

# Discerning the impact of human-mediated factors on biodiversity using bioclimatic envelope models and partial regression techniques

Noelia Zafra-Calvo<sup>1</sup>, Miguel Á. Rodríguez<sup>1</sup> and Jorge M. Lobo<sup>2\*</sup>

<sup>1</sup>Departamento De Ecología, Facultad de Biología, Universidad de Alcalá, 28871 Alcalá de Henares, Madrid, Spain, <sup>2</sup>Dpto. de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006. Madrid, Spain

## ABSTRACT

**Aim** Human-related pressures are growing in species-rich regions and pose a threat to the conservation of biodiversity. Here, we use the available data for five taxonomic groups (ferns, monocotyledons, dicotyledons, birds and monkeys) to exemplify a procedure directed to discriminate the degree of conflict between human actions and biodiversity.

**Location** Bioko island, Equatorial Guinea.

**Methods** Using bioclimatic envelope modelling techniques devoted to produce estimations of the potential distributions, we generated geographical representations of the variation in the total number of species as well as in the number of endemic and threatened species. We then employed partial regression techniques to determine how and to what extent current environmental, habitat and human-derived variables are associated with these potential species richness values.

**Results** Although the type of associations we looked for was sometimes difficult to discern since the same patterns could be explained by different types of variables, our results show that potential species richness values are generally positively associated with human-related factors (mainly agriculture and bushmeat hunting activities), suggesting that the localities with environmental conditions favourable to higher species richness tend to be those exploited by humans.

**Main conclusions** We propose that the combined use of distribution models and partial regression techniques can support a better understanding of the relationship between species occurrences/preferences and human-related factors and inform future conservation initiatives, particularly in small but hyperdiverse territories, in which dispersal limitations do not play a prominent role.

## Keywords:

Bioclimatic envelope modelling, Bioko island, Equatorial Guinea, human–biodiversity relationships, partial regressions.

\*Correspondence: Jorge Miguel Lobo, Dpto. de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006. Madrid, Spain. E-mail: mcnj117@mncn.csic.es

## INTRODUCTION

One of the most important problems facing conservation biology today is the increase in human-induced pressures on ecosystems across the world, particularly in hotspots of biodiversity. Although biodiversity and human populations

are frequently positively correlated at regional scales (Balmford *et al.*, 2001; Araújo, 2003; Luck *et al.*, 2004; Evans *et al.*, 2006; Vázquez & Gaston, 2006; Luck, 2007), the occurrence of a species generally declines when human activities increase at a local scale (Brashares *et al.*, 2001; Koh *et al.*, 2006; Pautasso, 2007). Human alteration of habitats for agriculture

(Vitousek *et al.*, 1997), increases in human population density (Cincotta *et al.*, 2000; McKee *et al.*, 2003), building of infrastructure (Burgess *et al.*, 2007) and bushmeat hunting (Wilkie & Carpenter, 1999; Fa *et al.*, 2003) are all serious threats for biodiversity. Therefore, more effort needs to be put towards understanding the association between human-related variables and biodiversity and to incorporate this knowledge into conservation planning, particularly at local scales, since it is at these fine-grained levels where most practical management actions take place (Chown *et al.*, 2003; O'Connor *et al.*, 2003; Rouget *et al.*, 2003).

Data on species distributions are usually incomplete and biased towards particular species groups and ecosystems in almost any country, but especially in developing regions, where species inventories often remain largely incomplete even for the most commonly studied groups (Hortal & Lobo, 2005, 2006; Hortal *et al.*, 2007). Under such circumstances, however, biodiversity patterns can be approached using niche-modelling techniques that give quick estimations of the potential distribution of species. The potential distribution of a species can be considered the set of localities with favourable environmental conditions, in which a species can maintain a net positive rate of population increase without immigration (Guisan & Zimmerman, 2000; Soberón & Peterson, 2005; Soberón, 2007; Jiménez-Valverde *et al.*, 2008) and might be used for conservation-related purposes (e.g. see Bini *et al.*, 2006 and references therein). A possible utility of these techniques, yet unexplored, is their capacity to help unveiling potential conflicts between biodiversity and human activities. Specifically, we notice that if these modelling techniques are applied using non-anthropogenic environmental variables (e.g. climate variables), then the resulting species' ranges as well as their overlap will reflect a potential without-human influence scenario, which in turn may serve to evaluate to what extent the areas that are best suited environmentally for higher species richness coincide with existing human activities.

In the present study, we exemplify this idea for the case of the Equatoguinean island of Bioko, a recognized African hotspot of biodiversity (Myers *et al.*, 2000; Burgess *et al.*, 2006) for which a large database of plant and vertebrate species inventory records was compiled in a previous study to generate bioclimatically based potential richness values for a range of species groups. Here, we apply regression diagnostic techniques on these predicted richness patterns to explore their relationships with human factors that are expected to affect biodiversity negatively; namely, roads/tracks, population density, agriculture and bushmeat hunting (see earlier and Juste & Fa, 1994; Wilkie & Carpenter, 1999; Fa *et al.*, 2005). We assume that the degree of conflict between biodiversity and human actions can be indicated by the strength and sign of these relationships, with potentially high conflict levels being reflected by positive and significant relationships (i.e. environmentally suitable areas for most species tend to coincide with those used by humans), and low levels by negative, null or reduced relationships. We conclude that these kinds of results

may serve to identify future management actions and conservation priorities.

