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Prioritizing areas for conservation and vegetation restoration in post-agricultural landscapes: A Biosphere Reserve plan for Bioko, Equatorial Guinea

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ABSTRACT

Although the conversion of natural vegetation to agriculture threatens biodiversity, post-agricultural lands may provide an opportunity to preserve biodiversity if they are allowed to regenerate. We develop a framework for incorporating abandoned agricultural fields into the design of a Biosphere Reserve using former cocoa plantations on Bioko, Equatorial Guinea, as a case study. First, we used BIOCLIM to model the potential distribution of 62 ferns, 327 monocotyledons, 749 dicotyledons, seven primates, and 104 birds on Bioko. Next, we quantitatively assessed the representation of these distributions in conservation areas proposed by the Equatoguinean administration (hereafter "EPAs"). In addition, we used an area prioritization algorithm implemented in the ResNet software package to select an initial set of sites to serve as the Biosphere Reserve's core areas, that is, intact forest in Bioko's montane regions. Then, to augment the beta-diversity of the Reserve, we used the area prioritization algorithm to prioritize buffer zones in lowland sites including rainforest remnants and abandoned plantations that have partially regenerated to forest. We also compared the representation of biodiversity in the EPAs to its representation in Biosphere Reserves designed with ResNet. The representation of vegetation types and species in Reserves selected by ResNet that occupy 25% of the land on Bioko is equivalent to the representation achieved by the EPAs, which would cover 42% of Bioko. To conclude, we propose a conservation plan for Bioko.

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1. Introduction

The contraction of species' distributions due to anthropogenic land use change threatens biodiversity in many terrestrial hotspots of biodiversity (Fahrig, 2003; Myers et al., 2000). A consensus has emerged that the use of systematic conservation planning methods implemented in software tools provides numerous benefits over ad hoc planning approaches that are based primarily on expert opinion (Sarkar et al., 2006). Systematic conservation planning is particularly important in transformed landscapes with ongoing land conversion because, besides showing where conservation areas should be located, it can identify areas where natural vegetation should be restored (Fuller et al., 2006). Recent work has demonstrated the value of some transformed areas for conservation inso-

far as such areas maintain and increase the connectivity of a conservation area network (Fischer and Lindenmayer, 2006; Kupfer et al., 2006). Transformed areas may be particularly important when remnants of intact vegetation are small and spatially distant from each other (Rubinoff and Powell, 2004).

Bioko Island, Equatorial Guinea has been recognized as a priority area for biodiversity conservation at the regional and global scales (Burgess et al., 2005; Myers et al., 2000). However, despite its exceptional natural value, no effective conservation plan has been implemented to date. Since the early 1960s several conservation area networks have been proposed but have never been implemented on the ground (Castroviejo et al., 1994; Fa, 1992). Since Bioko is relatively small with a total area of only 2019 km^2, we wanted to design a conservation area network that would represent the island's biodiversity adequately without taking up too much land. At the start of the planning exercise, we hypothesized that UNESCO's Man and the Biosphere (MAB) strategy of implementing Biosphere Reserves might constitute an appropriate planning tool on a small island like Bioko.

Biosphere Reserves are comprised of core areas, which are managed strictly to protect plant and animal genetic resources, buffer zones, where some extractive activities such as agriculture are permitted, and transition zones (Heijnis et al., 1999; Stanvliet et al., 2004). The core areas are typically established at the sites with the greatest number of rare species (Mendez-Larios et al., 2006). Thus, there may be significant differences in beta-diversity between a Biosphere Reserve's core area and buffer zone (Striganova et al., 2001). At the start of the present analysis, we hypothesized that: (i) intact forests on Pico Basilé and in the Southern Highlands contained the greatest number of rare species (see Fig. 1) and (ii) there would be significant differences in beta-diversity between Bioko's montane regions and former plantations in Bioko's lowlands, but the plantations would contain fewer rare species. We tested these hypotheses as follows. First, we compiled a database of species' occurrences on Bioko. Next, we constructed models of species' potential distributions based on the occurrence data and abiotic variables. Finally, we used an algorithm based on rarity and complementarity to prioritize sites on Bioko to represent a targeted percentage of each species' potential distribution. The algorithm first selects the site that contains the rarest species then breaks ties in rarity by selecting the site that, if added to the network, would result in the greatest increase in beta-diversity (Sarkar et al., 2009; see Section 2.3.2). If hypotheses (i) and (ii) are correct, then montane sites should be selected first and lowlands should be selected later to complement the flora and fauna of the montane sites. If hypothesis (i) is correct, then it may be appropriate to establish core areas of a Biosphere Reserve in Bioko's northern and southern massifs due to the rarity of the species in these sites. If hypothesis (ii) is correct, then post-agricultural lands in Bioko's lowlands might be suitable as the buffer zones of a Biosphere Reserve.

