No more trouble: An economic strategy to protect taxonomic, functional and phylogenetic diversity of continental turtles

Ricardo Lourenço-de-Moraesa[b,*], Felipe S. Campos[c,*], Ana C. Carnavald[e],
Mileny Otani[a], Frederico G. R. França[b], Pedro Cabral[c], Evanilde Benedito[a]

[a]Programa de Pós-graduacão em Ecologia de Ambientes Aquáticos Continentais (PEA), Departamento de Ciências Biológicas, Universidade Estadual de Maringá, 87020-900 Maringá, PR, Brazil

[b] Present address: Programa de Pós-graduação em Ecologia e Monitoramento Ambiental (PPGEMA), Universidade Federal da Paraíba, 58297-000, Rio Tinto, PB, Brazil

[c]NOVA Information Management School (NOVA IMS), Universidade Nova de Lisboa, 1070-312 Lisboa, Portugal

[d]Department of Biology, City College of New York, New York, NY, 10031 USA

[e]Graduate Center, City University of New York, New York, NY 10016, USA

*Corresponding authors

E-mail addresses: rlm@academico.ufpb.br (R. Lourenço-de-Moraes); fcampos@novaims.unl.pt (F.S. Campos); acarnaval@ccny.cuny.edu (A.C. Carnaval); milenyotani1@gmail.com (M. Otani); fredericogrf@gmail.com (F.G.R. França); pcabral@novaims.unl.pt (P. Cabral); eva@nupelia.uem.br (E. Benedito).

Lourenço-de-Moraes, R., Campos, F. S., Carnaval, A. C., Otani, M., França, F. G. R., Cabral, P., & Benedito, E. (2021). No more trouble: An economic strategy to protect taxonomic, functional and phylogenetic diversity of continental turtles. Biological Conservation, 261, 1-10. [109241]. https://doi.org/10.1016/j.biocon.2021.109241

Funding Information:

We thank Anders G.J. Rhodin (Chelonian Research Foundation, Tortoise and Freshwater Turtle Specialist Group) and John Iverson (Earlham College) for spatial data of species and Carlos E. Guidorizzi (ICMBio-RAN) for spatial data of species Chelonoidis denticulatus. RLM thanks CNPq (151473/2018-8) for providing fellowship. FSC and PC thank the Portuguese Foundation for Science and Technology (PTDC/CTA-AMB/28438/2017) and Management Research Center – MagIC/NOVA IMS (UIDB/04152/2020). This study was financed in part by the CAPES - Finance Code 001.

No more trouble: an economic strategy to protect taxonomic, functional and phylogenetic diversity of continental turtles

Ricardo Lourenço-de-Moraes[a,b,*], Felipe S. Campos[c,*], Ana C. Carnaval[d,e], Mileny Otani[a], Frederico G. R. França[b], Pedro Cabral[c], Evanilde Benedito[a]

[a] *Programa de Pós-graduacão em Ecologia de Ambientes Aquáticos Continentais (PEA), Departamento de Ciências Biológicas, Universidade Estadual de Maringá, 87020-900 Maringá, PR, Brazil*

[b] *Present address: Programa de Pós-graduação em Ecologia e Monitoramento Ambiental (PPGEMA), Universidade Federal da Paraíba, 58297-000, Rio Tinto, PB, Brazil*

[c] *NOVA Information Management School (NOVA IMS), Universidade Nova de Lisboa, 1070-312 Lisboa, Portugal*

[d] *Department of Biology, City College of New York, New York, NY, 10031 USA*

[e] *Graduate Center, City University of New York, New York, NY 10016, USA*

*Corresponding authors

E-mail addresses: rlm@academico.ufpb.br (R. Lourenço-de-Moraes); fcampos@novaims.unl.pt (F.S. Campos); acarnaval@ccny.cuny.edu (A.C. Carnaval); milenyotani1@gmail.com (M. Otani); fredericogrf@gmail.com (F.G.R. França); pcabral@novaims.unl.pt (P. Cabral); eva@nupelia.uem.br (E. Benedito).

ABSTRACT

One key strategy to publicise the benefits of nature more effectively to people is to correlate indicators of human well-being with conservation needs. Turtles are important and publicly visible ecological indicator groups. We use continental turtles as flagship umbrella species in the Brazilian Atlantic Forest hotspot to design a conservation strategy that incorporates taxonomic (TD), functional (FD) and phylogenetic diversity (PD) for improved cost-effective outcomes. We first analyse the effectiveness of the current arrangement of protected areas (PAs) in safeguarding species by calculating the mean percentage overlap. We create three conservation models that differ in the amount of TD, FD and PD preserved. Each model defines a distinct plan (and cost) of paying landowners to participate in set-aside programs to preserve local habitats. We also analyse the performance of indicator species in representing TD, FD and PD gains and economic costs induced by payments for ecosystem services. The results show that species of continental turtles are not well conserved in the PAs. The spatial distribution of TD is highly correlated with that of FD and PD in the biome with high values in the central region, extreme North, and South of the Atlantic Forest, due to the co-existence of the evolutionary lineages. We suggest a program for conservation planning to protect a threatened biodiversity hotspot, the ecosystem functions provided by flagship umbrella species, and its associated ecological and evolutionary values. Our findings are providing a representation of ecological and evolutionary values of continental turtles with annual economic benefits from environmental management tools.

Keywords:

Atlantic Forest, biodiversity hotspot, conservation priorities, protected areas, freshwater turtles, tortoises

1. Introduction

The importance of continental turtles for the stability and functioning of ecosystems is widely recognised (Hansen et al., 2010; Vitt and Caldwell, 2014; Matsumoto et al., 2014; Viana et al., 2017; Stanford et al., 2018). Their vast ecological contributions play a key role in aquatic and terrestrial habitats, as well as the flux between them, which are directly related to their sensitivity to environmental change (Schneider et al., 2009; Matsumoto et al., 2014). Affected by pollution, habitat loss, predatory hunting, and the pet trade (TEWG, 2015), more than half of the species of continental turtles (i.e., freshwater turtles and tortoises) are endangered with extinction (Rhodin et al., 2017), making them one of the most threatened vertebrate groups on Earth (Rhodin et al., 2018). In addition to controlling trophic dynamics in many ecosystems, continental turtles have significant environmental functions (Junk, 1997; Viana et al., 2017; Stanford et al., 2018). For one, these species can affect nutrient cycling at the ecosystem level, which in many cases ensures habitat quality for other species groups (Fuentes et al., 2014). Their interactions in the functioning of ecosystems also include soil bioturbation, seed dispersal, and ecosystem engineering processes (Hansen et al., 2010; Vitt and Caldwell, 2014; Viana et al., 2017). Loss of continental turtles in ecosystems can alter primary production and the community structure of faunal food chains, reduce energy transfer between ecosystems, and impact the quality of drinking water (Hopkins et al., 2013). However, turtles' important contributions to natural ecosystems are highly threatened by habitat loss, pollution, and climate change -

with broad ecological consequences to human well-being (Fuentes et al., 2014; Stanford et al., 2018).

To simplify complex conservation problems into feasible strategies, the flagship and umbrella species concepts were developed for common ecological proxies (Veríssimo et al., 2011; Stuber and Fontaine, 2018). Based on similar ecological requirements, the concept of umbrella species suggests the protection of a wide range of co-occurring species as a shortcut for the conservation in ecosystems (Fleishman et al., 2000: Seddon and Leech, 2008). Charismatic and well-known species to the public can be named as flagships species, are primarily intended to promote public awareness and to raise funds for conservation (Veríssimo et al., 2011). In this context, continental turtles can be defined as flagship umbrella species (i.e., flagship and umbrella species) whose conservation confers both functions (Caro, 2010). Many continental turtle species are freshwater, so actions that promote public and political involvement with these iconic freshwater species would give greater visibility to freshwater ecosystems and can motivate the public to take conservation action (Kalingat et al., 2017). However, the efficiency of such selected shortcuts in achieving conservation goals depends on how well represented are their ecological components (Dietz et al., 2015). Additional conservation actions are needed to safeguard the effectiveness of these conservation shortcuts among taxonomic groups without protection, particularly for continental turtles, which have only 10% of their range protected (Roll et al., 2017).

