

CONSERVATION ECOLOGY

Cost-effective conservation of amphibian ecology and evolution

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Habitat loss is the most important threat to species survival, and the efficient selection of priority areas is fundamental for good systematic conservation planning. Using amphibians as a conservation target, we designed an innovative assessment strategy, showing that prioritization models focused on functional, phylogenetic, and taxonomic diversity can include cost-effectiveness-based assessments of land values. We report new key conservation sites within the Brazilian Atlantic Forest hot spot, revealing a congruence of ecological and evolutionary patterns. We suggest payment for ecosystem services through environmental set-asides on private land, establishing potential trade-offs for ecological and evolutionary processes. Our findings introduce additional effective area-based conservation parameters that set new priorities for biodiversity assessment in the Atlantic Forest, validating the usefulness of a novel approach to cost-effectiveness-based assessments of conservation value for other species-rich regions.

INTRODUCTION

Ecosystem functioning and evolutionary processes are usually linked, carrying a series of short-term implications for ecological and human well-being (1). The consequences of human activities go beyond species loss, with various studies also reporting losses of functional traits and evolutionary history in various human-influenced landscapes (2). These losses are increasing demands for effective strategies on biodiversity conservation (3), which have been also subject to the incorporation of economic costs with the objective of providing more feasible conservation strategies on the ground (4). Given that habitat loss is the most important threat to species survival, the protected sites chosen by decision makers determine what species and how many of these will be able to survive in nature (5). The effectiveness of these selected sites in achieving conservation goals depends on how well the ecological diversity is represented in a given area (6). Several studies have focused on spatial prioritization to represent taxonomic diversity (TD), not highlighting the importance of capturing other biodiversity components, such as functional diversity (FD) and phylogenetic diversity (PD) (7). Moreover, to date, their conservation strategies have been blind to the functions these other components perform in a cost-effective conservation policy.

FD is a biodiversity dimension that represents the extent of functional differences among species based on the distinction of their morphological, physiological, and ecological traits (8). PD adds value to theoretical and applied ecology studies by distinguishing species according to their evolutionary histories (9), reflecting the time and mode of divergence across the tree of life (10). In addition, FD and PD can better predict ecosystem function and stability than TD (11, 12). However, using TD, FD, and PD in a simultaneous approach can help predict differential effects of competition and environmental filtering on the community assembly (13). Nonetheless, consistency in the relationships between TD, FD, and PD can provide insights into the extent to which community assembly is driven by deterministic versus stochastic processes (14).

A central question in community ecology and conservation biology is related to determining how biodiversity patterns can influence ecosystem functioning (15–17). The key strategy to address this issue is to assess the relationships between functional and phylogenetic biodiversity components of the ecosystem (11, 18). Understanding the associations between ecological similarity and phylogenetic relatedness among species helps in the formulation of a hypothesis about the impact of evolutionary changes on functional ecology (19). Focusing on both functional and phylogenetic traits of a community can improve our understanding of the consequences of biodiversity loss (20). However, to describe how environmental actions can protect multiple dimensions of biodiversity, comparative methods on the consequences of species extinction in relation to ecological and evolutionary traits still need to be applied (21).

Approaches to setting conservation priorities recommend ranking ecosystems on several criteria, including level of endangerment and metrics of species value such as evolutionary distinctiveness, ecological importance, and social significance (21). On the other hand, these approaches have not yet been implemented in practice and therefore remain as theoretical studies, not applied effectively in ecological landscape planning (22). Although the role of protected areas (PAs) in conserving biological communities is essential for natural systems (23), conservation planning needs to include the ecological functions performed by species that occur not only inside PAs but also throughout the biome (24). In this context, environmental set-asides on private land have been shown to be a promising strategy for conservation of species and ecological functions across farmlands (25). Nevertheless, set-asides of private land for conservation generally come with economic costs to the landowners (26). Therefore, environmental strategies that incorporate payment for ecosystem services (PES) can provide an efficient tool for increasing landowner participation in conservation programs (25). This strategy's feasibility is reflected in the ever-increasing number of PES projects around the world (27, 28). Despite this trend, most PES projects are relatively local initiatives that may not adequately represent the full range of conservation needs and economic issues observed throughout biodiversity hot spots (28). On the other hand, many environmental organizations are developing systematic planning tools to help identify opportunities that offer the greatest return on investment in biodiversity protection (29). In a conservation context, this investment can be indicated by cost-effectiveness-based estimates of land values, that is, the trade-off between biodiversity gains and economic costs of paying landowners to participate in set-aside programs (26).