## METHODS

### Study area

Located in the Gulf of Guinea 32 km from the coast of Cameroon, the Equatorial Guinean island of Bioko (3°48' N–8°27' E) has an area of 2019 km<sup>2</sup>. The origin of this island is volcanic, with three volcanoes ranging from 2009 m to 3011 m in altitude. The climate is typically equatorial, with a dry season from November to March and a rainy season from April to October. However, the rugged topography of Bioko creates large climatic differences in temperature and precipitation across the island. The mean annual temperature varies between 27°C in the north coast and 12°C on the highest peak of the island, while precipitation ranges from 1557 mm per year on the north part of the island to 10934 mm per year in the south (Nosti, 1942).

The vegetation, made up of an estimated 6000 plant species (M. Velayos personal communication), includes coastal plant formations, lowland rainforest (up to an elevation of 800 m) which alternates with monsoon forest in the south (up to 1000 m), montane rainforest (from 800 to 1800 m), mossy forest (from 1800 to 2500 m) and high elevation shrubs alternating with subalpine meadows at the top of the volcanoes. Human activities have caused noticeable changes in these natural communities, the most important being the replacement of most lowland rainforest (formerly representing almost half of the natural vegetation of the island) with cocoa plantations (*Theobroma cacao*) at the end of the 19th century (Nosti, 1948; Terán, 1962; Juste & Fa, 1994). There were also some oil palm (*Elaeis guineensis*) and abaca (*Musa textilis*) plantations, but these covered much less area. Today, almost all of the plantations are abandoned and appear to be covered by secondary forest. In addition to this agricultural transformation affecting lowland rainforests, humans have also cleared a small area of montane and mossy forest for grassland to promote cattle grazing (Ocaña García, 1962); an activity that has also nearly ceased even though the grassland area persists.

The fauna of the island is characterized by a richness of animal species as well as a high degree of endemism. The faunal richness has been estimated to include 33 amphibian species and 50 reptile species (Jones, 1994), 191 bird species (Pérez del Val, 1996) and 65 mammal species, including 26 bats (Juste & Ibáñez, 1994) and seven monkeys (Butynski & Koster, 1994; González Kirchner, 1994). One of the most alarming human impacts is the hunting of terrestrial wild mammals. The current absence of livestock on the island has forced the human population to turn to bushmeat for consumption and trade. This is having dramatic consequences on Bioko (Fa *et al.*, 1995, 2000; Albrechtsen *et al.*, 2007) where a number of prey populations have already gone extinct because of overexploitation (Castroviejo *et al.*, 1994).

## Data origin

Plant data came from the 'Flora de Guinea Equatorial' database (available at <http://www.floradeguinea.com>; accessed October 2008) which includes distributional data for 1138 plant species, including 62 ferns (158 database records), 327 monocotyledons (715 database records) and 749 dicotyledons (1818 database records). Bird data were comprised of 104 island resident species (708 database records) studied by Pérez del Val (1996) between 1988 and 1992. Data on the seven species of monkey that are present on the island (73 database records) were collected by Butynski & Koster (1994) between 1986 and 1990. Endemic and threatened taxa were specifically considered. Fourteen species of plants and 33 species of birds have been categorized as island endemics (Fa, 1992; Figueiredo, 1994; Jones, 1994; Pérez del Val *et al.*, 1994; Pérez del Val, 1996). Five of the seven species of monkey inhabiting Bioko are considered endemic subspecies (Butynski & Koster, 1994; González Kirchner, 1994; Jones, 1994). For threatened species, we included all the species belonging to the four categories of the IUCN Red List (2006) that identify some degree of threat: near threatened, vulnerable, endangered and critically endangered. In total, 22 species of plants, two species of birds and five monkeys were considered threatened species. All the data were georeferenced at a UTM (Universal Transverse Mercator System) of 1 km<sup>2</sup>. The island comprises 2070 1 × 1 km UTM cells.

Three climatic variables (annual precipitation, maximum temperature of the warmest month and minimum temperature of the coldest month) were used for bioclimatic envelope modelling. These variables were chosen from an initial set of 21 variables including two topographic variables (elevation and slope) and the 19 bioclimatic variables of the WorldClim database (Hijmans *et al.*, 2005a). A Principal Component Analysis (PCA) with all these variables produced three axes

with eigenvalues higher than one and that jointly represented 92.5% of the total environmental variability. Each of these axes was characterized by one of the three climatic variables chosen attending to their respective factor loadings, for which these variables were retained as the ones most representative of the island climate.