Among the objectives of the MAB Program is the integration of conservation and the economic use of ecosystems (Matysek et al., 2006). Bioko provides an opportunity for such integration because the island has a rich endemic fauna and flora but also a long history of extractive land use (Juste and Fa, 1994). Until Equatorial Guinea's independence from Spain in 1968, the main economic activity on Bioko was cocoa production that cleared most lowland rainforest for the establishment of plantations. Since the 1970s, agriculture has declined and some of the agricultural land has returned to a semi-natural state. These secondary-growth forests or post-agricultural lands may have value as dispersal corridors or connectivity areas. One approach to conservation planning in fragmented landscapes might be to regenerate transformed areas, such as the ones found in Bioko, so that they can serve as stepping stones for vertebrates dispersing between patches of intact natural vegetation (Aerts et al., 2008; Alagador and Cerdeira, 2007). Many studies assessing the impacts of croplands on local biodiversity have concluded that shaded plantations, particularly those of cocoa, are among the least deleterious of human land uses, and that they even promote the persistence of native flora and fauna (Bhagwat et al., 2008; Franzen and Mulder, 2007; Rice and Greenberg, 2000). In Bioko, shaded cocoa plantations were the most common form of agriculture, which means that the post-agricultural lands that currently exist stand a good chance of successfully regenerating, if provided protection, and also of retaining a large proportion of the native floral composition.

Because of the limited resources allocated to conservation and the increasing competition for extractive land uses on Bioko, careful planning is needed to ensure the most economical (minimum area) and effective (maximum coverage of relevant biodiversity features) selection of conservation areas. Area prioritization algorithms are becoming a critical tool in the practice of biodiversity
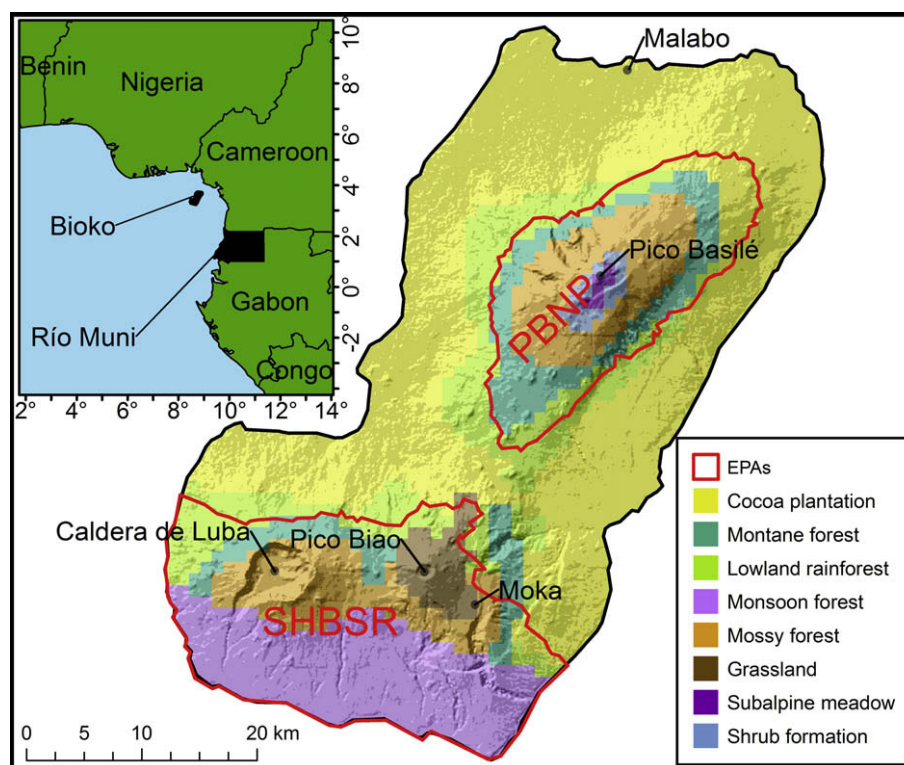
Fig. 1. Study region. Inset: location of Equatorial Guinea in West Africa. Equatorial Guinea comprises the continental region of Río Muni and two islands in the Gulf of Guinea including Bioko (shown in black) and Annobón (not shown). Main panel: sites on Bioko are colored by vegetation type (resolution: 1 × 1 km). The vegetation types are displayed as semi-transparent and are overlaid on a hillshade that represents the topographic relief of sites on Bioko (CUREF, 1999). "PBNP" = Pico Basilé National Park. "SHBSR" = Southern Highlands of Bioko Scientific Reserve. Absolute scale = 1: 400,000.

conservation (Sarkar et al., 2006). The design of biodiversity conservation areas was first formulated as an optimization problem in the early 1980s (Pressey, 2002). During the 1980s and 1990s a variety of optimization models were formulated for the design of conservation areas, most of which were deterministic and had a single temporal stage. In the last 10 years these models have been generalized to incorporate multiple stages, climate change, and uncertainty about species' distributions (reviewed in Moilanen et al., 2009). Although these newer area prioritization models are more realistic, they are also more difficult to solve for large data sets. Since our analysis included 1249 species, we chose to use a relatively simple deterministic, one-stage model to prioritize conservation areas on Bioko. The objective of our prioritization model was to select sites to represent a targeted percentage of the potential distribution of as many species as possible. However, the optimization was constrained by a land budget, meaning that there was a ceiling on the total number of sites that could be selected. This optimization problem is appropriate to real world scenarios where budget constraints are commonplace (see Illoldi-Rangel et al., 2008). In addition, this optimization model allowed us to analyze the effect of different land budgets on the representation of Bioko's biodiversity. Sites that are selected when the budget is low might be prioritized as the core areas of a Biosphere Reserve whereas sites selected when the budget is more liberal could become the Reserve's buffer areas.

