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ESTRATÉGIAS E ÁREAS PRIORITÁRIAS À CONSERVAÇÃO DE QUELÔNIOS AQUÁTICOS E SEMI-AQUÁTICOS NA AMAZÔNIA

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Manaus, Amazonas
Abril, 2015

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Sinopse

Este estudo tem como objetivo prever áreas ambientalmente adequadas para a ocorrência dos quelônios de água doce na Amazônia, e avaliar se o grupo é protegido pela rede atual de áreas Protegidas (APAs) na Amazônia Brasileira (Gap analysis). Nós analisamos também a vulnerabilidade do grupo em relação ao desmatamento na Amazônia Brasileira. Áreas prioritárias para a conservação de quelônios foram selecionadas levando em consideração o desmatamento, o requerimento de habitat das espécies e a rede de APAs existente. Espécie com ampla extensão de ocorrência na Amazônia podem apresentar requerimentos distintos em diferentes áreas geográficas. Assim, nós testamos a transferência dos modelos de distribuição de espécies. Com a finalidade de entender como as mudanças climáticas afetam a razão sexual de espécies onde o sexo é dependente da temperatura, nós modelamos a "norma de reação" do crescimento do embrião e a sexualização em temperaturas de ninhos naturais em uma praia de areia e em uma área de Várzea na Amazônia central.

Palavras-chave: tartarugas, Análise de Lacunas, vulnerabilidade, mudanças climáticas, modelo de razão sexual

Dedico este trabalho à minha mãe,

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"*There is no part of natural history more interesting or instructive,*

than the study of the geographical distribution of animals."

Alfred Russell Wallace – Travels on the Amazon, 1911.

RESUMO

ESTRATÉGIAS E ÁREAS PRIORITÁRIAS À CONSERVAÇÃO DE QUELÔNIOS AQUÁTICOS E SEMI-AQUÁTICOS NA AMAZÔNIA

Este estudo teve como objetivo avaliar ameaças relacionadas a tartarugas de água doce na Amazônia brasileira, a fim de propor estratégias e áreas prioritárias para a sua conservação. No primeiro capítulo, foram utilizados dados de distribuição de quelônios para prever áreas ambientalmente adequadas para a ocorrência do grupo (modelos de distribuição de espécies - SDM) e avaliar se as tartarugas são protegidas pela rede de reservas atuais (Gap Analysis). Identificamos apenas uma espécie-lacuna, *Mesoclemmys nasuta*. Outras espécies de quelônios tiveram pelo menos uma parte de sua área de distribuição incluída em áreas protegidas. Considerando Áreas de Proteção Integral (IPA), apenas *Rhinoclemmys punctularia* e *Kinosternon scorpioides* estão protegidas. A inserção de Áreas de Uso Sustentável (SUA) e Áreas de Territórios Indígenas (ITA) foram cruciais para considerar protegida a maioria das espécies. Quelônios podem ser sobreexplorados em áreas que não são protegidas integralmente. É necessário reestruturar as áreas protegidas na Amazônia, a fim de contemplar locais de captação dos rios. No segundo capítulo foi avaliada a exposição das tartarugas de água doce ao desmatamento. Nós também identificamos áreas prioritárias para a conservação do grupo com base nas exigências do habitat das espécies, o desmatamento e a rede de áreas protegidas atuais. As áreas prioritárias para conservação estão localizadas no norte do Amazonas e elas não abrangem áreas de grande desmatamento. No entanto, o maoir número de espécies afetadadas pelo desmatamento está no centro-nordeste da Amazônia, onde o desmatamento está progredindo. *Phrynops geoffroanus, Kinosternon scorpioides* e *Rhinoclemmys punctularia* apresentaram maior porcentagem de SDMs perdidos devido ao desmatamento. As reservas incluíram grande quantidade de área exigida na conservação de quelônios, mas elas não estão localizadas em áreas de maior riqueza. Nossos resultados destacam as regiões mais importantes para investir na conservação das tartarugas de água doce na Amazônia brasileira. No terceiro capítulo, nós analisamos se os Modelos de Nicho Ecológico (ENM) de uma espécie amplamente distribuída, *Podocnemis expansa*, são transferíveis para outras partes de seu *range* geográfico. Todos os valores de TSS foram baixos, indicando que os modelos não podem ser transferidos de uma área da Amazônia para outra. Por outro lado, a AUC apresentaram excelentes e bons valores, não importa o conjunto de dados e a seleção de preditores. A área predita para a ocorrência da espécie em número de pixels mostrou forte relação com os valores de AUC e TSS. Nosso estudo demonstra a importância de capturar mudanças relevantes nas necessidades da espécie em cada região. Devido à falta de transferência, a soma das áreas adequadas prevista para ambas as regiões do conjunto de dados que produziram modelos mais acurados podem ser utilizados para representar a distribuição das espécies. No quarto capítulo, determinamos a razão sexual de filhotes de *P. unifilis* baseado na dependência da taxa de crescimento do embrião a partir de uma série histórica de temperaturas de incubação de ninhos naturais na Amazônia central. O nosso estudo é a primeiro a mostrar que a temperatura influencia a taxa de desenvolvimento do embrião e a determinação do sexo de um modo diferente. Temperatura média diária do ninho foi relacionada com a distância dele até a vegetação, temperatura do ar e da área. Variação termal diária está relacionada com a temperatura diária do ninho e ambas são responsáveis pela determinação do sexo. A praia de areia mostra alto padrão de feminização, mas a praia de Várzea ainda é um importante local de produção do sexo masculino e parece ser crucial para a manutenção da viabilidade populacional.

ABSTRACT

STRATEGIES AND PRIORITY AREAS FOR THE CONSERVATION OF AQUATIC AND SEMI-AQUATIC AMAZON TURTLES

This study aimed to evaluate some threats to freshwater turtles in Brazilian Amazon in order to propose strategies and priority areas to their conservation. In the first chapter, we used chelonian distribution data to generate species distribution model (SDM) that predict suitable areas for the occurrence of the group and to evaluate if turtles are protected by the current reserve networks (Gap Analysis). We identified only one gap species, *Mesoclemmys nasuta.* Other chelonian species had at least a portion of their distribution range included in protected areas. Considering Integral protected Areas (IPA), only *Rhinoclemmys punctularia* and *Kinosternon scorpioides* are protected. The insertion of Sustainable Use Areas (SUA) and Indigenous Territories Areas (ITA) was crucial to consider protected most of turtles. Chelonians may be overharvested in non-integral protected areas due their importance as a food resource. It is necessary to restructure the protected areas in Amazon in order to contemplate river catchment sites. In the second chapter we evaluated the exposition of the freshwater turtles to deforestation. We also identified priority areas to the group conservation based on the habitat requirements of the species, deforestation and the network of protected areas. The priority areas to freshwater chelonian conservation are located in northern Amazon and they do not encompass high deforestation areas. However, higher vulnerability of turtle richness to deforestation is located in central-northeastern Amazon, where the deforestation is currently progressing. *Phrynops geoffroanus*, *Kinosternon scorpioides* and *Rhinoclemmys punctularia* had higher percentage of their SDMs lost due to deforestation. Protected areas included large amount of sites required by chelonian conservation but they are not located in areas with higher turtle richness. Our results highlight the regions more important to invest in conservation of freshwater turtles in Brazilian Amazon. In the third chapter, we analized if the Ecological Niche Model (ENM) of a large distributed species, *Podocnemis expansa*, are transferable to other parts of its geographical range. All TSS values were low, indicating that the models cannot be transferred from one Amazon area to another. On the other hand, AUC showed excellent and good values, no matter the dataset and predictor selection. The predicted area in number of pixels showed strong relationship with the TSS and AUC values using both predictor selections. Our study demonstrates the importance of capture relevant drivers of change in the requirements of the species in each region. Given the lack of transferability, the sum of the suitable areas predicted to both regions of the dataset which produced the more accurate model may be used to represent species distribution. In the fourth chapter, we determined sex ratio of *P. unifilis* hatchlings based on the dependency of the embryo growth rate from a time series of incubation temperatures of natural nests in central Amazonia. Our study is the first one to show that temperature influences the embryo developmental rate and sex determination in a different way. Daily mean nest temperature was related to distance to vegetation, air temperature and area. Daily thermal variance is related to daily mean nest temperature and both are responsible to sex determination. The sand beach shows high feminization pattern, but the flooding site is still an important source of male production and it seems to be crucial to the maintenance of the population viability.

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INTRODUÇÃO GERAL

A biogeografia de quelônios possui forte concordância com a fragmentação da Pangea no Jurássico. Durante o Cretáceo, o grupo (exceto as tartarugas marinhas) apresentou padrões fortes de provincianismo, relacionados aos conjuntos de terra resultantes daquela cisão (Hirayama *et al.*, 2000). Um dos maiores padrões de distribuição é a separação das duas subordens de quelônios existentes hoje no Cretáceo, onde Pleurodira exerceu domínio na Gondwana, na parte sul e Cryptodira exerceu domínio na Laurásia, na parte norte (Broin e De la Fuente, 1993). Na América do Sul, a diversidade de quelônios parece ser bastante influenciada pelo tempo de especiação, pois as famílias mais diversas nessa região são de origem Gonduânica (Hirayama *et al.*, 2000; De la Fuente *et al.*, 2014). Eventos de especiação geográfica alopátrica são tidos como os responsáveis pela riqueza de espécies na Amazônia (Haffer, 1969; Bush, 1994; Haffer, 1997; Moritz *et al.*, 2000; Cheviron *et al.*, 2005). Haffer (2008) afirma que a explicação mais plausível da origem da maioria das espécies na região Neotropical é resultado de eventos ecológicos simultâneos de vicariância através de flutuações globais climático-vegetacionais que separaram repetidos "refúgios" ecológicos por muitos milhões de anos. O avanço final do rio Amazonas em direção ao seu curso moderno ocorreu com a elevação final da Cordilheira Central dos Andes (Gregory-Wodzicky, 2000) e o aumento do arco Purus (Lundberg *et al.*, 1998). Depois de regressões marinhas, a dinâmica andina levou à fragmentação do Alto Amazonas, com diversos arcos que formaram o estabelecimento final dos principais afluentes (Rasanen *et al.*, 1987; 1992; Hoorn *et al.*, 1995). A diversidade de peixes amazônicos e suas áreas de endemismo podem ser atribuídas ao aumento dos arcos e à persistência de água doce na terra emergida durante a transgressão marinha no Mioceno-Plioceno (Albert e Reis, 2011). Os mesmos eventos também devem ter influenciado na diversidade e áreas de endemismo de quelônios de água doce.

Atualmente existem 442 espécies de quelônios, sendo 327 espécies e 115 subespécies (van Dijk *et al.*, 2014). A riqueza de quelônios segue um gradiente latitudinal, com aproximadamente 250 espécies localizadas nas regiões tropical e subtropical (Bour *et al.*, 2008). A precipitação anual é a variável responsável pela riqueza global de tartarugas quando diferentes bacias hidrográficas são avaliadas (Iverson, 1992; Hecnar, 1999; Moll e Moll, 2004). E o mesmo padrão é verificado na América do Sul (Souza, 2005). Além disso, os padrões espaciais dos quelônios continentais sul-americanos estão relacionados a formações geológicas e vegetacionais (abertas e fechadas) e outras variáveis climáticas, resultando em diferentes áreas de endemismo (Pritchard e Trebbau, 1984; Hecnar, 1999; Ippi e Flores, 2001; Souza, 2005). A Amazônia é uma região com grande riqueza de quelônios (Buhlmann et al., 2009), onde 12 são endêmicas (Rhodin *et al.*, 2010). O Brasil, por sua vez, é o quinto país em riqueza de quelônios juntamente com a China (Rhodin *et al.*, 2010), apresentando 35 espécies (Sbh, 2015).

As espécies de quelônios, tanto as extintas como as atuais, apresentam características morfológicas muito semelhantes, sugerindo que a manutenção da forma como o grupo explora o ambiente foi bem sucedida evolutivamente e conservada (Ernst e Barbour, 1989; Páez *et al.*, 2012). Entretanto, atualmente o grupo está entre os vertebrados mais ameaçados (Klemens, 2000): 10% das espécies existentes são consideradas criticamente ameaçadas (Buhlmann *et al.*, 2002; IUCN, 2011) e aproximadamente 74% se encontram em algum grau de ameaça (Turtle Taxonomy Working Group - van Dijk *et al.*, 2012). O declínio mundial do grupo é atribuído em grande parte pela perda de habitats aquáticos, a fragmentação de habitats devido a fatores antrópicos de uso da terra (Millennium Ecosystem Assessment, 2005) e sobre-exploração (Gibbons *et al.*, 2000; Klemens, 2000). International Union for Conservation of Nature (IUCN, 2011) classificou sete espécies Amazônicas em alguma categoria de ameaça.

Uma grande ameaça aos quelônios na região da Amazônia consiste na sua importância como recurso alimentar para as populações indígenas e ribeirinhas e o comércio ilegal. Indivíduos adultos têm sido capturados e seus ovos têm sido colhidos há muitas gerações (Pritchard e Trebbau, 1984; Fachín-Terán *et al.*, 1996; Vogt, 2001). A maior pressão de caça encontra-se na família Podocnemididae (Klemens e Thorbjarnarson, 1995; Vogt, 2001), tendo provocado uma drástica redução de suas populações (Mittermeier, 1975; Vogt, 2001). Em geral, *Podocnemis expansa* (tartaruga-da-amazônia) e *P. unifilis* (tracajá) são as espécies mais consumidas, devido ao fato de atingirem tamanhos maiores, mas a preferência no consumo de quelônios varia de acordo com a região (Fachín-Terán, 2000; Vogt, 2001; Silva, 2004), estação do ano (Pezzuti *et al.*, 2010) e disponibilidade (Fachín-Terán, 2000). Uma análise conservativa sugeriu que nas décadas de 80 e 90 cerca de 38.790 a 95.110 adultos de *P. unifilis* e de 59.150 a 145.020 adultos de *P. expansa* foram consumidos anualmente por famílias ruuais na Amazônia Brasileira (Peres, 2000).

Na família Podocnemididae, a maioria das espécies tem o sexo dos filhotes determinado pela temperatura no interior dos ninhos (TSD), onde maiores temperaturas são favoráveis à produção de fêmeas (Ewert *et al.*, 1994; Viets *et al.*, 1994). Grandes padrões de mudanças climáticas tem sido descritos para as próximas décadas e TSD espécies são particularmente vulneráveis a essas modificações (Karl *et al.*, 1996; Magnusson, 2001; Intergovernmental Panel on Climate Change - IPCC, 2007; Deutsch *et al.*, 2008; Kallimanis, 2010; Mitchell e Janzen, 2010). O aquecimento global pode aumentar a proporção de fêmeas nas populações (Hawkes *et al.*, 2009; Hays *et al.*, 2010; Limpus, 2006; Schwanz, 2013), modificar a sobrevivência dos ninhos (Broderick *et al.*, 2001; Godley *et al.*, 2001; Hawkes *et al.*, 2007) e alterar a distribuição de espécies (Brown *et al.*, 1997; Parmesan *et al.*, 1999; Walther *et al.*, 2002). Quelônios podem mudar seu comportamento, escolhendo locais de nidificação mais frios ou mudando a época de desova para diminuir uma razão sexual desproporcional (Hawkes *et al.*, 2007; Schwanz e Janzen, 2008). Entretanto, não está claro se as tartarugas podem se adaptar tão rapidamente ao aquecimento global atual. Quelônios são organismos de longa duração, possuem maturidade tardia (Avise *et al.*, 1992; Zug *et al.*, 2002) e tem evoluído para mudanças climáticas a um ritmo muito mais lento do que as projeções sugerem para os próximos cem anos (Hamann *et al.*, 2007).

Os preditores da paisagem mais importante no declínio de tartarugas são a cobertura florestal e a quantidade de habitats aquáticos (Reese e Welsh, 1998; Gibbons *et al.*, 2000; Quesnelle *et al.*, 2013). Apesar de não existir estudos que quantifiquem os impactos da fragmentação florestal nas populações de quelônios da região amazônica, a perda e degradação de habitat são apontadas por serem grandes ameaças ao grupo nesse bioma (Rhodin *et al.*, 2009; Berry e Iverson, 2011; Magnusson e Vogt, 2014; Mittermeier *et al.*, 2015). O índice atual e a extensão cumulativa do desmatamento na Amazônia abrangem áreas enormes, principalmente em função de políticas de desenvolvimento na região (Fearnside, 2005), tais como pecuária bovina, exploração madeireira e agricultura (Fearnside, 2003; Alencar *et al.*, 2004; Laurance *et al.*, 2004). Quando a floresta é convertida para usos tais como as pastagens, as funções da bacia hidrográfica são perdidas (Fearnside, 2005).

A conservação dos ecossistemas muitas vezes entra em conflito com outros interesses socioeconômicos. Assim, a criação de áreas protegidas parece ser a melhor técnica para diminuir os impactos antrópicos sobre as espécies e conservar populações viáveis nos seus ambientes naturais (Rodrigues *et al.*, 2004; Loucks *et al.*, 2008). No entanto, várias análises de lacunas a nível regional e continental revelam que as áreas existentes para a proteção da biodiversidade são inadequadas (Scott *et al.*, 2001; Ochoa-Ochoa *et al.*, 2007). Áreas com elevada riqueza podem apresentar uma composição similar no que diz respeito às espécies que ocorrem nesses locais. Assim, a escolha de áreas prioritárias para a conservação deve ser embasada na complementaridade de áreas que representem toda biodiversidade (Bonn e Gaston, 2005). Para a avaliação desses parâmetros é necessário o conhecimento da distribuição das espécies. Esses dados, entretanto, são raramente disponíveis, especialmente em regiões tropicais pobremente amostradas (Crisci, 2001).

Modelos de Distribuição de Espécies (SDM) ou Modelos de Nicho Ecológico (ENM), entre outros nomes (Araújo e Perteson, 2012; Peterson e Soberón, 2012) podem constituir uma importante ferramenta para preencher as lacunas na informação sobre a distribuição das espécies (Raxworthy *et al.*, 2003; Costa *et al.*, 2010). Esses modelos definem a adequabilidade ambiental para a sobrevivência das populações (Guisan e Thuiller, 2005; Elith e Leathwick, 2009; Franklin, 2010; Peterson *et al.*, 2011) por meio da identificação de relações estatísticas entre suas ocorrências e um grupo de preditores ambientais (Guisan e Zimmermann, 2000). As áreas adequadas são projetadas no espaço geográfico para estimar a distribuição das espécies (Peterson, 2001).

A falta de conhecimento sobre padrões de distribuição de quelônios e sua vulnerabilidade em escala Amazônica dificulta o planejamento adequado de ações conservacionistas para o grupo nesse bioma. As ações de manejo desenvolvidas para quelônios focam na proteção dos sítios de desova para a proteção de filhotes, entretanto, usualmente não existem informações sobre a sua razão sexual. Devido a grande proporção de ameaças que o grupo enfrenta, torna-se urgente o desenvolvimento de medidas de proteção em locais além dos seus sítios reprodutivos.

Com base no exposto, a presente tese foi dividida em quatro capítulos. O primeiro capítulo tem como objetivo prever áreas ambientalmente adequadas para a ocorrência dos quelônios de água doce na Amazônia; e avaliar se o grupo é protegido pela atual rede de áreas Protegidas na Amazônia Brasileira (Gap Analysis). O segundo capítulo trata da vulnerabilidade das tartarugas de água doce em relação ao desmatamento na Amazônia brasileira e identifica áreas prioritárias para a conservação do grupo. A seleção dessas áreas foi baseada no desmatamento, no requerimento das espécies, além de considerar a rede atual de áreas protegidas no bioma.

As espécies com distribuição ampla podem apresentar requerimentos distintos em diferentes áreas geográficas. A compreensão dos fatores ecológicos que determinam a adequabilidade de habitats em cada local é importante para a conservação das espécies em toda a sua extensão de ocorrência. Assim, para a maior aplicação de modelos de predição nas ações de manejo, no terceiro capítulo nós testamos a transferência de modelos de distribuição de *P. expansa* para diferentes áreas da Amazônia. O desempenho dos modelos foi baseado na seleção de preditores para controlar autocorrelação e escolha do background. Discutimos também a aplicabilidade e limitações da abordagem da transferabilidade na conservação de organismos.

O conhecimento da relação entre as alterações climáticas e a proporção de fêmeas e machos produzida em cada período de tempo é muito importante para entender como o aquecimento global pode afetar a sobrevivência das espécies onde o sexo é dependente da temperatura. Assim, no quarto e último capítulo nós modelamos a “norma de reação” do crescimento do embrião e a sexualização sob temperaturas de ninhos naturais em uma praia de areia e em uma área de Várzea na Amazônia central, com a finalidade de predizer proporção de machos e fêmeas, e de determinar os fatores que influenciam a temperatura do ninho. O nosso estudo é o primeiro a mostrar que a temperatura influencia a taxa de desenvolvimento do embrião e a determinação do sexo de uma maneira distinta e os modelos feitos até então não modelaram essas características separadamente.

OBJETIVOS

O objetivo geral da tese foi:

Avaliar ameaças relacionadas a tartarugas de água doce na Amazônia Brasileira e propor estratégias e áreas prioritárias à sua conservação.

Os objetivos específicos de cada capítulo foram:

Capítulo 1: Predizer áreas adequadas à ocorrência de quelônios de água doce na Amazônia. Avaliar se o grupo é protegido pela atual rede de áreas Protegidas na Amazônia Brasileira.

Capítulo 2: Verificar a vulnerabilidade das tartarugas de água doce na Amazônia brasileira ao desmatamento. Além disso, esse capítulo teve como objetivo indicar áreas prioritárias para a conservação do grupo.

Capítulo 3: Testar a transferabilidade dos Modelos de Nicho Ecológico (ENMs) de *Podocnemis expansa* para outras partes de sua extensão geográfica na Amazônia.

Capítulo 4: Modelar a “norma de reação” do crescimento do embrião e a sexualização de filhotes de *Podocnemis unifilis* em relação a temperaturas de incubação de ninhos naturais. Determinar fatores que afetam a temperatura dos ninhos.

Capítulo 1

Fagundes, C.K., Vogt, R. C. & De Marco Jr., P. 2015. Are Amazonian megareserves efficient to conserve freshwater turtles: A Gap analysis based on a species distribution modelling approach. Aceito na Diversity and Distribution

TESTING THE EFFICIENCY OF PROTECTED AREAS IN THE AMAZON FOR CONSERVING FRESHWATER TURTLES

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Short running title: A gap analysis for amazonian freshwater turtles

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 if these turtles 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 statistical methods. 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 targets 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 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, deforestation in the Amazon Basin is driven by socio-economic development, mainly cattle ranching (Fearnside, 2005a, 2008; Macedo *et al.*, 2012; Castello *et al.*, 2013; Souza & De Marco Jr, 2013). A large proportion of the basin has been deforested or altered, and deforestation rates since 1991 have trended upward (Fearnside, 2005a). 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). 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 are 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 (SDM) (Araújo & Peterson, 2012; Peterson & Soberón, 2012) and in this study we use this term because we are trying 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 statistical methods for modelling, 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 Junior, 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 Jr, 2011). Thus, these models are advantageous for evaluating the efficiency of existing protected area 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, 2003; Sánchez-Azofeifa *et al.*, 2003; Veríssimo *et al.*, 2011). However, gap analyses have demonstrated that existing protected area (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 threatened groups of vertebrates (van Dijk *et al.*, 2000; Gibbons *et al.*, 2000; Turtle Conservation Fund 2002; IUCN, 2008). Böhm *et al.* (2013) estimated that 52% of freshwater turtles are threatened. There are 16 freshwater species of turtles in the Brazilian Amazon, seven of which 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 if 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 geo-referencing, 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).

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 environmental variables 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 in Supporting Information). We then used these principal components as predictor variables to develop our species distribution models (Guisan & Truiller, 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/pseudo-absence' approach via Generalized Linear Modeling (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 "pseudo-absences" 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 species distribution models 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 pseudo-absence localizations for GLM and SVM methods and 10.000 background data for Maximum Entropy. For species that had less than 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 modeled distributions (Liu *et al.*, 2009). We judged models acceptable only if they had TSS values $\geq$ 0.5 (Fielding & Bell, 1997). We calculated the TSS confidence interval as proposed by Allouche *et al*. (2006). We used repeated measures ANOVAs to compare differences in TSS values of each species using different statistical methods for modelling. The significant level of this analysis was 0.05.

Gap Analysis

We based the Gap Analysis on the presence of a particular set of environmental conditions appropriate to the species occurrence in protected areas (Rodrigues *et al.*, 2003). We used the statistical method 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 principle 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 sub-categories (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 protected areas 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 (< 1.000 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 500m 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 if 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 in Supporting Information). 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 in Supporting Information). Species that have a more restricted distribution in the Amazon, such as *Acanthochelys macrocephala*, *M. nasuta*, *M. vanderhaegei* and *R. rufipes* exhibited the highest TSS values. The confidence interval for the TSS values can be seen in Appendix S3 in Supporting Information.

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 seen in Appendix S4 in Supporting Information. We identified only one full gap 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 partial gap species or as fully protected species.

