UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO

CENTRO DE CIÊNCIAS HUMANAS E NATURAIS

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Modelos de nicho, mudanças climáticas e a vulnerabilidade do clado Perissodactyla ao longo do tempo

Andressa Gatti

Vitória, ES
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Orientador: Paulo De Marco Júnior

Tese submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para a obtenção do grau de Doutor em Biologia Animal.

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5ª ATA DE DEFESA DE TESE DE DOUTORADO EM BIOLOGIA ANIMAL

Ata da sessão de defesa da 5ª Tese de Doutorado em Biologia Animal do Centro de Ciências Humanas e Naturais da Universidade Federal do Espírito Santo, da aluna ANDRESSA GATTI, candidata ao grau de Biologia Animal. Às 14:00 horas do dia 20/06/2013, Auditório IC-II, o presidente da Comissão Examinadora, Prof. Paulo De Marco Júnior, iniciou a sessão apresentando a Comissão constituída, além dele próprio, que é o Orientador, pelos professores EMÍLIA PATRÍCIA MEDICI (Examinador Externo) - IPE, NATÁLIA MUNDIM TÔRRES (Examinador Externo) - UFU, Sérgio Lucena Mendes (Examinador Interno) - UFES, Albert David Ditchfield (Examinador Interno) - UFES, Paulo De Marco Júnior (Orientador) - UFES. A seguir, o presidente passou a palavra à candidata, que, em 50 minutos, apresentou a sua tese, intitulada "Modelos de nicho, mudanças climáticas e a vulnerabilidade do clado Perissodactyla ao longo do tempo.". Finda a apresentação, o presidente passou a palavra aos membros da Comissão para procederem à arguição da candidata. Finda a arguição, o presidente convidou a Comissão para dirigir-se a uma sala reservada, para deliberação. Após a deliberação, a Comissão retornou, e o presidente informou aos presentes que a tese fora Aprovada. Logo após, o presidente declarou encerrada a sessão, e eu, Ariel Sessa, lavrei a presente Ata, que é assinada pelos membros da Comissão Examinadora, Vitória, 20/06/2013.

EMÍLIA PATRÍCIA MEDICI

Natália Mundim Tôrres.
NATÁLIA MUNDIM TÔRRES

Sérgio Lucena Mendes

Albert David Ditchfield.
Albert David Ditchfield

Paulo De Marco Júnior
Paulo De Marco Júnior

“*Não há parte da história natural mais interessante ou instrutiva do que o estudo da distribuição geográfica dos animais.*” Alfred Russell Wallace (1823-1913)

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Aprendi logo cedo na minha vida profissional que um trabalho não se faz sozinho, uma ideia não se sustenta somente com o seu "criador" em longo prazo, que ninguém é autossuficiente e que as parcerias que criamos precisam ser mantidas com respeito e cuidado. E antes de tudo, antes do trabalho, está o respeito pelas pessoas, pelos amigos. Logo, estes agradecimentos são feitos de coração para os meus amigos.

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SUMÁRIO

RESUMO

A Terra sofreu várias mudanças climáticas no passado e as mais recentes ocorreram durante os ciclos glacial-interglacial no Quaternário resultando na perda de habitat, em expansões e reduções do nível dos oceanos, produzindo mudanças nos ecossistemas e alterações significativas no habitat disponível para os herbívoros terrestres, principalmente. Muitas extinções dessa época são associadas às mudanças climáticas "naturais", no entanto, as predições indicam que as alterações climáticas, ocasionadas pelas atividades antrópicas, serão uma das principais ameaças à biodiversidade no futuro. Em resposta às flutuações climáticas, a distribuição de algumas espécies poderá sofrer mudanças ou, ainda, as espécies poderão se deslocar para novas áreas adequadas. Contudo, isso dependerá de sua capacidade em dispersar e de características ambientais. Assim, é fundamental identificar quais são as características que tornariam as espécies mais vulneráveis a essas mudanças. Nesse contexto, os Perissodactyla mostraram-se um modelo adequado para testarmos nossas hipóteses, pois compreendem um grupo de grandes mamíferos herbívoros, extremamente ameaçados, que passaram por inúmeras mudanças ambientais desde a sua origem. Nosso principal objetivo foi avaliar a influência das alterações climáticas sobre os mamíferos do clado Perissodactyla, em uma escala temporal ampla, abrangendo desde o Quaternário (a partir do Último Interglacial) até o futuro (ano 2080). Utilizamos duas abordagens: i) a relação entre as características do nicho e a vulnerabilidade do clado no futuro; e ii) a influência do clima na distribuição de áreas ambientalmente adequadas, de *Tapirus terrestris*, no passado e no futuro. Para testar nossas predições nos baseamos na Modelagem de Nicho Ecológico, que tem sido uma das abordagens mais empregadas e relevantes para predizer as mudanças na distribuição das espécies. Nós usamos diferentes conjuntos de modelos climáticos (paleoclimáticos, atuais e futuro) e procedimentos de modelagem. Os resultados indicam que os Perissodactyla apresentaram características de nicho distintas, e que espécies consideradas generalistas também podem sofrer negativamente com os efeitos das mudanças climáticas. Além disso, grande parte das respostas das espécies foi idiossincrática. Outro ponto importante são as barreiras que podem limitar a dispersão dessas espécies para novas áreas ambientalmente adequadas, pois concluímos que várias espécies do clado ocorrem em áreas altamente ameaçadas pelas mudanças climáticas. Dentre os Perissodactyla, *T. terrestris*, se mostrou a espécie mais climaticamente generalista. Contudo, a avaliação da resposta da espécie em relação às diferentes mudanças climáticas, sugere que as condições mais críticas, que prevaleceram durante o Último Máximo Glacial, reduziram a extensão geográfica das áreas climaticamente adequadas para a anta, com uma subsequente expansão. Se o clima não foi um problema muito sério na história evolutiva da espécie, os desafios para a sua conservação na atualidade e no futuro podem ser bem maiores. Mesmo que a extensão da distribuição geográfica da anta em si não se altere como resposta às alterações climáticas, predizer as mudanças da adequabilidade ambiental ao longo dessa distribuição nos auxiliará na priorização de áreas para a conservação da espécie. Dessa forma, o desaparecimento das condições climáticas e a emergência de novas áreas ambientalmente adequadas devem ser considerados em planos de manejo futuros, especialmente na criação de novas unidades de conservação tanto para *T. terrestris* quanto para os demais Perissodactyla.

Palavras-chave: Mudanças climáticas, Mamíferos, Perissodactyla, Paleoclima, Modelagem de distribuição de espécies, Unidades de conservação.

ABSTRACT

The Earth has undergone several climate changes in the past, and the latest occurred during the glacial-interglacial cycles in the Quaternary, resulting in habitat loss, during ocean expansions and reductions, and several ecosystem changes. Numerous extinctions of that time are associated with "natural” climate change. However, the predictions indicated that climate change caused by human activities is now the major threat to biodiversity. In response to climatic fluctuations, the distribution of some species may change, or species can move to new suitable areas. But this will depend on their ability to disperse and environmental characteristics in an anthropic ecosystem. Thus, it is essential to identify the most important characteristics that make species more vulnerable to those changes. In this context, the clade Perissodactyla was a good model to test our hypotheses, because they are a group of large herbivorous mammals extremely threatened, that went through numerous environmental changes since its origin. I evaluated the influence of climate change on the Perissodactyla clade, on a wide time scale, ranging from the Quaternary (from the Last Interglacial) to the future (2080). I used two approaches: i) the relationship between the characteristics of the niche and the vulnerability of the clade in the future, and ii) the influence of climate on the distribution of environmentally suitable areas of *Tapirus terrestris*, in the past and future. To test the predictions, I used an Ecological Niche Modeling, which has been one of the most relevant approaches to predict changes in the species distributions. I used different sets of climate models (i.e. paleoclimate, present and future climates) and modeling procedures. The results indicated that the Perissodactyla showed distinct niche characteristics. Generalist species may also suffer negative effects of climate change. Furthermore, most of the species had idiosyncratic responses. Another important point is that barriers may have limited the dispersion of these species to new areas environmentally appropriate because several of these Perisodactyla occurred in areas highly threatened by climate change. The evaluation of the response of *T. terrestris* (the species most climatically generalist), to different climate scenarios, suggests that the most critical condition that prevailed during the UMG reduced the geographical extent of areas climatically suitable, with subsequent expansion. If the weather was not a very serious problem in the evolutionary history of the lowland tapir, the challenge to conserve this taxon today and in the future may be much higher. Even if the total size range itself does not change as a response to climate variations, predicting the suitability of the environmental changes, along the distribution of tapirs, can help us to prioritize areas for their conservation. Thus, the disappearance of the climatic conditions and the emergence of new environmentally suitable areas should be considered in future management plans, especially concerning to creation of new protected areas for both *T. terrestris* as for other Perissodactyla species.

Keywords: Climate change, Mammals, Perissodactyla, Paleoclimate, species distribution modeling, Conservation Units

1. INTRODUÇÃO GERAL E FUNDAMENTAÇÃO TEÓRICA

1.1. História evolutiva dos Perissodactyla

A Era Cenozóica, há 66 milhões de anos, é comumente conhecida como a "Era dos Mamíferos", mesmo abrangendo apenas o terço final da fase de maior diversificação na evolução dos mamíferos (Archibald & Deutschman, 2001). O máximo de diversidade dos mamíferos placentários na Terra foi no início do Eoceno, durante o ótimo climático (55–52 Ma; Zachos *et al.*, 2001). Esse foi considerado um período de grande produtividade primária, com altas temperaturas, favorecendo o surgimento de uma grande área habitável. A vegetação nas altas latitudes foi similar às florestas tropicais modernas no que diz respeito à diversidade de plantas (Collinson *et al*., 1981; Wolfe, 1985), o que provavelmente favoreceu o desenvolvimento de mamíferos florestais e sua diversificação.

Foi neste cenário que o clado Perissodactyla -- constituído por mamíferos ungulados que mantêm o apoio corporal sobre número ímpar de dedos -- tornou-se um grupo importante de herbívoros, especialmente folívoros, de médio e grande porte, sendo considerado o grupo mais abundante no início do Terciário. Existem opiniões divergentes sobre as relações entre os Perissodactyla, resultantes dos paralelismos que ocorreram no início de sua radiação. Uma hipótese é que a origem do clado tenha sido a partir dos Condylarthra (Phenacodontidae) baseada nas similaridades da estrutura bilofodonte dos dentes, no final do Paleoceno (Radinsky, 1969). Já McKenna *et al*. (1989) propõem que *Radinskya*, um Condylarthra – Phenacolophidae, tenha sido o ancestral do clado. Existe também discordância sobre qual grupo dentre os Perissodactyla é o mais primitivo (tapiróides, brontotérios ou equóideos) (Radinsky, 1963).

Neste momento inicial, três ou talvez quatro das cinco superfamílias de Perissodactyla teriam surgido. No registro fóssil, existem evidências de espécimes representativos de cinco superfamílias (Tapiroidea, Rhinocerotoidea, Chalicotheroidea, Equoidea and Brontotheroidea), incluindo 14 diferentes famílias (Holbrook, 1999).

Os primeiros Perissodactyla originaram-se na América do Norte e Europa (Prothero & Schoch, 1989). Em adição a estes, uma radiação adaptativa inicial ocorreu após o surgimento da ordem com novas formas de ungulados representadas, por exemplo, pelos brontotérios (Titanotheriomorpha), mamíferos semelhantes a rinocerontes (Kemp, 2005). Os Equoidea também diversificaram neste período, particularmente na Europa (Radinsky, 1969), onde *Palaeotherium*, um ungulado similar a uma anta, foi bastante comum (Kemp, 2005). A terceira linhagem dos Perissodactyla diversificou-se na fase mais quente (15 milhões de anos antes do presente), coincidindo com o segundo pico de diversidade dos mamíferos no Cenozóico. Novamente, a alta produtividade vegetal criou oportunidades para uma diversificação de mamíferos herbívoros e seus predadores (Janis, 1993). Os Chalicoteriidae (*Chalicotherium*) foram os maiores e mais especializados do Oligoceno até o Pleistoceno, embora estivessem presentes no Eoceno, a principal radiação ocorreu no Mioceno.

A linhagem dos Tapiroidea e Rhinocerotoidae divergiu do ancestral comum há 50 milhões de anos (Colbert & Schoch, 1998). Os Tapiroidea foram amplamente diversos durante o Eoceno, quando houve uma abundância de gêneros na América do Norte, Europa e Ásia, e algumas dessas formas originais (e.g., *Heptodon* da família Helaletidae), mostraram muitas semelhanças com as antas atuais (gênero *Tapirus*). Os Rhinocerotoidae, aparentemente derivados de radiações secundárias dos Tapiroidea (Radinsky, 1969), foram muito mais diversos desde o Eoceno até o Mioceno do que são atualmente, incluindo desde formas pequenas semelhantes a uma anta até o gigante *Indricotherium*. Foi apenas durante o Oligoceno e Mioceno que ocorreu o surgimento dos rinocerontes verdadeiros (família Rhinocerotidae), os quais se tornaram abundantes em todos os continentes do Norte e na África (Kemp, 2005). Os Rhinocerotidae foram um dos grupos de mamíferos de maior sucesso na América do Norte. Após a extinção dos titanotérios no Eoceno Superior, os rinocerontes foram os maiores mamíferos até o aparecimento dos mastodontes no Mioceno Médio. Entretanto, no final do Mioceno os rinocerontes foram extintos da América do Norte, muito provavelmente devido à perda de habitats florestais subtropicais durante o resfriamento e aridificação.

Diferentes hipóteses foram propostas para justificar o sucesso dos Perissodactyla durante milhões de anos. Uma das mais difundidas está relacionada à sua fisiologia. O sistema de fermentação alimentar realizado no ceco (*hindgut*) possibilita o consumo de itens alimentares altamente fibrosos, incluindo diferentes espécies de plantas encontradas durante o Eoceno (Janis, 1989). Mais da metade dos ungulados, no início do terciário, foram fermentadores de ceco, uma condição plesiomórfica para estes mamíferos (Janis, 1989). No entanto, os padrões de diversidade dos Perissodactyla mostraram uma mudança no final do Mioceno em paralelo a uma mudança similar na diversidade dos Artiodactyla. Na América do Norte, por exemplo, a diversidade de ungulados foi alta e incluiu além dos Perissodactyla, os mamíferos da ordem Artiodactyla.

Desde o final do Eoceno, a diversidade genérica dos Perissodactyla declinou enquanto que a dos Artiodactyla aumentou (Janis, 1989, 1993; Cifelli, 1981). Chalicotérios e tapirídeos continuaram a aparecer como elementos raros da fauna durante o Ótimo Climático do Mioceno (Blois & Hadly, 2009), no entanto, há o registro do surgimento do gênero *Tapirus* durante este período (25–5 maa). Existem alguns debates e hipóteses propostas sobre o declínio dos

Perissodactyla em relação à diversificação dos Artiodactyla (Cifelli, 1981; Mitchell & Lust, 2008; Janis, 1989, 2009). Janis (1989) argumenta que a interação competitiva não foi um fator impactante, mas sim, as mudanças climáticas, pois o clado Artiodactyla continuou a crescer a partir do Oligoceno e desde o Mioceno Médio o número dos perissodáctilos foi constante.

A transição Eoceno/Oligoceno marca o início de profundas diferenças sazonais na disponibilidade e abundância de vegetação. Janis (1976) sugeriu que em resposta a essas diferenças, os artiodáctilos desenvolveram um trato digestivo ruminante e diferentes estratégias de seleção de habitat, além da melhora na locomoção, facilitando a adaptação a áreas abertas. Mitchell & Lust (2008) chamam a atenção para a habilidade termorregulatória dessas espécies e consequente vantagem competitiva sobre os Perissodactyla, durante o clima altamente sazonal pós-Eoceno. No entanto, Cifelli (1981) não evidencia competição nem substituição entre as ordens, ao contrário, argumenta que as ordens evoluíram independentemente. De qualquer forma, analisar o evento da radiação dos Artiodactyla é extremamente importante para entendermos quais fatores (biótico, abiótico ou a combinação entre eles) podem ter contribuído para moldar a história evolutiva dos Perissodactyla.

Alguns eventos geológicos e climáticos também contribuíram na formação da história evolutiva dos Perissodactyla e, em diferentes períodos, houve migrações entre os continentes. Imigrações em combinação com mudanças climáticas podem ter um grande efeito sobre estrutura e composição de comunidades. Há 20-16.5 Ma (final do Mioceno Inferior), um decréscimo no nível do mar (Keller & Barron, 1983) permitiu o intercâmbio extensivo entre África e Eurásia, e também entre Eurásia e América do Norte. Conexões intermitentes entre América do Norte e Ásia, através do Estreito de Bering, favoreceram o aparecimento das antas na Eurásia (Medici, 2011).

A história da fauna na América do Sul, a partir do Plioceno, está intimamente ligada à emergência do Istmo do Panamá, que ocorreu entre 7.0-2.5 milhões de anos, possibilitando o fluxo de fauna entre América do Norte e América do Sul, evento este donominado Grande Intercâmbio da Biota Americana (Marshall, 1988). Este evento proporcionou a imigração das antas para a América do Sul, originando no continente pelo menos cinco espécies já extintas e as espécies viventes: *Tapirus pinchaque* e *T. terrestris* (Marshall, 1988; Holanda *et al*., 2011; Medici, 2011). Antes deste intercâmbio, a fauna da América do Sul era diferente de qualquer outra e foi representada por ungulados nativos, tais como os Meridiungulata (por exemplo, Litopterna, *Toxodonte*), que durante o intercâmbio permaneceram. No entanto, estes sobreviventes foram extintos no final do Pleistoceno.