Current environmental challenges facing humanity – including that of preserving key groups such as continental turtles – require effective approaches to biodiversity conservation planning (Corlett, 2015). Although controversial (Silvertown, 2015), one of the most realistic options is to incorporate the economic values of environmental management into biodiversity policy-making (Atkinson et al., 2012). Given that conservation efforts are often limited by time and money (Naeem et al., 2016), a multifaceted framework of biodiversity components is key to ensure functioning ecosystems that provide social and ecological benefits in changing landscapes (Pollock et al., 2017). Ecological (functional) and evolutionary (phylogenetic) diversity are also needed to ensure biodiversity persistence in a changing world (Pressey et al., 2007). Functional diversity is a biodiversity dimension that represents the extent of ecological differences between species, based on differences in their morphological (e.g., body size), physiological (e.g., poisonous), or life history (e.g., habit) (Petchey and Gaston, 2006). Phylogenetic diversity reflects the evolutionary histories of the species that coexist in a given area and quantifies how much of the Tree of Life is represented locally – an issue particularly relevant when one aims to preserve the evolutionary and adaptive potential of a biota over time (Magurran, 2004). Understanding the associations between the functional and phylogenetic components among species helps to formulate a hypothesis about evolutionary changes in the structure of communities (Hof et al., 2010). Any well-planned strategy for the conservation of functional and phylogenetic diversity requires detailed prior knowledge of the geographic distribution of the species to be evaluated (Campos et al., 2017), along with knowledge of their phenotypes and evolution.

Here, we exemplify how the integration of information sources (spatial ranges and species richness, their phenotypes and life history, and evolutionary history) can be added to cost-effectiveness–based assessments for improved conservation outcomes. While crucial to protect threatened biodiversity hotspots and their ecosystem functioning relationships (Lawler and White, 2008), most analyses to date have not yet compared and selected effective strategies for benefit-targeting conservation while considering multiple dimensions of biodiversity – particularly those reflecting their ecological and evolutionary legacies (Carbayo and Marques, 2011). How much does it cost to preserve these multiple dimensions within one group of organisms, and which targets should be selected by conservation strategies? While the evolutionary and ecological monetary value of species and taxonomic groups are often implicitly acknowledged in conservation planning, only a few studies have addressed this issue in an ecological landscape planning framework (e.g., Banks-Leite et al., 2014; Petersen et al., 2016).

We use continental turtles (i.e., freshwater turtles and tortoises) as flagship umbrella species to illustrate how to incorporate knowledge of taxonomic, functional, and phylogenetic diversity in the Brazilian Atlantic Forest while integrating economic costs into practical conservation planning. We show a multifaceted framework of biodiversity components proposed as strong drivers of ecological and evolutionary processes in feasible conservation strategies. To verify the effectiveness of the existing protected areas (PAs), we first evaluate whether their current distribution in the Brazilian Atlantic Forest is efficient to protect the species of continental turtles. We then conduct a spatial prioritization scheme for biodiversity conservation and management by estimating cost-effective values for land set-asides under three scenarios that differ in the amount of taxonomic (TD), functional (FD) and phylogenetic diversity (PD) of continental turtles that they preserve.

2. Methods

2.1. Study area

We focus our analyses on the Brazilian Atlantic Forest Biodiversity Hotspot (Myers et al., 2000), which once covered around 150 million ha, and yet is now reduced to 6-10% of its Pre-Columbian range (Ribeiro et al., 2009). In this domain, heterogeneous environmental conditions are provided by a wide range of climatic belts and vegetation formations (Ribeiro et al., 2009): the forest has an altitudinal range that extends from sea level to up to 2,000 m above sea level in the mountain chains of the Serra do Mar and Serra da Mantiqueira (Cavarzere and Silveira, 2012). The longitudinal range of the forest allows it to harbour differences in tree composition due to a diminishing gradient in rainfall from the coast to the interior, and its latitudinal range extends into tropical and subtropical environments (Ribeiro et al., 2009) (Fig. 1 and Fig. S1).

2.2. Spatial data

We obtained spatial data from 15 species of continental turtles (two tortoises and 13 freshwater turtles) that occur in the Brazilian Atlantic Forest to create an updated database of geographic distribution maps for all species. For that, we gathered the species distribution maps provided by the Chelonian Research Foundation and Turtle Conservancy (Rhodin et al., 2017; https://iucn-tftsg.org/checklist/) in association with the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Turtle Conservation Fund, Global Wildlife Conservation, Conservation International, and IUCN Red List database (www.iucnredlist.org/), version 2020.3 (IUCN, 2020). We also consulted Brazil’s Chelonian Red List (Vogt et al., 2015) and the Reptile Red List of the Espirito Santo State (Bérnils et al. in press) to confirm the geographic distribution of *Chelonoidis denticulatus* (see Table S1 for details).

To compile a list of species supported by the existing network of protected areas (PAs), we then compiled spatial data on the distribution of PAs of the Atlantic Forest from the Brazil's Ministry of Environment database (MMA, 2017). We used only those PAs falling within IUCN (www.iucnredlist.org) categories (I to IV, IUCN 2020), which represent National, State, and Municipal PAs, a total of 133 protected areas. We then superimposed the species distribution data on a gridded representation of the PAs and the Brazilian Atlantic Forest, with a spatial resolution of 0.1 degrees (~10km^2 grid cell). In preparation for the subsequent analyses, we used ArcGIS Pro software (ESRI, 2019) to create a presence/absence matrix of species per grid cell (10,359 grid cells) and a matrix describing the percentage of the grid cell occupied by PAs (133 PAs covered 876 grid cells vs. 10,359 grid cells).

2.3. Effectiveness of the existing PAs network

To demonstrate the level of representativeness of the existing network of PAs in protects continental turtle diversity in the Atlantic Forest, we calculated the Mean Percentage Overlap - MPO. The MPO corresponds mean percentage of spatial overlap between the units in which the species occurs in the studied area and the protected areas (Sanchez-Fernandez and Abellán, 2015; Lourenço-de-Moraes et al., 2019a). First, we obtained the spatial overlap (%) of each cell of the study area with the polygons of PAs. After, we used null models to test if the level of the MPO of each species was significantly different (lower or higher) than would be expected by chance, considered the number of occupied cells of each species (i.e., range size). For that, we used the software R (R Development Core Team, 2019) to compare the observed MPO value of each species with MPO values obtained from 1,000 randomizations using a significance level of $p < 0.05$.

2.4. Estimating Taxonomic, Functional and Phylogenetic diversity

To estimate and map Taxonomic Diversity (TD), we added the number of turtle species in each one of the 10,359 grid cells of the Brazilian Atlantic Forest. To map Functional Diversity (FD), we built a database of six major categories of functional traits of continental turtles, representing morphology, life history, and behaviour characteristics (e.g., Vogt et al. 2015; see Table S2). The traits are: 1) body size (maximum length of the species); 2) habitat (open area, forest, or both); 3) habit (semi-aquatic or terrestrial); 4) time of activity (day, night, or both); 5) diet (annelids, molluscs, arthropods, fishes, amphibians, mammals, birds, aquatic plants, or terrestrial plants/seeds); 6) environment (forest floor, swamp/lake, stream, river, or stream and river). For details of specific functions and ecosystem supporting services of each one of the functional traits assessed, see Table S3. To estimate the FD at each grid cell we followed Petchey and Gaston (2006) and 1) constructed a species-trait matrix; 2) converted the species-trait matrix into a species distance matrix, using Gower distances (Pavoine et al., 2009); 3) clustered the distance matrix into a dendrogram (UPGMA); and 4) calculated the total functional diversity in each grid cell by summing the dendrogram branch lengths leading to all species expected to be found in each grid cell in the biome.

To estimate the Phylogenetic Diversity (PD) represented by continental turtles of the Brazilian Atlantic Forest, we used the turtle phylogeny inferred by Crawford et al. (2015) to calculate Faith’s (1992) PD index. Faith’s PD has been shown to appropriately account for relatedness between taxa and evolutionary history in a conservation context (Pio et al., 2011). This PD index comprises the sum of the branch lengths in a phylogenetic tree of all species assessed and is often used in studies of phylogenetic diversity of co-occurring species (e.g., Rodrigues and Gaston, 2002; Safi et al., 2011; Trindade-Filho et al., 2012).

To verify whether FD and PD were influenced by species richness (Devictor et al., 2010), we then applied independent swap null models (Swenson, 2014) in each cell of the 10,359 grid cells in Brazilian Atlantic Forest. Through them, we were able to ask if functional and phylogenetic diversity estimates were significantly different (lower or higher) than would be expected by chance at each cell. We computed 1,000 replicates of FD and PD, obtaining a p-value of predicted FD and PD as compared to the distribution of the random replicates. We then used simple linear regression models (testing normality through the Shapiro-Wilk test (Shapiro and Wilk, 1965) to evaluate correlations between TD, FD, and PD in each grid cell. All spatial analyses were performed using the packages "ade4", "picante", "FD", and "vegan" through the R software (R Development Core Team, 2019).