In the highest level of protected area (IPA), only *Rhinoclemmys 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 partial gap (see Fig. 2b and Fig. 3b). The partial gap species occurring in this category of protected areas were *M. vanderhaegei* and *A. macrocephala*. These species have the smallest suitable areas in the Amazon, and IPA+SUA protected areas were not sufficient to attain conservation targets for these species. 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 partial gap 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 Indigenous Lands 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 Sustainable Use Areas (SUA) and Indigenous Lands (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, 2005a). 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 non-protected areas (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 southwest to northwest part of the Amazonian Basin (Fearnside, 2005a). 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 & Pezzutti, 2007; Vogt, 2008; Schneider *et al*., 2011). Over-collection 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; Fachín-Terán, 2005; Caputo *et al*., 2005; Vogt, 2008). One conservative analysis suggested that in the 80's and 90's, between 38.79-95.11 adults of *P. unifilis* and from 59.15-145.02 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 southeast region, and the species also occurs in the Brazilian Pantanal, northern Paraguay 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 exists 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 program, regulation of immigration into PAs, establishment of sustainable harvest quotas, and the creation of intangible zones within reserve boundaries.

In our study, species distribution models 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; Siqueira *et al.*, 2008). SDMs have also be critical for rigorous gap analyses and the establishment of conservation priorities (Loiselle *et al.*, 2003; Martinez *et al.*, 2006; Nóbrega & De Marco, 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 *P. 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 protected areas 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.

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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}

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BIOSKETCH

The overall aim of this project was to evaluate if freshwater turtles are protected by the current network of Amazonian Conservation Units (Gap Analysis). The lead author of this paper is Camila Kurzmann Fagundes, doctoral researcher at National Institute for Amazonian Research (INPA) in Brazil. Her research interests focus on vulnerability of freshwater turtle to land use/land cover changes, the effects of global change on hatchlings sex ratio 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, acting on the following themes: community ecology, population ecology, conservation biology and quantitative ecology. Richard Carl Vogt is a permanent researcher at the National Institute for Amazonian Research (INPA) and advisor in graduate programs 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 evaluate the effect of incubation temperature on sex determination in turtles and in vocalization studies of aquatic turtles.

Author contributions: C.K.F and P.D.M. originally formulated the ideas presented in this paper. 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.

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), proportion of the conservation targets (%) and the proportion of the conservation targets attained (%) for those species using (a) only the Integral Protection Areas (IPA), (b) Integral Protection Areas + Sustainable Use Areas (IPA + SUA) and (c) 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

APPENDIX S1

The 42 environmental variables used for predicting freshwater turtle habitat suitability in Amazon. The table also shows the variables code, their description and source

Variables (units)	Code	Description
Annual Mean Temperature (°C) [1]	Bio 01	Calculated from the minimum and maximum temperatures
Mean Diurnal Range (°C) [1]	Bio 02	Calculated from the minimum and maximum temperatures: (Mean of monthly (max temp - min temp))
Isothermality [1]	Bio 03	Calculated from the minimum and maximum temperatures: (Bio02/Bio07)
Temperature Seasonality (CV) [1]	Bio 04	Calculated from the minimum and maximum temperatures: (standard deviation *100)
Max Temperature of Warmest Month (°C) [1]	Bio 05	The maximum temperature of warmest month
Min Temperature of Coldest Month (°C) [1]	Bio 06	The minimum temperature of clodest month
Temperature Annual Range (°C)[1]	Bio 07	Calculated from the minimum and maximum temperatures: (Bio5-Bio6)
Mean Temperature of Wettest Quarter (°C) [1]	Bio 08	Calculated from the minimum, maximum temperatures and rainfall (mm month^{-1})
Mean Temperature of Driest Quarter (°C) [1]	Bio 09	Calculated from the minimum, maximum temperatures and rainfall (mm month^{-1})
Mean Temperature of Warmest Quarter (°C) [1]	Bio 10	Calculated from the minimum and maximum temperatures
Mean Temperature of Coldest Quarter (°C) [1]	Bio 11	Calculated from the minimum and maximum temperatures
Annual Precipitation (mm) [1]	Bio 12	Calculated from the rainfall (mm month^{-1})
Precipitation of Wettest Month (mm) [1]	Bio 13	Calculated from the rainfall (mm month^{-1})
Precipitation of Driest Month (mm) [1]	Bio 14	Calculated from the rainfall (mm month^{-1})
Precipitation Seasonality (mm) [1]	Bio 15	Calculated from the rainfall (mm month^{-1})
Precipitation of Wettest Quarter (mm) [1]	Bio 16	Calculated from the rainfall (mm month^{-1})
Precipitation of Driest Quarter (mm) [1]	Bio 17	Calculated from the rainfall (mm month^{-1})
Precipitation of Warmest Quarter (mm) [1]	Bio 18	Calculated from the minimum, maximum temperatures and rainfall (mm month-^{1})
Precipitation of Coldest Quarter (mm) [1]	Bio 19	Calculated from the minimum, maximum temperatures and rainfall (mm month-^{1})
Annual mean radiation (W m-^{2}) [2]	Bio 20	Calculated from the radiation (W m^{-2}d^{-1})
Highest weekly radiation (W m^{-2}) [2]	Bio 21	Calculated from the radiation (W m^{-2}d^{-1})

Lowest weekly radiation (W m$^{-2)}$ [2]	Bio 22	Calculated from the radiation (W m^{-2}d^{-1})
Radiation seasonality (CV) [2]	Bio 23	Calculated from the radiation (W m^{-2}d^{-1})
Radiation of wettest quarter (W m^{-2}) [2]	Bio 24	Calculated from the rainfall (mm month-1) and radiation (W m^{-2}d^{-1})
Radiation of driest quarter (W m^{-2}) [2]	Bio 25	Calculated from the rainfall (mm month-1) and radiation (W m^{-2}d^{-1})
Radiation of warmest quarter (W m^{-2}) [2]	Bio 26	Calculated from the minimum, maximum temperatures and radiation (W m^{-2}d^{-1})
Radiation of coldest quarter (W m-^{2}) [2]	Bio 27	Calculated from the minimum, maximum temperatures and radiation (W m^{-2}d^{-1})
Annual mean moisture index[2]	Bio 28	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Highest weekly moisture index[2]	Bio 29	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Lowest weekly moisture index[2]	Bio 30	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Moisture index seasonality (CV) [2]	Bio 31	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of wettest quarter [2]	Bio 32	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of driest quarter [2]	Bio 33	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of warmest quarter [2]	Bio 34	Calculated from the minimum, maximum temperatures, rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of coldest quarter [2]	Bio 35	Calculated from the minimum, maximum temperatures, rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Flow accumulation (number of cells) [3]	FACC	Defines the amount of upstream area draining into each cell
Flow direction (number of cells) [3]	FDIR	Defines the direction of flow from each cell in the conditioned DEM to its steepest down-slope neighbor
Shuttle Radar Topography Mission (m) [4]	SRTM	Digital elevation data
Slope (°) [5]	SLP	The maximum rate of elevation between each cell and its eight neighbors
Compound Topographic Index [5]	CTI	Reflects a function of the upstream contributing area and the slope of the landscape
Annual Actual Evapotranspiration (mm) 6	AAE	Effective quantity of water that is removed from the soil due to evaporation and transpiration processes, alternative indicator of energy availability
Annual Water Balance (mm) [6]	AWB	Defines the fraction of Water Content available for evapotranspiration processes

The layers references and website for download: [1] Hutchinson et al. (2009), available on http://www.worldclim.org/download; [2] Hutchinson et al. (2009), available on https://www.climond.org/Download.aspx; [3] Lehner et al. (2006), available on http://hydrosheds.cr.usgs.gov/index.php; [4] Farr et al. (2007), available on https://lta.cr.usgs.gov/SRTM2; [5] Moore et al (1991), available on https://lta.cr.usgs.gov/HYDRO1K; [6] Ahn & Tateishi (1994), available on http://edit.csic.es/Climate.html.

APPENDIX S2

Summary of the principal components (PCA) used as environmental layers. Each cell value represents the individual loadings of variables in each PC. The proportion of individual and cumulative explanation of each PCA is also shown

Environmental variables	Principal components											
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12
Annual Actual Evapotranspiration (mm)	0.190	0.012	-0.047	-0.011	0.080	-0.002	-0.034	0.015	-0.071	0.310	-0.209	-0.450
Annual Mean Temperature (°C)	0.171	-0.221	-0.055	-0.178	-0.014	-0.065	-0.018	-0.016	0.059	-0.015	0.009	0.065
Mean Diurnal Range (°C)	-0.185	0.025	0.122	-0.029	0.243	0.027	0.037	-0.009	0.050	0.019	-0.381	0.330
Isothermality	0.140	0.160	-0.041	0.119	-0.243	-0.243	-0.152	-0.020	-0.199	-0.146	-0.183	0.126
Temperature Seasonality (CV)	-0.167	-0.004	-0.112	-0.130	0.079	0.382	0.246	0.022	0.326	-0.083	0.087	-0.066
Max Temperature of Warmest Month (°C)	0.126	-0.273	-0.024	-0.200	0.069	-0.028	0.019	-0.018	0.120	0.013	-0.097	0.169
Min Temperature of Coldest Month (°C)	0.199	-0.162	-0.076	-0.091	-0.117	-0.101	-0.048	-0.013	0.006	-0.032	0.072	-0.014
Temperature Annual Range (°C)	-0.190	-0.036	0.099	-0.072	0.271	0.136	0.101	0.001	0.124	0.068	-0.228	0.212
Mean Temperature of Wettest Quarter (°C)	0.154	-0.226	-0.068	-0.232	0.002	-0.021	0.007	-0.014	0.098	-0.018	0.048	0.063
Mean Temperature of Driest Quarter (°C)	0.185	-0.208	-0.048	-0.115	-0.055	-0.097	-0.035	-0.016	0.027	-0.018	-0.014	0.061
Mean Temperature of Warmest Quarter (°C)	0.158	-0.235	-0.070	-0.195	-0.015	-0.023	0.011	-0.014	0.104	-0.026	0.023	0.066
Mean Temperature of Coldest Quarter (°C)	0.184	-0.206	-0.032	-0.139	-0.032	-0.119	-0.054	-0.018	0.006	0.000	-0.004	0.075
Annual Precipitation (mm)	0.214	0.057	-0.045	0.086	0.194	0.020	0.027	-0.009	0.053	-0.017	-0.026	0.128
Precipitation of Wettest Month (mm)	0.172	-0.088	-0.034	0.227	0.287	-0.038	0.003	-0.022	0.024	-0.160	0.064	0.004
Precipitation of Driest Month (mm)	0.162	0.214	-0.138	-0.063	-0.062	0.066	0.039	0.010	0.029	0.016	-0.141	0.321
Precipitation Seasonality (mm)	-0.170	-0.187	0.091	0.096	0.069	-0.041	0.014	-0.028	0.016	-0.298	-0.028	-0.002
Precipitation of Wettest Quarter (mm)	0.177	-0.080	-0.015	0.206	0.306	-0.031	0.006	-0.025	0.034	-0.140	0.048	0.016
Precipitation of Driest Quarter (mm)	0.172	0.208	-0.135	-0.052	-0.048	0.065	0.042	0.009	0.043	0.017	-0.127	0.271
Precipitation of Warmest Quarter (mm)	0.077	0.199	-0.044	-0.220	0.378	0.042	0.019	-0.021	0.088	0.015	0.247	0.055

Precipitation of Coldest Quarter (mm)	0.169	0.007	-0.058	0.268	-0.152	0.141	0.138	0.014	0.227	-0.279	-0.195	0.011
Annual mean radiation (W m-2)	-0.136	-0.044	-0.386	0.054	0.043	0.014	-0.001	-0.001	-0.014	-0.037	-0.036	-0.007
Highest weekly radiation (W m-2)	-0.103	-0.174	-0.284	0.191	-0.053	0.176	0.041	0.042	-0.043	0.258	0.102	0.133
Lowest weekly radiation (W m-2)	-0.125	0.047	-0.390	-0.024	0.054	-0.081	-0.035	-0.021	-0.031	-0.165	-0.075	-0.106
Radiation seasonality (CV)	0.092	-0.135	0.341	0.130	-0.082	0.185	0.052	0.050	-0.008	0.330	0.164	0.171
Radiation of wettest quarter (W m-2)	-0.124	0.034	-0.397	-0.069	0.033	-0.003	0.007	-0.010	0.056	-0.136	-0.001	-0.133
Radiation of driest quarter (W m-2)	-0.059	-0.209	-0.192	0.297	-0.027	0.077	-0.025	0.045	-0.166	0.345	0.048	0.234
Radiation of warmest quarter (W m-2)	-0.062	-0.196	-0.321	0.163	-0.059	0.152	0.055	0.026	0.039	0.144	0.121	0.032
Radiation of coldest quarter (W m-2)	-0.141	0.019	-0.213	-0.123	0.223	-0.276	-0.187	-0.034	-0.306	0.136	-0.111	0.132
Annual mean moisture index	0.216	0.110	-0.032	0.089	0.100	0.011	-0.007	0.004	-0.031	0.092	0.086	-0.017
Highest weekly moisture index	0.175	-0.049	-0.004	0.272	0.257	-0.054	-0.028	-0.014	-0.069	-0.063	0.110	-0.041
Lowest weekly moisture index	0.167	0.230	-0.112	-0.051	-0.091	0.062	0.019	0.014	-0.002	0.064	0.000	0.148
Moisture index seasonality (CV)	-0.162	-0.217	0.094	0.095	0.149	-0.082	-0.021	-0.027	-0.041	-0.168	-0.094	0.079
Mean moisture index of wettest quarter	0.180	-0.041	0.013	0.251	0.271	-0.050	-0.030	-0.015	-0.073	-0.031	0.100	-0.042
Mean moisture index of driest quarter	0.176	0.221	-0.106	-0.034	-0.079	0.063	0.020	0.015	0.007	0.077	0.027	0.098
Mean moisture index of warmest quarter	0.089	0.269	-0.035	-0.157	0.245	0.061	0.011	-0.010	0.012	0.079	0.296	-0.073
Mean moisture index of coldest quarter	0.188	0.025	-0.057	0.233	-0.174	0.116	0.099	0.022	0.159	-0.175	-0.078	-0.073
Flow accumulation (number of cells)	0.008	-0.007	0.011	0.015	-0.033	0.346	-0.455	-0.819	0.032	-0.004	-0.029	-0.005
Flow direction (number of cells)	-0.001	-0.012	0.012	-0.010	0.046	0.268	-0.764	0.545	0.194	-0.069	-0.040	-0.012
Slope (°)	-0.119	0.162	0.003	0.153	-0.076	-0.280	-0.123	-0.054	0.248	-0.124	0.331	0.386
Shuttle Radar Topography Mission (m)	-0.167	0.210	0.040	0.203	0.003	0.038	0.001	0.015	-0.065	0.034	-0.024	-0.023
Compound Topographic index	0.089	-0.046	0.027	-0.153	0.001	0.460	0.088	0.114	-0.672	-0.381	0.088	0.144
Annual Water Balance (mm)	0.185	0.052	-0.017	0.065	0.165	0.073	0.053	0.013	0.039	0.138	-0.481	-0.066
Proportion explained by each PC	42.646	17.080	9.983	7.569	5.688	2.620	2.407	2.320	1.958	1.424	1.060	0.988
Accumulated variation proportion	42.646	59.726	69.709	77.278	82.966	85.586	87.993	90.312	92.270	93.694	94.754	95.742

APPENDIX S3

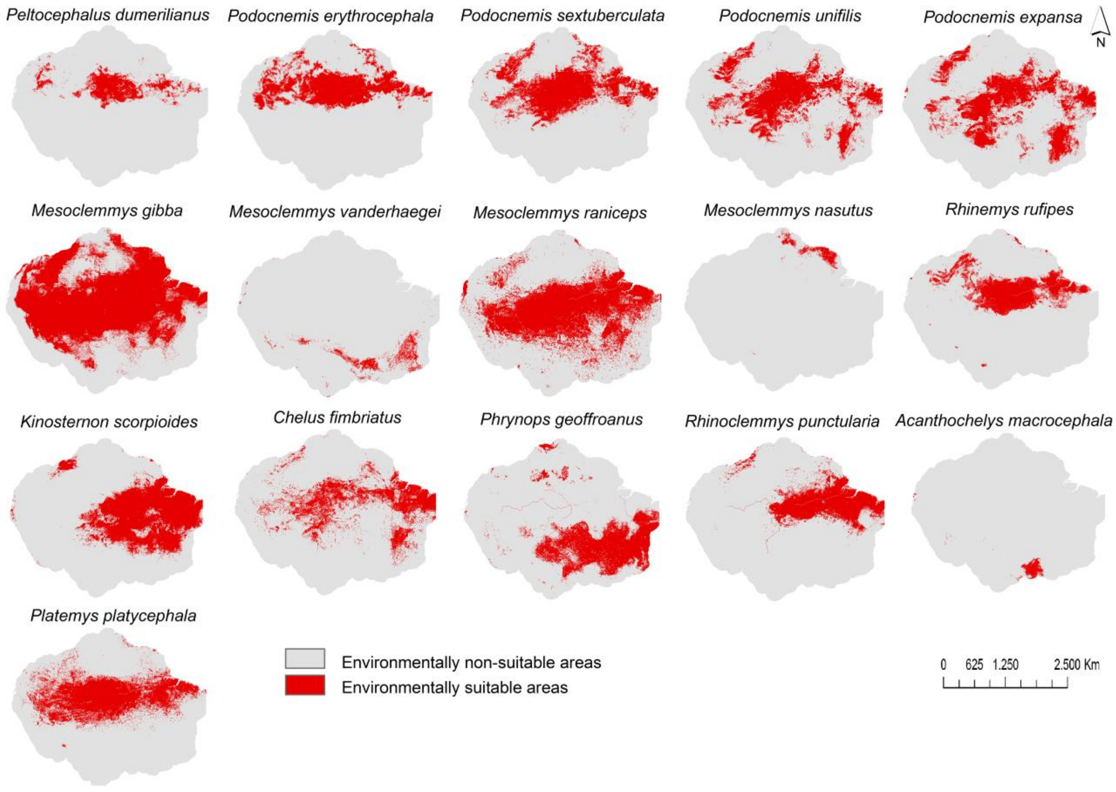
Summary of the evaluation of the species distribution models (SDMs) according True Skilled Statistics (TSS) method to each statistical method for modelling to each chelonian species and its confidence interval

Species	TSS1	TSS2	TSS3	TSS4
Podocnemis expansa	0.09 (0.06-0.97)	0.36 (0.21-0.92)	0.59 (0.55-1)	0.60 (0.51-1)
Podocnemis erythrocephala	0.04 (0.03-0.98)	0.39 (0.25-0.91)	0.78 (0.75-1)	0.43 (0.34-0.99)
Podocnemis unifilis	0.09 (0.05-1)	0.50 (0.39-1)	0.62 (0.57-1)	0.64 (0.52-0.97)
Podocnemis sextuberculata	0.06 (0.03-0.98)	0.36 (0.20-0.96)	0.71 (0.68-1)	0.50 (0.44-0.97)
Peltocephalus dumerilianus	0.05 (0.05-1)	0.27 (0.13-91)	0.76 (0.68-1)	0.35 (0.31-0.91)
Mesoclemmys gibba	0.01 (0.01-0.96)	0.15 (0.07-0.96)	0.38 (0.31-1)	0.20 (0.16-0.89)
Rhinemys rufipes	0.01 (0.01-1)	0.17 (0.10-0.97)	0.85 (0.85-1)	0.72 (0.60-1)
Mesoclemmys raniceps	0.00 (0.00-0.95)	0.15 (0.09-0.99)	0.50 (0.37-1)	0.05 (0.02-0.95)
Acanthochelys macrocephala	0.14 (0.09-1)	0.34 (0.21-0.93)	0.99 (0.98-1)	0.65 (0.52-0.92)
Platemys platycephala	0.01 (0.01-0.94)	0.15 (0.11-0.97)	0.63 (0.53-1)	0.08 (0.05-0.94)
Phrynops geoffroanus	0.01 (0.01-0.95)	0.13 (0.08-0.97)	0.56 (0.43-1)	0.11 (0.07-0.92)
Chelus fimbriatus	0.03 (0.02-0.97)	0.30 (0.22-0.95)	0.59 (0.49-1)	0.17 (0.09-0.94)
Kinosternon scorpioides	0.02 (0.02-0.96)	0.22 (0.16-0.98)	0.64 (0.57-1)	0.20 (0.14-0.89)
Mesoclemmys vanderhaegei	0.02 (0.02-0.95)	0.16 (0.09-0.94)	0.80 (0.63-1)	0.16 (0.16-0.90)
Rhinoclemmys punctularia	0.02 (0.02-0.94)	0.52 (0.46-1)	0.75 (0.66-1)	0.35 (0.22-0.94)
Mesoclemmys nasuta	0.09 (0.06-1)	0.11 (0.06-0.98)	0.98 (0.98-1)	0.69 (0.58-1)

The numbers indicate the statistical methods for modelling: 1 – BIOCLIM; 2- Generalized Linear Model (GLM); 3- Maximum Entropy; 4- Support Vector Machines (SVM).

APPENDIX S4

Environmentally suitable areas for the occurrence of 16 freshwater turtles in the Amazon using Maximum Entropy statistical method



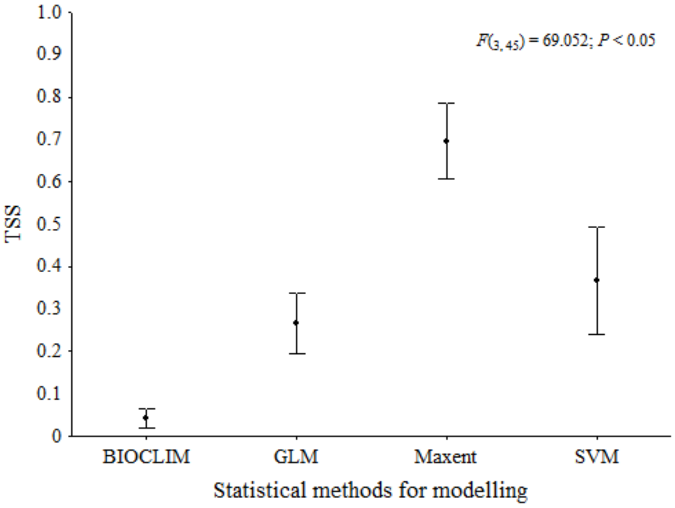


Figure 1

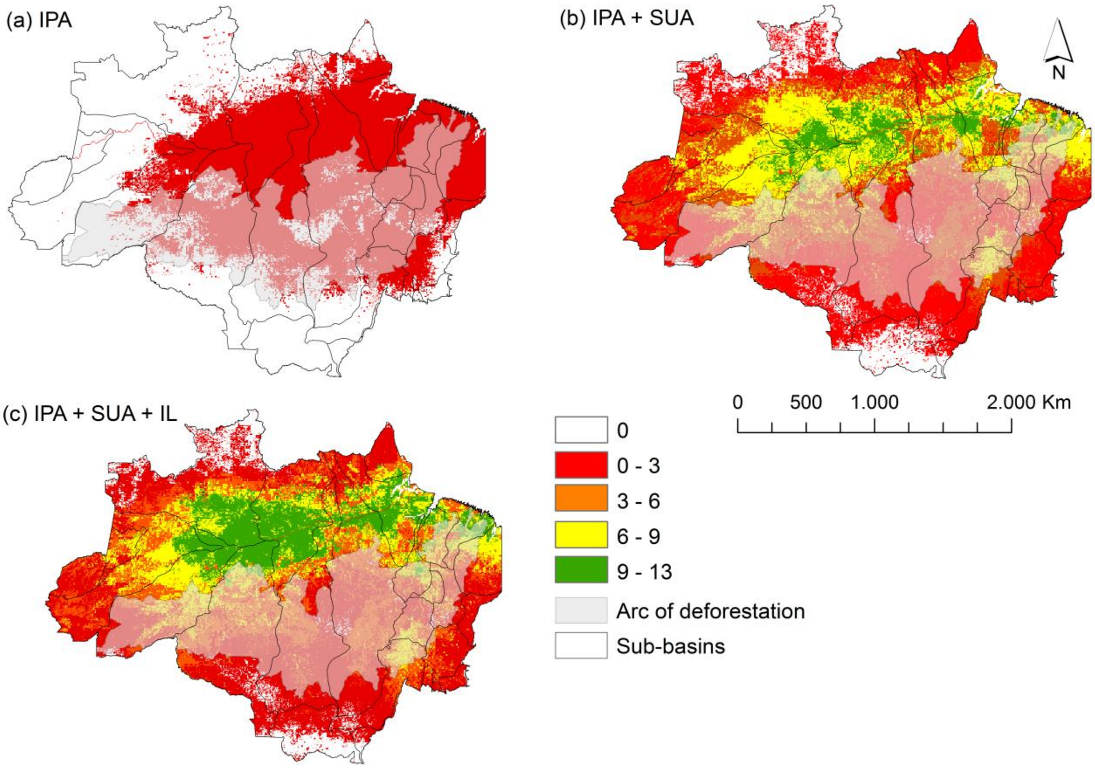


Figure 2

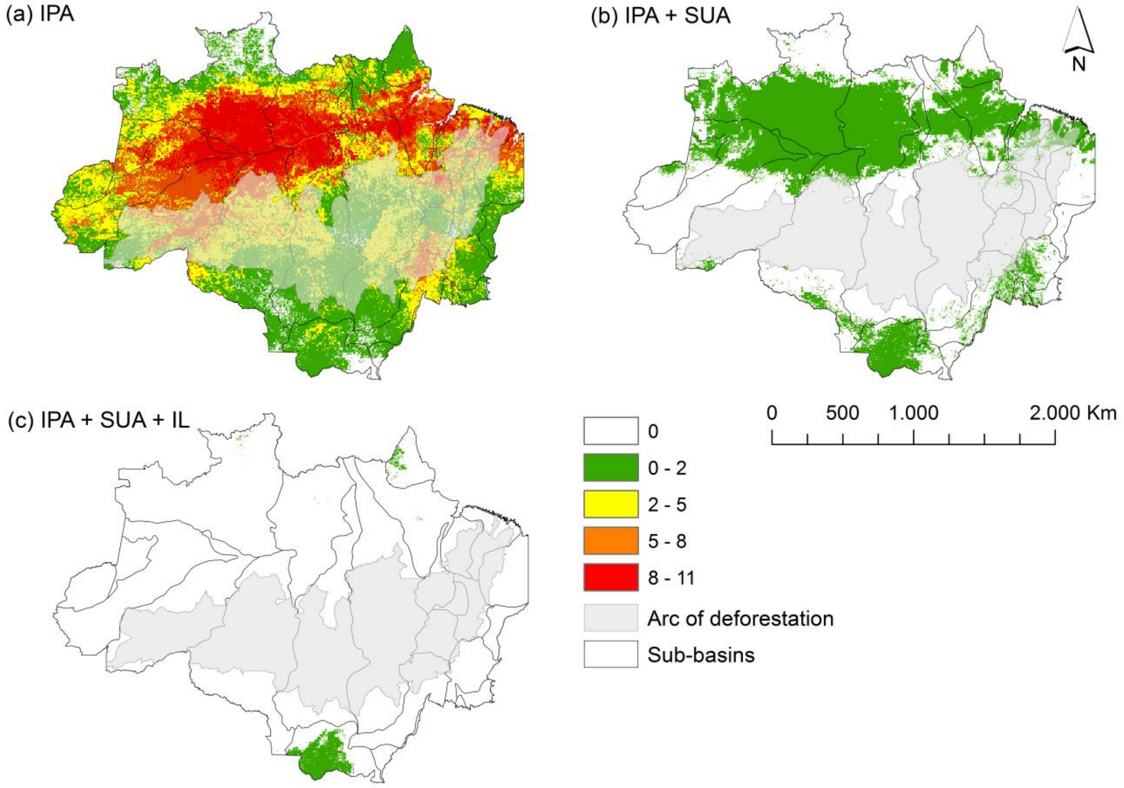

(a) IPA
(b) IPA + SUA
(c) IPA + SUA + IL
N
0
500
1.000
2.000 Km
0
0 - 2
2 - 5
5 - 8
8 - 11
Arc of deforestation
Sub-basins

Figure 3

Figure captions

Figure 1 Differences in TSS values calculated for turtle species using different statistical methods for modelling.