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A conservation dilemma arises from the question of how much cost and which biodiversity components should be chosen in large-scale conservation programs. This context suggests a need for development of conservation plans that optimally balance economic costs and ecological constraints (30). However, effective conservation plans should also take into account the maintenance of functional and evolutionary processes as a justification for investments, mainly in biodiversity hot spots (31–33). Here, we explore how FD, PD, and TD are distributed in the most endangered biodiversity hot spot on Earth—the Brazilian Atlantic Forest (34)—focusing on the most threatened vertebrate group worldwide, amphibians (35). Given that spatial patterns of diversity and distribution of tropical amphibians are a consequence of their ecological and phylogenetic relations (36), we conducted a spatial prioritization of conservation management for the biodiversity components FD, PD, and TD, concerning threatened species (TS), PAs, and their respective land cost-effective values. We centered our land cost-effective estimations on the average PES values of \$13,273 for each square kilometer given annually to the private forest landowners in the Brazilian Atlantic Forest (26, 28). We aimed to incorporate the functions that amphibians perform with cost-effective considerations, exploring adequate conservation models that can allow us to preserve endangered species at a low cost. Therefore,

we report for the first time that the selection of priority sites based on PD and FD can be extended to include not only high species richness and threatened taxonomic groups but also land cost-effective outcomes.

RESULTS

Our results revealed a high FD and PD in the eastern Atlantic Forest, with the highest rates in the east central region rising to the northeast (Fig. 1, A and B). We found high correlations between TD with FD and PD ($r^2 = 0.86$, $P < 0.001$ and $r^2 = 0.82$, $P < 0.001$, respectively) (fig. S1, A and B). However, we observed that the values of FD and PD significantly differ from the random expectation of the null models ($P < 0.001$). Moreover, using paired t tests to validate these differences, we found highly significant differences between the observed distributions of FD and PD and the null models ($P < 10^{-16}$, t test). When we compared FD, PD, and TD with TS, we found low but significant correlations ($r^2 = 0.31$, $P < 0.001$; $r^2 = 0.26$, $P < 0.001$; and $r^2 = 0.33$, $P < 0.001$, respectively) (fig. S1, D to F). Mapping these relationships, we revealed important spatial mismatches and congruencies among these biodiversity components (Fig. 1, A to D). Our spatial analysis revealed a wide disparity among the biodiversity these various measures of biodiversity: We observed a