2.5. Cost-effective conservation targets

We used the cost-effective conservation strategy proposed for the Brazilian Atlantic Forest by Banks-Leite et al. (2016) to attribute an economic value for each km^2 of forest remnant preserved. These values of payment for ecosystem services paid annually per hectare were based on 21 pre-established pilot programs supported by the Ministry of Environment of Brazil. These pilot projects were strictly related to payment for the establishment and maintenance of settlements in the Atlantic Forest. Following

Banks-Leite et al. (2016), we set the value to be given to private forest owners analysing only non-PAs (areas under no protection). We assumed that areas that are already protected, through payment of ecosystem services in set-aside programs, as US$ 13,273 for each km^2, annually. To compare the trade-offs between biodiversity gains and economic costs, we implemented and contrasted three set-aside models, each based on a different conservation scenario, adapted from Campos et al. (2017):

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

$$\text{Model } 2_{(70\%)} = \{FD \geq [(0.7\ ((\textstyle\sum_{i=0}^{n} FD)/N))/0.5] + PD \geq [(0.7\ ((\textstyle\sum_{i=0}^{n} PD)/N))/0.5] + TD \geq [(0.7\ ((\textstyle\sum_{i=0}^{n} TD)/N))/0.5]\} - \text{Model } 1_{(90\%)}$$

$$\text{Model } 3_{(50\%)} = \{FD \geq [(0.5((\textstyle\sum_{i=0}^{n} FD)/N))/0.5] + PD \geq [(0.5((\textstyle\sum_{i=0}^{n} PD)/N))/0.5] + TD \geq [(0.5\ ((\textstyle\sum_{i=0}^{n} TD)/N))/0.5]\} - \text{Model } 2_{(70\%)}$$

Model 1 identifies areas that hold very high levels of per-cell FD, PD, and TD ≥ 90% (0.9) of the total observed in each cell of the 10,359 grid cells in the Brazilian Atlantic Forest; Model 2 identifies areas that hold high levels of per-cell FD, PD, and TD ≥ 70% (0.7) of the total observed; Model 3 identifies areas that hold medium levels of per-cell FD, PD, and TD ≥ 50% (0.5) of the total observed (N). We did not consider areas with FD, PD, and TD values lower than 50% of the total observed in the conservation targets assessed (i.e., Model 1, Model 2, and Model 3).

Validating the implications of these models for applied ecology, we show a practical example of how to use this modelling approach in landscape planning, integrating biodiversity gains and economic costs through payments for ecosystem services (Fig. 2).

2.6. Continental turtles as indicator species of conservation priority

To evaluate the efficiency of species indicator groups in representing one of the models for each priority model proposed, we calculated the Indicator Value Index (IndVal) of Dufrene and Legendre (1997). The IndVal index ranges from 0 to 1 and represents the proportional association between a species and a site group (i.e., Model 1, 2, or 3) (Dufrene and Legendre, 1997). To verify the performance of each species as a potential indicator, we used optimization routines based on the concept of complementarity (Vane-Wright et al., 1991; Howard et al., 1998; Cabeza and Moilanen, 2001). Thus, we evaluated whether the performance of the species indicator groups was higher or lower than that expected randomly, under a 95% confidence interval with 1,000 permutations. Within a random distribution, species with $p \leq 0.05$ were considered as potential species indicators of the spatial extent of each conservation scenario (i.e., Model 1, 2, or 3). This analysis was performed through the R software (R Development Core Team, 2019), using the "labdsv" package (Roberts, 2016).

3. Results

Estimates of MPO (i.e., mean percentage overlap) demonstrate that protected areas comprise a very small percentage of the range of the continental turtles that occupy the Brazilian Atlantic Forest. On average, only 1.5% of the species ranges are currently protected (individual species ranging from 0.1 to 5.9 %, SD ±1.6%; Table 1, Fig. 3). In 47% of the species, the level of protection is not significantly different than that expected by chance. Only 33% of the species (*Acanthochelys radiolata, Chelonoidis denticulatus*, *Hydromedusa maximiliani*, *H. tectifera*, and *Trachemys dorbigni*) had their distribution patterns significantly higher than expected by chance (Table 1, Fig. 3) with well level of representativeness of PAs network.

The maps show high taxonomic, functional and phylogenetic diversity in the east-central region, mainly in the regions of the mountain ranges of the Serra do Mar, the Central Corridor of the Atlantic Forest (CCAF), and the Pernambuco Endemism Centre (PEC) (Fig. 4 and Fig. S2). The highest values of TD, FD, and PD are distributed in the north-eastern portion of the forest (PEC), the central region (north and centre of Serra do Mar and south of CCAF), and south region (Rio Grande do Sul state) (Fig. 4 and Fig. S1). Null models suggest that FD and PD values are different from those expected by chance ($p < 0.001$), indicating a non-random pattern of FD and PD. Functional, phylogenetic and taxonomic diversity are highly correlated (Fig. 5).

Our results show that Model 1 (i.e., 90% of TD, FD, and PD) selects the region north of the Serra do Mar and south of CCAF. Model 1 represents the highest-priority regions due to having 90% of TD, FD, and PD for conservation. The Model 2 (i.e., 70% of TD, FD, and PD) select the region from the south, centre, and north of the Serra do Mar, to the south of CCAF, and the PEC. Model 3 (i.e., 50% of TD, FD, and PD) selects most of the Atlantic Forest domain, north, centre and south of Serra do Mar, south of CCAF, north, centre, and south of PEC, and western of Paraná and Santa Catarina. Model 1 has a small area when compared to Model 2 and 3 that showed larger land areas, which require higher investments. It is also important to note that Model 2 covers areas with high PD values in the northern, centre and southern of biome (see Table 2, Fig. 6, and Fig. S1).

Our results show that the species that indicate the models with areas with higher TD, FD and PD are *Mesoclemmys hogei* (IndVal 0.84) and *C. denticulatus* (IndVal 0.74) for Model 1; *C. carbonarius* (IndVal 0.57) and *Kinosternon scorpioides* (IndVal

0.53) for Model 2; and *Rhinoclemmys punctularia* (IndVal 0.15) for Model 3 (Fig. 7, Table 3).

4. Discussion

Focusing on freshwater turtles and tortoises as flagship umbrella species, our findings report new priority areas for conservation in the Brazilian Atlantic Forest that may maximize the representation of biodiversity components at the lowest economic cost. In a world where conservation action is often limited by land-use costs (Lawler and White, 2008), the inclusion of economic factors is crucial in determining effective priorities for applied conservation (Silvertown, 2015; Sutton et al., 2016). In the book “Turtles in Trouble”, Stanford et al. (2018) highlighted a need to conserve endangered continental turtles on Earth. We suggest set-asides conservation scenarios through potential trade-offs for ecological and evolutionary processes with economic benefits. Under such ecological planning, biodiversity contribution to economic growth can be assessed in multiple ways of environmental protection.

In general**,** the approach to choosing umbrella species is limited by differences in the ecological conditions required by individual species, and with a large number of species co-occurring, their needs are more likely to be different from those of umbrella species (Wang et al., 2018). In our approach, we use several species of continental turtles and map the points with the highest TD, FD and PD, to get the most information and consequently many sympatric species in terrestrial and aquatic ecosystems. Our approach does not only take into account species richness but their ecological and evolutionary values that would not be found using only species richness, mainly in continental turtles that have two distinct phylogenetic origins. Therefore, this approach can have important evolutionary consequences that can also benefit co-occurring species. Functional traits arise through natural selection processes based on ecological pressures to which species are subjected the evolutionary changes (e.g., Grant and Grant, 2014). Thus, it is expected that co-occurring species will benefit from this strategy since many researchers have found an evolutionary congruence between different taxonomic groups (e.g., Zhou et al., 2019). However, we suggest further studies to confirm this spatial pattern in different taxonomic groups, which limits the dispersion and distribution of species.

Similar to studies of Atlantic Forest snakes (Lourenço-de-Moraes et al., 2019a), we reveal that the ranges of most species of continental turtles lay outside of the current network of PAs in the Brazilian Atlantic Forest. The conservation scenario is worrisome, as 67% of the species have restricted distributions and a low level of representativeness in the PA network. The species *Mesoclemmys vanderhaegei* is the most alarming case; the present configuration of PAs fails to overlap with its range entirely. In this context, the ecological and evolutionary values promoted by these animals in the Atlantic Forest are threatened. However, this species (*M. vanderhaegei*) occurs in other biomes such as Pantanal and Cerrado, suggesting further studies on this species to ensure its conservation.