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: (a) IPA (Integral Protection Areas); (b) IPA + SUA (Integral Protection Areas + Sustainable Use Areas); (c) IPA+ SUA + IL (Integral Protection Areas + Sustainable Use Areas + Indigenous Lands).

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: (a) IPA (only Integral Protection Areas); (b) IPA + SUA (Integral Protection areas + Sustainable Use Areas); (c) IPA+ SUA + IL (Integral Protection Areas + Sustainable Use Areas + Indigenous Lands).

Capítulo 2

Fagundes, C.K., Vogt, R. C. & De Marco Jr., P. 2015. Vulnerability of freshwater chelonian in Brazilian Amazon to deforestation: indicating priority areas for conservation. Padronizado de acordo com as normas da Conservation Biology

Title: Vulnerability of freshwater chelonian in Brazilian Amazon to deforestation: indicating priority areas for conservation

Running head: Priority areas for freshwater chelonian conservation in Amazon

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Vulnerability of freshwater chelonian in Brazilian Amazon to deforestation: indicating priority areas for conservation

Abstract: Forest cover is accounted to play a great role in freshwater turtle decay. Amazon forest has been quickly fragmented due to the development policies in the region. Thus, this study aimed to evaluate the exposition of the freshwater turtles to deforestation in Brazilian Amazon and evaluate biological traits that are more vulnerable to habitat loss. We also identified priority areas to the group conservation based on the habitat requirements of the species, deforestation and the network of protected areas. The only component of vulnerability that we analyzed was exposure. We calculated the areas of species distribution modelling (SDM) lost by deforestation and identified the most vulnerable regions to turtle richness. We used the software Zonation to identify priority areas for chelonian conservation. We assigned higher conservation weight to semi-aquatic turtles and a negative weight to the deforestation areas, running scenarios with and without reserve networks. The priority areas to freshwater chelonian conservation are located in northern Amazon and they do not encompass high deforestation areas. However, higher vulnerability of turtle richness to deforestation is located in central-northeastern Amazon, where the deforestation is currently progressing. *Phrynops geoffroanus, Kinosternon scorpioides* and *Rhinoclemmys punctularia* had higher percentage of their SDMs lost due to deforestation. Protected areas included large amount of sites required by chelonian conservation but they are not located in areas with higher turtle richness. Despite of we did not consider the social importance of chelonian as a food resource, our results have significant practical implications for conservation agencies because it highlights the

regions more important to invest in conservation of freshwater turtles in Brazilian Amazon and the exposition of the species to deforestation.

Introduction

Chelonians are among the most threatened vertebrate groups (Klemens 2000) and they show a particular conservation concern because they are long-lived animals with late sexual maturity and low reproductive output. Impacts in their populations may remain unnoticed by many decades (Klemens 2000). The worldwide decline of freshwater turtles is largely attributed to wetland loss and habitat fragmentation due to anthropogenic land-uses (Millennium Ecosystem Assessment 2005) and overexploitation (Gibbons et al. 2000). Brazil is the fifth country in turtle richness along with China (Rhodin et al. 2010) and Amazon is the region with the higher chelonian diversity, where 12 freshwater species are endemic (Rhodin et al.,2010). In this biome, seven Amazonian turtles were classified in some threatened category by the International Union for Conservation of Nature (IUCN 2011). It is well reported that turtles have vast importance as a food resource for indigenous and riverine populations in Amazon (Pritchard & Trebbau 1984; Fachín-Terán et al. 1996; Vogt 2001). The higher hunting pressure is focused on Podocnemididae family (Klemens & Thorbjarnarson 1995; Vogt 2001), resulting in a drastic reduction of their populations (Mittermeier 1975; Vogt 2001).

Despite the relevance of overexploitation on chelonian conservation, freshwater turtles are largely influenced by anthropogenic change on the landscape level (Rizkalla & Swihart 2006; Sterrett et al. 2011). Forest cover is accounted to be the most important landscape predictor to chelonian occurrence and plays a greater role in freshwater turtle decay (Quesnelle et al. 2013). In some locals, decline of turtle populations is also related to the decrease of the amount of natural wetland habitats (Reese & Welsh 1998; Gibbons et al. 2000). Amazon forest has been quickly fragmented due to the development policies in the region (Alencar et al. 2004; Laurance et al. 2004; Fearnside, 2005; Pereira et al. 2010). Fragmentation converts previously continuous landscapes in a set of disconnected fragments surrounded by an anthropic matrix and this process encompasses two components: habitat loss and connectivity loss (Fahrig 2003). The main drivers of the Amazon deforestation are the expansion of infrastructure and agriculture (Soares-Filho et al. 2006; Pereira et al. 2010), which is usually the greatest threat to some turtle species (Richter et al. 1996) because of its high potential to fragment landscapes and induce wetland loss (Rytwinski & Fahrig 2012). Many freshwater species use a variety of wetlands types and exhibit interwetland movements that are dependent of the habitat isolation (Joyal et al. 2001). Uplands connect aquatic habitats and are critical in the dispersion of the freshwater turtles that use terrestrial habitats in greater extension (Gray 1995; Marchand & Litvaitis 2004) and may be determinant in the maintenance of the populations of many chelonian species (Semlitsch & Jensen 2001).

Vulnerability is the extent which a species or population is threatened and it is usually partitioned into three components: exposure, sensitivity and adaptive capacity (Dawson et al. 2011). The exposition is directly measured based on the overlap between species distribution and the threat. Nevertheless, both sensitivity to threat and adaptive capacity to new conditions are difficult to predict without large amount of knowledge on individual species ecology (Dawson et al. 2011). Clearly, habitat changes affect species differently, according to aspects of their natural history, as migration patterns, habitat use, among others (Pearman 1997; Becker et al. 2007). Semi-aquatic chelonians should be particularly affected by forest loss, because forest provides complementary resources to this species such as seasonally abundant food, rehydration and mating and nesting sites (Buhlmann & Gibbons 2001; Grgurovic & Sievert 2005; Beaudry et al. 2009). Turtle movement depends on the amount of vegetation (Buhlmann & Gibbons 2001), since some species prefer to move in forest than in open areas, probably to reduce thermal stress (Bowne 2008). During overland movements in altered areas species may be more exposed to natural predation and human exploitation (Gibbons 1986; Buhlmann & Gibbons 2001). In addition, human altered watersheds may show overall reduced water quality of wetlands (Trebitz et al. 2007; DeCatanzaro et al. 2009). However, even aquatic turtles should depend on the matrix composition of landscapes. Nesting sites may be more easily accessed in regions with high forest cover (Quesnelle et al. 2013), because the density of vegetation may be important in determinate the distance that turtle moves in land to nest. Forest loss can also affect the water temperature and reduce the microhabitats produced by fallen logs in wetland forests (Sterrett et al. 2011), depth heterogeneity and amount of sediments (Walser & Bart 1999).

The creation of Conservation Units may be the best option to conserve viable populations of species in their natural environments (Rodrigues et al. 2004; Loucks et al. 2008) and it is usually one of the strategies implemented to restrain deforestation and biodiversity loss in Amazon region (Ferreira et al. 2005; Nepstad et al. 2006). Protected areas are an effective way to break agricultural expansion (Gaston et al. 2008; Soares-Filho et al. 2010). However, gap analysis reveal that areas converted to biodiversity conservation are inadequate in many parts of America (Scott et al. 2001; Ochoa -Ochoa et al. 2007). Some notable gaps in protection of Amazon freshwater turtles were identified, where Integral Protection Areas (IPA) network alone is inefficient in conserving suitable areas for group distribution. The insertion of Sustainable Use Areas (SUA) and Indigenous Territories (ITA) Areas was crucial to attain the conservation targets to the most of chelonian species that occur in Brazilian Amazon (Fagundes et al. unpubl. data). However, hunting may be unsustainable in SUA and ITA and those protected areas may not be effective in protecting some turtle species (Peres & Lake 2003). Many populations of game species have been eradicated in extractive reserves (Peres & Palacios 2007).

The choice of priority areas for conservation should prioritize complementary locals in order to represent the overall biodiversity, since high richness regions may have similar species composition among different sites (Margules & Pressey 2000; Bonn & Gaston 2005). Some studies have already analyzed the effect of habitat degradation in freshwater turtle populations (Lindeman 1996; Marchand & Litvaitis 2004; Browne & Hecnar 2007). Nevertheless, no study has yet measured the spatial vulnerability on turtle species and explored the relationships between species richness and human disturbances in a broad-scale. Turtles are good organisms to evaluate the impacts of habitat loss because they require both wetlands and terrestrial environments in their life cycle (Congdon & Gibbons 1996; Klemens 2000). Thus, the objective of this study was to evaluate the exposition of the freshwater turtles in relation to deforestation and evaluate biological traits that are more vulnerable to habitat loss. We also identified priority areas to the group conservation. The selection of those areas was based on the habitat requirements of the species and considering or not the current network of protected areas in the biome.

Methods

Species Distribution Modelling (SDM)

We reviewed the occurrence registers for 16 freshwater turtles that occur in Brazilian Amazon. The database was composed by literature information, Brazilian scientific collections and museums, unpublished data from our research group and from government and by distribution maps depicted in EMYSystem Global Turtle Database (Iverson et al. 2003). Only one occurrence point in each cell of our spatial resolution was considered (unique points). We used 42 environmental variables to characterize the occurrence areas of the species (Supplementary material 1). We performed a principal components analysis (PCA) among environmental predictors to decrease their collinearity and used the PCA scores as environmental layers in the SDM procedures. Considering the Kaiser-Guttman criterion (Peres-Neto et al. 2005), we selected 12 principal components which were responsible for more than 95% of the variation on the environmental variables data. All layers were converted into a grid resolution of approximately 4 km^2. Thus, the Amazon freshwater turtle occurrence points were correlated to the principal components to project their distribution into a geographical space that encompass similar environments from known occurrences (Guisan & Truiller 2005; Peterson et al. 2011).

Maximum Entropy was the method chosen to build the models and the software MaxEnt was used to run the algorithm (Phillips et al. 2006; Phillips & Dudik 2008; Elith et al. 2010). The freshwater turtle species that had more than 15 spatially unique points were divided into 80-20% training-test subsets. The training subsets were used to produce the turtle SDMs and the test subsets were used to evaluate the predictions. We used 10.000 background values. For the species that had less than 15 spatially unique points we accomplished the same methodology but we used only one dataset.

The conversion of the SDMs into a binary prediction of a 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, that is a balance between omission and commission errors (hereafter Balance threshold) (Pearce & Ferrier 2000; Jiménez-Valverde & Lobo 2007). The models were evaluated using a threshold-independent method, the area under the ROC curve (AUC - Fielding & Bell 1997), and a threshold-dependent method, the True Skilled Statistics (TSS - Allouche et al. 2006; Liu et al. 2011).

Deforestation model

We used the Amazonian deforestation model created by Souza & De Marco Jr. (2014), where they used deforestation data from automatic classification analysis of LANDSAT- 5/TM images of the Deforestation Monitoring Program - PRODES (INPE, 2010). The models were built with Maximum Entropy algorithm in MaxEnt Software and had higher predictive power than other existing models for the Amazon (Souza & De Marco Jr. 2014). The center point of each deforestation polygon was used as deforestation occurrence and features as density of deforestation until 2007, roads, agriculture, livestock, urban areas, IBAMA offices, embargo, indigenous land, protected areas and settlements of land reform were used as functional variables. They ran MaxEnt varying the layers of predictors and using different settings of MaxEnt software to each deforestation area. The models were trained with data from 2008 and tested with data from 2010 and the authors compared predicted deforestation from distinct models with the real observed deforestation in 2010. In our study, we used the model that had the higher predictive power and obtained it to all Brazilian Amazon. This model used the distance from previous deforestation (PRODES) as a functional variable and the automatic features of MaxEnt software. The predicted deforestation did not forecast some areas where the deforestation has already occurred. Thus, we corrected those omission errors including all the current deforested areas in the model of predicted deforestation.

Vulnerability to deforestation

The only component of vulnerability that we analyzed was exposure, which in our study is the extent of deforestation likely to be experienced by a species (Dawson et al. 2011). We used the Souza & De Marco Jr. (2014) deforestation model to evaluate the exposure of freshwater turtle species and their richness to deforestation in Brazilian Amazon. We calculated the SDMs portion of each species that was found inside the current deforestation area and the predicted deforestation area, assuming that chelonians are eradicated in those regions. Thus, we evaluated the areas of SDMs lost by deforestation and identified the most vulnerable regions to turtle richness in relation to this threat.

Priority areas for conservation

We used the spatial prioritization software Zonation (Moilanen 2005) to identify priority areas that attempt to determined conservation aims for chelonian conservation in Brazilian Amazon. The management units were defined in 4 km^2 cells. The input species layers were the SDMs (environmental suitability) previously produced. The species geographic ranges were overlaid to extract data on species richness for each grid cell. Zonation algorithm is based on the complementarity principle, which measures the frequency that a determined management unit is selected to a set of conservation goals (Pressey 1994). Initially, all the area is considered to be protected and then, the algorithm removes the cells that incur the smallest marginal loss in conservation value (Moilanen & Kujala 2008). The algorithm results in a conservation priority-ranked map that maximizes the frequency of environmental suitable area of species occurrence divided by the cost associated to each cell (Moilanen et al. 2009). We used the additive benefit function removal rule that prioritizes the sites with higher species richness (Moilanen 2007 for details).

Zonation allows to attribute priority weights and to insert the existing protected areas (Moilanen et al. 2005; Moilanen & Kujala 2008). We assigned higher conservation weight to semi-aquatic turtles (Table 1) and a negative weight to the deforestation, forcing the exclusion of sites with little conservation value in deforestation areas (Fahrig 2001). We run the analysis with and without the network of

State and Federal Conservation Units in Amazon to verify if the priority areas to chelonian conservation overlap the current protected areas. The protected areas in Brazil can be classified in two groups: Integral Protection Areas (IPA), which is 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 Territories Areas (ITA). Thus, we tested different scenarios to verify the influence of deforestation and the categories of protected areas in conservation planning: (1) deforestation + protected areas; (2) deforestation + not considering protected areas; (3) not considering deforestation + protected areas and (4) not considering deforestation + not considering protected areas. The scenarios with the current protected areas were run (a) using only the Integral Protected Areas (IPA) as a mask, (b) using IPA and Sustainable Use Areas (SUA) as a mask and (c) using IPA, SUA and Indigenous Territories Areas (ITA) as a mask. For practical purposes our conservation goals are based on the top 17% and 50% sites of landscape in all scenarios. According to the Aichi Biodiversity Targets to 2020, the aim of conservation for terrestrial environments is 17% (Convention on Biological Diversity 2010). This value may not be appropriate for aquatic organisms, since they show a linear dispersion along areas. The properties in the Amazon region had to maintain 50% of the legal reserve until 2001, when was signed the law that increased those areas to 80% (IPAM 2011). Thus, we considered that at least the top 50% of sites is required by chelonian species.

Results

Species Distribution Modelling (SDM)

Species distribution models had good predictive accuracies with TSS > 0.5 to 14 species and AUC > 0.7 to all species (from 0.73 to 0.99) (Supplementary material 2). The environmental suitability areas (Supplementary material 3) showing higher chelonian richness is concentrated in northeast and central-northern Brazilian Amazon in lowlands of Amazon River basin. Some tributaries of Amazon River that have high chelonian richness are Madeira River, Negro River, Purus River, Xingu River, Tapajós River, Trombetas River, Uatumã River and Nhamundá River.

Vulnerability to deforestation

The impact of deforestation is more pronounced in the east and south part of the environmentally suitability areas for turtle species occurrence (Fig. 1). The species that had the highest potential distribution area lost by the current deforestation was *Kinosternon scorpioides*, followed by *Mesoclemmys gibba* and *M. raniceps* (Table 1). The same species will be more affected by predicted deforestation. However, when we consider the percentage of total area lost (current and future deforestation) in relation to the species suitable areas, *Phrynops geoffroanus*, *K. scorpioides* and *Rhynoclemmys punctularia* were the species with higher exposition to deforestation. Regarding the Brazilian Amazon, the only species that could be threatened in this biome according to the decrease of extension of occurrence (criterion B of IUCN) is *M. nasuta*. That criterion takes into account the restricted distribution and decline or fluctuation of species populations by (1) extension of occurrence or (2) occupation area.

The current and predicted deforestation areas that affect the highest richness of freshwater turtle are located on northeast Amazon and in central Amazon region (Fig. 2).

Priority areas for conservation

Excluding the protected areas, the conservation priorities for turtles are located in extensive continuous sites in northern Amazon and in smaller areas in southern Amazon and those areas usually do not overlap areas with high forest loss (Fig. 3). The scenarios considering deforestation removed priority sites to chelonian conservation only in northeastern Amazon, where deforestation is currently progressing. In other regions, the use of deforestation to select sites with high conservation value results in small differences in relation to the results without forest loss, with decreasing effect when we include other protected areas such as SUA and ITA (Fig. 3).

The extent of priority areas in northern Amazon reduced when we forced the inclusion of protected areas (Fig. 3D, F, H). IPA + SUA + ITA scenarios encompass large amount of areas required by chelonian conservation in our conservation goals but they are not located in sites with higher turtle richness. Thus, the insertion of all categories of protected areas was still not enough to attain the goal of protect the top 50% priority sites (Fig. 3H). IPA category alone was not sufficient to achieve the imposed preservation targets even when our conservation goal decreases to the top 17% sites. Thus, the result allows us to conclude that many areas of high conservation value are not protected by IPA in central-northern Amazon (Fig. 3C). The inclusion of SUA and ITA makes that the top 17% priority sites be inside protected areas only, showing that the current reserve networks in not efficient in protect freshwater turtle richness (Fig. 3 E, G).

The percentage of the species distribution protected with landscape loss is a little bit higher when we did not use deforestation, mainly between 20% and 40% of Amazon lost (Fig. 4). The deviations in the performance curves that measure the effectiveness of spatial conservation plans are related to the forced exclusion of deforestation areas in sites with high frequency of distribution and to the inclusion of protected areas in sites with low frequency of distribution (Fig. 4).

Discussion

The priority areas to freshwater chelonian conservation in Brazilian Amazon are located mainly in extensive continuous sites in northern Amazon and they do not encompass high deforestation areas. However, vulnerability analysis identified higher threat to turtle richness in relation to deforestation in central-northeastern Amazon, where the deforestation is currently progressing. *Phrynops geoffroanus, K. scorpioides* and *R. punctularia* are the species most exposed to deforestation, showing higher percentage of their suitable areas lost due to this threat. Protected areas included large amount of sites required by chelonian conservation but they are not located in areas with higher turtle richness. Even considering only the top 17% sites to turtle conservation, reserve networks were not efficient in protecting freshwater chelonian richness.

Large areas of the Amazon Basin have already been deforested due to development policies (Soares-Filho et al. 2006; Hansen et al. 2010). Watershed functions are lost with forest loss because in deforested areas the flooding patterns become irregular, reducing rainfall (Fearnside 2005; Coe et al. 2011) and this is the climatic factor more associated to chelonian diversity in South America (Souza 2005). Forest cover and the amount of aquatic habitats are important landscape predictors in turtle decline (Gibbons et al. 2000; Quesnelle et al. 2013), possibly because they require both wetlands and terrestrial environments to complete their life cycle (Congdon & Gibbons 1996; Klemens 2000). Semi-aquatic chelonians may be more affected by forest loss, because they use terrestrial ecosystems in many aspects of their biology and ecology (Buhlmann & Gibbons 2001; Grgurovic & Sievert 2005; Beaudry et al. 2009). In Amazon, some aquatic turtles such as *Rhinemmys rufipes*, *Mesoclemmys vanderhaegei* and *Acanthochelys macrocepahala* are also considered to be threatened by the habitat destruction (Rhodin et al. 2009; Magnusson & Vogt 2014; Marques et al. 2014). *Podocnemis erythrocephala* feeds on fruits and seeds and is highly dependent on the flooded forest to survive (Mittermeier et al. 2015). The same pattern could be inferred to other species of the *Podocnemis* genus.

In the current study, *K. scorpioides*, *M. gibba* and *M. raniceps* had the highest potential distribution area lost by the current and predicted deforestation. Those species show the higher size of environmentally suitable areas and occur in all Amazon (Pritchard & Trebbau 1984; Iverson 1992; McCord et al. 2001; Rueda-Almonacid et al. 2007; Vogt 2008). Habitat degradation and alteration of aquatic habits are known to be factors of strong impact on *K. scorpioides* populations (Berry & Iverson 2011). Considering the perceptual of total area lost in relation to the species suitable areas, *P. geoffroanus*, *K. scorpioides* and *R punctularia* are the most affected species. *Phrynops geoffroanus* seems to be a complex of sibling species (Pritchard & Trebbau 1984) and in Amazon its distribution is concentrated in the “arc of deforestation region”. Despite the concern about the impact of deforestation in the distribution areas of *K. scorpioides* and *R punctularia*, they are the only species protected by the Integral Protection Areas (IPA) in a previous gap analysis (Fagundes et al. unpubl. data). IPAs were not specially designed to protect turtle species (Fagundes et al. unpubl. data) and its occurrence in those protected areas could be explained only by consequence of random protection, since they show large distribution in Amazon.

Despite of deforestation to be a large threat to chelonians, the forest loss in Amazon is concentrated in a region from southwest to northeastern Amazon called “arc of deforestation”, which do not overlap areas of higher turtle richness. In recent years, the deforestation rates in Pará state have increased and a new advancement of deforestation outside the arc has been registered towards the West in Trans-Amazonian Highway and Cuiabá-Santarém Highway (Vieira et al. 2008; INPE 2015). Some of those areas encompass priority areas for chelonian conservation. Another relevant aspect is that the deforestation model used in this study does not account for the effect of planned highways, hydroelectric power plants, mining and waterways on predicted deforestation (Fearnside & Graça 2009; Souza & De Marco Jr. 2014). The government plan to build 277 hydroelectric power plants in Amazon and establish 15.114 km of navigable waterways (Castello et al. 2013). Thus, turtles may be threatened in locals other than the predicted by the deforestation model. The construction of dams prevent aquatic turtle movements, because they disrupt the longitudinal connectivity of rivers (Agostinho et al. 2008) and lateral connectivity between rivers channels and floodplains and riparian zones (Poff & Hart 2002). This characteristic makes difficult the migration of these organisms to non-deforested and non-impacted areas, reducing the adaptive capacity of species. Large dams were already constructed in locals that possess large turtle richness such as Madeira River, Uatumã River, Xingu River, Tocantins River and other dams are planned to be built in those areas in rivers such as Tapajós, Curuapanema, Maicuru, Jari, Cupari, Curuá and so on.