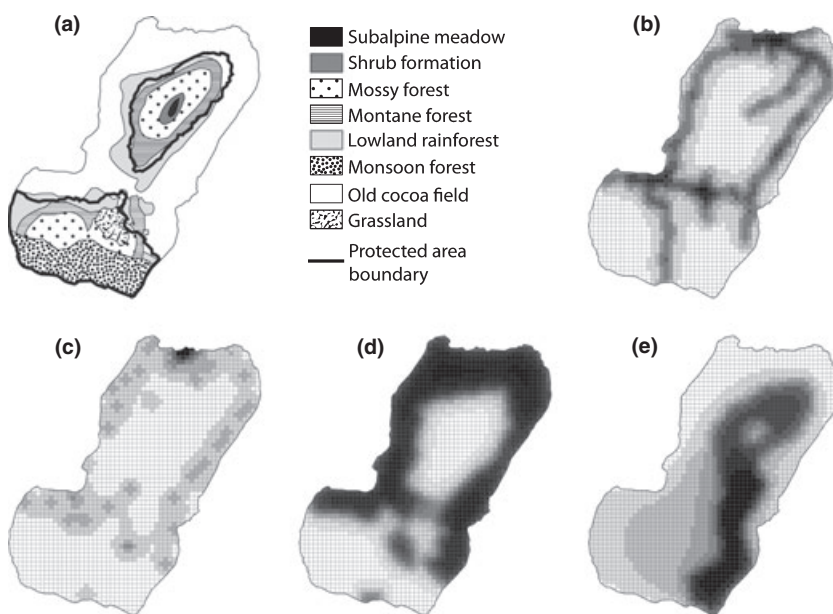
The habitat variables came from Pigeonniere (2001) which differentiates eight habitat types: subalpine meadows (6 km<sup>2</sup>), shrub formations (18 km<sup>2</sup>), mossy forests (249 km<sup>2</sup>), montane rainforests (178 km<sup>2</sup>), lowland rainforests (268 km<sup>2</sup>), monsoon forest (244 km<sup>2</sup>), secondary forests occupying abandoned cocoa plantations (926 km<sup>2</sup>) and grasslands for cattle grazing (49 km<sup>2</sup>). These habitat types were considered as binomial (1/0) habitat variables (see Fig. 1).

Human-related variables reflect the population density and presence of roads/tracks, agriculture and bushmeat hunting in each cell. All roads and main tracks on the island were digitized from Pigeonniere (2001), and the map of the Servicio Geográfico del Ejército Español carried out in 1979, and the cells overlapping them were identified. We then generated interpolated values ( $V$ ) of road/track influence for each cell  $i$  using the following formula:

$$V_i = \sum_{j=1}^n C_j / D_{ij}^2 \quad (1)$$

where  $C$  reflects whether cell  $j$  does (1) or does not (0) overlap with a road/track,  $D_{ij}^2$  is the squared Euclidean distance value [obtained with horizontal (X and Y) coordinates and elevation (vertical) differences expressed in kilometres] between cells  $i$  and  $j$ , and  $n$  represents the number of 1 × 1 km cells in our database (2070).

Geographical locations and raw numbers of inhabitants were obtained from Pigeonniere (2001) for cities and large towns. The map of the Servicio Geográfico del Ejército Español (1979) was used for small villages, and the report entitled 'The



**Figure 1** Habitat types and proposed protected areas in the Bioko Island (a), and human-related variables: proximity to roads (b), population density (c), area with agricultural and cattle grass land (d) and hunting (e), ranging from black (higher values) to white (lower values).

Economics of the Primate Trade in Bioko, Equatorial Guinea' (Reid *et al.*, 2003) was used for hunting camps. As the area of each small village and hunting camp was smaller than one cell (1 km<sup>2</sup>), we assigned their corresponding inhabitant numbers to the cells that overlapped them most. For cities and large towns, the number of inhabitants was divided by the number of overlapping cells, and that number was assigned to every city cell. We then generated interpolated values of population influence for all cells using Equation 1, in which the  $C_j$  value corresponding to each cell became the number of assigned inhabitants (see Fig. 1).

Reid *et al.* (2003) also provide a map dividing the island into four quadrants of different bushmeat hunting intensity (expressed for each quadrant as the number of animals that have been hunted in it). We first assigned each of these values to the cells overlapping each quadrant (divided in each case by the number of cells comprising the quadrant), but then we generated a continuous variable of bushmeat hunting influence by interpolating these values across all cells using Equation 1 (with the  $C_j$  of each cell now reflecting its assigned hunting intensity).

To take agricultural effects on species richness into account, we first used Pigeonniere (2001) data to identify all cells that have ever been devoted to agriculture or cattle grasslands. We then generated interpolated values of agricultural influence for all cells using Equation 1, so that agricultural/grassland cells entered into the formula with a  $C_j$  value of 1, while the rest of the cells entered in with a  $C_j$  value of 0.

## Data analysis

The potential distribution of all species on the island was estimated using the presence data of each species, the three climatic variables that we had selected as representative of the main climatic trends on the island (see earlier) and a simple bioclimatic envelope technique that linked all the 1 × 1 km cells with similar climatic conditions to the observed presences (see Busby, 1986; Nix, 1986; Beaumont *et al.*, 2005). We used Diva GIS 5.2. (Hijmans *et al.*, 2005b) to identify all the cells whose climatic conditions were within the range of those in which the species was observed (the species' predicted potential distribution). Bioclimatic envelope models such as the one we employed tend to over-predict 'real' species distributions, because reliable absences and forces restricting distribution are not considered in the modelling process (Chefaoui & Lobo, 2008). Thus, the output provided by this simple procedure can be considered a representation of the potential distribution of species in the absence of dispersal limitations (Jiménez-Valverde *et al.*, 2008). All the potential distributions were overlapped to generate predicted potential species richness representations for each group as well as for endemic and threatened species.

