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Vulnerability of turtles to deforestation in the Brazilian Amazon: Indicating priority areas for conservation

Camila K. Fagundes[a,*], Richard C. Vogt[b], Rodrigo A. de Souza[c], Paulo De Marco Jr.[d]

[a] Wildlife Conservation Society, Brazil Program, Av. Rodrigo Octavio, 6200, Setor Sul, Bloco H, 69077-000, Manaus, AM, Brazil
[b] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. André Araújo, 2936 – Petrópolis, CP 2223, CEP 69067-375 Manaus, AM, Brazil
[c] Remote Sensing Center from Brazilian Institute of Environment and Renewable Natural Resources (CSR/IBAMA), Trecho 2, Ed. Sede, Bloco F, P.O. 09566, 70.818-900 Brasília, DF, Brazil
[d] Laboratório de Teoria, Metacomunidades e Ecologia da Paisagem, ICB 5, Universidade Federal de Goiás, CP 131, 74001-970 Goiânia, GO, Brazil

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ABSTRACT

The loss of forest cover has been considered to be an important factor in the decline of turtle populations. We used Species Distribution Models (SDM) to identify the potential distribution areas of several turtle species in the Brazilian Amazon and to calculate amount of area possibly lost to deforestation (vulnerability). We then used the software Zonation to prioritize areas for turtle conservation. We assigned higher conservation weight to terrestrial, semi-aquatic and threatened turtles and forced the exclusion of deforested areas. Different scenarios were run to assess the effectiveness of PAs in protecting turtles. Priority areas for turtle conservation are located in central-northern Amazon. These regions usually do not encompass high deforestation areas. Areas that turtles are most vulnerable to deforestation are located in central-northeastern Amazon, but only three species lost more potential distribution area to current and predicted deforestation than the percentage of total deforestation in the Brazilian Amazon. *Phrynops geoffroanus*, *Podocnemis unifilis*, *Mesoclemmys gibba* and *Kinosternon scorpioides* had a highest proportion of their potential distribution area lost due to deforestation. Many priority sites for turtle conservation are located outside of PAs, even when considering only the top 17% of priority sites. Although we did not explicitly take into consideration the social importance of turtles as a food resource in our analysis, our results highlight the most important regions for investing in conservation of turtles in the Brazilian Amazon. These results have significant practical implications for conservation.

1. Introduction

Forest ecosystems have been quickly fragmented in the Amazon basin, mainly due to development policies related to the expansion of infrastructure and agriculture (Laurance et al., 2004; Fearnside, 2005; Soares-Filho et al., 2006). The creation of Protected Areas (PAs) is one of the key conservation strategies used in the Amazon to avoid biodiversity loss (Ferreira et al., 2005; Nepstad et al., 2006), and may be the best option to prevent human impacts (Gaston et al., 2008; Soares-Filho et al., 2010) and conserve viable populations (Rodrigues et al., 2004; Loucks et al., 2008). However, a previous gap analysis revealed that areas reserved for biodiversity conservation may be inadequate (Scott et al., 2001). The choice of priority areas for conservation should incorporate the complementary principle (Rodrigues et al., 2003), which prioritizes sites that complement each other in relation to biodiversity composition rather than those that have high richness, since such sites may have redundant species composition (Margules and Pressey, 2000; Bonn and Gaston, 2005).

In general, aquatic species are only indirectly included in the creation of PAs (Roux et al., 2008). This holds true for Amazon, where the spatial location of PAs was mainly established to protect terrestrial taxa from overharvesting and to decrease deforestation (Peres and Terborgh, 1995; Veríssimo et al., 2011). The protection of large terrestrial areas based on biogeographic units was considered to be adequate to conserve the diversity of freshwater ecosystems and their related fauna in the Amazon (Peres and Terborgh, 1995; Peres, 2005). However, significant gaps in the protection of aquatic species have been recently identified in the biome, including freshwater turtles (Fagundes et al., 2016) and stream-dwelling fish fauna (Frederico et al., 2018). Those studies question the ability of large PAs to conserve aquatic

* Corresponding author at: Wildlife Conservation Society, Brazil Program, Av. Rodrigo Octavio, 6200, Setor Sul, Bloco H, 69077-000 Manaus, AM, Brazil.
E-mail addresses: cfagundes@wcs.org (C.K. Fagundes), vogt@inpa.gov.br (R.C. Vogt), rasouzamail@gmail.com (R.A. de Souza), pdemarcojr@gmail.com (P. De Marco Jr.).

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elements of biodiversity. Castello et al. (2013) had already highlighted the importance of shifting the Amazon conservation paradigm to encompass the freshwater ecosystems, since they comprise a large area of the Amazon basin and are highly sensitive to anthropogenic impacts occurring in both freshwater and terrestrial habitats.

Turtles are considered useful organisms to include in spatial prioritization planning and for examining broader impacts of habitat loss on ecosystems, as all species require both wetlands and terrestrial environments to complete their life cycle (Klemens, 2000). Moreover, the group is among the most threatened vertebrate taxa and its worldwide decline is largely attributed to wetland loss and habitat fragmentation due to anthropogenic land-use (Reese and Welsh Jr., 1998) and exploitation (Gibbons et al., 2000). In the Amazon, seven turtle species have been classified in some threat category by the IUCN's (International Union for Conservation of Nature) Tortoise and Freshwater Turtle Specialist Group (TFTSG) (Turtle Taxonomy Working Group et al., 2017. In that region, turtles are an important food resource for indigenous and riverine populations (Fachín-Terán et al., 1996; Vogt, 2008), but are also affected by anthropogenic impacts at landscape level (Rhodin et al., 2009; Berry and Iverson, 2011; Magnusson and Vogt, 2014; Mittermeier et al., 2015). The landscape predictor that plays the greatest role in the decline of turtles is vegetation loss (Quesnelle et al., 2013), but turtles are particularly dependent on habitat connectivity to maintain their populations (Semlitsch and Jensen, 2001; Rizkalla and Swihart, 2006; Sterrett et al., 2011; Quesnelle et al., 2013).

