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Priority areas for biodiversity conservation in mainland Ecuador

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Ecuador's territory harbors a unique set of species and ecosystems, many of them endemic to the country's territory and subject to different sources of threat of anthropogenic origin. Despite national and subnational conservation strategies developed in Ecuador to conserve its biodiversity in the long run, including the National System of Protected Areas (PANE) and the forest conservation incentive program SocioBosque (PSB), further actions are needed to mitigate and reverse the effects of threats for the persistence of biodiversity. This study was designed to identify the most important areas for biodiversity conservation in mainland Ecuador that can contribute to preserving key species (i.e. endemic, threatened) and ecosystems in the wider landscape, thus complementing current conservation efforts (i.e. PANE). Species distribution models and recent maps were used to identify a set of 744 species and 87 ecosystems as surrogates of the country's biodiversity. Marxan, a systematic reserve selection algorithm was used to identify important biodiversity areas that could represent between 10% and 20% of the remnant distribution of the surrogates. The optimized solution generated by Marxan included 24% (3.64 million ha) of Ecuador's remnant vegetation, of which 35% is within the current national protected area system and 13% (456 000 ha) are included within SocioBosque communal and private conservation agreements. Major conservation shortfalls of the PANE were concentrated in the Southern Andes, Central Amazonia, and the Central and Southern portions of the Coastal plain. The incidence of complementary criteria to prioritize conservation strategies, related to climate change, ecosystem conversion, carbon and accessibility, and population density change in relation to the important biodiversity areas was heterogeneous among regions. This confirms the need to implement differentiated conservation and sustainable landscape management strategies. Fourteen priority landscapes were identified based on these important biodiversity areas, including remnant ecosystems considered critical for maintaining large-scale connectivity among regions and preservation of restricted range and threatened species. Further work is needed to expand base information about distribution patterns of biodiversity, improve the representation of endemic and threatened species in conservation strategies, and to fully integrate conservation priorities among a wider set of goals in land use planning exercises at different scales.

Keywords: threatened species; ecosystems; Marxan; protected areas; conservation targets

1. Introduction

Ecuador is the smallest of the 17 megadiverse countries [1] and harbors an astounding number of ecosystems and species, with many endemic species occurring in small geographic ranges [2–4]. Unfortunately, the country has experienced a profound change of its natural habitats. For the year 2014, the country reports an estimated forest area of 12.75 million hectares, a 14% (i.e. 1.83 million ha) reduction with respect to 1990 [5]. The annual deforestation rate for the period 2008–2014 was –0.37%, equivalent to an average annual loss of 47,000 hectares [5]. These figures, added to the historical changes occurred during the middle decades of the twentieth century (1940–1970), set up a scenario where only ~30% of the original natural vegetation remains in the Coastal plains, 60% in the Andean region, and 88% in the Amazon lowlands. Considering the accelerated pace of habitat transformation, it is important to identify important areas that require land management goals

aligned to the preservation of biodiversity from both national and local authorities.

As with most countries that are members of the Convention on Biological Diversity (CBD), Ecuador's major strategy to conserve its biodiversity has been the establishment of a network of protected areas. Ecuador's efforts to preserve its natural heritage are noteworthy; currently, the national protected area system (PANE hereafter) is composed of 48 units,¹ which cover nearly 20% of the country landmass (~4.3 million ha, Figure 1). Establishing a representative protected areas network, in which biodiversity can persist in the long term, has also become a public policy goal [6]. Additionally, the Ministry of the Environment has created a national incentive program of payments for biodiversity conservation (i.e. SocioBosque Program) involving both private and community lands [7] that by the end of 2015 is conserving almost 1.5 million ha.

Nevertheless, important conservation gaps still remain for species, many of them endemics [8,9], and

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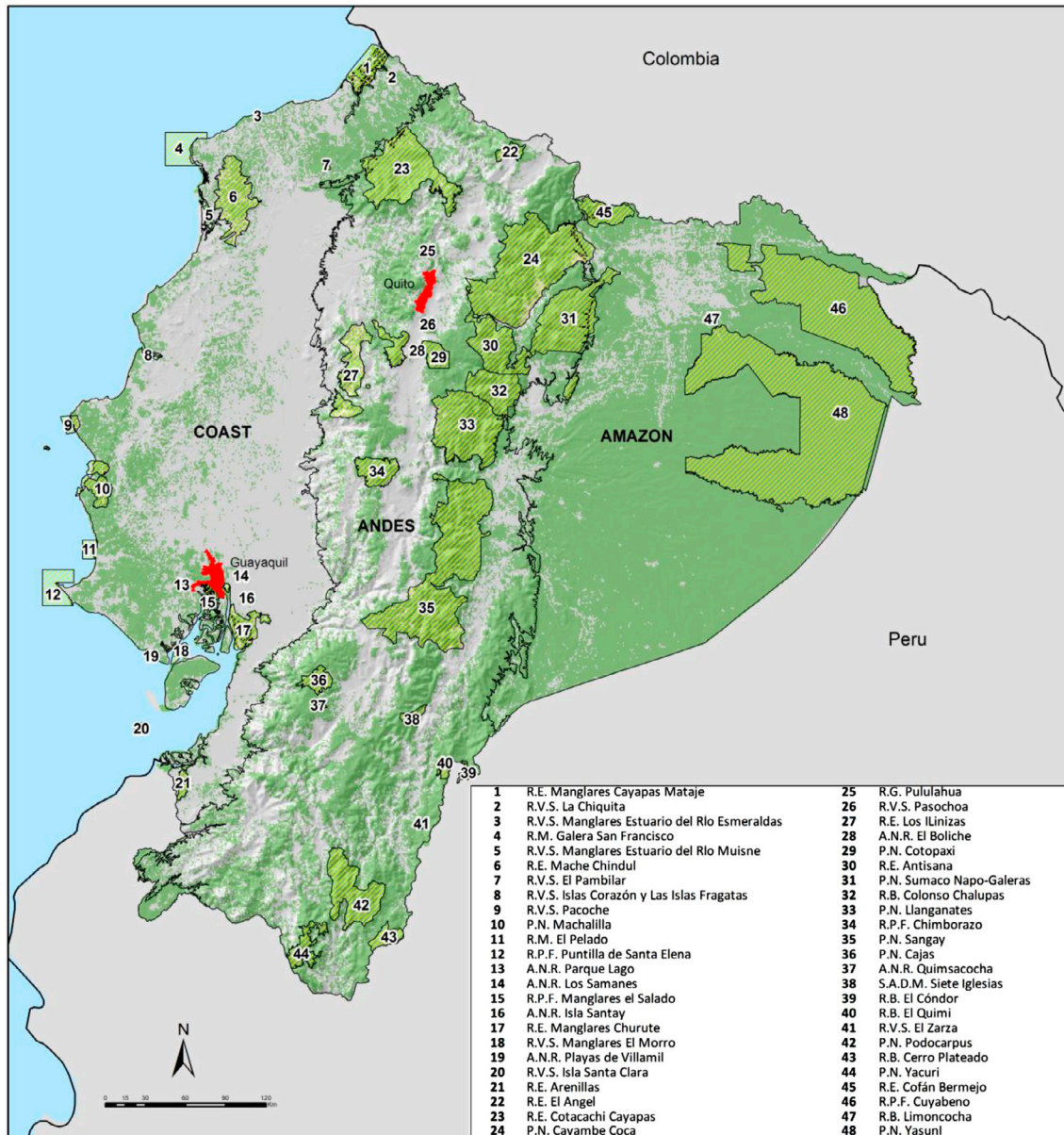