We find that continental turtles of the Brazilian Atlantic Forest exhibit taxonomic diversity characteristics that are correlated with their ecological and evolutionary diversity patterns. This observed pattern is similar to the previously reported for the Atlantic Forest amphibians (Campos et al., 2017; Lourenço-de-Moraes et al., 2019b). Moreover, distribution patterns show that the species that co-exist in the north of Serra do Mar, south of CCAF, extreme north-eastern and southern regions of the Brazilian Atlantic Forest are phylogenetically distinct from each other, much more so than the species that co-exist out of those areas. This leads to a spatial pattern of accumulation of phylogenetic diversity that is unique to this group and an important issue to be considered in the conservation process. The pattern results from the joint presence of representatives of the suborder Cryptodira and Pleurodira: these two distinct evolutionary lineages occur in sympatry mainly in the extreme north (e.g., *Kinosternon scorpioides* and *Phrynops geoffroanus*) and in the extreme south of the biome (e.g., *Trachemys dorbigni* and *Hydromedusa tectifera*). Given the absence of PAs in these regions, our results point to conservation gaps and help to guide the establishment of new private and public reserves.

Apart from this accumulation of PD in the south and north, other areas that hold high ecological and evolutionary diversity values (i.e., TD, FD and PD) of continental turtles agree with several studies of other endemic groups (i.e., Serra do Mar, CCAF, and PEC). These regions have been considered important refuges for biodiversity, especially amphibians (Carnaval et al., 2014; Campos et al., 2014; Santos et al., 2020) and snakes (Moura et al., 2017).

We argue for the use of Model 1 (i.e., very high priority) and Model 2 (i.e., high priority) as an indicator of new key conservation areas in the Atlantic Forest with crucial implications in landscape planning (see Fig. 2). The regions prioritized by Model 1 and 2 – that is, those sites that hold 90 % and 70% of the TD, FD and PD diversity dimensions respectively in continental turtles – also corresponds to the approximate location of Pleistocene climatic refugee inferred for amphibians (Carnaval et al., 2009), and a known Anthropocene refugee for amphibians and snakes (Lourenço-de-Moraes et al., 2019a, b; Santos et al., 2020). Because these same areas are poorly protected by the current PA network (2.9% of its extension), and given that turtles and amphibians are the most endangered vertebrates (Hoffman et al., 2010; Rhodin et al., 2018), they seem especially appropriate for conservation efforts under limited budgets (Campos et al., 2017). Indicator species of the prioritization arrangement flagged by Model 1 include *Mesoclemmys hogei*, which is listed as critically endangered by the Tortoise and Freshwater Turtle Specialist Group (TFTSG) and the Brazilian Red List (Vogt et al., 2015), and recognized as endangered by IUCN (2020). According to Rhodin et al. (2017), the tortoise *Chelonoidis denticulatus* was considered outside of the Atlantic Forest. However, the species already has been found in the forests of south Bahia and Espirito Santo states (Vogt et al., 2015; Bérnils et al. in press). Our findings suggest this species as a potential indicator group for the conservation of evolutionary and ecological values of continental turtles in the Brazilian Atlantic Forest (Model 1 – very high priority), which is also listed as near threatened by TFTSG and vulnerable by the IUCN (2020).

While we acknowledge that our models present solutions for the current time, the conservation of Atlantic Forests corridors (Campos et al., 2020) may allow species to take shelter in known climatic refuges (i.e., Serra do Mar, CCAF, and PEC), which are also protected by the models presented here. Continental turtles are under intense pressure from humans (Stanford et al., 2018; Fagundes et al., 2018), being negatively affected by the advancement of human development, agriculture, and land and water pollution (Lourenço-de-Moraes et al., 2018; Stanford et al., 2018; Figueiredo et al., 2019). In the Atlantic Forest, natural areas have been heavily impacted by anthropogenic activity over the last 500 years (Dean, 1995), giving way to agriculture and pasture mainly (Ribeiro et al., 2009); human-made fires also are a known cause of freshwater turtle death (Oliveira et al., 2018). Despite previous analyses of extinction risks (e.g., Vogt et al., 2015), our results show that the taxonomic, functional and phylogenetic dimensions of the diversity of Atlantic Forest continental turtles are still not protected – and propose a novel way to prioritize new areas for conservation that effectively preserve the ecological and evolutionary dimensions of regional turtle diversity, even under financial stress. The fact that new species of continental turtles are still expected to be discovered and described makes the expansion of PAs even more desirable (Oliveira et al., 2018).

The current political crisis and budget cuts to Brazilian science demand improved environmental action and funding for land-based investments guided by an understanding of biodiversity values and contributions. Although applied here to freshwater turtles and tortoises, our approach can be expanded and used in conservation plans of any other taxonomic group. We hope this framework can be useful for decision-makers and key conservation players aiming to protect the multiple dimensions of biodiversity under limited budgets.

Data availability statement

All data and codes used in our analysis are available in an online repository (https://doi.org/xxxxx).

CRediT authorship contribution statement

Ricardo Lourenço-de-Moraes and Evanilde Bendito: conceived the ideas of the study; Ricardo Lourenço-de-Moraes: wrote the manuscript with important contributions for the others authors, in particular Felipe S. Campos and Ana Carnaval; Ricardo

Lourenço-de-Moraes and Felipe S. Campos: designed methodology; Ricardo Lourenço-de-Moraes and Mileny Otani collected the data; Ricardo Lourenço-de-Moraes and Felipe S. Campos: analysed the data and created the figures. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Anders G.J. Rhodin (Chelonian Research Foundation, Tortoise and Freshwater Turtle Specialist Group) and John Iverson (Earlham College) for spatial data of species and Carlos E. Guidorizzi (ICMBio-RAN) for spatial data of species *Chelonoidis denticulatus.* RLM thanks CNPq (151473/2018-8) for providing fellowship. FSC and PC thank the Portuguese Foundation for Science and Technology (PTDC/CTA-AMB/28438/2017) and Management Research Center – MagIC/NOVA IMS (UIDB/04152/2020). This study was financed in part by the CAPES - Finance Code 001.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/xxxxx.

References

Ackerly, D.D., Schwilk, D.W., Webb, C.O., 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. Ecology. 87, 50–61.

Atkinson, G., Bateman, I., Mourato, S., 2012. Recent advances in the valuation of ecosystem services and biodiversity. Ox. Rev. Econ. Pol. 281, 22–47.

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T.,... Condez, T.H., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science. 3456200, 1041–1045.

Bérnils, R.S., Castro, T.M., Almeida, A.P., Argôlo, A.J., Costa, H.C., Oliveira, J.C.F., Silva-Soares, T., Nobrega, Y.C., Cunha, C.J. (in press). Répteis ameaçados de extinção no estado do Espírito Santo. In Fauna e Flora ameaçadas de extinção no estado do Espírito Santo (Fraga, C.N.F., Formigoni, M.H., Chaves, F.F., eds.) 1ed. Santa Teresa: Instituto Nacional da Mata Atlântica. 270–293

Cabeza, M., Moilanen, A., 2001. Design of reserve networks and the persistence of biodiversity. T. Ecol. Evol. 165, 242–248.

Campos, F.S., Brito, D., Solé, M., 2014. Diversity patterns, research trends and mismatches of the investigative efforts to amphibian conservation in Brazil. A. Braz. Acad. Sci. 864, 1873–1886.

Campos, F.S., Lourenço-de-Moraes, R., Llorente, G.A., Solé, M., 2017. Cost-effective conservation of amphibian ecology and evolution. Sci. Adv. 36, e1602929.

Carbayo, F., Marques, A.C., 2011. The costs of describing the entire animal kingdom. T. Ecol. Evol. 26, 154–155.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T., Moritz, C., 2009. Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. Science. 323, 785–789.

Carnaval, A.C., Waltari, E., Rodrigues, M.T., Rosauer, D., VanDerWal, J., Damasceno, R.,… Prates, I., 2014. Prediction of phylogeographic endemism in an environmentally complex biome. Proc. R. Soc. B Biol. Sci. 281, 20141461.

Caro, T., 2010. Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington, D.C.

Cavarzere, V., Silveira, L.F., 2012. Bird species diversity in the Atlantic Forest of Brazil is not explained by the Mid-domain Effect. Zoologia. 29, 285–292.

Corlett, R.T., 2015. The Anthropocene concept in ecology and conservation. T. Ecol. Evol. 30, 36–41.

Crawford, N.G., Parham, J.F., Sellas, A.B., Faircloth, B.C., Glenn, T.C., Papenfuss, T.J., … Henderson, J.B., 2015. A phylogenomic analysis of turtles. Mol. Phyl. Evol. 83, 250–257.

Dean, W., 1995. With Broadax and Firebrand: The Destruction of the Brazilian Atlantic Forest. University of California Press, Berkeley.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol. Lett. 13, 1030–1040.

Dietz, M.S., Belote, R.T., Aplet, G.H., Aycrigg, J.L., 2015. The world’s largest wilderness protection network after 50 years: An assessment of ecological system representation in the U.S. National Wilderness Preservation System. Biol. Conserv. 184, 431–438.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for flexible asymmetrical approach. Ecol. Monog. 63, 345–366.