Deforestation affects migration patterns and habitat use in different ways depending on the natural history of species (Pearman, 1997; Becker et al., 2007). In this context, terrestrial and semi-aquatic turtles are more affected by forest loss and habitat fragmentation than the aquatic species, because they move between ecosystems through forests rather than open areas to reduce thermal stress (Bowne, 2008) and exposure to natural predation and human exploitation (Buhlmann and Gibbons, 2001). Semi-aquatic turtles are species that use terrestrial habitats to obtain complementary resources such as food, rehydration and mating and nesting sites (Buhlmann and Gibbons, 2001; Grgurovic and Sievert, 2005; Beaudry et al., 2009). Furthermore, even exclusively aquatic turtles depend on the landscape matrix composition and might be vulnerable to forest cover changes, as they inhabit a variety of wetland types (Joyal et al., 2001) and eventually use uplands to move among aquatic habitats (Marchand and Litvaitis, 2004). The vegetation density may be particularly important in determining how far those species will travel to nest in riverbanks (Quesnelle et al., 2013), the quality of wetlands (Trebitz et al., 2007; DeCatanzaro et al., 2009), water temperature, depth heterogeneity and the amount of sediments (Walser and Bart, 1999). All those characteristics may constitute important threats to the group.

Despite habitat loss and habitat degradation are reported as important threats to turtle species in the Amazon (Rhodin et al., 2009; Berry and Iverson, 2011; Magnusson and Vogt, 2014; Mittermeier et al., 2015), no study has yet evaluated the vulnerability of an Amazon turtle to deforestation. Vulnerability is the extent which a species or population is threatened and is usually divided into three components: exposure, sensitivity, and adaptive capacity (Dawson et al., 2011). Our objective here was to evaluate the exposure of turtle species to deforestation in the Brazilian Amazon to indicate geographic locations where species are most vulnerable to forest loss. We focused on the exposure component because it is easily estimated by measuring the overlap between a distribution of a species distribution and a threat. Both sensitivity to threat and adaptive capacity to new conditions are difficult to predict without a large amount of knowledge on the ecology of individual species (Dawson et al., 2011). Thus, for the majority of individual species, vulnerability to anthropogenic impacts can be suggested only in general terms (Kozlowski, 2008).

Lack of information about the distribution of organisms (Diniz et al., 2010) is an important limitation for conservation planning (Peres, 2005), especially in tropical regions (Myers et al., 2000). Species distribution models (SDMs) can be an important tool to fill gaps in knowledge about species' distributions (Raxworthy et al., 2003; Costa et al., 2010) because they identify suitable habitat for populations of a species (Guisan and Thuiller, 2005; Peterson et al., 2011). These models are advantageous for identifying sites that species are most vulnerable to particular threats and for selecting priority areas for conservation. Spatial prioritization is critical for broad-scale conservation actions. Thus, in addition to the evaluation of the vulnerability of turtles to deforestation, this paper also aims to assess the efficiency of existing protected area (PA) networks in representing the distribution of turtle species in the Brazilian Amazon. The selection of priority areas was based on the habitat requirements of the species in each basin, the current location of PAs and deforested areas.

2. Material and methods

2.1. Species distribution modeling (SDM)

We used Species Distribution Modeling (SDM) to provide an estimate of turtle distribution (Guisan and Thuiller, 2005; Peterson et al., 2011) because observed records for most turtle species in the Amazon are limited to a few localities within their ranges (Souza, 2004, 2005; Brito et al., 2012). We ran maximum entropy algorithm using the MaxEnt software (Phillips et al., 2006) because it had the best evaluation values among the statistical methods previously used to estimate the distribution of Amazon turtles (Fagundes et al., 2016) and has been extensively evaluated and considered to be consistent over a large range of modeling scenarios (Pearson et al., 2007; de Siqueira et al., 2009). This approach correlates the environment at the locations of known records with the environment across the entire study area (Peterson et al., 2011).

To analyze the statistical relationship between species' occurrences and environmental predictors, we compiled occurrence records for 17 Amazon turtles (15 freshwater species and two terrestrial species) and used 42 environmental variables: 37 climatic predictors, three variables that reflect terrain shifts and two predictors that characterize the aquatic environment (Appendix A). Only one occurrence record of each species in each cell was considered (spatially unique records) to help avoid effects of sampling bias (Kadmon et al., 2004). We performed a principal components analysis (PCA) of the 42 environmental variables to decrease collinearity among them and to avoid model overfitting. Then, we used the PCA scores (12 axes - responsible for $>$ 95% of the variation) as environmental layers in the SDM procedures (Peres-Neto et al., 2005; Dormann et al., 2012; Fagundes et al., 2016). We divided occurrence data of species that had $>$ 15 spatially unique records into 80–20% training–test subsets. We used the training subset to fit the SDMs and the test subset to evaluate the predictions. For species that had $<$ 15 spatially unique records, we fit and tested the SDMs with the same dataset. We used 10,000 random points as background data. The models had a resolution of 4 km^2 and were created and evaluated for the entire Amazon basin.

Species distribution models based on presence-only data are expected to be good predictors of species suitability at a macroscale (Guisan and Thuiller, 2005) and are widely used in spatial conservation prioritization (Faleiro et al., 2013; Lemes and Loyola, 2013; Frederico et al., 2018). Nevertheless, the conversion of those models into potential distribution is based on the assumption that all predicted areas are accessible for the species during their evolutionary history (Barve et al., 2011). The coverage of SDMs to the entire Amazon basin and the possibility of dispersal along the rivers for the majority of turtle species favor the acceptance of this assumption. To convert the continuous suitability into a binary distribution model we used a threshold derived from the ROC curve. By plotting the sensitivity against 1-specificity for all existing thresholds, the method identifies the value at which the omission and commission errors intersect and minimize them (Pearce and Ferrier, 2000; Jiménez-Valverde and Lobo, 2007). The models were evaluated using, the True Skilled Statistics (TSS - Allouche et al., 2006), a threshold-dependent method. Acceptable models had TSS values ≥ 0.5 (Fielding and Bell, 1997). The variance equation for TSS proposed by Allouche et al. (2006) was used to calculate the 95% confidence interval for TSS. Although models were produced and evaluated for the entire Amazon basin, our analysis focused only on the Brazilian Amazon.