The objectives of this study are: (i) to evaluate the potential performance of the protected areas system of Bioko that, although not formally implemented yet, is currently being considered by the Equatorial Guinean administration (hereafter "existing protected areas" – EPAs); (ii) to prioritize areas for the core zone of a Biosphere Reserve by applying systematic conservation planning tools; and (iii) to suggest areas for the restoration of vegetation communities based on the results of the area prioritization exercise under different land budgets. To do this, we structured our analysis as follows: (a) an evaluation of the performance of the EPAs; (b) a concise account of the modeling of species' distributions (for details, see Zafra-Calvo, 2008; Zafra-Calvo et al., in press); (c) prioritization of areas using the rarity-complementarity algorithm in the ResNet software package (Sarkar et al., 2009); and finally (d) comparison of the performance of the conservation area networks selected by ResNet to the current EPAs. Finally, (e) we propose a conservation plan for Bioko using endemic primates, birds, and plants as biodiversity surrogates.

2. Methods

Our study required adapting techniques of systematic conservation planning to a tropical region where biodiversity has been poorly sampled and data parameters typically required for the prioritization are not available. Mapping biodiversity on Bioko is especially challenging because the island has a hyperdiverse flora and fauna that has not been sampled adequately to date (Zafra-Calvo et al., in press). Results indicate that biological inventories conducted on Bioko since the 18th century have been biased toward sites with flat slopes that are close to roads. In addition, it is estimated based on species accumulation curves that only about half of the island's monocotyledons have been described. Since biological sampling on Bioko has been biased and floral inventories are incomplete, we modeled species' potential distributions using a simple presence-only method, BIOCLIM (see Section 2.2).

Our methodology is based on the following sequential scheme. First, we carried out completeness analysis of the database using species accumulation curves (for a summary, see Section 2.2; for details, see Zafra-Calvo et al., in press). The motivation for the completeness analysis was to assess the quality and coverage of inventories of Bioko's biodiversity. Second, we constructed models of species' potential distributions using BIOCLIM, a simple model based on abiotic factors (Section 2.2) because a more complex model of species' realized distributions would have required data on true absences and biotic variables (Jiménez-Valverde et al., 2008), which is not available for Bioko. Third, the BIOCLIM models were used to prioritize conservation areas on Bioko with a rarity- and complementarity-based algorithm (Section 2.3.2). This three-stage protocol – estimation of sampling completeness, niche modeling, and area prioritization – has been applied previously to tropical conservation planning by Peralvo et al. (2007).

2.1. Study area

With a surface area of 2019 km^2, the volcanic island of Bioko is a province of Equatorial Guinea located in the Gulf of Guinea (between latitudes 13°48' and 03°59' North, and longitudes 11°20' and 08°26' East), approximately 30 km off the coast of Cameroon (Fig. 1). Its topography is abrupt due to the presence of three volcanoes with altitudes ranging between 2009 m and 3011 m. The climate is typically equatorial, with a dry season from November to March and a rainy season from April to October, and is characterized by large topographically-driven variation in mean annual temperatures (from 26.5 °C on the northern coast, to 12 °C at the highest peak) and annual precipitation (1557 mm in the north, and 10934 mm in the south) (Nosti, 1942).

The natural vegetation of the island, estimated to comprise more than 6000 species (M. Velayos unpublished data), includes a wide variety of formations (Fig. 1): coastal vegetation; 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 and subalpine meadows (>2500 m). However, human activities have produced important modifications in these natural communities, causing the practical disappearance of coastal vegetation and the transformation of large areas of lowland rainforest into cocoa plantations (most of which are currently abandoned and occupied by secondary forests). Some of the original mossy forest has also been transformed into grasslands for cattle (Ocaña, 1960). The fauna of the island, which is characterized by high species richness and endemism, comprises 33 amphibian species, 50 reptiles, 191 birds (Pérez del Val, 1996) and 65 mammals, among which there are 26 bats (Juste and Ibáñez, 1994) and seven primates (Butynski and Koster, 1994). Bushmeat hunting is the main threat to fauna (Albrechtsen et al., 2007) and a number of species have already become extinct due to overexploitation (Castroviejo et al., 1994).

The EPAs of the island consist of two conservation areas covering approximately 42% of its land (see Fig. 1). The legal implementation of these areas is currently being reevaluated by the Equatoguinean government and, if finally approved, they would be included within IUCN categories Ia and II. These are the Pico Basilé National Park in the northern half of the island (hereafter "PBNP") and the Southern Highlands of Bioko Scientific Reserve (hereafter "SHBSR").