ESRI., 2019. Arcgis Software. Version 10.1. Available from www.esri.com/products/index.html

Fagundes, C.A., Vogt, R.C., Souza, R.A., De Marco Jr.P., 2018. Vulnerability of turtles to deforestation in the Brazilian Amazon: Indicating priority areas for conservation. Biol. Cons. 226, 300–310.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Cons. 61, 1–10.

Famelli, S., Adriano, L.R., Pinheiro, S.C.P, Souza, F.L., Bertoluci, J., 2014. Reproductive Biology of the Freshwater Turtle *Hydromedusa maximiliani* Chelidae from Southeastern Brazil. Chel. Cons. Biol. 131, 81–88.

Figueiredo, G.T., Storti, L.F., Lourenço-de-Moraes, R., Shibatta, O.A., Anjos, L., 2019. Influence of microhabitat on the richness of anuran species: a case study of different landscapes in the Atlantic Forest of southern Brazil. A. Acad. Bras. Ciênc. 91, e20171023.

Fleishman, E., Murphy, D. D., Brussard, P. F., 2000. A new method for selection of umbrella species for conservation planning. Ecol. App. 10,569–579.

Fuentes, M.S., Sterli, J., Maniel, I., 2014. Origin, Evolution and Biogeographic History of South American Turtles. Springer Cham Heidelberg New York Dordrecht London.

Grant, P.R., Grant, B.R., 2014. Synergism of Natural Selection and Introgression in the Origin of a New Species. Am. Nat. 183, 671–681.

Hansen, D.M., Donlan, C.J., Griffiths, C.J., Campbell, K.J., 2010. Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions. Ecography. 33, 272–284.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., ... Carpenter, K.E., 2010. The impact of conservation on the status of the world's vertebrates. Science. 330, 1503–1509.

Hopkins, B.C., Hepner, M.J., Hopkins, W.A., 2013. Mercury exposure is associated with negative effects on turtle reproduction. Envir. Sci. Tec. 47, 2416–2422.

IUCN., 2020. IUCN Red List of Threatened Species. Version 2020.2. Available from www.iucnredlist.org.

Junk, W.J., 1997. The Central Amazon System: Ecology of a Pulsing System. Berlin: Springer Verlag.

Kalinkat, G., Cabral, J.S., Darwall, W., Ficetola, G.F., Fisher, J.L., Giling, D.P., ... Jarić, I., 2017. Flagship umbrella species needed for the conservation of overlooked aquatic biodiversity. Cons. Biol. 31(2), 481–485. https://doi.org/10.1111/cobi.12813

Lawler, J., White, D., 2008. Assessing the mechanisms behind successful surrogates for biodiversity in conservation planning. Anim. Cons. 11, 270–280.

Loucks, C., Ricketts, T.H., Naidoo, R., Lamoreux, J., Hoekstra, J., 2008. Explaining the global pattern of protected area coverage: Relative importance of vertebrate biodiversity, human activities and agricultural suitability. J. Biog. 358, 1337–1348.

Lourenço-de-Moraes, R., Malagoli, L.R., Guerra, V.B., Ferreira, R.B., Affonso, I.P., Haddad, C.F.B.,… Sawaya, R.J., 2018 Nesting patterns between Neotropical species assemblages: Can reserves in urban areas be failing to protect anurans? U. Ecos. 17, 17–18.

Lourenço-de-Moraes, R., Lansak-Tohâ, F.M., Schwind, L.T.F., Arrieira, R.L., Rosa, R.R., Terribile, L.C.,...Lemes, P., 2019a. Climate change will decrease the range size of snake species under negligible protection in the Brazilian Atlantic Forest hotspot. Sci. Rep. 9, 8523.

Lourenço-de-Moraes, R., Campos, S.C., Ferreira, R.B., Solé, M., Beard, K.H., Bastos, R.P., 2019b. Back to the future: conserving functional and phylogenetic diversity in amphibian climate-refuges. Biod. Cons. 285, 1049–1073.

Margules, C.R., Sarkar, S., 2007. Systematic conservation planning. Cambridge University Press, Cambridge, U.K.

Magurran, A.E., 2004. Measuring biological diversity, 2nd ed. Blackwell Publishing, Oxford.

Martins, F.I., Sousa, F.L., 2008. Estimates of Growth of the Atlantic Rain Forest Freshwater Turtle *Hydromedusa maximiliani* Chelidae. J. Herp. 421, 54–60.

Matsumoto, Y., Hannigan, B., Crews, D., 2014. Embryonic PCB exposure alters phenotypic, genetic, and epigenetic profiles in turtle sex determination, a biomarker of environmental contamination. Endocrinology. 155, 4168–4177.

Ministério do Meio Ambiente, Cadastro Nacional de Unidades de Conservação., 2017. http://mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature. 403, 853–858.

Moilanen, A., 2008. Generalized complementarity and mapping of the concepts of systematic conservation planning. Cons. Bio. 22, 1655–1658.

Mouchet, M., Villéger, S., Mason, N.W.H., Mouillo, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Func. Ecol. 24, 867–876.

Moura, M.R., Argôlo, A.J., Costa, H.C., 2017. Historical and contemporary correlates of snake biogeographical subregions in the Atlantic Forest hotspot. J. Biog. 443, 640–650.

Naeem, S., Chazdon, R., Duffy, J.E., Prager, C., Worn, B., 2016. Biodiversity and human well-being: an essential link for sustainable development. Proc. R. Soc. B. 283, 20162091.

Neuteleers, S., Engelen, B., 2015. Talking money: How market-based valuation can undermine environmental protection. Ecol. Econ. 117, 253–260.

Oliveira, J.C.F., Castro, T.M., Silva-Soares, T., Rocha, C.F.D., 2018. First-order effects of fire and prolonged-drought effects on an undescribed semi-aquatic turtle in Atlantic rainforest in southeastern Brazil. J. Coast. Cons. 232, 367–372.

Pavoine, S., Vallet, J., Dufour, A-B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos. 118, 391–402.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Petersen, A.H., Strange, N., Anthon, S., Bjørner, T.B., Rahbek, C., 2016. Conserving what, where and how? Cost-efficient measures to conserve biodiversity in Denmark. J. Nat. Cons. 29, 33–44.

Pio, D.V., Broennimann, O., Barraclough, T.G., Reeves, G., Rebelo, A.G., Thuiller, W., Guisan, A., Salamin, N., 2011. Spatial predictions of phylogenetic diversity in conservation decision making. Cons. Biol. 256, 1229–1239.

Pollock, L.J., Thuiller, W., Jetz, W., 2017. Large conservation gains possible for global biodiversity facets. Nature. 5467656, 141–144.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. T. Ecol. Evol. 2211, 583–592.

R Development Core Team., 2019. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available from http://www.R-project.org.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for Conservation. Biol. Cons. 1426, 1141–1153.

Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B., van Dijk, P.P., 2017. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status 8th Ed.. In A. G. J. Rhodin, et el. eds. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chel. Res. Mon. 7, 1–292.

Rhodin, A.G.J., Stanford, C.B., van Dijk, P.P., Eisemberg, C., Luiselli, L., Mittermeier, R.A., ... Hudson R., 2018. Global conservation status of turtles and tortoises Order Testudines. Chel. Cons. Biol. 17, 135–161.

Roberts, D.W., 2016. labdsv: Ordination and Multivariate Analysis for Ecology. R Package version 1.8-0. Available from https://CRAN.R-project.org/package=labdsv.

Rodrigues, A.S.L., Gaston, K.J., 2002. Maximising phylogenetic diversity in the selection of networks of conservation areas. Biol. Cons. 105, 103–111.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., ...Meiri, S., 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. Nat. Ecol. Evol. 1(11), 1677–1682.

Safi, K., 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. Phil. Trans. R. Soc. S. B. 366, 2536–2544.

Sánchez-Fernández, D., Abellán, P., 2015. Using null models to identify under-represented species in protected areas: A case study using European amphibians and reptiles. Biol. Cons. 184, 290–299.

Santos, M.T.T., de Magalhães, R.F., Lyra, M.L., Santos, F.R., Zaher, H., Giasson, L.O., ... Haddad, C.B.F., 2020. Multilocus phylogeny of Paratelmatobiinae Anura: Leptodactylidae reveals strong spatial structure and previously unknown diversity in the Atlantic Forest hotspot. Mol. Phyl. Evol. 148, 106819.

Schneider, L., Belger, L., Burger, J., Vogt, R.C., 2009. Mercury bioacumulation in four tissues of *Podocnemis erythrocephala* Podocnemididae: Testudines as a function of water parameters. Sci. T. Env. 4073, 1048–1054.