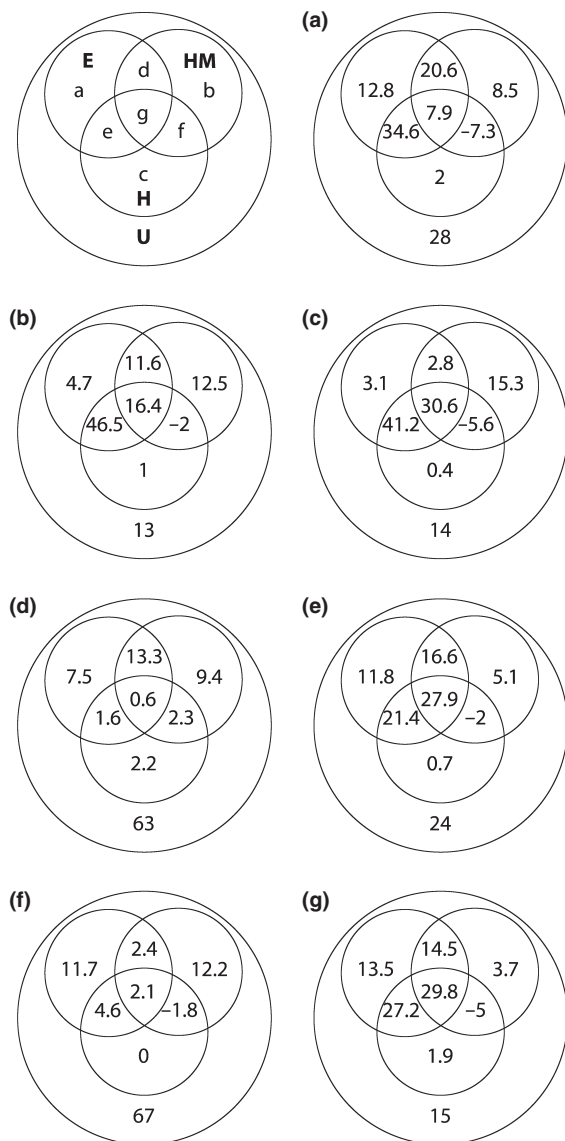
Partial regression analysis was used to estimate the single and shared variability accounted for by the three groups of explanatory variables; i.e. environmental (E), human (HM)

and habitat (H) related variables. This regression diagnostics procedure facilitates exploring the relevance of different factors in determining species richness patterns by quantifying how much of the species richness variation can be unequivocally attributed to a group of predictor variables (single effects), and how much is indistinguishable between two and three groups of variables (shared effects; see Borcard *et al.*, 1992; Legendre & Legendre, 1998; Lobo *et al.*, 2002). These analyses were carried out using Generalized Linear Models (GLMs; McCullagh & Nelder, 1989) assuming a Poisson error distribution for the dependent variable and a logarithmic link function. Variation of species richness estimates with continuous explanatory variables (i.e. those comprising the E and HM sets in our case) are often curvilinear. Accordingly, we examined the nature of relationships between our species richness variables and each of our predictors by introducing linear, quadratic and cubic functions in the multiple regression models and then retaining the function in which all of the terms are statistically significant ( $P < 0.05$ ). Thus, we calculated the percentages of unexplained (U) and explained variation of the species richness variables with eight different combinations of the E, HM and H predictors: single effects of either environmental variation alone (i), human variables alone (ii), or habitat variables alone (iii), and variability explained by joined effects of either environment and human components (iv), environmental and habitat components (v), human and habitat components (vi) or the three components together (vii). Further details on this analysis can be seen in Qinghong & Bråkenhielm (1995) and Anderson & Gribble (1998).

Finally, we estimated the variability accounted for by the four human variables as well as their respective individual effects. For this, each species richness variable was first regressed against environmental and habitat variables with the residuals retained as the variability not accounted for these types of predictors. These residuals were then regressed against the four human-related variables to estimate their individual effects. All statistical analyses were carried out using the Statistica 6.0. (Statsoft Inc, 2003).

## RESULTS

Multiple regression models accounted for >70% of the deviance in our potential species richness variables except for birds (37%) and endemic species (33%). A large amount of the explained variability can be attributed to a single predictor from the three sets of analysed predictors (E, H or HM) for dicotyledons, monkeys and threatened species (see Fig. 2). Habitat distribution is expected to depend strongly on climatic gradients, so it is not surprising that habitat characteristics and environmental variables (mostly reflecting climatic variation) jointly explained a great deal of the deviance of potential species richness values for the three plant groups (ferns: 35%; monocotyledons: 46% and dicotyledons: 41%), monkeys (21%) and threatened species (27%). In addition, relatively large fractions of total deviance were also explained by the combined effects of human and



**Figure 2** Diagram showing the variation in the dependent variable (potential species richness) due to three groups of explanatory variables: E (environmental), HM (human) and H (habitat). Letters *a*, *b* and *c* are the single effects of environmental, human and habitat variables, respectively; while *d*, *e* and *f* are the shared variability accounted for by the joint effect of environmental and human variables, the joint effect of environmental and habitat variables, and the joint effect of habitat and human-related variables, respectively; *g* is the combined variation due to the joint effect of all three types variables, and *U* is the unexplained variation. We carried out a variation partitioning procedure for the number of ferns (a), monocotyledons (b), dicotyledons (c), birds (d), monkeys (e), endemic (f) and threatened species (g) between the three sets of explanatory variables. The decomposition of the variation has been carried out using a partial regression analysis utilizing generalized linear models and the percentage of total explained deviance as the measure of explained variability.

environmental factors for the richness of ferns (21%), monkeys (17%), threatened species (15%), birds (13%) and monocotyledons (11%).

With regard to the variation that can be attributed simultaneously to habitat and human-related variables, it is interesting to note that, in spite of being relatively low in general, it was negative in all cases except for birds. These negative values suggest that the joint effects of habitat and human factors on richness are higher than the sum of their individual effects (Legendre & Legendre, 1998). The effects of each group of predictors independent from the effects of other groups were low ( $\leq 15.3\%$ ), especially in the case of habitat factors ( $\leq 2.2\%$ ). It should be noted that the highest single effects of human factors are those affecting dicotyledons, monocotyledons, birds and endemic species. In the remaining groups (ferns, monkeys and threatened species), most of the variation explained by human factors is indistinguishable from that accounted for by climatic and habitat variables.