2.2. Deforestation model

The deforestation model used in analysis was created by de Souza and De Marco Jr (2014) for the entire Brazilian Amazon. The authors used current deforestation data from automatic classification analysis of LANDSAT- 5/TM images from the Deforestation Monitoring Program - PRODES (INPE) to predict potential deforestation sites. Deforestation models were built with the Maximum Entropy algorithm in MaxEnt Software by varying the predictors and settings. Deforestation data was treated as "species data" and its future occurrence was determined as "potential species distribution". The central point of each deforestation polygon was used as deforestation occurrence data and variables such as deforestation density, roads, agriculture, livestock, urban areas, environment agency offices, protected areas, and land reform settlements were used as predictors. The models were trained with 2008 data and tested with 2010 data by comparing the models of predicted deforestation with real deforestation data from 2010. The models predicted deforestation better than all other existing models for the Amazon region (de Souza and De Marco Jr, 2014), and we used the model that had the higher predictive power. This model used the distance from previous deforestation (PRODES) as a functional variable and the automatic features of MaxEnt software. The conversion output into a binary prediction of the deforestation was based on a threshold derived from the ROC curve which balances the omission and commission errors. The predicted deforestation model did not forecast some areas where the deforestation has already occurred. Thus, we corrected those omission errors by including the current deforested areas in the predicted deforestation model.

2.3. Vulnerability to deforestation

The only component of vulnerability analyzed in this study was exposure, which we define as the extent of deforestation likely to be experienced by the species (Dawson et al., 2011). We used the de Souza and De Marco Jr (2014) deforestation model to evaluate both the exposure of each turtle species and turtle richness to forest loss in the Brazilian Amazon. SDMs had a resolution of 4 km^2. Thus, we evaluated the overlap of potential distribution areas of each turtle species to current and predicted deforestation in a 4 km^2 pixel, assuming that turtles are eradicated in deforested sites. We also calculated the number of turtle species in each pixel based on their potential distribution areas to identify the regions where turtle richness is most vulnerable to this threat.

We performed a regression between the potential distribution area of turtles and their remaining potential distribution area, considering the habitat lost to current and predicted deforestation. We expected that the potential distribution area lost to deforestation would correspond to the same percentage of total deforestation in the Brazilian Amazon if forest loss was random across this biome (expected potential distribution = potential distribution area x percentage of remaining forest). The current forest loss in the Brazilian Amazon is 14.85%, while the predicted forest loss is 22.75% (de Souza and De Marco Jr, 2014).

2.4. Priority areas for conservation

The spatial prioritization software Zonation (Moilanen, 2005) was used to identify priority areas for turtle conservation in the Brazilian Amazon. The Zonation algorithm is based on the principle of complementarity and produces a balanced ranking of conservation priority over the entire study area (Pressey, 1994). Initially, the entire area is considered protected, then the algorithm removes the planning units that incur the smallest aggregate loss of conservation value, while the most important planning units for biodiversity remaining until the end (Moilanen and Kujala, 2008). Each planning unit has a value that correspond to the occurrence level of each biodiversity feature, and the manner in which conservation loss is aggregated across those features depends on the removal rule of the planning unit. The algorithm accounts for the conservation weight attributed to biodiversity features, the distribution and connectivity of those features, and the cost associated to each planning unit (Moilanen et al., 2005; Moilanen and Kujala, 2008; Moilanen et al., 2009).

Basins were used as planning units. We extracted the mean of the environmental suitability from the SDMs previously produced of each species for all the planning units in ArcGIS 10.3 (ESRI, Inc.) and used them as the input species layers. The basins we used (Basin Level 7) were developed for the entire Amazon and are subdivided into drainage units from 300 km^2 to 1000 km^2 (Venticinque et al., 2016). This approach is part of a new spatially uniform multi-scale GIS framework, which prioritizes the high water drainage patterns in the delineation of floodplain drainage polygons (Venticinque et al., 2016). The design of planning units may be visualized in Appendix B.

We used the additive benefit function removal rule to prioritize the sites with higher species richness (Moilanen, 2007 for details). Moreover, we assigned higher conservation weight to terrestrial and semi-aquatic turtles, because they are potentially more impacted by forest loss, and a higher conservation weight to threatened turtles (Table 1), because they should have priority in conservation planning. Thus, if a species is terrestrial or semi-aquatic and threatened it had higher weight than a terrestrial or semi-aquatic species that is not threatened. We forced the exclusion of current and predicted deforested areas (de Souza and De Marco Jr, 2014) if they were included in the top of priority areas for conservation by giving a negative weight to them. We believe that removing areas of greatest socioeconomic conflicts makes conservation planning more applicable to decision makers and guarantee the persistence of species (Fahrig 2001; Faleiro et al., 2013).

To test the effectiveness of Amazonian PAs in protecting turtle species, we conducted a replacement cost analysis (Cabeza and Moilanen, 2006). PAs in Brazil are classified in two groups: Integral Protected Areas (IPA), which are free of any human interference; and Sustainable Use Areas (SUA), where the sustainable extraction of natural resources is allowed based on management strategies. The country also has a large percentage of Indigenous Lands (IL). We ran different scenarios to analyze if PAs overlap with priority areas for turtle conservation: (a) first, we ran the analysis with no constraints, not considering PAs – which would be the optimal solution for turtle conservation; and then we considered (b) IPA as a mask; (c) IPA + SUA as a mask and (d) IPA + SUA + IL as a mask to determine suboptimal constrained solution. The mask forced the inclusion of PA categories in the top priority areas for turtle conservation, indicating areas that complement the current network of PAs. According to the target defined for terrestrial and inland water ecosystems from Aichi Biodiversity Targets to 2020 (Convention on Biological Diversity, 2010), we based our conservation goals on the top 17% of priority sites in all scenarios. However, this value may not be appropriate to conserve some aquatic organisms, since they show a linear dispersion along areas. Therefore, this study also considered the top 50% of priority sites, as land owners in the Amazon region have to maintain at least 50% of their properties in legal reserve (IPAM (Instituto de Pesquisa Ambiental da Amazônia), 2011).

Table 1
Vulnerability of turtle species to current and predicted deforestation in the Brazilian Amazon and their threat categories according to the IUCN Tortoise and Freshwater Turtle Specialist Group (TFTSG).