Seddon, P.J., Leech, T., 2008. Conservation short cut, or long and winding road? A critique of umbrella species criteria. Oryx 42, 240–245. doi:10.1017/S003060530806119X

Silva, J.M.C., Casteleti, C.H.M., 2003. Status of the Biodiversity of the Atlantic Forest of Brazil. In C. Galindo-Leal I. G. Câmara Eds., The Atlantic Forest of South America: Biodiversity Status, Threats and Outlook Washington, DC: Island Press. pp. 43–59.

Silvertown, J., 2015. Have Ecosystem Services Been Oversold? T. Ecol. Evol. 30, 641–648.

Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality complete samples. Biometrika. 523–4, 591–611.

Sobral-Souza, T., Lautenschlager, L., Morcatty, T.Q., Bello, C., Hansen, D., Galetti, M., 2017. Rewilding defaunated Atlantic Forests with tortoises to restore lost seed dispersal functions. Persp. Ecol. Cons. 154, 300–307.

SOS Mata Atlântica INPE., 2019. Atlas dos Remanescentes Florestais da Mata Atlântica - Relatório Técnico Período 2017–2018. São Paulo: Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais - INPE.

Souza, F.L., Cunha, A.F., Oliveira, M.A., Pereira, G.A.G., Reis, S.F., 2002. Estimating dispersal and gene flow in the neotropical freshwater turtle *Hydromedusa maximiliani* Chelidae by combining ecological and genetic methods. Gen. Mol. Biol. 252, 151–155.

Stanford, C.B., Rhodin, A.G.J., van Dijk, P.P., Horne, B.D., Blanck, T., Goode, E.V.,... Hudson, R., 2018. Turtles in Trouble: The World's 25+ Most Endangered Tortoises and Freshwater Turtles. pp. 1–80

Stuber, E.F., Fontaine, J.J., 2018. Ecological neighborhoods as a framework for umbrella species selection. Biol. Cons. 223, 112–119

Sutton, N.J., Cho, S., Armsworth, P.R., 2016. A reliance on agricultural land values in conservation planning alters the spatial distribution of priorities and overestimates the acquisition costs of protected areas. Biol. Conserv. 194, 2–10.

Swenson, N.G., 2014. Functional and Phylogenetic Ecology in R. Springer, USA.

Trindade-Filho, J., Carvalho, R.A., Brito, D., Loyola, R.D., 2012. How does the inclusion of Data Deficient species change conservation priorities for amphibians in the Atlantic Forest? Biod. Cons. 21, 2709–2718.

Turtle Extinctions Working Group (TEWG)., 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. In: Rhodin, A.G.J., Pritchard, P.C.G., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., Mittermeier, R.A. (Eds.), Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chel. Res. Monog. 5, 1–66.

Uetz, P., 2019. The reptile database. Accessed 14 March 2020 from http://www.reptile-database.org/.

Wang, F., McShea, W.J., Li, S., Wang, D., 2018. Does one size fit all? A multispecies approach to regional landscape corridor planning. Divers. Distrib. 24, 415–425. https://doi.org/10.1111/ddi.12692.

Whiles, M.R., Lips, K.R., Pringle, C.M., Kilham, S.S., Bixby, R.J., Brenes, R.,… Connelly, S., 2006.The effects of amphibian population declines on the structure and function of neotropical stream ecosystems. Front. Ecol. Envir. 41, 27–34.

Vasconcelos, T.S., Prado, V.H.M., 2019. Climate change and opposing spatial conservation priorities for anuran protection in the Brazilian hotspots. J. Nat. Cons. 49, 118–124.

Veríssimo, D., MacMillan, D.C., Smith, R.J., 2011. Toward a systematic approach for identifying conservation flagships. Cons. Lett. 4, 1–8.

Viana, M.N.S., Oliveira, J.A., Agostini, M.A.P., Erickson, J., Morais, G.M., Monjeló, L.A.S., Andrade, P.C.M.,... Félix-Silva, D., 2017. Population Genetic Structure of the Threatened Amazon River Turtle, *Podocnemis sextuberculata* Testudines, Podocnemididae. Chel. Cons. Biol. 162, 128–138.

Vitt, L.J., Caldwell, J.P., 2014. Herpetology: An Introductory Biology of Amphibians and Reptiles. Elsevier's Science & Technology Rights Department in Oxford, UK.

Vogt, R.C., Fagundes, C.K., Bataus, Y.S.L., Balestra, R.A.M., Batista, F.R.Q., Uhlig, V.M.,...Silveira, A.L., 2015. Avaliação do Risco de Extinção de *Mesoclemmys hogei* (Mertens, 1967) no Brasil. Processo de avaliação do risco de extinção da fauna brasileira. ICMBio. Répteis – Quelônios Continentais. http://www.icmbio.gov.br/portal/faunabrasileira/estado-de-conservacao/2791-repteis-quelonios-continentais

Zhou, Y., Wang, S., Njogu, A.W., Ochola, A.C., Boru, B.H., Mwachala, G, Hu, G., Wang, Q., 2019. Spatial congruence or mismatch between phylogenetic and functional structure of seed plants along a tropical elevational gradient: different traits have different patterns. Front. Ecol. Evol. 7, 100. doi: 10.3389/fevo.2019.00100

Tables

Table 1

Mean percentage of spatial overlap (MPO) between the range of continental turtle species and protected areas in the Brazilian Atlantic Forest. Results of null models describing the representativeness of the species in protected areas: (+) denotes values significantly higher than expected by chance, (-) denotes values significantly lower than expected by chance, and (*) denotes non-significant ($p < 0.05$) values. The nomenclature follows Uetz (2019).

N	Species	MPO Observed	MPO randomised	Representativeness
sp1	*Acanthochelys radiolata*	3.06	2.07	+
sp2	*Acanthochelys spixii*	2.39	2.07	*
sp3	*Chelonoidis carbonarius*	1.89	2.06	*
sp4	*Chelonoidis denticulatus*	3.80	2.05	+
sp5	*Hydromedusa maximiliani*	5.98	2.06	+
sp6	*Hydromedusa tectifera*	3.51	2.07	+
sp7	*Kinosternon scorpioides*	2..02	2.09	*
sp8	*Mesoclemmys hogei*	2.21	2.06	*
sp9	*Mesoclemmys tuberculata*	1.44	2.06	*
sp10	*Mesoclemmys vanderhaegei*	0.88	2.06	-
sp11	*Phrynops geoffroanus*	1.75	2.07	-
sp12	*Phrynops hilarii*	1.40	2.06	*
sp13	*Phrynops williamsi*	2.21	2.09	*

sp14	*Rhinoclemmys punctularia*	0.12	2.06	-
sp15	*Trachemys dorbigni*	3.53	2.10	+

Table 2

Table 2: Cost-effective conservation of evolutionary and ecological values (TD, FD, and PD) of continental turtles in the Brazilian Atlantic Forest. Model 1, very high priority (90% of TD, FD, and PD); Model 2, high priority (70% of TD, FD, and PD); Model 3, medium priority (50% of TD, FD, and PD). Percentage of rivers, forest remnants, protected areas (PAs), and area (km^2) are also provided.

Priority Scenarios	Rivers (%)	Forest remnants (%)	PAs (%)	Area (km^2)	Cost-effectiveness (million dollars/year)
Model 1	1.15	12.10	6.90	1,377.76	18.28
Model 2	17.61	14.20	6.85	62,106.92	824.34
Model 3	19.69	15.04	5.96	95,028.13	1,261.30

Table 3

Species indicator groups for the conservation of evolutionary and ecological values (TD, FD, and PD) of continental turtles in the Brazilian Atlantic Forest. Model 1, very high priority (90% of TD, FD, and PD); Model 2, high priority (70% of TD, FD, and PD); Model 3, medium priority (50% of TD, FD, and PD). The nomenclature follows Uetz (2019).