Figure 1. Study area in mainland Ecuador showing the distribution of remnant vegetation. The internal black lines limit the three major physiographic regions: (1) the Coastal plain, (2) the Andean highlands, and (3) the Amazon. Remnant native vegetation is shown in green, whereas converted areas are presented in gray. The red polygons are the two biggest cities in the country.

ecosystems [10]. In many cases, reserves were set up based on ad hoc approaches rather than biogeographic distributional information of the conservation targets. These ad hoc approaches have resulted in a bias in the distribution of the reserve network, with the majority of the reserves occurring at higher elevations, on steeper slopes, and in inaccessible lands of marginal interest for production [11,12]. This leaves important areas for biodiversity conservation outside the PANE and in a context where the creation of new protected areas is less viable as pressure to allocate land for agriculture and other land uses increases [13]. In this context, there is an urgent need to rethink biodiversity conservation strategies to mitigate the effects of climate change, land use – land

cover change among other drivers, by maintaining and increasing the connectivity between reserves and regions (e.g. between the Andes and the Amazon) at local to national scales.

In the last decades, considerable advances have been made to develop science-based methodologies to select priority areas for biodiversity conservation [14,15] and secure the provision of environmental services [16–18]. These methods emerged from the field of systematic conservation planning, aimed at defining explicit conservation goals and objective rules for reserve selection in order to obtain maximized benefits (i.e. accomplish conservation goals in as little area as possible). Therefore, these methods can also be applied to identify

complementary scenarios aimed at guiding land use planning exercises at local and national scales.

Previous studies focused on identifying priority areas for biodiversity conservation in mainland Ecuador used either species [9] or ecosystems [10,12] as biodiversity surrogates. Thus, complementary studies aimed at identifying areas that ensure both species and ecosystems conservation in mainland Ecuador are of utmost importance in order to inform policy formulation and definition of conservation strategies in the short term [19].

Prioritization exercises are valuable tools for megadiverse countries that need to accommodate for multiple land management goals in heterogeneous landscapes [13]. These exercises provide valuable information for land use planning, as priority areas for conservation can be compared and contrasted with areas important for other goals, and synergies and trade-offs can be made explicit spatially [20]. Further, these important areas for conservation can be contrasted to different *in situ* conservation strategies already implemented in the country, and identify gaps where further actions, involving local stakeholders and authorities, could be promoted. With this context in mind, this paper addresses the following interrelated questions: (1) What are the most important areas for biodiversity conservation in mainland Ecuador? (2) How does different conservation strategies are contributing to conserving them? (3) Where should additional efforts be developed, considering multiple drivers of environmental change and distinctive land management objectives?

2. Study area

The study area covers the full extent of mainland Ecuador, which corresponds to nearly 25.3 million hectares, and it's commonly classified into three major physiographic regions: (1) the Coastal plain, (2) the Andean highlands, and (3) the alluvial plains of the Amazon [21,22] (Figure 1). Ecuador is a country with high environmental heterogeneity due primarily to its latitudinal position (which determines its tropical condition), the existence of the Andean chain with active strato-volcanoes in its northern portion, the climatic influence of the trade winds of the Atlantic together with the effects of the warm current of the Pacific Ocean and the cold waters of the Humboldt current [22–24]. These environmental setting have promoted the creation of a diverse array of ecological niches that have been filled with one of the most diverse sets of biological organisms on Earth. Ecuador's biodiversity has been classified in 91 ecosystems [25] and comprises ~17,300 vascular plant species of which nearly 26% are reported as endemic to the country [8,26], 1659 bird species [27], 416 mammals [28], 558 amphibians [29], 450 reptiles [30], and 951 freshwater fishes [31] (Table S1, SOM).

3. Methods

The methodology incorporates three main steps: (1) identification of important areas for biodiversity conservation,

using tools from systematic conservation planning [32,33], (2) the assessment of how current conservation efforts (e.g. PANE, SocioBosque) are effectively contributing to conserving important biodiversity areas in mainland Ecuador, and (3) comparing biodiversity priority areas with other areas relevant drivers of environmental change to assess patterns of spatial coincidence at the regional level.

3.1. Conservation surrogates

Two types of biodiversity surrogates were selected: (a) ecosystems, and (b) species. At the ecosystem level, 87 ecosystems² were included based on the recent ecosystem map published by the Ministry of Environment of Ecuador [25]. The area of remnant ecosystems in the referred map comprises 61% of the country's landmass (~15.2 million hectares); the remaining 39% (~9.65 million hectares) corresponds to transformed areas, mainly agricultural and pasture lands. Only seven ecosystems cover an area larger than 500,000 ha; at the other end, 19 out of 87 ecosystems occur in an area smaller to 10,000 ha (Appendix 1, SOM). At the species level, 744 species were chosen (Appendix 2, SOM), including vascular plants ($n = 234$), birds ($n = 278$), amphibians ($n = 120$), and reptiles ($n = 112$). Among these, 196 species (26%) are currently listed within the IUCN red list categories (Appendix 3, SOM).

