants might reveal a different gradient of species richness, and this would be likely to correlate differently with human population density. Unless this bias was coincident with some undocumented and similar bias in the African data, results should be interpreted with caution.

Besides the similarities, there were also some important differences between the African and European studies. Birds were the group most strongly correlated with people in Africa ($\rho = 0.59$, Balmford *et al.*, 2001a) and the least correlated with people in Europe ($\rho = 0.19$). Unlike a previous study exploring the correlation between human population density and threatened species richness in the United States (Dobson *et al.*, 2001), I found no particular trend between human density and richness of species with different levels of threat. For example, the correlation between people and richness among species of favourable conservation status that concentrate in Europe (i.e. 83 species classified in SPEC category 4, as defined by Tucker & Heath, 1994) is $\rho = 0.31$, and $\rho = 0.30$ with species of unfavourable conservation status that concentrate in Europe (37 species, SPEC 2). In contrast, the correlation between human density and richness among species of global conservation concern (17 species, SPEC 1) is $\rho = 0.21$, and $\rho = 0.15$ for species of unfavourable conservation status that do not concentrate in Europe (113 species, SPEC 3).

Combined vertebrate species richness among the 25% most restricted species in the Africa database produced a lower correlation with people than overall species richness, although a still relatively strong one ($\rho = 0.39$). In Europe, the same measure of 'endemism' produced a very weak correlation with people ($\rho = 0.17$). Similarly, there was no correlation of human density with richness among the most restricted European endemic species ($\rho = 0.09$). Richness among combined European endemic species followed a similar trend of positive correlation as the combined data for all species. Analyses lead to the observation that the most restricted species seem to be those that deviate most from the overall pattern of correlation with people.

Taken together, these results can lead to at least two opposing interpretations. One is that the observed congruence between patterns of human density and biodiversity may be accidental. In other words it may be related to unmeasured factors, which may not interact with people and biodiversity in the same way across the planet. Thus, it would be unsurprising if analysis of correlation between human population density and species richness gave inconsistent results with different data (e.g. such as that observed for birds and narrow endemics in Europe and Africa). However, this is perhaps too simplistic. The similarities between the results obtained for the African and European studies support the possibility that mechanisms causing an area to be suitable for people might

indeed be coincident to those causing an area to be suitable for large numbers of extant species, or, alternatively, that some kinds of human actions might contribute to boost total numbers of species per unit area (e.g. due to landscape heterogeneity) (for discussion see Blondel & Aronson, 1999). An interesting feature of both the African and European studies is that scatter diagrams depicting the relationship between human density and species richness report top scores for species richness at intermediate levels of human density and not in the areas with highest human densities (although it is also at intermediate human densities that species richness scores are most variable, possibly confounding any clear statement about this relationship: see Fig. 1). This feature was even observed among those groups of species that showed no, or only weak correlation with human density (e.g. bird and endemic species richness in this study). This is consistent with the idea that highly urbanized areas, such as the conurbations of London and southern England, Paris and its surroundings, or the vast urbanized areas linking Brussels, Amsterdam and Berlin, are not particularly rich in biodiversity. Our maps in Fig. 2 confirm this suspicion, as all these areas show blue residuals (departures of people over biodiversity). Similar patterns are observed for the most industrialized areas of Italy, the north-west of Iberia and the Balkans. Nevertheless, areas with the highest human densities still have a generally greater numbers of species than do areas with very low human densities.

It is difficult to disentangle the causes and effects of such large-scale patterns, not least because many of the possible underlying mechanisms may be correlated among themselves (e.g. Loreau *et al.*, 2001). For example the diversity–disturbance hypothesis (for reviews see Huston, 1994; Rosenzweig, 1995) postulates the existence of a unimodal relationship between diversity and disturbance with highest diversities at intermediate levels of disturbance. Because human density can be seen as a large-scale surrogate for disturbance (e.g. Maurer, 1996; Thomson & Jones, 1999), we could associate the tendency for species richness to peak at intermediate levels of human density with such a line of argument. On the other hand, human density can also be related to human interference in the landscape and its associated spatial heterogeneity. Spatial heterogeneity can be seen as a form of disturbance, but also as a natural property of landscapes (e.g. in the mountains). In either case it is expected that areas of ecological transition or mosaics of different kinds of habitats will have a greater number of species than do more homogeneous areas (e.g. Araújo, 2002). In some cases these areas might coincide with intermediately high human densities (especially if heterogeneity is caused by people), while in others cases it might not (see green residuals, i.e. departures of biodiversity over people, in mountainous areas in Fig. 2). Nevertheless, with the European data used in this paper it would be difficult to make such assertions because of the high variability of richness scores, particularly at intermediate levels of human density (see Fig. 1).