Assim, os Perissodactyla atuais são remanescentes de uma ampla radiação no Terciário, seguida de uma redução na sua diversidade, permanecendo apenas quatro famílias até o Quaternário. Atualmente apenas três famílias são representadas em 16 espécies distribuídas em seis gêneros. Tradicionalmente, os Perissodactyla têm sido divididos em duas subordens: i) Hippomorpha, que é representada pela família Equidae, e ii) Ceratomorpha, compreendendo as famílias modernas Tapiridae e Rhinocerotidae (Radinsky, 1966; Prothero & Schoch, 1989). Diferentes trabalhos examinaram as relações filogenéticas do clado Perissodactyla (Norman & Ashley, 2000; Price & Bininda, 2009; Willerslev *et al*., 2009; Steiner & Ryder, 2011) e, de maneira geral, os resultados suportam a monofilia das subordens Ceratomorpha e Hippomorpha, e as famílias Rhinocerotidae, Tapiridae e Equidae. Recentemente, dois trabalhos sobre a filogeografia das espécies viventes de *Tapirus* foram publicados (Thoisy *et al*., 2010; Ruíz-Garcia, 2012). Thoisy *et al*. (2010) sugerem que os eventos climáticos no final do Pleistoceno podem ter moldado a história de *T. terrestris*, além de indicar a Amazônia Ocidental como o ponto de dispersão da espécie para as demais regiões da América do Sul.

1.1.1. A história dos Tapiridae: uma abordagem mais detalhada sobre *Tapirus terrestris*

Os registros mais antigos da família Tapiridae são datados do Oligoceno da Europa (33-37 Maa) e seus fósseis têm sido frequentemente encontrados na Europa, América do Norte e Ásia (Hulbert, 1995). A evolução da família envolveu, principalmente, um refinamento da probóscide, a molarização dos pré-molares e o aumento geral no tamanho corporal. A família incluiu os gêneros *Protapirus* (1º tapirídeo verdadeiro), *Tapirus*, *Miotapirus* e *Tapiravus* (América do Norte), *Megatapirus* e *Plesiotapirus* (Ásia), e *Tapiriscus*, *Eotapirus* e *Palaeotapirus* (Europa) (Colbert, 2007). Cerca de 20 diferentes espécies de *Tapirus* são reconhecidas paras regiões da América do Norte, Europa e Ásia. O registro mais antigo do gênero *Tapirus* na América do Sul data do Pleistoceno Inferior-Médio na Argentina (Tonni, 1992; Cione & Tonni, 2005; Nabel *et al*., 2000). Os três gêneros com origem na América do Norte compartilham a condição derivada de Tapiridae que envolve a redução relativa no comprimento dos ossos frontais, a migração posterior dos ossos nasais e o aumento na altura vertical pós-craniana (Medici, 2011).

As antas são consideradas “fósseis vivos” (Janis, 1984; Medici, 2011), pois dentre os Perissodactyla, foram as espécies que mais retiveram características similares dos ungulados primitivos (por exemplo, *Hyracotherium*), especialmente do esqueleto pós-cranial, como os membros anteriores tetradáctilos e os posteriores tridáctilos. A dentição de *Tapirus* também é considerada plesiomórfica (padrão bilofodonte estabelecido no início da história do grupo). Além disso, as antas também retiveram vários aspectos comportamentais, como o hábito solitário e a geração de um único filhote por gestação (são raros os casos de gêmeos), o que é uma condição derivada nos ungulados (Janis, 1984).

A família Tapiridae (Gray 1821) é composta, atualmente, por um único gênero, *Tapirus* (Brünnich 1772), com cinco espécies viventes: *T. bairdii*, *T. indicus*, *T. pinchaque, T. kabomani* e *T. terrestris*. *Tapirus kabomani* foi descrita recentemente por Cozzuol *et al.* (2013). As relações monofiléticas entre as antas da América do Sul, *T. pinchaque* e *T. terrestris* (Thoisy *et al*., 2010; Ruíz-Garcia, 2012) são consistentes com a hipótese de que elas se originaram de um único evento de dispersão de seu ancestral pelo Istmo do Panamá. *Tapirus terrestris*, a Anta Brasileira ou Sul-Americana, é o tapirídeo vivente com a mais ampla distribuição georgráfica ocorrendo nas zonas tropicais da América do Sul, em 11 países: Argentina, Bolívia, Brasil, Colômbia, Equador, Guiana, Guiana Francesa, Paraguai, Peru, Suriname e Venezuela (Medici *et al*., 2007; IUCN, 2012), onde a espécie habita uma multitude de diferentes ambientes. Quatro subespécies de *T. terrestris* são reconhecidas: *terrestris*, *colombianus*, *aenigmaticus* e *spegazzinii* (para mais detalhes sobre a distribuição das subespécies veja Medici, 2011).

Tapirus terrestris é um dos últimos remanescentes de dispersores a longa-distância de espécies vegetais com grandes sementes, que já foram uma vez dispersadas por mamíferos no Pleistoceno, especialmente nos Neotrópicos (Janzen & Martin, 1982; Hansen & Galetti, 2009). É provável que as antas tenham vivido em áreas mesotermais úmidas, onde a diversidade e a quantidade de folhagem eram grandes. O desenvolvimento da probóscide e de estratégias de forrageamento seletivas podem ter permitido que os tapirídeos do Oligoceno e Mioceno maximizassem a utilização de recursos em refúgios mesotermais restritos – áreas ripárias em ambientes mais secos (Rose, 2006).

Desde a sua origem, a distribuição das antas vem mudando ao longo do tempo eessas mudanças foram provavelmente causadas por migrações, mudanças continentais e climáticas, e consequentemente a distribuição das florestas (García *et al*., 2012). De fato, os habitats ocupados pelas antas na atualidade incluem, sobretudo, florestas tropicais associadas a corpos de água e ambientes ripários (Medici, 2010). No entanto, é possível que *T. terrestris* e as demais espécies do clado Perissodactyla não consigam lidar com as futuras mudanças climáticas uma vez que grande parte das espécies encontra-se extremamente ameaçada de extinção devido às pressões antrópicas.

1.2. Mudanças climáticas: passado e futuro

A Terra tem passado por diferentes cenários climáticos. No passado, as principais alterações de clima foram associadas com a formação periódica de supercontinentes, episódios glaciais e vulcanismo. Durante os últimos 100 milhões de anos houve inicialmente uma ligeira tendência de resfriamento, que foi gradualmente revertida há cerca de 80 milhões de anos. Em seguida, houve um breve e intenso período de aquecimento, há aproximadamente 55 milhões de anos atrás. Este período corresponde à transição do Paleoceno-Eoceno, ou seja, coincide com o início da Era Cenozóica, no período Terciário, o qual foi marcado por vários eventos climáticos críticos (Zachos *et al*., 2001). A paleogeografia do início do Terciário difere consideravelmente dos dias atuais (Janis, 1993) e o aquecimento no início do Paleoceno (66–57 Maa) foi seguido por clima mais tropical (Paleoceno Médio) (Janis, 1993). Nesta fase, as florestas eram aparentemente mais densas do que no Cretáceo, possivelmente porque a precipitação era maior e menos sazonal (Krause & Maas, 1990).

O rápido aquecimento no final do Paleoceno foi seguido por um ótimo climático no início do Eoceno (55–52 Ma; veja Zachos *et al*., 2001). Segundo Janis (1993), os eventos tectônicos podem ter influenciado essa tendência, resultando em atividades vulcânicas e consequente aumento na atividade hidrotermal dos oceanos, o que pode ter aumentado os níveis de CO_2 (Rea *et al*., 1990; Gingerich, 2006). Esse aquecimento possivelmente favoreceu a expansão das florestas tropicais em maiores latitudes (Wolfe, 1985; Wing & Tiffney, 1987). Em seguida a essa fase, houve um episódio de frio extremo nas maiores latitudes, com o surgimento de uma vegetação decidual há 45 Ma (Janis, 2008), preparando um cenário de clima mais temperado no Oligoceno, com ambientes mais áridos em médias latitudes. As temperaturas começaram a aumentar no Oligoceno, em torno de 25 Ma, e depois de uma breve queda alcançaram um novo pico, chegando ao ótimo climático há aproximadamente 15 Ma, durante o Mioceno Médio (Zachos *et al.*, 2001), com períodos mais quentes e mais secos. Diferentes trabalhos indicaram uma tendência de decréscimo de CO_2 durante a transição Oligoceno/Mioceno (Pagani *et al*., 2005; Plancq *et al*., 2012; Grein *et al*., 2013), quando ocorreu um período de glaciação (Miller *et al*., 1991).

No final do Mioceno (~ 6 Ma) as savanas da América do Norte foram substituídas por pradarias (Retallack, 2001). A expansão da vegetação C4 (adaptadas a maior luminosidade e climas mais quentes) foi registrada durante o Mioceno, entre 10 e 6 Ma (Cerling *et al*., 1997; Uno *et al*., 2011), determinada principalmente pela mudança na dieta de equídeos e rinocerontes fósseis (identificada a partir de análise de dentição). Porém, segundo Feakins *et al*. (2013), antes dessa expansão das plantas C4 existiam extensos e produtivos campos durante o Mioceno Médio dominados por vegetação C3, no norte da África. Esse período exibiu um declínio mais estável das temperaturas e uma continuação das estiagens (Wolfe, 1978).

No entanto, o início do Plioceno foi um período de aquecimento global e transgressões marinhas (Ravelo *et al.*, 2004) com uma transição para o final (cerca de 2.5 Maa), representada por glaciação no Ártico e um resfriamento global significante. Tipos modernos de desertos e semi-desertos foram comuns nessa época, assim como pradarias, estepes e pampas (Wolfe, 1985). Ao mesmo tempo, surge o Istmo do Panamá, conectando as Américas do Norte e do Sul e interrompendo a circulação circum-equatorial (Janis, 2008). Comparativamente ao período atual, o período quente do Plioceno foi caracterizado por temperaturas mais altas em pelo menos 3ºC(Raymo *et al.*, 1996; Ravelo & Andreasen, 2000). Um evento importante que ocorreu durante o Mioceno foi a elevação dos Andes, sendo crucial para a formação da biota antes do Quaternário (Hoorn *et al.*, 2010). Além disso, as oscilações do nível do mar nos últimos 4 Ma foram associadas com os ciclos de Milankovitch, desencadeando significativas mudanças na paisagem da América do Sul (Dynesius & Jansson, 2000; Hoorn & Wesselingh, 2010).

Mais precisamente, a dinâmica do clima foi particularmente dramática durante o Quaternário, que abrangeu os últimos 2.0-1.8 Ma. Composto pelas épocas do Pleistoceno e Holoceno-Atual, este período foi caracterizado por pelo menos 20 avanços e retrações glaciais. Condições glaciais dominaram esse período, com intervalos quentes de efeito estufa (~100 mil anos) e com apenas alguns milhares de anos cada (Ruddiman, 2001). Esse período foi caracterizado por muita variabilidade climática, incluindo súbitos desvios às condições mais quentes ou mais frias, que ocorreram em menos de 1000 anos, por exemplo, o evento Younger Dryas (12.9–11.6 mil anos atrás) que marcou a transição glacial-interglacial mais recente (Rodbell, 2000). Após estas oscilações, o clima tornou-se muito estável e tem persistido como tal durante os últimos 11.000 anos. Além disso, durante o Quaternário os períodos relativamente secos (glaciais) foram mais frios também nos trópicos.

De forma geral, o clima tornou-se progressivamente mais frio e mais seco desde o último período interglacial (~125 mil anos atrás) até o Último Máximo Glacial (UGM; ~21 mil anos atrás) e, então, tornou-se mais quente e úmido no Holoceno Médio (~ 6 mil anos atrás) (Nogués-Bravo *et al*., 2008). No Pleistoceno, durante o UGM (~21.000 anos atrás), o clima alcançou o máximo do resfriamento em diferentes locais do mundo, com condições mais secas (Ledru *et al*., 1998). Segundo Mayle *et al*. (2004), as florestas tropicais expandiram mais do que uma vez no final do Holoceno devido ao aumento da precipitação. Além disso, estudos mostram que espécies de florestas tropicais persistiram durante o UGM, por exemplo, nas terras baixas da região Amazônica (Colinvaux *et al*., 1996).

Todas essas evidências suportam fortemente que as mudanças climáticas que ocorreram no passado foram eventos chave para entender a mudança da vegetação tanto em escala espacial quanto temporal. Mas será que o aumento na velocidade das mudanças climáticas preditas para o futuro permitirá o entendimento de tais processos? Atualmente, uma das principais causas das rápidas mudanças climáticas pode ser a liberação de gases de efeito estufa, tais como CO_2 e metano. No passado, tais liberações podem ter ocorrido naturalmente a partir das erupções vulcânicas, por exemplo. Entretanto, as emissões atuais têm efeitos massivos sobre o ciclo global do carbono e direcionam as principais mudanças no clima.

A estimativa é de que a concentração de CO_2 na atmosfera tenha aumentado mais do que 30% no século passado, devido principalmente à queima de combustíveis fósseis. As últimas previsões do Painel Intergovernamental sobre Mudanças Climáticas (em inglês, *Intergovernmental Panel on Climate Change – IPCC*) indicam ainda que a média da temperatura do ar na superfície global vai continuar a aumentar ao longo do século 21 (IPCC, 2007). As projeções feitas para o fim do século (2090–2099) apontam para um aumento da temperatura média global da ordem de 1.8 a 4ºC (IPCC, 2007). Na região Neotropical, as previsões apontam para aquecimento de 0.4°C a 1.8°C até 2020, e de 1°C a 7.5°C até 2080. Os valores de aquecimento mais elevados são projetados para a região tropical da América do Sul, como a região Amazônica (Magrin *et al.*, 2007). Ao mesmo tempo, temperaturas extremas e chuvas também se tornarão mais comum, enquanto que a cobertura de neve e gelo do mar vai diminuir contribuindo para a elevação do nível do mar (IPCC, 2007).

Diante desse cenário, um dos maiores desafios da atualidade é entender quais novos riscos as mudanças climáticas trarão para a conservação de espécies a nível global. É provável que muitas dessas mudanças não façam parte das experiências prévias vividas por cada organismo no passado, afetando assim a habilidade das espécies em responder a essas mudanças. Dessa forma, é crucial identificar como as espécies, e a dinâmica e composição dos ecossistemas locais podem ser afetados pelas mudanças climáticas e como eles poderão potencialmente responder a essas perturbações.

1.3. Vulnerabilidade às mudanças climáticas globais

O aumento nas emissões de gases de efeito estufa, como o CO2, implicará em uma mudança climática significativa nas próximas décadas. Desta forma, o potencial para a perda de biodiversidade e rompimento de serviços ecológicos deverá ser seriamente avaliado no processo de tomada de decisões relativas à conservação. No passado geológico, muitas extinções de espécies podem ter sido associadas a mudanças climáticas “naturais” resultando em perda de habitat e mudanças nos ecossistemas (McKinney, 1997). No entanto, as mudanças climáticas observadas na atualidade são reconhecidas como uma das principais ameaças à biodiversidade global e vem causando extinções locais em diferentes partes do mundo. Espera-se que essas alterações tenham um profundo efeito tanto sobre indivíduos quanto em populações animais (Thomas *et al*., 2004; Schloss *et al*., 2012) e vegetais (Thuiller *et al*., 2006; Franklin *et al*., 2013). A multiplicidade de resultados observados nas projeções realizadas para diferentes taxa e tipos de história de vida enfatizam as respostas do passado, que provavelmente refletem no presente e no futuro (Dawson, 2011), indicando que nem todas as espécies responderão da mesma forma, mesmo em níveis similares de alterações climáticas (Arribas *et al*., 2012).

Lorenzen *et al*. (2011) demonstraram que o clima tem sido o principal direcionador de mudanças populacionais nos últimos 50 mil anos. No entanto, cada espécie responde diferentemente aos efeitos das alterações climáticas. Por exemplo, o clima por si só explicou a extinção do rinoceronte lanudo, *Coelodonta antiquitatis*, comum na Europa e norte da Ásia. Em geral, a proporção de espécies extintas foi maior nos continentes que estiveram mais expostos a mudanças climáticas mais drásticas, reservando ao clima o papel principal na perda dessas espécies. Além disso, espécies expostas a intensas alterações climáticas em combinação com suscetibilidade intrínseca a essas alterações enfrentarão um maior risco de extinção (Foden *et al*., 2008).

Em resposta às flutuações climáticas, a distribuição de algumas espécies poderá sofrer contrações, expansões ou as espécies poderão se deslocar para habitats climaticamente mais favoráveis (Parmesan & Yohe 2003). De acordo com Schloss et al. (2012), as mudanças climáticas provavelmente ultrapassarão a capacidade de resposta de muitos mamíferos e a sua vulnerabilidade a essas alterações poderá ser muito maior do que previsto anteriormente. Espera-se que 90% das espécies de mamíferos experimentem reduções em sua distribuição e que essas reduções serão, provavelmente, devidas às limitadas habilidades de dispersão, que potencialmente proporcionaria a ocupação de novas áreas ambientalmente adequadas. Espécies com maior habilidade de dispersão podem expandir rapidamente sua distribuição após mudanças no ambiente, por exemplo, após as glaciações que ocorreram durante o Pleistoceno (Dynesius & Jansson, 2000).

A compreensão da capacidade das espécies em expandir sua distribuição para novos habitats adequados quando expostas a mudanças climáticas é importante, uma vez que indica as probabilidades de extinção espécie-específica (ou espécies-específicas) (Thomas *et al*., 2004; Loarie *et al*., 2008) e a estrutura da comunidade no futuro (Lawler *et al*., 2009; Gilman *et al*., 2010). Thuiller *et al*. (2005) e Broennimann *et al*. (2006) colocam que a sensibilidade de uma dada espécie às mudanças climáticas dependerá de sua distribuição geográfica e suas propriedades do nicho ecológico, tais como amplitude e marginalidade.