3.1.1. Species distribution models (SDMs)

Species distribution information in the Tropics, including Ecuador, is fragmented and incomplete [34], thus we used species distribution model techniques (SDMs) to project their geographic distribution at the country scale (see Appendix 3 in SOM for details). We applied an asymmetric modeling technique to build up the SDMs since true absence data were not available [35]. SDMs were developed using Maxent, a machine learning algorithm based on the maximum entropy theory, which is used as a general-purpose method for making predictions or inferences from incomplete information [36]. We chose Maxent over other algorithms as it has been tested extensively and has been found to suitably perform as an advanced modeling technique for predicting current and future species niche distributions [37–39]. Maxent estimates species' distributions by finding the distribution of maximum entropy (i.e. closest to uniform) based on species records and environmental niche variables [40]. SDMs were developed with Maxent 3.3.3e following the parameters settings of [41] and using eight environmental niche variables: Annual Precipitation, Precipitation Seasonality (Coefficient of Variation), Precipitation of Wettest Quarter, Precipitation of Driest Quarter, Temperature Seasonality (standard deviation), Ombrothermic index, Ombrothermic index of the driest two-months of the driest quarter, Terrain ruggedness index, and Topographic exposure index (see Appendix 3 in SOM for

details). We modeled only species with at least five distinct locations, as a compromise between model quality and sufficient coverage of limited-range species [42]; species with less than five records were used as an indicator of species distribution in Marxan (see below).

Probability distributions were reclassified to presence-absence data using the ‘prevalence threshold’ [43]. This threshold is defined as the average probability over all input data points used to fit the model (i.e. training presence points). To obtain a better approximation of the species realized niche, the binary distributions were evaluated by comparing them with published literature [29,30,44,45]. Finally, to avoid over-prediction we removed from the species distribution model all non-natural areas based on a recently produced land-cover map of Ecuador [5].

3.2. Conservation goals

Conservation goals are related to the amount of area or number of biodiversity surrogates that should be protected, or in other words, the minimum representation of biodiversity features in protected areas [46]. Goals should be defined based on a quantitative basis that translates concepts of representativeness and persistence in operational use. Additionally, goals should consider constraints related to costs and historical and geographic patterns of land use in a way that results are achievable [47,48].

In this study, conservation goals were set using as a reference 10% of the species or ecosystem remnant distribution to be included in the site-selection algorithm within the selected portfolio. This proportion has been suggested as a conservation target by the Convention on Biological Diversity [49,50] as well as in other conservation planning exercises meant to inform policy formulation [51]. This proportion was adjusted up to 20% for species listed under the IUCN red list categories or for species with a restricted distribution range (<1,000,000 ha); the same proportion was applied to ecosystems with a remnant distribution below 20,000 hectares. This threshold was chosen considering that 30 out of 87 ecosystems (i.e. 35%) had a remnant distribution below 20,000 ha and can be considered the equivalent to a species with a restricted distribution range [52].

The distribution of each species derived by the SDMs was contrasted with the national land cover map for the year 2008 to determine the remnant distribution and the rate of conversion. For ecosystems, a conversion rate was estimated for each one based on the deforestation maps produced by the Ministry of Environment for the period 1990–2008 [5]. A relative low conservation goal was adopted, recognizing that a higher goal is too demanding in terms of the area that needs to be included. In regions with high levels of ecosystem conversion and high level of species richness such as the Ecuadorian coastal plains, a higher threshold would

require conserving almost all the remnant vegetation and no prioritization would be required. The conservation targets defined here are lower than previous studies carried out in Ecuador (9, 10), but these represent a compromise between politically and socially viable scenarios to support policy-making at the national level and more robust scenarios to promote biodiversity conservation in the long term.

3.3. Selection of priority areas for biodiversity conservation

Reserve selection algorithms are generally based on the principles of complementarity, singularity, and persistence [15,33,53]. For this study, we used the conservation planning software Marxan V. 1.8.2 [14] which provides analytical support to a range of conservation planning problems, including biodiversity’s representativeness of current conservation schemes as well as the identification of important areas that should be managed with conservation goals.

Marxan aims to find reserve systems that meet biodiversity targets in the least number of planning units (PUs) in which all conservation targets are met, while minimizing cost and addressing spatial design objectives [54]. This is achieved by minimizing the value of an objective function, which is a combination of the cost (usually area) of each planning unit (PU) included in the resulting reserve network, an additional cost related to the fragmentation of the network, and a penalty for unmet biodiversity targets:

$$\text{Total cost} = \sum_{\text{PUs}} \text{Cost} + \text{BLM} \sum_{\text{PUs}} \text{Boundary} + \sum_{\text{goals}} \text{Penalty} \quad (1)$$

where $\sum_{\text{PUs}} \text{Cost}$ equals the total cost of the reserve network; $\sum_{\text{PUs}} \text{Boundary}$ is a cost related to the total reserve perimeter length multiplied by a boundary length modifier (BLM). The BLM factor defines the relative importance of the border, where higher values of BLM translate into solutions with lower perimeter (i.e. more aggregated); $\sum_{\text{goals}} \text{Penalty}$ is the costs imposed for not adequately representing conservation targets in the solution modified by a Species Penalty Factor (SPF) that increases the penalty for missing the goal for each species. Higher SPF values will influence the solution to increase the total cost up to the conservation goals are met [55]. Following the Marxan good practice guidelines [46], the boundary cost modifier (BLM) was set in 0.55 following a sensitivity analysis in which different BLM values were assessed against the resulting total cost of the solution (i.e. number of PUs) and the total border length. This value represents a good compromise on the compactness level of resulting areas at the national level taking into account differences in the spatial configuration of remnant vegetation in the country. The SPF

parameter was set to 1.0 following the same procedure applied for the BLM (Appendix 3, SOM).

Ecuador's mainland territory was divided into 50,683 hexagonal planning units of 500 ha each. This PU size was selected because it constitutes a reasonable landscape extent to harbor adequate representations of the selected biodiversity surrogates. Additionally, the same PU size was chosen in previous GAP assessments of Ecuador's reserve network [10]. Each planning unit was set to a standardized cost of 1 since all units have the same area, allowing each PU to have the same probability of being included in the final solution. Additionally, each boundary length was set to 1. Marxan runs were performed using the simulated annealing method, followed by iterative improvement, using 10^7 iterations and 100 runs. Two output results were generated: the best solution for all runs and the summed solution. The best solution is the solution with the lowest objective function value (i.e. the most efficient solution of the 100 runs) [46]. The summed solution reports the number of times (i.e. frequency) a planning unit was selected as part of a good solution across the 100 runs; consequently, it can be used as irreplaceability proxy [46]. The solution generated by Marxan using these settings represents the important areas for biodiversity conservation in mainland Ecuador (the priority biodiversity areas hereafter).

3.4. Assessment of conservation strategies in continental Ecuador

The biodiversity priority areas scenario was overlaid with the PANE to analyze the patterns of coincidence and differences between the two maps. Additionally, the areas under contracts belonging to the SocioBosque Program [7] were overlaid to the biodiversity priority areas with similar purposes.