Table 1 shows the degree of association of species richness values (expressed as a percentage of described deviance) with each human factor as well as the amount of association independent from environmental and habitat effects (described deviances represented in parentheses). With regard to the relevance of human factors independent of environmental and habitat effects, it is worth noting that neither factor had strong independent effects on any species richness variable (all described deviances  $< 8\%$ ). On the other hand, agricultural transformation of land (mostly consisting of abandoned cocoa plantations evolving into secondary forests) was positively correlated and of great importance, especially for the potential richness of monocotyledons, dicotyledons, monkeys and threatened species (all described deviances  $\geq 29\%$ ). For monkeys and threatened species, most of the effect associated with agricultural transformation of land was shared with the effects caused by other variables.

Bushmeat hunting variable was important and positively related with the richness of monkeys (27%) and threatened species (30%), although the effect independent of other variables did not exceed 3%. In addition, proximity to roads and human population densities was moderately associated (10–17%) with the potential richness of dicotyledons (a predominantly positive relationship) and those of monkeys and threatened species (predominantly negative relationships). Finally, in contrast to what was observed for the other species groups, this analysis also indicated that the potential richness values for birds and endemic species were weakly associated with human predictors (all described deviances  $\leq 11.2\%$  with very few single explanatory capacities). Bearing in mind that most island endemics were birds, these results suggest that bird species are less sensitive to human activities.

## DISCUSSION

Using predicted potential species richness values obtained by applying bioclimatic envelope modelling techniques, we investigated how environmental factors, habitat characteristics and human influences relate to the potential richness patterns of three plant groups (ferns, monocotyledons and dicotyledons), birds, monkeys, and endemic and threatened species.

**Table 1** Percentage of deviance explained by the four considered human variables on the variation in potential richness of the different species groups and estimations of the single effects of these variables (in parentheses) by a partial regression analysis (see Legendre & Legendre, 1998). Potential species richness values were regressed against environmental predictors and habitat variables, retaining the residuals as the variability not accounted for by these types of predictors. These residuals were subsequently regressed against the four human-related variables to estimate single effects. Quadratic and cubic terms of each variable were included in the models when they accounted for a significant change in the amount of explained deviance ( $P < 0.05$ ). The sign columns indicate the signs of the terms included in each model.

Species group	Proximity to roads		Population density		Agricultural land		Hunting	
Ferns	2.2 (1.1)	+ -	3.8 (0.7)	+ -	16.3 (3.4)	+ - +	16.1 (1.4)	+ - +
Monocotyledons	4.3 (1.3)	+ - +	6.0 (1.2)	+ -	29.0 (6.4)	+ - +	5.3 (4.5)	+ - +
Dicotyledons	13.2 (1.2)	- + -	14.8 (1.3)	+ -	42.3 (7.9)	+ - +	4.7 (1.8)	+ - +
Birds	1.0 (0.0)	+	4.5 (0.0)	-	11.2 (0.0)	+	6.7 (0.0)	+ -
Monkeys	15.5 (1.0)	-	16.0 (0.2)	-	40.9 (1.0)	- +	26.6 (2.3)	+ - +
Endemism	0.9 (0.8)	+	3.3 (0.0)	-	9.9 (7.0)	+	4 (2.5)	+ -
Threatened species	10.3 (1.0)	- + -	16.8 (0.5)	+ -	36.1 (1.2)	- +	29.9 (2.7)	+ - +

Through partial regression analyses, we found that environmental factors, chiefly reflecting gradients of temperature, precipitation and primary productivity, drive the spatial variation of potential richness both directly and/or indirectly through their effects on habitat distributions. On average, habitat and environmental variables are able to explain around 36% of potential species richness variability, depending on the group (from 53% to 11%). These results are not unexpected, because potential species' ranges used to generate species richness values have clear climatic limits and the influence of contingent factors such as dispersal limitations of biotic interactions on species distributions are minimized. These results are also consistent with what can be expected regarding the ecological processes that likely drive species richness patterns on an equatorial island like Bioko. The rugged topography of this island is likely to create steep gradients of climate and primary productivity across it thereby creating strong habitat zonation and mesoclimatically driven local diversity gradients (Janzen, 1967; Ghalambor *et al.*, 2006).

The main challenge of this study was not estimating the degree of association between climate or environmental variables and species richness but examining the coincidence of potential species richness patterns with human variables that reflect the use and transformation of the territory. Our results show that human variables tend to have a high single explanatory capacity (around 10%); 71% of the relationships between human variables and potential species richness are positive, and the eight regression analyses able to account for more than 2% of variability are also positive (see Table 1). Thus, current human uses seem to be located in areas with high potential species richness values, suggesting the existence of a conflict between biodiversity and human actions. Although this does not take place across the entire island, our results show, as expected, that human populations frequently appear in those localities where the climatic conditions would permit high levels of biodiversity (Pautasso, 2007).

For the specific case of the Bioko island, agriculture seems to be the main human factor positively correlated with the

potential species richness patterns in all groups (especially for monocotyledons, dicotyledons, monkeys and threatened species). These relationships imply that the localities with environmental conditions favourable to harbouring higher numbers of species tend to be those that have been devoted to agricultural activities (i.e. agricultural alterations have taken place in potentially species-rich areas). Thus, agriculture could be the principal human agent affecting the species richness patterns of plants on the island (Juste & Fa, 1994). Interestingly, it should be noted that the variable we call 'agriculture' mainly consists of secondary forests that were abandoned after the Equatorial Guinea gained its independence in 1968. Thus, it is possible that the abandonment of agriculture is actually promoting biodiversity in the island because of the re-colonization of species at these environmentally favourable places (Zapfack *et al.*, 2002; Bobo *et al.*, 2006).