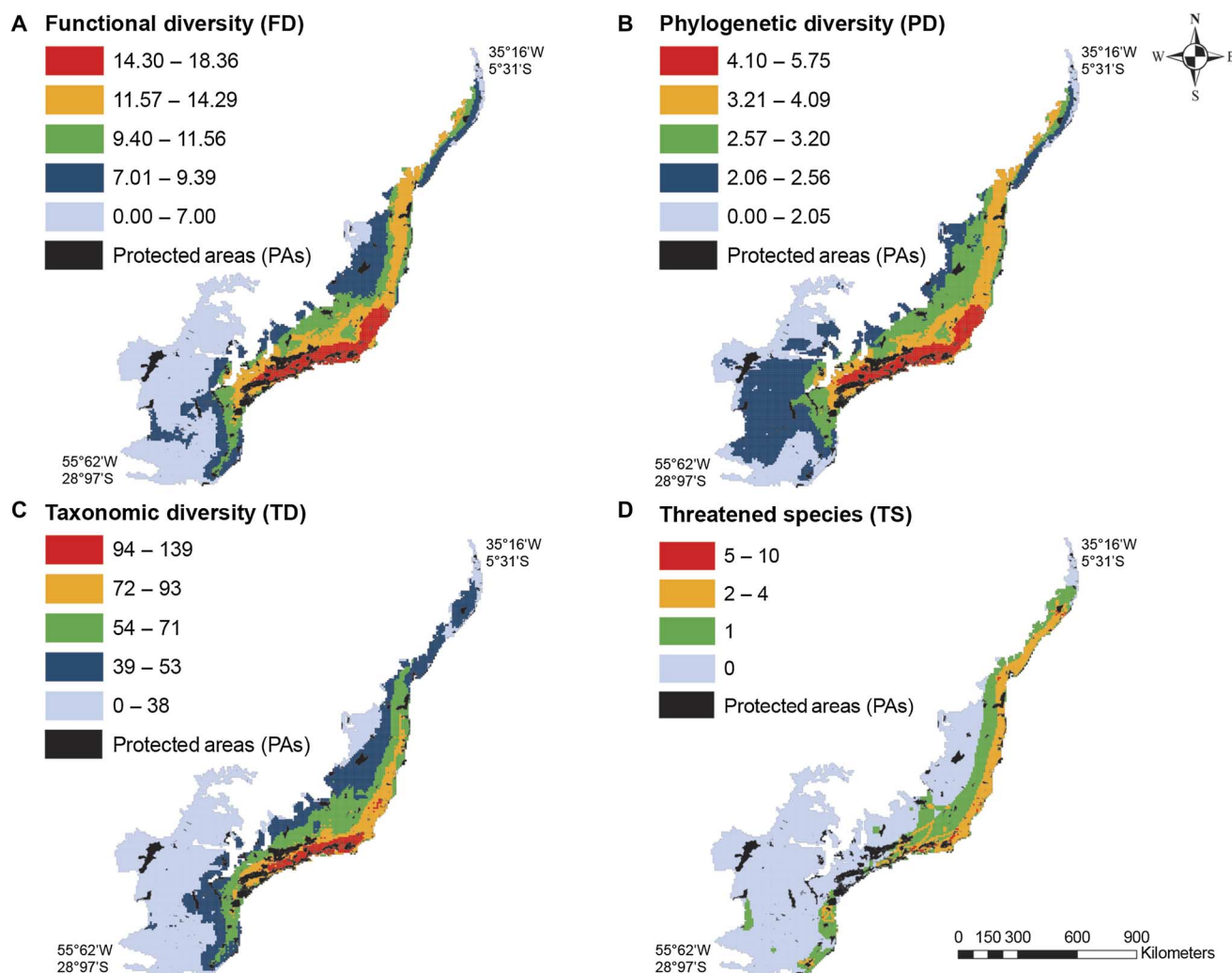


Fig. 1. Spatial distribution of FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

proportional difference of 5% between FD and PD, 14% between FD and TD, 12% between PD and TD, 44% between FD and TS, 42% between PD and TS, and 29% between TD and TS (fig. S2).

Through mapping and calculating the spatial data of the PAs, we found that a 9309.15-km² protected area in the Brazilian Atlantic Forest corresponded to only 9% of the region's entire area, comprising 2316.74 km² of strict protection areas and 6992.41 km² of sustainable use areas. This PA network comprises ~10% of FD, PD, and TD and almost 30% of TS, according to their spatial distributions across the Brazilian Atlantic Forest (Table 1). In total, we found 38 TS, corresponding to 17 critically endangered, 10 endangered, and 11 vulnerable species, with ~70% of their total geographical range distributed outside the PAs (Table 1). Incorporating cost-effectiveness assessments of land values into evaluation of PAs and non-PAs, we showed the amount of investment needed for proportional values of FD, PD, TD, and TS of amphibians in the Brazilian Atlantic Forest (Table 1). Permutational multivariate analysis of variance (PERMANOVA) results reveal that cost-effectiveness assessment of land values can be considered as a strong predictor for those biodiversity attributes assessed as conservation targets (table S1).

Our three prioritization models illustrate several scenarios for integrative assessments of FD, PD, TD, and TS attributes (Fig. 2). However, model 1 best represents the highest-priority regions for conservation (Table 2). Alternatively, models 2 and 3 show larger land areas, which also require higher investment. Although our results are area-dependent (square kilometers), we found a mismatch between percentage forest cover and overall land area in each model (Table 2). We recommend model 1 as the best cost-effective strategy, which has a greater capability to safeguard larger forest areas in addition to being the cheapest alternative (figs. S3 to S5). Moreover, model 1 has the lowest presence of PAs, which reinforces the urgent need to develop conservation efforts in these sites (Table 2). We also note that the priority sites indicated by this model corroborate the two larger climatic refuges for Neotropical species during the late Pleistocene [see the study of Carnaval *et al.* (37) for details], located in the central corridor of the Atlantic Forest and the Serra do Mar coastal forests.

DISCUSSION

Our findings provide different optimization scenarios for the conservation of amphibian diversity aspects. FD and PD indices have been proposed as effective techniques for capturing potential niche

complementarity in a community (11, 38). Some studies have highlighted the potential role of PD as a proxy for FD, yet this association is premised on the assumption that phylogenetic diversity generates ecological trait diversification, which in turn can result in greater niche complementarity (20). Despite the increasing evidence for positive correlations between taxonomic, functional, and phylogenetic attributes and ecosystem stability (39), the mismatch among TD, FD, and PD (7) is creating a conservation impasse, which demands a practical approach to assessing relative conservation values of these components of biodiversity. From a conservation viewpoint, FD and PD can be considered as two key attributes of diversity for safeguarding ecosystem goods and services (40), as well as for representing evolutionary processes and features of conservation interest (41). Therefore, measuring each of these biodiversity components in a complementary way is crucial for understanding the composition and dynamics of natural communities (10).

Mason *et al.* (42) showed that the FD component may reveal changes in community assembly processes along an environmental gradient, suggesting that this index may be a strong predictor of complex processes structuring communities. A multifaceted framework of the FD metrics behind these assembly processes facilitates the development of predictive models and more adequate tools for understanding how community structure is related to ecosystem functioning (43). In this context, the FD index can provide a potentially efficient power analysis to differentiate assembly rules for different degrees of species richness (43). On the other hand, null model approaches provide a robust means to test whether species with similar functional traits are more or less probable to occur together than expected at random (44). Therefore, use of the FD index associated with null models has shown to be the approach that best relates to community functioning and ecosystem processes (8, 43).