3.5. Identifying additional criteria to prioritize biodiversity conservation

The biodiversity priority areas scenario was contrasted with a set of maps that represent different drivers of social and environmental change. The purpose was to assess the degree of spatial coherence between the solution generated by Marxan and these maps that are relevant for different and complementary land management strategies and goals. Hence, four binary maps were generated using the same planning units (i.e. hexagons) used for the Marxan runs (Appendix 3 'Extended Methods' in SOM).

The first map corresponds to areas of recent ecosystem conversion in the period 2008–2014 as represented by the maps of land use–land cover change at the national level generated by the Ministry of Environment [5]. Priority areas were defined as those PUs where ecosystem conversion was greater than 40.5 ha (upper

quartile of the national distribution of conversion per PU) and the PUs immediately adjacent to these. These areas are used as proxies of deforestation and forest conversion risk in the near future.

The second map corresponds to the turnover of species per PU calculated using the modeled distribution of 667 species of vascular plants, birds, amphibians, and reptiles using SDMs generated in Maxent for the reference period 1950–2000 and for 2050 for six models of the A1B emissions scenario [56]. The turnover rate is a value between 0 (no change in the composition of species) and 100 (complete change between base and future conditions). The threshold used to generate the binary map corresponds to the upper quartile of the mean value per PU of the turnover index (Appendix 3 'Extended Methods' in SOM). The resulting binary map represents areas where high impacts on the structure and composition of biotic communities are expected under novel bioclimatic conditions.

The third binary map depicts areas with high carbon contents in above ground biomass and with a high degree of accessibility. Carbon content was estimated for each PU as the mean value according to the map generated by Saatchi et al. [57]. Accessibility was estimated as the mean travel time in hours to the closest province capital or municipality seat city per PU. Travel time was calculated using an adaptation of a cost weighted distance model developed by Jarvis et al. [58]. Priority areas were identified using the lower quartile for accessibility and the upper quartile for mean carbon content for each of the three regions in continental Ecuador: coastal plains, Andes and Amazon (Appendix 3 'Extended Methods' in SOM). By combining carbon and accessibility, the goal of this map is to represent areas of importance for the provision of ecosystem services (i.e. carbon storage) that could be sensitive to processes of ecosystem conversion or degradation.

Finally, the fourth binary map was generated using values of change in population density in the period 2001–2010 per parish using data from the two last national censuses (<http://www.ecuadorencifras.gob.ec/sis-tema-integrado-de-consultas-redatam/>). The percentage of change in population density in relation to the value in 2001 was calculated for each PU, and the priority areas were those with values above the threshold for the upper quartile at the national level (Appendix 3 'Extended Methods' in SOM). This map represents an important underlying driver of ecosystem conversion associated to the increasing demand for ecosystem goods and services associated to increasing human population.

For each map, the percentage of the priority areas at the national level, for each region and in relation to the biodiversity priority areas were calculated. This allowed assessing coherence between areas where land management goals focus on different aspects of the persistence of biodiversity in the long term.

4. Results

4.1. Important areas for biodiversity conservation in mainland Ecuador

The Marxan best solution produced an optimized scenario in which nearly 4.14 million ha were included in the solution (Figure 2), equivalent to almost 24% of Ecuador's remnant vegetation (Table 1). The solution includes a higher proportion of the remnant vegetation in the Coast (30%) and the Andes (26%) than in the Amazon region, where the selected PUs represents nearly 20% of the remnant vegetation (Table 1). The areas selected in this scenario accomplished the conservation goals for nearly the entire set of biodiversity indicators ($n = 840$), except for two ecosystems and two species (Appendix 4 in SOM).

Of the 4.14 million ha included in the solution, 3.64 million ha (88%) correspond to natural vegetation and the remaining ~ 500 thousand ha (12%) correspond to mosaics of agricultural uses and scattered fragments of natural vegetation. Almost 40% (0.2 million ha) of these cases are in the Coast, whereas only 8% are located within the Amazon. Thus, evidencing the high degree of

fragmentation of the relic vegetation in the Ecuadorian coast (Table 1).

4.2. Contribution of national conservation strategies in conserving important biodiversity areas

The planning units (PU) selected in the solution have a moderate spatial correspondence with the current reserve system. From the 3.64 million of hectares, 1.18 million ha (32%) are located inside of an existing reserve, being among the most important Yasuní et al. (Figure 2). The remaining 2.36 million ha (65%) included in the Marxan solution are located outside the PANE, depicting a large proportion of important biodiversity areas beyond management of the national protected area system. The most critical areas that demand further conservation efforts are located in Southern Amazonia (Pastaza), the lowland (between the Cotacachi-Cayapas and the Pambilar reserves) and the piedmont forests (between the Illinizas and the Pululahua reserves) of the Chocó region, the xerophytic and mesic forests of the Coastal Mountain range, the mountain forests of the Southern Andes and the Cónдор-Kutukú Mountain ranges (Figure 2).

The contribution of the PSB to conserve Ecuador's mainland biodiversity is noteworthy. Currently, the PSB program protects almost 1.47 million ha of native vegetation of which almost one-third (0.46 million ha) has a spatial correspondence with the biodiversity priority areas (Table 2). This is particularly evident in the Pastaza region (southern Amazonia), in the coastal mountain range and in the Cónдор-Kutukú ridges (Figure 2).

Additionally, we assessed the achievement of ecosystems and species conservation goals by the current national protected areas. In general, the national reserve system had a better performance representing the geographic ranges of the species, while for ecosystems, the PANE revealed significant limitations (Appendix 6 SOM). Of the 87 ecosystems, 41 (47%) are well represented in the existing national protected areas (i.e. more than 20% of its remnant distribution); yet, 24 (28%) are not represented in the PANE, and 22 (25%) are under-represented (i.e. less than 10% of its remnant distribution is within the reserve network). Most conservation gaps at the ecosystem level are in the southern Andes, including the Kutukú and Cónдор ridges, central Amazonia (Pastaza), and in particular, in the central and southern portions of the Coastal plain (Appendix 6 SOM).