2.2. Biodiversity mapping

We constructed models of species' potential distributions on Bioko for ferns (62 species), monocotyledons (327 species) and dicotyledons (749 species), primates (seven monkey species), and birds (104 species). To do this, we compiled data on species' occurrences on Bioko from the primary literature and museum records (Zafra-Calvo, 2008; Zafra-Calvo et al., in press). Completeness analyses (Baselga and Novoa, 2006; Soberón and Llorente, 1993) indicated that this database includes almost all species of resident

birds and primates inhabiting the island, and more than half of the expected diversity of ferns, monocots, and dicots (Zafra-Calvo, 2008, Chapter 3; Zafra-Calvo et al., in press). Nevertheless, the data that we have compiled provides scarce coverage of the island's biodiversity. Studies of Red List Lepidoptera in Europe have constructed ecological niche models based on more than one hundred presence points for a single species (Chefaoui and Lobo, 2007). In contrast, no species in our database had more than 33 presences. Since our data on species' occurrences were scant and presence-only, it was more appropriate to model species' potential distributions with a simple presence-only method instead of a complex presence–absence method (Jiménez-Valverde et al., 2008).

These occurrences served as the input for BIOCLIM based on precipitation and temperature gradients (Busby, 1986; Nix, 1986), which modeled the potential distribution of all 1249 species at the 1×1 km resolution (at this resolution, Bioko comprises 2070 terrestrial sites). Specifically, the three climatic variables used for modeling (namely, annual precipitation, maximum temperature of the warmest month, and minimum temperature of the coldest month) 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., 2005). A principal component analysis with all these variables produced three first axes with eigenvalues higher than 1 that jointly represented 92.5% of the total environmental variability. Each of these axes was characterized by one of the three climatic variables chosen based on their respective factor loadings. For this reason, we retained these three variables as the ones most representative of the island's climate. The use of this bioclimatic procedure allowed us to identify the cells whose climatic conditions were within the range of those in which each species was observed. We assume that the effect of dispersal limitations on the delimitation of species' ranges is not important. This assumption is plausible for a small island such as Bioko. As a result, it is plausible that the maps we generated adequately represent the potential distributions of the species considered.

In addition, we classified each 1×1 km site into one of the following land cover types based on the Atlas of Africa, Equatorial Guinea (2002): lowland rainforest (total area: 268 km^2), montane rainforest (178 km^2), mossy forest (249 km^2), shrub formations (18 km^2), subalpine meadows (6 km^2), monsoon forest (244 km^2), agricultural fields which mostly consist of secondary forests occupying abandoned cocoa plantations (926 km^2), and cattle grasslands (49 km^2) (see Fig. 1). We carried out this classification in order to test the hypothesis that current vegetation communities inside of and outside of Bioko's conservation areas are similar (see Section 2.3).

We identified endemic and threatened species on Bioko through a literature review. We determined that 14 species of plants, one species and 32 subspecies of birds were island endemics (Fa, 1992; Figueiredo, 1994; Jones, 1994; Pérez del Val, 1996; Pérez del Val et al., 1994). In addition, Bioko has five subspecies of endemic primates (Butynski and Koster, 1994; González Kirchner, 1994; Jones, 1994). Twenty two species of plants, two species of birds, and five species of primates on Bioko are classified as near threatened, vulnerable, endangered, or critically endangered according to the IUCN Red List (IUCN Standards and Petitions Working Group, 2008; see Table 1 of the Supplementary material).

2.3. Prioritization of biodiversity conservation areas

2.3.1. Evaluation of the EPAs

We digitized published maps of PBNP and SHBSR (CUREF, 1999) and overlaid them to the grid of cells described in Section 2.2. Eight hundred and seventy six cells were within PBNP or SHBSR. Next,

we assessed the representation of land cover types in PBNP and SHBSR. For each land cover type, we used a two-sample t-test to evaluate the null hypothesis that the proportion of the type that was represented in the EPAs was equal to the proportion of this land cover type on the entire island. For a given land cover type, the rejection of the null hypothesis implies that the representation of that type in the EPAs is disproportionate. For all 1249 species described in Section 2.2, we also measured the proportion of the potential distribution of each species that was not included within the EPAs (Jennings, 2000). We ranked the species according to the resulting proportions. Next, we examined five conventional targets of representation (1%, 12%, 25%, 50%, and 100%). For each target, we determined the number of species that had the targeted percent of its potential distribution represented in PBNP and SHBSR.

2.3.2. Area prioritization

When the total area of the planning region is large or the region has a large human population, it is customary to exclude sites that are close to towns as unsuitable for conservation management (e.g., Fuller et al., 2006). However, in light of the small total area of Bioko, we decided to retain all 2070 of the 1×1 km sites in the planning exercise. We carried out area prioritization with a rarity-complementarity algorithm implemented in the ResNet software package (Sarkar et al., 2009), because such algorithms are known to find near-optimal solutions to maximum representation problems rapidly (Csuti et al., 1997). We initialized the area prioritization procedure by the selection of the first cell on the basis of rarity. We disambiguated ties in rarity by appeal to complementarity, which selects the site that contains the largest number of surrogates that have not met their targets in sites selected in previous iterations of the algorithm. We broke ties in complementarity with the adjacency rule, which gives preference to a site that is located next to a site selected in a previous iteration. We used the adjacency rule because it results in more compact conservation areas, which may be easier to manage (Fuller et al., 2006; Sarkar et al., 2009). We terminated area selection when the land budget was exceeded.