Considering the role of amphibian species in community functioning, the ecological contributions of these species can affect aquatic and terrestrial ecosystems as a whole, as well as the flux between these ecosystems (45). Amphibians have varied and significant roles in ecosystems, from soil bioturbation and nutrient cycling to pest control and ecosystem engineering (46). Some studies suggest that the loss of amphibians from stream ecosystems can alter primary production, algal community structure, faunal food chains (from aquatic insects up to riparian predators), and reduce energy transfers among diverse ecosystems through their role in nutrient cycling (45–47). Amphibians have frequently been cited as potential biological indicators of environmental change due to their permeable skin, high rates of contaminant bioaccumulation, climate-sensitive breeding cycles, and the fact that many species are dependent on both terrestrial and aquatic habitats during their life cycle (48–51). In addition, some amphibian taxa from small areas within the Atlantic Forest have been identified as potential indicators of general biodiversity (52).

Although a particular individual diversity component could be used as a surrogate for other biological attributes, biodiversity assessment should benefit from integrative approaches connecting evolutionary and functional ecology (40). Using integrative conservation strategies, we showed a congruence of ecological and evolutionary processes in the proposed models, yet they also revealed mismatches between land area and priority rank. Because of the large area considered for conservation, economic costs become an obstacle; but if insufficient land area is set aside, biological gains are weak (26). Our results thus demonstrate that local conservation policies for the Brazilian Atlantic Forest PAs do not guarantee the survival of most amphibian species in this region (~90% of TD). Moreover, the current PA network effectively protects only less

Table 1. Land cost-effectiveness and percent land covered by PAs and non-PAs, according to the spatial distribution of the FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.				
	FD	PD	TD	TS
PAs				
Land cost-effectiveness (million dollars)	159.49	152.71	127.86	36.36
Land covered (%)	11.60	11.10	9.38	29.37
Non-PAs				
Land cost-effectiveness (million dollars)	1215.45	1222.32	1245.97	87.07
Land covered (%)	88.40	88.90	90.62	70.63

