Diversity and Distributions, (Diversity Distrib.) (2016) 22, 123–135

A Journal of Conservation Biogeography
Diversity and Distributions

BIODIVERSITY RESEARCH

Testing the efficiency of protected areas in the Amazon for conserving freshwater turtles

Camila K. Fagundes[1]*, Richard C. Vogt[2] and Paulo De Marco Júnior[3]

[1]*Wildlife Conservation Society, Brazil Program, Av. Rodrigo Octavio, 6200, Setor Sul, Bloco H, 69077-000, Manaus, AM, Brazil,* [2]*Departamento de Biologia Aquática, Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo, 2936 – Petrópolis, CP 2223, 69067-375, Manaus, AM, Brazil,* [3]*Laboratório de Teoria, Metacomunidades e Ecologia da Paisagem, ICB 5, Universidade Federal de Goiás, CP 131, 74.001-970, Goiânia, GO, Brazil*

*Correspondence: Camila K. Fagundes, Wildlife Conservation Society, Brazil Program, Av. Rodrigo Octavio, 6.200, Setor Sul, Bloco H, 69077-000 Manaus, AM, Brazil.
E-mail: cfagundes@wcs.org

ABSTRACT

Aim We used chelonian distribution data to (1) predict suitable areas of the occurrence for freshwater turtle species using species distribution models and (2) evaluate whether these species are protected by the current network of protected areas (PAs).

Location The Brazilian Amazon.

Methods We generated predictions of suitable areas for chelonian occurrence based on BIOCLIM, SVM, GLM and maximum entropy modelling procedures. We used maximum entropy to run the gap analysis and compared the effectiveness of three kinds of protected areas with different levels of protection: (1) integral protection areas (IPA) only; (2) integral protection areas + sustainable use areas (IPA+SUA); and (3) integral protection areas + sustainable use areas + indigenous lands (IPA + SUA + IL).

Results We identified only one full gap species, *Mesoclemmys nasuta*, whose distribution is not included in any PAs. Other chelonian species have at least a portion of their distribution included in PAs. Some protected species and partial gap species occur in areas with high rates of deforestation. Considering PAs with the highest level of protection (IPA), only *Rhinoclemmys punctularia* and *Kinosternon scorpioides* achieve their conservation targets. In the IPA + SUA scenario, conservation targets of some species with small range sizes are not achieved. When all PA types were considered (IPA + SUA + IL), only two species fail to achieve their conservation targets, *Acanthochelys macrocephala* and *M. nasuta*.

Main conclusions Despite the large number of PAs in the Brazilian Amazon, IPAs alone are not sufficient for capturing suitable areas for freshwater turtles. The inclusion of SUA and IL is crucial for achieving coverage targets for most species. However, chelonians may be overharvested in SUAs and ILs, due to their importance as a food resource. Areas that have high turtle richness next to existing PAs and the needs of traditional cultures should be considered in management planning for freshwater turtles.

Keywords
Amazon, gap analysis, turtle conservation, vulnerability of freshwater organisms.

INTRODUCTION

The need for conservation planning is particularly urgent in the tropics (Klink & Machado, 2005; Cayuela *et al.*, 2009) where habitat loss and degradation contribute to the decline in fauna, generating what is known as the 'biodiversity crisis' (Myers, 1996). For instance, most megadiverse areas currently occur in the tropics (Myers *et al.*, 2000) and the Amazon includes ecoregions with high levels of richness and endemism of aquatic organisms (Abell *et al.*, 2008). Deforestation in the Amazon basin is driven by socio-economic development, mainly cattle ranching (Fearnside, 2005, 2008;

DOI: 10.1111/ddi.12396
http://wileyonlinelibrary.com/journal/ddi

Macedo *et al.*, 2012; Castello *et al.*, 2013; Souza *et al.*, 2013). A large proportion of the basin has been deforested or altered, and deforestation rates since 1991 have trended upward (Fearnside, 2005). To decrease threats associated with deforestation, it has been suggested that megareserves be created to represent different biological assemblages, including aquatic vertebrates (Peres & Terborgh, 1995; Peres, 2005).

Knowledge about species' distributions is an important basic piece of information for conservation planning and prioritization (Peres, 2005; Thieme *et al.*, 2007). Lack of information about biogeography and the distribution of organisms, the so-called Wallacean shortfall (Lomolino, 2004; Diniz *et al.*, 2010), is widely recognized as a critical limitation for effective management actions, especially in tropical regions (Myers *et al.*, 2000; Brooks *et al.*, 2001). Frequently the only available information about species distributions is range maps, which are typically coarse overestimates of species occurrence (Rodrigues *et al.*, 2003; Rondinini *et al.*, 2006; Hurlbert & Jetz, 2007). Records for most chelonian species in the Amazon are limited to a few localities within their ranges (Souza, 2004, 2005; Brito *et al.*, 2012). In this context, predictive distribution models can be an important tool to fill gaps in knowledge about species' distributions (Raxworthy *et al.*, 2003; Costa *et al.*, 2010). These models are commonly called species distribution models (SDMs) (Araújo & Peterson, 2012; Peterson & Soberón, 2012) specially in studies that try to generate hypotheses about species distributions, rather than modelling their niche (Van Loon *et al.*, 2011).

Independent of the terminologies that are used, predictive distribution models have the same purpose, to identify suitable habitat for populations of a species (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Franklin, 2010; Peterson *et al.*, 2011), through identification of statistical relationships between species' occurrences and a set of environmental predictors (Guisan & Zimmermann, 2000). Suitable areas can be then projected into geographic space to estimate species' geographic distribution (Peterson, 2001). These analyses are performed using different modelling procedures, depending on different theoretical conditions and assumptions (Elith *et al.*, 2006; Austin, 2007; Elith & Leathwick, 2009). Different methods often show substantial variation in performance (Elith *et al.*, 2006; Peterson *et al.*, 2007).

Species distribution models are useful for management (Peterson *et al.*, 2001; Guisan & Thuiller, 2005; Araújo *et al.*, 2011; Crowder & Heppell, 2011; Nóbrega & De Marco, 2011) because they produce maps showing the environmental suitability for species occurrence in areas that have not been previously sampled and can produce valuable information about overall spatial patterns in biological diversity (Cayuela *et al.*, 2009; Nóbrega & De Marco, 2011). Thus, these models are advantageous for evaluating the efficiency of existing protected area (PA) networks in representing species distribution, as assessed in formal gap analyses (Rodrigues, 2003; Phillips *et al.*, 2006; Loucks *et al.*, 2008). Protected areas have been an effective tool for maintaining viable populations of threatened species or species potentially impacted by human occupation (Rodrigues *et al.*, 2003; Sánchez-Azofeifa *et al.*, 2003; Veríssimo *et al.*, 2011). However, gap analyses have demonstrated that existing PA networks in the Americas are usually inadequate to conserve biodiversity (Scott *et al.*, 2001; Ochoa-Ochoa *et al.*, 2007).

The applicability of SDMs in the freshwater aquatic realm has been poorly explored (Wiley *et al.*, 2003) due to the lack of distribution data for freshwater species (Thieme *et al.*, 2007) and limited data describing local environmental conditions (Iguchi *et al.*, 2004; McNyset, 2005; Oakes *et al.*, 2005). Freshwater biodiversity has been more impacted than the most of terrestrial organisms (Sala *et al.*, 2000). However, priority areas for conservation are typically established based on terrestrial species and ecosystems (Brooks *et al.*, 2006; Castello *et al.*, 2013), and aquatic habitats are only protected by chance (Skelton *et al.*, 1995; Peres, 2005). Conservation planning and strategies that encompass both terrestrial and aquatic environments are crucial for effective management, especially in Amazon, where freshwater ecosystems cover between 14 and 29% of the basin area (Thieme *et al.*, 2007; Castello *et al.*, 2013).