Species indicator groups	Conservation targets	IndVal	p-value
Mesoclemmys hogei	Model 1	0.84	0.001
Chelonoidis denticulatus	Model 1	0.74	0.001
Hydromedusa maximiliani	Model 1	0.66	0.001
Acanthochelys radiolata	Model 1	0.51	0.002
Phrynops geoffroanus	Model 1	0.44	0.003
Chelonoidis carbonarius	Model 2	0.57	0.001
Kinosternon scorpioides	Model 2	0.53	0.001
Mesoclemmys tuberculata	Model 2	0.45	0.001
Rhinoclemmys punctularia	Model 3	0.16	0.025

Figures

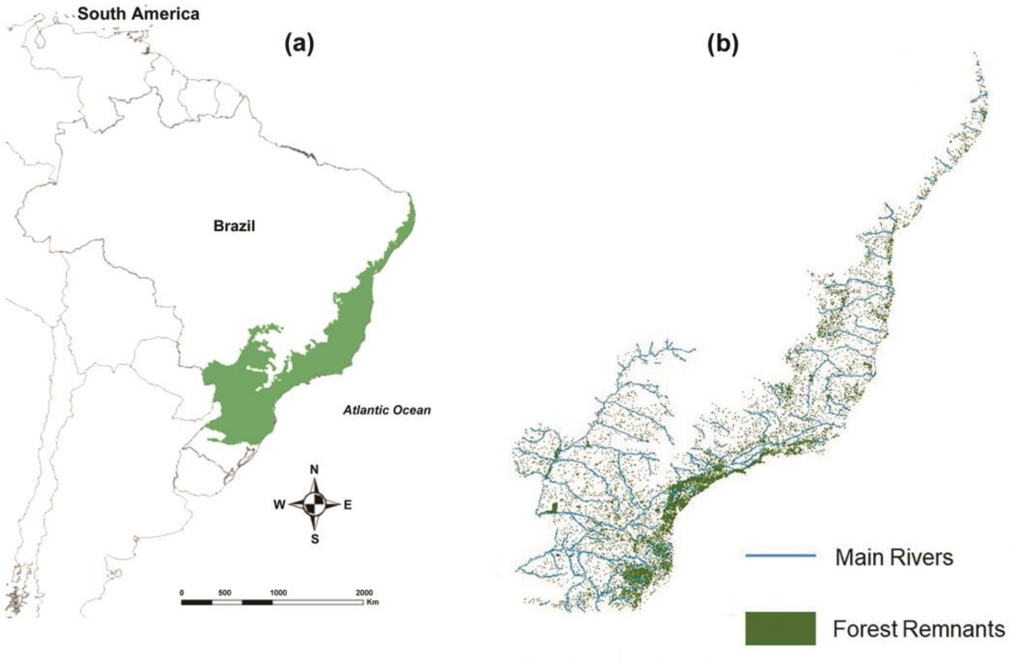

Fig. 1. Spatial distribution of the Brazilian Atlantic Forest. (a) Pre-Columbian distribution of Brazilian Atlantic Forest in South America; (b) forest remnants and main rivers in the Brazilian Atlantic Forest. Source: SOS Mata Atlântica & INPE (2019).

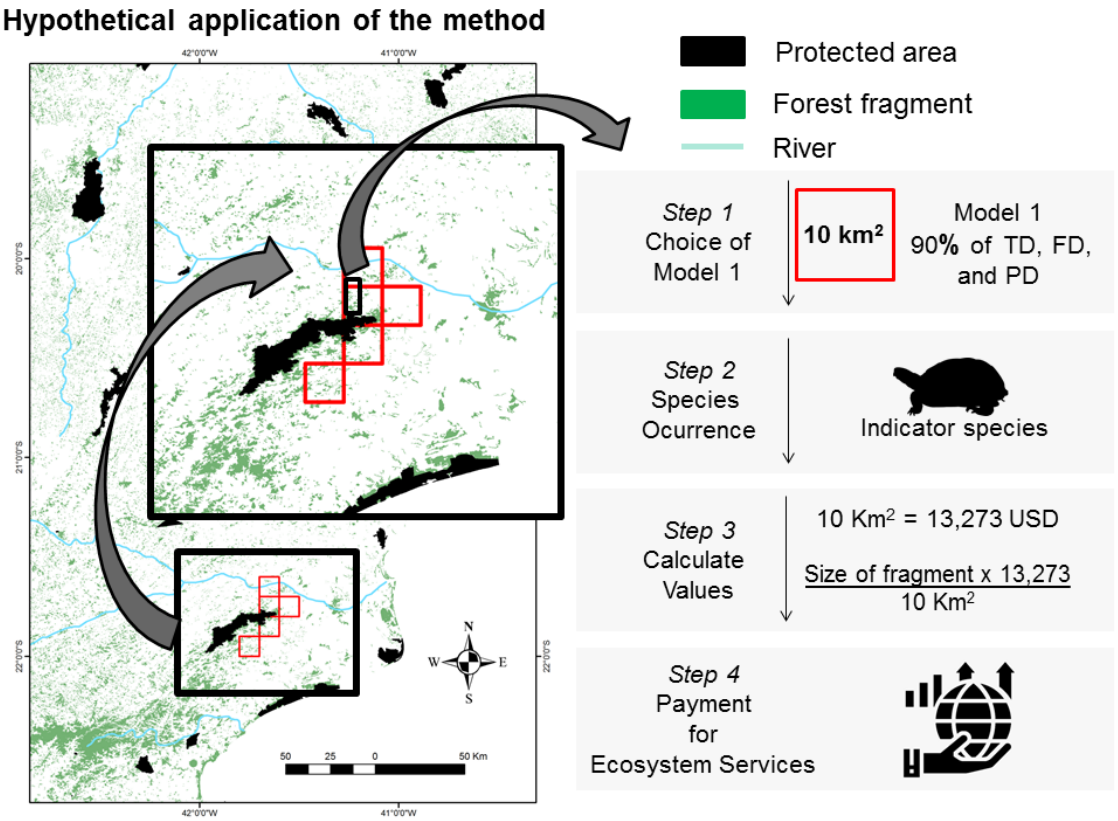

Fig. 2. The figure shows the hypothetical application of Model 1 (very high priority) for the conservation of continental turtles in four-steps landscape planning. In step 1, the choice of the Model which can help in the area where the decision-maker will conserve; in step 2, to find in the specialized literature or field research, the indicator species of the chosen model; in step 3, to calculate the size of the area to be conserved using the formula indicated in the figure (in American dollar USD); and finally, in step 4, the payment to the landowner to maintain the area conserved by the ecosystem services provided.

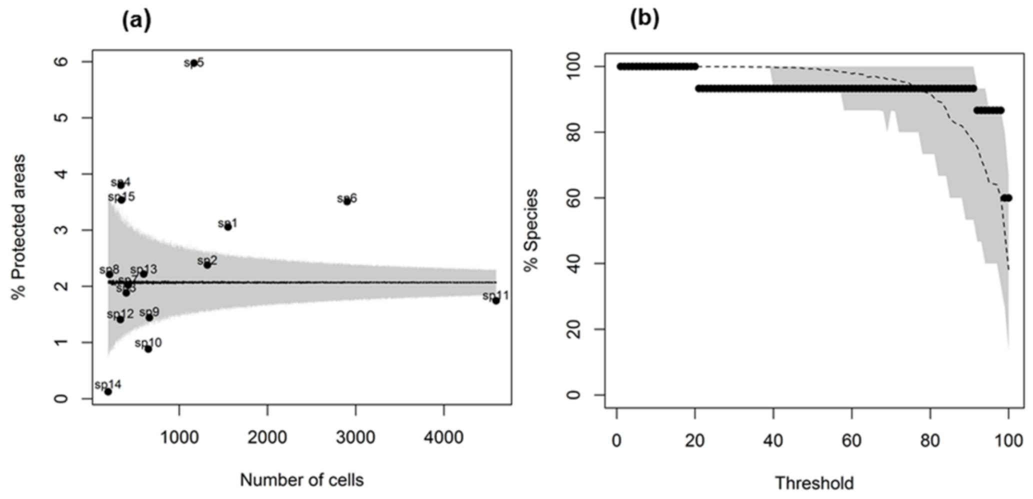

Fig. 3. Relationship of the Mean Percentage Overlap (MPO), percentage of spatial overlap between continental turtles' distribution and PAs in the Brazilian Atlantic Forest, and the number of cells occupied by the species. (a) Species are numbered and represented by black dots. The dashed lines show mean percentage overlap from 1,000 randomisations, and grey surface represents the random range, which indicates the range of 95% of the randomised data; (b) percentage of continental turtles' species that are well represented by MPO.