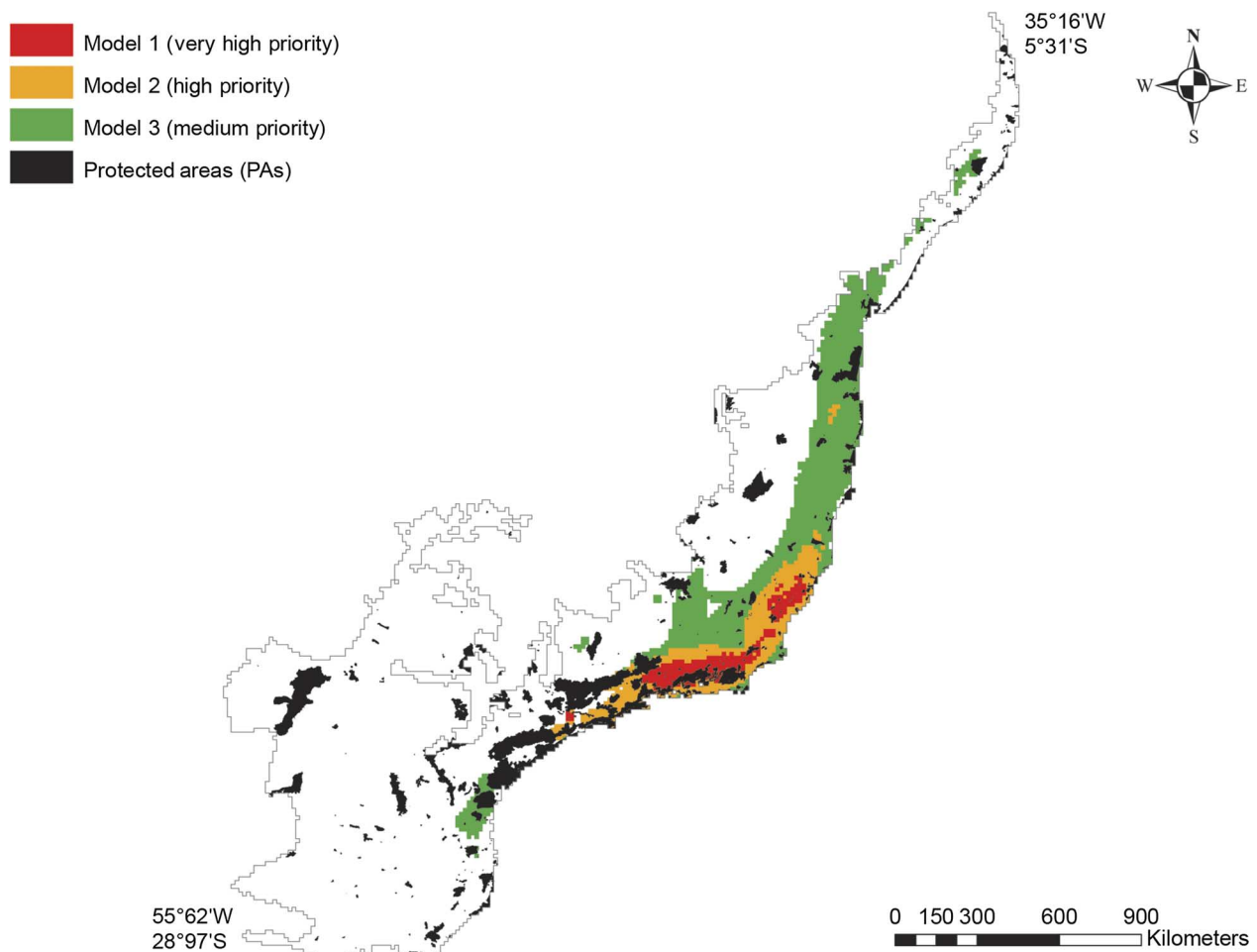


Fig. 2. Spatial distribution of the PAs and the three prioritization models proposed to amphibian conservation in the Brazilian Atlantic Forest.

Table 2. Area, excluded PAs, forest cover, and land cost-effectiveness by three priority scenarios to amphibian conservation in the Brazilian Atlantic Forest. Model 1, very high priority; model 2, high priority; model 3, medium priority.				
Priority scenarios	Area (km ²)	Excluded PAs (km ²)	Forest cover (%)	Land cost-effectiveness/year (million dollars)
Model 1	1,995.28	293.62	24.25	26.48
Model 2	4,555.12	934.02	15.30	60.46
Model 3	13,213.50	1406.28	11.86	175.38

than 10% of the total Atlantic Forest remnants (53). Although this reduced PA area seems inadequate, our results revealed that 28% of this network does nevertheless safeguard important eco-evolutionary processes, represented by those areas showing a $\geq 50\%$ FD, PD, and TD value of the total observed.

The selection of PAs is normally aimed to preserve species of different taxonomic groups, communities of high biological relevance, or combinations of different abiotic conditions favorable to local ecosystems, assuming that these sites will protect a wider range of biodiversity (54). However, many case studies reveal the inadequacy of the PA

network in representing species diversity (55). In north-eastern Brazil, Campos *et al.* (56) showed that the size of the PAs along the geographical range of threatened amphibian species does not necessarily safeguard their persistence, a finding also observed in this study. Moreover, it is predicted that the number of amphibian species of the Brazilian Atlantic Forest will decline within the PA network due to changing climate conditions (57). This network faces an additional risk because of its location within the economic center of Brazil (53), with a high human population density (~70% of the total Brazilian population) (58) and the presence of mining and logging industries in the region (57). To make

matters worse, a recent mining dam burst on 5 November 2015 destroyed one of the main river basins of the central corridor of Atlantic Forest, leading to the worst environmental disaster in the history of Brazil (59), which further accentuates the urgency for implementation of conservation strategies in this region. The federal and state Brazilian governments have sued the mine's owner companies with \$5 billion in damages (59), which have been said to be designated for funding of conservation plans aimed to restore this highly degraded ecosystem.

We centered our prioritization models on a return-on-investment framework to simulate how limited conservation funds could be spent on biodiversity protection, which were not based on agriculture land values, in accordance with the suggestions proposed by Sutton *et al.* (29). Our study demonstrates how the cost-effectiveness-based methods for assessing land values developed by our models could work as a functional PES, which, in comparison with agrarian activities, corresponds to 24.13% of the median yearly gross profit per square kilometer of agricultural land distributed in the Atlantic Forest domain (26). However, considering that only 12.30% of the total area covered by our models is represented by forest remnants, we recommend active reforestation practices in the nonforest areas (degraded livestock lands and abandoned agricultural lands). These practices would require an additional cost of up to \$500,000/km² for the first 3 years of restoration in the most degraded sites [see the study of Melo *et al.* (60) and Brancalion *et al.* (61) for details], corresponding to 0.02% of the Brazilian gross domestic product (26). On the other hand, most areas would follow natural regeneration simply by stopping the drivers of disturbance (60), taking into account that at least 20% of the area considered for restoration needs some active reforestation practice (61).