Species	Potential distribution area	Remaining potential distribution area under current deforestation	Remaining potential distribution area after total deforestation[a]	Potential area lost to current deforestation	Potential area lost to predicted deforestation	Total potential area lost[a] (%)	TFTSG threat category[b]
Aquatic turtles[c]							
Mesoclemmys nasuta	163,824	154,256	143,184	9568	11,072	12.60	Data deficient
Podocnemis erythrocephala	1,126,016	1,038,368	981,760	87,648	56,608	12.82	Vulnerable
Peltocephalus dumerilianus	1,517,264	1,300,896	1,223,184	181,840	112,24	19.38	Vulnerable
Rhinemys rufipes	1,482,736	1,391,184	1,332,688	91,552	58,496	10.12	Least concern
Podocnemis sextuberculata	1,996,080	1,799,568	1,680,304	196,512	119,264	15.82	Vulnerable
Podocnemis unifilis	3,018,160	2,659,056	2,442,944	359,104	216,112	19.06	Endangered
Podocnemis expansa	2,260,000	1,948,672	1,780,944	311,328	167,728	21.20	Critically endangered
Mesoclemmys raniceps	1,298,544	1,232,240	1,190,256	66,304	41,984	8.34	Data deficient
Chelus fimbriata	2,426,656	2,135,440	1,975,408	291,216	160,032	18.60	Least concern
Phrynops geoffroanus	2,168,800	1,769,776	1,559,584	399,024	210,192	28.09	Least concern
Semi-aquatic turtles[c]							
Platemys platycephala	2,349,392	2,195,312	2,096,688	154,080	98,624	10.76	Least concern
Mesoclemmys gibba	3,459,904	3,116,112	2,899,072	343,792	217,04	16.21	Least concern
Mesoclemmys heliostemma	245,328	243,168	242,128	2160	1,04	1.30	Data deficient
Rhinoclemmys punctularia	1,565,456	1,247,168	1,076,096	318,288	171,072	31.26	Least concern
Kinosternon scorpioides	1,411,584	1,066,992	898.752	344,592	168,24	36.33	Least concern
Terrestrial tortoises[c]							
Chelonoidis denticulatus	1,823,168	1,646,432	1,526,800	176,736	119,632	16.25	Near threatened
Chelonoidis carbonarius	1,329,744	1,226,256	1,140,464	103,488	85,792	14.23	Vulnerable

[a] Considering current and predicted deforestation.
[b] Threat categories from the IUCN Tortoise and Freshwater Turtle Specialist Group (TFTSG) (Turtle Taxonomy Working Group et al., 2017).
[c] The habits were compiled from Rueda-Almonacid et al. (2007) and Vogt (2008).

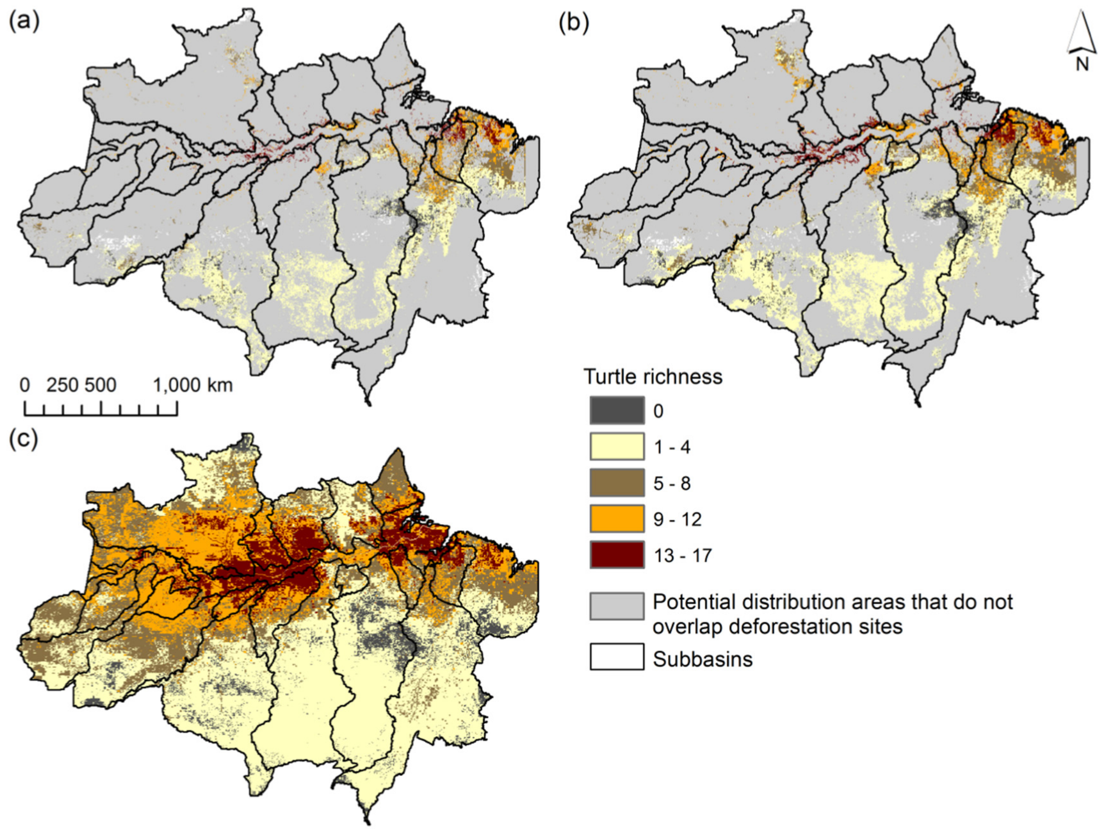

Fig. 1. Number of turtle species exposed to (a) current deforestation, (b) current deforestation + predicted deforestation and (c) the turtle richness in the Brazilian Amazon. The calculation of the number of turtle species in each pixel of 4 km^2 was based on the sum of potential distribution areas from all species. Then, it was evaluated the overlap of turtle richness to deforestation sites.

3. Results

3.1. Species distribution modeling (SDM)

Species distribution models had good predictive accuracies, TSS ≥ 0.5 to 11 species (from 0.33 to *Phrynops geoffroanus* to 0.95 to *Mesoclemmys heliostemma*) (Appendix C).

3.2. Vulnerability to deforestation

High turtle richness usually does not occur in areas with high deforestation rates (Fig. 1). Nevertheless, turtle richness is more exposed to current and predicted deforestation in areas of central Amazon and in northeastern Amazon (Fig. 1). Potential distribution areas exposed to deforestation to each turtle species in the Brazilian Amazon are showed in Appendix D.