Our results also showed that bird potential richness patterns were the least associated with human variables, suggesting that there is no conflict between birds and humans due probably to their greater mobility (Thiollay, 1999; Daily *et al.*, 2001; Fairbanks, 2004). While the agricultural transformation of lowland rainforests on Bioko was considerable, it was not complete. Nearly 25% of the area originally covered by lowland forests (about 268 km<sup>2</sup>, see Fig. 1) remains unaffected by agriculture. The greater mobility of birds coupled with the persistence of original lowland rainforests and other unaffected habitats on the island may explain why the richness of this group appears to be less sensitive to the anthropogenic influences analysed in this study.

On the contrary, for monkeys and threatened species, the proximity to roads and human population density had noticeable and predominantly negative effects on potential species richness (see Table 1). This suggests that roads as well as densely populated areas do not occur where the best conditions for monkeys and threatened species are, indicating a low level of conflict with human actions in these cases. On the other hand, agriculture (firstly) and bushmeat hunting (secondarily) were the most important predictors of the

potential richness of these two species groups, both showing a positive relationship. This indicates that the areas best environmentally suited to harbour more species of both groups are also areas that have been selected for agriculture and bushmeat hunting activities. Again, the abandonment of agriculture could have increased the distribution range of these species. With regard to the bushmeat hunting, there is a great deal of evidence showing that it is a major threat for the fauna inhabiting the Congo River Basin (Wilkie & Carpenter, 1999; Fa *et al.*, 2005), particularly the fauna of Bioko (Fa *et al.*, 1995, 2000; Albrechtsen *et al.*, 2007). Bearing this in mind, a sensible interpretation of our results is that bushmeat hunting tends to take place where faunal communities happen to be rich in monkeys and threatened species. Because of this, these areas may have suffered a loss of their rich assemblages, because hunters tend to focus their energies on places that are rich in the prey species they want to capture. Thus, our results can be taken as additional evidence that hunting is a major threat for the biodiversity of this island.

Our results constitute the first attempt to examine the coincidence between human activities and biodiversity in a territory with scarce taxonomical and distributional information by using potential distribution simulations and partial regression analysis. However, the frequent bias in the available distributional information (Freitag *et al.*, 1998; Hortal *et al.*, 2007) can influence the obtained results of this and other similar analyses. Survey biases may affect the detected relationship between potential species distributions and human-related factors when: (i) there is a survey bias towards areas under human use, (ii) the climatic conditions in these anthropogenically transformed localities are different from those prevailing in the remaining territory, and/or (iii) the species detected in these more surveyed but anthropogenically transformed localities are not in fact adapted to these specific climatic conditions. In our case, Spearman rank correlations ( $r_s$ ) showed that the number of observations available in each cell increased weakly, but significantly along with three of the anthropic variables we analysed: proximity to roads, population density and area with agricultural and cattle grass land ( $r_s \leq 0.30$ ,  $P < 0.001$  in all cases). These anthropic variables were also correlated negatively with annual precipitation ( $r_s \leq -0.53$ ,  $P < 0.001$  in all cases) and positively with temperature of the warmest month ( $r_s \geq 0.25$ ,  $P < 0.001$ ) and minimum temperature of the coldest month ( $r_s \geq 0.24$ ,  $P < 0.001$ ). This indicates that anthropogenically transformed localities experiencing warmer and drier conditions may have had more survey effort. Hence, model predictions from those species with few data coming from these localities will have a limited potential distribution, thus inflating the spatial coincidence between species richness and human actions. However, these species may be also adapted to the specific climatic conditions prevailing in these anthropogenically transformed localities. Is the well-known positive correlation between humans and species richness an artefact because of the higher survey effort existent around such areas or is it the consequence of

the increase in productivity because of human actions and/or the coincidence in the climatic requirements between humans and biodiversity? This is a question subjected to an open debate (Pautasso & McKinney, 2007) that may only be solved by carrying new surveys.

The proposed procedure has been possible by the joint use of a technique devoted to identify the single explanatory capacity of correlated variables and distribution models that are able of approximating the potential distribution of species in scarcely surveyed areas. However, potential distributions may only be partially approached by using actual distributional data and cannot be strictly validated except by using physiological data or other information able to reflect the species' niches (Jiménez-Valverde *et al.*, 2008; Colwell & Rangel, 2009; Soberón & Nakamura, 2009). Our approach is thus especially appropriate for those territories in which dispersal limitations have had a smaller role in shaping current biodiversity patterns (e.g. hyperdiverse and small regions with a low level of taxonomic effort). The application of this procedure to the Bioko Island suggests that the relationship among human actions and biodiversity is conflicting (Evans *et al.*, 2006). As humans tend to select those localities with the most favourable environmental conditions to harbour a higher number of species, our results suggest that the conservation of biodiversity requires active designs able to promote the sustainable use of the territory.