Considered individually, no single forest remnant reaches the minimum land values proposed by the Aichi Biodiversity Target 11, which concluded that the terrestrial PAs should be expanded to at least 17% by 2020 (62). In this context, models 1, 2, and 3 rise to about 5, 7, and 16%, respectively, from the current Brazilian Atlantic Forest PAs. We draw attention to the critical need for amphibian conservation efforts in Atlantic Forest, and to the critical fact that ~90% of FD, PD, and TD remain outside the PAs. Conservation strategies such as PES are essential to maintain the ecological and evolutionary process. Although the strength of this study is its innovative approach to incorporating biodiversity components into considerations of cost-effectiveness in conservation, our results rest heavily on good research in ecosystem service provisioning. According to the environmental message reported by Naem *et al.* (17), we also highlight the precautionary principle, in which "biodiversity conservation ensures ecosystem functions that in turn ensure ecosystem services benefiting humanity." Although we know that some ecosystem services cannot be subject to pricing, they should be considered on the basis of their biological value. Stakeholders and decision makers are key actors whose contribution is essential to putting these reports into practice. This situation demands political will and improved environmental services based on cost-effective designations of the highest-priority conservation areas, to reduce extinction risk and avoid species loss. Our research highlights the importance of maintaining the forest cover remnants in the Atlantic Forest, to provide a maximum representation of biodiversity components with the lowest economic cost. This innovative approach is not only amphibian-specific but can also be used in conservation plans for other taxonomic groups. This work has advanced knowledge of the analytical methods that can be used to plan effective environmental actions to protect multiple biodiversity components with limited resources.

MATERIALS AND METHODS

Study area

Considered as the most threatened biodiversity hot spots on Earth (34), the Atlantic Forest had an original of area around 1,500,000 km², of which only about 12.9% (~194,500 km²) still remains in Brazil, Paraguay, and Argentina (53), corresponding to about 100,000 km² of Brazilian forest remnants (63). The large fragments are located in hilly terrain, which hinder human occupation (64). Moreover, the ranges of different altitudinal and latitudinal gradients where these remnants were found have favored high biodiversity and endemic species compared to other biomes in Brazil (53).

Although having a high rate of habitat loss (65), which is one of the main risk factors for amphibian extinction (35), the Atlantic Forest is the leader biome in amphibian diversity in Brazil, with 543 described species, comprising ~90% endemics and corresponding to more than 50% of all amphibian species of the entire country (66). However, despite the legal restrictions on deforestation in the Brazilian Atlantic Forest, vegetation is still extracted illegally, representing a mean rate of forest loss of around 0.15%/year (67). Here, we used the term Brazilian Atlantic Forest with regard to the vegetation remnant map reported by the SOS Mata Atlântica/Instituto Nacional de Pesquisas Espaciais in 2015 (67).

Data acquisition

We obtained spatial data on amphibian species with three procedural approaches. First, we built a data set with all the species distributed in the Atlantic Forest according to Haddad *et al.* (66); second, we included maps of geographical ranges for each species from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species database (68); and third, we conducted complementary fieldwork comprising the major Atlantic Forest remnants of Brazil, to supplement the data set with additional data on distribution and observed functional traits (body size, reproductive mode, habitat, activity, poison patterns, habit, and calling site).

We led the survey in seven Brazilian PAs located in the central corridor of the Atlantic Forest and the Serra do Mar coastal forests, stretching from the south to the northeast of the country (fig. S6). We sampled each area for 10 days between January and March 2015 (wet season), which are the months of highest activity of amphibians in the Atlantic Forest (69). In all localities, we conducted the survey using acoustic and visual nocturnal/diurnal assessments (70, 71), through an active search around water bodies, streams, and along 2000 m of forest transects for each assessed PA.

Next, we used ArcGIS 10.1 software (72) to build presence/absence matrices from the species distribution data by superimposing a grid system with cells of 0.1° latitude/longitude, creating a network with 10,359 grid cells for the Brazilian Atlantic Forest. We also used spatial data on the Atlantic Forest PAs through the Brazil's Ministry of Environment database (73), including their categories (IUCN categories I to IV) and land coverage.

Data analyses

We characterized 453 amphibian species through eight functional traits from 56 categories that determine different dimensions of the amphibians' ecological niches regarding morphology, life history, and behavior. We used the trait categories reported by Haddad *et al.* (66), with some additional complementary data obtained in our fieldwork (see data file S1). Data file S1 describes the functional traits and their references for 453 amphibian species sampled in the Brazilian Atlantic Forest:

(i) body size (millimeter), (ii) members (apodal and tetrapod), (iii) activity (nocturnal, diurnal, and both), (iv) toxicity (toxic, nontoxic, unpalatable, or bad odor), (v) habitat (forested area, open area, and both), (vi) habit (arboreal, phytotelmata, terrestrial, cryptozoic, fossorial, rheophilic, semiaquatic, and aquatic), (vii) calling site (bamboo grove, swamp or lake, bromeliad, forest floor, tree canopy, caves or burrows, rock wall, backwater river, stream, river, shrubs, grasslands, and not sings), and (viii) reproductive mode [1 to 39 modes; see the study of Haddad and Prado (74)]. These functional traits primarily contribute to ecosystem-supporting services through direct and indirect changes on ecosystem functions and processes (46). These functions can be structural (habitat and habit) and ecological (body size, members, activity, poisonous, calling site, and reproductive mode). For further details, see the Supplementary Materials (table S2), where we show the specific functions and the ecosystem-supporting services of each one of the functional traits assessed (46, 66, 74–77).