Além da avaliação das consequências das mudanças climáticas sobre as espécies e sobre os ecossistemas, é necessário considerar a sinergia entre tais mudanças e o acelerado aumento das ameaças à biodiversidade, tais como perda de habitat e fragmentação, caça, disseminação de doenças, invasão de espécies, entre outras. Tais ameaças podem intensificar o efeito das mudanças climáticas sobre os organismos, aumentando a sua vulnerabilidade (para mais detalhes veja a revisão feita por Brook *et al*., 2008). Estudos sugerem que o advento das mudanças climáticas poderá superar a destruição de habitat no ranking de ameaças mundiais à biodiversidade (Leadley *et al*., 2010). É tarefa fundamental da comunidade conservacionista, em todo o mundo, identificar as características das espécies que as tornem resistentes ou suscetíveis a mudanças climáticas. Desta forma, poderemos subsidiar melhores avaliações de risco de extinção e desenvolver estratégias de conservação efetivas. Neste aspecto, como é possível avaliar a vulnerabilidade das espécies e de seus habitats, e a distribuição do seu nicho climático sob o efeito das mudanças climáticas, especialmente de um grupo extremamente ameaçado, como é o caso dos grandes mamíferos herbívoros pertencentes à ordem Perissodactyla?

1.4. Teoria do Nicho Ecológico

Um dos principais impactos causados pelas mudanças climáticas é a alteração na adequabilidade ambiental nas áreas ocupadas pelas espécies ou em potenciais locais que virão a ocupar no futuro. Em teoria, os indivíduos estabelecem-se em habitats onde as condições ambientais locais são propícias à sua sobrevivência e reprodução. No entanto, os fatores climáticos e físicos podem afetar a distribuição das espécies, expressa pela ecologia e história evolutiva de cada uma delas, em diferentes intensidades e escalas (Pearson & Dawson 2003), por um longo período de tempo (Soberón & Peterson, 2005). Algumas das teorias mais fundamentais sobre as condições ambientais que influenciam a distribuição de espécies foram apresentadas por Joseph Grinnell há mais de 90 anos, quando foi registrado o primeiro uso da palavra “nicho” (Grinnell, 1917, 1924).

Grinnell referiu-se ao "nicho ecológico ou ambiental" como a unidade de distribuição final de uma espécie, sem levar em consideração a presença de interações com outras espécies, considerando somente os locais que possuem as condições ambientais necessárias para uma espécie sobreviver. Dessa forma, o nicho Grinnelliano pode ser definido por variáveis fundamentalmente não interativas (cenopoéticas) (James *et al*., 1984; Austin, 2002) e pelas condições ambientais em ampla escala, relevantes ao entendimento de propriedades ecológicas e geográficas em grande escala (Jackson & Overpeck, 2000; Peterson, 2003). Outro conceito de nicho foi proposto por Elton, em 1927, com enfoque nas interações bióticas e na dinâmica de recursos-consumidor, que Hutchinson (1978) definiu como variáveis bionômicas, e que pode ser medido, principalmente, em uma escala local. Ambas as classes de nichos são relevantes para a compreensão da distribuição dos indivíduos de uma espécie (Soberón, 2007).

O conceito de nicho evoluiu ao longo do tempo. Hutchinson (1957) definiu nicho ecológico como: “Hipervolume n-dimensional limitado pelas interações com outros organismos, que envolve todas as respostas fisiológicas às condições do meio e depende da disponibilidade de recursos, sob as quais as populações apresentam taxa de crescimento positivo”. Adicionalmente, Hutchinson dividiu o conceito de nicho em fundamental (fisiológico ou potencial) e realizado (ecológico, atual). Nicho fundamental é definido como o conjunto de todas as condições ambientais que permitem o crescimento e a reprodução da espécie, distinguindo-se de nicho realizado no qual os efeitos da competição reduzem o nicho fundamental de uma espécie, ou ainda a área que ela pode ocupar Soberón (2007). Para Vandermeer (1972), talvez essa distinção tenha sido o mais importante princípio derivado do conceito original de Hutchinson. De forma geral, Hutchinson definiu nicho como uma propriedade da espécie e não do ambiente, como discutido por Pulliam (2000).

Sobéron & Peterson (2005) e Guisan & Thuiller (2005) apresentam três fatores que podem determinar a área em que uma espécie pode ser encontrada e que, consequentemente, corresponde ao nicho da espécie: 1. Fatores abióticos, que impõem os limites fisiológicos sobre a capacidade de sobrevivência de uma espécie; 2. Fatores bióticos, o conjunto de interações com outras espécies que afetam a habilidade da espécie em manter suas populações; 3. As regiões que são acessíveis à dispersão pela espécie. Deve-se considerar ainda que uma espécie somente estará presente em um dado local, onde os três primeiros fatores estiverem reunidos, apesar de outros fatores também contribuírem, como por exemplo, a capacidade evolutiva da espécie (Sobéron & Peterson, 2005).

Dessa forma, Soberón & Peterson (2005) e Soberón (2007) apresentaram um diagrama, que descreve alguns resultados da interação dos fatores que determinam a distribuição de espécies: diagrama Biótico-Abiótico-Mobilidade, mais conhecido como diagrama BAM. Os autores usam o diagrama como uma representação abstrata do espaço geográfico. A região geográfica que apresenta somente as condições cenopoéticas favoráveis é chamada de “A”, que Peterson & Soberón (2012) chamam de "nicho fundamental existente", onde a taxa de crescimento intrínseco da espécie pode ser positiva (Soberón, 2010). A região identificada como “B” é a área onde as condições bióticas estão disponíveis para a espécie e a terceira região, a “M”, inclui áreas que têm sido acessíveis à espécie ao longo de períodos de tempo relevantes (Soberón & Peterson, 2005; Peterson & Soberón, 2012) e foi previamente discutida por (Barve *et al*., 2011).

Embora o nicho realizado possa ser mapeado, essa não é uma tarefa fácil do ponto de vista conceitual e nem facilmente exequível do ponto de vista prático, pois as interações bióticas são muito difíceis de mensurar. Dessa forma, reduzindo a definição de nicho ao conceito Grinnelliano (ou nicho fundamental de Hutchinson), a dualidade entre os espaços ambiental e geográfico se torna uma questão apenas operacional (Colwell & Rangel, 2009), porém de extrema importância para modelagem em Ecologia, especialmente sob a perspectiva paleoecológica e das mudanças climáticas futuras.

1.5. Modelagem de Nicho Ecológico

A teoria de nicho ecológico suporta fortemente uma das principais ferramentas utilizadas atualmente, a Modelagem de Nicho Ecológico (mais à frente discutiremos as diferentes denominações para esta ferramenta) (Guisan & Zimmermann, 2000; Soberón, 2007), a qual é baseada principalmente no nicho Grinnelliano. Consequentemente, a teoria do nicho será a base central do presente trabalho. Conforme apresentado anteriormente, as primeiras aplicações desta teoria foram as de Joseph Grinnell, que utilizou a distribuição espacial de ocorrência de espécies para inferir os fatores limitantes de suas distribuições, estabelecendo uma base sólida para os trabalhos subsequentes neste campo. A diversidade de tais aplicações, no entanto, já cresceu consideravelmente, mas de uma forma geral, estes estudos têm como principal objetivo reconstruir os requerimentos ecológicos das espécies e/ou predizer suas distribuições potenciais (Peterson, 2006). Resumidamente, os modelos são simplificações da realidade (Franklin, 2009), formulados a partir de parâmetros observados na natureza.

Antes de considerarmos as demais questões envolvendo o uso dessa ferramenta, é preciso entender as diferentes terminologias utilizadas. Os modelos de nicho ecológico (MNEs) (Peterson *et al*., 1999) são também chamados de modelos de envelope bioclimático (Araújo & Peterson, 2012) ou modelos de distribuição de espécies (MDEs) (Elith & Leathwick, 2009). Segundo Peterson & Soberón (2012), o debate entre MNE e MDE está longe de ser meramente semântico. É preciso entender que a distribuição geográfica normalmente obtida por tais modelos não reflete os efeitos de dispersão e interações bióticas (Soberón, 2010). Desta forma, na maioria das vezes não estamos lidando com a distribuição real da espécie, mas sim com sua distribuição potencial. De acordo com a análise feita por Peterson & Soberón (2012), a terminologia MNE deve ser usada somente quando o foco seja estimar o nicho fundamental ou o conjunto de áreas que atendam às condições do nicho fundamental de uma espécie. Ou ainda, qualquer distribuição potencial frente às mudanças nas condições ambientais e as circunstâncias utilizadas pelo modelo. Considerando-se o foco central deste estudo, especialmente no que diz respeito àdistribuição potencial de áreas ambientalmente adequadas para as espécies avaliadas, e limitações técnicas, será adotado em todo o trabalho o termo "Modelos de Nicho Ecológico - MNEs".

Independentemente de terminologias, o princípio geral da MNE é obter um mapa de adequabilidade ambiental, a partir de um modelo que descreva o nicho das espécies (Pearce & Ferrier, 2000; Guisan *et al*., 2002; Thuiller, 2003). Este é um dos campos de pesquisa mais ativos em Ecologia (Zimmermann *et al*., 2010), sendo aplicado a estudos com diferentes metas (Peterson *et al*., 2011; Svenning *et al*., 2011), desde a descoberta da biodiversidade, passando pela discussão de padrões biogeográficos, predição da invasão das espécies até a predição para o futuro dos efeitos das mudanças climáticas sobre as espécies, buscando estabelecer estratégias efetivas de conservação para as espécies e seus ambientes (Pearson *et al*., 2007; Keith *et al*., 2008; Rood *et al*., 2010; Nóbrega & De Marco, 2011; Araújo *et al*., 2011; Hof *et al*., 2011, Ochoa-Ochoa *et al*., 2012). Além disso, os MNEs também têm sido utilizados para reconstruir nichos de espécies no passado buscando entender, por exemplo, a dinâmica de distribuição das espécies e dos ecossistemas sob cenários de mudanças climáticas passadas, e a extinção da megafauna no final do Pleistoceno (Nogués-Bravo *et al*., 2008, Varela *et al*., 2010, Lorenzen *et al*., 2011, Lima-Ribeiro *et al*., 2012; Werneck *et al*., 2012).

Tecnicamente o MNE é sustentado por três pilares fundamentais: 1) a informação sobre as espécies (tolerância fisiológica a partir de dados de ocorrência), 2) as variáveis ambientais (variáveis preditoras), e 3) os métodos analíticos (funções ou modelos que relacionam as informações sobre as espécies aos preditores ambientais). As projeções para o futuro ou reconstruções para o passado são um resultado da distribuição conhecida da espécie e das variáveis climáticas da região onde a espécie se encontra, identificando, assim, outras regiões as quais a espécie possa potencialmente habitar ou as mudanças na distribuição das áreas ambientalmente adequadas tanto no futuro quanto no passado (Heikkinen *et al*., 2006). O mapa de adequabilidade define quais locais são mais ou menos adequados à sobrevivência da espécie focal, dados seus requerimentos ecológicos (isto é, o modelo), o que é chamado de distribuição geográfica modelada ou mapa preditivo (Elith & Leathwick, 2009, Franklin, 2009).

Existem várias classes de métodos analíticos utilizados para determinar o nicho ecológico de uma espécie. Estes podem ser divididos em dois grupos de acordo com seus princípios metodológicos: modelos mecanísticos e modelos correlativos. Em um modelo mecanístico, o nicho é predito por um conjunto de funções baseadas em seu conhecimento fisiológico (Kearney & Porter, 2009). Modelos correlativos são mais gerais e utilizam a informação ambiental contida em um conjunto de pontos de ocorrência de uma espécie para determinar suas condições ambientais favoráveis (Franklin, 2009). Os modelos correlativos assumem que a distribuição geográfica da espécie focal é resultado de seus requerimentos ambientais (Soberón, 2007; Soberón & Nakamura, 2009; Peterson *et al*., 2011). Dessa forma, é possível ajustar os modelos utilizando tanto simulações paleoclimáticas, quanto as condições climáticas projetadas para o futuro, a partir dos modelos climáticos globais de acordo com diferentes cenários de emissão de gás carbônico (Hannah, 2011). Por essa razão, apenas modelos correlativos serão apresentados e discutidos neste trabalho.

Com base em todas as informações, os MNEs têm se mostrado úteis especialmente no planejamento de ações de conservação, chamando a atenção para espécies ou ecossistemas ameaçados. É importante ressaltar, entretanto, que os modelos projetados precisam ser analisados com cautela, considerando, principalmente, as características biológicas e ecológicas de cada espécie avaliada, assim como outras variáveis como a fragmentação ambiental e outros impactos antrópicos.

2. APRESENTAÇÃO DOS CAPÍTULOS

O clima foi um importante direcionador na história evolutiva dos Perissodactyla, mas entender o que ocorreu no passado e prever o que acontecerá com seus representantes e, principalmente, com os ambientes onde habitam no futuro, é desafiador. A base teórica consultada nos incentivou a realizar uma abordagem integrada e propor hipóteses sobre a influência do clima nesses grandes mamíferos herbívoros, em diferentes períodos temporais (125 mil anos antes do presente até 2080). O grau de vulnerabilidade das espécies do clado Perissodactyla, em particular *Tapirus terrestris*, a diferentes cenários climáticos, foi avaliado no intuito de acrescentar mais uma abordagem às análises de priorização de estratégias de conservação. A base metodológica para testar nossas predições foi centrada na Modelagem de Nicho Ecológico, a qual é sustentada especialmente pela Teoria do Nicho. Resultados e discussões são apresentados na forma de três artigos, aqui denominados como capítulos.

O **Capítulo 1** apresenta os aspectos de nicho climático que podem determinar a vulnerabilidade do clado Perissodactyla às mudanças climáticas. Projeções resultantes de modelos de nicho ecológico, baseadas em um cenário pessimista de emissão de gás carbônico, foram utilizadas para examinar tais relações e testar se as espécies mais marginais e com baixa tolerância climática teriam distribuição potencial mais restrita e se espécies com menor tolerância e mais marginais teriam maior perda de áreas ambientalmente adequadas no futuro. Resultados das análises demonstraram que a anta brasileira (*Tapirus terrestris*) é considerada a mais generalista climaticamente enquanto que o cavalo de Przewalski é o mais especialista.

Os Perissodactyla apresentaram características de nicho distintas e, de acordo com as análises, nem sempre a espécie mais especialista foi predita a sofrer mais seriamente os efeitos das mudanças climáticas. Além disso, grande parte das respostas das espécies foi idiossincrática, mesmo apresentando valores similares de marginalidade, como as espécies que habitam áreas de montanhas. Isso sugere que é preciso avaliar cada espécie isoladamente, considerando suas características biológicas e as características de sua área de ocorrência. Adicionalmente, é crucial considerar as barreiras e características biológicas que poderiam potencialmente limitar a dispersão dessas espécies a novas áreas ambientalmente adequadas. Deve-se considerar também que muitas dessas espécies estão em áreas afetadas e ameaçadas por mudanças climáticas e por alterações da paisagem produzidas pelo homem, além de outras pressões como a caça, que vem dizimando centenas de indivíduos de todas as espécies avaliadas neste trabalho. Dessa forma, consideramos que não somente as pressões antrópicas, mas também as mudanças nas condições climáticas e a potencial emergência de novas áreas ambientalmente adequadas são fatores que devem ser considerados em planos de ação futuros.

Uma questão que chamou a atenção neste capítulo está ligada à hipótese de que espécies generalistas, com ampla distribuição, seriam menos ameaçadas pelas mudanças climáticas. A Anta Brasileira foi a espécie mais generalista deste trabalho e, mesmo assim, quando foram projetados os cenários mais pessimistas (maior emissão de gás carbônico e seleção apenas de áreas consideradas altamente adequadas) demonstrou alto grau de vulnerabilidade. Tal resultado, indicando que uma espécie generalista podeser altamente vulnerável a mudanças climáticas, leva a uma nova pergunta: O que poderia contradizer a hipótese proposta por diferentes autores? Os dois próximos capítulos foram estruturados com base nisso, focando somente na Anta Brasileira, a qual se mostrou uma espécie intrigante, pois sobreviveu a fortes oscilações climáticas no passado e, diferentemente do restante da megafauna que habitava a América do Sul naquele momento, não desapareceu do continente.

Logo, o **Capítulo 2** está bastante focado em como as áreas ambientalmente adequadas para a anta estavam distribuídas no passado, considerando os impactos das oscilações climáticas durante o Quaternário, e em como o clima pode ter contribuído para moldar a distribuição atual da espécie. A hipótese utilizada foi a da mudança climática, que propõe que as reduções de áreas climaticamente favoráveis podem ter levado à redução da distribuição da espécie, aumentando sua suscetibilidade à extinção. Foram também trabalhadas hipóteses filogeográficas e paleontológicas, as quais sugerem que a distribuição de *T. terrestris* sofreu retração durante o Último Máximo Glacial (UGM), com uma rápida expansão após este período. Dessa forma, duas predições foram testadas: 1. As áreas ambientalmente adequadas para a espécie foram restritas durante o UGM; e 2. Houve expansão de áreas ambientalmente adequadas após esse período.

A fim de testar essas predições, dados atuais (pontos de ocorrência) de *Tapirus terrestris* foram projetados para condições paleoclimáticas no Quaternário (Último Interglacial ~125 mil anos atrás; Último Máximo Glacial ~21 mil anos atrás; Holoceno Médio ~6 mil anos atrás), a partir de modelos de nicho ecológico, utilizando quatro diferentes algoritmos. As condições paleoclimáticas têm sido razoavelmente bem estimadas para estes períodos geológicos, que são considerados os períodos importantes do Pleistoceno e Holoceno, utilizando os modelos de circulação geral. Para avaliarmos as mudanças na distribuição de um período a outro, tais como expansão e contração, nós usamos duas métricas, mudança relativa e perda proporcional, as quais têm sido frequentemente utilizadas em estudos com enfoque em mudanças climáticas.