The selection of areas with high conservation values is crucial to conciliate biological diversity into development plans (Theobald et al. 2000; Pierce et al. 2005). The lack of integration between socioeconomic interests and conservation planning makes the last issue less relevant to decision makers (Faith & Walker 2002; Polasky 2008), since frequently important areas for biodiversity overlaps human activities (Eklund et al. 2011). Thus, the complementarity principle has been used in spatial prioritization of conservation sites (Possingham et al. 2000) using aspects like land-use changes (Faleiro et al. 2013). In the current work, the turtle overall distribution included in sites ranked in the top 50% priority areas decreased when we used deforestation. Areas showing high conservation value were forced to be excluded in deforested sites. The goal of conservation that has been used for terrestrial environments is 17% (Convention on Biological Diversity 2010). The top 17% priority areas for freshwater turtle conservation had practically the same species distribution with or without deforestation. At this conservation goal, the inclusion of protected areas makes that the sites with priority to be fragmented.

The current protected areas in Amazon cover 22.2% of its territory and Indigenous lands 21.7%, which the majority was created in areas subjacent to high anthropogenic pressures (Veríssimo et al. 2011). However, the reserve networks seem to be inefficient in conservation of species that depend of the aquatic ecosystems in a large scale. Many protected areas are out of the priority sites for chelonian conservation. Some sites with high conservation value are not contemplated by IPA, even when only the top 17% priority sites are required. The addition of Sustainable Use Areas (SUA) and Indigenous Territories Areas (ITA) in our analyses shows higher cover of the priority sites for turtle conservation. The reserve networks are sufficient to complete the established conservation effort in the scenarios considering the top 17% priority sites. Nevertheless, the amount of sites for turtle conservation is widespread in Amazon and not contemplates the continuous areas with higher turtle richness in north. Besides, the effectiveness of SUA has been questioned, because they frequently show high human population and the resulting high hunting and forest loss rates (Peres & Palacios 2007; Peres 2011; Veríssimo et al. 2011).

In general, aggregated terrestrial protected areas are assumed to perform better because they may decrease edge effects and support metapopulation persistence (Moilanen 2005; Moilanen & Wintle 2006; Nicholson et al. 2006). Freshwater organisms may demand the conservation of parts of river systems (e.g. headwaters) that are geographically distant from the biological features of interest (Moilanen et al. 2008). Turtles migrate from high productivity feeding areas to nesting sites usually next from headwaters regions (Peres 2005) and use terrestrial environments to accomplish many activities (Congdon & Gibbons 1996; Klemens 2000). Thus, the conservation of top 17% priority sites may be not adequate to the group and freshwater turtles may require goals higher than 17%. A better design of protected areas should be based in large areas with high conservation value in both terrestrial and aquatic habitats (Crawford & Semlitsch 2007; Gardner et al. 2007). A good option is to select freshwater conservation areas, maybe entire watersheds, in the high priority turtle conservation sites (Abell 2002; Thieme et al. 2007). This measure can prevent future threats upstream (Peres 2005).

The choice of priority sites is usually complicated due to the limited knowledge about aspects of biology and species distribution (Lomolino 2004; Diniz et al. 2010). In addition, vulnerability to ecological changes driven by anthropic impacts can be suggested only in general terms for the majority of individual species (Kozlowski 2008). Species distribution modelling can fill the referred gaps of information and has been used in conservation planning when evaluated together with threats to biodiversity (Phillips et al. 2006; Cabeza et al. 2010). Those models can overestimate or omit true species range and do not take into account species interactions and dispersal ability of species (Soberón & Nakamura 2009). However, SDMs performed better than analysis using few data from the extent of occurrence of the species (Diniz-Filho et al. 2010). Detailed occurrence data of freshwater Amazonian turtles is uncommon and the distribution maps for these species are frequently created based on small numbers of occurrence data, mainly for Chelidae (Iverson 1992; Rueda-Almonacid 2007). The lack of information makes that some species are not classified in IUCN list and/or to be categorized as data deficient in Brazilian Ministry of Environment (MMA) (IUCN 2011; MMA 2014).

Studies that show priority sites to conservation of particular groups within large areas are very important to decision making and to reduce the budgets in conservation practices. The results of our study have significant practical implications for conservation agencies. Studies on priority areas for the conservation of aquatic organisms are still relatively incipient in comparison with terrestrial organisms (Moilanen et al. 2008). However, our findings should be interpreted cautiously with respect to applied conservation. We did not take into account the social importance of chelonian as a food resource in Amazon. Socioeconomic and cultural forces are largely necessary in the process of negotiation with all stakeholders to implement conservation actions (Margules & Pressey 2000; Ferrier & Wintle 2009). Despite of those limitations, our study highlights which regions would be more important to invest in conservation of freshwater turtles in Brazilian Amazon and how the species are exposed to deforestation. Biodiversity loss seems to be inevitable unless land-use changes be balanced with land protection. Thus, the assessment of the vulnerability of organism to anthropic impacts, the efficiency and the expansion of the protected areas considering current and predicted land-use are crucial to the conservation of species.

Supporting Information

Figures related to (Appendix S1), (Appendix S2) and (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

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

Figure S2. Summary of the evaluation of the models using Maximum Entropy algorithm by two methods: the area under the ROC curve (AUC) and True Skilled Statistics (TSS).

Figure S3. The environmentally suitable areas showing higher richness of freshwater turtles in the Amazon.

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Table 1. Vulnerability of the 16 freshwater turtles to the current and predicted deforestation in Brazilian Amazon and their threat category according International Union for Conservation of Nature (IUCN) and Brazilian Ministry of Environment (MMA).

Species	Potential distribution area	Potential distribution with total deforestation	Potential area lost in current deforestation	Potential area lost in predicted deforestation	Total potential area lost	Total potential area lost (%)	IUCN[1]	MMA[2]
Aquatic turtles[3]								
Mesoclemmys nasuta	10.336	10.048	288	0	288	2.79	Not listed	Data deficient
Podocnemis erythrocephala	1.537.360	1.324.144	130.784	82.432	213.216	13.87	Vulnerable A1bd	Data deficient
Peltocephalus dumerilianus	802.768	681.536	72.128	49.104	121.232	15.10	Vulnerable A1acd	Data deficient
Rhinemys rufipes	1.416.640	1.195.648	135.808	85.184	220.992	15.60	Near threatened	Least concern
Podocnemis sextuberculata	2.085.968	1.742.928	214.928	128.112	343.040	16.45	Vulnerable A1acd	Near threatened
Podocnemis unifilis	2.107.616	1.715.936	246.704	144.976	391.680	18.58	Vulnerable A1acd	Near threatened
Podocnemis expansa	2.147.648	1.671.328	311.888	164.432	476.320	22.18	Least concern	Near threatened
Mesoclemmys raniceps	3.489.664	2.685.936	509.840	293.888	803.728	23.03	Not listed	Data deficient
Chelus fimbriata	1.676.768	1.209.904	320.496	146.368	466.864	27.84	Not listed	Least concern
Phrynops geoffroanus	1.799.584	1.207.312	395.104	197.168	592.272	32.91	Not listed	Least concern
Semi-aquatic turtles[3]								
Platemys platycephala	2.281.552	1.895.296	241.072	145.184	386.256	16.93	Not listed	Least concern
Mesoclemmys vanderhaegei	222.864	179.680	33.696	9.488	43.184	19.38	Near threatened	Data deficient
Acanthochelys macrocephala	91.360	85.456	5.472	432	5.904	6.46	Near threatened	Data deficient
Mesoclemmys gibba	4.111.632	3.229.520	552.736	329.376	882.112	21.45	Not listed	Data deficient
Rhinoclemmys punctularia	1.602.432	1.110.608	323.744	168.080	491.824	30.69	Not listed	Least concern
Kinosternon scorpioides	2.915.552	2.002.016	596.672	316.864	913.536	31.33	Not listed	Data deficient

[1] Threat categories of the International Union for Conservation of Nature (IUCN) from the last updating in 1996; [2] Threat categories of Brazilian Ministry of Environment (MMA) from the last updating in 2014. [3] The habits were compiled from Rueda-almonacid et al. (2007) and Vogt (2008).

Figure legends

Figure 1. Potential distribution areas of 16 freshwater turtles in Brazilian Amazon affected by current and predicted deforestation.

Figure 2. Richness of freshwater turtles affected by deforestation in Amazon. A) Current deforestation, B) Current deforestation + Predicted deforestation.

Figure 3. Top 17% and 50% priority areas for freshwater turtle conservation in Brazilian Amazon considering different scenarios. The orange areas represent the priority sites for models with or without deforestation and yellow areas represent sites that only show conservation value for one that those models. (A - B) depicture the scenarios without Protected Areas (-PA); (C - D) depicture the scenarios using Integral Protected Areas (+IPA); (E – F) depicture the scenarios using Integral Protected Areas and Sustainable Use Areas (IPA + SUA); (G – H) depicture the scenarios using Integral Protected Areas, Sustainable Use Areas and Indigenous Territories Areas (IPA + SUA + ITA). The location of the current protected areas is shown in the black circle sites.

Figure 4. Performance curves to different conservation scenarios for freshwater turtles in Brazilian Amazon. (A - D) Graphs show the proportion of the landscape lost and their correspondent proportion of species distribution remaining. The full line represents scenarios considering the deforestation and the dot-dash line represents scenarios not considering deforestation. Models without Protected Areas (-PA); scenario using Integral Protected Areas (+IPA); scenarios using Integral Protected Areas and

Sustainable Use Areas (IPA + SUA); and scenarios using Integral Protected Areas, Sustainable Use Areas and Indigenous Territories Areas (IPA + SUA + ITA)

Figure 1

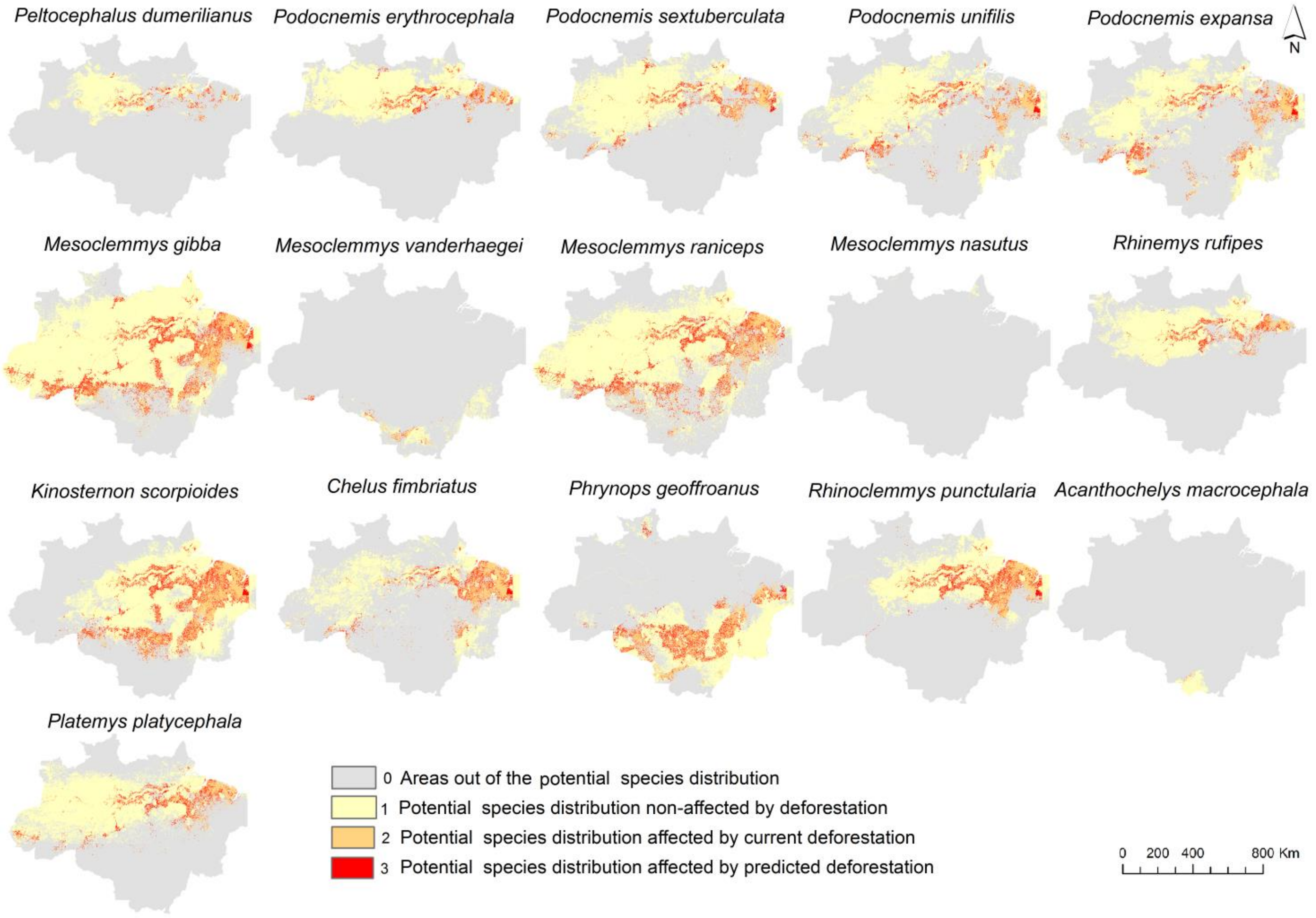

Peltocephalus dumerilianus
Podocnemis erythrocephala
Podocnemis sextuberculata
Podocnemis unifilis
Podocnemis expansa
N
Mesoclemmys gibba
Mesoclemmys vanderhaegei
Mesoclemmys raniceps
Mesoclemmys nasutus
Rhinemys rufipes
Kinosternon scorpioides
Chelus fimbriatus
Phrynops geoffroanus
Rhinoclemmys punctularia
Acanthochelys macrocephala
Platemys platycephala
0 Areas out of the potential species distribution
1 Potential species distribution non-affected by deforestation
2 Potential species distribution affected by current deforestation
3 Potential species distribution affected by predicted deforestation
0 200 400 800 Km

Figure 2

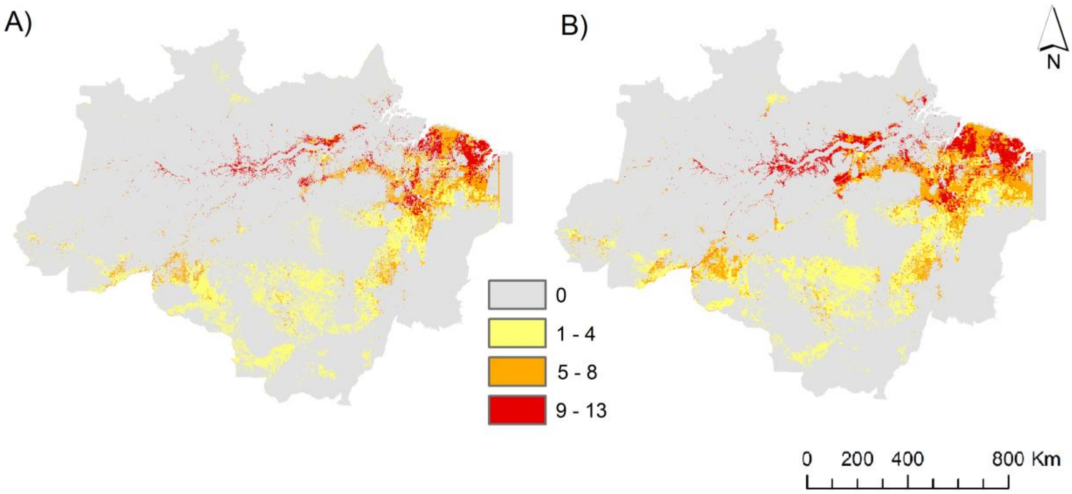


Figure 3

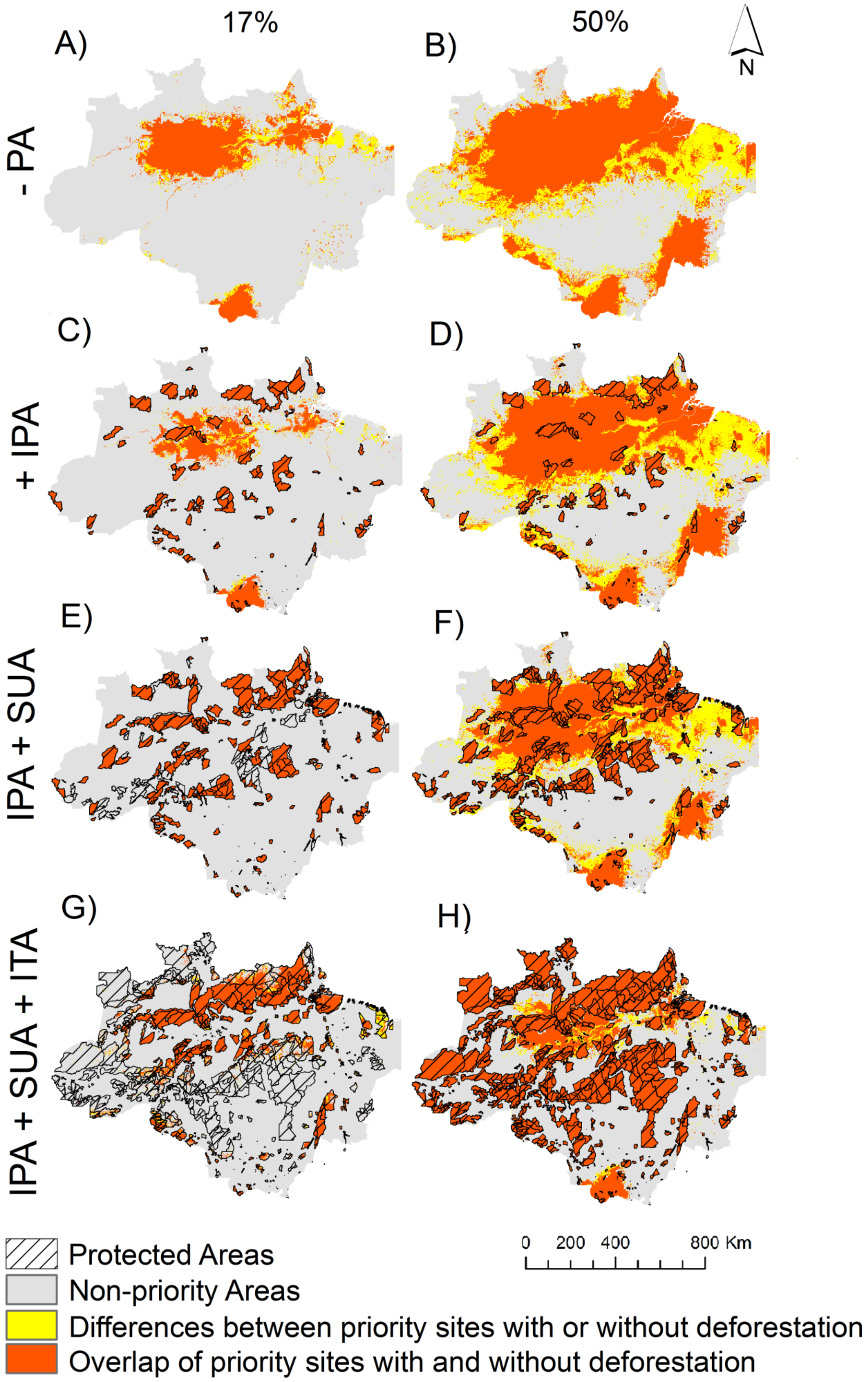

17%
50%
A)
B)
N
- PA
C)
D)
+ IPA
E)
F)
IPA + SUA
G)
H)
IPA + SUA + ITA
0 200 400 800 Km
Protected Areas
Non-priority Areas
Differences between priority sites with or without deforestation
Overlap of priority sites with and without deforestation

Figure 4

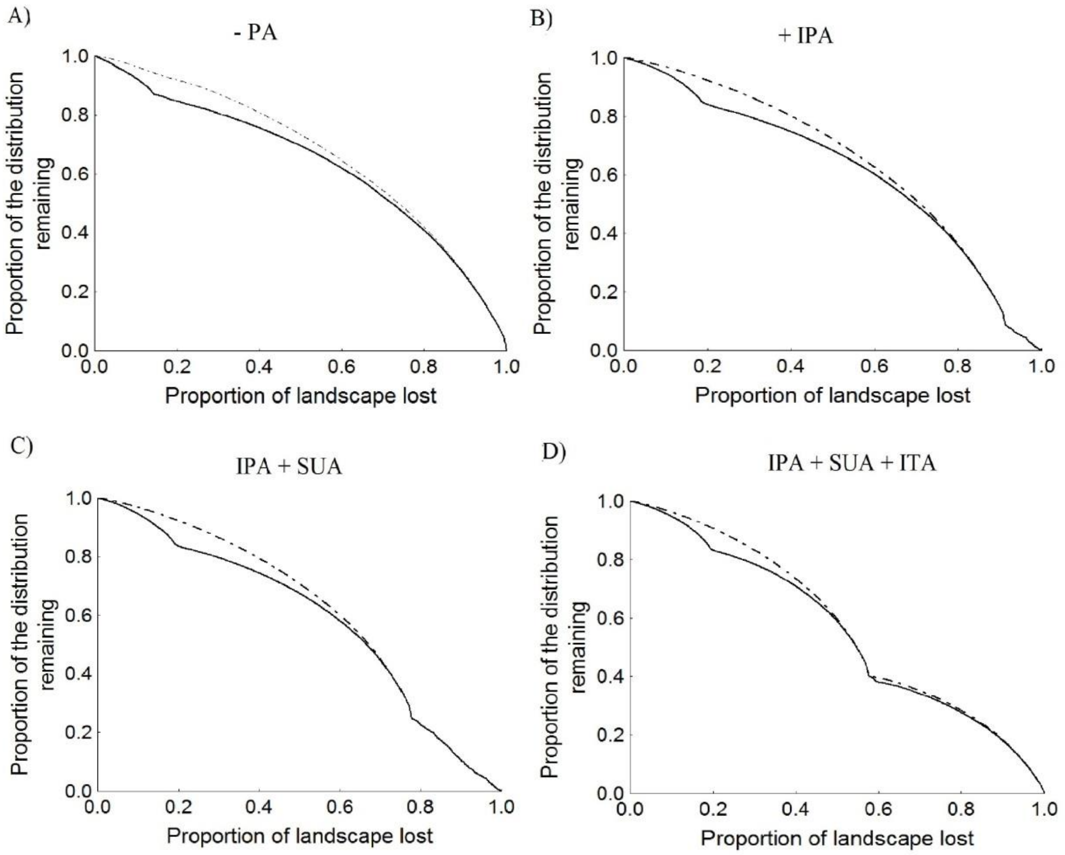

A)
- PA
B)
+ IPA
C)
IPA + SUA
D)
IPA + SUA + ITA
Proportion of the distribution remaining
Proportion of landscape lost
0.0
0.2
0.4
0.6
0.8
1.0

Figure S1

Variables (units)	Code	Description
Annual Mean Temperature (°C) [1]	Bio 01	Calculated from the minimum and maximum temperatures
Mean Diurnal Range (°C) [1]	Bio 02	Calculated from the minimum and maximum temperatures: (Mean of monthly (max temp - min temp))
Isothermality [1]	Bio 03	Calculated from the minimum and maximum temperatures: (Bio02/Bio07)
Temperature Seasonality (CV) [1]	Bio 04	Calculated from the minimum and maximum temperatures: (standard deviation *100)
Max Temperature of Warmest Month (°C) [1]	Bio 05	The maximum temperature of warmest month
Min Temperature of Coldest Month (°C) [1]	Bio 06	The minimum temperature of clodest month
Temperature Annual Range (°C)[1]	Bio 07	Calculated from the minimum and maximum temperatures: (Bio5-Bio6)
Mean Temperature of Wettest Quarter (°C) [1]	Bio 08	Calculated from the minimum, maximum temperatures and rainfall (mm month^{-1})
Mean Temperature of Driest Quarter (°C) [1]	Bio 09	Calculated from the minimum, maximum temperatures and rainfall (mm month^{-1})
Mean Temperature of Warmest Quarter (°C) [1]	Bio 10	Calculated from the minimum and maximum temperatures
Mean Temperature of Coldest Quarter (°C) [1]	Bio 11	Calculated from the minimum and maximum temperatures
Annual Precipitation (mm) [1]	Bio 12	Calculated from the rainfall (mm month^{-1})
Precipitation of Wettest Month (mm) [1]	Bio 13	Calculated from the rainfall (mm month^{-1})
Precipitation of Driest Month (mm) [1]	Bio 14	Calculated from the rainfall (mm month^{-1})
Precipitation Seasonality (mm) [1]	Bio 15	Calculated from the rainfall (mm month^{-1})
Precipitation of Wettest Quarter (mm) [1]	Bio 16	Calculated from the rainfall (mm month^{-1})
Precipitation of Driest Quarter (mm) [1]	Bio 17	Calculated from the rainfall (mm month^{-1})
Precipitation of Warmest Quarter (mm) [1]	Bio 18	Calculated from the minimum, maximum temperatures and rainfall (mm month-^{1})
Precipitation of Coldest Quarter (mm) [1]	Bio 19	Calculated from the minimum, maximum temperatures and rainfall (mm month-^{1})
Annual mean radiation (W m-^{2}) [2]	Bio 20	Calculated from the radiation (W m^{-2}d^{-1})
Highest weekly radiation (W m^{-2}) [2]	Bio 21	Calculated from the radiation (W m^{-2}d^{-1})
Lowest weekly radiation (W m$^{-2)}$ [2]	Bio 22	Calculated from the radiation (W m^{-2}d^{-1})
Radiation seasonality (CV) [2]	Bio 23	Calculated from the radiation (W m^{-2}d^{-1})