The species that had the greatest amount of potential distribution area overlapping current deforestation sites are *P. geoffroanus* (399,024 km^2) and *Podocnemis unifilis* (359,104 km^2), followed by *Mesoclemmys gibba* (343,792 km^2) and *Kinosternon scorpioides* (344,592 km^2) (Table 1). The same species would be more affected by predicted deforestation. On the other hand, considering the percentage of potential distribution area lost to current and predicted deforestation, the species most exposed to this threat are *K. scorpioides, Rhinoclemmys punctularia*, *P. geoffroanus* and *Podocnemis expansa* (Table 1).

Species with the largest potential distribution area have the largest potential distribution area lost to current ($R^2 = 0.98$; $p < 0.001$, Fig. 2a) and predicted deforestation ($R^2 = 0.97$; $p < 0.001$, Fig. 2b). We expected that species would lose the same potential distribution area as the percentage of total deforestation in the Brazilian Amazon if forest loss occurred at random across this biome. Nevertheless, the majority of the species lost less potential distribution area under current and predicted deforestation than the percentage of total deforestation in the Amazon (Fig. 2). Only three turtle species (*K. scorpioides, R. punctularia* and *P. geoffroanus*) lost more potential distribution area than the random expectation, about 36%, 31% and 28%, respectively (Fig. 2; Table 1).

3.3. Priority areas for turtle conservation

According to the optimal solution (not considering PAs), priority areas for turtle conservation are located in the central-northern Amazon (mainly in Japurá-Caquetá, Negro, Uatumã, Trombetas, Jari, Amazon River main stem, northern coastal basin, Purus, Abacaxis, and Tefé basins) and in some areas of Tocantins basin in the eastern Amazon. With the exception of the Tocantins basin, those priority sites do not overlap areas with higher deforestation levels (Fig. 3). If 17% or 50% of the Brazilian Amazon were chosen for conserving turtles, the average proportion of species distribution remaining in the priority areas selected for conservation (31.02 ± 16.21% and 70.42 ± 45.63%, respectively) would be higher than the suboptimal constrained solutions, which forced the inclusion of the current network of PAs (Fig. 4).

The species distribution area decreased in the priority sites for turtle conservation in the scenarios considering PA categories for both conservation goals (Fig. 4). For instance, to conserve the top 17% landscape sites, the average proportion of species distribution remaining in the priority areas for turtle conservation decreases to 25.2% ± 16.86% including IPA, and to 17.4 ± 13.3% including all PA types (Fig. 4). The deviations in the performance curves that measure the effectiveness of spatial conservation plans are related to the inclusion of PAs in sites with low frequency of species distribution and the exclusion of sites with high frequency of species distribution in areas with high

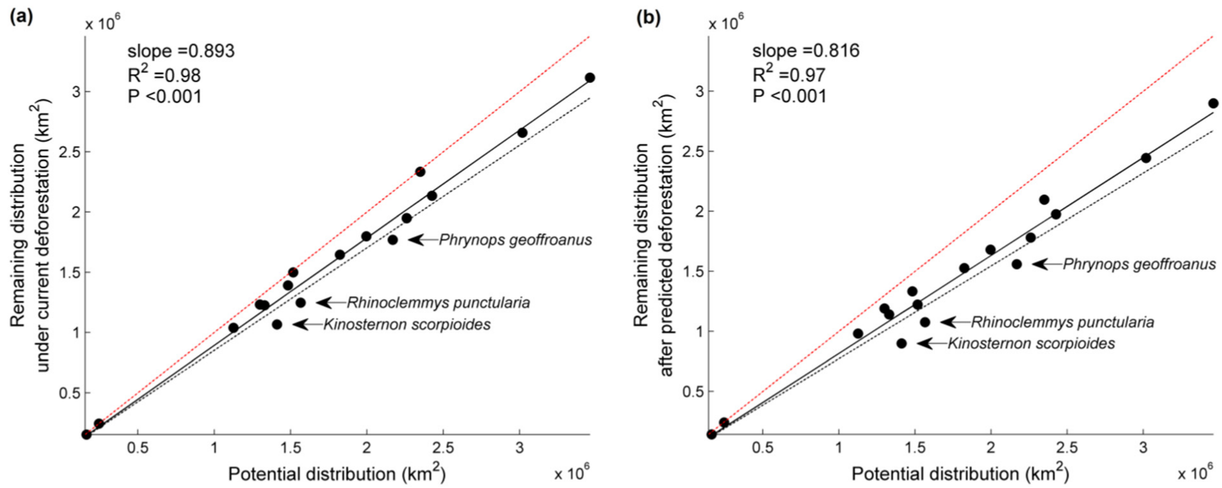

Fig. 2. Relationship between the potential distribution area of Amazon turtles and their remaining potential distribution area, considering habitat lost to (a) current and (b) predicted deforestation. Each point represents a turtle species. The potential distribution area is estimated based on species distribution models (SDMs) using the ROC threshold. Remaining potential distribution area is estimated considering the potential distribution lost to (a) current and (b) predicted deforestation. Solid red line represents the expected results for no change in potential distribution area. Dash-dotted black line represents a regression line between the potential and remaining distribution constrained to a zero intercept. Solid black line represents the expected remaining potential distribution if habitat loss was random across Brazilian Amazon. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

deforestation levels (Fig. 4).

The use of PA networks as a mask in the analysis forced the inclusion of some areas that are not necessarily located in sites with high conservation priority for turtles (Fig. 3). Considering the protection of the top 17% landscape sites, the inclusion of Integral Protected Areas (IPA) covered only 14.38% of priority sites for turtle conservation identified in the optimal solution (Fig. 3c). After including Sustainable Use Areas (SUA) and Indigenous Lands (IL), almost all the top 17% landscape sites are inside PAs: 96.35% and 97.32%, respectively (Fig. 3e, g).

Regarding the scenarios based on the top 50% of landscape sites, IPA covered only 19.69% (Fig. 3d) of priority sites for turtle conservation found in the optimal solution. The inclusion of SUA and IL covered a larger amount of priority areas identified using this conservation goal: 45.59% and 86.78%, respectively (Fig. 3f, h). The results demonstrate that all PAs were still not enough to include the top 17% and the top 50% landscape sites for turtle conservation (Fig. 3h).