At the species level, the current national protected areas system contains the majority of the species ranges (i.e. according to the SDMs). Nearly 60% of the target species ($n = 445$) meet the conservation targets used in the analysis (i.e. >20% of their remnant habitat) within the PANE (Appendix 6 SOM). Nevertheless, our results evidence that endemic and restricted-range species (e.g. *Chaetocercus berlepschi*, *Eriocnemis nigrivestis*, *Pyrrhura orcesi*) are not appropriately protected considering the current design and distribution of the national protected areas. From the 744 species selected for this

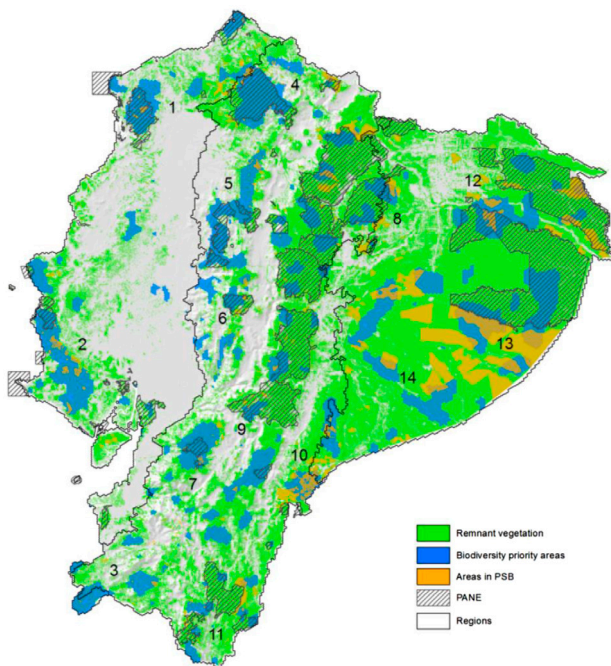


Figure 2. Important biodiversity areas in continental Ecuador selected from the best solution in Marxan. Numbers depicts 14 priority landscapes to improve the representation of the priority biodiversity areas within the National Protected Areas System. Notes: Landscape 1: Mache-Chindul, Landscape 2: Chongon-Colonche mountain range, Landscape 3: Dry and mesic forest of Zapotillo, Landscape 4: Cotacachi-Cayapas, Landscape 5: Illinizas-Mindo-Nambillo mountain range, Landscape 6: Central Andes, Landscape 7: Cajas massif, Landscape 8: Sumaco-Napo Galeras, Landscape 9: Sangay- Siete Iglesias, Landscape 10: Condor Kutukú mountain ranges, Landscape 11: Southern Andes, Landscape 12: Cuyabeno-Pañacocha, Landscape 13: Yasuní, Landscape 14: Pastaza & Santiago Watershed.

Table 1. Remnant vegetation included in the areas identified as biodiversity conservation priorities by Marxan solutions (blm 0.5; Spf 1.0) per region and at the national level.

Region	Total area* (ha)	Remnant vegetation (ha)	Remnant vegetation as % of region	Priority areas (ha)	Remnant vegetation in priority BD areas	
					ha	%
Coast	6,839,350	2,023,679	29.59	800,500	602,394	29.8
Andes	10,583,935	6,409,254	60.56	1,928,000	1,669,281	26.0
Amazonia	7,545,961	6,895,613	91.38	1,408,500	1,366,821	19.8
Ecuador	24,969,246	15,328,546	61.39	4,137,000	3,638,496	23.7

*Continental Ecuador.

Table 2. Contribution of the Patrimony of National Protected Areas of Ecuador (PANE by its Spanish acronym) and of the areas under ecosystem conservation agreements of the Socio Bosque Program (PSB by its Spanish acronym) to the protection of remnant vegetation in priority biodiversity areas.

Region	Remnant vegetation in priority areas (ha)	Remnant vegetation in priority areas in PANE (ha)	Percentage (%)	Remnant vegetation in priority areas in PSB (ha)	Percentage (%)
Coast	602,394	126,584	21.01	48,880	8.11
Andes	1,669,281	633,328	37.94	113,201	6.78
Amazon	1,366,821	420,525	30.77	294,572	21.55
National	3,638,496	1,180,437	32.44	456,653	12.55

study, 106 (14%) are endemic or have a restricted range (<5000 km²), of which only 4 are well represented in PANE. The remaining 102 endemic species are usually found outside ($n = 10$) the protected areas or are underrepresented ($n = 92$) (Appendix 6 SOM). A similar pattern was found for the threatened species. All of the species ($n = 8$) classified as critically endangered (CR) are underrepresented in PANE, being especially important the cases of *Atelopus elegans*, *A. balios*, *A. guanujo*, and *Synallaxis maranonica*. From the 25 species classified as Endangered (EN), only one is well represented in the national protected areas network, 21 are underrepresented and three are completely outside the reserve system (i.e. *Anolis proboscis*, *Bothrops lojanus*, *Geonoma irena*). In the same way, from the 36 species listed as Vulnerable (VU), 34 are underrepresented and one is out of the protected areas boundaries (i.e. *Wetmorethraupis sterrhopteron*).

4.3. Additional criteria to prioritize biodiversity conservation strategies

The binary maps for the four criteria selected (i.e. (a) land use change, (b) species turnover, (c) carbon stocks and accessibility, (d) changes in population density), and the spatial distribution of biodiversity priority areas are presented in Figure 3. As expected, the spatial patterns of the contextual factors varied markedly among factors and regions. This is related to the complex interactions of the underlying processes that drive potential impacts on the persistence of biodiversity across scales [59]. For example, habitat conversion poses a continuous threat to biodiversity priority areas that distributed

in areas with good accessibility (e.g. in the Coast and the southern Andes), whereas potential impacts from climate change related to species turnover reveals patterns associated to the global processes built into the GCMs used (Figure 3).

Combining the binary maps for the four criteria with the priority biodiversity areas reveals differentiated levels of spatial coherence (Table 3). For example, areas with recent and potentially future ecosystem conversion are prevalent in the Andean region (44%). However, it is in the Coast where the overlap of these areas is highest with the biodiversity priority areas (47%), especially in the northern and southwestern portions of this region. In contrast, the overlap in the Amazon is the lowest (7%) and occurs mostly in the northern portion of this region (Figure 3).

Critical areas due to the risk of high species turnover in scenarios of climate change are more prevalent in the Amazon region, especially in the eastern Amazon and represent 28% of the region (Figure 3). The overlap with biodiversity priority areas is of ca. 31% in the Amazon. In the Andes, the overlap is 12% and it is concentrated in the central and western areas (Table 3). In this last region, the areas of overlap are concentrated in the central Andes and in the external slopes of the western Andean range (Table 3).