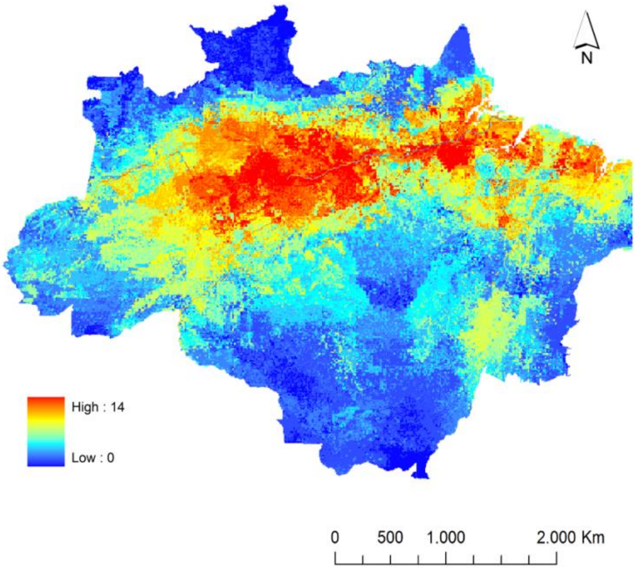
Radiation of wettest quarter (W m^{-2}) [2]	Bio 24	Calculated from the rainfall (mm month-1) and radiation (W m^{-2}d^{-1})
Radiation of driest quarter (W m^{-2}) [2]	Bio 25	Calculated from the rainfall (mm month-1) and radiation (W m^{-2}d^{-1})
Radiation of warmest quarter (W m^{-2}) [2]	Bio 26	Calculated from the minimum, maximum temperatures and radiation (W m^{-2}d^{-1})
Radiation of coldest quarter (W m-^{2}) [2]	Bio 27	Calculated from the minimum, maximum temperatures and radiation (W m^{-2}d^{-1})
Annual mean moisture index[2]	Bio 28	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Highest weekly moisture index[2]	Bio 29	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Lowest weekly moisture index[2]	Bio 30	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Moisture index seasonality (CV) [2]	Bio 31	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of wettest quarter [2]	Bio 32	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of driest quarter [2]	Bio 33	Calculated from the rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of warmest quarter [2]	Bio 34	Calculated from the minimum, maximum temperatures, rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Mean moisture index of coldest quarter [2]	Bio 35	Calculated from the minimum, maximum temperatures, rainfall (mm month^{-1}) and pan evaporation (mm d^{-1})
Flow accumulation (number of cells) [3]	FACC	Defines the amount of upstream area draining into each cell
Flow direction (number of cells) [3]	FDIR	Defines the direction of flow from each cell in the conditioned DEM to its steepest down-slope neighbor
Shuttle Radar Topography Mission (m) [4]	SRTM	Digital elevation data
Slope (°) [5]	SLP	The maximum rate of elevation between each cell and its eight neighbors
Compound Topographic Index [5]	CTI	Reflects a function of the upstream contributing area and the slope of the landscape
Annual Actual Evapotranspiration (mm) 6	AAE	Effective quantity of water that is removed from the soil due to evaporation and transpiration processes, alternative indicator of energy availability
Annual Water Balance (mm) [6]	AWB	Defines the fraction of Water Content available for evapotranspiration processes

The layers references and website for download: [1] Hutchinson et al. (2009), available on http://www.worldclim.org/download; [2] Hutchinson et al. (2009), available on https://www.climond.org/Download.aspx; [3] Lehner et al. (2006), available on http://hydrosheds.cr.usgs.gov/index.php; [4] Farr et al. (2007), available on https://lta.cr.usgs.gov/SRTM2; [5] Moore et al (1991), available on https://lta.cr.usgs.gov/HYDRO1K; [6] Ahn & Tateishi (1994), available on http://edit.csic.es/Climate.html.

Figure S2

Species	AUC	TSS
Podocnemis expansa	0.87	0.59
Podocnemis erythrocephala	0.95	0.78
Podocnemis unifilis	0.86	0.62
Podocnemis sextuberculata	0.91	0.71
Peltocephalus dumerilianus	0.94	0.76
Mesoclemmys gibba	0.73	0.38
Rhinemys rufipes	0.97	0.85
Mesoclemmys raniceps	0.82	0.50
Acanthochelys macrocephala	0.99	0.99
Platemys platycephala	0.87	0.63
Phrynops geoffroanus	0.78	0.56
Chelus fimbriatus	0.87	0.59
Kinosternon scorpioides	0.88	0.64
Mesoclemmys vanderhaegei	0.96	0.80
Rhinoclemmys punctularia	0.94	0.75
Mesoclemmys nasuta	0.99	0.98

Figure S3



Capítulo 3

Fagundes, C.K., Vogt, R. C. & De Marco Jr., P. 2015. Modelling amazon freshwater turtle: addressing the transferability problems. Padronizado de acordo com as normas da Ecological Modelling

MODELLING AMAZON FRESHWATER TURTLE: ADDRESSING THE TRANSFERABILITY PROBLEMS

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Abstract: Ecological Niche Models (ENM) are usually evaluated and applied within the region in which they were fitted. However, transfer ENMs to other parts of a species' geographical range is recommended to the proper evaluation of the models and for management actions. Given the conservation concern regarding the turtle *Podocnemis expansa*, we tested the transferability of the ENMs to this species in Amazon. We divided the occurrence points in six pairs of datasets. The occurrence points from one region of each pair were used to calibrate the model, whereas the occurrences from the other region of each pair were used to evaluate the model and vice-versa. The background points were chosen only in the training data area. We modeled using raw environmental variables and principal components as environmental predictors. The process resulted in 24 regional Amazon models. We modeled the distribution of the species with Maximum Entropy and they were evaluated using the area under the ROC curve (AUC), and the True Skilled Statistics (TSS). The similarity between the suitable areas for *P. expansa* occurrence to both regions of a dataset is low no matter which predictor selection we use. However, the use of raw variables as environmental predictors produced models that predict suitable areas far from the known distribution of the species. All TSS values were low, indicating that the models cannot be transferred from one Amazon area to another. On the other hand, AUC showed excellent and good values. The predicted area in number of pixels showed strong relationship with the TSS and AUC values using both predictor selections. The use of distinct datasets and principal components did not change the transferability to TSS and AUC values. Our study demonstrates the importance of capture relevant drivers of change in the requirements of the species in each region, especially widespread species like *P. expansa*. However, care should be taken when a modeled distribution of a species is projected into geographic regions with heterogeneous areas, such as the Amazon. Given the lack of transferability, the sum of the suitable areas predicted to both regions of the dataset which produced the more accurate model may be used to represent species distribution.

Keywords: Ecological Niche Models; Maximum Entropy; transferability; prevalence; *Podocnemis expansa*

1. Introduction

The knowledge of species distribution is the basic unit information used in both macroecology and conservation (Cayuela et al., 2009; Guisan and Thuiller, 2005; Nóbrega and De Marco Junior, 2011). The information regarding the distribution of organisms allows the evaluation of diversity patterns and their ecological and evolutionary process (Diniz-Filho et al., 2010). The lack of the species' proper distribution data, the so-called "Wallacean shortfall", hampers the evaluation of the biogeographical patterns. Such scenario is more evidenced in tropical regions (Brooks et al., 2001; Myers et al., 2000) and on freshwater species, which usually have poorer distribution database in comparison with terrestrial groups (Peres, 2005; Peres and Terborgh, 1995; Thieme et al., 2007). Detailed occurrence data of freshwater Amazonian turtles is uncommon and the distribution maps for these species are frequently created based on their known occurrence extent (Iverson, 1992b; Rueda-Almonacid, 2007). However, range maps may overestimate the distribution areas of the species (Rondinini et al., 2006), and the inclusion of unoccupied areas may inflate the species richness, producing a false biodiversity pattern (Bombi et al., 2011).

Ecological Niche Models (ENM) can be an important tool to fill the gaps about distribution data (Costa et al., 2010; Raxworthy et al., 2003). Those models estimate the environmental suitability to a given species from the association of abiotic variables and the known occurrence records in order to generate a projection of their distribution in geographical space (Guisan and Zimmermann, 2000; Peterson, 2001). Other terms have been used to refer those predictive models, but we used ENM in the current study because transferability issue requires hypotheses related to niche (Peterson and Soberón, 2012). The usage of ENMs allows the discovery of new species and new populations (Guisan et al., 2005; Raxworthy et al., 2003), to study introduction of alien species and extinctions (Broennimann et al., 2007; Ervin and Holly, 2011; Wang and Jackson, 2014), to assess the impact of accelerated land use and climate change (Araújo et al., 2005b; Araújo and Rahbek, 2006; Randin et al., 2006) and to answer several conservation problems (Loiselle et al., 2003; Marini et al., 2010; Martinez et al., 2006; Nóbrega and De Marco Junior, 2011). However, ENMs are usually evaluated and applied within the region in which they were fitted (Randin et al., 2006).

Despite the importance of the habitat relationships within individual landscapes, a desirable feature of ENMs is that the results can be transferred to other parts of a species' geographical range (Fielding and Haworth, 1995; Kleyer, 2002; McAlpine et al., 2008; Schröder and Richter, 1999; Thomas and Bovee, 1993) and across time (Araújo et al., 2005b; Schröder and Richter, 1999). Geographical or temporal transference of models is defined as generality (Fielding and Haworth, 1995) or transferability (Glozier et al., 1997; Kleyer, 2002; Schröder and Richter, 1999; Thomas and Bovee, 1993). A model with good generality should have good performance in different dataset in a similar spatial scale of what it was firstly developed (Barbosa et al. 2009; Pearce and Ferrier, 2000; Wenger and Olden, 2012). Transferability is recommended for a proper evaluation of the model (Fielding and Bell, 1997; Guisan and Zimmermann, 2000) and it is particularly relevant for models which purpose is conservation planning (Peterson, 2006; Soberón and Peterson, 2004; Vanreusel et al., 2007).

Projecting the species response to environmental conditions different from the studied range is not trivial (Elith et al., 2010; Zurell et al., 2012) and some obstacles to model transferability has been identified. For instance, sets of abiotic predictors which support the establishment and the survival of species may show spatial differences (Austin, 2002). However, even when environment is constant, historical influences, dispersal capacity and biotic pressure can generate local niche variation in a species range (Murphy and Lovett-Doust, 2007; Pulliam, 2000). Dispersal has significant influence on local adaptation of the species through both demographic and genetic rescue effects and can change the species distribution (Holt, 2003). On the other hand, it can prevent divergences in niche evolution, mainly at marginal populations (Hendry et al., 2001). Although some species occupy specialized habitats and show lower niche breadth next to the limit of their distributional ranges (Brown et al., 1995), other species can occupy similar niche positions in different regions (Hill et al., 2000; Prinzing et al., 2002; Thompson et al., 1993).

Studies involving different modelling techniques have been developed to address transferability (Araújo et al., 2006; Bakkenes et al., 2002; Guisan and Zimmermann, 2000; Peterson et al., 2002; Thuiller et al., 2005; Verbruggen et al., 2013). It is still not completely clear how and under what conditions distribution models can be transferred (Araújo et al. 2005a, 2005b; Graf et al., 2006; McAlpine et al., 2008; Pearson et al. 2006; Randin et al., 2006; Vernier et al., 2008), although some considerations may be discussed. Non-systematic sampling negatively influences ENMs and their transferability because the available species localities may not represent all the environmental conditions in which species occurs. Samples are often collected near from accessible locals (Hortal et al., 2008; Kadmon et al., 2004; Reddy and Davalos, 2003). Thus, ENMs may reflect survey effort rather than species distribution. Spatial sampling bias can generate unrealistic models and it is particularly serious in models based on presence-only databases (Phillips et al., 2009). Some authors postulate that models incorporating spatial or temporal autocorrelation are difficult to transfer from one region to another (Araújo et al., 2005a; Guisan and Thuiller, 2005; Hampe, 2004). Conversely, model generality is markedly improved by the choice of appropriate predictor variables, and in lower proportion by the distribution of the occurrence points in the geographic space, model complexity and background choice (Verbruggen et al., 2013). Indirect variables may fail to express the true habitat requirements of the species in distinct geographical areas (Guisan and Zimmermann, 2000; Randin et al., 2006).

Effective management actions require an understanding of the ecological factors determining habitat suitability in each local (Rushton et al., 2004). The distribution of Brazilian Amazonian freshwater turtles is poor, except for some species from the Podocnemididae family. *Podocnemis expansa* shows a large extent of occurrence in Amazon, which is desired property to test local responses of the species to different conditions. The species faces high hunting pressure by both adults and eggs (Rebêlo & Pezzuti, 2000; Schneider et al., 2011; Vogt, 2008). In this context, transferring models of *P. expansa* to areas where data are incomplete or lacking may help to solve conservation problems over its entire range and compensate low budgets in research (Whittingham et al., 2007). Hence, given the conservation concern regarding this species and the need for applicable models across the species distribution area, we tested the models transferability of the ENMs for *P. expansa* in Amazon. The performance was based on selection of predictors to control autocorrelation and background choice. We also discuss the applicability and limitations of the transferability approach for conservation.

2. Materials and methods

2.1. Species occurrence data

The occurrence database for *P. expansa* is composed of an extensive literature review, unpublished data obtained by our research group, data from a governmental project for turtle conservation ("Quelônios da Amazônia") and data from Brazilian scientific collections and museums provided on CRIA's Species Link (http://splink.cria.org.br/). Besides, we used species records data published on The EMYSystem Global Turtle Database (Iverson et al., 2003), which depict the maps yielded by Iverson (1992a, 1992b, 1992c). Extremes or obvious errors were eliminated as a protocol to control the data quality. Datasets frequently exhibit a spatial bias (Dennis and Thomas, 2000; Kadmon et al., 2004). In order to decrease the effect of sampling bias in the quality of model and transferability (Verbruggen et al., 2013), we consider only one occurrence point in each cell of our spatial resolution, which is designated unique points. This process resulted in 306 occurrences for *P. expansa* in all Amazonian area. The software MaxEnt used in modelling already discards redundant records that occur in a single cell, but does not correct the lack of data in some areas.

2.2. Environmental predictors

Despite the difficulty to obtain local variables that influence aquatic organisms (Mendonça et al., 2005), some studies reveal that macroscale variables are good predictors to be used in distribution models of aquatic species, including in Amazon area (Frederico et al., 2014; Porter et al., 2000; Watson and Hillman,1997). Following this reasoning, we used 42 variables: 37 climatic predictors, three variables that reflect terrain shifts and two predictors that characterize the aquatic environment (Fagundes et al., unpubl. data) to create the ENMs. Predictor variables usually show high collinearity and interfere in the interpretation of the models and its transferability (Dormann et al., 2012; Graham, 2003; Verbruggen et al., 2013). Thus, in order to reduce the parameters overfitting, we performed a principal components analysis (PCA) of those environmental variables to create new axes that summarized their variation (Dormann et al., 2012; Jiménez-Valverde et al., 2011). It was selected 12 principal components considering the Kaiser-Guttman criterion (Peres-Neto et al. 2005), which together explained more than 95% of the overall rate in predictors (Table 1). The 42 raw variables and the 12 principal components (PCA scores) were used separately in the modelling procedures to analyze which predictor selection improves transferability and the ability to predict species distribution. All layers were converted into a grid resolution of approximately 4km^2.

2.3. Analytical design

We built a global model using all the occurrence points of *P. expansa* using principal components as environmental variables. The median latitude and median longitude of the unique occurrence points were then used to divide the dataset into two parts in relation to the longitudinal and latitudinal Amazonian areas. Besides, the same process was used to divide the entire Amazon area in four quadrants. We obtained six pairs of datasets: two pairs in both latitude and longitude direction, two pairs in diagonals and two pairs in southern and northern Amazon areas (Fig. 1). To evaluate the transferability of ENMs under different locals, each pair of dataset was used separately. Thus, the occurrence data from one region of a pair of dataset were used to calibrate the model (training data/ partition A) and the occurrence data from the correspondent region of the same pair of dataset were used to evaluate the model (validation data/ partition B) and vice-versa. The background points in each model were chosen only in the training data area. Calibration data and evaluation data should use different environmental data as background to the model to be transferable (Phillips, 2008). We used 10.000 background points.

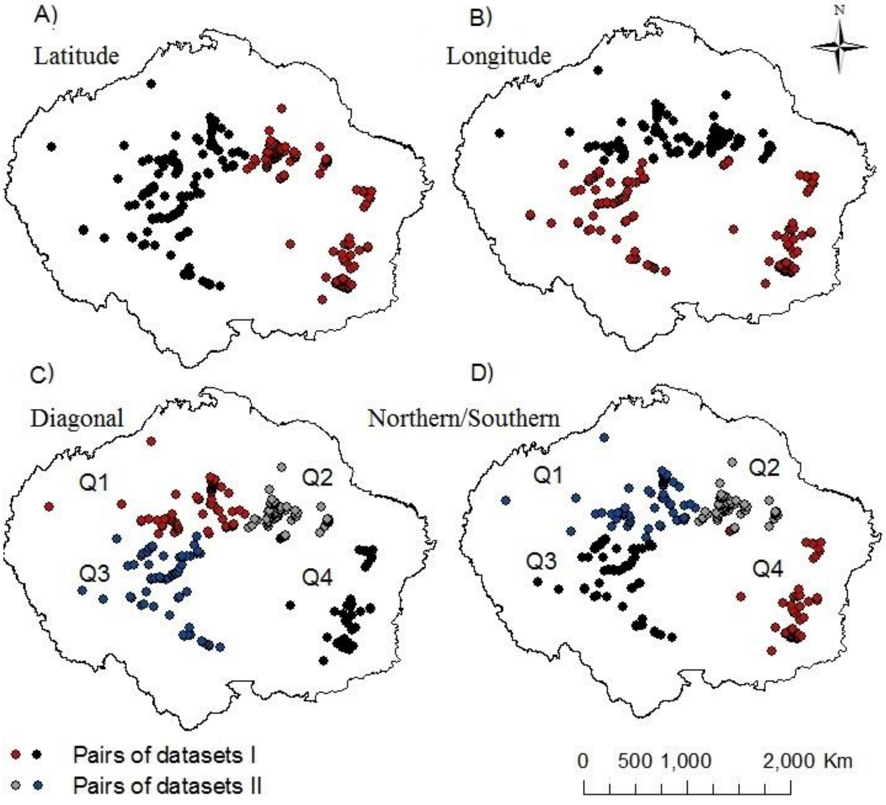

Fig. 1. Partition of *Podocnemis expansa* occurrence points in six pairs of datasets in Amazonian area in order to test transferability. A – Dataset partitioned by longitude; B – Dataset partitioned by latitude; C- Datasets partitioned by both diagonals (Q1Q4, Q2Q3) and

D –Datasets partitioned by southern and northern Amazon regions (Q1Q2, Q3Q4). Q1= quadrant 1, Q2= quadrant 2, Q3= quadrant 3, Q4= quadrant 4.

We have two conditions to test ENM performance in transferability: (a) datasets of occurrence points + raw environmental variables, (b) datasets of occurrence points + principal components. Thus, the process resulted in 24 regional Amazon models to test transferability, 12 models to each condition previously reported.

2.4. Modelling procedures and evaluation statistics

Maximum Entropy was the ‘presence/background’ algorithm chosen to build the models (Elith et al., 2010; Phillips and Dudik, 2008; Phillips et al., 2006). It is considered one of the most efficient methods, especially when the algorithm is used with few or biased occurrence data (Elith et al., 2006; Pearson et al., 2007; Siqueira et al., 2009). We used the software MaxEnt to run Maximum Entropy (Phillips et al., 2006) and the models were fitted by linear and quadratic features in order to decrease underparametrization. Verbruggen et al. (2013) verified that this condition allows a higher predictive power in the models.

The conversion of the modeled environmental suitability into a binary prediction of a 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 (Th ROC) and balances both omission and commission errors, reducing the risk of selecting sites with low suitability for species (Jiménez-Valverde & Lobo, 2007; Pearce and Ferrier, 2000). The models were evaluated using a threshold-independent method, the area under the ROC curve (AUC - Fielding and Bell, 1997), and a threshold-dependent method , the True Skilled Statistics (TSS - Allouche et al., 2006; Liu et al., 2011). We followed the criteria of Araújo et al. (2005a) adapted from Swets (1988) to classify the models into excellent (AUC > 0.90), good (0.80 > AUC < 0.90), fair (0.70 > AUC < 0.80), poor (0.60 > AUC < 0.70), and fail (0.50 > AUC < 0.60) as indicators of transferability. In relation to the TSS evaluation, acceptable values show at least the value of 0.5 (Fielding and Bell, 1997).

We compared the similarity of the suitable areas predicted for *P. expansa* occurrence to both regions of a pair of dataset using the Sorensen similarity index. This index was also used to calculate the similarity between the predicted area to each dataset and the environmentally suitable areas predicted to the global model. The overlap comparison was made only to the models built with principal components.

The equation of Sorensen similarity index is $Ss = \frac{2a}{(2a+b+c)}$, where a is the number of pixels containing predicted area to *P. expansa* occurrence to both zones used in the comparison, b is the number of pixels with predicted area to the zone 1 and c is the number of pixels with predicted area to the zone 2.

We use pairwise *t*-tests to compare the similarity of the predicted areas to both regions of a dataset using raw or principal components as environmental data. We also compared the effect of the dataset and predictor selection on transferability to both AUC and TSS evaluation methods using main effect ANOVA. The relationship between the number of pixels predicted to be suitable to *P. expansa* occurrence and TSS/AUC values using both set of environmental predictors were evaluated by simple linear regression. All statistical tests were conducted using Statistica 8.0 (Statsoft Inc, Tulsa, USA).

3. Results

The maps of the environmentally suitable areas to *P. expansa* occurrence show large changes in predicted area according to each dataset and predictor variables used to generate the potential distribution for the species (Fig. 2 and Fig. 3). The common predicted area to both regions (partition A and partition B) of a dataset was low in all models (Fig. 2 and Fig. 3). The higher similarity was found to the latitude model built with principal components (43%). When we use the raw variables as environmental predictors Q1Q4 and Q3Q4 models predict suitable areas far from the species distribution in Andean region. However, predictor selection have no significant difference in similarity of the predicted areas to both regions of a dataset (*t*= -0.33; *P*=0.75) (Table 1).