We used endemic species and subspecies (plants, birds, and monkeys) as biodiversity surrogates because these are the most vulnerable taxa on Bioko (Das et al., 2006; Eken et al., 2004) and they can only be protected by conservation management within Bioko. We defined targets of representation based on the conservation status of each species (Illoldi-Rangel et al., 2008; Pressey et al., 2003). Because all of the surrogates were endemic and had some level of threat, we set a 100% target for all of them.

Using ResNet, we generated four nominal conservation area networks corresponding to four different land budgets. Initially, we analyzed a budget of 42% because PBNP and SHBSR occupy 42% of Bioko. Since the actual amount of land that can plausibly be put under a conservation plan on Bioko is unknown, we carried out sensitivity analysis to investigate the effect of lower budgets (12% and 25%) and a higher budget (50%) on the conservation area network. Although the budgets that we considered are arbitrary, there is no convention about suitable budget values in the conservation planning literature. Indeed, previous planning exercises have analyzed budgets as low as 2.5% and as high as 100% (Camm et al., 2002; Polasky and Solow, 2001). We measured the representation of land cover types and species' potential distributions in the conservation area network selected at each land budget using the same methodology that was applied to the EPAs (see Section 2.3.1).

Exploratory data analysis indicated that, for a given land budget, there were many alternative conservation area networks. Each network prioritized the same number of sites to be put under a conservation plan but the different networks selected distinct sites to serve as conservation areas. In order to account for the variation

among alternative networks, we constructed 100 conservation area networks with ResNet for each of the four budgets. We computed the frequency of selection of each site in the 100 solutions. We considered sites that were selected more frequently to be of higher priority to be put under a conservation plan than sites selected less frequently (see Fuller et al., 2006 for a comparable approach).

3. Results

3.1. Accuracy assessment of species' distribution models

The mean percentage of species' occurrences predicted correctly by BIOCLIM was 82.2% (Zafra-Calvo et al., in press). To determine whether a different niche modeling algorithm would provide better and more robust predictions than BIOCLIM, we also computed the percentage of presences predicted correctly by Maxent (for a comparison of Maxent and environmental envelope methods such as BIOCLIM, see Jiménez-Valverde et al., 2008). The percentage of presences predicted correctly by Maxent ranged from 56.51% to 60.7%, leading us to conclude that BIOCLIM provides more accurate predictions for our data set (for details, see "Comparison of Maxent and BIOCLIM" in the Supplementary material).

3.2. Performance of the EPAs

Except for subalpine meadows, the proportion of each land cover type in the EPAs differs significantly from the proportion of the land cover type on Bioko (Table 1). The most underrepresented land cover type in the EPAs is agricultural land (only 3% of the secondary forests occupying these lands are within PBNP or SHBSR). A moderate proportion of lowland rainforest sites are covered by the EPA system (PBNP and SHBSR include one third of Bioko's lowland rainforests). The remaining vegetation communities are well represented in the EPAs sites with more than 85% of their area within them.

Evaluation of species' representation indicates that 14 species of ferns (23%), 64 monocotyledons (20%), 263 dicotyledons (35%), 12 birds (11%), nine endemic species (19%) and two Red List species (7%) are not represented in PBNP or SHBSR (Fig. 2). Next, we measured the representation of species' potential distributions in the EPAs. Very few species have more than 25% of their potential distribution represented within the EPAs (Fig. 3). At a representation target of 50% or higher, there was a marked increase in the percentage of species that did not meet their targets in PBNP or SHBSR.

Table 1

Column 2 is the percentage of Bioko occupied by each land cover type. Column 3 is the percentage of sites in the EPAs that belong to each land cover type. We used a two-tailed t-test to test H_0: Bioko (%) = EPAs (%). The font in column 3 represents the p-value resulting from the test. Bold: $p \leqslant 0.001$, italics: $0.001 < p \leqslant 0.01$, underline: $0.01 < p < 0.05$. Columns 4–7 list the percentage of the sites in the Biosphere Reserves designed using ResNet that belong to each land cover type. Column 4 describes the ResNet results when the land budget is 12% of the total area of Bioko. In columns 5, 6, and 7, the budgets are 25%, 42%, and 50%, respectively. In column 4, we used a two-tailed t-test to test H_0: ResNet-12% = EPAs (%). In columns 5, 6, and 7 we carried out the corresponding tests for the budgets of 25%, 42%, and 50%. The fonts in columns 4–7 have the same meaning as in column 3.