Turtles are one of the most endangered groups of vertebrates (Gibbons *et al.*, 2000; Van Dijk *et al.*, 2000; Turtle Conservation Fund 2002; IUCN, 2011). Böhm *et al.* (2013) estimated that 52% of freshwater turtles are threatened. Of the 16 freshwater species of turtles in the Brazilian Amazon, seven are in some threat category (IUCN, 2011). In this context, the knowledge about current distribution patterns of turtles and the contribution of PAs to their conservation could not be more important (Iverson, 1992a; Stuart & Thorbjarnarson, 2003; Rhodin, 2006). Thus, our objectives in this study are to (1) predict suitable areas of occurrence for freshwater Amazon chelonians and (2) evaluate whether the group is protected by the existing network of Amazonian PAs.

METHODS

Species occurrence records

We compiled an occurrence database for 16 freshwater turtles (see Table 1) including data from the following sources: an extensive literature review, Brazilian scientific collections and museum specimens obtained from Species Link (CRIA, 2015), unpublished data from our research group and from a governmental project, Projeto Quelônios da Amazônia (IBAMA, 2015a). In addition, we utilized species data provided by the EMYSystem Global Turtle Database (Iverson *et al.*, 2003), which records depict the maps produced by Iverson (1992a,b,c). To minimize modelling problems caused by errors in georeferencing, we deleted occurrence records that were obviously erroneous, records with imprecise geographic coordinates, and generalized location descriptions. This process resulted in 1826 occurrence records (Table 1).

Table 1 The number of spatially unique occurrence records (at 4 km^2 resolution) for 16 freshwater turtles in Brazilian Amazon. We also show the amount of suitable habitats (km^2), the proportion of the conservation targets (%) and the proportion of the conservation targets attained (%) for those species using (i) only the integral protection areas (IPA), (ii) integral protection areas + sustainable use areas (IPA + SUA) and (iii) integral protection areas + sustainable use areas + indigenous lands (ITA + SUA + IL).

Species	Unique records	Suitable habitats	Conservation target	IPA	IPA + SUA	IPA + SUA + IL
Semi-aquatic						
Kinosternon scorpioides	67	2,915,552	10	10.7	27.3	45.1
Rhinoclemmys punctularia	40	1,602,432	10	11.3	21.2	44.2
Acanthochelys macrocephala	13	91,360	50.5	19.3	25.4	40.5
Mesoclemmys vanderhaegei	18	222,864	35.9	9.9	23.8	43.4
Mesoclemmys gibba	48	4,111,632	10	6.4	15.6	29.3
Platemys platycephala	45	2,281,552	10	7.1	12.9	27.7
Aquatic						
Chelus fimbriata	71	1,676,768	10	5.5	22.5	34.1
Mesoclemmys raniceps	28	3,489,664	10	7.7	22.9	39.6
Mesoclemmys nasuta	11	10,336	81.7	0	0	0.07
Phrynops geoffroanus	39	1,799,584	10	5.8	11.9	29.9
Rhinemmys rufipes	13	1,416,640	10	9.1	29.2	42.9
Peltocephalus dumerilianus	78	802,768	10	9.8	28.1	37.6
Podocnemis erythrocephala	97	1,537,360	10	8.7	23.1	35.8
Podocnemis expansa	305	2,147,648	10	7.1	22.1	35.1
Podocnemis sextuberculata	168	2,085,968	10	7.4	22.8	37.1
Podocnemis unifilis	329	2,107,616	10	7.5	22.9	35.5

We included in the analyses not only exclusively aquatic species, but also semi-aquatic species, that live in small temporary and perennial water bodies in forests. As such, we covered the entire area of the Brazilian Amazon in our modelling efforts, as opposed to only including the aquatic ecosystems. The area was divided into a grid of approximately 4 km^2 cells. We considered only one occurrence record of each species in each cell (spatially unique records) to help avoid effects of sampling bias (Dennis & Thomas, 2000; Kadmon *et al.*, 2004) (Table 1).

Environmental data

Aquatic organisms are influenced by a suite of local environmental variables (Mendonça *et al.*, 2005) for which spatial information is not readily available. However, some studies have shown that macroscale variables performed similarly to local variables when modelling the distribution of aquatic species (Watson & Hillman, 1997; Porter *et al.*, 2000). In the Brazilian Amazon, limnological and macroscale predictors are highly correlated (Frederico *et al.*, 2014). Following this reasoning, we used 42 variables: 37 climatic predictors, three variables that reflect terrain shifts and two predictors that characterize the aquatic environment (see Appendix S1 in Supporting information). We performed a principal components analysis (PCA) of the environmental variables to decrease collinearity among them and to avoid model overfitting. For the PCA, we compiled all layers at a resolution of 4 km^2. The PCA scores were used as environmental layers in the SDM procedures (Jiménez-Valverde *et al.*, 2011; Dormann *et al.*, 2012). Considering the Kaiser-Guttman criterion of principal components selection (Peres-Neto *et al.*, 2005), we selected 12 principal components which were responsible for more than 95% of the variation in the environmental variables data (see Appendix S2). We then used these principal components as predictor variables to develop our SDMs (Guisan & Thuiller, 2005; Peterson *et al.*, 2011).

Species distribution modelling

We calculated four different statistical methods for modelling to provide a more reliable estimate of the distribution of turtles (Rocchini *et al.*, 2011): a 'presence-only' method called BIOCLIM (Nix, 1986; Piñero *et al.*, 2007); a 'presence/pseudoabsence' approach via generalized linear modelling (GLM – Stockwell & Peters, 1999;. Guisan *et al.*, 2002); and two-class support vector machines (SVM – Schölkopf *et al.*, 2001; Tax & Duin, 2004; Guo *et al.*, 2005). These methods relate known occurrence localities with 'pseudoabsences' extracted from sites at which the species is not known to occur in the study area (Peterson *et al.*, 2011). In addition, we used one 'presence/background' approach, maximum entropy (Phillips *et al.*, 2006; Phillips & Dudik, 2008; Elith *et al.*, 2010). This approach assesses the relation between the environment at the locations of known records and the environment across the entire study area (Peterson *et al.*, 2011). We used the software MaxEnt to run maximum entropy (Phillips *et al.*, 2006), and the 'dismo' package on R Software (R Development Core Team 2012) to run the other modelling methods. Considering possible restriction of accessibility (Barve *et al.*, 2011), we created and evaluated all models for the entire Amazon basin.

We divided occurrence data of species that had more than 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. We based the evaluation of model performance on the elements of a confusion matrix or on the measures derived from this matrix (Elith *et al.*, 2006; Peterson *et al.*, 2011). We used 10,000 random pseudoabsence localizations for GLM and SVM methods and 10,000 background data for maximum entropy. For species that had < 15 spatially unique records, we fit and tested the SDMs with the same dataset.

The conversion of the continuous suitability gradient produced by the SDMs into binary predictions of species distribution requires the choice of a threshold (Elith *et al.*, 2006; Peterson, 2006). The threshold that we chose is 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 (Pearce & Ferrier, 2000; Jiménez-Valverde & Lobo, 2007). The models were evaluated using a threshold-dependent method, the True Skilled Statistics (TSS – Allouche *et al.*, 2006; Liu *et al.*, 2011;). The TSS varies from −1 to +1. Negative and near-zero values are no better than random and values near +1 denote the same observed and modelled distributions (Liu *et al.*, 2009). We judged models acceptable only if they had TSS values ≥ 0.5 (Fielding & Bell, 1997). We used the variance equation for TSS proposed by Allouche *et al.* (2006) to calculate the 95% confidence interval for TSS values obtained in this study. We used repeated-measures ANOVAs to compare differences in TSS values of each species using different statistical methods for modelling.

Gap analysis

We based the gap analysis on the presence of a particular set of environmental conditions appropriate to the species occurrence in PAs (Rodrigues *et al.*, 2003). We used the modelling procedure that showed higher TSS values to assess the degree that PAs overlap the distribution of turtle species considered as conservation target.