Os resultados sugerem que as condições mais críticas que prevaleceram durante o UMG reduziu a extensão geográfica das áreas climaticamente adequadas para a anta, expandindo durante o período interglacial atual, com temperaturas mais quentes. Dessa forma, a modelagem da paleodistribuição suportou fortemente hipóteses propostas previamente por estudos filogeográficos e paleontológicos. O amplo nicho ambiental da anta, conforme observado no Capítulo 1, pode ter favorecido que a anta expandisse rapidamente sua distribuição geográfica, como proposto por outros estudos. Além disso, foi identificada uma grande área estável que foi mantida ao longo do tempo, indicando que o efeito do clima para a anta pode ter sido bem menor do que para as espécies de mamíferos extintas da megafauna.

Embora o clima não pareça ter sido um problema muito sério na história evolutiva da espécie, o desafio para a sua conservação atualmente e no futuro pode ser bem maior. O efeito combinado das mudanças climáticas com a perda e fragmentação de habitat, caça e outras ameaças podem afetar severamente as populações da espécie e seu habitat. Esta questão gerou a temática para o **Capítulo 3** desta tese, o qual está focado no impacto futuro das mudanças climáticas sobre as populações da anta brasileira. Adicionalmente, as predições foram utilizadas para avaliar se as unidades de conservação atuais serão efetivas para a proteção da espécie no futuro. Para a modelagem da distribuição das áreas adequadas nas condições climáticas atuais e futuras foram utilizados dois procedimentos de modelagem diferentes (algoritmos). As condições atuais foram projetadas para três modelos climáticos e dois níveis de emissão de gás carbônico, um mais otimista (com menores taxas de emissão) e outro mais pessimista (com maiores taxas). Para avaliar a efetividade das áreas protegidas, foram compilados dados do ICMBio (Instituto

Chico Mendes de Conservação da Biodiversidade) e selecionadas apenas as unidades com tamanho ≥ 500 km^2. Este valor foi considerado, por estudos anteriores, como o mínimo ideal para manter populações viáveis de antas na Mata Atlântica, dessa forma, decidimos seguir este cenário mais conservativo.

Os modelos gerados predizem uma acentuada perda na adequabilidade ambiental, especialmente nas áreas de florestas tropicais úmidas, por exemplo, as florestas úmidas das Guianas. Já em outras áreas, como na Floresta de Araucária, é predito um aumento no número de áreas adequadas. Embora não tenham sido observadas grandes mudanças no tamanho total da distribuição da anta brasileira, os modelos predizem acentuadas mudanças na distribuição espacial da adequabilidade climática, inclusive onde as Unidades de Conservação estão presentes. Estes resultados demonstram a importância na análise das mudanças na adequabilidade ambiental, especialmente para espécies generalistas, como a anta. Mesmo que o tamanho da distribuição em si não altere ou sofra pequenas expansões como uma resposta às alterações climáticas, identificar as mudanças na adequabilidade ambiental em toda a distribuição da anta brasileira contribuirá para a priorização de áreas para a conservação da espécie. Embora a anta brasileira tenha resistido às alterações de clima ao longo de milhares de anos, seu sucesso futuro não é uma certeza. Deve-se considerar que a sinergia entre a perda na adequabilidade ambiental, fragmentação do habitat, caça e muitas outras ameaças podem intensificar os efeitos das mudanças climáticas, aumentando a vulnerabilidade da espécie. Além disso, os modelos gerados demonstram que muitas das Unidades de Conservação que ainda mantêm populações de antas certamente enfrentarão ambientes extremos, muito provavelmente não suportando populações viáveis de grandes mamíferos, como a anta, em longo prazo.

Os resultados apresentados nos três capítulos desta tese reforçam fortemente a importância dos modelos de nicho ecológico como ferramenta de predição e suas perspectivas de aplicabilidade para modelagem do passado, presente e futuro, particularmente para um grupo de espécies tão ameaçado e com características climáticas razoavelmente distintas entre si. Além disso, mesmo espécies, como os representantes da Ordem Perissodactyla com uma longa história evolutiva, que experimentaram diferentes alterações no clima e mudanças no ambiente, poderão não se manter no futuro, uma vez que tanto seus ambientes quanto suas populações já estão em níveis críticos de ameaça.

3. REFERÊNCIAS

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

Archibald, J.D. & Deutschman, D.H. (2001) Quantitative analysis of the timing of the origin and diversification of extant placental orders. *Journal of Mammalian Evolution*, **8**, 107-124.

Arribas, P., Abellán, P., Velasco, J., Bilton, D.T., Millán, A. & Sánchez-Fernández, D. (2012) Evaluating drivers of vulnerability to climate change: a guide for insect conservation strategies. *Global Change Biology*, **18**, 2135-2146.

Austin, M. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157**, 101–118.

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

Blois, J.L. & Hadly, E.A. (2009) Mammalian Response to Cenozoic Climatic Change. *Annual Review of Earth and Planetary Sciences*, **37**, 8.1-8.28.

Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.M.R. & Guisan, A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology*, **12**, 1079–1093.

Brook, B., Sodhi, N. & Bradshaw, C. (2008) Synergies among extinction drivers under global change. *Trends in ecology and evolution*, **23**, 453–460.

Brooks, D.M., Bodmer, R.E. & Matola, S. (1997) Tapirs: Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V. & Ehleringer, J.R. (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature*, **389**, 153–158.

Cifelli, R.L. (1981) Patterns of evolution among Artiodactyla and Perissodactyla (Mammalia). *Evolution*, **35**, 433–440.

Cione, A.L. & Tonni, E.P. (2005). Bioestratigrafía basada em mamíferos del Cenozóico Superior de la Província de Buenos Aires, Argentina. Geología y recursos minerales de Província de Buenos Aires (ed. by E. Barrio, R.O. Etcheverry, M.F. Caballé and E. Llambias), pp. 183–200. Quick Press, La Plata, Argentina.

Colbert, M.W. & Schoch, R.M. (1998) Tapiroidea and other moropomorphs. Evolution of Tertiary Mammals of North America (eds. by C.M. Janis, K.M. Scott and L.L. Jacobs), pp. 569-582. Cambridge University Press, Cambridge, United Kingdom.

Colbert, M. (2007) New fossil discoveries and the history of *Tapirus*. *Tapir Conservation*, **16**, 12-14.

Collinson, M.E., Fowler, K. & Boulter, M.C. (1981) Floristic changes indicate a cooling climate in the Eocene of southern England. *Nature*, **291**, 315-317.

Colinvaux, P., De, P. & Bush, M. (2000) Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, **19**, 141-169.

Colwell, R. & Rangel, T. (2009) Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, **106 Suppl 2**, 19651–19658.

Cozzuol, M.A., Clozato, C. L., Holanda, E.C., Rodrigues, F.H.G., Nienow, S., Thoisy, B. de, Redondo, R. A. F & Santos, F. R. (2013) A new species of tapir from the Amazon. *Journal of Mammalogy*, **94 (6)**: 1331-1345.

Dawson, T., Jackson, S., House, J., Prentice, I. & Mace, G. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science (New York, N.Y.)*, **332**, 53–58.

Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 9115–9120.

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.

Elton, C. (1927) Animal Ecology. Sedgwick and Jackson, London.

Feakins, S.J., Levin, N.E., Liddy, H.M., Sieracki, A., Eglinton, T.I. & Bonnefille, R. (2013) Northeast African vegetation change over 12 m.y. *Geology*, **41**, 295-298.

Foden, W., Mace, G., Vié, J.-C., Angulo, A., Butchart, S., DeVantier, L., Dublin, H., Gutsche, A., Stuart, S. & Turak, E. (2008) Species susceptibility to climate change impacts. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species (ed. by J.-C. Vié, C. Hilton-Taylor and S. N. Stuart), pp.77–87, Gland, Switzerland: IUCN.

Franklin, J. (2009) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cam-bridge, UK.

Franklin, J., Davis, F., Ikegami, M., Syphard, A., Flint, L., Flint, A. & Hannah, L. (2013) Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology*, **19**, 473–483.

García, M., Medici, E., Naranjo, E., Novarino, W. & Leonardo, R. (2012) Distribution, habitat and adaptability of the genus *Tapirus*. *Integrative Zoology*, **7**, 346–355.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution*, **25**, 325–331.

Gingerich, P. (2006) Environment and evolution through the Paleocene-Eocene thermal maximum. *Trends in ecology & evolution*, **21**, 246–53.

Grein, M., Oehm, C., Konrad, W., Utescher, T., Kunzmann, L. & Roth-Nebelsick, A. (2013) Atmospheric CO2 from the late Oligocene to early Miocene based on photosynthesis data and fossil leaf characteristics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **374**, 41-51.

Grinnell, J. (1917) The niche-relationships of the California Thrasher. *The Auk*, **34(4)**, 427-433.

Grinnell, J. (1924) Geography and evolution. *Ecology*, **5(3)**, 225-229.

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

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

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

Hannah, L.J. (2011) Climate Change Biology. Academic Press, Burlington, MA.

Hansen, D.M. & Galetti, M. (2009) The Forgotten Megafauna. *Science*, **324**, 42-43.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, **30**, 1-27.

Hof, C., Levinsky, I., Araújo, M.B. & Rahbek, C. (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, **17**, 2987-2990.

Holanda, E.C., Ferigolo, J. & Ribeiro, A.M. (2011) New Tapirus species (Mammalia: Perissodactyla: Tapiridae) from the upper Pleistocene of Amazonia, Brazil. *Journal of Mammalogy*, **92**, 111-120.

Holbrook, L.T. (1999) The phylogeny and classification of tapiromorph perissodactyls (Mammalia). *Cladistics*, **15**, 331-250.

Hoorn, C. & Wesselingh, F.P. (2010) Amazonia—landscape and species evolution: a look into the past. Blackwell Publishing Ltd.

Hulbert, R.C. (1995) The giant tapir, *Tapirus haysii*, from Leisey Shell Pit 1A and other Florida Irvingtonian localities. *Bulletin of the Florida Museum of Natural History*, **37**, 515–551.

Hutchinson, G.E. (1957) Concluding remarks. Cold Spring Harb.Symp. *Quantitative Biology*, **22**, 415–427.

Hutchinson, G.E. (1978) An Introduction to Population Ecology. Yale University Press, New Haven.

IPCC, Climate Change. (2007). Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

IUCN (2012). IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>. Downloaded on **20 June 2013**.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

James, F.C., Johnston, R.F., Warner, N.O., Niemi, G. & Boecklen, W. (1984) The Grinnellian niche of the Wood Thrush. *American Naturalist*, **124**, 17–47.

Janis, C.M. (1984). The significance of fossil ungulate communities as indicators of vegatation structure and climate. In Fossils and Climate (ed. by P.J. Brenchley), pp. 85-104. New York: Wiley.

Janis, C. (1976) The evolutionary strategy of the Equidae, and the origin of rumen and cecal digestion. *Evolution*, **30**, 757–774.

Janis, C.M. (1989) A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology*, **32**, 463–481.

Janis, C. (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual* Review of *Ecology*, Evolution, and Systematics, **24**, 467–500.

Janis, C. (2008) The Ecology of Browsing and Grazing. An Evolutionary History of Browsing and Grazing Ungulates (ed. by I.J. Gordon and H.H.T. Prins), pp. 21-45. Ecological Studies.

Janis, C. (2009) Artiodactyl "success" over perissodactyls in the late Palaeogene unlikely to be related to the carotid rete: a commentary on Mitchell & Lust (2008). *Biology letters*, **5**, 97–98.

Janzen, D. & Paul S.M. (1982) Neotropical anachronisms: The fruits the gomphotheres ate. *Science*, **215**, 19-27.

Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.

Keith, D., Akçakaya, H., Thuiller, W., Midgley, G., Pearson, R., Phillips, S., Regan, H., Araújo, M. & Rebelo, T. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560-563.

Keller, G. & Barron, J.A. (1983) Paleoceanographic implications of Miocene deep-sea hiatuses. *Geological Society of America Bulletin*, **94**, 590-613.

Kemp, T.S. (2005). The Origin and Evolution of Mammals. New York: Oxford University Press.

Krause, D.W. & Maas, M.C. (1990) The biogeographic origins of late Paleocene-early Eocene mammalian immigrants to the Western Interior of North America. Dawn of the Age of Mammals in the northern part of the Rocky Mountain Interior, North America (ed. by T. M. Bown and K. D. Rose). *Geological Society of America*, Special Paper, **243**, 71-105.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, 90, 588–597.

Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarres, J.F., Proenca & V., Scharlemann, J.P.W. (2010) Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. Secretariat of the Convention on Biological Diversity (ed. by Diversity SotCoB), pp. 1-132. Published by the Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 50.

Ledru, M.P., Labouriau, M. L.S. & Lorscheitter, M. L. (1998) Vegetation dynamics in southern and central Brazil during the last 10,000 year B. P. *Review* of *Palaeobotany* and *Palynology*, **99**, 131 – 142.

Lima-Ribeiro, M.S., Varela, S., Nogués-Bravo, D. & Diniz-Filho, J.A.F. (2012) Potential suitable areas of giant ground sloths dropped before its extinction in South America: the evidences from bioclimatic envelope modeling. *Natureza & Conservação*, **10**, 145-151.

Loarie, S., Duffy, P., Hamilton, H., Asner, G., Field, C. & Ackerly, D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Lorenzen, E., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., *et al.* (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature*, **479**, 359–364.

McKenna, M.C., Chow, M., Ting, S. & Luo, Z. (1989) "*Radinskya yupingae*, a perissodactyl-like mammal from the late Paleocene of China". The evolution of perissodactyls (ed. by D.R. Prothero and R.M. Schoch), pp. 24-36. Oxford monographs on geology and geophysics **15**. New York: Oxford University Press.

Magrin, G., García, C.G., Choque, D.C., Giménez, A.R.M.J.C., Nagy, G.J., Nobre, C. & Villamizar, A. (2007) Latin America. Climate Change 2007: Impacts, Adaptation and

Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (ed. by M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden and C. E. Hanson), pp. 581-615. Cambridge University Press, Cambridge, UK.

Marshall, L.G. (1988) Land Mammals and the Great American Interchange. *American Scientist*, **76**: 380-388.

Mayle, F.E., Beerling, D.J., Gosling, W.D. & Bush, M.B. (2004) Responses of Amazonian ecosystems to climatic and atmospheric CO2 changes since the Last Glacial Maximum. *Philosophical Transactions of the Royal Society, London B*, **359(1443)**, 499–514.

Medici, E.P. (2011). Family Tapiridae (Tapirs). Handbook of the Mammals of the World, Volume 2: Hoofed Mammals (ed. by D.E. Wilson, R.A. Mittermeier), pp. 182–204. Lynx Edicions, Spain.

McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views.*Annual Review of Ecology and Systematics*, 495–516.

Miller, K.G., Wright, J.D. & R.G. (1991) Fairbanks, Unlocking the Ice House: Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion. *Journal of Geophysical Research*, **96**, 6829-6848.

Mitchell, G. & Lust, A. (2008) The carotid rete and artiodactyl success. *Biology Letters*, **4**, 415–418.

Nabel, P.E., Cione, A. & Tonni, E. P. (2000) Environmental changes in the Pampean area of Argentina at the Matuyama– Brunhes (C1r–C1n) Chrons boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **162**, 403–412.

Nóbrega, C.C. & Marco, P.D. (2011) Unprotecting the rare species: a niche-based gap analysis for odonates in a core Cerrado area. *Diversity and Distributions*, **17**, 1-15.

Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. & Araújo, M. (2008) Climate change, humans, and the extinction of the woolly mammoth. *PLoS biology,* **6**, e79.

Norman, J. & Ashley, M. (2000) Phylogenetics of Perissodactyla and test of the molecular clock. *Journal of Molecular Evolution*, **50**, 11–21.

Ochoa-Ochoa, L.M., Rodríguez, P., Mora, F., Flores-Villela, O. & Whittaker, R.J. (2012) Climate change and amphibian diversity patterns in Mexico. *Biological Conservation*, **150**, 94-102.

Pagani, M., Zachos, J., Freeman, K., Tipple, B. & Bohaty, S. (2005) Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. *Science (New York, N.Y.)*, **309**, 600–603.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pearce, J., & Ferrier, S. (2001) The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation*, **98**, 33–43.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

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

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Peterson, A. (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology*, **78**, 419–433.

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

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Nakamura, M., Martinez-Meyer, E., & Araújo, M. B. (2011) Ecological niches and geographical distributions. Princeton University Press, Princeton, New Jersey, USA.

Peterson, A.T. & Soberón, J. (2012) Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right. *Natureza & Conservação*, **10**, 102-107.

Plancq, J., Grossi, V., Henderiks, J., Simon, L. & Mattioli, E. (2012). Alkenone producers during the late Oligocene–early Miocene revisited. *Paleoceanography*, **27**.

Price, S.A. & Bininda-Emonds, O.R.P. (2009) A comprehensive phylogeny of extant horses, rhinos and tapirs (Perissodactyla) through data combination. *Zoosystematics and Evolution*, **85**, 277-292.

Prothero, D.R. & Schoch, R.M. (1989) The Evolution of Perissodactyls. Oxford: Oxford Univ. Press.

Pulliam, H. (2000) On the relationship between niche and distribution. *Ecology letters*, **3**, 349-361.

Radinsky, L.B. (1963) Origin and early evolution of North American Tapiroidea. *Bulletin of the Peabody Museum of Natural History*, **17**, 100-106.

Radinsky, L.B. (1966) The Families of the Rhinocerotoidea (Mammalia, Perissodactyla). *Journal of Mammalogy*, **47**, 631-639.

Radinsky, L.B. (1969) The Early Evolution of the Perissodactyla. *Evolution*, **23**, 308-328.

Ravelo, A.C. & Andreasen, D.H. (2000) Enhanced circulation during a warm period. *Geophysical Research Letters*, **27**, 1001–1004.