| Land cover type | Bioko (%) | EPAs (%) | ResNet | | | |
			12%	25%	42%	50%
Lowland rainforest	13.2	<u>10.6</u>	11.2	13	<u>15.9</u>	<u>14.3</u>
Montane forest	8.6	**17.8**	2.4	*12.5*	12.1	11.3
Monsoon forest	13.83	32.7	4.9	17.9	20.9	21.7
Mossy forest	11.7	**27.4**	43.8	27.7	22.7	19.8
Shrub formation	0.9	<u>2.1</u>	2.4	2.7	1.8	1.8
Subalpine meadow	0.3	0.6	0.9	0.9	0.7	0.5
Agricultural land	49.1	**3.5**	27.8	19.04	16.6	25.7
Grassland	2.5	*5.3*	6.7	6.2	5.2	4.8
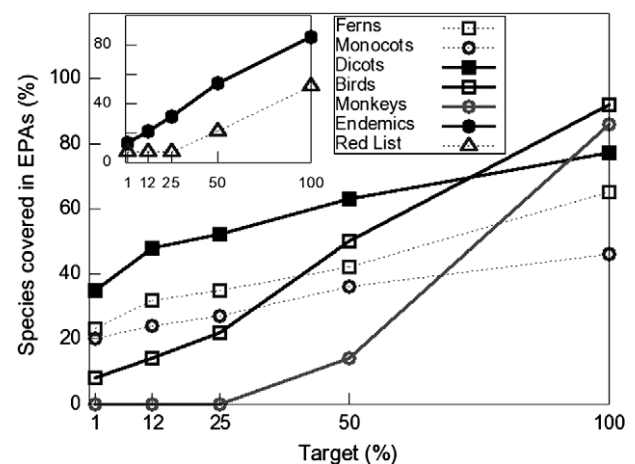
Fig. 2. Effect of the conservation target on the percentage of species represented in the EPAs. Main panel: each line represents one taxonomic group. The x-coordinate of each point is a percentage of the total potential distribution of the species that belong to the taxonomic group on Bioko. The y-coordinate is the fraction of the species in the taxonomic group that have the targeted percentage of their potential distributions represented in the EPAs. Inset: the upper line represents all species endemic to Bioko and the lower line represents the species on Bioko in the IUCN Red List. The x- and y-coordinates have the same meaning as in the main panel.
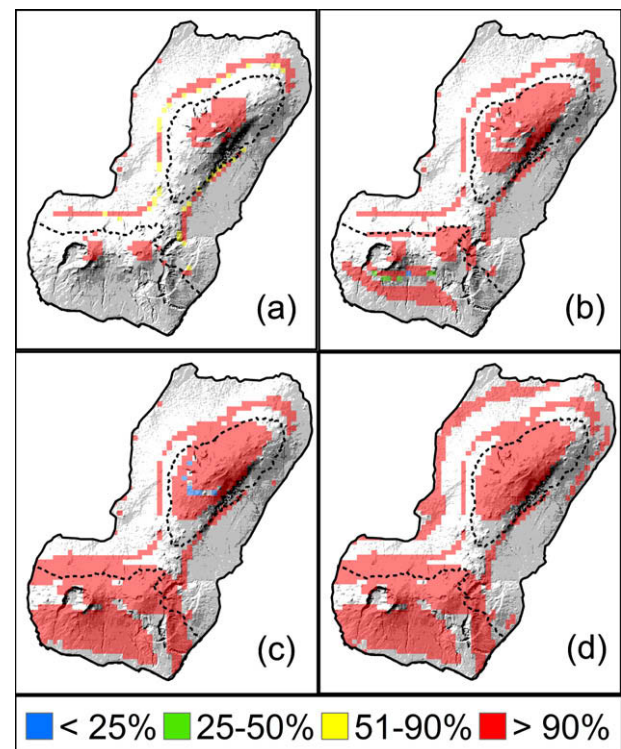
Fig. 3. Frequency of selection of sites on Bioko by the area prioritization algorithm according to different land budgets. Land budget: (a) 12% of the total area of Bioko, (b) 25%, (c) 42%, (d) 50%. Sites shown in red were selected frequently in 100 runs of the area prioritization algorithm. Sites shown in blue were seldom selected. Sites shown in grayscale were never selected. The selection frequency data are overlaid on a hillshade that represents the topographic relief of sites on Bioko. The discontinuous black lines represent Bioko's EPAs (see Fig. 1 for details).

3.3. Performance of conservation areas selected using ResNet

Fig. 3 shows four maps of Bioko corresponding to the land budgets of 12%, 25%, 42%, and 50%. Sites shown in warm colors were selected frequently in 100 alternative conservation area networks and

should be prioritized to be put under a conservation plan. The conservation area networks that we generated at the 12% land budget prioritized sites on the three peaks of Pico Basilé, Pico Biao, and Caldera de Luba (Fig. 3a). However, sites containing remnants of lowland rainforest as well as agricultural land (former cocoa plantations) were also selected. The abandoned plantations that were selected by the rarity-complementarity algorithm form a linear strip of land linking Bioko's northern and southern massifs. Similarly, areas prioritized at the 25% land budget included Bioko's montane areas, lowland rainforest remnants, and post-agricultural lands located between the island's three volcanoes (Fig. 3b). In addition, the monsoon forest in southern Bioko was selected. At the 42% land budget, we observed a substantial increase in the number of selected sites in montane and lowland rainforest surrounding mountain areas as well as monsoon forests and agricultural land (Fig. 3c). At the 50% land budget, the spatial configuration of the prioritized sites is similar, but even more agricultural land and lowland rainforest are selected (Fig. 3d). Land linking Bioko's northern and southern volcanoes was also selected by ResNet when we prioritized areas based on Maxent models of the species' potential distributions (Supplementary material, Fig. 1).