In Brazil, there are two main categories of PAs: integral protected areas (IPA), which are created for biodiversity preservation and to be free of human interference, and sustainable use areas (SUA) where the sustainable extraction of natural resources is allowed based on management strategies. Each of these types is further divided into various subcategories (SNUC, 2002). In addition, the country has a large percentage of indigenous lands (IL), where indigenous populations have possession and usage rights. We downloaded the official maps of the state and federal PAs from the government website (MMA, 2015) and converted to a resolution of 4 km^2 for performing the gap analysis.

We ran the analysis considering three kinds of PAs with different levels of protection: (1) IPA only; (2) IPA + SUA; and (3) IPA + SUA + IL. According to Rodrigues *et al.* (2003), the target amount for protecting species should be related to species range sizes. Small range size species (< 1000 km^2) should have 100% of their distributions captured in PAs, and species with large ranges (> 250,000 km^2) should have at least 10% of their distributions captured in PAs. Targets for species with intermediate range sizes were based on a logarithmic interpolation between 10% and 100%.

We evaluated the protection targets considering the Brazilian Amazon region, where most turtle species are widely distributed. Thus, we classified species as protected (P) when the target percentage of the distribution size was in fact included within PAs, partial gap (PG) when only a portion of the target percentage was included within PAs; and full gap (FG) when the entire range of the species was outside of the PA network (Rodrigues *et al.*, 2003). For fully aquatic species of turtles, we made a 500 m buffer zone around the Amazonian streams and performed the gap analysis only in this portion of the SDMs.

The annual rates of deforestation in the Brazilian Amazon are concentrated in a region known as 'arc of deforestation'. To determine whether P, PG and FG species are located in areas that show high anthropic pressure, we overlapped the arc of deforestation with species distribution maps. We obtained the arc of deforestation map from the government website (IBAMA, 2015b).

RESULTS

Species distribution modelling

According to the TSS evaluation method, BIOCLIM produced non-acceptable models for all turtle species (0.0–0.14) (see Appendix S3). GLM generated acceptable models only for *Rhinoclemmys punctularia* and *Podocnemis unifilis* (0.11–0.52). The TSS values for SVM methods ranged from 0.05 to 0.72, producing non-acceptable models for 11 species and acceptable models for five species. Maximum entropy generated acceptable models for 14 species (0.38–0.99) (see Appendix S3). Species that have a more restricted distribution in the Amazon, such as *Acanthochelys macrocephala*, *Mesoclemmys nasuta*, *M. vanderhaegei* and *Rhinemmys rufipes* exhibited the highest TSS values. The confidence interval for the TSS values can be seen in Appendix S3.

Repeated-measures ANOVAs indicated that the best statistical method for modelling in relation to TSS values ($F = 69.052$; $P < 0.05$) was maximum entropy (see Fig. 1).

Gap analysis

Turtle species richness was higher in the sedimentary portion of the Amazon basin, in the Amazon/Solimões River drainage and in the Rio Negro drainage. These basins comprise an important region for freshwater chelonian conservation.

To perform the gap analysis, we used suitability maps produced by the maximum entropy method, because it produced the best TSS values. These suitability maps can be

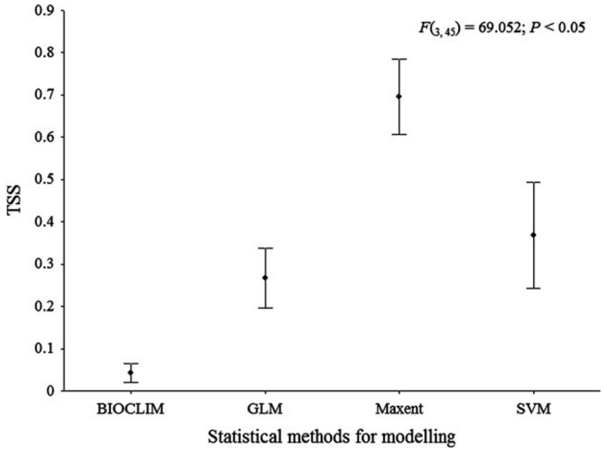

Figure 1 Differences in True Skilled Statistics (TSS) values calculated for turtle species using different statistical methods for modelling.

seen in Appendix S4. We identified only one FG species, *M. nasuta*. The suitable areas for the occurrence of this species were not protected by any category of PA. Other chelonian species were classified as PG species or as fully protected species.

In the highest level of protected area (IPA), only *R. punctularia* and *Kinosternon scorpioides* achieved their protection targets (see Fig. 2a). Thus, IPAs alone do not effectively capture the most suitable areas for turtle occurrence. Under the second level of protected areas (IPA + SUA), we identified 13 species (68.7%) as protected and two species (12.5%) as PG (see Figs 2b and 3b). The PG species occurring in this category of PAs were *M. vanderhaegei* and *A. macrocephala*. These species have the smallest amount of suitable areas in the Amazon, and IPA + SUA were not sufficient to attain conservation targets for them. The species considered fully protected in IPA+SUA scenario had a maximum of 29.2% of their suitable habitat captured in PAs (Fig. 2b, Table 1). Considering all categories of conservation areas (IPA + SUA + IL), *A. macrocephala* and *M. nasuta* were the only species that still did not achieve their conservation targets and were classified as PG species (Fig. 3c). All the other species in this scenario were classified as protected, and they had 27.7–45.1% of their suitable habitat captured by PAs (Table 1).

DISCUSSION

Despite the fact that PAs cover 22.2% the Amazon and IL cover an additional 21.7% (Veríssimo *et al.*, 2011), we found some notable gaps in protection of freshwater turtles. The network of integral protection areas is insufficient in capturing the suitable areas for chelonian occurrence. Only *R. punctularia* and *K. scorpioides* are protected by IPAs. These species are semi-aquatic turtles that live in a wide variety of habitats, mostly in small temporary or perennial water bodies in forests. *Kinosternon scorpioides* is a polytypic species that has a wide distribution, from Mexico to northern Argentina (Rueda-Almonacid *et al.*, 2007; Vogt, 2008). For all other species, we found it was also necessary to consider SUA and IL to reach target protection values, demonstrating the importance of these PA types for effective conservation of freshwater turtles in the Brazilian Amazon.

Our results support the claim that PAs in the Amazon were primarily established to protect terrestrial taxa from overharvesting and deforestation (Peres & Terborgh, 1995; Veríssimo *et al.*, 2011). However, such strategies to protect terrestrial species and ecosystems usually do not effectively conserve freshwater ecosystems and their associated fauna (Thieme *et al.*, 2007; Castello *et al.*, 2013). Much of the existing PA network ignores river catchment sites (Wishart & Davies, 2003) and freshwater threats like dams, waterways, oil exploration, pollution (Castello *et al.*, 2013) and flow modification (Abell, 2002; Dudgeon *et al.*, 2006; Davidson *et al.*, 2012; Castello *et al.*, 2013). The mitigation of the impacts of these threats on freshwater ecosystems in Amazon is particularly important because these habitats cover a large area of the basin (Castello *et al.*, 2013) and contribute to the well-being and sustenance of a large number of people (Kvist & Nebel, 2001).

Peres (2005) suggested that megareserves based on biogeographic units defined primarily by the overlap of main river barriers and a vegetation matrix would be adequate to protect Amazon flora and fauna, including aquatic ones. However, we suggest that a catchment-based system for conserving basins would be more appropriate, with identification of areas where terrestrial and freshwater conservation priorities overlap (Castello *et al.*, 2013). Amis *et al.* (2009) noticed that integrating priority areas for conservation of freshwater and terrestrial biodiversity improved management plans in South Africa. Only in particular cases should ecosystems be maintained separately (Thieme *et al.*, 2007). Creating additional PAs in a region where existing PAs already cover a large portion of land is a huge challenge. Thus, a potentially effective strategy for improving protection of freshwater resources would be to prioritize important areas that are also adjacent to existing or proposed PAs, reducing costs (e.g. start-up costs, stakeholder engagement costs) by adding more freshwater biodiversity to existing management efforts (Abell, 2002; Thieme *et al.*, 2007).