Raymo, M.E., Grant, B., Horowitz, M. & Rau, G.H. (1996) Mid-Pliocene warmth: Stronger greenhouse and stronger conveyer. *Marine Micropaleontology*, **27**, 313–326.

Ravelo, A., Andreasen, D., Lyle, M., Olivarez Lyle, A. & Wara, M. (2004) Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature*, **429**, 263–267.

Rea, D.K., Zachos, J.C., Owen, R.M. & Gingerich, P.D. (1991) Global change at the Paleocene-Eocene boundary: climatic and evolutionary consequences of tectonic events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **79**, 117-128.

Retallack, G.J. (2001) Cenozoic expansion of grasslands and climatic cooling. *The Journal of Geology*, **109**, 407–426.

Rodbell, D.T. (2000) The Younger Dryas: Cold, Cold Everywhere? *Science*, **290**, 285-286.

Rood, E., Ganie, A.A. & Nijman, V. (2010) Using presence-only modelling to predict Asian elephant habitat use in a tropical forest landscape: implications for conservation. *Diversity and Distributions*, **16**, 975–984.

Rose, K.D. (2006) The Beginning of the Age of Mammals. Baltimore: Johns Hopkins University Press.

Ruddiman, W.F. (2001) Earth's Climate: past and future. W.H. Freeman & Sons, New York.

Schloss, C., Nuñez, T. & Lawler, J. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 8606–8611.

Ruiz-García, M., Vásquez, C., Pinedo, M., Sandoval, S., Kaston, J., Thoisy, B., & Shostell, J. (2012) Phylogeography of the mountain tapir (*Tapirus pinchaque*) and the Central American tapir (*Tapirus bairdii*) and the molecular origins of the three South American tapirs. Current Topics in Phylogenetics and Phylogeography of Terrestrial and Aquatic Systems (ed. by K. Anamthawat-Jónsson). Rijeka, Croatia: In Tech.

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1-10.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America*, **106 Suppl 2**, 19644–19650.

Soberón, J. (2010) Niche and area of distribution modeling: a population ecology perspective. *Ecography*, **33,** 159-167.

Steiner, C.C. & Ryder, O.A. (2011) Molecular phylogeny and evolution of the Perissodactyla. *Zoological Journal of the Linnean Society*, **163**, 1289–1303.

Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nógues-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews*, **30**, 2930–2947.

Thoisy, B. de, da Silva, A., Ruiz-García, M., Tapia, A., Ramirez, O., Arana, M., Quse, V., Paz-y-Miño, C., Tobler, M., Pedraza, C. & Lavergne, A. (2009) Population history, phylogeography, and conservation genetics of the last Neotropical mega-herbivore, the lowland tapir (Tapirus terrestris). *BMC Evolutionary Biology*, **10**, 278.

Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., Erasmus, B., De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A., Midgley, G., Miles, L., Ortega-Huerta, M., Peterson, A., Phillips, O. & Williams, S. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller, W. (2003) BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Thuiller, W., Lavorel, S., Sykes, M.T. & Araújo, M.B. (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, **12**, 137–152.

Tonni, E.P. (1992) *Tapirus* Brisson, 1762 (Mammalia, Perissodactyla) en el Lujanense (Pleistoceno superior–Holoceno inferior) de la Provincia de Entre Rios, Republica Argentina. *Ameghiniana*, **29**, 3–8.

Uno, K.T., Cerling, T.E., Harris, J.M., Kunimatsu, Y., Leakey, M.G., Nakatsu-kasa, M., and Nakaya, H., 2011, Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 6509–6514.

Vandermeer, J. (1972) Niche theory. *Annual Review of Ecology, Evolution, and Systematics*, **3**, 107-132.

Varela, S., Lobo, J.M., Rodríguez, J. & Batra, P. (2010) Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. *Quaternary Science Reviews*, **29**, 2027-2035.

Werneck, F.P., Nogueira, C., Colli, G.R., Sites, J.W. & Costa, G.C. (2012) Climatic stability in the Brazilian Cerrado: implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, **39**, 1695–1706.

Wing, S.L. & Tiffney, B. H. (1987) Interactions of angiosperms and herbivorous tetrapods through time. The origins of angiosperms and their biological consequences. (ed. by E. M. Friis, W. G. Chaloner and P. R. Crane), pp. 203–224. Cambridge University Press, Cambridge.

Willerslev, E., Gilbert, M., Binladen, J., Ho, S., Campos, P., Ratan, A., Tomsho, L., da Fonseca, R., Sher, A., Kuznetsova, T., Nowak-Kemp, M., Roth, T., Miller, W. & Schuster, S. (2008) Analysis of complete mitochondrial genomes from extinct and extant rhinoceroses reveals lack of phylogenetic resolution. *BMC Evolutionary Biology*, **9**, 95.

Wolfe, J.A. (1978) A Paleobotanical Interpretation of Tertiary Climates in the Northern Hemisphere: Data from fossil plants make it possible to reconstruct Tertiary climatic changes, which may be correlated with changes in the inclination of the earth's rotational axis. *American Scientist*, **66**, 694-703.

Wolfe, J.A. (1985) Distribution of major vegetational types during the Tertiary. The Carbon Cycle and Atmospheric CO2 Natural Variations Archean to Present (ed. by E.T. Sundquist & W.S. Broecker), pp. 357-375. American Geophysical Union, Washington D.C.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and ab-errations in global climate 65 Ma to present. *Science*, **292**, 686–693.

Zimmermann, N.E., Edwards, T.C., Graham, C.H., Pearman, P.B. & Svenning, J.-C. (2010) New trends in species distribution modelling. *Ecography*, **33**, 985-989.

CAPÍTULO 1

A ser submetido para: Global Ecology and Biogeography

Climatic niche and vulnerability to global climate change: an analysis of clade Perissodactyla

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Short Running Title: Vulnerability of Perissodactyla to Climate Change.

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ABSTRACT

Aim We explored the relationship between climate niche and the species distributional properties to evaluate if the vulnerability of Perissodactyla clade is related to the distribution of their climatic niches.

Location Afrotropical, Indomalayan, Neotropical, Paleartic bioregions

Methods The niche properties were estimated using a multivariate analysis. The future potential distribution for 15 species from the Perissodactyla clade was predicted by ecological niche models. We calculated the range changes for each species from the difference between the climatically suitable habitats. Then, we related the ranges changes to the species niche properties, using generalized linear models. To quantify the accessible area for each species, we used two dispersal scenarios.

Results Thirteen Perissodactyla species were considered more specialized in terms of climate conditions, and the marginality was negatively related with tolerance between species. The lowland tapir was close to the origin of the axes, i.e., most general habitat conditions (low marginality) and with greater tolerance. In contrast, the Przewalski's horse was the more specialized. We did not find any correlation between tolerance/marginality and habitat loss, but projections from climate models indicated that five of the species will lose more than 50% of their environmentally suitable areas.

Main conclusions We understand that each species may have unique answer to this threat, once marginal species, of Perissodactyla clade, are not always the most vulnerable to climate change. Although our models did not consider the limitations of dispersal which is important to consider in ecological niche models, especially to species that inhabit endangered regions, such some of

those large herbivores. Furthermore, we must consider that climatic tolerance of a species may be underestimated because some climatically distinct, but tolerable, areas cannot be accessible to the individuals. Thus, changes in the current climatic conditions and the emergence of new climatic scenarios should be considered in future management and conservation strategies.

INTRODUCTION

INTRODUCTION

Climate change is a long-term phenomenon that can affect the biodiversity negatively (Miles *et al*., 2004; Parmesan, 2006; D'Amen *et al*., 2011; Torres *et al*., 2013), with consequences often irreversible (Parmesan & Yohe, 2003; Lapola *et al*., 2009; Leadley *et al*., 2010). It can create cascading effects on ecosystem functioning by changing the interactions between species (Memmott *et al*., 2007; Altermatt, 2010), increasing the vulnerability of thousands of species, eventually driving them to extinction (Thomas *et al*., 2004; Hof *et al.*, 2010; Dawson *et al.*, 2011; Bellard *et al*., 2012). Even if overall habitat suitability does not change in the future, species range can become fragmented and individual populations may not be able to migrate to new environmentally suitable areas (Massot *et al.*, 2008; Vos *et al*., 2008). This poses a challenge for current ecological theory, which in response will need to produce empirical support to understand these changes as well as generate models to predict the vulnerability of species and ecological systems to future impacts.

The vulnerability of a given species to climate change will depend on both its ability to maintain current populations as well as its ability to shift its geographical range to future suitable environments. In general, vulnerability is an integrated measure that quantifies the degree of threats that a species or an ecosystem is susceptible to as well as its inability to cope with adverse impacts of climate change (Smit *et al.*, 2000; Füssel & Klein, 2006; IPCC, 2007). Vulnerability includes three aspects: exposure (external dimension or environmental conditions), sensitivity (internal dimension or intrinsic characteristics of species) and inherent ability of species to adapt to changes (adaptive capacity) (Füssel & Klein, 2006; Williams *et al*., 2008; Dawson *et al.*, 2011). Specifically, species characteristics such as dispersal ability and temperature tolerance can influence the species distribution and, consequently, species vulnerability to climate change (Calosi *et al*., 2008). Recently, a study carried out by Schloss *et al*. (2012) showed that the speed of climate change will most likely exceed the ability of various mammals to respond and, thus, their vulnerability will be higher than it was expected, especially for species with narrower climatic niches.

Furthermore, Thuiller *et al*. (2005) and Broennimann *et al*. (2006) demonstrated that the sensitivity of a species to climate change depends on its geographic range and niche properties, such as niche breadth and marginality. Emphasis has been given to the assumption that marginal species (climate specialists), i.e., species with requirements which do not correspond to the mean climate conditions in an area, should be more susceptible to climate change than generalist species (Swihart *et al*., 2003; Williams *et al*., 2007). Marginal species may be less tolerant in terms of climate and likely to have problems to colonize new areas that may become climatically suitable in the future (Jansson, 2009). Or because they have restricted geographic distributions with little or no opportunity for range expansion (Learmonth *et al*., 2006).

Assessments of vulnerability considering the three components is complex. However, one promising approach involves tools as the ecological niche models (ENMs). They are perhaps the most widely used of all climate change biological models (Hannah, 2011) to evaluate climate change impacts on biodiversity with different conservation purposes (Thomas *et al*., 2004; Thuiller *et al*., 2005; Bradley *et al*., 2010; Araújo *et al*., 2011; Fordham *et al*., 2012; Zimbres *et al*., 2012; Bagchi *et al*., 2013). ENMs have been used more frequently to identify exposure to climate change, one of the three components of vulnerability. Most ENMs are correlative models (Kearney & Porter, 2009) and do not integrate physiological characteristics, such as climatic tolerance, as mechanistic models do (Beerling *et al*., 1995; Thuiller *et al*., 2008). Nevertheless, this evaluation is important given that the intensity of the climate change varies widely among species and the exposure to these alterations is inevitable, especially if we consider the life history and the evolutionary history of the species. For instance, groups such as the Perissodactyla have diversified at least 60 million years ago and have coped with a variety of climatic fluctuations during this time.

However, each species can be unique in its response to climate. Exploring the relationship between climate niche and distributional properties of species, such as niche position, tolerance and range size, and their sensitivity to climate change can provide information about the potential distribution of climatic niche of the Perissodactyla may be related to their vulnerability. We used projections from ENMs to examine these relationships. We expected that: 1) Marginal species (outlying niches) and with lower climatic tolerance have more restricted potential distribution, making them more vulnerable; 2) Species with lesser tolerance and more marginal are predicted to have greater habitat loss, in the future.

METHODS

Studied species

The Perissodactyla order or odd-toed ungulates is a very old group of mammals, the first appearing in the beginning of the Eocene, approximately 55 Mya, and comprising a group of strict herbivores adapted for running and dietary specialization (Janis, 2008; Steiner & Ryder, 2011). In the fossil record, there are representative specimens from five main superfamilies

(Holbrook, 1999) and currently, only three superfamilies and three families are present (Equidae, Rhinocerotidae and Tapiridae) (Rose, 2006). The family Equidae includes only one genus and seven species survive to the present day: four in Africa (African wild ass *E. africanus*, Grevy's zebra *E. grevyi*, plains zebra *E. quagga* and mountain zebra *E. zebra*)*;* and three Asian horses (Przewalski's horse *E. ferus*, Asiatic wild ass *E. hemionus*, Kiang *E. kiang*) (Moehlman, 2002). The family Tapiridae includes five living species of tapirs that belong to a single genus: three in South America (lowland tapir *Tapirus terrestris*, *T. kabomani* (new species) and mountain tapir *T. pinchaque*), one in Central America and northwestern South America (central american tapir *T. bairdii*), and one in Southeast Asia (Malayan tapir *T. indicus*) (Cozzuol *et al.*, 2013; Medici, 2011). The family Rhinocerotidae includes five surviving species of rhinoceroses in four genera: two species of African rhinoceros -- the black rhino (*Diceros bicornis*) and the white rhino (*Ceratotherium simum*); and three species of Asian rhinos: the Indian rhinoceros (*Rhinoceros unicornis*), the Javan rhinoceros (*R. sondaicus*), and the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) (Foose & van Strien, 1997; Emslie & Brooks, 1999). The estimation of divergence times used in the analysis was based in the complete phylogeny of living Perissodactyla (Equidae, Rhinocerotidae and Tapiridae), published by Steiner & Ryder (2011).

Species records

We compiled 829 occurrence records for 15 species of Perissodactyla (Table 1). The Javan rhinoceros was not included in the analysis, since the number of records is very small and the species in present in only two areas and very small populations (IUCN, 2012). The set of geographic records of Tapiridae was mostly gathered from data provided by experts from the IUCN/SSC Tapir Specialist Group (TSG). Information on the species of the family

Rhinocerotidae and Equidae were mostly compiled from previously published action plans and other documents prepared and provided by IUCN/SSC Specialist Groups (Foose & van Strien, 1997; Emslie & Brooks, 1999; Moehlman, 2002). The IUCN/SSC rhino specialist groups do not release accurate locations of rhinos in the wild. Hunting has strongly impacted populations over time, therefore much of the data refer to the location of the region where the species occur.

Environmental Variables and Climate Change Models

Environmental data were obtained from the WorldClim Database (www.worldclim.org) and included six variables (from 19 variables available): annual mean temperature, temperature seasonality (coefficient of variation), mean temperature of the driest quarter, annual precipitation, precipitation seasonality (coefficient of variation) and precipitation during the warmest quarter. These data were used at a 5’ spatial resolution (~ 9 km of cell-side size).

We used future climate datasets derived from three general circulation models (GCMs), for the year 2080 (www.ccafs-climate.org/data): 1) Canadian Centre for Climate Modelling and Analysis (CCCma) Coupled Global Climate Model (CGCM2), Second Version (Flato & Bôer, 2001); 2) CSIRO Atmospheric Research Mark 2b Climate Model (Hirst *et al.*, 1996, 2000), and 3) HadCM3, which is the coupled ocean–atmosphere general circulation model developed by the Hadley Centre for Climate Prediction and Research (Gordon *et al.*, 2000). These GCMs projected the mean climate under a rather extreme scenario, the A2 - considered more severe, assuming 1 % yr^{-1} CO2 increase and do not take into account effects of sulfate aerosols - describes a heterogeneous world, in continuously increasing global population. All climate layers were used at a 5’ spatial resolution.

Modeling approach

We use MaxEnt Software (Version 3.3.3e) (Phillips *et al*., 2006) to predict the size of the current distribution and potential future habitats and thus relate to characteristics of climatic niches of species and their distributions. MaxEnt is a general-purpose machine-learning approach that uses a simple mathematical formulation for modeling geographic distribution of species with presence-only data (Phillips *et al*., 2006). Absence data are generated by randomly selecting ‘‘pseudo-absence’’ points or the background of the area. MaxEnt models were built using 1000 iterations, the logistic output format, as well as removing all duplicates. Recent studies have shown that MaxEnt models suffer from over-parameterization leading to transferability problems (Peterson *et al*., 2007) that may effect its predictions, especially for future climate (Elith *et al*., 2010). In order to control for over-parameterization, we developed the MaxEnt models using the “simple” setting, including only the two features: (i) linear, which constrains the output distribution for each species as having the same expectation for each of the continuous environmental variables and the sample locations for that species; and (ii) the quadratic feature, which models the tolerance of the species to variation from its optimal conditions (Phillips *et al*., 2006; Phillips & Dudík, 2008). This choice generated models with a substantial decrease in the total number of parameters, which helps control known problems of MaxEnt related to model transferability (Peterson *et al*., 2007; Elith *et al*., 2010).

Models were evaluated through True Skill Statistics (TSS), which seems to be more appropriate when compared to other similar measures (Liu *et al.*, 2011), mostly because it is less sensitive to differences in prevalence among models (Allouche *et al.*, 2006). TSS takes into account both omission and commission errors and ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random. And selected a threshold-independent measure, the AUC that values range from 0 to 1, where a score of 1 indicates perfect discrimination and a score of 0.5 implies discrimination that is no better than random (Elith *et al.*, 2006).

The thresholds are used to convert continuous species distribution model outputs in binary maps predicting presence/absence of each species. Values smaller than the threshold were considered zero whereas values higher than threshold were considered one. For this, we adopted the “ROC plot-based approach” threshold, which minimizes the commission error. The potential future distributions were obtained by intersection the binary maps from three AOGCMs resulting from modeling procedure, and considering one scenario more conservative, in which only the areas predicted by the three common climatic models were considered. The binary maps are included as Supporting Information (Appendix S1).