3.4. Comparison of the EPAs and the ResNet results

At the four land budgets that we considered, the conservation area networks constructed using ResNet were not able to provide 100% representation to all surrogate species. At the 12% budget, 16 species of ferns (26%), 181 monocotyledons (55%), 249 dicotyledons (33%), eight birds (8%), one primate (14%), four endemics (8%) and five threatened species (17%) are not represented in any one of the conservation areas selected by ResNet. At the 25% budget, ResNet improved the representation of these species slightly. In this case, 15 species of ferns (24%), 146 monocotyledons (44%), 308 dicotyledons (41%), three birds (3%), and three Red List species (10%) were not represented in any area selected by ResNet to be put under a conservation plan. Our results show that the 42% land budget provides the best representation for ferns; it outperforms the EPAs for dicotyledons, birds, endemics, and performs as well as the EPAs for primates and threatened species (Supplementary material, Fig. 2). At the 50% land budget, the sites prioritized by ResNet provided the best representation for the species considered here. However, even at this budget, 12 species of ferns (19%), 116 monocotyledons (35%), 187 dicotyledons (25%), one bird (1%), and one Red List species (3%) are still not covered in any site selected by ResNet. For most taxa, the budget constraint of 50% provided the best representation, with the exception of monocotyledons and primates. For the latter two, the EPAs offer better coverage (Supplementary material, Fig. 2).

With increasing land budgets, there is a concomitant increase in the representation of lowland rainforest in the conservation area networks selected by ResNet (Supplementary material, Fig. 2). Shrub formations, subalpine meadows, and grasslands are equally represented in the EPAs and the ResNet results. Although the EPAs represent less agricultural land than the areas prioritized by ResNet, montane rainforest and monsoon forest are better represented within the EPAs. The aforementioned results assume that managers want to represent 100% of each species' potential distribution in the conservation areas prioritized by ResNet. In some planning contexts, it may be acceptable to lower the target of representation to 1–12% of the potential distribution of each species. In this setting, the representation of species' potential distributions in sites selected by ResNet at the 25% land budget is equivalent to the representation achieved by the EPAs that cover 42% of the island. To this extent, a conservation plan formulated using ResNet provides a marked increase in economy compared to the proposed protected areas at PBNP and SHBSR.

4. Discussion

High-altitude vegetation communities (shrubs formations and subalpine meadows) contain rare vegetation types that are only located at the top of Pico Basilé National Park; therefore, it is particularly important to conserve them. In our analysis, the rarity-complementarity algorithm implemented in ResNet selects these two vegetation communities as other conservation assessments have done in the past (Castroviejo et al., 1994; Fa, 1992). To this extent, our use of a stepwise algorithm results in a conservation plan that is quite similar to earlier plans developed based on criteria decided by experts. Protection of highlands is also essential for biodiversity conservation on Bioko because of the presence of endemics and threatened species (Bergl et al., 2007; Smith et al., 2000). Our results show that when more land is available for preservation (i.e. if the land budget is increased), monsoon forests are also selected. The monsoon forest is a minimally disturbed vegetation community on Bioko, only located in the south of the island, supports a significant amount of species from lowland primary forest, and has one of the highest densities of primates in the world (Castroviejo et al., 1994). At land budgets of 42% and higher, areas that are not typically set as priorities for conservation are selected by the algorithm. For example, lowland vegetation communities and modified human landscapes (e.g. post-agricultural lands) are selected. In connection with this, it should be noted that the raw data used in our selection procedures consist of species' potential distributions that were generated by taking into account existing gradients of temperature and precipitation (see Section 2.2). To what extent these potential distributions match reality cannot be assessed with the data currently available for the island, but certainly is an aspect that should be taken into account when using our results for practical purposes. In particular, it can be expected that mismatches will be stronger for the case of modified human areas, for which we suggest that the current degree of regeneration of each of these sites be evaluated when designing conservation plans as discussed below.

A shortcoming of the system of EPAs that has been proposed for Bioko is that the representation of lowland landscapes (lowland rainforests and post-agricultural lands) is disproportionately small. Previous proposals for protected areas on Bioko have also been biased towards montane vegetation, as have proposals for other geographical regions (Oldfield et al., 2004; Trisurat, 2007). Although, on Bioko, most of the lowland rainforest was transformed into cocoa plantations by the end of the 19th century, after independence in 1968, the departure of agricultural workers resulted in the collapse of the cocoa exporting business. Abandoned cocoa plantations have subsequently grown into secondary-growth forests and results indicate that they are important for local biodiversity (see Zafra-Calvo, 2008; Zafra-Calvo et al., in press). Elsewhere in Africa, the complement of species in lowland areas is relatively depauperated (Burgess et al., 2005; De Klerk et al., 2004). However, on Bioko, lowlands contain the only vegetation community that is part of the potential distribution of a large number of species (for example, dicotyledons and most endemic birds). Lowland sites classified as agricultural land were selected under each land-budget constraint (Table 1) because these areas harbor the appropriate climatic conditions for a high number of species. If lowland sites are prioritized to be put under a conservation plan based on their regeneration status, they can establish a geographical link between the two great mountainous areas of Bioko, particularly if their regeneration is encouraged (see below).