Similar complications can be envisaged for the climate stability hypothesis (e.g. Fjelds  & Rahbek, 1998). This idea postulates that glacier refuges allowed humans and species to persist in the same areas and this could contribute to a contemporary coincidence between people and extant biodiversity. However, glacier refuges were located commonly alongside coastal areas, deep valleys and lowlands and these are often productive sites. Therefore, an alternative causal relationship between people-diversity and productivity could also be proposed (although a recent review on the productivity and species richness hypothesis has revealed too great a variation of response curves for anyone to foresee any clear relationship: see Waide *et al.*, 1999).

Whatever the mechanisms underlying the reported correlation between human density and extant species richness, this should always be contingent on historical patterns of species' persistence and extinction. For example, if persistence of species was favoured by climatic stability and people concentrated in such areas in the past, it is likely that this coincidence might have led to an intensification of conflicts and subsequent extinctions of the most intolerant species to humans. Therefore, once species were able to expand out of climatically stable areas only the more tolerant might have been there to do so. More generally, if we accept the idea that humans acted as major extinction filters (for review see Balmford, 1996), then we have to recognize that present-day biodiversity should be biased toward species that are generally more tolerant of humans. Hence, it would be unsurprising to find a correlation between people and extant biodiversity because species that were intolerant of humans are either extinct, or persist at low abundances in the most undisturbed areas. In the latter case their contribution to the overall pattern of correlation between people and biodiversity might be negligible. This could also partly explain the tendency of species richness to peak at intermediate levels of human density. At high levels of current pressure only few opportunistic species might survive (e.g. McKinney & Lockwood, 1999). At lower levels of pressure we might report low numbers of species because the most intolerant species might have gone extinct, or be reduced to few isolated spots. At intermediate levels of pressure we might have a confluence of species with different degrees of tolerance to pressure, i.e. those that are tolerant of humans and those that are relatively intolerant of present-day high levels of human pressure (e.g. species adapted to low-intensive farming practices), but less so than those already extinct or isolated in the most undisturbed mountainous areas (e.g. forest interior species). Similarly, if the relationship between human density and species richness was mainly determined by the landscape heterogeneity, we could envisage a situation where too much human activity could lead to a reduction in heterogeneity (e.g. cities), hence a decrease in the numbers of species.

One consequence of the correlation between people and species richness is that important areas for biodiversity con-

servation might coincide with areas of high human pressure. Empirical evidence partly supports this prediction. For example, Cincotta *et al.* (2000) brought to attention that 16 of the 25 global biodiversity hotspots, identified by Myers *et al.* (2000), had more people than the world average, although it could be argued that there is nonindependence in this coincidence as global biodiversity hotspots were also selected on the basis of their level of threat. Other studies do not have this problem. Balmford *et al.* (2000a) showed that 110 of 235 areas needed to represent all species of African terrestrial vertebrates belong to the 25% most densely populated areas in sub-Saharan Africa. Ara jo *et al.* (2002) found that complementarity hotspots for terrestrial vertebrates in Europe had more people living within than expected by chance ($P < 0.05$). However, they also found that constraining selection of areas to top quality habitats within every species' range would reduce the total number of people within selected areas. That is, although Ara jo *et al.* (2002) noted a positive relationship between the location of biodiversity hotspots and human density, they also found that species had generally better conditions for persistence away from highly populated areas. Therefore, if the goal of a reserve network is to ensure local persistence of species – rather than to obtain blind representation of as many species as possible – then there might be opportunities to conserve them away from some of the most populated areas. Downscaling the analysis from a coarse scale to the local scale, and from multiple species to individual species, might provide us with further insights on the relationship between people, biodiversity and priority areas for conservation.

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BIOSKETCH

Miguel Araújo has a PhD from the University of London. His research focuses on the development of quantitative methods to select conservation areas that are more robust to local extinctions of species. An important part of his work also includes analysis of coarse-scale patterns and processes affecting occurrence and persistence of biodiversity at different temporal scales.