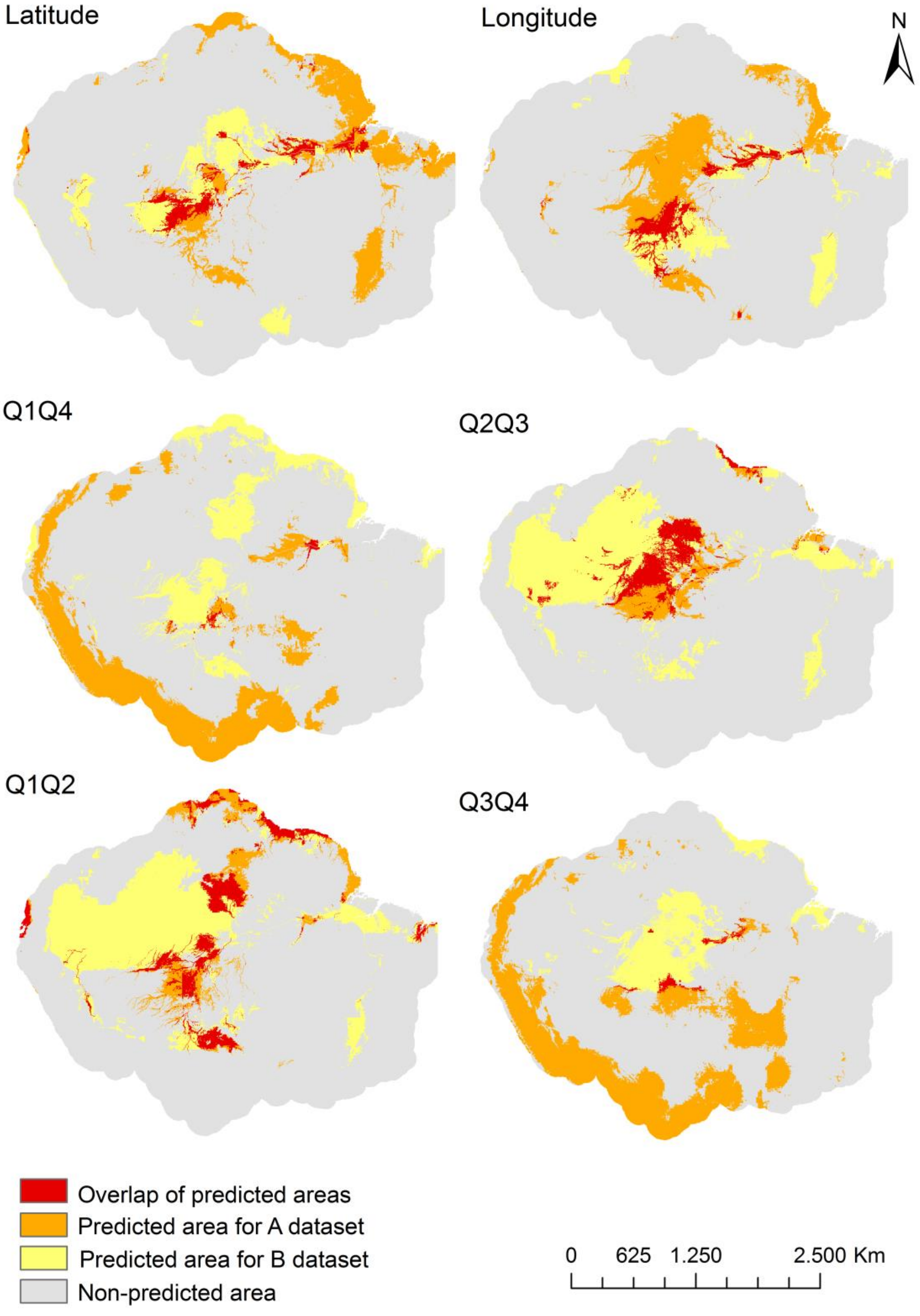

Fig. 2. Maps of the environmentally suitable areas for *Podocnemis expansa* occurrence in Amazon to each region of dataset. The models were built considering raw variables as environmental predictors. The red areas show the overlap of suitable areas predicted by a pair of dataset, indicating transferability.

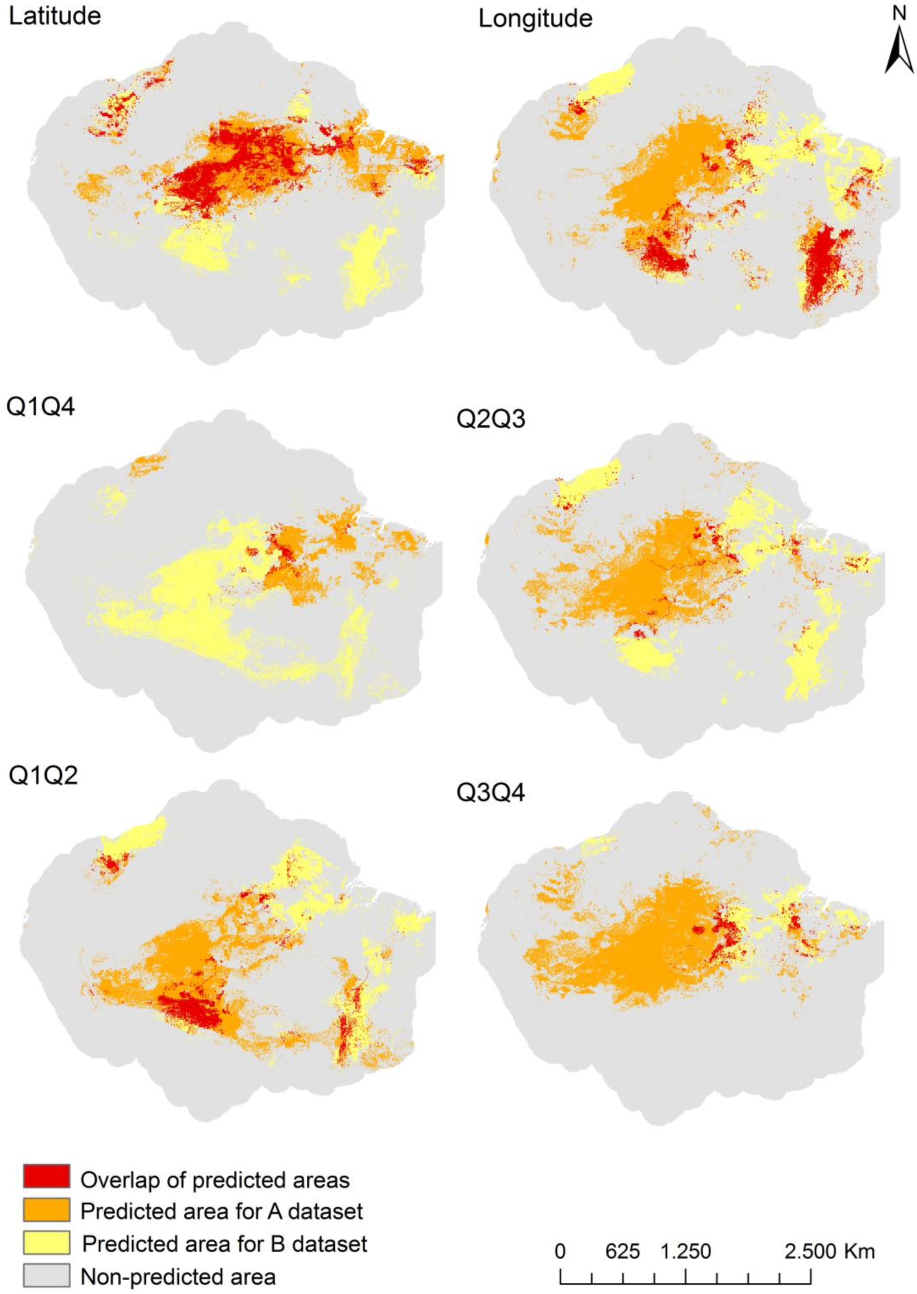

Fig. 3. Maps of the environmentally suitable areas for *Podocnemis expansa* occurrence in Amazon to each region of a dataset. The models were built considering principal components as environmental predictors. The red areas show the overlap of suitable areas predicted by a pair of dataset, indicating transferability.

Table 1. Similarity values of suitable areas predicted for *Podocnemis expansa* occurrence in Amazon between each region of a dataset. We considered principal components and raw variables as environmental predictors. The table also show the number of occurrence points used to run the models.

	Raw variables	Principal components	Occurrence points
Latitude	0.22	0.43	153
Longitude	0.24	0.32	153
Q1Q2	0.23	0.22	75
Q1Q4	0.02	0.04	78
Q2Q3	0.28	0.08	75
Q3Q4	0.03	0.10	78

The suitable areas predicted to each dataset (partition A + partition B) show high similarity to the global model built with principal components (Fig. 4). Thus, the sum of the suitable areas predicted to both regions of a dataset may be used to represent species distribution when models show lack of transferability. Latitude and longitude models showed higher overlap of predicted areas in relation to the global model (Table 2).

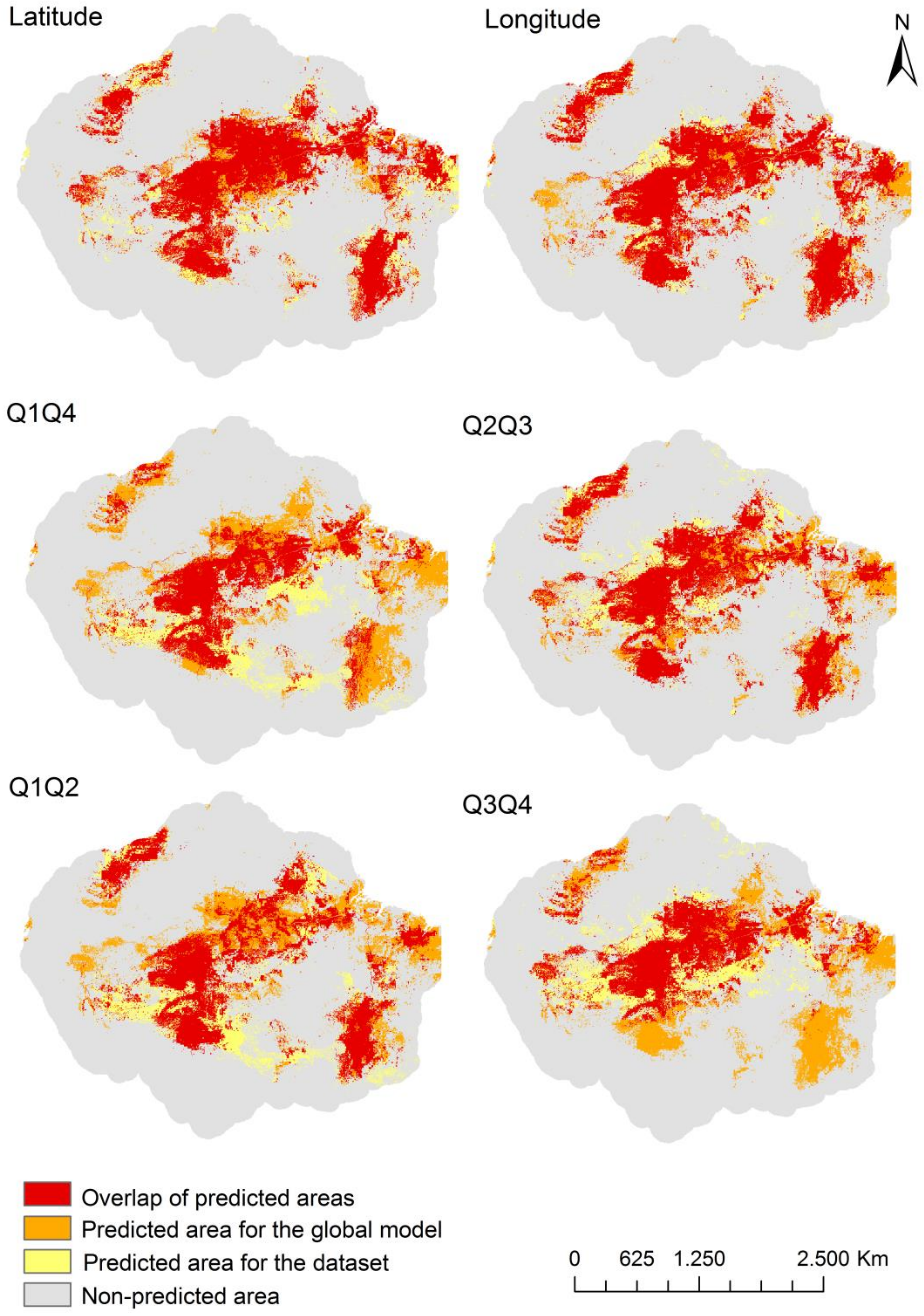

Fig. 4. Maps of the environmentally suitable areas for *Podocnemis expansa* occurrence in Amazon to each dataset and global model. The models were built considering principal components as environmental predictors. The red areas show the overlap of suitable areas predicted by a dataset and global model, indicating transferability.

Table 2. Similarity values of suitable areas predicted for *Podocnemis expansa* occurrence in Amazon between each dataset and global model. We considered only principal components as environmental predictors.

	Global Model
Latitude	0.81
Longitude	0.82
Q1Q2	0.65
Q1Q4	0.58
Q2Q3	0.74
Q3Q4	0.57

None of the models had acceptable value when TSS was used as evaluation method to assess the transferability of the models (values ≤ 0.50). The conditions present in training regions were not verified in testing data and vice-versa. Thus, the models developed in this study for *P. expansa* cannot be transferred from one Amazon area to another. On the other hand, almost all models had excellent and good AUC values (values ≥ 0.80) (Table 3).

Table 3. Transferability values of the Ecological Niche Models developed for *Podocnemis expansa* in Amazon to each region of a dataset and with different predictor selection. The models were evaluated using the Area under the ROC curve (AUC) and True Skilled Statistics (TSS) methods. A and B is related to the region of the datasets used to train the models.

Method	Predictor selection	Latitude		Longitude		Q3Q4		Q2Q3		Q1Q4		Q1Q2	
		A	B	A	B	A	B	A	B	A	B	A	B
TSS	PCA	0.082	0.081	0.075	0.095	0.050	0.061	0.045	0.128	0.059	0.049	0.041	0.139
TSS	Raw variables	0.100	0.136	0.110	0.154	0.076	0.024	0.070	0.047	0.027	0.090	0.077	0.033
AUC	PCA	0.909	0.927	0.910	0.957	0.954	0.958	0.943	0.973	0.954	0.948	0.938	0.980
AUC	Raw variables	0.929	0.960	0.955	0.961	0.959	0.790	0.954	0.879	0.811	0.972	0.967	0.834

The predicted area in number of pixels showed strong negative relationship with the TSS and AUC values and this pattern did not change when we used different sets of environmental predictors (Fig. 5). The use of principal components did not improve the TSS evaluation values (*F*= 1.26; *P*= 0.38) and the AUC values (*F*= 1.25; *P*= 0.38). The use of distinct datasets do not change the transferability measure to both TSS (*F*= 1.23; *P*= 0.39) and AUC (*F*= 0.39; *P*= 0.92) methods.

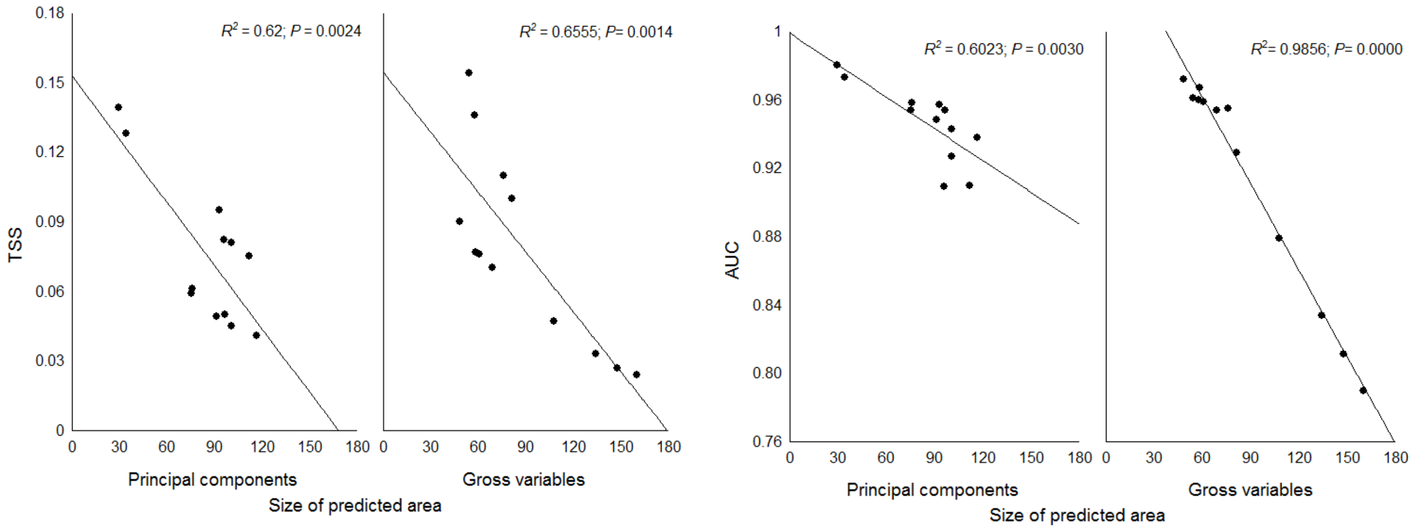

Fig. 5. Regression analyses between the size of predicted area for *Podocnemis expansa* occurrence in Amazon (in number of pixels) and True Skilled Statistics (TSS) and under the ROC curve (AUC) values. The regressions were calculated using raw variables and principal components as environmental predictors.

4. Discussion

A good evaluation of the models requires testing them with an independent dataset. The similarity between the suitable areas for *P. expansa* occurrence to both regions of a dataset is low no matter which predictor selection we use. However, when we used the raw variables, the models predict areas largely out of the extent of occurrence known for *P. expansa*. The use of AUC to measure model transferability indicated good performance in all partitions considered, but such result may be false (Wenger and Olden, 2012). The AUC and TSS values had strong relationship with the predicted area in number of pixels and this pattern did not change when we used different sets of environmental predictors. We did not identify differences in transferability of predictive species distribution when we used modelling techniques such as distinct selection of predictor variables and data partition. However, variation in transferability of ENMs using different occurrence datasets and modelling procedures have been observed in other studies (Randin et al., 2006; Verbruggen et al., 2013).

The representation of the niche of the species require that training data is in all suitable environments to the species occurrence, otherwise when we transfer the model to a different area (test area), a portion of the its niche that was not sampled before may not be recognized by the models (Fitzpatrick et al., 2007; Rödders et al., 2009). Thus, lack of transferability of ENMs is mainly related to the differences in environmental conditions between areas and does not mean niche shift or if those changes are situated at the fundamental or realized niche. The variable being modeled is the environmental suitability not site occupation. Transferability issue only supports assumptions about differences of realized niche between areas, since correlative models estimate that niche part (Verbruggen et al., 2013). Amazon shows an east-west gradient in climate, soils and elevation (Albert and Reis, 2011; Marengo, 2004). The northwest area encompasses the rainy regions while southern and eastern Amazon shows a more wet/dry climate (Davidson et al., 2012). McPherson et al. (2004) found that differences in altitudinal range between areas may reduce transferability. It can be particularly important in chelonians because in general the altitude is a limiting factor to their distribution. Besides, turtle richness is largely determined by precipitation (Iverson, 1992a, 1992c; Souza, 2005).

Species can show different environmental requirements in diverse sites according to the contrast of each geographic area (Randin et al, 2006; Walter and Breckle, 1985). However, other features can influence the distribution of the species between regions. Transferability of ENMs may be affected by the biotic interactions in a regional species pool, mainly in broader scales (Hill et al., 2000; Odland and Birks, 1999; Prinzing et al., 2002; Thompson et al., 1993; Zobel, 1997). Unequal abundance of a species in its extent of occurrence also can cause niche restriction or dispersal limitations and decrease transferability (Dirnböck and Dullinger, 2004; Groom, 1998; Pulliam, 2000). Another factor that influences the model generality is the existence of different ecotypes between regions (Joshi et al., 2001; Walter and Breckle, 1985). Amazon shows a mosaic of vegetation types related to different freshwater ecosystems (Sioli, 1985; Davidson et al., 2012). The flooded forest várzea in western part of Amazon is composed by 85–90% of low-várzea type, which has more prolonged inundations (Wittmann et al., 2002; Wittmann et al., 2006). Pritchard and Trebbau (1984) commented that flooded and non-flooded areas from Amazonia drive the geographical distribution of large river turtles as Podocnemididae. Adult males and females of *P. expansa* migrate from flooded forests areas to the nesting beaches in the reproductive period and return to flooding areas after the birth of the hatchlings (Alho and Pádua, 1982; Ferrara et al., 2012; Vogt, 2008).

Failure to correct for geographical sampling bias can result in unrealistic models (Phillips et al., 2009). In some situations, we can expect significant deviations from predicted omission rates (Peterson et al., 2007) or commission rates, mainly on presence-only models (Phillips et al., 2009). Models with dramatic errors can be generated and influence conservation actions in a negative way. Thus, dividing the occurrence data to smaller dataset can help to decrease the sample bias effect and we can more precisely account for suitable sites to the species occurrences. This is particularly true for species with large geographical and/or environmental range as *P. expansa* (Osborne and Suárez-Seoane, 2002). Many studies show that predictive models can be transferred to new areas and reduce budgets in conservation actions (Vanreusel et al., 2007; Verbruggen et al., 2013). However, some authors conclude that transferability of models is hardly possible (Graf et al., 2006; Guay et al., 2003; Mallet et al., 2000; Randin et al., 2006). The capacity for transferability is highly species specific (Randin et al., 2006) and depends on ecological traits, such as mobility, specialization and prevalence (Angert et al., 2011; Pöyry et al., 2009).

Larger areas are most likely to encompass larger variation of environmental variables than more-restrictive training geography (Graf et al., 2006; Phillips, 2008). Some studies show that the model accuracy depends more precisely on the relationship between the environmental range of the occurrence data and background points (Stokland et al., 2011). Thus, the reduction of the background selection to narrow areas in the design to evaluate transferability may affect the model performance (Thuiller et al., 2004; Vanderwal et al., 2009). It is particularly important in widely distributed species (Barve et al., 2011), which are inherently difficult to model (Eskildsen et al., 2013). According to the above assumptions, our study found that models trained in largest areas (latitude/longitude models) showed higher transferability values and higher similarity values between the environmentally suitable areas predicted to both regions of those datasets. However, distinct datasets did not show a significant change on transferability to both TSS and AUC methods.

The AUC may provide misleading results, suggesting that all models had good or excellent performance. Transferability is frequently verified in studies that use AUC measure (Eskildsen et al., 2013; Verbruggen et al., 2013). The AUC method appears to be sensitive to background choice. Larger backgrounds increase the AUC values because it includes points with different environmental characteristics, but it does not mean a significant higher predictive power (Jiménez-Valverde, 2012; Lobo et al., 2008). Conversely, this method is also dependent of the proportion of presences relative to the number of sites (prevalence), and small areas may have higher prevalence and higher AUC values. Some studies highlight that high AUC values can be obtained even for models with strong biases and may poorly reflect model accuracy (Fourcade et al., 2014; Jimenez-Valverde et al., 2012; Lobo et al., 2008). The maps produced in this study reveal that although AUC values were very high, the predicted areas to the species occurrence to both regions of a datasets had low overlap. In this respect, TSS appears to be more sensitive to low transferability and may be a better measure to evaluate the models, and according to the results obtained here, all the models were not transferable according to this method. Allouche et al. (2006) conclude that TSS is a good measure of the model accuracy because it is not affected by prevalence and by the size of the validation set. However, in the current study both AUC and TSS measures had a strong relationship with the predicted area in number of pixels. The dependency of prevalence makes difficult to estimate the performance of the models (Lantz and Nebenzahl, 1996).

The choice of the predictors may have also a drastic effect on the transferability (Peterson and Nakazawa, 2008; Rödder and Lötters, 2010; Rödde et al., 2009; Tuanmu et al., 2011; Vanreusel et al., 2007), but we could not find this effect on *P. expansa* models. Usually environmental predictors show high autocorrelation (Phillips, et al., 2006). Multicollinearity changes model structure and the relationship between species occurrence and environment suitability, affecting the significance of the tests (Graham, 2003; Mac Nally, 2000). Principal components are commonly used to reduce correlated variables (Graham, 2003; Verbruggen et al., 2013) and are useful in ENMs that predict environmental conditions within the same area and during the same time of a train model (Viña et al., 2010). On the other hand, in some occasions the use of indirect environmental variables and intermediate predictors such as principal components on the niche similarity may not increase the transferability of the models (Austin, 2002; Graf et al., 2006; Phillips, 2008). In the current study, PCA did not improve the transferability values and the similarity of the predicted areas to both regions of a dataset. Peterson et al. (2007) postulate that indirect variables can overpredict the distribution area (Peterson et al., 2007). However, the use of principal components does not change the relation verified in this study, where higher AUC and TSS values were found to the lower predicted areas. Although we did not find significant differences in results using PCA, some models built with raw variables produced exaggerated predictions to areas such as Andean mountains and should reflect less the species distribution.

Transferring models to new sites represent a new approach to consider species-specific requirements into a reserve network and conservation actions (Vanreusel et al., 2007). Local and regional managements depend on a detailed knowledge of the variation in response shown by a species across its range. In this context, our study demonstrates the importance of considering transferability to evaluate the models and increase their accuracy. Model validation has showed good predictive accuracy when the non-independent data are from the same time (Araújo et al., 2005a; Eskildsen et al., 2013). However, we showed that care should be taken when ENMs are projected to different geographic regions, especially in heterogeneous areas such as Amazon. Assessment of performance should focus on the ability of models to capture relevant drivers of change (Rapacciuolo et al., 2012), since that local adaptations of the species may overestimated species distribution (Stockwell and Peterson, 2002). *Podocnemis expansa* shows high dispersal capacity (Valenzuela, 2001) and the differences in environmental conditions across Amazon seem to drive the requirements of the species in each region. The nesting beaches could limit *P. expansa* occurrence in different parts of its range. Those sites appear to be more abundant in western Amazon (Cantarelli and Herde, 1989). In case of lack of transferability, the sum of the suitable areas predicted to both regions of the dataset which produced the more accurate model may be used to represent species distribution. The results presented here are specific to the current spatial scale. Other resolution could generate different patterns because the importance of the variables is dependent on the scale (Luoto, 2007; Pearson et al., 2004).