The conservation area networks constructed in our analyses all include a continuous area of residual lowland rainforest that runs between Bioko's northern and southern massifs (Fig. 3). These rainforests and the post-agricultural land adjacent to them could be used to establish connectivity between Pico Basilé and the

Southern Highlands. Future research should investigate the suitability of these post-agricultural lands as dispersal corridors for Bioko's endemic fauna. To date, there have been relatively few studies of the effects of vegetation on the movement of animals in natural tropical forests. However, forest plantations with intact epiphytes are known to serve as dispersal corridors for passerines in the Neotropics (Cruz-Agnón et al., 2008). Ideally, corridors on Bioko would be able to sustain populations, becoming a source instead of just serving as sinks for the various species that make use of them (Hess and Fischer, 2001). The latter could be accomplished if abandoned plantations are put under a conservation plan and allowed to regenerate with time to become part of species' real distributions. The likelihood of such progression will depend on the level of degradation and the activities that originally modified the landscape (Bhagwat et al., 2008).

Post-agricultural landscapes have a higher probability of regeneration if agroforestry has taken place rather than other forms of agriculture, because it promotes the persistence of native trees and biodiversity (Bhagwat et al., 2008). In Bioko, shaded cocoa plantations were the most commonly used form of forest farming (Juste and Fa, 1994; Nosti, 1948), which is probably why natural regeneration in some of the less disturbed areas and the use of these areas by local fauna have been observed (N. Zafra-Calvo, unpublished data). Protection of former cocoa plantations could potentially promote the regeneration of vegetation communities that are part of the potential distribution of many endangered and endemic species whose narrow ranges often result in their neglect when conservation area design decisions are ad hoc (Araújo et al., 2007).

No conservation area network presented here represents 100% of the potential distribution of all of the surrogate species. To meet the representation target for all surrogates, all of Bioko would have to be put under a conservation plan. Such a plan would be politically unviable. Therefore, we suggest that an approach based on sustainable development, such as those implemented in the MAB Program (UNESCO, 1987), is better suited to accomplish the protection of biodiversity on Bioko. We propose dividing Bioko into three zones according to the MAB design: (1) core, (2) buffer, and (3) transition zone, each with a distinct conservation role. The core zone should be delineated based on the areas selected by the 25% land budget. This area mainly includes intact vegetation in mountain and monsoon areas. However, it is also important to note some major threats to biodiversity that will pose some management challenges: (i) the illegal bushmeat trade (Albrechtsen et al., 2007); (ii) overexploitation of a medicinal tree, the African cherry (*Prunus africana*) (Sunderland and Tako, 1999); (iii) impacts associated with the road that links Malabo with the top of Pico Basilé where the national aerial communication facilities are situated; and (iv) the economic activities of the town of Moka (mainly agriculture and cattle grazing). These threats can be overcome and the management of this area for conservation is possible with enough political will. The buffer zone should include the complementary areas selected by the algorithm at a 42% land budget. These complementary areas include: montane as well as lowland rainforest surrounding mountain areas, monsoon forest, and post-agricultural land. Conservation action and management of biodiversity should be explored with the government but participation of local residents and private landowners is also crucial. The rest of the island could be considered a transition zone where more sustainable methods should be devised for urban development and the extraction of oil and other natural resources.

Post-agricultural land plus lowland rainforests are potentially of high conservation value due to their likely importance for several endemic species. These would be the areas that serve as corridors. On the other hand, it is also interesting to note that the plant formations occurring in this strip comprise lowland rainforest and abandoned plantations of cocoa, oil palm, and abaca. Except for the abaca areas (which are still heavily occupied by *Musa textilis* plants) the other old plantations are occupied by secondary-growth forests, thus suggesting that, if this strip were to be converted into a conservation corridor, the regeneration of vegetation would only be needed to convert the abaca areas into more natural forests. Additionally, future conservation regulations for this potential corridor should take into account the two important towns and several bushmeat-hunters' camps that lay within its confines.

To conclude, our results should be viewed as a preliminary assessment of the representation of biodiversity in notional conservation area networks on Bioko. Our analysis is intended to be refined via consultation with stakeholders to address economic and social criteria. Systematic conservation planning is an iterative process in which conservation priorities may change due to new biological data (Sarkar et al., 2006). Priorities for future field surveys include the validation of the models of species' distributions utilized here. Future work should also incorporate data on additional taxa into conservation plans for Bioko, such as arthropods and herpetofauna (Larison et al., 1999).

The framework for the design of a Biosphere Reserve on Bioko that we put forward can be used for other islands. The case of island conservation is interesting and challenging at the same time because land constraints are more pressing as are the human needs that conflict with biodiversity conservation goals. Although Biosphere Reserves have been established in 480 sites in 100 countries (Isacch, 2008), our analysis is the first time that systematic conservation planning methods have been used to select which areas should be assigned to the core and buffer zones in a Biosphere Reserve.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.12.022.

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