Since 1991, most PAs created by the Brazilian government as a policy action for biodiversity protection are sustainable-use reserves (Peres, 2011). Conservation strategies that attempt to reconcile biodiversity conservation and human needs are among the most effective conservation measures (Peres, 2011). However, use of natural resources is often not properly supervised in sustainable-use PAs (Peres & Terborgh, 1995; Peres, 2011). Human pressure induces forest loss, and this impact is one of the major causes of biodiversity loss (Laurance, 1999; Fearnside, 2005). The rural population in Amazon has increased from 6 million in 1960 to 25 million in 2010 (Davidson *et al.*, 2012). Human population densities in Amazonian reserves are frequently larger than in

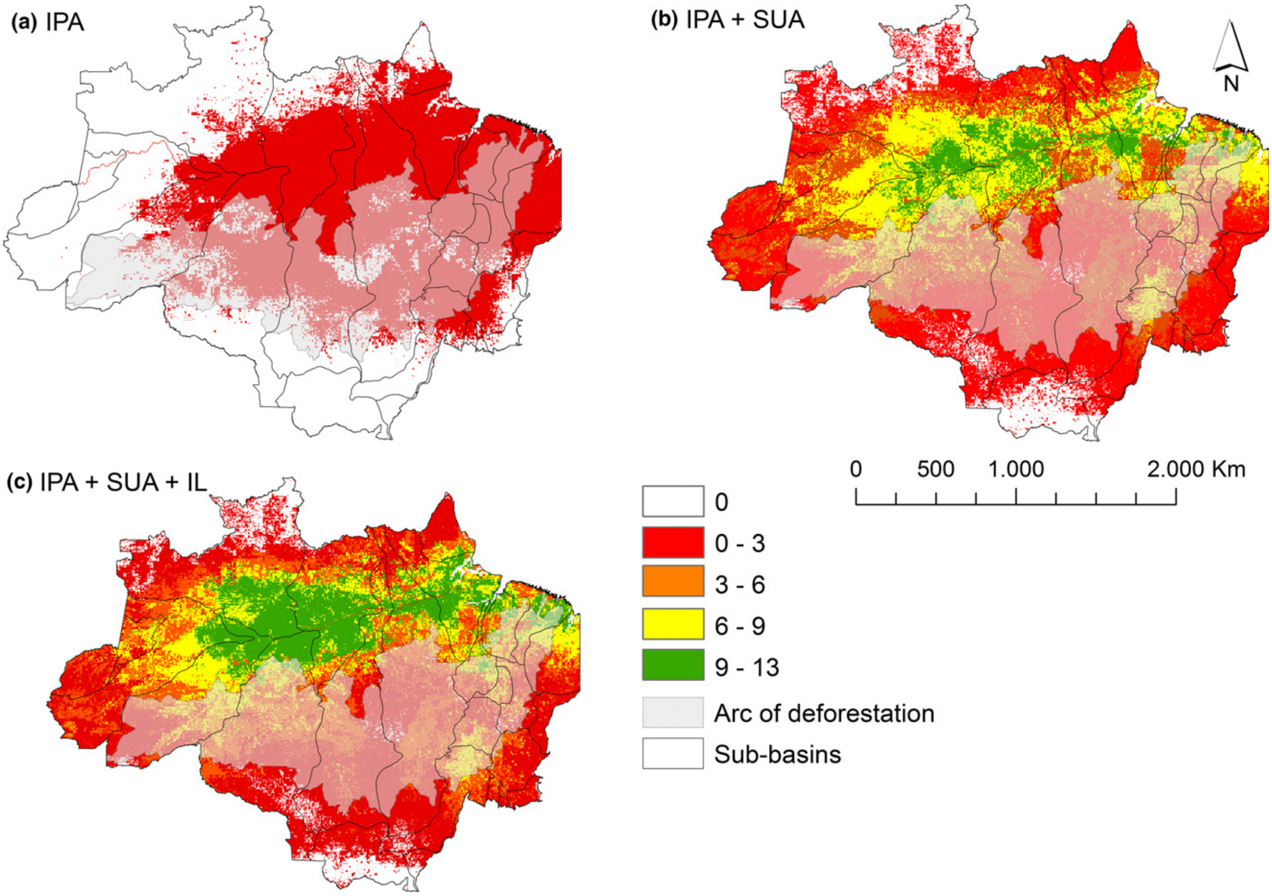

Figure 2 Number of freshwater turtles in Brazilian Amazon fully protected by the reserve networks. The conservation targets are based on the amount of suitable areas generated by maximum entropy method in protected areas. Different levels of protected areas evaluated include the following: (a) integral protection areas (IPA); (b) integral protection areas + sustainable use areas (IPA + SUA); and (c) (integral protection areas + sustainable use areas + indigenous lands (IPA + SUA + IL).

non-PAs (Peres, 2011) and even strictly protected reserves in Brazilian Amazon contain illegal human communities (SNUC, 2002). Since their formal establishment, SUAs have lost 298.500 ha of forest (Veríssimo *et al.*, 2011). Because development in the Amazon is concentrated around waterways, aquatic and semi-aquatic wildlife species are likely heavily impacted (Peres, 2000, 2011).

Conservation success has often been judged by measuring vegetation cover change across large scales (Gaston *et al.*, 2008). The rates of forest loss in Amazon are higher in 'arc of deforestation', a continuous area stretching from the south-west to north-west part of the Amazonian basin (Fearnside, 2005). According to our analysis, suitable areas for several chelonian species occur in this region and are partly captured by the existing PA network, primarily SUAs and ILs. However, turtles may be overharvested even in well forested areas, because hunting is usually unsustainable in an extraction scale (Peres & Lake, 2003). Many populations of game species have been eradicated in extractive reserves (Peres & Palacios, 2007), and chelonians are important in the diet of traditional communities in the Amazon (Kemenes & Pezzuti, 2007; Vogt, 2008; Schneider *et al.*, 2011). Overcollection of adult females and eggs have been reported as the main threats to the survival of turtle populations, mainly Podocnemididae (Fachín-Terán & Von Mülhen, 2003; Caputo *et al.*, 2005; Fachín-Terán, 2005; Vogt, 2008). One conservative analysis suggested that in the 1980s and 1990s, between 38.79 and 95.11 adults of *P. unifilis* and from 59.15 to 145.02 adults of *P. expansa* were consumed annually by the low-income rural communities in the Brazilian Amazon (Peres, 2000). Hence, sustainable-use reserves may not be sufficient on their own to conserve some freshwater turtles.

According to our analysis, a substantial amount of suitable habitat for species of genus *Podocnemis* is captured in IPAs and SUAs. However, these PAs are not sufficient to capture suitable habitats for species that have restricted distributions in the Brazilian Amazon, such as *M. vanderhaegei*, *M. nasuta* and *A. macrocephala*. *Acanthochelys macrocephala* and *M. nasuta* are not protected in the Amazon, even when we considered all the categories of PAs (IPA + SUA + IL). The distribution of *Acanthochelys macrocephala* in the Amazon is limited to a small part of the south-east region, and the species also occurs in the Brazilian Pantanal, northern Paraguay