To calculate the FD, we followed the protocol proposed by Petchey and Gaston (8): (i) construction of a species-trait matrix, (ii) conversion of species-trait matrix into a distance matrix, (iii) clustering distance matrix into a UPGMA (Unweighted Pair-Group Method with Arithmetic Average) dendrogram, and (iv) calculating FD by summing dendrogram branch lengths of species community. According to Petchey and Gaston (8), FD is the functional metric that best relates to the functioning of communities. To create the distance matrices, we used the method proposed by Pavoine *et al.* (78), through the Gower distance. We constructed the dendrograms using a hierarchical clustering, where only the species found in both the functional trait data set and the amphibian occurrence database were considered. To verify whether FD was influenced by species richness, we used independent swap null models (79), according to the protocol proposed by Swenson (80). The values provided by these models are more sensitive in preserving both site diversity and species frequency of occurrence while randomizing the pairs of species/sites, which ensure that patterns of trait assembly do not simply reflect differential occurrence of particular species (80, 81). We tested whether the observed FD was higher, equal, or lower than that expected by chance for each grid cell, assuming a random distribution in which every species could occupy any grid cell in the biome. For this, we computed 1000 random replicates of the remaining FD, allowing us to obtain a *P* value of FD as compared to the distribution of the random replicates. Although observed and null FD metrics indicate very similar responses (43, 80), the values generated by these metrics do not necessarily represent redundant information. Observed FD is highly correlated with species richness, whereas its null model is totally independent of the species richness of an assemblage (80), which provides expected values at different species richness levels (43). In addition, we compared relative changes of observed and null FD distributions using paired *t* test. Given their different ability to discriminate community assembly rules, where the predictive accuracy of null FD is clearly better than the observed FD (43, 80), we used the null model approach to detecting patterns in the overlap among species in functional character space. Therefore, we used the term FD with regard to the null FD distributions in all further comparisons. We performed all analyses using the packages “ade4,” “picante,” “FD,” and “vegan” through the R software (82).

For PD, we used the Faith’s PD index (83), comprising the sum of the lengths of the branches from the phylogenetic tree of all species assessed. We based the phylogenetic distance on 207 species nucleotide sequences obtained from GenBank (data file S2) [see the study of Benson *et al.* (84)], provided by the National Center for Biotechnology Information. Following the protocol proposed by Pyron and Wiens (85)

in an extant amphibian phylogeny, we used 12 genes to produce a novel phylogeny estimate for the Atlantic Forest amphibians (11,906 base pairs for each species), through three mitochondrial (Cyt-b, 12s, and 16s) and 9 nuclear (CXCR4, H3A, NCX1, POMC, RAG1, ROHD, SIA, SLC8A3, and TYR) genes. For length-variable regions, we performed multiple pairwise comparisons using the online version of MAFFT 6.8 with the G-INS-i algorithm (86). Next, we put together alignments of all genes in the same alignment, using the software Sequence Matrix 1.7.7 (87) to concatenate the supermatrix previously produced.

We reconstructed phylogenetic relationships with Bayesian analyses using BEAST 1.8 (88). We performed the phylogenetic analysis based on the combined data matrix through the Hasegawa, Kishino, and Yano (HKY) model of sequence evolution for one partition for all genes, using a Yule speciation process as the tree prior under an uncorrelated relaxed clock. We ran the Yule process for 100 million generations, ensuring that the number of generations convergence was sufficiently assessed with Tracer 1.6 (88), removing a conservative 10% burn-in fraction for the final tree. We combined these results with the use of LogCombiner 1.8.1 and TreeAnnotator 1.8.1 (88). We considered the nodes strongly supported if they received a posterior probability of ≥ 0.95 . To edit the new phylogenetic tree, we used R software (82), from the package “ape” (89), using the Mesquite software 3.04 (90) as an additional viewing tool. As provided on the functional metrics, we also built null models to PD according to the same protocol used to obtain the null FD expectations (80). Therefore, we computed 1000 random replicates of remaining PD, obtaining a *P* value of PD as compared to the distribution of the random replicates. We also compared relative changes of observed and null PD distributions using paired *t* test. As proposed in the FD analyses and considering the predictive accuracy of the null PD compared with the observed PD, we used the term PD with regard to the null PD distributions in all further comparisons. We performed the null model analyses using the packages ade4, picante, and vegan through the R software (82).