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Capítulo 4

Fagundes, C.K., Vogt, R. C. & De Marco Jr., P. 2015. Predicting the hatchling sex ratio from natural nest temperatures in a temperature-dependent sex determination (TSD) turtle species in central Amazon. Padronizado de acordo com as normas da American Naturalist

Predicting the hatchling sex ratio from natural nest temperatures on in a TSD turtles species in central Amazonia

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List of essential elements: Introduction, Results, Discussion, Material and Methods.

ABSTRACT: Some species show temperature-dependent sex determination (TSD), where the offspring sex ratio is determined by the incubation temperature of the embryo. Climate is under dramatic modifications and TSD species may be particularly threatened. *Podocnemis unifilis* is classified as vulnerable by IUCN and conservation actions do not contemplate hatchling sex ratio estimates. Thus, we used a more general method to determine sex ratio based on the dependency of the embryo growth rate on temperature from a time series of incubation temperatures of natural nests. The study was developed in a seasonally flooded whitewater forest (Várzea) area and in a sand beach area in central Amazonia. A linear mixed model (lme) was run to evaluate the correlation between daily mean nest temperatures and fixed effects (air temperature, nest distance to vegetation, nesting distance to water, area and female track width), and between thermal variance and daily mean nest temperature and area in order to determine the factors that influence the nest temperature. Our study is the first one to show that temperature influences the embryo developmental rate and sex determination in a different way. Daily mean nest temperature was related to distance to vegetation, air temperature and area. Daily thermal variance is related to daily mean nest temperature and both are responsible to sex determination. The sand beach shows high feminization pattern, but the flooding site is still an important source of male production and it seems to be crucial to the maintenance of the population viability.

Introduction

Temperature has a strong influence on all biological taxes in ectothermic animals (Angilletta et al. 2002; Gillooly et al. 2002). Particularly in chelonians, characteristics related to reproduction like incubation period, hatchling success, embryonic growth and hatching morphology are strongly depend on incubation temperature (Mrosovsky and Provancha 1989; Du and Ji 2003; Limpus 2006). Some species show temperature-dependent sex determination (TSD), where the offspring sex ratio is determined by the incubation temperature of the embryo (Bull and Vogt 1979; Pieau 1996). In the TSD pattern present in most turtles, high temperatures produced females and low temperatures produced males (Ewert et al. 1994; Viets et al. 1994). More precisely, the sex in TSD turtle species depends on the cumulative effect of temperature during the second third of the embryonic development, designed as thermosensitive period (TSP) (Bull and Vogt 1979; Yntema 1979; Bull and Vogt 1981; Vogt and Bull 1982; Yntema and Mrosovsky 1982). Besides, the cumulative effect of temperature varies with the amplitude of its fluctuation (Georges 1989).

Incubation temperature is the basic element of the sexual determination, because it regulates the oestrogen production (Georges et al. 1994; Wibbels et al. 1994). The hormone has a feminizing role in gonadal differentiation (Wibbels et al. 1994; Dorizzi et al. 1996; Pieau and Dorizzi 2004) and is related to the aromatase activity in TSP (Jeyasuria and Place 1997). During TSP, the embryogenesis reaches temperature values where both sexes are produced in equal proportion, the pivotal temperature (P), and temperatures values where both sexes are yielded in variable proportions, the transitional range of temperatures (TRT) (Mrosovsky and Pieau 1991). Only a small shift in incubation temperature (~1ºC) (Godfrey et al. 1999; Broderick et al. 2000; Godley et al. 2001; Schwanz et al. 2010) or an increase in the temperature fluctuations at low and high mean temperatures is sufficient to alter de embryo sex ratio (Neuwald and Valenzuela 2011). Different parameters were already used to find a non-invasive method to predict correctly hatchling sex ratio: mean nest temperature (Bull 1980; Schwarzkopf and Brooks 1987; Valenzuela 2001), incubation period (Marcovaldi et al. 1997), the mean and variance of incubation temperature (Bull 1985; Souza and Vogt 1994) and the number of hours at or above pivotal temperature during TSP (Bull 1985; Mrosovsky and Provancha 1992; Souza and Vogt 1994). However, experimental studies showed that those approaches had poor predictive power (Valenzuela 2001; Georges et al. 2004). Natural nests experience daily and seasonal temperature fluctuations that influence the embryo development time and sex ratio (Bull 1985; Georges 1992; Janzen 1994; Shine and Harlow 1996).

Georges (1989) developed a model where the results from constant temperatures are transformed in predictions about natural conditions. The constant temperature equivalent method (CTE) converts fluctuating temperature into constant temperature that shows the same effect on sex ratio (Georges 1989; Georges et al. 1994). However, the model is restricted to temperatures around a stationary mean that have a linear effect on embryo development (Georges et al. 2004; Georges et al. 2005). In order to concern about natural nest temperatures outside the optimal temperature range (OTR), different methods have been developed to evaluate the cumulative and differential effects of temperature on sex determination (Georges et al. 2004; Georges et al. 2005; Parrott and Logan 2010; Neuwald and Valenzuela 2011). Recently, CTE has been improved by accounting for physiological response of the embryo to temperature (Delmas et al. 2008; Girondot et al. 2010) and for the effect of nesting phenology on hatchling sex ratio (Telemeco et al. 2013). The mentioned models require large data sets on embryo growth though. To deal with the lack of data, Girondot and Kaska (2014) provided a more general method to determine sex ratio based on the dependency of the embryo growth rate on temperature (reaction norm) from a time series of incubation temperatures in natural nests. In the current study, however, we evaluated the difference in the influence of temperature on embryo growth rates and sex determination (Neuwald and Valenzuela 2011).

Climate is under dramatic modifications (Karl et al. 1996; Magnusson 2001). Intergovernmental Panel on Climate Change (IPCC) described large changes in climatic patterns for recent decades (IPCC 2007). Climate changes, especially in higher latitudes affect annual mean temperatures (Parry et al. 2007) and TSD species are particularly vulnerable (Deutsch et al. 2008; Kallimanis 2010; Mitchell and Janzen 2010). In those species, global warming has the potential to increase the proportion of female hatchlings that are produced (Limpus 2006; Hawkes et al. 2009; Hays et al. 2010; Schwanz 2013) and to alter species distribution (Brown et al. 1997; Parmesan et al. 1999; Walther et al. 2002) and nest survivorship (Miller 1985; Broderick et al. 2001; Godley et al. 2001; Hamann et al. 2007; Hawkes et al. 2007). Turtles have persisted during dramatic period of climate changes (Hamann et al. 2007; Hawkes et al. 2009), however, the climate projections for the next hundred years are expected to occur more accelerated than in the past (Brohan et al. 2006; IPCC 2007). It is uncertain if turtles can adapt their behavior or physiological characteristics quickly (Hamann et al. 2007). Turtles are long-lived animals with late maturity (Zug et al. 2002) and pivotal temperature is a relatively conservative characteristic among populations and species (Freedberg and Wade 2001). Despite that Bull et al. (1982b) showed pivotal temperatures to vary within a climate from northern to southern USA in the same species.

Podocnemis unifilis is a TSD species classified as vulnerable by the International Union for Conservation of Nature and Natural Resources (IUCN) (Vogt 2008; IUCN 2010). The knowledge of the relation between climate change and the proportion of females and males yielded each time period is very important to understand how temperature can affect the species survival (Hulin et al. 2009; Hamann et al. 2010) and to the development of conservation policies (Saba et al. 2012). Most of conservation activities for chelonians are focused on the protection of the nesting beaches in order to protect adult females and to increase the number of hatchlings. However, we usually do not have any information about the natural hatchling sex ratio. Thus, given the conservation concern regarding *P. unifilis*, the objectives of this study are (1) to model the "reaction norm" of embryo growth and sexualization under natural fluctuating temperatures in a sand beach and in a Várzea area (seasonally flooded whitewater forest) in central Amazonia in order (2) to predict sex ratio; and (2) to determine the factors that influence the nest temperature.

Results

Embryo growth reaction norm and its confidence interval

Nest temperatures varied between 24.35°C and 52.73°C (fig. 2). The incubation period ranged from 58 to75 days and it decreases at higher mean nest temperatures. The lower incubation length mean occurred at a temperature mean of 30.06ºC (fig. 3).

The data were fit better with the four parameters Schoolfield et al. (1981) equation (ΔAIC=0.00, Akaike weight=0.87). The embryo growth rate increases at higher values. Taking into account the registered nest temperatures, the embryo growth is lower at 24.35ºC, reaching only 30% of the observed growth rate value at 37°C, which is the temperature of the maximum embryo growth (fig. 4). After the peak value the embryo growth return to decrease. The confidence interval for the reaction norm was lower when a range of temperatures was well represented among nest samples (fig. 4).

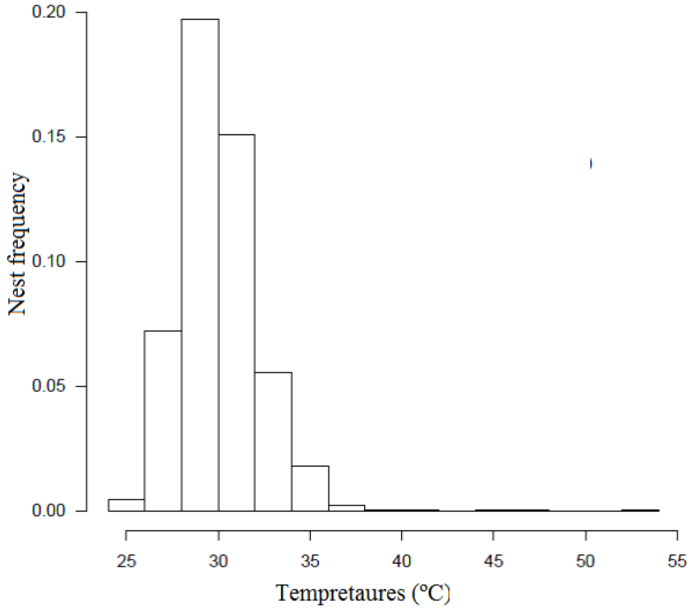

Figure 2: Distribution of nest temperatures for *Podocnemis unifilis* in a seasonally flooded whitewater forest (Várzea) and in a sand beach in Brazilian central Amazonia.

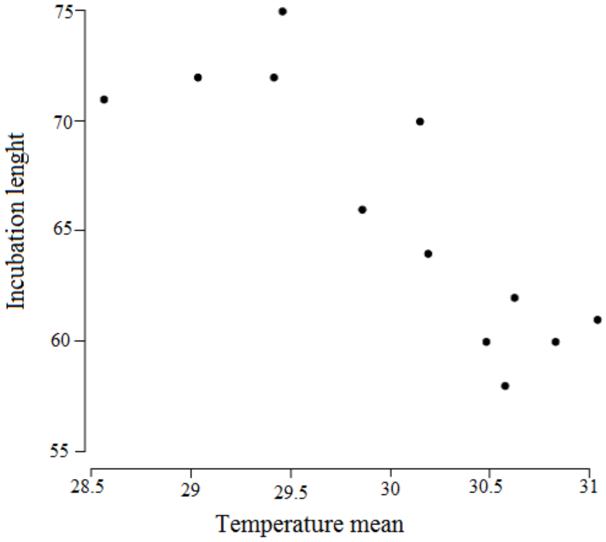

Figure 3: Relationship between incubation temperature mean and incubation period. The points represent the 12 studied nests of *Podocnemis unifilis* in a seasonally flooded whitewater forest (Várzea) and in a sand beach in Brazilian central Amazonia.

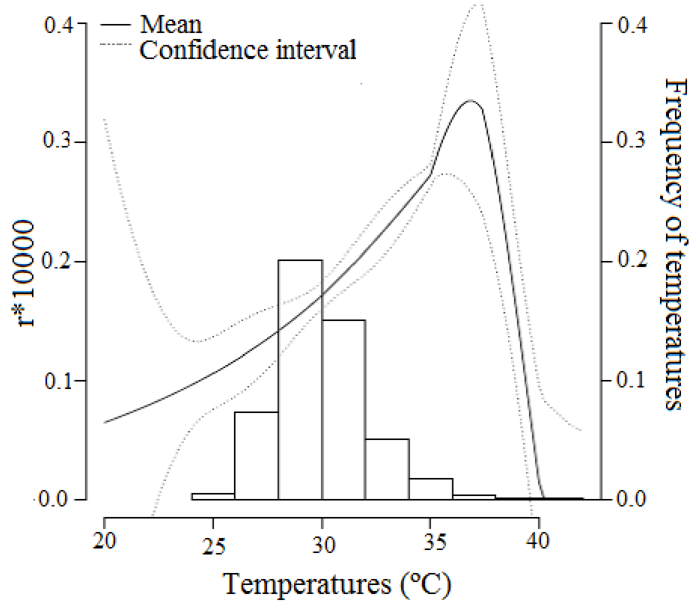

Figure 4: Mean and confidence interval for embryo reaction norm r(T) with nest temperature data of *Podocnemis unifilis* from Brazilian central Amazonia. The graphic is based on the anchored model.

Predicting time series of nest temperature

The daily mean nest temperatures ranged between 25ºC and 42ºC, and they were higher in sand beach than flooding area. Using the daily mean local temperatures from data loggers, the lme model nest showed that the measures of distance to vegetation (t_{12}= 3.22, $p < 0.01$), air temperature (t_{920}= 29.51, $p < 0.01$) and area (t_{12}= -4.32, $p < 0.01$) were correlated to daily mean nest temperature. Comparison of the model using all the fixed effects (AIC = 2529.50, n = 936) to the model using only distance to vegetation, air temperature and area (AIC = 2502.69, n = 936) suggested that the last one is better. However, when we use the daily mean air temperature from ECMWF, the daily mean nest temperatures are correlated with air temperature (t_{920}= 13.44, $p < 0.01$) and area (t_{13}= -5.04, $p < 0.01$) only. This model had lower

Akaike (AIC = 2445.74, n = 936) than the model that encompass all independent variables (AIC = 2477.19, n = 936).

The daily amplitude of nest temperatures was higher in sand beach (1.8 – 11.5 ºC) than in flooding area (0.5 – 4.3 ºC). According to the lme model the daily amplitude of nest temperatures is correlated with the daily mean nest temperatures ($t = 7.25$, $p < 0.01$) and area ($t = -5.19$, $p < 0.01$) (fig. 5).

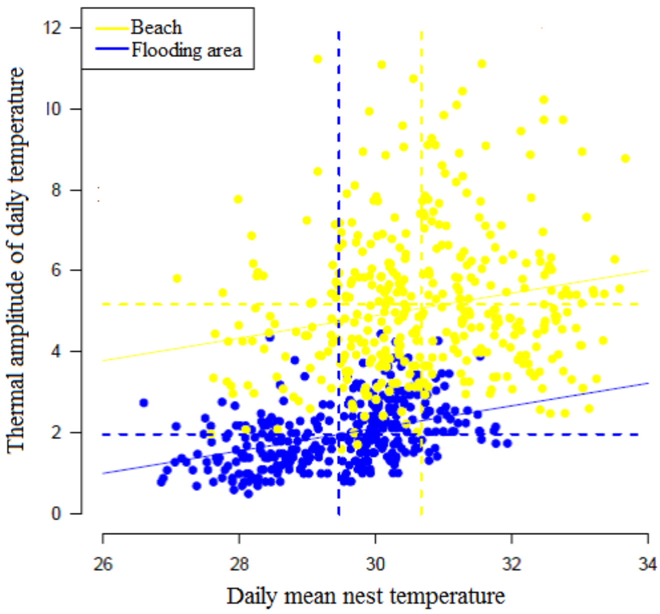

Figure 5: Relationship between daily mean nest temperature and thermal amplitude of daily temperature to seasonally flooded whitewater forest (Várzea) area and sand beach area in Brazilian central Amazonia.

Reaction norm for sexualization model

The seasonally flooded whitewater forest (Várzea) area show high proportion of males and the opposite is verified at sand beach where we found high proportion of females. Higher incubation period and TSP period produce higher male frequency, while higher incubation temperatures decrease male frequency (fig. 6, fig. 8).

The curve of thermal reaction norm for sexualization shows a higher peak than we found for embryo growth. Thus, when the embryo growth starts to become slow, the sexualization continues to increase its performance. Sexualization has higher extent with higher frequency of temperatures around from 35ºC to 39ºC in relation to embryo growth (fig. 7). The temperature where the reaction norm for sexualization reaches the maximum of its activity is 37 ºC.

The temperature which the both sexes were yielded in equal proportion (pivotal temperature) was 31.43 ± 0.09. The transitional range of temperature l=5% is 6.903 ± 0.335. The frequency of males decreases above the pivotal temperature. The male proportion from 33ºC is less than 10% to Souza and Vogt (1994) and 0% in the current study. However, in a 34.8°C temperature, one nest showed a male frequency around 30% (fig. 8).

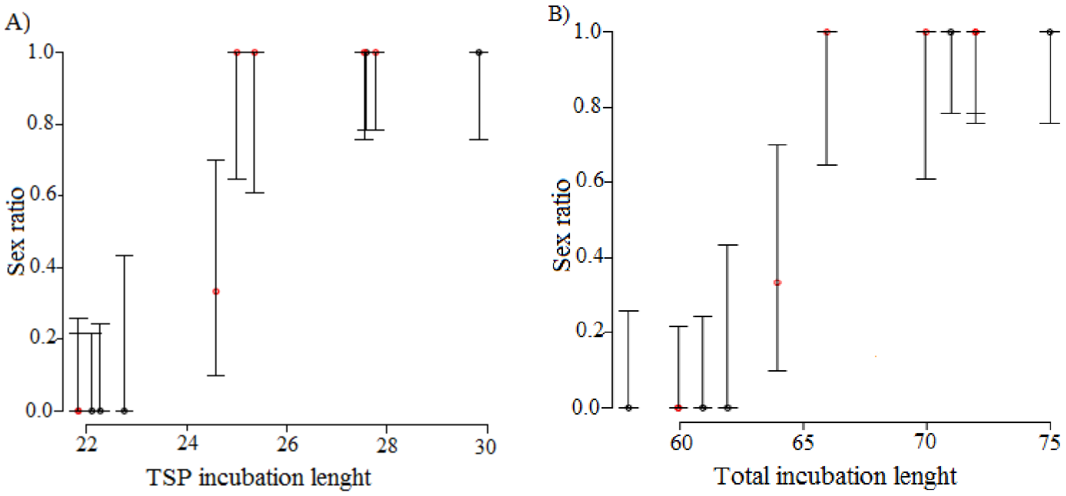

Figure 6: Mean of male frequency of *Podocnemis unifilis* yielded in different A) incubation lengths and B) TSP incubation lengths. The blue dots correspond to the data from seasonally

flooded (Várzea) area and the red dots correspond to the data from sand beach in Central Amazonia.

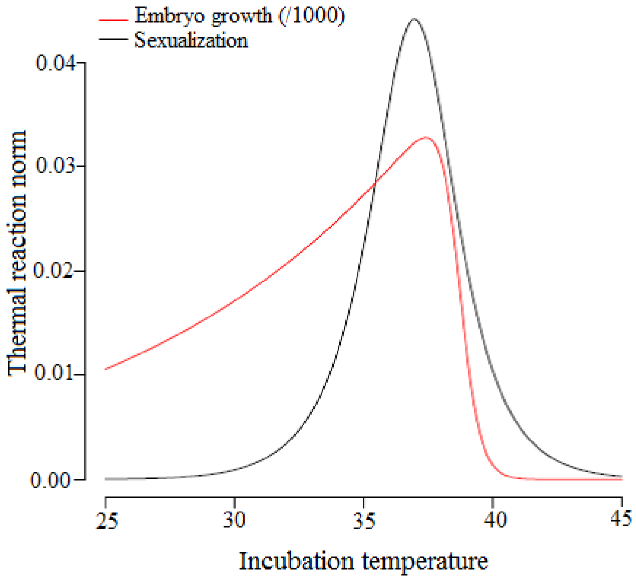

Figure 7: Thermal reaction norm of embryo growth and sexualization of *Podocnemis unifilis* in different nest temperatures (ºC) in Brazilian central Amazonia.

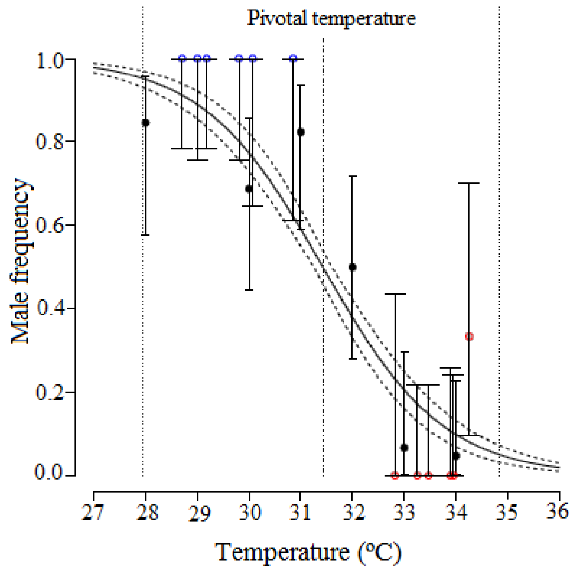

Figure 8: Mean of male frequency of *Podocnemis unifilis* yielded in different temperatures (ºC) and its confidence interval. The black dots are based on the results showed by Souza and

Vogt (1994) study. The blue dots correspond to the data from the seasonally flooded (Várzea) area and the red dots correspond to the data from sand beach in Central Amazonia.

Discussion

The current study shows for the first time that the temperature influences the embryo developmental rate and sex determination in a different way and it is a fundamental question to understand and estimate sex ratio in turtle populations. Daily thermal variance is related to daily mean nest temperature and both are responsible to sex determination. The sand beach area had higher temperatures and thermal variance. High nest temperatures are not lethal to embryo when its frequency is low. The sand beach shows high feminization pattern, but the flooding site is still an important source of male production and it seems to be crucial to the maintenance of the population viability.

Eggs of *P. unifilis* experienced temperatures higher than the temperatures that are accounted to support high success of eggs hatching (Bustard 1971; Yntema and Mrosovsky 1980; Binckley et al. 1998; Valverde et al. 2010). None eggs hatched at a constant temperature of 36ºC to *C. caretta* species (Yntema and Mrosovsky 1980) and at 33ºC to *Dermochelys coriacea* (Binckley et al. 1998). However, extreme temperatures occur in natural nests. Low frequency of the extreme incubation temperatures is not lethal (Valenzuela 2001). The mortality is high only when the thermal variance is high above the optimal temperature range (OTR) (Neuwals and Valenzuela 2011). Natural nests that exceed 35ºC can show high hatching success (Hewavisenthi and Parmenter 2002; Read et al. 2013). *Natator depressus* has lethal limit to embryo in temperatures above 37ºC in the end of incubation and some hatching sea turtles survive temperatures exceeding 40ºC (Drake and Spotila 2002).

The incubation period verified in this study is similar to the Solimões River in Amazon, where the hatchling occurred from 56 to 73 days (Fachín-Teran and von Mülhen

2003). In Javaés River, the incubation time ranged from 67 to 86 days (Malvasio et al. 2002), while in Colombian Amazon it was from 67 to 82 days. High mean nest temperatures can reduce the incubation period (Du et al. 2009). Incubation duration may also be affect by the mineralogical composition of the sediment and grain size (Souza and Vogt 1994; Milton et al. 1997; Ferreira-Júnior and Castro 2006). In general, the incubation period is lower in sand beaches (Fachín-Terán 1993; Thorbjarnarson et al. 1993; Soini 1997) and higher when the nests are deposited in bankss and borders of rivers and lakes, where the vegetation quickly covers them (Fachín-Terán 1993; Soini and Coppula 1995). Besides the physical characteristics of the nests and the soil where they are laid, the incubation temperatures result from the climate in each year (Vogt and Bull 1982; Vogt and Bull 1984; Schwarzkopf and Brooks 1987). In Amazonas, the nesting activity is related to regional hydrologic cycle. When the water levels of the rivers begin to lower, turtles migrate to nesting areas (Nascimento 2002; Haller and Rodrigues 2006).

The embryo development depends on the accumulated effect of the nest temperature, but it is also influenced by the thermal variance (Georges et al. 2005). The dependency of embryo growth on nest temperatures has been modeled at constant temperature experiments (Bull 1985; Mrosovsky and Provancha 1992; Souza and Vogt 1994). However, the relationship between fluctuating temperatures and sex determination in nature remains little known (Georges 1989; Georges et al. 1994; Valenzuela et al. 1997). Few studies take into account non-constant temperatures, using linear degree-hour model (Georges et al. 2005), empirical curvilinear model (Georges et al. 2005; Delmas et al. 2008), biophysical model (Georges et al. 2005; Girondot et al. 2010), and polynomial model (Georges et al. 2005). We used a sigmoidal model of embryo growth, because morphological characters usually follow this shape (Girondot and Kaska 2014). This model fitted well in our natural incubation data. In the current study, the embryo growth was better described by the Schoolfield et al. (1981)

model using four parameters. The embryonic development increases at higher temperatures and above 37ºC, it is suggested that embryo growth is injured. Embryo development also was faster at higher mean temperatures for the congeneric species *P. expansa* (Valenzuela 2001).