## ACKNOWLEDGEMENTS

We thank Luis Cayuela, Mauricio Velayos and Jaime Pérez del Val for their valuable suggestions and comments, and Miguel Á. Olalla-Tárraga and Fabio S. de Albuquerque for technical assistance. N.Z.-C. thanks the Spanish Agency for Development and Cooperation (AECID) for its financial support through a MAE/AECI Grant. Work by M. Á. R. was supported by the Spanish Ministry of Science and Innovation (grant CGL2006-03000/BOS). An anonymous referee and Mark Robertson provided helpful comments and suggestions for the improvement of this manuscript.

## REFERENCES

- Albrechtsen, L., McDonald, D.W., Johnson, P.J., Castelo, R. & Fa, J.E. (2007) Faunal loss from bushmeat hunting: empirical evidence and policy implications in Bioko Island. *Environmental Science & Policy*, **19**, 654–667.
- Anderson, M.J. & Gribble, N.A. (1998) Partitioning the variation among spatial, temporal and environmental components in a multivariate dataset. *Australian Journal of Ecology*, **23**, 158–167.
- Araújo, M.B. (2003) The coincidence of people and biodiversity in Europe. *Global Ecology and Biogeography*, **12**, 5–12.
- Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P. & Rahbek, C. (2001) Conservation conflicts across Africa. *Science*, **291**, 2616–2219.

- Beaumont, L., Hughes, L. & Poulsen, M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling*, **186**, 250–269.
- Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Pereira Bastos, R. & Plaza Pinto, M. (2006) Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. *Diversity and Distributions*, **12**, 475–482.
- Bobo, K., Waltert, M., Sainge, N., Njokagbor, J., Fermon, H. & Mühlberg, M. (2006) From forest to farmland: species richness patterns of trees and understorey plants along a gradient of forest conversion in Southwestern Cameroon. *Biodiversity and Conservation*, **15**, 4097–4117.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- Brashares, J.S., Arcese, P. & Sam, M.K. (2001) Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 2473–2478.
- Burgess, N., Hales, J.D., Ricketts, T.H. & Dinerstein, E. (2006) Factoring species, non species values and threats into biodiversity prioritisation across the ecoregions of Africa and its islands. *Biological Conservation*, **127**, 383–401.
- Burgess, N.D., Balmford, A., Cordeiro, N.J., Fjeldså, J., Küper, W., Rahbek, C., Sanderson, C.W., Scharlemann, J.P.W., Henning-Sommer, J. & Williams, P.H. (2007) Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation*, **134**, 164–177.
- Busby, J.R. (1986) A biogeoclimatic analysis of *Nothofagus cunninghamii* in southeastern Australia. *Australian Journal of Ecology*, **11**, 1–7.
- Butynski, T. & Koster, S. (1994) Distribution and conservation status of primates in Bioko Island, Equatorial Guinea. *Biodiversity and Conservation*, **3**, 893–909.
- Castroviejo, J., Juste, J., Castelo, R. & Pérez del Val, J. (1994) The Spanish cooperation programme in Equatorial Guinea: a ten-year review of research and nature conservation in Bioko. *Biodiversity and Conservation*, **3**, 951–961.
- Chefaoui, R.M. & Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling*, **210**, 478–486.
- Chown, S.L., van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & van Jaarsveld, A.S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications*, **13**, 1233–1241.
- Cincotta, R.P., Wisniewski, J. & Engelman, R. (2000) Human population in the biodiversity hotspots. *Nature*, **404**, 990–992.
- Colwell, R.K. & Rangel, T.F. (2009) Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19651–19658.
- Daily, G.C., Ehrlich, P.R. & Sánchez-Azofeifa, G.A. (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications*, **11**, 1–13.
- Evans, K.L., van Rensburg, B.J., Gaston, K.J. & Chown, S.L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography*, **15**, 625–636.
- Fa, J.E. (1992) *Conservación de los Ecosistemas Forestales de Guinea Ecuatorial*. IUCN Gland and Cambridge, UK.
- Fa, J.E., Juste, J., Pérez Del Val, J. & Castroviejo, J. (1995) Impact of market hunting on mammalian species in Equatorial Guinea. *Conservation Biology*, **9**, 1107–1115.
- Fa, J.E., García Yuste, J. & Castelo, R. (2000) Bushmeat markets on Bioko Island as a measure of hunting pressure. *Conservation Biology*, **14**, 1602–1613.
- Fa, J.E., Currie, D. & Meeuwig, J. (2003) Bushmeat and food security in the Congo Basin: linkages between wildlife and people's future. *Environmental Conservation*, **30**, 71–78.
- Fa, J.E., Ryan, S.F. & Bell, D.J. (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afro-tropical forests. *Biological Conservation*, **121**, 167–176.
- Fairbanks, D.H.K. (2004) Regional land-use impacts affecting avian richness patterns in Southern Africa—insights from historical avian atlas data. *Agriculture, Ecosystems & Environment*, **101**, 269–288.
- Figueiredo, E. (1994) Diversity and endemism of angiosperms in the Gulf of Guinea islands. *Biodiversity and Conservation*, **3**, 785–793.
- Freitag, S., Hobson, C., Biggs, H.C. & van Jaarsveld, A.S. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Animal Conservation*, **1**, 119–127.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46**, 5–17.
- González Kirchner, J.P. (1994) *Ecología y conservación de los primates de Guinea Ecuatorial*. Ceiba Ediciones, Cantabria, Spain.
- Guisan, A. & Zimmerman, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005a) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hijmans, R.J., Guarino, L., Bussink, C., Mathur, P., Cruz, M., Barrientes, I. & Rojas, E. (2005b) *DIVA-GIS Version 5.2*. A geographic information system for the analysis of biodiversity data. User Manual freely available at <http://www.DIVA-GIS.org>.
- Hortal, J. & Lobo, J.M. (2005) An ED-based protocol for optimal 499 sampling of biodiversity. *Biodiversity and Conservation*, **14**, 2913–2947.
- Hortal, J. & Lobo, J.M. (2006) A synecological framework for systematic conservation planning. *Biodiversity Informatics*, **3**, 14–45.