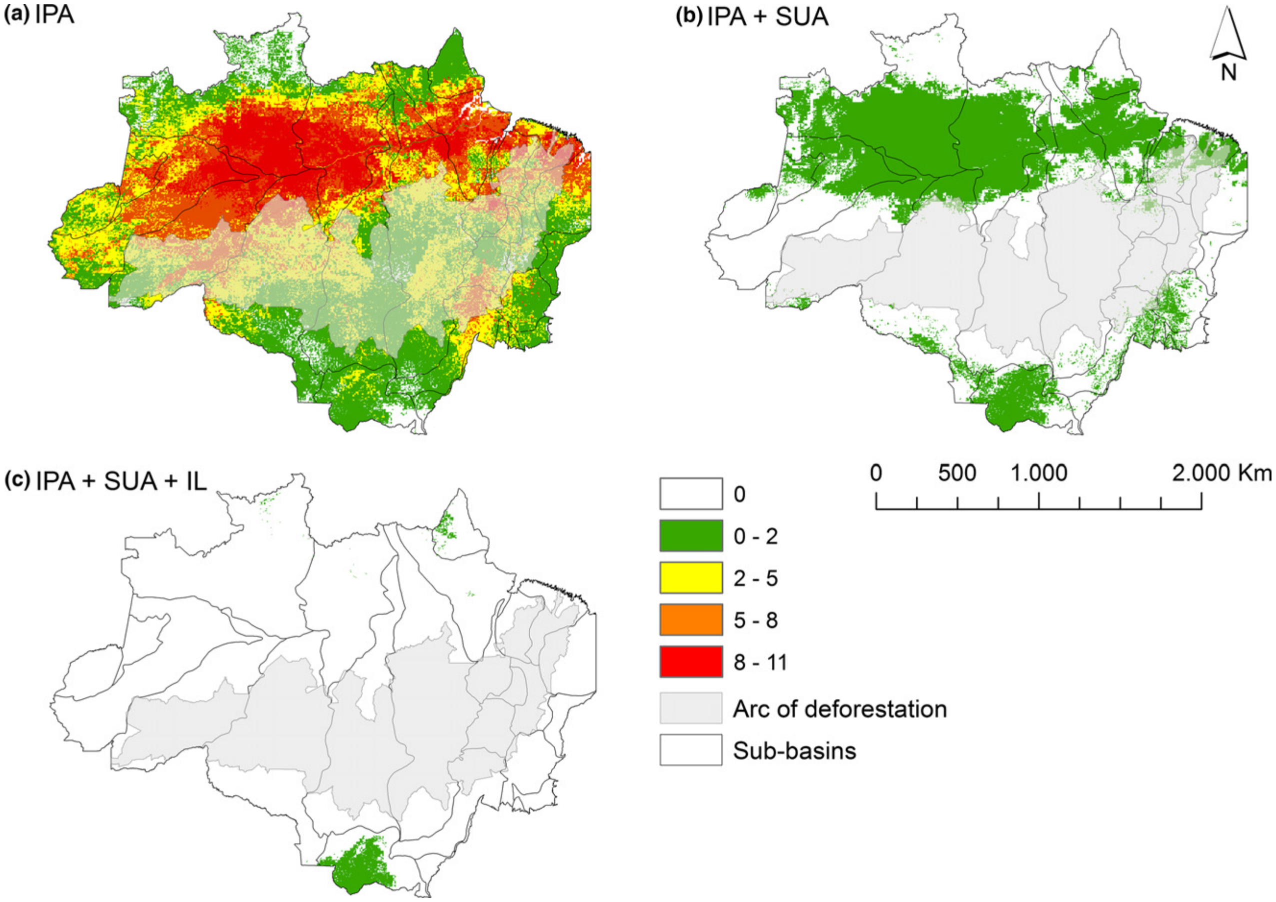

Figure 3 Number of freshwater turtles in Brazilian Amazon that are not protected by the reserve networks (partial gap). The conservation targets are based on the amount of suitable area generated by maximum entropy method in protected areas. Different levels of protected areas evaluated include the following: (a) only integral protection areas (IPA); (b) integral protection areas + sustainable use areas (IPA + SUA); and (c) integral protection areas + sustainable use areas + indigenous lands (IPA + SUA + IL).

and a very small part of Chaco ecoregion in Bolivia, where the effectiveness of PAs could be different (Rhodin *et al.*, 2009). *Mesoclemmys nasuta* is restricted to the Guianas and northernmost Amazon, in the state of Amapá (Bour & Zaher, 2005). Practically, no data concerning the biology and ecology of *M. nasuta* currently exist considering that, until recently, *M. nasuta* was considered conspecific with *M. raniceps*. Future genetic studies may recombine these allopatric species.

The sedimentary basin in northern Amazon is recognized as an important region in terms of turtle richness, as identified by Buhlmann *et al.* (2009). The area includes priority areas for freshwater turtle conservation. In this region, some of IPAs, such as Reserva Biológica do Rio Uatumã, Reserva Biológica do Rio Trombetas, Reserva Biológica do Abufari and Estação Ecológica de Jutaí-Solimões, have already implemented conservation actions for the most impacted species (*P. expansa*, *P. unifilis* and *P. sextuberculata*). Nevertheless, current activities are restricted to environmental education for traditional communities and protection of nesting beaches during the nesting season (Instituto Chico Mendes de Conservação da Biodiversidade, personal communication; Wildlife Conservation Society Brazil, personal communication). A more local analysis would be an important step for identifying specific sites for protection and specific management actions. Conservation targets should be developed in agreement with local communities and, in most cases, management activities should be carried out by them. According to Peres & Lake (2003), effective community-based conservation requires a capacity-building programme, regulation of immigration into PAs, establishment of sustainable harvest quotas and the creation of intangible zones within reserve boundaries.

In our study, SDMs were useful to predict the geographic range of chelonian species. The distribution of the majority of freshwater turtles in South America is poorly known (Souza, 2004). The predictive capacity of SDMs has been important in addressing urgent conservation problems, especially for rare and unknown species (Pearson *et al.*, 2007; de Siqueira *et al.*, 2009). SDMs have also been critical for rigorous gap analyses and the establishment of conservation priorities (Loiselle *et al.*, 2003; Martinez *et al.*, 2006; Nóbrega &

De Marco Jr., 2011). For particular turtle species, several studies have applied SDMs to help develop conservation policies (Forero-Medina *et al.*, 2012; Ihlow *et al.*, 2012; Millar & Blouin-Demers, 2012). However, the only other study that uses SDMs to generate conservation priorities based on geographic patterns of species richness and vulnerability information for a large group of chelonian species (Trionychidae and Pelomedusidae) was for African freshwater turtles (Bombi *et al.*, 2011).

Comparatively, maximum entropy produced the most reliable SDMs, according to the performance evaluation method we used (TSS). Elith *et al.* (2006) and Pearson *et al.* (2007) suggested that this statistical method is one of the most reliable SDM methods, especially for biased data. However, even using the TSS, which may control for differences in prevalence (Allouche *et al.*, 2006), models for some species, such as *M. raniceps*, *M. gibba* and *Phrynops geoffroanus*, were not acceptable. There are known identification and taxonomic challenges with these species that may contribute to poor model performance. *Phrynops geoffroanus* does not have a clear distribution pattern and is absent only at high southern latitudes (Souza, 2005). The species also seems to be a complex of sibling species (Pritchard & Trebbau, 1984). *Mesoclemmys gibba* has a wide distribution, rather similar to that of *M. raniceps* (Pritchard & Trebbau, 1984; Iverson, 1992b; McCord *et al.*, 2001) and may be misidentified in some occasions (Ferronato *et al.*, 2011). To improve SDMs and conservation planning for these species, we recommend that taxonomic revision efforts be continued for these groups and that new inventory studies be completed.

CONCLUSIONS

Amazonia covers an area of large turtle richness (Buhlmann *et al.*, 2009), composing an important region for their conservation. However, suitable areas for freshwater turtle's occurrence are not protected by the current network of IPA. The insertion of SUA and IL was crucial to consider protected large-range species, but some chelonians may be overharvested in those areas. Facing the current condition, it is necessary to shift the Amazon conservation focus and restructure the PAs in order to contemplate river catchment sites in whole basins. It is necessary to include protection actions that handle the upstream drainage network, the riparian area and, in the case of migratory species, the downstream drainage (Pusey & Arthington, 2003). At this level of PA coverage, not only turtles but all freshwater species would benefit (Dudgeon *et al.*, 2006). The approach would require a new distribution of the PAs and the use of large portions of land as PAs. Thus, a more practical manner to develop a chelonian conservation planning could take into account important areas for turtle richness conservation next to existent PAs and consider features of the traditional cultures in conservation planning in order to attend their needs.