Areas of high carbon content and high accessibility are more prevalent in the Andes (20%) and the Amazon (18%) regions. The high percentage of these areas in the Andean region is related to the remnant distribution of montane forest ecosystems in the external flanks of the western and eastern Andean ranges (Table 3). The highest overlap with biodiversity

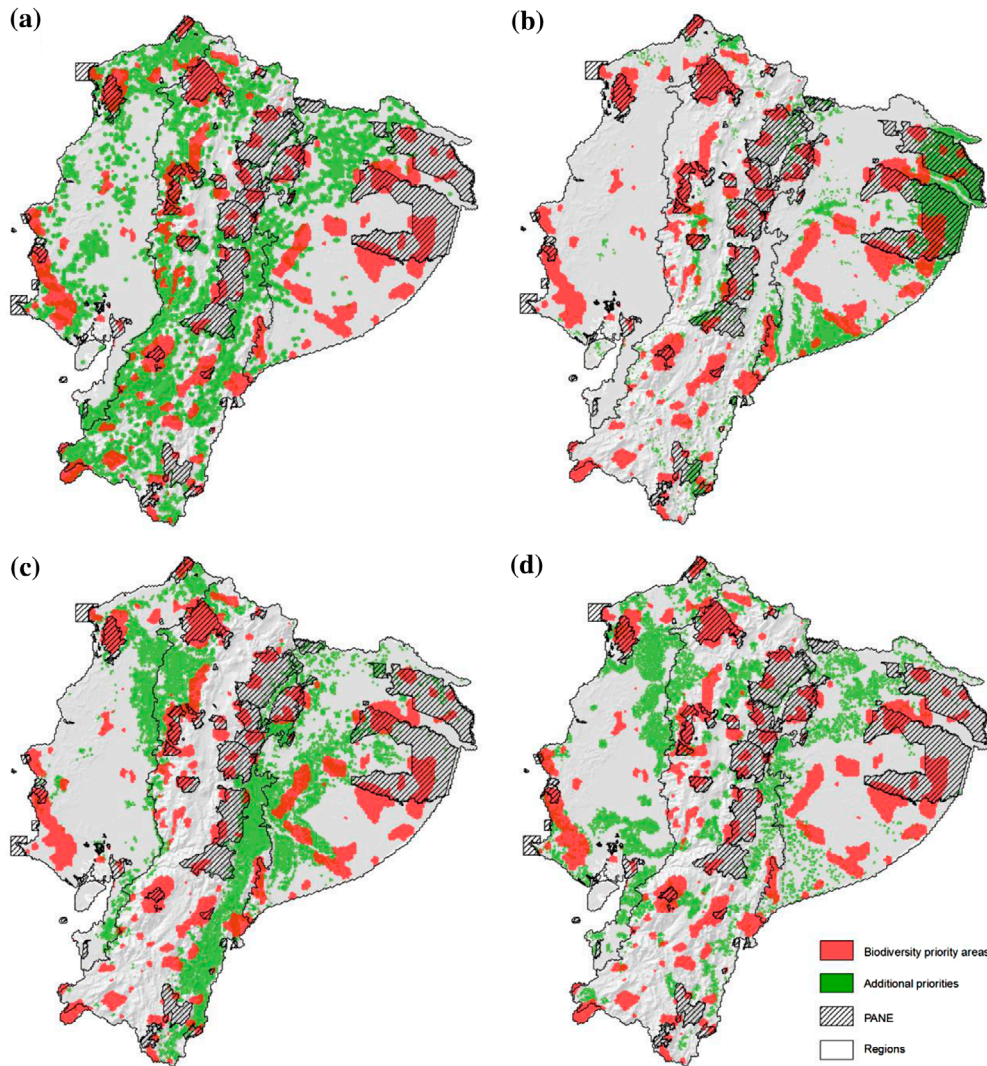


Figure 3. Additional criteria to prioritize biodiversity conservation strategies: (a) recent ecosystem conversion for the period 2008–2014, (b) species turnover due to climate change for the year 2050 under A1B emissions scenario, (c) carbon/accessibility, (d) change in population density 2001–2010. See details in the supplementary material Tables S5 and S6.

Table 3. Percent distribution of priority areas derived from drivers of environmental change in relation to the area of each region and to the distribution of priority biodiversity areas.

Region	Ecosystem conversion 2008–2014		Species turnover (2050 A1B emissions scenario)		Carbon and accessibility		Population density change 2001–2010	
	% Region	% of Priority areas	% Region	% of Priority areas	% Region	% of Priority areas	% Region	% of Priority areas
Coast	34.16	46.78	1.81	1.37	14.12	7.62	21.60	13.87
Andes	43.51	30.29	9.33	11.51	20.49	12.55	10.48	3.55
Amazon	20.15	6.96	28.20	30.56	17.96	15.94	9.57	3.44
National	33.76	25.54	13.23	16.04	18.02	12.75	13.13	5.51

priority areas (16%) occurs in the Amazon region, especially in the central and western portions of this region (Figure 3).

Finally, areas with high changes in population density during the period 2001–2010 were more concen-

trated in the Coast (22%). Overlaps with priority biodiversity areas likewise were concentrated in this region, whereas the incidence in the Amazon and Andean region is fairly low in both regions as well as at the national scale (Figure 3, Table 3).

5. Discussion

5.1. The important areas for biodiversity conservation in mainland Ecuador

The important biodiversity areas identified in this study are a sound tool to guide biodiversity conservation efforts at national and subnational scales in mainland Ecuador based on the following reasons. Firstly, the use of a robust set of biodiversity surrogates (87 ecosystems and 840 species) allowed us to improve the identification of key biodiversity areas reported in the previous work of Cuesta et al. [10] and Sierra et al. [12]. The use of an important number of endemic and threatened species from different taxa, highlighted areas of specific conservation interest that were overlooked in the aforementioned studies (e.g. Illinizas, Cajas massif).

On the other hand, several of the selected areas outside the PANE by our findings converge with the results of Lessmann et al. [9], which is pertinent as it confirms the importance of the prioritized areas by two independent exercises carried out with a different set of biodiversity surrogates. Different conservation planning studies have argued that results using ecosystems as biodiversity surrogates may differ from the studies using species as the focal group [60,61]. Previous studies focused on ecosystems in Ecuador [10,12] diverge from a study in which priority areas were set up using species as the only biodiversity surrogate [9]. Thus, our research is a step forward in selecting priority areas for biodiversity conservation, as it combines surrogates, species, and ecosystems. As pointed out by Lessmann et al. [9], combining species- and ecosystem-based studies would improve the decision-makers' solution portfolio, minimizing biases, and allowing better-informed decisions.