- Hortal, J., Lobo, J.M. & Jiménez-Valverde, A. (2007) Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology*, **21**, 853–863.
- IUCN (2006) 2006 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**, 233–249.
- Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, **14**, 885–890.
- Jones, P. (1994) Biodiversity in the Gulf of Guinea: an overview. *Biodiversity and Conservation*, **3**, 772–785.
- Juste, J. & Fa, J.E. (1994) Biodiversity conservation in the Gulf of Guinea islands: taking stock and preparing action. *Biodiversity and Conservation*, **3**, 759–777.
- Juste, J. & Ibáñez, C. (1994) Contribution to the knowledge of the bat fauna of Bioko island, Equatorial Guinea (Central Africa). *Zeitschrift Säugetierkunde*, **59**, 274–281.
- Koh, C.N., Lee, P.F. & Lin, R.S. (2006) Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Diversity and Distributions*, **12**, 546–554.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.
- Lobo, J.M., Lumaret, J.P. & Jay-Robert, P. (2002) Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. *Global Ecology and Biogeography*, **11**, 265–277.
- Luck, G.W. (2007) The relationships between net primary productivity, human population density and species conservation. *Journal of Biogeography*, **34**, 199–200.
- Luck, G.W., Ricketts, T.H., Daily, G.C. & Imhoff, M. (2004) Alleviating spatial conflict between people and biodiversity. *Proceedings of the National Academy of Sciences*, **101**, 182–186.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*. Chapman & Hall, London.
- McKee, J.K., Sciulli, P.W., Fooce, C.D. & Waite, T.A. (2003) Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, **115**, 161–164.
- 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.
- Nix, H.A. (1986) *A biogeographic analysis of Australian elapid snakes*. *Atlas of elapid snakes* (ed. by R. Longmore) pp. 4–15. Australian Government Publishing Service, Canberra.
- Nosti, J. (1942) *Climatología de los territorios españoles del Golfo de Guinea*. Instituto de Estudios Africanos, CSIC, Madrid.
- Nosti, J. (1948) *Agricultura de Guinea. Promesa de España*. Instituto de Estudios Africanos. CSIC, Madrid.
- Ocaña García, M. (1962) Factores que influncian la distribución de la vegetación en Fernando Poo. *Archivos del Instituto de Estudios Africanos*, **14**, 57–85.
- O'Connor, C., Marvier, M. & Kareiva, P. (2003) Biological vs. social, economic and political priority-setting in conservation. *Ecology Letters*, **6**, 706–711.
- Pautasso, M. (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology Letters*, **10**, 16–24.
- Pautasso, M. & McKinney, M.L. (2007) The botanist effect revisited: plant species richness, county area and human population size in the United States. *Conservation Biology*, **21**, 1333–1340.
- Pérez del Val, J. (1996) *Las aves de Bioko*. Edileasa, León, Spain.
- Pérez del Val, J., Fa, J.E., Castroviejo, J. & Purroy, F.J. (1994) Species richness and endemism of birds in Bioko. *Biodiversity and Conservation*, **3**, 868–892.
- Pigeonniere, A. (2001) *Atlas de Guinea Equatorial*. Les Editions J.A., Madrid.
- Qinghong, L. & Bråkenhielm, S. (1995) A statistical approach to decompose ecological variation. *Water, Air and Soil Pollution*, **85**, 1587–1592.
- Reid, J., Morra, W., Posa, C. & Fernandez, D. (2003) *The economics of the primate trade in Bioko, Equatorial Guinea*. Conservation Strategy Found. Arcata, CA.
- Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation*, **112**, 63–85.
- Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distribution of species. *Ecology Letters*, **10**, 1115–1123.
- Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19644–19650.
- Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1–10.
- Statsoft Inc (2003) STATISTICA version 6.0. (Data analysis software system). <http://www.statsoft.com>.
- Terán, M. (1962) *Síntesis geográfica de Fernando Poo*. Instituto de Estudios Africanos. CSIC, Madrid.
- Thiollay, J.M. (1999) Responses of an avian community to rain forest degradation. *Biodiversity and Conservation*, **8**, 513–534.
- Vázquez, L.B. & Gaston, K.J. (2006) People and mammals in Mexico: conservation. conflicts at a national scale. *Biodiversity and Conservation*, **15**, 2397–2414.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Wilkie, D.S. & Carpenter, J.F. (1999) Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodiversity and Conservation*, **8**, 927–955.

Zapfack, L., Engwald, S., Sonnke, B., Achoundong, G. & Madong, B.A. (2002) The impact of land conversion on plant biodiversity in the forest zone of Cameroon. *Biodiversity and Conservation*, **11**, 2047–2061.

## BIOSKETCHES

**Noelia Zafra-Calvo** recently finished her PhD thesis on the conservation of biodiversity in Equatorial Guinea. She is interested in the international cooperation with African countries as well in the training of local people in conservation management.

**Miguel Á. Rodríguez's** main interests include the study of factors and processes conditioning patterns of biodiversity at local, regional and global scales.

**Jorge M. Lobo** is interested in the patterns and processes of species distributions and in the management of biodiversity information.

---

Editor: Mark Robertson