ACKNOWLEDGEMENTS

We are grateful to Elizangela Silva de Brito, Karl Didier and Camila Rudge Ferrara for valuable suggestions to this paper. We thank the referees for their constructive comments on the study which helped us to improve our work, CNPq, CAPES, FAPEAM and Programa Petrobras Ambiental for financial support. P.D.M and R.C.V. have been supported by continuous CNPq productivity grants.

REFERENCES

Abell, R. (2002) Conservation biology for the biodiversity crisis: a freshwater follow-up. *Conservation Biology*, **16**, 1435–1437.

Abell, R., Thieme, M.L., Revenga, C. *et al.* (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, **58**, 403–414.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.

Amis, M.A., Rouget, M., Lotter, M. & Day, J. (2009) Integrating freshwater and terrestrial priorities in conservation planning. *Biological Conservation*, **142**, 2217–2226.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.

Austin, M. (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling*, **200**, 1–19.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, **222**, 1810–1819.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R. & Ram, M. (2013) The conservation status of the world's reptiles. *Biological Conservation*, **157**, 372–385.

Bombi, P., Luiselli, L. & D'Amen, M. (2011) When the method for mapping species matters: defining priority areas for conservation of African freshwater turtles. *Diversity and Distributions*, **17**, 581–592.

Bour, R. & Zaher, H. (2005) A new species of *Mesoclemmys*, from the open formations of northeastern Brazil (Chelonii, Chelidae). *Papeis Avulsos de Zoologia*, **45**, 295–311.

Brito, E.S., Strüssman, C., Kawashita-Ribeiro, R.A., Morais, D.H., Ávila, R.W. & Campos, V.A. (2012) New records and distribution extensions of three species of *Mesoclemmys* Gray, 1863 (Testudines: Chelidae) in Mato Grosso state, Brazil, with observations on terrestrial movements. *Check List*, **8**, 294–297.

Brooks, T.M., Balmford, A., Burgess, N.D., Fjeldsa, J., Hansen, L.A., Moore, J., Rahbek, C. & Williams, P.H. (2001) Toward a blueprint for conservation in Africa. *BioScience*, **51**, 613–624.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.

Buhlmann, K.A., Akre, T.S.B., Iverson, J.B., Karapatakis, D., Mittermeier, R.A., Georges, A., Rhodin, A.G.J., Van Dijk, P.P. & Gibbons, J.W. (2009) A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. *Chelonian Conservation and Biology*, **8**, 116–149.

Caputo, F.P., Canestrelli, D. & Boitani, L. (2005) Conserving the Terecay (*Podocnemis unifilis,* Testudines: Pelomedusidae) through a community-based sustainable harvest of its eggs. *Biological Conservation*, **126**, 84–92.

Castello, L., McGrath, D.G., Hess, L.L., Coe, M.T., Lefebvre, P.A., Petry, P., Macedo, M.N., Renó, V.F. & Arantes, C.C. (2013) The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, **6**, 217–229.

Cayuela, L., Golicher, D., Newton, A., Kolb, H., de Alburquerque, F.S., Arets, E.J.M.M., Alkemade, J.R.M. & Pérez, A.M. (2009) Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. *Tropical Conservation Science*, **2**, 319–352.

Costa, G.C., Nogueira, C., Machado, R.B. & Colli, G.R. (2010) Sampling bias and the use of ecological niche modeling in conservation planning: a field evaluation in a biodiversity hotspot. *Biodiversity and Conservation*, **19**, 883–899.

CRIA - Reference Center for Environmental Information (2015) Available at: http://splink.cria.org.br/ (acessed 21 January 2013).

Crowder, L. & Heppell, S. (2011) The decline and rise of a sea turtle: how Kemp's Ridleys are recovering in the Gulf of Mexico. *Solutions*, **2**, 67–73.

Davidson, E.A., de Araújo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., Bustamante, M.M.C., Coe, M.T., DeFries, R.S., Keller, M., Longo, M., Munger, J.W., Schroeder, W., Soares-Filho, B.S., Souza, C.M. & Wofsy, S.C. (2012) The Amazon basin in transition. *Nature*, **481**, 321–328.

Dennis, R.L.H. & Thomas, C.D. (2000) Bias in butterfly distribution maps: the influence of hot spots and recorder's home range. *Journal of Insect Conservation*, **4**, 73–77.

Diniz, J.A.F., De Marco, P. Jr & Hawkins, B.A. (2010) Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, **3**, 172–179.

Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B. & Singer, A. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–2131.

Dudgeon, D., Arthington, A., Gessner, M., Kawabata, Z., Knowler, D., Leveque, C., Naiman, R., Prieur-Richard, A., Soto, D., Stiassny, M. & Sullivan, C. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*, **40**, 677–697.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.

Fachín-Terán, A. (2005) Participação comunitária na preservação de praias para reprodução de quelônios na Reserva de Desenvolvimento Sustentável Mamirauá, Amazonas, Brasil. *Uakari*, **1**, 9–18.

Fachín-Terán, A. & Von Mülhen, M. (2003) Reproducción de la taricaya *Podocnemis unifilis* Troschel 1848 (Testudines: Podocnemididae) en la várzea del medio Solimões, Amazonas, Brasil. *Ecología Aplicada*, **2**, 125–132.

Fearnside, P.M. (2005) Deforestation in Brazilian Amazonia: History, rates and consequences. *Conservation Biology*, **19**, 680–688.

Fearnside, P.M. (2008) The roles and movements of actors in the deforestation of Brazilian Amazonia. *Ecology and Society*, **13**, 23.

Ferronato, B.O., Molina, F.B., Molina, F.C., Espinosa, R.A. & Morales, V.R. (2011) New locality records for chelonians (Testudines: Chelidae, Podocnemididae, Testudinidae) from Departamento de Pasco, Peru. *Herpetology Notes*, **4**, 219–224.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

Forero-Medina, G., Cárdenas-Arévalo, G. & Castaño-Mora, O.V. (2012) Habitat modeling of Dahl's toad-headed turtle (*Mesoclemmys dahli*) in Colombia. *Herpetological Conservation and Biology*, **7**, 313–322.

Franklin, J. (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.

Frederico, R.G., De Marco, P. Jr & Zuanon, J. (2014) Evaluating the use of macroscale variables as proxies for local aquatic variables and to model stream fish distributions. *Freshwater Biology*, **59**, 2303–23014.

Gaston, K.J., Jackson, S.F., Cantú-Salazar, L. & Cruz-Piñón, G. (2008) The ecological performance of protected areas. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 93–113.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S. & Winne, C.T. (2000) The global decline of reptiles, deja vu amphibians. *BioScience*, **50**, 653–666.

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Guisan, A., Edwards, T.C. Jr & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89–100.

Guo, Q., Kelly, M. & Graham, C. (2005) Support vector machines for predicting distribution of Sudden Oak Death in California. *Ecological Modelling*, **182**, 75–90.

Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence or range maps in ecology and conservation. *Proceedings of National Academy of Sciences USA*, **104**, 13384–13389.

IBAMA - Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (2015a). Available at: http://www.ibama.gov.br/fauna-silvestre/programa-quelonios-da-amazonia (accessed 10 March 2013).

IBAMA - Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (2015b). Available at: http://siscom.ibama.gov.br/ (accessed 15 September 2014).

Iguchi, K., Matsuura, K., McNyset, K.M., Peterson, A.T., Scachetti-Pereira, R., Powers, K.A., Vieglais, D.A., Wiley, E.O. & Yodo, T. (2004) Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Transactions of the American Fisheries Society*, **133**, 845–854.

Ihlow, F., Dambach, J., Engler, J.O., Flecks, M., Hartman, T., Nekum, S., Rajaei, H. & Rodder, D. (2012) On the brink of extinction? How climate change may affect global chelonian species richness and distribution. *Global Change Biology*, **18**, 1520–1530.

International Union for Conservation of Nature (IUCN) (2011) *2011 IUCN Red List of Threatened Species*. Available at: www.iucnredlist.org (accessed 5 January 2015).