The thermosensitive period in TSD species is determined by the knowledge of the dependency of embryo growth on thermal regimes (Mrosovsky and Pieau 1991). TSP occurs at the middle third of embryo development and can be measured as the progression of embryonic stages (Yntema 1968). However, due to diel and seasonal shifts on temperature during all incubation period, the middle third of embryo development will not correspond to the middle third in time. Although the gonad growth happens at the same time as the embryo growth during TSP, the sexual differentiation is controlled by oestrogen levels through endogenous aromatase activity. In fact, the sexualization reaction norm follows the same pattern previously observed to aromatase activity (Desvages et al. 1993) and it continues to increase its performance after embryo growth attained its maximum value. This result highlights for the first time that sex determination cannot be understood only using the embryo growth reaction norm, but sexualization should be modeled separately. Neuwald and Valenzuela (2011) had already commented that the existent TSD models do not predict the sex ratio correctly because the temperature influences the embryo developmental rate and sex determination in a different way.

The temperature that both sexes were produced (pivotal temperature =31.43) is similar to the values found by Souza and Vogt (1994). Those authors registered that the pivotal temperature for *P.unifilis* is between 31ºC and 32°C. The male frequency largely decreases above the pivotal temperature in turtles (Mrosovsky and Pieau 1991; Souza and Vogt 1994; Valenzuela 2001). For, *P. expansa*, a sex ratio of 100% of males was reported at 29.5ºC (Valenzuela 2001). However, the temperature of 34.8ºCs produced around 30% of males. High temperatures may yield male offspring, since CTE values initially fall when nest temperatures exceed the maximum temperature (Neuwald and Valenzuela 2011). The TSD model built by Telemeco et al. (2013) predicts this situation under extreme conditions, when the mean temperature on the first day of TSP and slope of temperature during TSP were not adjusted. In the warmest years, Schwanz et al. (2010) verified that the sex ratio is not 100% females. At extreme temperatures behavioral or physiological plasticity may have a promising compensatory effect (Kearney et al. 2009; Huey et al. 2012).

The mean nest temperature was correlated to area, nest distance to vegetation and air temperature from data loggers. Air temperature is known to show a linear relationship with the nest temperatures (Godley et al. 2001; Mitchell et al. 2008). The daily mean nest temperatures were lower in flooded area. This site has clay soil, which retains less heat than sandy soils. In addition, nests closer to vegetation can show cooler temperatures because they are usually shaded by canopy (Vogt and Bull 1984; Weisrock and Janzen, 1999; Morjan, 2003). Lower incubation temperatures are favorable to male production (Ewert et al. 1994; Viets et al. 1994). Thus, the study areas were very different in sex ratio production, with flooding area showing 100% of male frequency and sand beach showing high female sex-bias. Populations with lower TRT values have higher probability of producing unisexual nests (Hulin et al. 2008). The differences between nesting sites according to sex ratio ensure a distinct range of thermal profiles to produce male and female hatchlings (Fuentes et al. 2010). When we use air temperature from ECMWF, however, the nest temperatures are not correlated with distance to vegetation. This characteristic can be explained because the ECMWF is a coarser data base and may not account for finer temperature variation at sampled localities.

The daily amplitude of nest temperatures is correlated with the daily mean nest temperatures and area. The sex ratio response to mean temperature is mediated by amplitude of thermal fluctuations and the females production occurs is a more complex way (Georges et al. 1994; Du et al. 2009, Les et al. 2007; Neuwald and Valenzuela, 2011). The daily amplitude of nest temperatures was higher on the sand beach, when we also had higher temperatures. It is possible to change sex ratios from 100% male to 100% female only altering the daily amplitude of temperature (Georges et al. 1994). Under limited magnitude of diel temperature, the increase of mean temperature below OTR enhances the male production and the increase of mean temperature within OTR enhances the female production (Valenzuela and Lance 2004; Neuwals and Valenzuela 2011). On the other hand, if the thermal variance is high below the OTR, the embryo development decreases, while high thermal variance within OTR accelerates embryo development. Both thermal amplitude cases have a feminizing effect, but the mortality is not affected (Neuwals and Valenzuela 2011).

The sand beach shows a high feminization pattern. Sea turtle populations have already shown highly female-biased sex ratios (Limpus 2006; Hawkes et al. 2007, Patino-Martinez et al. 2012). In addition, Telemeco et al. (2013) predicts 100% female sex ratios according to the changes in mean air temperature over the twenty-first century. The consequences of climate change can be dramatic in TSD turtle populations if the nests do not experience any temperatures where the sexual differentiation is achievable. Although hatchling female bias may be maintained in juvenile and adult turtles (Heithaus et al. 2005; Limpus 2008), primary sex ratio may not be the same as the sex ratio of adults (Wibbels et al. 1987, 1991; Delgado et al. 2010). In warming scenarios, male hatchlings may be produced in nests lower along the shorelione, in deeper nests, in smaller nests and in the periphery of nests, where the effects of metabolic heating would be smaller (Patino-Martinez et al. 2012). Sex ratio of one male to two or three females seems to be sufficient to ensure viable populations (Fuentes et al. 2009)

TSD is an adaptive trait (Charnov and Bull 1977) and may induce a transition on sex determination mechanism. The transition between TSD and genomic (GSD) over 200 m.y. appears to coincide with climate change events (Valenzuela and Adams 2011). Turtles have already supported dramatic climate changes in the past by shifting their nesting sites distribution and their migratory routes (Hamman et al. 2007; Limpus 2008). However, at this time, global warming is much more accelerated due to anthropic impacts (Johannes and Macfarlane 1991; Harris et al. 2000; Brohan et al. 2006; Moore et al. 2009). We do not know if turtles can adapt so fast to climate change. It is possible that TSD species can change the P and/or TRT value through natural selection. TRT could be potentially more adaptive (Girondot 1999), but P could evolve too slowly in relation to global warming (Freedberg and Wade 2001; Morjan 2003; Nelson et al. 2004). Shallow nesting TSD species, such as *P. unifilis*, may be more affect by climate change, since the thermal variance in the nest can be higher and expose eggs lethally (Georges et al. 1994).

In a large scale, variation in nesting characteristics in different populations seems to be the most important factor to decrease sex ratio bias (Bull et al. 1982a; Doody et al. 2006). Maternal effects such as oestrogen concentrations in eggs (Bowden et al. 2004), nesting time (Doody et al. 2006) and nest-site selection (Morjan 2003; Ewert et al. 2004) can mediate local adaptations to climate change. Nesting earlier can increase the male production. Hawkes et al. (2007) verified that turtles would have to alter the nesting period by up to a week for warming of 3ºC in a worst scenario. However, the nesting date plasticity alone has small effect on sex ratio (Schwanz and Janzen 2008). Changes on nest depth also do not compensate for climate change (Refsnider et al. 2013). The sex ratio seems to be managed better by the control of the temperatures at beginning of the TSP (Telemeco et al. 2013). Females might reduce the mean temperature on the first day of TSP nesting in wetter or more shaded areas (Foley et al. 2006; Kamel and Mrosovsky 2006). Shade cover is a significant predictor of mean daily temperature and sex ratio (Doody et al. 2006; Refsnider et al. 2013). Thus, this strategy could offer the most likely adaptive mechanism to climate change.

Turtles are largely consumed in the Amazon Region and a decline of their populations can impact traditional people that depend on these animals as a food resource (Kemenes and Pezzutti 2007; Vogt 2008; Schneider et al. 2011). Thus, management actions are very important to mitigate the predicted impacts from climate change. Modify the sand temperature by artificial shading or sprinkling cool water may also be a good strategy to maintain temperatures within the thermal tolerance and avoid the high female frequency (Naro-Maciel et al. 1999). This strategy is better than nest translocation, which can decrease survivorship and show high effect on one-sex production (Chan and Liew 1995). In addition to knowing the localities that yield a high male frequency it is also important to promote the viability of the populations (Mrosovsky et al. 1984; Booth and Astill 2001; Hawkes et al. 2007). In this context, the flooded site evaluated in this study is an important source of male production. *Podocnemis unifilis* shows multiple paternity (Fantin et al. 2008) and males may not be a limitation to reproduction. However, this species has late sexual maturity and the effects of climate on sex ratio may take some time to become apparent (Patino-Martinez et al. 2012).

Material and Methods

Study area

The study was developed in two sites of the Piagaçu-Purus Sustainable Development Reserve (PP-SDR) in Brazilian central Amazonia. The reserve covers 809.268 ha, of which 50% consist of Várzea floodplains and it is located between the Purus and Madeira rivers (fig. 1). Nests of *P. unifilis* were monitored in a sand beach located near from the Ayapuá Lake (04º26'030" S 62º17'427" W) and in a flooding area in the municipality of Beruri (4°15'28.1" S 61°55'52.9" W). The nests in the flooding area occurred in inclined clay soils, which differ largely from the sandy soil beaches of the margins of Ayapuá Lake.

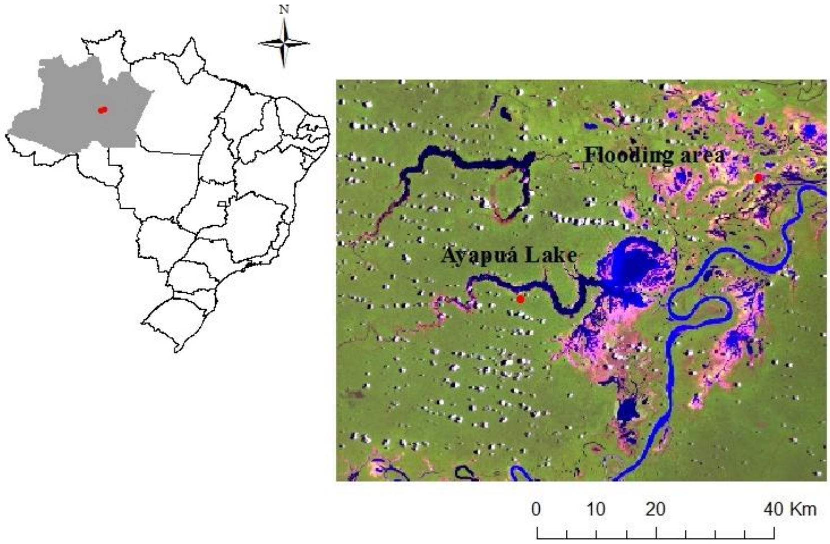

Figure 1: Map showing the seasonally flooded whitewater forest (Várzea) area and the sand beach area at Ayapuá Lake in Brazilian central Amazonia, where the nest temperatures of *Podocnemis unifilis* were recorded.

Data collection

The sand beach and Várzea areas were checked from the end of August to the beginning of November (depending on the year) in order to determine the number of nests in the sites. On the sand beach the monitoring occurred during 2010-2014 nesting seasons and at the flooding area during 2011-2014. Incubation temperatures of 12 nests of *P. unifilis*, six in each study area, were recorded using data loggers (HOBO Pendant Temp/Light Logger, temperature accuracy of ±0.47°C at 25ºC, Size 58mm x 33mm x 23mm) in the 2013 nesting season. The data loggers were inserted among the eggs (c.a. 8 cm depth) in the morning following nesting and were programmed to measure the temperature inside the nests every hour until the hatching. Hatching was considered when at least one individual hatched inside the nest. The local air temperatures were also obtained at each hour from a data logger that was placed in both Várzea and sand beach sites. Air temperatures from the studied period were also obtained from The European Centre for Medium-Range Weather Forecasts (ECMWF).

A subset of hatchlings in each nest (from six to 16 hatchlings) was euthanized with intramuscular anesthetic and sexed via histological analysis of gonads. The straight line carapace length (SCL) of the hatchlings was measured with digital caliper with 0.1 mm of accuracy.

Modelling the embryo growth reaction norm

We used the same methodology applied by Girondot and Kaska (2014). The SCL measure, like other morphological characters, follows a sigmoidal shape. The SCL growth is slow at the beginning, gets higher in some part of the incubation period and returns to be slower again before hatchling emergence (Miller 1982). Thus, sigmoidal equations should be used to describe embryo development. In this study we used a modified Gompertz model (Laird 1964):

$$\mathrm{X(t) = Kexp}\left(\ln\left(\frac{\mathrm{X(0)}}{\mathrm{K}}\right)\mathrm{exp(-r(T)t)}\right) \qquad (1)$$

The equation uses the embryo size or mass at nesting time X(0), the growth rate at the beginning of the curve r(T) and the carrying capacity (K) with lim x(t) = K. X(0) cannot be obtained from observation data. However, the gastrula disk size of *Caretta caretta* (approximately 1.7 mm) was used as X(0) (Kaska and Downie 1999) because the preovipositional development in turtles are similar (Miller 1982). K parameter can be simply a manner to decrease the growth when the embryo is close to the hatching size. The rate of decrease can be manipulated with K. Thus, the model was fitted varying K from 45 to 100 adding each time the value of 5. For each K value the model was run again using constant temperatures from 20ºC to 35°C along with the fitted parameters and the sum of the square of difference between the 21° and 26° embryonic stages were calculated. Those embryonic stages designate the limits of the middle third of the development in marine turtles, when the incubation occurs at constant temperatures (Pieau and Dorizzi 1981; Bull 1987). The K value that minimizes this statistic is *K*=82.33 and it was estimated by interpolation using a fifth order polynomial equation. The alternative parameterization proposed by those authors and used in the current study is the *rK*=2.0933, where *K*= *rK* x [Hatchling SCL]. This measure is independent of the hatchling size of the species.

The model of Schoolfield et al. (1981) with four or six parameters and an incubation temperature were used to calculate r(T). This model removed the high correlation among the parameters used on the equations of temperature-dependent models developed by Sharpe and DeMichelle (1977). r(T) specifically in this equation is the mean development rate at temperature T (time $^{-1}$) and T is the temperature in K (298 K=24.85°C). The simplificated four parameter model is similar to the Johnson and Lewin (1946) equation. For more details see Girondot and Kaska (2014).

After obtaining values of X(0), K and a time series of r (T) we evaluated the pattern of changes in the size of embryo using the Runge-Kutta method of order 4. The method approximates solutions of ordinary differential equations. The estimation of parameters was performed using maximum likelihood with an identity link and a Gaussian distribution of SCL (μ= 37.11 mm, SD=3.92 mm). The four and six parameters models were compared by Akaike information criteria (AICs), using the Akaike weight (Akaike, 1973).

Confidence interval of embryo growth reaction norm

Maximum likelihood (Hamby 1994) was used to evaluate the sensitivity of the Schoolfield et al. (1981) model. The local sensitivity analysis successively varies one parameter while the others are fixed. The parameters used have more influence on the peak of the reaction norm in relation to the area of higher and lower temperatures. Thus, the confidence interval of the reaction norm is higher around the peak. A phenocopy of the fitted model was created using local regression (LOESS method) with seven anchor points spread from 20°C to 35°C to ensure that the confidence interval reflects the constraint of the reaction norm. The Schoolfield et al. (1981) models with four or six parameters were replaced by the anchor point model that best reproduce them. A method of Markov Chain Monte Carlo (MCMC), Metropolis-Hastings algorithm (Chib and Greenberg 1995) with 5.000 iterations was used to estimate the probability distribution of the parameters. For initial values we applied those ones that maximized likelihood. The posterior distribution was compared with the initial distribution to verify if the values were chosen properly. The standard error of parameters was corrected for being calculated from a time series (Plummer *et al*. 2012).

Factors that affect the nest temperature

We obtained the daily mean nest temperatures, the daily mean local air temperatures (data loggers) and the daily mean air temperatures from ECMWF in both sand beach and Várzea areas during the studied period. Autoregressive Moving Average Models (ARMA) makes a regression of the values of each unit of measure with its past values. Thus, ARMA(p, q) was used to evaluate the relationship between the daily mean nest temperatures with its previous values. This model describes a weakly stationary stochastic process in terms of two polynomials, one for the auto-regression AR(p) and the second for the moving average MA(q). The ARMA model is defined as:

$$X_t = c + \varepsilon_t + \sum_{i=1}^{p} \varphi_i X_{t-i} + \sum_{i=1}^{q} \theta_i \varepsilon_{t-i} \tag{2}$$

where $\theta_{1,\dots}\theta_q$ are the parameters of the model; μ is the expectation of X_t; and the $\varepsilon_{t;}\ \varepsilon_{t-1,\dots}$ are the white noise terms.

A linear mixed model (lme), which contains fixed effects and random effects was run to evaluate multiple correlated measurements on each unit of interest for each air temperatures database, separately. The lme in matrix form is determined as:

$$y_i = X_i\beta + Z_i b_i + \varepsilon_i \qquad (3)$$

Where y_i is the $n_i{\times}1$ response vector for observations in the ith group; X_i is the $n_i{\times}p$ model matrix for the fixed effects for observations in group i; β is the $p{\times}1$ vector of fixed-effect coefficients; Z_i is the $n_i{\times}q$ model matrix for the random effects for observations in group i; b_i is the $q{\times}1$ vector of random-effect coefficients for group i; ε_i is the $n_i{\times}1$ vector of errors for observations in group i.

ARMA model was used in lme model as a correlation factor. Thus, the daily nest temperature was a dependent factor of the fixed effects like nest distance to vegetation; nesting distance to water; nest distance to vegetation x nesting distance to water; air temperature (from data logger or ECMWF datasets), area, area x nest distance to water; area x nest distance to vegetation and female track width. The nests corresponded to the random effects. The parameters where p value was not significant were removed and then the lme was run again until we reached correlation significance in all parameters.

We also generate the daily amplitude of nest temperatures for the studied period to sand beach and flooding sites. ARMA model was used to evaluate the relationship between the daily amplitude nest temperatures with its previous values and lme was used to analyze the correlation between amplitude , the dependent factor, and the fixed effects mean nest temperature + area + mean nest temperature X area.

Modelling sexualization reaction norm and its confidence interval

The reaction norm for sexualization model was developed to the sand beach and Várzea areas and fitted with the four-parameter parametric model built for embryo growth reaction norm. We included the information about male proportion and hatchling number from each nest. Thus, we obtained the male proportion and its confidence interval at each temperature.

We used a confidential interval for binomial probabilities, where the vector with successes for binomial variates was the male proportion and the vector with the number of correspondent observations was the hatchling number. The interval method used is the Wilson interval which is based on score-test (Agresti and Coull 1998). This interval has good properties even for a small number of trials and/or an extreme probability.

All analyzes were run in R program. The model is implemented as an R package “embryogrowth” available on Comprehensive R Archive Network (http://cran.r-project.org).

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SÍNTESE

Encontramos algumas lacunas notáveis na proteção de tartarugas de água doce na Amazônia. Áreas de Proteção Integral (IPA) sozinhas são ineficientes na conservação das áreas ambientalmente adequadas para a ocorrência de quelônios. Somente *Rhinoclemmys punctularia* e *Kinosternon scorpioides* são protegidos por IPAs. Estas espécies são tartarugas semi-aquáticas, e vivem em uma grande variedade de habitats, a maioria em pequenos corpos d’água temporárias ou perenes em florestas. *Kinosternon scorpioides* é uma espécie politípica que mostra uma ampla distribuição, do México ao norte da Argentina (Rueda-Almonacid *et al*., 2007; Vogt, 2008). A inserção de Áreas de Uso Sustentável (SUA) e territórios indígenas Áreas (ITA) foram fundamentais para a proteção da maioria das tartarugas de água doce que ocorrem na Amazônia brasileira. Nossos resultados destacam o fato de que as Unidades de Conservação na Amazônia foram estabelecidas para proteger organismos terrestres (Peres & Terborgh, 1995; Veríssimo *et al*., 2011). Quelônios podem ser sobreexplorados em áreas que não são protegidas integralmente. Com base no exposto, é necessário mudar o foco conservação da Amazônia e reestruturar as áreas protegidas, a fim de contemplar locais de captação fluviais na bacia inteira. Neste cenário, não só as tartarugas, mas todas as espécies de água doce se beneficiariam (Dudgeon *et al*., 2006). A abordagem exige uma nova distribuição das Unidades de Conservação e uso de grandes porções de terras como áreas protegidas. Assim, a maneira mais prática para desenvolver um planejamento de conservação para quelônios poderia levar em consideração às áreas de lacunas parciais próximas as áreas protegidas já existentes.

As áreas prioritárias para a conservação dos quelônios de água doce da Amazônia Brasileira são localizadas principalmente em extensivas áreas no norte da Amazônia e não abrangem áreas com alta taxa de desmatamento. Entretanto, a análise de vulnerabilidade identificou maior riqueza de tartarugas ameaças ao desmatamento no centro-nordesre da Amaônia, onde o desmatamento está avançando. *Phrynops geoffroanus, K. scorpioides* and *R. punctularia* são as espécies mais vulneráveis ao desmatamento, mostrando maior porcentagem das suas áreas adequadas perdidas por esta ameaça. Apesar da preocupação em relação a essas espécies, *K. scorpioides* and *R punctularia* são protegidas por IPAs. Essas reservas não foram designadas a proteger tartarugas e sua ocorrência nessas áreas é consequência da aleatoriedade, uma vez que se trata de espécies amplamente distribuídas na

Amazônia. As áreas protegidas atuais abrangem grande quantidade de áreas requeridas na conservação de quelônios, mas elas não estão localizadas em áreas com maior riqueza de tartarugas. Até mesmo quando consideramos somente os melhores 17% para a conservação de quelônios, a rese de reserve não foi efeiciente em proteger a riqueza do grupo. Nossos resultados tem importante significado prático para agências de conservação, pois evidencia as regiões mais importantes para investor na conservação de quelônios de água doce na Amazônia e a exposição dessas espécies ao desmatamento. Entretanto, nossos resultados devem ser interpretados com precaução, uma vez que nós não consideramos a importância social dos quelônios como recurso alimentar.

Modelos de Nicho Ecológico (ENM) evidenciam áreas ambientalmente adequadas à ocorrência de organismos e eles são frequentemente avaliados e aplicados dentro da região na qual eles foram ajustados. Entretanto, a transferência de ENMs para outras partes da extensão geográfica da espécie estudada é recomendada para uma avaliação adequada desses modelos e para o desenvolvimento de ações de manejo. A técnica representa uma nova abordagem para considerar requisitos específicos da espécie em cada parte de sua distribuição geográfica (Vanreusel *et al*., 2007). A semelhança entre as áreas adequadas para a ocorrência de *Podocnemis expansa* entre regiões de um conjunto de dados é baixa, não importa qual a seleção de preditores. No entanto, quando utilizamos variáveis brutas, os modelos prevêem áreas em grande parte fora da extensão de ocorrência conhecida para a espécie. O uso de AUC para medir a transferabilidade dos modeloso indicada bom desempenho, enquanto que para o TSS os modelos construídos em uma área da Amazônia não podem ser transferidos para outra. Os valores de AUC e TSS teve forte relação com a área adequada prevista em número de pixels e esse padrão não foi modificado quando usamos diferentes conjuntos de preditores ambientais. Nosso estudo demonstra que deve ser tomado cuidado quando ENMs são projetados para diferentes regiões geográficas, especialmente em áreas heterogêneas como a Amazônia. A avaliação dos modelos deve se concentrar na sua capacidade de capturar fatores de mudanças no requerimento da espécie e suas adaptações em cada local (Rapacciuolo *et al*., 2012). A soma das áreas adequadas previstas para as duas regiões de um mesmo conjunto de dados podem ser mais bem utilizadas para representar a distribuição das espécies.

O nosso estudo é o primeiro a mostrar que a temperatura influencia a taxa de desenvolvimento do embrião e a determinação do sexo de uma maneira diferente. Temperatura média diária do ninho foi relacionada com a distância do ninho a vegetação, temperatura do ar e da área. Variação térmica diária está relacionada com a temperatura média diária do ninho e ambas são responsáveis na determinação do sexo. A praia de areia apresenta alto padrão de feminização, mas a área de Várzea é importante na produção do sexo masculino e que parece ser crucial para a manutenção da viabilidade populacional. Além do seu valor biológico, tartarugas são amplamente consumidas na região Amazônica e o declínio de suas populações pode afetar povos tradicionais que dependem desses animais como um recurso alimentar (Vogt, 2008; Schneider *et al*., 2011). Assim, ações de manejo são muito importantes para mitigar os impactos previstos das mudanças climáticas. Modificar a temperatura da areia pelo sombreamento artificial ou regar os ninhos com água fria podem ser boas estratégias para manter as temperaturas dentro da tolerância térmica e evitar a elevada frequência do sexo feminino (Naro-Maciel *et al*., 1999). Esta estratégia é melhor do que a translocação ninho, que pode diminuir a sobrevivência dos filhotes e produzir razão sexual desproporcional (Chan & Liew, 1995). Além disso, conhecer as localidades que produzem uma elevada frequência do sexo masculino é importante para promover a viabilidade das populações (Mrosovsky *et al*, 1984; Hawkes *et al*., 2007). Neste contexto, o local inundado avaliado neste estudo é uma fonte importante de produção de machos. *Podocnemis unifilis* apresenta paternidade múltipla (Fantin *et al*., 2008) e os machos podem não ser uma limitação para a reprodução. No entanto, esta espécie tem a maturidade sexual tardia e os efeitos do clima sobre a razão sexual pode levar algum tempo para se tornar aparente (Patino-Martinez et *al*., 2012).

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