Species range shift

The evaluation of the shift in environmentally suitable areas, both in the past as well as in the future, has been carried out by different research studies (Thuiller *et al*., 2005; Broennimann *et al*., 2006; Waltari & Guralnick, 2009; Nenzén & Araújo, 2011; Loyola *et al*., 2012). Changes in distribution range for each species were calculated from the difference between the current climatically suitable habitat, defined as the grid cells suitable, relative to the number of grid cells lost or gained under the scenario of climate change. Thus, based on these preliminary studies, we used the following metrics of changes in climatically suitable areas: 1) Of the currently suitable areas, the remaining grid cells, predicted to become unsuitable, resulted in the percentage of habitat loss (proportional loss); 2) The relative change of the distribution (values >1 and <1 represent expanding and shrinking climates, respectively) calculated by dividing the area occupied under the future projections by the area occupied under current climates; 3) We also quantified the number of overlapping suitable cells in the present and the future.

Quantification of accessible area

Recently, Barve *et al*. (2011) discussed the importance of considering "M", one of the three classes of factors of the BAM diagram, proposed by Soberón & Peterson (2005). "M" refers to areas of the world that have been accessible to a given species over certain periods of time. Barve *et al*. (2011) identified three approaches to estimate "M" that should be considered before starting the analysis and we selected the first approach, that uses the selection of biotic regions and is considered more operational. Using this approach, we adjusted the models to consider the biogeographic regions - Neotropical, Afrotropical, Paleartic and Indo-Malayan - where each species of the Perissodactyla clade occurs.

The modelling process can produce areas outside M (where the species cannot occur) will generally be predicted at lower suitability levels or not connected to areas where there are occurrence records of the species. According to Barve et al. (2011), it is crucial to understand the areas which the species can potentially visit. Thus, in order to be able to to quantify the accessible areas for each species in this study two dispersal scenarios were used, unlimited or no dispersal. The first scenario assumes that species can track their shifting climate envelopes. The second assumes that suitable habitat and climate for the establishment, survival, and reproduction if a given species will only exist in areas where the predicted current and future climate envelopes overlap and that individuals will disperse directly toward the closest suitable grid cell. This means that we only considered as accessible the suitable areas that have current records of the species and those connected to them.

Quantification of climatic niche

For characterization of climatic niches of species we used an ordination approach termed ‘‘Outlying Mean Index’’ (OMI), published by Dolédec *et al*. (2000). OMI is a multivariate method based on the evaluation of marginality of species, *i.e.*, gives the species average position (‘‘niche position’’) within environmental space, which in turn represents the distance between the climatic conditions used by the species and the mean environmental conditions of the sampling area (origin G) (Dolédec *et al*., 2000). These conditions were measured as a function of 19 climatic variables, which are detailed in Hijmans *et al*. (2005), for the entire distribution area of Perissodactyla clade. A high OMI index for a given species is interpreted as higher habitat specialization (Galassi *et al.*, 2009). We used 1000 Monte Carlo randomizations in order to access the statistic significance of the marginality of each taxon and to determine the mean marginality of the species (Dolédec *et al.*, 2000).

The variability of species niches was also represented by two others components: tolerance index or niche breadth, and residual tolerance. The first quantifies the variability in the species response to environmental variables, which is presented by the standard deviation along their OMI axes (Thuiller *et al*., 2004, 2005). The second represents the proportion of variability in habitat that is not explained by measured environmental variables. Furthermore, OMI analysis also compute the total inertia, which expresses the influence of environmental variables on the separation of species niche and contributes to the characterization of the overall overlap of the species global niche (Dolédec *et al.*, 2000). OMI analysis was performed using the ade-4 package in R (Chessel *et al*., 2004, R Development Core Team 2008).

RESULTS

Of the 15 species analyzed, 13 can be considered more specialized in terms of climate, *i.e.*, high values of OMI (Table 2). Two tapir species (*T. terrestris* and *T. bairdii*) are among the most generalists, with OMI values ≤50%; and two horses (*E. ferus* and *E. kiang*) are the most specialists (OMI values ≥90%). Thirteen of the 15 species showed a significant deviation of their niche from the origin suggesting a more marginal position in the environmental space.

The response of climatic tolerance and evolutionary time may present stationary (equal rate of divergence through time) and non-stationary (varying rates of divergence) behavior. We found a strong non-stationarity in observed variables, with contrasting directions between recent and early species. Recent species as *T. pinchaque* and the equids increase tolerance with divergence time, but early species which includes the rhinos and the other three tapir species decrease tolerance as the divergence time among species increase (Fig. 2). The threshold for this difference appears to be near 3 Mya.

The marginality is negatively related to tolerance among species ($R^2 = 0.785$; $p<0.05$; Fig. 1). The lowland tapir was close to the origin of the axes, *i.e.*, most general habitat conditions (low marginality) and with greater tolerance. In contrast, the Przewalski's horse was the species with most specialized climatic niche, showing high OMI value and less tolerance. Three species, mountain zebra, Sumatran rhinoceros and mountain tapir showed similar OMI value (Table 2), but the mountain zebra is the less tolerant of the three.

We did not find any correlation between tolerance/marginality and habitat loss, which contradicts our original hypothesis that Perissodactyla species with high marginality and low tolerance would be more sensitive to climate change. However, projections from three climate models indicated five species -- four horses *E. ferus*, *E. grevyi*, *E. quagga* and *E. zebra*; and one tapir *T. terrestris* -- could lose more than 50% of suitable environmentally area. In addition, five other species are predicted to lose area in the future: *Diceros bicornis* and *C. simum*, based on CCCma and HadCM3 climate models; *T. pinchaque* and *Dicerorhinus sumatrensis,* based on CSIRO and HadCM3, respectively, and *E. kiang* based on CCCma and CSIRO (Table 4).

Three of the ten species that were predicted to lose suitable area are considered more generalist in terms of climate according with OMI values. Furthermore, the models predict that the African ass, Baird's tapir and Indian rhinoceros will have a gain of environmentally suitable areas. The AUC and TSS values for all resulting models of each species show an excellent fit and the ROC threshold choice was reinforced by TSS values, which were higher than TSS values from LPT in the three climate models (Table 3).

We did not find correlation between potential current distribution predicted by models and tolerance/marginality values, as well as the suitable habitat in the future not increased with niche position (marginality) and breadth (tolerance). Restricting the potential distribution area of the species, there is a decrease on average of 1.50 times compared to the current distribution estimated by MaxEnt (Fig. 3). The species with higher reduction of areas were *T. bairdii* and *E. hemionus*. When evaluating by bioregion the reduction of distribution area is predicted to occur most intensely (>50%) in species located in the Afrotropical region, regardless of the climate model. Five of the six species can be considered vulnerable in this context, except African ass inhabiting regions in eastern Africa.

DISCUSSION

Our original prediction that more marginal Perissodactyla species of would be less tolerant was corroborated by the results, as it was suggested by previous studies (Swihart *et al*., 2003; Thuiller *et al*., 2005). Furthermore, contradicting our expectations, the oldest species were not found to be more tolerant than the more recent species. In addition, we did not identify a relationship between niche properties and the vulnerability of each species, expressed here by the size of environmentally suitable areas and loss of these areas in the future. Moreover, we observed that marginal species are not always the most vulnerable to climate change, but we understand that each species may present a unique response to this threat, as previously discussed by Broennimann *et al*. (2006) and I-Ching Chen *et al*. (2011). Thus, we suggest that species sensitivity to climate change may depend on their ecological characteristics related to regional patterns of exposure to climate change.

These large herbivore mammals have survived and persisted through major climatic events since the Eocene. Today, they are distributed in four bioregions (Afrotropical, Neotropical, Paleartic and Indomalayan), which are predicted to be impacted by climate change in different ways and degrees of intensity (IPCC, 2007). Our data suggest that there was an increase in the climatic tolerance from approximately 26 kyr BP to 3.0 kyr BP and these values decreased until the period of more recent species origin. One possible explanation is that the diversification of species with low tolerance occurred in critical climatic periods and, the persistence of these species may have been favored, probably by resistance, i.e., the ability of a species to withstand an environmental perturbation. For instance, the Asian species, the first to diversify (Oligocene) (Steiner & Ryder, 2011) experimented an episode of extreme cold, with temperatures starting to rise again in the late Oligocene (Zachos *et al*., 2001). In addition, the more recent species, as the genus *Equus* and *T. pinchaque* were exposed to relatively rapid climate shifts during the Quaternary.

Although we have not investigated if there is niche conservatism here, there are two scenarios related to this phenomenon: i) species may have evolved their temperature niches (tolerance) and are, hence, able to readily cope with environmental changes (Wiens *et al.*, 2010; Cooper *et al.*, 2011); ii) species may have retained their climatic niche over time and their niche has always been restricted. The degree of niche conservatism in mammals varies among tropical and temperate, large-ranged and small-ranged, and generalist and specialist species (Cooper *et al.*, 2011).

There is an assumption that generalist species can tolerate a wide range of environmental conditions and, thus, will have a larger range size than specialist species with a more restricted environmental niche (Brown, 1984). In this context, we identified the species with extreme traits, in terms of tolerance and marginality, and both are predicted to lose climatically suitable areas. The lowland tapir is the more generalist species and the Przewalski's horse is the more specialized. The lowland tapir has the widest geographic distribution among the Perissodactyla. However, the species faces several threats throughout its distribution including habitat loss and fragmentation, unsustainable hunting, road-kill and infectious diseases (Medici *et al.*, 2012). Furthermore, our models predict a marked loss in the highly suitable areas, indicating suitable areas in the future, principally, in portions of the Brazilian Atlantic Forest, where the species is already endangered (Gatti *et al.*, 2011; Medici *et al.*, 2012).

The geographic ranges of all species of the Equidae family have declined significantly during the past 200 years (Moehlman, 2002). The Przewalski's horse is regionally extinct in eight countries, which occurred until the late 18th century (Sokolov & Orlov, 1986). The species formerly inhabited steppe and semi-desert habitats, but most of this range became degraded or was occupied by domestic livestock (Van Dierendonck *et al*., 1996). Today, the species occurs only in Mongolia, a reintroduced population (IUCN, 2012). The models predict a loss of 80% of the environmentally suitable areas in relation to the current climate conditions, especially in the Gobi desert. The models indicated a gain of new suitable areas in the East Siberian Taiga, located in Russia, in which the species occurred historically. However, whether the species would persist in this ecoregion, through a possible reintroduction, is not possible to say. Or maybe these new potential areas predicted as environmentally suitable may be inaccessible to the species, especially by habitat loss and fragmentation (Thomas *et al*., 2004). Thus, the synergy between low climatic tolerance, preference for specific habitats (Kaczensky *et al*., 2008; Van Dierendonck & de Vries, 1996), competition with livestock, increasing land use pressure and climate change can intensify the susceptibility to extinction.

The mountain zebra, mountain tapir and Sumatran rhinoceros are equally marginal, *i.e.* are positioned at close distance from the average conditions of the environmental space sampled. These species inhabit mountainous regions, but with different altitudes and specific characteristics: 1) Mountain tapirs occur in Andean mountains in the South America, in five habitat types between 2200–4800 m (Downer, 1997; Medici, 2011); 2) Mountain zebras occur in Namibia and South Africa (Eastern Cape Province, Northern Cape Province), particularly in broken mountainous and escarpment areas up to around 2000 m (Novellie, 2008); and 3) Sumatran rhinoceros occur in montane forests in Sumatra (> 1000 m) (IUCN, 2012). However, different species can present different sensitivities to climate change (Williams *et al*., 2008) and these mammals respond idiosyncratically to climate change. Amont the three of them, mountain zebras arepredicted to lose more suitable areas according with our results.

These habitats are generally occupied by species with narrow habitat tolerance and low dispersal capacity, which may increase the risk from the environmental effects of climate change (Broennimann *et al*., 2006; Ruiz *et al*., 2008). Furthermore, these habitats have been drastically impacted by extensive agriculture and livestock grazing, threatening the water supply, for example, in high mountain Andean forests and *páramos* (high Andean savanna/grassland habitat) (Anderson *et al*., 2011). A good example is *D. sumatrensis*, a species that although being confined to protected lowland forests or high-altitude forests that are largely inaccessible to conversion, is currently threatened by small population size (Uryu *et al*., 2010; Zafir *et al*., 2011). Thus, these large herbivores, with distribution restricted by climate, declining populations and close association with perennial water sources, may be unable to adapt to new climate conditions and, hence, have a higher risk of extinction (Isaac, 2009; Wasserman *et al*., 2013).

In theory, a species located in regions most exposed to climate change is expected to be more sensitive than a species in a region less exposed (Thuiller *et al*., 2005). The Intergovernmental Panel on Climate Change (IPCC) projects that the average annual temperature in South Asia and Tibet, region of the occurrence of *E. kiang* and *E.hemionus*, will increase by 3-4ºC by 2080-2099, while annual precipitation is expected to increase throughout this region as well (Christensen *et al*., 2007). These species are now under different threats levels -- the Kiang is considered as Least Concern and the Asiatic Wild ass is listed as Endangered (IUCN, 2012). However, although Kiang has a wide distribution and large populations, it is more climatically specialist than Asiatic Wild ass and according to the models. Kiang is predicted to lose nearly 55% of its suitable habitats, being considered more vulnerable to climate change when compared to the Asiatic wild ass. In this approach, is interesting to discuss the climate change impact in each bioregion de occurrence of the species, because the response of these mammals can be linked to the characteristics of the region and especially as the changes can affect the vegetation. Obviously, the consequences of this impact to large herbivores can be drastic, principally if we associate the alterations in the landscape by anthropogenic activities and the intrinsic traits of the species. For example, studies in South Africa identified that species with distributions in Fynbos and the Namib Desert biomes, and the Cape Floristic Region, will suffer consequences of future global changes (Broennimann *et al*., 2006; Yates, 2009; Abbott & Le Maitre, 2010), and consequently the larger part of wildlife, such as the equids and rhinoceros, that today already at critical levels of threat will be affected.

Some species that are currently listed as Endangered or Critically Endangered are predicted to gain environmentally suitable areas based in our models, such as the African Wild ass and the Baird's tapir. Nevertheless, we have to consider if the areas are geographically available/or environmentally accessible. Our models do not consider dispersal trajectories: topography, rivers, roads, cities and other barriers to dispersal. It is important to consider dispersal limitations (the "M" set of Soberón & Peterson, 2005) in the models and discussions, since the loss of suitable areas in the future may restrict access to new suitable areas (Barve *et al*., 2011). Furthermore, we must consider the idea that climatic tolerance of a species may be underestimated because some climatically distinct areas, but tolerable, cannot be accessible to the individuals due to non-climatic constraints on dispersal (e.g. urban areas, roads, industrial and agricultural belts, intense used rivers). Peterson *et al.* (2011) defined this as the "existing fundamental niche".

One extremely important variable for modeling future distribution and which is never included in projections is that dispersal barriers, mostly related to economic development, are expected to increase, particularly in developing countries. These barriers may decrease available suitable habitat for the majority of species and became a dominant effect on their future distribution. It is quite possible that most of these mammals will depend on protected areas for their conservation in the future, notwithstanding the environment within them may change, especially with climate change (Wiens *et al.*, 2011; see Chapter 3). Changes in the current climate conditions and emergence of new conditions should be taken into consideration in future management actions. The creation and establishment of protected areas should consider potential range shifts for both both threatened and non-threatened species.

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REFERENCES

Abbott, I. & Maitre, D.L. (2009) Monitoring the impact of climate change on biodiversity: The challenge of megadiverse Mediterranean climate ecosystems. *Austral Ecology*, **35**, 406–422.

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

Altermatt, F. (2010) Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change. *Ecology letters*, **13**, 1475–1484.

Anderson, E.P., Marengo, J., Villalba, R., Halloy, S., Young, B., Cordero, D., Gast, F., Jaimes, E. & Ruiz, D. (2011) Consequences of climate change for ecosystems and ecosystem services in the tropical Andes. Climate Change and Biodiversity in the Tropical Andes (ed. by S.K. Herzog, R. Martínez, P.M. Jørgensen and H. Tiessen), pp. 1-5. MacArthur Foundation, Inter-American Institute for Global Change Research (IAI), Scientific Committee on Problems of the Environment (SCOPE).

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

Bagchi, R., Crosby, M., Huntley, B., Hole, D.G., Butchart, S.H.M., Collingham, Y., Kalra, M., Rajkumar, J., Rahmani, A., Pandey, M., Gurung, H., Trai, L.T., Quang, N.V. & Willis, S.G. (2013) Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty.*Global Change Biology*, **19**, 1236-1248.

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

Beerling, D.J., Huntley, B. & Bailey, J.P. (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *Journal of Vegetation Science*, **6**, 269–282.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology letters*, **15**, 365–377.

Boyd, L. & King, S.R.B. (2011) *Equus ferus*. IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2.

Bradley, B.A., Wilcove, D.S. & Oppenheimer, M. (2009) Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions*, **12**, 1855–1872.

Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.M.R. & Guisan, A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology*, **12**, 1079–1093.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.

Calosi, P., Bilton, D. & Spicer, J. (2008) Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biology letters*, **4**, 99–102.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, **333**, 1024-1026.

Chessel, D., Dufour, A.-B. & Thioulouse, J. (2004) The ade4 package-I- One-table methods. *R News*, **4**, 5–10.

Cifelli, R.L. (1981) Patterns of evolution among Artiodactyla and Perissodactyla (Mammalia). *Evolution*, 35, 433–440.

Cooper, N., Freckleton, R. & Jetz, W. (2011) Phylogenetic conservatism of environmental niches in mammals. *Proceedings. Biological sciences / The Royal Society*, **278**, 2384–2391.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A. & Whetton, P. (2007) Regional Climate Projections. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (ed. By S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignorand H.L. Miller). Cambridge University Press. Cambridge, United.

D'Amen, M., Bombi, P., Pearman, P.B., Schmatz, D.R., Zimmermann, N.E. & Bologna, M.A. (2011) Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? *Biological Conservation*, **144**, 989–997.

Dawson, T., Jackson, S., House, J., Prentice, I. & Mace, G. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science (New York, N.Y.)*, **332**, 53–58.