Secondly, not forcing the inclusion of protected areas in the solution allowed us to assess the effective contribution of the PANE and SocioBosque Program, as complementary national conservation efforts, to conserve important areas for terrestrial biodiversity in mainland Ecuador. It highlights priority biodiversity areas that are currently outside the national protected area system (Figure 2, Table 1). These areas should be conceived as conservation priority as in many cases reflects areas with a high concentration of restricted range and threatened species. Thirdly, the use of reserve selection algorithms

and its calibration together with the applied sensitivity tests (Appendix 3 'Extended Methods' in SOM) on the results provided us with optimized solutions to identify key conservation areas in a rather small area (3,638,496 ha), particularly those outside the current reserve system (2,458,059 ha) (Table 4). Although previous exercises to identify priority areas for biodiversity are not completely comparable, due to the underlying differences in the approach adopted in each case (e.g. conservation goals established), the amount of area prioritized in this study is almost a third lower than previous studies (Table 4).

5.2. How well represented is Ecuador's ecosystem and species diversity within the current reserve system and the SocioBosque Program?

This study has shown that Ecuador's protected areas system (PANE) offers protection to an important number of ecosystems and species. Half of the ecosystem diversity is well represented in the natural reserves as well as the majority of the analyzed species (~60%). A similar proportion was documented for the entire bird taxa of Ecuador [62] and in a recent publication Fajardo et al. found a higher ratio in Peru in which 71% of the species are well represented in the current reserve system and using a conservation goal that varied between 5 and 50% of their current distribution. Globally, [53] found that from 11,633 species analyzed, 12% ($n = 1423$) were considered to be a gap species of all protected areas analyzed. That figure increased to 25% if only protected areas higher than 1,000 ha were analyzed.

Nonetheless, we found the endemic and threatened species are poorly represented in the current national protected areas system. Only four species of the 106 endemic or restricted range species are contained in the reserve system. A similar result was reported by Lessmann et al. who found that nearly 75% of the threatened species were inadequately represented in Ecuador's reserve system. A similar proportion was reported for the endemic plants of Ecuador [8] evidencing a similar trend when all the species of a specific group are analyzed. Likewise, Fajardo et al. [13] found that all the Critically Endangered, 86% of the Endangered, and 62% of the Vulnerable species are major conservation gaps of the Peruvian reserve system. Our findings are in line with

Table 4. Comparison of key elements used by published studies aimed at defining priority biodiversity areas in continental Ecuador.

Study reference	Biodiversity surrogates	Conservation goal	Area selected (ha)	Area selected outside PANE (ha)
Lessmann et al. [9]	Species	15–30% of species remnant distribution	9,037,500	4,984,300
Cuesta et al. [10]	Ecosystems and small set of species	10–90% of the species and ecosystem remnant distribution	7,316,000	3,410,893
Sierra et al. [12]	Ecosystems	10% of the potential ecosystem distribution	1,376,000	765,235
This study	Species and ecosystems	10–20% of the species or ecosystem remnant distribution	3,638,496	2,458,059

the results of the global gap assessment of Rodrigues et al. [53] who argued that on average ~36% of the 3896 threatened species are not protected by the global protected area network. In the same study, Rodrigues et al. [53] reported that amphibians were the least represented taxon of all taxa in which 50% of the 1543 threatened amphibian species are outside the protected areas' network. We found a similar pattern in which threatened birds and amphibians were the least protected groups, with 44 and 33% respectively.

Our findings have implications for the strategies needed to cover identified gaps, particularly those of endangered and endemic species which are a high priority [63]. Covering these gaps is not related to a linear increase in areas under conservation since patterns of biodiversity distribution are not homogeneous in space [64,65]. As such, restricted range species reflect aggregate patterns in specific regions resulting from current environmental conditions and past biogeographical and geological events [66]. Thus, priority should be given to preserving the endemism centers where these species occur [67].

The PSB program constitutes an important complementary strategy to secure the preservation of critical biodiversity areas. In the Coast, the PSB protects 8% of the selected priority areas of which the majority are located outside PANE. Especially important are the areas located in the Chongón-Colonche mountain ridge and between Pambilar and the Cotacachi-Cayapas reserve (Figures 1 and 2). On the Andes, the PSB program covers ~7% of the priority areas and, in different locations, these areas are located around the protected areas functioning as buffer zones and stepping stones between national protected areas (Figure 2). Lastly, in the Amazon, the contribution of PSB increased up to nearly 22%. A great portion of these areas improves substantially the representation of the priority areas in conservation schemes (Figure 2). Our findings have strong implications for the biodiversity national strategic planning. A priority action is to secure the long-term sustainability of the PSB incentive program. Of utmost important will be to secure the 500 thousand hectares directly linked to the priority areas for biodiversity conservation.

5.3. Conservation priorities and land use planning

The important biodiversity areas provide a spatially explicit framework to focus conservation efforts at the national level (Figure 2). However, in a small country such as Ecuador, increasing competition among alternative land uses requires a flexible framework to formulate land management goals and identify key areas to attain these goals. For example, modeling the potential effects of climate change on the composition of biotic communities reveal that important biodiversity areas in the western and southern Ecuadorian Amazon (Figure 3) are key to enhance the resilience of these ecosystems, and that

maintaining habitat connectivity can be important to hold up the persistence of species tracking their climatic niches [68].

In the short term, the prevalence of processes leading to ecosystem conversion and degradation highlights the need to protect threatened important biodiversity areas and the biotic communities these harbor. The most threatened ecosystem remnants from this perspective are the ones located in coastal Ecuador, where 47% of the important biodiversity areas identified in this study are close to recent (2008–2014) areas of habitat conversion due to deforestation (Table 4, Figure 3). The risk of future ecosystem conversion is attached to a broader set of socioeconomic factors, such as demographic processes, markets fluctuations and infrastructure expansion [69–71]. Recent growth (2001–2010) in population density reinforce the necessity of concentrating additional efforts in the Coast of Ecuador, where important demographic changes have occurred around important biodiversity areas (Table 4, Figure 3).

Another important pattern is the concentration of ecosystems with high carbon content and potentially high level of threat (modeled by accessibility patterns) surrounding important biodiversity areas and PANE areas in the northern Ecuadorian coast and in the external slopes of the Andean ranges, particularly in the Eastern flank [72] (Figure 3). This supports the need to engage in conservation strategies that address drivers of habitat conversion in the context of rapid social and economic change. These areas can become ideal candidates for mechanisms such as REDD+, which target threatened ecosystems with high potential to mitigate the emission of GHG and, at the same time, generate additional benefits through the conservation of biodiversity. The important areas for biodiversity add an explicit link to these types of efforts by providing a specific geographic focus where biodiversity co-benefits can be optimized [73].