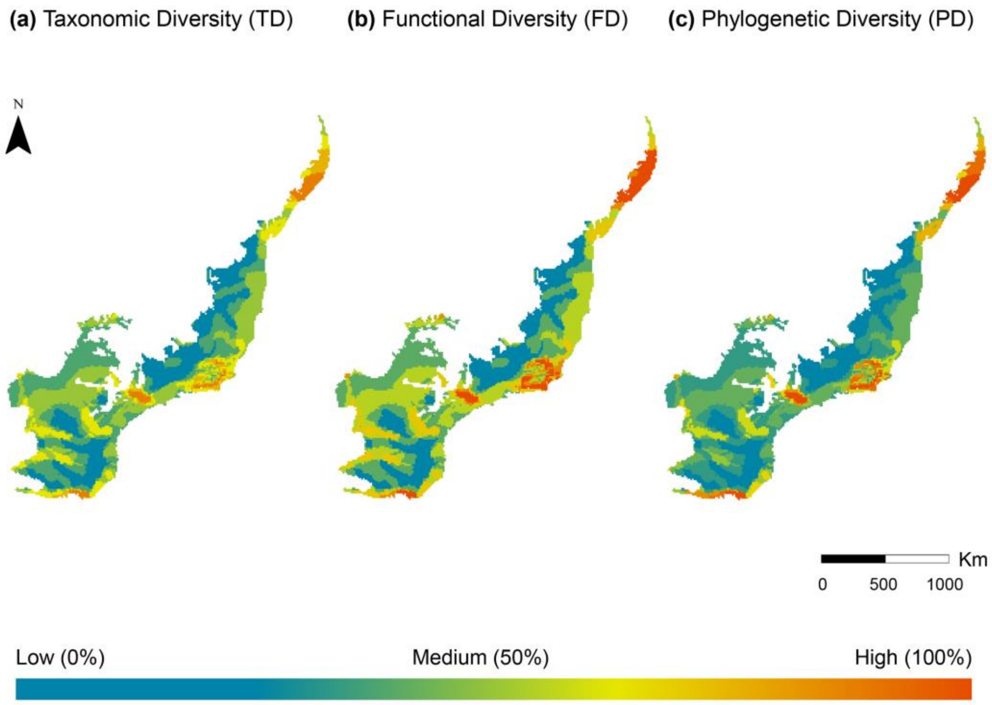

Fig. 4. Spatial distribution of Taxonomic Diversity (TD), Functional diversity (FD), and Phylogenetic Diversity (PD) of continental turtles in the Brazilian Atlantic Forest.

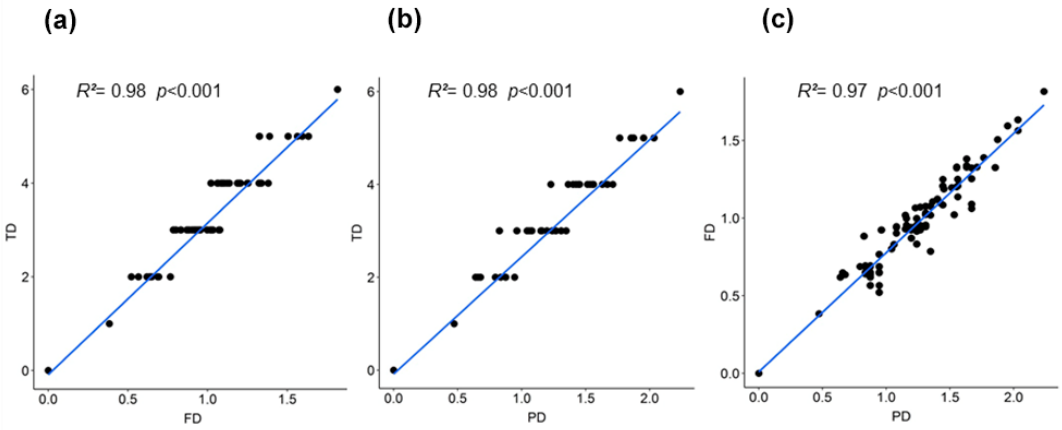

Fig. 5. Relationships between Taxonomic Diversity (TD), Functional diversity (FD), and Phylogenetic Diversity (PD) of continental turtles in the Brazilian Atlantic Forest. (a) TD vs. PD, (b) TD vs. FD, and (c) FD vs. PD.

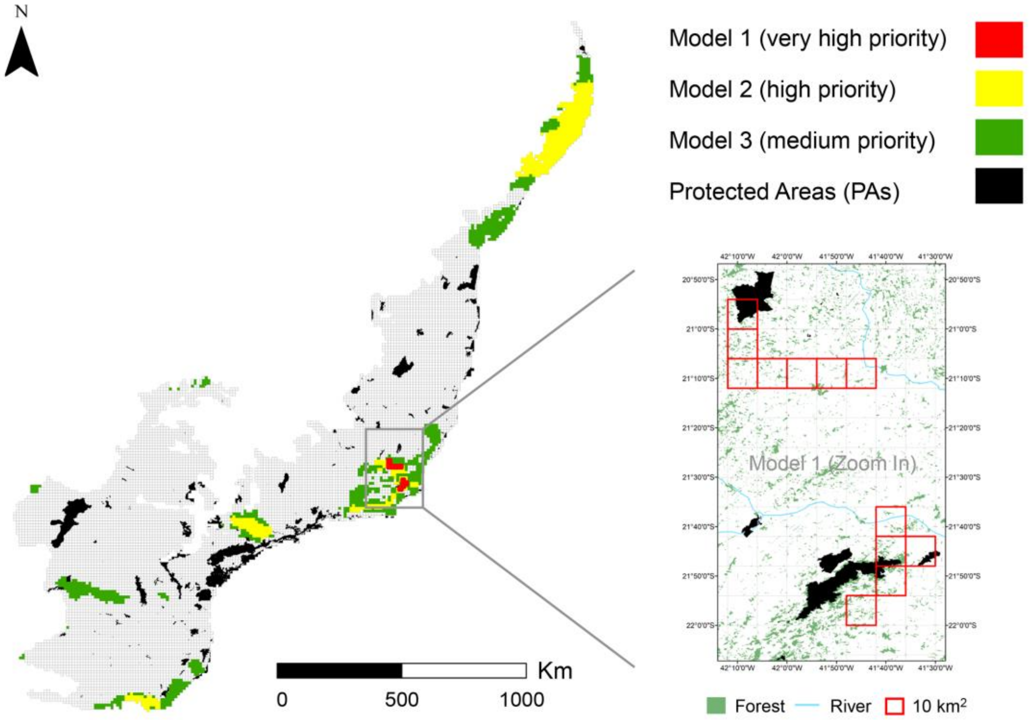

Fig. 6. Spatial distribution of the three prioritization models for the conservation of evolutionary and ecological values (TD, FD, and PD) of continental turtles in the Brazilian Atlantic Forest. Model 1 flags areas holding 90% of TD, FD and PD; Model 2, 70% of TD, FD and PD; Model 3, 50% of TD, FD and PD.

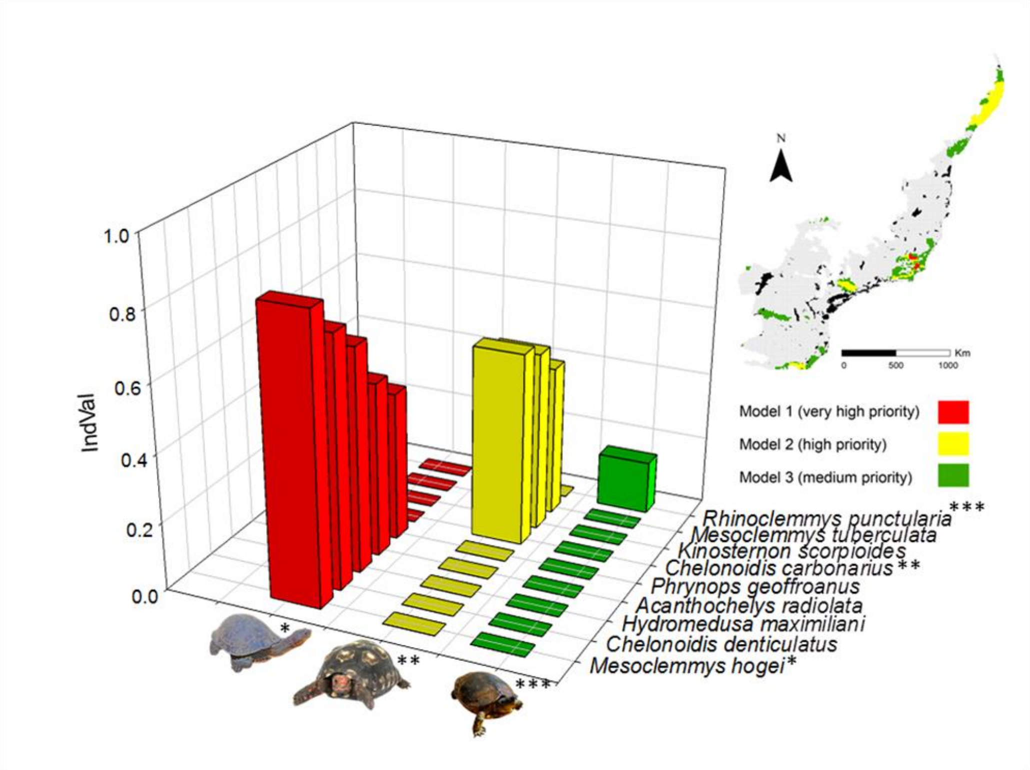

Fig. 7. Species indicator groups for the conservation of evolutionary and ecological values (TD, FD, and PD) of continental turtles in the Brazilian Atlantic Forest. Model 1, very high priority (90% of TD, FD and PD); Model 2, high priority (70% of TD, FD and PD); Model 3, medium priority (50% of TD, FD and PD). (*) Species with the highest IndVal values. The nomenclature follows Uetz (2019).