Dolédec, S., Chessel, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.

Downer, C.C. (1997). Status and Action Plan of the Mountain Tapir (*Tapirus pinchaque*). Tapirs - Status Survey and Conservation Action Plan (ed. by D.M. Brooks, R.E. Bodmer and S. Matola), pp. 10-22. IUCN, Gland, Switzerland and Cambridge, UK.

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

Emslie, R.H. & Brooks, M. (1999) African Rhinos: Status Survey and Conservation Action Plan. IUCNISSC African Rhino Specialist Group, Gland and Cambridge.

Fisher-Reid, M., Kozak, K. & Wiens, J. (2012) How is the rate of climatic-niche evolution related to climatic-niche breadth? *Evolution; international journal of organic evolution*, **66**, 3836–3851.

Flato, G.M. & Boer, G.J. (2001). Warming asymmetry in climate change simulations. *Geophysical Research Letters*, **28**, 195-198.

Fordham, D.A., Akçakaya, H.R., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C. & Brook, B.W. (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.

Foose, T.J. & van Strien, N. (1997) Asian Rhinos – Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland.

Füssel, H.-M. & Klein, R.J.T. (2006) Climate Change Vulnerability Assessments: An Evolution of Conceptual Thinking. *Climatic Change*, **75**, 301–329.

Galassi, D.M.P., Stoch, F., Fiasca, B., Lorenzo, T.D. & Gattone, E. (2009) Groundwater biodiversity patterns in the Lessinian Massif of northern Italy. *Freshwater Biology*, **54**, 830–847.

Gatti, A., Brito, D. & Mendes, S.L. (2011) How many lowland tapirs (*Tapirus terrestris*) are needed in Atlantic Forest fragments to ensure long-term persistence? *Studies on Neotropical Fauna and Environment*, **46(2)**, 77-84.

Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B. & Wood, R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16**, 147-168.

Hannah, L.J. (2011) Climate Change Biology. Academic Press, Burlington, MA.

Hirst, A.C., Gordon, H.B. & OFarrell, S.P. (1996) Global warming in a coupled climate model including oceanic eddy-induced advection. *Geophysical Research Letters*, **23**, 3361-3364.

Hirst, A.C., OFarrell, S.P. & Gordon, H.B. (2000). Comparison of a Coupled Ocean-Atmosphere Model with and without Oceanic Eddy-Induced Advection. Part I: Ocean Spinup and Control Integrations. *Journal of Climate*, **13**, 139-163.

Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography*, **33**, 242-250.

Holbrook, L.T. (1999) The phylogeny and classification of tapiromorph perissodactyls (Mammalia). *Cladistics*, **15**, 331-350.

IPCC, Climate Change. (2007) Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, Cambridge.

Isaac, J. (2009) Effects of climate change on life history: implications for extinction risk in mammals. *Endangered Species Research*, **7**, 115–123.

IUCN (2012). IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>. Downloaded on **01 June 2013**.

Janis, C.M. (2008) An evolutionary history of browsing and grazing ungulates. The Ecology of Browsing and Grazing (ed. by I.J. Gordon, H.H.T. Prins), pp. 21–45. Berlin: Springer.

Jansson, R. (2008) Extinction risks from climate change: macroecological and historical insights. *F1000 biology reports*, **1**, 1-5.

Kaczensky, P., Ganbaatar, O., Wehrden, H. von & Walzer, C. (2008) Resource selection by sympatric wild equids in the Mongolian Gobi. *Journal of Applied Ecology*, **45**, 1762–1769.

Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.

Lapola, D.M., Oyama, M.D. & Nobre, C.A. (2009) Exploring the range of climate biome projections for tropical South America: The role of CO 2 fertilization and seasonality. *Global Biogeochemical Cycles*, **23**, 1-16.

Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarres, J.F., Proenca & V., Scharlemann, J.P.W. (2010) Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. Secretariat of the Convention on Biological Diversity (ed. by Diversity SotCoB), pp. 1-132. Published by the Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 50.

Learmonth, J., MacLeod, C., Santos, M., Pierce, G., Crick, H. & Robinson, R. (2006) Potential effects of climate change on marine mammals. *Oceanography and Marine Biology*, **44**, 431.

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

Loyola, R.D., Lemes, P., Nabout, J.C., Trindade-Filho, J., Sagnori, M.D., Dobrovolski, R. & Diniz-Filho, J.A.F. (2012) A straightforward conceptual approach for evaluating spatial conservation priorities under climate change. *Biodiversity and Conservation*, **22**, 483-495.

Massot, M., Clobert, J. & Ferrière, R. (2008) Climate warming, dispersal inhibition and extinction risk.*Global Change Biology*, **14**, 461–469.

Medici, E.P. (2011). Family Tapiridae (Tapirs). Handbook of the Mammals of the World, Volume 2: Hoofed Mammals (ed. by D.E. Wilson, R.A. Mittermeier), pp. 182–204. Lynx Edicions, Spain.

Medici, E.P., Flesher, K., Beisiegel, B.M., Keuroghlian, A., Desbiez, A.L.J., Gatti, A., Pontes, A.R.M., Campos, C.B., Tófoli, C.F., Moraes, E.A., Azevedo, F.C., Pinho, G.M., Cordeiro, J.L.P., Santos, T.S.Jr., Morais, A.A., Mangini, P.R., Rodrigues, L.F. & Almeida, L.B. (2012).

Avaliação do Risco de Extinção da Anta brasileira *Tapirus terrestris* Linnaeus, 1758, no Brasil. *Biodiversidade Brasileira Ano II*, **3**, 103-116.

Memmott, J., Craze, P., Waser, N. & Price, M. (2007) Global warming and the disruption of plant-pollinator interactions.*Ecology letters*, **10**, 710–717.

Miles, L., Grainger, A. & Phillips, O. (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, **13**, 553–565.

Moehlman, P.D. (2002) Equids: Zebras, Asses and Horses. Status Survey and Conservation Action Plan, pp. 2-10. IUCN, Gland, Switzerland.

Nenzén, H.K. & Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling*, **222**, 3346-3354.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

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

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Nakamura, M., Martinez-Meyer, E. & Araújo, M. B. (2011) Ecological niches and geographical distributions. Princeton University Press, Princeton, New Jersey, USA.

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

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

Rose, K.D. (2006) The Beginning of the Age of Mammals. Baltimore: Johns Hopkins Univ. Press.

Ruiz, D., Moreno, H.A., Gutierrez, M.E. & Zapata, P.A. (2008) Changing climate and endangered high mountain ecosystems in Colombia. *Science of the Total Environment*, **398**, 122-132.

Schloss, C., Nuñez, T. & Lawler, J. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 8606–8611.

Smit, B., Burton, I., Klein, R. & Wandel, J. (2000) An anatomy of adaptation to climate change and variability. *Climatic Change*, **45**, 223–251.

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1-10.

Sokolov, V.E. & Orlov, V.N. (1986) Introduction of Przewalski horses into the wild. The Przewalski Horse and Restoration to its Natural Habitat in Mongolia. *FAO Animal Production and Health*, **61**, 77–88.

Steiner, C.C. & Ryder, O.A. (2011) Molecular phylogeny and evolution of the Perissodactyla. *Zoological Journal of the Linnean Society*, **163**, 1289–1303.

Swihart, R.K., Gehring, T.M., Kolozsvary, M.B. & Nupp, T.E. (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and Distributions*, **9**, 1–18.

Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., Erasmus, B., De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A., Midgley, G., Miles, L., Ortega-Huerta, M., Peterson, A., Phillips, O. & Williams, S. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller, W., Lavorel, S., Midgley, G.F., Lavergne, S. & Rebelo, T. (2004) Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* species in the Cape Floristic Region. *Ecology*, **85**, 1688 –1699.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137-152.

Torres, R., Jayat, J.P. & Pacheco, S. (2013) Modelling potential impacts of climate change on the bioclimatic envelope and conservation of the Maned Wolf (Chrysocyon brachyurus). *Mammalian Biology - Zeitschrift für Säugetierkunde*, **78**, 41-49.

Uryu, Y., Purastuti, E.P., Laumonier, Y., Setiabudi, A. & STUWE, M. (2010) Sumatra Snapshots: 1985–2008–2023. The Past, Present, and Future of Sumatra's Forests and Wildlife and What It Means for Our Climate. WWF–Indonesia Technical Report. Jakarta, Indonesia.

Van Dierendonck, M. & Wallis de Vries, M.F. (1996) Ungulate reintroductions: experiences with takhi or Przewalski horse (*Equus ferus przewalskii*) in Mongolia. *Conservation Biology*, **10**, 728-740.

Van Dierendonck, M., Bandi, N., Batdorj, D., Dugerlham, S. & Munkhtsog, B. (1996) Behavioural observations of reintroduced takhi or Przewalski horses (*Equus ferus przewalskii*) in Mongolia. *Applied Animal Behaviour Science*, **50**, 95-114.

Vos, C.C., Berry, P., Opdam, P., Baveco, H., Nijhof, B., O’Hanley, J., Bell, C. & Kuipers, H. (2008) Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology*, **45**, 1722–1731.

Waltari, E. & Guralnick, R.P. (2009) Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. *Journal of Biogeography*, **36**, 148-161.

Wasserman, T.N., Cushman, S.A., Littell, J.S., Shirk, A.J. & Landguth, E.L. (2012) Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context. *Conservation Genetics*, **14**, 529–541.

Wiens, J., Ackerly, D., Allen, A., Anacker, B., Buckley, L., Cornell, H., Damschen, E., Jonathan Davies, T., Grytnes, J.-A., Harrison, S., Hawkins, B., Holt, R., McCain, C. & Stephens, P. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters*, **13**, 1310–1324.

Wiens, J.A., Seavy, N.E. & Jongsomjit, D. (2011) Protected areas in climate space: What will the future bring? *Biological Conservation*, **144**, 2119–2125.

Williams, J., Jackson, S. & Kutzbach, J. (2007) Projected distributions of novel and disappearing climates by 2100 AD.*Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5738–5742.

Williams, S., Shoo, L., Isaac, J., Hoffmann, A. & Langham, G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS biology*, **6**, 2621–2626.

Yates, C.J., Elith, J., Latimer, A.M., Maitre, D.L., Midgley, G.F., Schurr, F.M. & West, A.G. (2009) Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: Opportunities and challenges. *Austral Ecology*, **35**, 374–391.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.

Zafir, A.W.A., Payne, J., Mohamed, A., Lau, C.F., Sharma, D.S.K., Alfred, R., Williams, A.C., Nathan, S., Ramono, W.S. & Clements, G.R. (2011) Now or never: what will it take to save the Sumatran rhinoceros Dicerorhinus sumatrensis from extinction? *Oryx*, **45**, 225–233.

Zimbres, B.Q.C., Aquino, P.D.P.U. de, Machado, R.B., Silveira, L., Jácomo, A.T.A., Sollmann, R., Tôrres, N.M., Furtado, M.M. & Marinho-Filho, J. (2012) Range shifts under climate change and the role of protected areas for armadillos and anteaters. *Biological Conservation*, **152**, 53–61.

BIOSKETCH

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Author contributions: A.G., C.C.N. and P.M.J. conceived the ideas; A.G. collected the data; N.M.T., C.C.N and P.M.J. analyzed the data; and A.G. led the writing.

TABLES

Table 1. Number of occurrence records (N) for each species of Perissodactyla clade.

Family	Species	Geographic Range	N
Tapiridae	*Tapirus terrestris*	South American	516
Tapiridae	*Tapirus pinchaque*	South American	106
Tapiridae	*Tapirus bairdii*	Central and northern South America	53
Tapiridae	*Tapirus indicus*	Asia	8
Rhinocerotidae	*Ceratotherium simum*	Africa	14
Rhinocerotidae	*Diceros bicornis*	Afica	18
Rhinocerotidae	*Dicerorhinus sumatrensis*	Asia	7
Rhinocerotidae	*Rhinoceros unicornis*	Asia	7
Equidae	*Equus africanus*	Africa	9
Equidae	*Equus ferus*	Asia	5
Equidae	*Equus grevyi*	Africa	18
Equidae	*Equus hemionus*	Asia	16
Equidae	*Equus kiang*	Asia	8
Equidae	*Equus quagga*	Africa	25
Equidae	*Equus zebra*	Africa	19
Total			**829**

Table 2. Niche parameters of 15 Perissodactyla species. The outlying mean index (OMI), the tolerance index (Tol), and the residual tolerance (RTol) are given as percentages of variability. Species are arranged in decreasing order of marginality (OMI).

Species	Inertia	OMI	TOL	RTol
Przewalski's horse (*Equus ferus*)	181.59	99.20	0.40	0.40
Kiang (*Equus kiang*)	141.05	95.40	1.20	3.40
African Wild ass (*Equus africanus*)	24.97	85.00	3.10	11.90
Indian rhinoceros (*Rhinoceros unicornis*)	25.64	81.80	1.90	16.30
Asiatic Wild ass (*Equus hemionus*)	98.04	79.30	6.00	14.70
Mountain tapir (*Tapirus pinchaque*)	27.85	78.90	7.50	13.70
Mountain zebra (*Equus zebra*)	25.68	78.70	1.90	19.50
Sumatran rhinoceros (*Dicerorhinus sumatrensis*)	11.80	78.60	3.40	18.00
Grevy's zebra (*Equus grevyi*)	17.23	75.00	2.80	22.20
White rhino (*Ceratotherium simum*)	16.17	72.00	12.30	15.80
Black rhino (*Diceros bicornis*)	15.42	66.50	7.60	26.00
Plain zebra (*Equus quagga*)	14.48	62.00	6.30	31.70
Malayan tapir (*Tapirus indicus*)	13.72	51.40	8.30	40.30
Baird's tapir (*Tapirus bairdii*)	16.12	43.00	20.40	36.70
Lowland tapir (*Tapirus terrestris*)	11.61	10.90	21.40	67.80

Table 3. The AUC (training data) and TSS values for each of the thresholds (ROC and LPT) determined by the MaxEnt (simple model) for all species of Perissodactyla clade.

Species	Unique points	AUC	TSS_LPT	TSS_ROC
Equus africanus	8	0.92	0.65	0.81
Equus ferus	5	1.00	1.00	1.00
Equus grevyi	17	0.93	0.60	0.80
Equus hemionus	15	0.91	0.63	0.68
Equus kiang	8	0.97	0.96	0.96
Equus quagga	24	0.84	0.10	0.67
Equus zebra	19	0.97	0.81	0.83
Dicerorhinus sumatrensis	7	0.96	0.92	0.92
Diceros bicornis	18	0.93	0.71	0.71
Ceratotherium simum	14	0.86	0.42	0.76
Rhinoceros unicornis	7	0.96	0.90	0.90
Tapirus indicus	8	0.89	0.67	0.63
Tapirus bairdii	38	0.94	0.40	0.78
Tapirus pinchaque	78	1.00	0.98	0.99
Tapirus terrestris	478	0.78	0.15	0.44

Table 4. Effects of climate changes on the proportion of remaining suitable areas for species of Perissodactyla clade based on future conditions. The values presented are proportional to the suitable cell number for the various climate change scenarios (Loss Proportional). All range size values for Present and Future conditions are expressed as the number of suitable cells (Resolution = ~ 9 km).

Species	**Present**			**CCCma**		**CSIRO**		**HadCM3**	
	Range size (IUCN)	Range size (with dispersion)	Range size (no dispersion)	Range size	Loss	Range size	Loss	Range size	Loss
Equus africanus	1215	34533	26378	117210	0.07	117210	0.09	97672	0.17
Equus ferus	128	24700	22485	15846	0.84	19629	0.87	22857	0.84
Equus grevyi	817	26181	21521	13327	0.58	13032	0.60	8085	0.75
Equus hemionus	5351	160041	51639	94371	0.45	92035	0.42	106670	0.34
Equus kiang	25240	27386	17021	26311	0.53	14779	0.68	34317	0.46
Equus quagga	28190	63983	55264	13186	0.80	15361	0.77	12389	0.81
Equus zebra	1285	14006	11400	8368	0.83	9011	0.78	7116	0.73
Dicerorhinus sumatrensis	106	14223	11417	12440	0.14	5477	0.59	3973	0.71
Diceros bicornis	88358	21180	16877	10183	0.53	11047	0.49	9367	0.57
Ceratotherium simum	67347	24717	20790	12350	0.50	14358	0.41	11263	0.55
Rhinoceros unicornis	48	12101	8537	22216	0.16	19260	0.18	19424	0.18
Tapirus indicus	1049	24112	16594	20233	0.16	21748	0.10	19872	0.18
Tapirus bairdii	9098	17687	5379	24126	0.24	41044	0.13	90309	0.20
Tapirus pinchaque	574	4063	3034	2768	0.38	2598	0.36	1824	0.55
Tapirus terrestris	135211	89746	77030	27713	0.71	25255	0.74	28203	0.77

FIGURE LEGENDS

Figure 1. Relationship between niche properties (Tolerance and OMI) of fifteen species of the Perissodactyla clade. OMI = Outlying mean index. The straight line shows a negative relationship between Tolerance and OMI. The points correspond to species.

Figure 2. Relationships between Tolerance Index and the divergence time of the fifteen species of Perissodactyla clade. The straight lines filled correspond to relationships.

Figure 3. Maps depicting the distribution of the environmental suitable areas for fifteen species of the Perissodactyla clade. The maps show the potential distribution for only one climate model (CCCma) and for the current climate using scenario with and no dispersion.