Rather than having a unique framework to define a ranking of priority biodiversity areas, the four criteria used in this analysis, suggest that a more nuanced land use planning process is needed (Table 4, Figure 3). Designing conservation strategies should provide opportunities to examine alternative priority scenarios under different assumptions and land use planning goals [74]. For example, setting conservation priorities based on the likelihood of future habitat conversion will generate a different scenario if compared with setting priorities that minimize the potential impacts of climate change on the structure and composition of ecosystems. In this context, the important areas for biodiversity conservation identified in our study provide a common baseline to incorporate synergies and trade-offs into land use planning under different goals and assumptions [75]. These factors are not meant to be exhaustive or representative of all the relevant processes related to the vulnerability of ecosystems. Rather, this recognizes the need to adopt and develop different conservation strategies adjusted to the importance of drivers of change at more local scales

to qualify the results from the optimization exercise at the national level.

5.4. Recommendations to conserve the priority biodiversity areas in the short term

The outcome of biodiversity priority areas and the overlay with the protected area system, depicts 14 priority landscapes, equivalent to nearly half (1,782,863 ha) of the area selected in the Marxan solution (Figure 2). In the context of scarce resources and limited opportunities to set aside these areas from other land uses, these landscapes should be considered as a first priority due to their specific relevance in preserving Ecuador's terrestrial biodiversity. In the last 10 years (2005–2014), 15 new areas have been created adding-up nearly 230,000 ha to the national reserve network; unfortunately, only 11% of these areas have a spatial correspondence with the priority areas defined here. It would be important to use these results to guide further protected areas design and declaration. The contrast of the priority landscapes for biodiversity conservation with the current reserve network highlights the following recommendations:

- (1) Higher proportions (68%) of the priority biodiversity areas are located outside the PANE (Figure 2, Table 2). Thus, a landscape approach is needed to effectively manage the areas located outside the national protected area system. Of primary importance is the contribution of the SocioBosque program to this aim. The areas included in this incentive program helps to protect an additional 13% (456,653 ha) of the priority biodiversity areas.
- (2) The protected areas that better capture the spatial distribution of the biodiversity priority areas are Mache-Chindul, Machalilla, Cotacachi-Cayapas, Illinizas, Cajas, Sumaco Napo-Galeras, Yasuní, and Cuyabeno. These protected areas should be prioritized to strengthen their conservation effectiveness and investments allocations.
- (3) From the 14 selected landscapes, three are entirely outside the PANE suggesting the urgent needs for designing sound-base actions to preserve these priority biodiversity areas (i.e. Zapotillo – Landscape 3; Condor-Kutukú – Landscape 10; and Pastaza-Santiago watersheds – Landscape 14).
- (4) The majority of the reserves of the PANE (74%) are less than 100,000 ha and therefore too small to accomplish their conservation goals of sustaining viable populations and functional ecosystems [76,77]. The majority of those small protected areas are located in the Coast and the Southern Andes (Figure 1). In various cases, these reserves are isolated and embedded in an agricultural matrix, making them more prone to edge and fragmentation effects. We propose the expansion

of many of the existing reserves together with the design of conservation corridors in which the existing reserves act as core areas. The priorities should be focused on the following landscapes: Mache-Chindul (Landscape 1), Chongón-Colonche mountain range (Landscape 2), Illinizas-Mindo-Nambillo mountain range (Landscape 5), Cajas Massif (Landscape 7), Sangay-Siete Iglesias (Landscape 9).

- (5) In many of the prioritized landscapes, the possibility to create new reserves, or modify the limits of the existing ones is challenging. Land tenure conflicts, competing economic interests and local needs that trigger resource use pressure might hamper the suggested modifications [78]. Consequently, placing environmental protection in the mainstream development agenda of local governments (i.e. municipalities and provinces) seems to be at the core of the solution to try to overcome the obstacles to policy implementation. In this context, establishing agreements for decentralizing protected areas is a promising path as it has been documented in the Brazilian state of Bahia [79] among others [80]. The rationale of this approach is to improve the delivery and impact of public sector services by increasing the role of local governments and rural communities in decision-making [81]. In this sense, the conformation of a reserve system managed by local governments aimed at preserving essential environmental services for local dwellers is one of the major goals of the Ecuadorian Ministry of Environment [6]. Complementarily, establishing conservation agreements through conservation incentives programs with private owners could also be an effective strategy, as it has been recently reported for the SocioBosque program [82].
- (6) Since the formulation of the Convention on Biological Diversity (CBD) in 1992, the mission of protected areas has expanded from biodiversity conservation to improving human welfare. The result is a shift in favor of protected areas allowing local resource use [83]. Nevertheless, in Ecuador, the different categories of protected areas still are managed as if their only goal is to preserve nature and preclude human use. In practice, the country has no sustainable-use management areas aimed at sustaining rural livelihoods while preserving biodiverse rich areas. A revision of the protected areas categories must be a priority for the PANE as a way to articulate biodiversity conservation and rural sustainable development.
- (7) An effective articulation of the conservation priorities identified and land use planning processes pose important challenges, especially in the definition of sound conservation and sustainable land

management strategies. Rather than embedding all the intervening variables in a rigid prioritization and feasibility analysis at a single scale (e.g. national level), a more productive effort should recognize the importance of different contexts at an optimal scale (e.g. landscapes, watersheds) to establish a set of measures that combine conservation of key areas with ecosystem restoration [84] and other sustainable land management strategies in the surrounding landscapes [85,86].

Author contribution

Francisco Cuesta, Pi, designed the study, analyzed data, and wrote the paper.

Manuel Peralvo, Co-Pi, designed the study, analyzed data, and wrote the paper.

Andres Merino-Viteri was responsible for the generation and edition of SDMs models, consolidation of amphibians' species database, and revision of priority areas based on Marxan results

Macarena Bustamante designed the study, revised the priority areas based on Marxan results, and wrote the paper.

Francis Baquero is the GIS analyst of Marxan scenarios, SDMs edition.

Juan F Freile consolidated birds' database, SDMs edition, revised the priority areas based on Marxan results, and wrote the paper.

Priscilla Muriel consolidated the species' database and consolidated vascular plants' database, SDMs edition, and revised the priority areas based on Marxan results

Omar Torres-Carvajal consolidated reptiles' database, SDMs edition and revised the priority areas based on Marxan results.

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Supplemental data

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/23766808.2017.1295705>.

Notes

1. The PANE at 2015 is composed of 48 continental reserves. In 2013, when the study was carried out, the PANE was composed of 47 units.
2. The version of the ecosystem map used in this study is from May 2012, date in which the map distinguished 87 ecosystems. The final version of the map, published in 2013, describes 91 units.

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