In addition, we calculated the TD and the number of TS present in each grid cell, correlating with the values obtained by the FD and PD indices through simple linear regression models. We also plotted the mismatches among the relative values of these biodiversity components in a spatial representation to show where the greatest disparity might be, which is also of interest. We classified TS according to the National Red List categories, using the official list of TS of the Brazilian fauna (91). We calculated the cost-effectiveness values according to the area required to represent each biodiversity component assessed (FD, PD, TD, and TS). Following Banks-Leite *et al.* (26), we based our cost-effectiveness analyses on the average value of PES across the Brazilian Atlantic Forest remnants, which corresponds to \$13,273 for each square kilometer given annually to the private forest landowners (28). In addition, to provide a comparative estimate of cost-effectiveness-based land values of PAs and non-PAs, we performed a gap analysis (92), measuring the amount of FD, PD, TD, and TS covered both by PAs and non-PAs. Thus, to assess the response of cost-effectiveness against the predicted variables FD, PD, TD, and TS, we used PERMANOVA, with 1000 permutations based on a Euclidean distance matrix, through the “adonis” function in the vegan R package (93). Finally, we provide three prioritization models based on different levels of complementary scenarios calculated as

$$\text{Model 1 (90\%)} = \left\{ \text{FD} \geq \left[\left(0.9 \left(\left(\sum_{i=0}^n \text{FD} \right) / N \right) \right) / 0.5 \right] + \text{PD} \geq \left[\left(0.9 \left(\left(\sum_{i=0}^n \text{PD} \right) / N \right) \right) / 0.5 \right] + \text{TD} \geq \right.$$

$$\left[\left(0.9 \left(\left(\sum_{i=0}^n \text{TD} \right) / N \right) \right) / 0.5 \right] + \left. \text{TS} \geq 1 \right\} \text{-PAs}$$

$$\text{Model 2 (70\%)} = \left\{ \text{FD} \geq \left[\left(0.7 \left(\left(\sum_{i=0}^n \text{FD} \right) / N \right) \right) / 0.5 \right] + \text{PD} \geq \left[\left(0.7 \left(\left(\sum_{i=0}^n \text{PD} \right) / N \right) \right) / 0.5 \right] + \text{TD} \geq \left[\left(0.7 \left(\left(\sum_{i=0}^n \text{TD} \right) / N \right) \right) / 0.5 \right] + \left. \text{TS} \geq 1 \right\} \text{-PAs}$$

$$\text{Model 3 (50\%)} = \left\{ \text{FD} \geq \left[\left(\sum_{i=0}^n \text{FD} \right) / N \right] + \text{PD} \geq \left[\left(\sum_{i=0}^n \text{PD} \right) / N \right] + \text{TD} \geq \left[\left(\sum_{i=0}^n \text{TD} \right) / N \right] + \left. \text{TS} \geq 1 \right\} \text{-PAs}$$

where model 1 refers to very high priority, and values of FD, PD, and TD are $\geq 90\%$ of the total observed (N); model 2 refers to high priority, where values of FD, PD, and TD are $\geq 70\%$ of the total observed (N); and model 3 refers to a medium priority, where values of FD, PD, and TD are $\geq 50\%$ of the total observed (N). We did not consider areas with FD, PD, and TD values lower than the average conservation targets assessed (FD, PD, and TD, $< 50\%$ of the total observed). The main reason for this approach was to establish prioritization models that indicate areas from medium to very high priority, leaving out areas with low priority. In these three models, we considered only areas containing at least one TS ($\text{TS} \geq 1$) and excluded all the PAs available, analyzing only non-PAs (areas under no protection). Under our prioritization approach, we assumed that areas that are already protected, such as PAs, do not have priority for additional conservation efforts.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/6/e1602929/DC1>

fig. S1. Plots of the relationships between FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

fig. S2. Mismatch maps among FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

fig. S3. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the very high priority sites covered by the proposed model 1 to amphibian conservation in the Brazilian Atlantic Forest.

fig. S4. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the high-priority sites covered by the proposed model 2 to amphibian conservation in the Brazilian Atlantic Forest.

fig. S5. Spatial distribution of the PAs, the forest remnants outside of the PAs, and the medium-priority sites covered by the proposed model 3 to amphibian conservation in the Brazilian Atlantic Forest.

fig. S6. Forest remnants and complementary fieldwork areas sampled in the Brazilian Atlantic Forest.

table S1. Results from the PERMANOVA on the land cost-effectiveness by the FD (Petchey and Gaston's FD), PD (Faith's PD), TD, and TS of amphibians in the Brazilian Atlantic Forest.

table S2. Specific functions, ecosystem-supporting services, and references related to the amphibian functional traits assessed in the Brazilian Atlantic Forest.

data file S1. Functional traits and references for 453 amphibian species sampled in the Brazilian Atlantic Forest (xlsx as a separate file).

data file S2. GenBank accession numbers for 207 amphibian species sampled in the Brazilian Atlantic Forest (xlsx as a separate file).

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