Iverson, J.B. (1992a) Species richness maps of the freshwater and terrestrial turtles of the world. *Smithsonian Herpetological Information Service*, **88**, 1–18.

Iverson, J.B. (1992b) *A revised checklist with distribution maps of the turtles of the world*. Privately Published, Richmond, IN.

Iverson, J.B. (1992c) Global correlates of species richness in turtles. *Herpetological Journal*, **2**, 77–81.

Iverson, J.B., Kiester, A.R., Hughes, L.E. & KimerlinG, A.J. (2003) *The EMYSystem World Turtle Database*. Available at: http://emys.geo.orst.edu (accessed 13 December 2014).

Jiménez-Valverde, A. & Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica*, **31**, 361–369.

Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragon, P. & Lobo, J.M. (2011) Use of niche models in invasive species risk assessments. *Biological Invasions*, **13**, 2785–2797.

Kadmon, R., Farber, O. & Danin, A. (2004) Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications*, **14**, 401–413.

Kemenes, A. & Pezzuti, J. (2007) Estimate of Trade Traffic of *Podocnemis* (Testudines, Pedocnemididae) from the Middle Purus River, Amazonas, Brazil. *Chelonian Conservation and Biology*, **6**, 259–262.

Klink, C.A. & Machado, R.B. (2005) Conservation of the Brazilian Cerrado. *Conservation Biology*, **19**, 707–713.

Kvist, L.P. & Nebel, G. (2001) A review of Peruvian flood plain forests: ecosystems, inhabitants, and resource use. *Forest Ecology and Management*, **150**, 3–26.

Laurance, W.F. (1999) Reflections on the tropical deforestation crisis. *Biological Conservation*, **91**, 109–117.

Liu, C., White, M. & Newell, G. (2009) Measuring the accuracy of species distribution models: a review. *Modelling and Simulation Society of Australia and New Zealand and International Association for Mathematics and Computers in Simulation* (ed. by R.S. Anderssen, R.D. Braddock and L.T.H. Newham), pp. 4241–4247. In: 18th World IMACS Congress and MODSIM09 International Congress on Modelling and Simulation, Cairns, Australia.

Liu, C., White, M. & Newell, G. (2011) Measuring and comparing the accuracy of species distribution models with presence–absence data. *Ecography*, **34**, 232–243.

Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G. & Williams, P.H. (2003) Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology*, **17**, 1591–1600.

Lomolino, M.V. (2004) Conservation biogeography. *Frontiers of Biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 293–296. Sinauer Associates, Sunderland, MA.

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. *Journal of Biogeography*, **35**, 1337–1348.

Macedo, M.N., DeFries, R.S., Morton, D.C., Stickler, C.M., Galford, G.L. & Shimabukuro, Y.E. (2012) Decoupling of deforestation and soy production in the southern Amazon during the late 2000s. *Proceedings of the National Academy of Sciences USA*, **109**, 1341–1346.

Martinez, I., Carreno, F., Escudero, A. & Rubio, A. (2006) Are threatened lichen species well-protected in Spain? Effectiveness of a protected areas network. *Biological Conservation*, **133**, 500–511.

McCord, W.P., Joseph-Ouni, M. & Lamar, W.W. (2001) A taxonomic reevaluation of *Phrynops* (Testudines: Chelidae) with the description of two new genera and a new species of *Batrachemys*. *Revista de Biología Tropical*, **49**, 715–764.

McNyset, K.M. (2005) Use of ecological niche modelling to predict distributions of freshwater fish species in Kansas. *Ecology of Freshwater Fish*, **14**, 243–255.

Mendonça, F.P., Magnusson, W.E. & Zuanon, J. (2005) Relationships between habitat characteristics and fish

Assemblages in small streams of central Amazonia. *Copeia*, **4**, 751–764.

Millar, C.S. & Blouin-Demers, G. (2012) Habitat suitability modelling for species at risk is sensitive to algorithm and scale: a case study of Blanding's turtle, *Emydoidea blandingii*, in Ontario, Canada. *Journal for Nature Conservation*, **20**, 18–29.

MMA – Ministério do Meio Ambiente (2015) Available at http://mapas.mma.gov.br/i3geo/datadownload.htm (accessed 16 September 2014).

Myers, N. (1996) The biodiversity crisis and the future of evolution. *The Environmentalist*, **16**, 37–47.

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

Nix, H.A. (1986) A biogeographic analysis of Australian elapid snakes. *Atlas of Elapid snapkes of Australia – Australian Flora and Fauna* (ed. by R. Longmore), Series Number 7, pp. 4–15. Australian Government Publishing Service, Canberra.

Nóbrega, C.C. & De Marco, P. Jr (2011) Unprotecting the rare species: a niche-based gap analysis for odonates in a core Cerrado area. *Diversity and Distributions*, **17**, 491–505.

Oakes, R.M., Gido, K.B., Falke, J.A., Olden, J.D. & Brock, B.L. (2005) Modelling of stream fishes in the Great Plains, USA. *Ecology of Freshwater Fish*, **14**, 361–374.

Ochoa-Ochoa, L., Vázquez, L.-B., Urbina-Cardona, J.N. & Flores-Villela, O. (2007) Análisis de vacíos y omisiones en conservación de la biodiversidad terrestre de México: espacios y espécies. *Anfibios y Reptiles*. pp. 32–35. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional de Áreas Naturales Protegidas, The Nature Conservancy-Programa México, Pronatura, A.C., Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, México, México.

Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.

Peres, C.A. (2000) Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology*, **14**, 240–253.

Peres, C.A. (2005) Why we need megareserves in Amazonia. *Conservation Biology*, **19**, 728–733.

Peres, C.A. (2011) Conservation in sustainable-use tropical forest reserves. *Conservation Biology*, **25**, 1124–1129.

Peres, C.A. & Lake, I.R. (2003) Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin. *Conservation Biology*, **17**, 521–535.

Peres, C.A. & Palacios, E. (2007) Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica*, **39**, 304–315.

Peres, C.A. & Terborgh, J.W. (1995) Amazonian nature reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. *Conservation Biology*, **9**, 34–46.

Peres-Neto, P.R., Jackson, D.A. & Somers, K.M. (2005) How many principal components? Stopping rules for determining the number of non-trivial axes revisited. *Computational Statistics & Data Analysis*, **49**, 974–997.

Peterson, A.T. (2001) Predicting species' geographic distributions based on ecological niche modeling. *The Condor*, **103**, 599–605.

Peterson, A.T. (2006) Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics*, **3**, 59–72.

Peterson, A.T. & Soberón, J. (2012) Species distribution modeling and ecological niche modeling: getting the concepts right. *Natureza & Conservação*, **10**, 102–107.

Peterson, A.T., Sánchez-Cordero, V., Soberón, J., Bartley, J., Buddemeier, R.H. & Navarro-Siguenza, A.G. (2001) Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling*, **144**, 21–30.

Peterson, A.T., Papes, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, **30**, 550–560.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological niches and geographic distributions*. Princeton University Press, Princeton.

Phillips, S.J. & Dudik, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Piñero, R., Aguilar, J.F., Munt, D.D. & Feliner, G.N. (2007) Ecology matters: Atlantic-Mediterranean disjunction in the sand-dune shrub *Armeria pungens* (Plumbaginaceae). *Molecular Ecology*, **16**, 2155–2171.

Porter, M.S., Rosenfeld, J. & Parkinson, E.A. (2000) Predictive models of fish species distribution in the Blackwater drainage, British Columbia. *North American Journal of Fisheries Management*, **20**, 349–359.

Pritchard, P.C.H. & Trebbau, P. (1984) *The Turtles of Venezuela*. Society for the Study of Amphibians and Reptiles, Athens.

Pusey, B.J. & Arthington, A.H. (2003) Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research*, **54**, 1–16.

R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. &

Peterson, A.T. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, **426**, 837–841.

Rhodin, A.G.J. (2006) Turtles and humans in Florida and the world: a global perspective on diversity, threats, and economic development (ed. by P.A. Meylan), *Biology and conservation of Florida turtles. Chelonian Research Monographs*, **3**, 18–27.