4. Discussion

We provided the first broad-scale evaluation of the vulnerability of turtles to forest loss in the Amazon. Our results indicate that some species lost a large amount of potential distribution area due to deforestation. However, we found that while individual species are vulnerable to forest loss, sites in the Brazilian Amazon that have high turtle richness usually do not occur in the “arc of deforestation”, the region extending from the southwest to northeast Amazon where forest loss is concentrated (Soares-Filho et al., 2006; Hansen et al., 2010). Deforestation in those areas is largely associated with agricultural activities, which are facilitated by an extensive road network (Barber et al., 2014). In addition, even though most of the potential habitat of turtles is not located in regions with high deforestation levels, our analysis indicates that central-northeastern Amazon, in between the Trans-Amazonia and Cuiabá-Santarém Highways (Vieira et al., 2008), contains a large number of sites where turtles are vulnerable to deforestation.

Deforestation is an important factor to consider when planning for turtle conservation because forest cover and the amount of aquatic habitats are important landscape predictors for the maintenance of their populations (Gibbons et al., 2000; Quesnelle et al., 2013). In deforested areas, rainfall is reduced and flooding patterns become irregular (Fearnside, 2005; Coe et al., 2011). It is particularly significant for turtles, as rainfall is the climatic variable most associated with their diversity in South America (Souza, 2005). Besides terrestrial turtles, semi-aquatic species are expected to be highly affected by deforestation because they use terrestrial ecosystems in different moments of their life cycle (Buhlmann and Gibbons, 2001; Grgurovic and Sievert, 2005; Beaudry et al., 2009). Nevertheless, even aquatic turtles such as *Rhinemmys rufipes* (Magnusson and Vogt, 2014) and *Podocnemis erythrocephala*, which are highly dependent on the flooded forests of Amazon basin to survive (Mittermeier et al., 2015), are considered threatened by habitat destruction. The same situation could be assumed relevant for other species of *Podocnemis* genus, such as *P. unifilis* and *P. expansa*, which are also directly affected by the destruction of the river banks and nesting beaches (Rodrigues, 2005; Arraes and Tavares-Dias, 2014).

Our analyses indicate that *Kinosternon scorpioides, R. punctularia*, *P. geoffroanus* and *P. expansa* are the species most affected by deforestation, based on the percentage of potential distribution area lost to current and predicted deforestation. These species may be particularly exposed to deforestation because they all have large geographic ranges. In addition, the first three species lost more potential distribution area than the percentage of total deforestation in the Amazon, which means that forest loss is concentrated in a large portion of their potential habitat. *Phrynops geoffroanus* distribution is already known to be concentrated in areas that have higher deforestation levels in the Amazon (Rueda-Almonacid et al., 2007; Ferrara et al., 2017). Recently, de Carvalho et al. (2016) proposed that the species should be reclassified into four different taxonomic units, which makes it difficult to determine the impact of forest loss on their populations. Berry and Iverson (2011) discussed the strong effect of habitat degradation and changes of aquatic habitats on *K. scorpioides*. However, a previous gap analysis (Fagundes et al., 2016) indicated that *K. scorpioides* and *R. punctularia* are the only species protected by the Integral Protection Areas (IPA). Protection of the species by IPA is at random, since those species occur extensively in the Amazon (Rueda-Almonacid et al., 2007; Vogt, 2008). Other species such as *P. unifilis* and *M. gibba* also had large amount of potential habitat overlapping both current and predicted deforestation sites.

It is important to highlight that the model used to predict deforestation does not account for the effect of planned highways, hydroelectric power plants, waterways, or mining (Fearnside and Graça, 2009; de Souza and De Marco Jr, 2014). The construction of dams