Rhodin, A.G.J, Parham, J.F, vanDijk, P.P & Iverson, J.B. (2009) Turtles of the world: annotated checklist of taxonomy and synonymy (ed. by A.G.J. Rhodin, P.C.H. Pritchard, van Dijk P.P., R.A. Saumure, K.A. Buhlmann, J.B. Iverson and R. A Mittermeier), *Conservation biology of freshwater turtles and tortoises*. A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. *Chelonian Research Monographs*, **5**, 39–84.

Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jiménez-Valverde, A., Ricotta, C., Bacaro, G. & Chiarucci, A. (2011) Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. *Progress in Physical Geography*, **35**, 211–226.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I. *et al.* (2003) Global gap analysis: towards a representative network of protected areas. *Advances in applied biodiversity science*, **5**, (ed. by P.J. Benson and N. Lindeman), pp. 1–98. Washington, DC: Conservation International.

Rondinini, C., Wilson, K.A., Boitani, L., Grantham, H. & Possingham, H.P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters*, **9**, 1136–1145.

Rueda-Almonacid, J.V., Carr, J.L., Mittermeier, R.A., Rodríguez-Mahecha, J.V., Mast, R.B., Vogt, R.C., Rhodin, A.G.J., deOssa-Velásquez, J.la., Rueda, J.N. & Mittermeier, C.G. (2007) *Las tortugas y los cocodrilianos de los países andinos del trópico*. Conservación Internacional, Serie Guias Tropicales de Campo, Bogotá.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, R., Huber-sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Sánchez-Azofeifa, G.A., Daily, G., Pfaff, A. & Busch, C. (2003) Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. *Biological Conservation*, **109**, 123–135.

Schneider, L., Ferrara, C.R., Vogt, R.C. & Burger, J. (2011) History of turtle exploitation and managements techniques to conserve turtles in the Rio Negro Basin of the Brazilian Amazon. *Chelonian Conservation and Biology*, **10**, 149–157.

Schölkopf, B., Platt, J.C., Shawe-Taylor, J., Smola, A.J. & Williamson, R.C. (2001) Estimating the support of a high dimensional distribution. *Neural Computation*, **13**, 1443–1471.

Scott, M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C. & Estes, J. (2001) Nature reserves: do they capture the full range of America's biological diversity? *Ecological Issues in Conservation: Ecological Applications*, **11**, 999–1007.

de Siqueira, M.F., Durigan, G., Junior, P.M. & Peterson, A.T. (2009) Something from nothing: using landscape similarity and ecological niche modeling to find rare plant species. *Journal for Nature Conservation*, **17**, 25–32.

Skelton, P.H., Cambray, J.A., Lombard, A. & Benn, G.A. (1995) Patterns of distribution and conservation status of freshwater fishes in South Africa. *South African Journal of Zoology*, **30**, 71–81.

SNUC (2002) *Sistema Brasileiro de Unidades de Conservação. MMA, SNU, Brasília*. Available at: http://www.mma.gov.br/areas-protegidas/sistema-nacional-de-ucs-snuc (accessed 16 December 2014).

Souza, F.L. (2004) Uma revisão sobre padrões de atividade, reprodução e alimentação de cágados brasileiros (Chelidae). *Phylllomedusa*, **3**, 15–27.

Souza, F.L. (2005) Geographical distribution patterns of South American side-necked turtles (Chelidae), with emphasis on Brazilian species. *Revista Española de Herpelogía*, **19**, 33–46.

Souza, R.A., Miziara, F. & De Marco, P. Jr (2013) Spatial variation of deforestation rates in the Brazilian Amazon: a complex theater for agrarian technology, agrarian structure and governance by surveillance. *Land Use Policy*, **30**, 915–924.

Stockwell, D. & Peters, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Information Science*, **13**, 143–158.

Stuart, B.L. & Thorbjarnarson, J. (2003) Biological prioritization of Asian countries for turtle conservation. *Chelonian Conservation and Biology*, **4**, 642–647.

Tax, D.M.J. & Duin, R.P.W. (2004) Support vector data description. *Machine Learning*, **54**, 45–66.

Thieme, M., Lehner, B., Abell, R., Hamilton, S.K., Kellndorfer, J., Powell, G. & Riveros, J.C. (2007) Freshwater conservation planning in data-poor areas: an example from a remote Amazonian basin (Madre de Dios River, Peru and Bolivia). *Biological Conservation*, **135**, 484–501.

Turtle Conservation Fund (2002) *A global action plan for conservation of tortoises and freshwater turtles*. Conservation International and Chelonian Research Foundation, Washington.

Van Dijk, P.P., Stuart, B.L. & Rhodin, A.G.J. (2000) Asian turtle trade. *Chelonian Research Monographs*, **2**, 1–164.

Van Loon, A.H., Sommers, H., Schot, P.P., Bierkens, M.F.P., Griffioen, J. & Wassen, M.J. (2011) Linking habitat suitability and seed dispersal models in order to analyse the effectiveness of hydrological fen restoration strategies. *Conservation Biology*, **144**, 1025–1035.

Veríssimo, A., Rolla, A., Maior, A.P.C.S., Monteiro, A., Brito, B.Souza, Jr, C., Augusto, C.C., Cardoso, D., Conrado, D., Araújo, E., Ricardo, F., Ribeiro, J., de Lima, L.M., Ribeiro, M.B., Vedoveto, M., Mesquita, M., Barreto, P.G., Salomão, R. & Futada, S.M. (2011) *Áreas Protegidas na Amazônia brasileira*. IMAZON/Instituto Socioambiental, Belém/São Paulo.

Vogt, R.C. (2008) *Tartarugas da Amazônia*. Gráfica Biblos, Lima, Peru.

Watson, G. & Hillman, T.W. (1997) Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. *North American Journal of Fisheries Management*, **2**, 237–252.

Wiley, E.O., McNyset, K.M., Peterson, A.T., Robins, C.R. & Stewart, A.M. (2003) Niche modeling and geographic range predictions in the marine environment using a machine-learning algorithm. *Oceanography*, **16**, 120–127.

Wishart, M. & Davies, B. (2003) Beyond catchment considerations in the conservation of lotic biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **5**, 429–437.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The 42 environmental variables used for predicting freshwater turtle habitat suitability.

Appendix S2. Summary of the principal components (PCA) used as environmental layers.

Appendix S3. Summary of the evaluation of the species distribution models (SDMs) according True Skilled Statistics (TSS) method.

Appendix S4. Environmentally suitable areas for the occurrence of 16 freshwater turtles in the Amazon.

BIOSKETCHES

The overall aim of this project was to evaluate whether freshwater turtles are protected by the current network of Amazonian conservation units (gap analysis). The lead author of this study is **Camila K. Fagundes**, researcher at Wildlife Conservation Society in Brazil. Her research interests focus on vulnerability of freshwater turtle to land use/land cover changes and species distribution modelling aimed to management practices. **Paulo De Marco Júnior** is currently Associate Professor of the Universidade Federal de Goiás and is permanent advisor in graduate courses of Ecology and Evolution and Environmental Sciences of the cited university. His experience has an emphasis on Theoretical Ecology: community ecology, population ecology, conservation biology and quantitative ecology. **Richard C. Vogt** is a permanent researcher at the National Institute for Amazonian Research (INPA) and advisor in graduate programmes of Tropical Ecology and Freshwater Biology and Inland Fisheries of INPA. His research interests are focused on biology and ecology of the Amazon turtles. He is one of the pioneers in evaluating the effect of incubation temperature on sex determination in turtles.

Author contributions: C.K.F and P.D.M. originally formulated the ideas presented in this study. C.K.F and R.C.V. provided the species data. C.K.F. supplied the environmental data. C.K.F and P.D.M. ran the species distribution models and the gap analysis. C.K.F. wrote the first draft of this manuscript, and P.D.M. and R.C.V. contributed extensively to the preparation of the final version.

Editor: Rafael Loyola