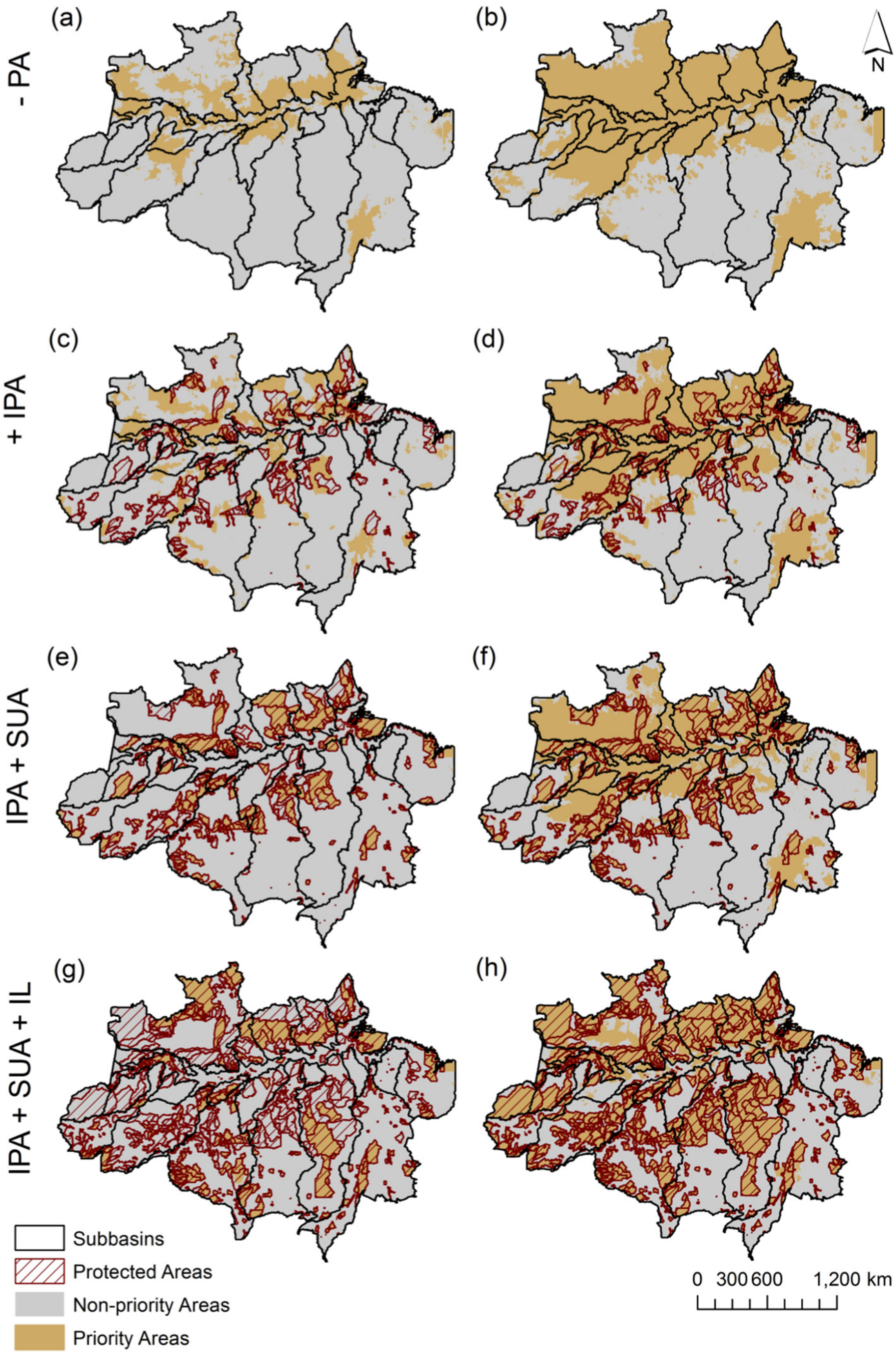

Fig. 3. Top 17% and 50% of priority areas for turtle conservation in the Brazilian Amazon considering different scenarios. (a–b) Optimal scenarios, which do not consider Protected Areas (-PA); (c–d) scenarios considering Integral Protected Areas as a mask (+IPA); (e–f) scenarios considering Integral Protected Areas and Sustainable Use Areas as a mask (IPA + SUA); (g–h) scenarios considering Integral Protected Areas, Sustainable Use Areas and Indigenous Lands as a mask (IPA + SUA + IL). The location of Protected Areas is shown in the striped polygons. Despite we used basin level 7 as management units in the analyses, which subdivides the entire Amazon basin into drainage units from 300 km^2 to 1000 km^2 (Venticinque et al., 2016), we show in the black polygons the largest subbasin level for Amazon (Venticinque et al., 2016) only to data visualization.

disturbs the movements of aquatic turtles because they induce the rupture of the longitudinal connectivity of rivers (Agostinho et al., 2008) and also lateral connectivity between river channels and their floodplains or riparian zones (Poff and Hart, 2002). This characteristic hinders turtle migration to non-deforested and non-impacted areas, reducing their adaptive capacity. A recent study demonstrated that Tapajós, Marañon, and Madeira are the most vulnerable sub-basins in terms of current dam, planned dams, and those under construction (Latrubesse et al., 2017). Other rivers, such as the Xingu, Trombetas, and Uatumã are also threatened by planned dams (Latrubesse et al., 2017). Changes in hydrology due to global warming also aggravate the conservation of aquatic organisms. Sorribas et al. (2016) reported that annual minimum river discharge will decrease in areas important for turtle conservation, especially in the lower Amazon River, lower Madeira River, middle Purus River, and middle Negro River. Changes in climate and hydrology can further influence aquatic species distribution and abundance (Lobón-Cervia et al., 2015) and nesting success (Eisemberg et al., 2016). Therefore, turtles are also vulnerable to human impacts in sites that were not identified by our analysis.

The priority sites for turtle conservation in the Brazilian Amazon are mostly located in the Amazon River main stem and the lower portions of its tributaries. The importance of those areas may be related to the fact that these regions integrates sub-basins flow and comprises distinct arrangements of geology, soil, and vegetation (MacClain and Naiman, 2008), allowing for the existence of a large diversity. Even though PAs (IPA + SUA + IL) cover a large proportion of the Brazilian Amazon, they seem to be not efficient in protecting turtles, especially aquatic and semi-aquatic species. Our results showed that many priority sites for

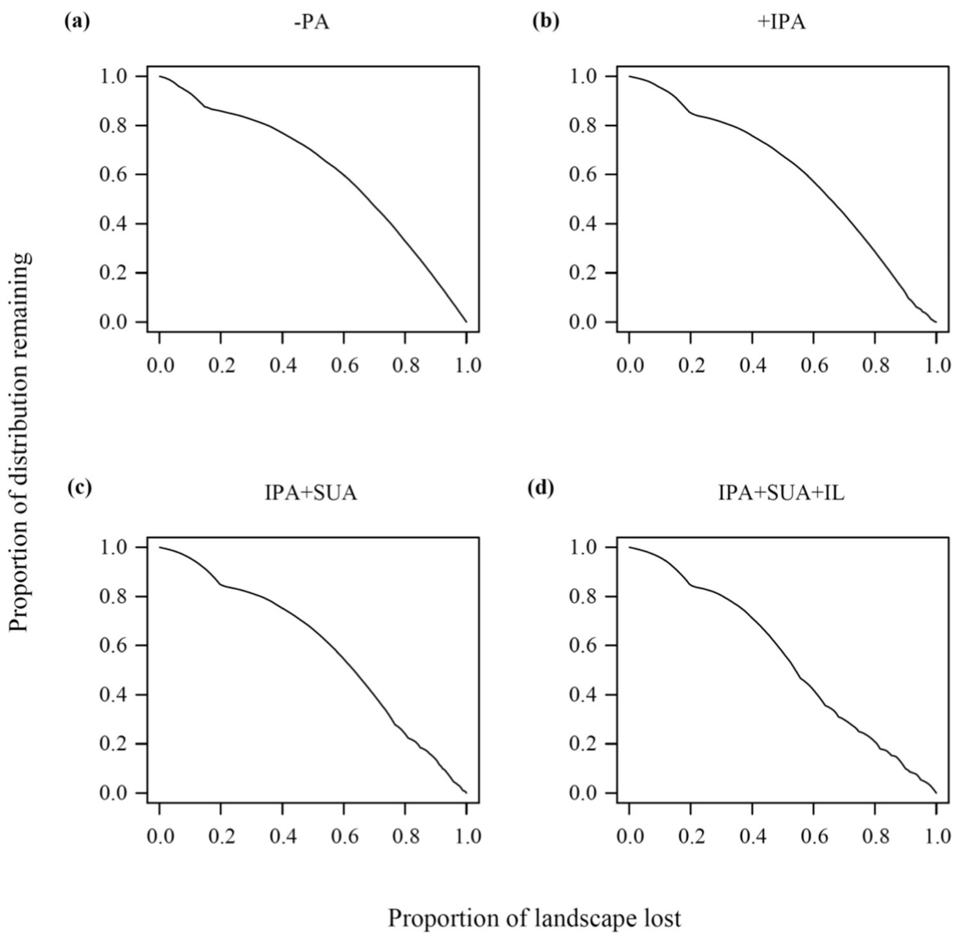

Fig. 4. Performance curves for different scenarios focused on turtle conservation in the Brazilian Amazon. The graphs show the proportion of the landscape lost and their correspondent average proportion of species distribution remaining. (a) optimal scenarios, which do not consider Protected Areas (-PA); (b) scenarios considering Integral Protected Areas (+IPA); (c) scenarios considering Integral Protected Areas and Sustainable Use Areas (IPA + SUA); and (d) scenarios considering using Integral Protected Areas, Sustainable Use Areas and Indigenous Lands (IPA + SUA + IL).

turtle conservation are located out of PAs even when only the top 17% of priority landscapes are required. Andrade (2017) also observed that, in the Amazonas state in Brazil, a large portion (> 80%) of important areas for management of turtles from the Podocnemididae family were outside PAs. The inclusion of SUAs and ILs in our analyses increased the amount of turtle habitats that are protected, but still many areas identified as priorities in the optimal scenarios (without PAs) remain outside of PAs. SUAs frequently have a high densities of human, and consequently high hunting rates and forest loss (Peres and Palacios, 2007; Peres, 2011), and may not be sufficient to conserve species of the Podocnemididae family and *Chelonoids* genus, which are the most exploited turtles in the Amazon (Kemenes and Pezzuti, 2007; Schneider et al., 2011; Morcatty and Valsecchi, 2015). Hunting has already eradicated many populations of species in extractive reserves (Peres and Palacios, 2007).

The lack of PAs in the priority sites for turtle conservation may be related to the fact that PAs in the Amazon were historically created in adjacent areas of high anthropogenic pressure (Veríssimo et al., 2011). In our analysis, to decrease land-use pressures on biodiversity, we forced the exclusion of deforested areas in the selection of priority sites (Pouzols et al., 2014). Studies of spatial conservation prioritization should take into account potential land-use change (Possingham et al., 2000; Faleiro et al., 2013), socioeconomic interests (Faith and Walker, 2002; Polasky, 2008) and vulnerability of biodiversity (Visconti et al., 2010) to prioritize sites that do not substantially overlap areas of intense human activities and sites where wildlife populations have a high chance of persisting over time (Cabeza and Moilanen, 2001).

It is also worth noting that the strategy of creating PAs mainly to protect terrestrial species (Veríssimo et al., 2011), does not effectively conserve species that are dependent on aquatic ecosystems. Turtles may demand the conservation of some parts of the drainage systems that are not close to the focal areas of concern (Moilanen et al., 2008). They migrate from high productivity feeding areas to nesting sites usually next to headwater regions (Peres, 2005) and use terrestrial environments to accomplish many activities (Klemens, 2000). Thus, a better design of PAs should be based on the selection of large areas with high conservation values in both terrestrial and aquatic habitats (Gardner et al., 2007), preferably including entire watersheds (Abell, 2002; Thieme et al., 2007). Large-scale conservation planning may decrease edge effects, support metapopulation persistence (Moilanen, 2005; Nicholson et al., 2006) and prevent future upstream threats (Peres, 2005).

The choice of priority sites is usually complex and limited by current information about the species distribution (Diniz et al., 2010). Records for most turtle species in the Amazon are available only in a few localities within their ranges (Souza, 2004, 2005; Brito et al., 2012) and most are located within 500 km of the home institutes/universities of researchers responsible for the observations (Salinéro and Michalski, 2016). Species distribution modeling can fill gaps in knowledge about species' distributions and has been largely used in conservation planning to assess the impacts of human threats on biodiversity (Phillips et al., 2006; Cabeza et al., 2010). These models can overestimate or omit portions of the species actual range and rarely take into account species interactions and the dispersal ability of species (Soberón and Nakamura, 2009). However, use of predictive SDMs is preferred over of relying only on sparse observation data delimiting the extent of occurrence of the species (Diniz et al., 2010). Here, some of our SDMs had low performance. This poor performance may be related to the important taxonomic challenges associated with some species, such as *P. geoffroanus* (de Carvalho et al., 2016) and *M. gibba*. *Mesoclemmys gibba* is often confused with *M. raniceps* (Ferronato et al., 2011) and *P. geoffroanus* is likely to be reclassified in several taxonomic units (de

Carvalho et al., 2016). It is important to state that, although the distribution of *K. scorpioides* and *P. geoffroanus* are much broader than Amazon basin, the SDMs for those species were created and evaluated to this biome because some environmental variables used in our analyses are not available for their entire extent of occurrence. This certainly had some impact on model performance.

4.1. Implications for conservation

Studies that indicate priority sites for species conservation at large scale are crucial for guiding spatial conservation planning (Theobald et al., 2000; Pierce et al., 2005) and maximizing the cost effectiveness of conservation actions. Biodiversity loss seems to be inevitable unless land-use changes are balanced with land protection. Thus, assessment of species vulnerability to anthropic impacts related to land-use activities and evaluation of the efficiency of PAs in protecting species are critical input for the development of public policies. Our results have significant practical implications for conservation agencies, as we identified regions where turtle species are most exposed to deforestation and showed the most important areas for turtle conservation in the Brazilian Amazon. Selecting priority areas for the conservation of aquatic species is still a relatively new undertaking compared to terrestrial organisms (Moilanen et al., 2008). The results can be used by decision makers to determine areas where infrastructure projects should be located to reduce or avoid impacts on turtles. However, our findings should be interpreted cautiously, as we did not take into account the social and cultural importance of turtles as a food resource in the Amazon. It is important to include socioeconomic and cultural aspects when planning or prioritizing conservation actions (Margules and Pressey, 2000; Ferrier and Wintle, 2009).

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Appendix A-D. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.08.009.

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