Figures

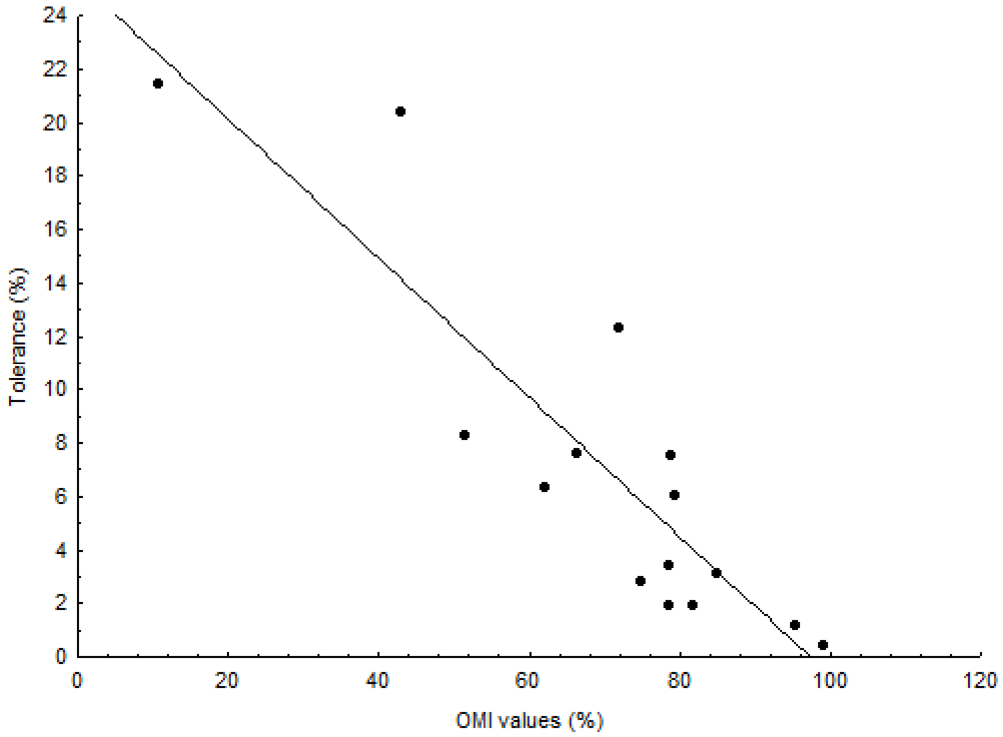


Figure 1.

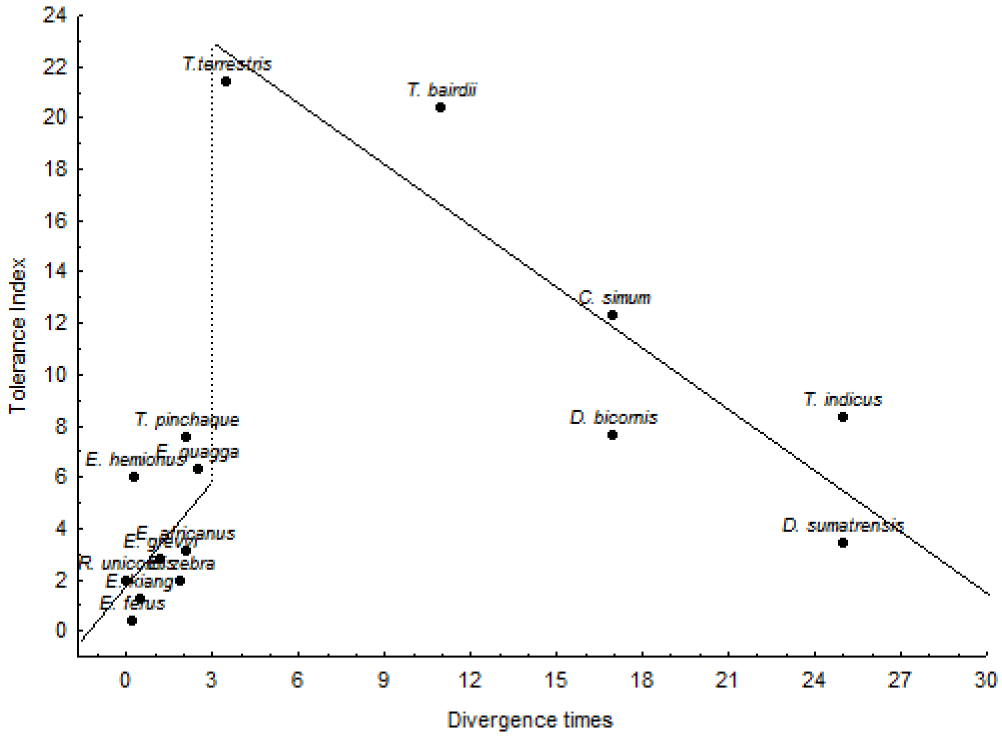

Tolerance Index
24
22
20
18
16
14
12
10
8
6
4
2
0
Divergence times
0
3
6
9
12
15
18
21
24
27
30
T.terrestris
T. bairdii
C. simum
T. indicus
D. bicornis
D. sumatrensis
T. pinchaque
E. hemionus
E. quagga
E. africanus
E. grevyi
R. unicornis
E. zebra
E. kiang
E. ferus

Figure 2.

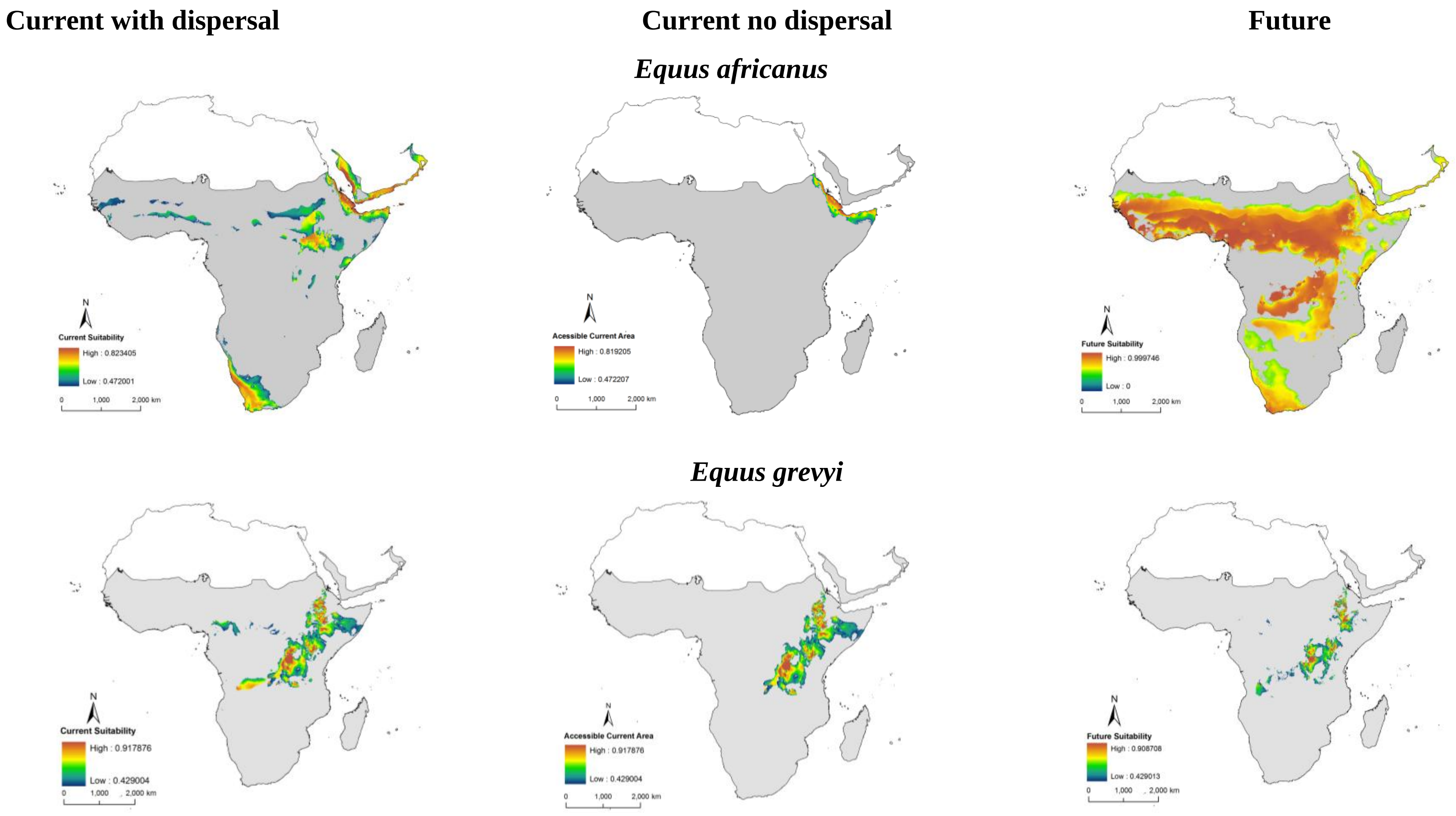
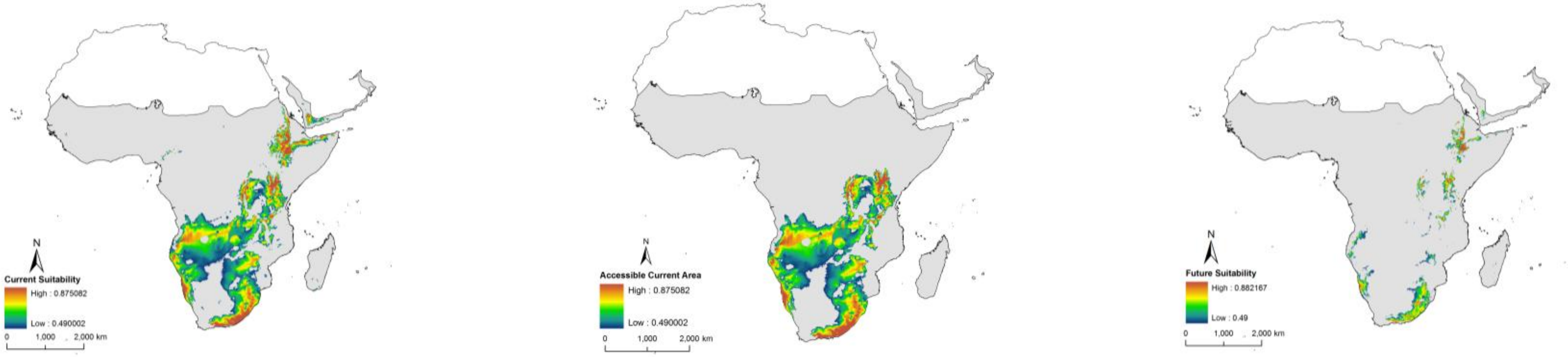

Current with dispersal
Current no dispersal
Future
Equus africanus
N
Current Suitability
High : 0.823405
Low : 0.472001
0 1,000 2,000 km
N
Acessible Current Area
High : 0.819205
Low : 0.472207
0 1,000 2,000 km
N
Future Suitability
High : 0.999746
Low : 0
0 1,000 2,000 km
Equus grevyi
N
Current Suitability
High : 0.917876
Low : 0.429004
0 1,000 2,000 km
N
Accessible Current Area
High : 0.917876
Low : 0.429004
0 1,000 2,000 km
N
Future Suitability
High : 0.908708
Low : 0.429013
0 1,000 2,000 km

Figure 3.

Current with dispersal **Current no dispersal** **Future**

Equus quagga



Equus zebra

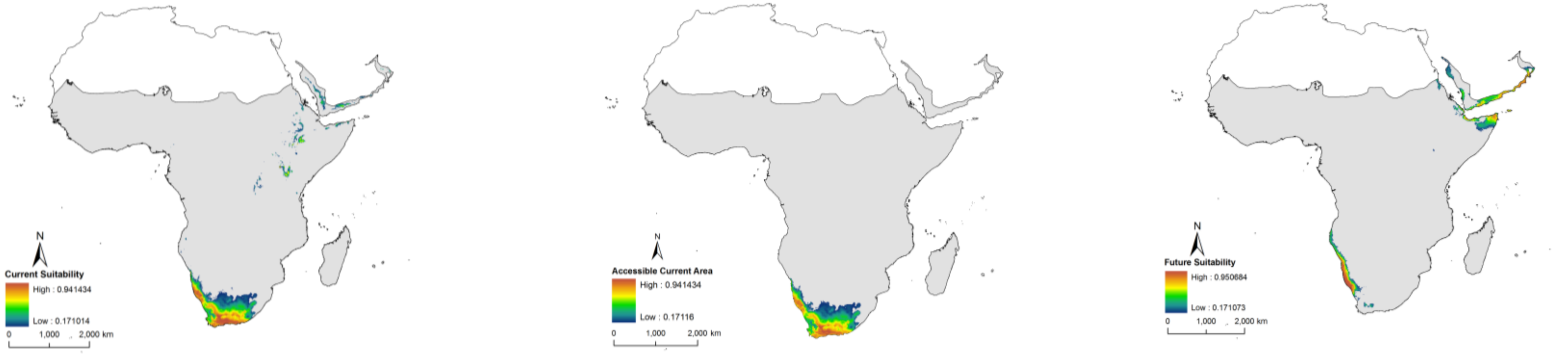
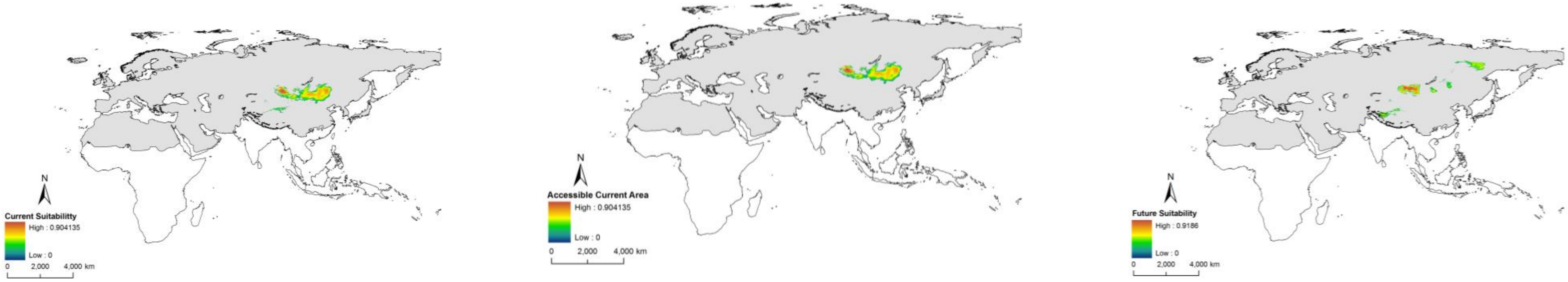


Figure 3. Continuation

Current with dispersal **Current no dispersal** **Future**

Equus ferus



Equus hemionus

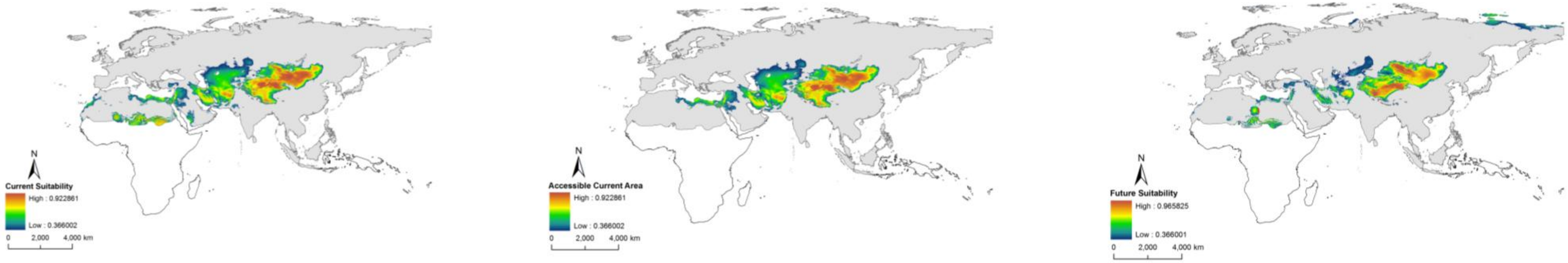


Figura 3. Continuation

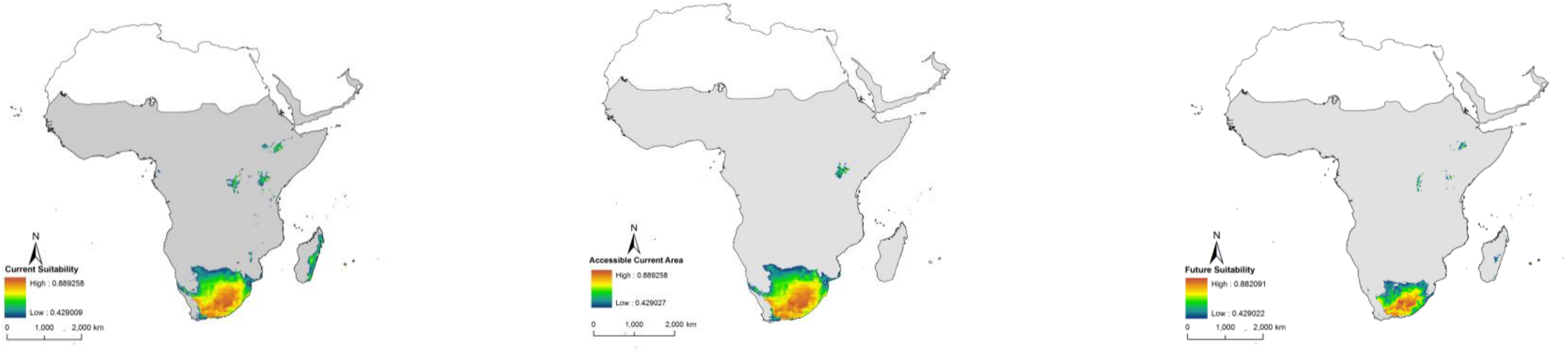
Current with dispersal **Current no dispersal** **Future**

Equus kiang

Figure 3. Continuation

Current with dispersal **Current no dispersal** **Future**

Ceratotherium simum



Diceros bicornis

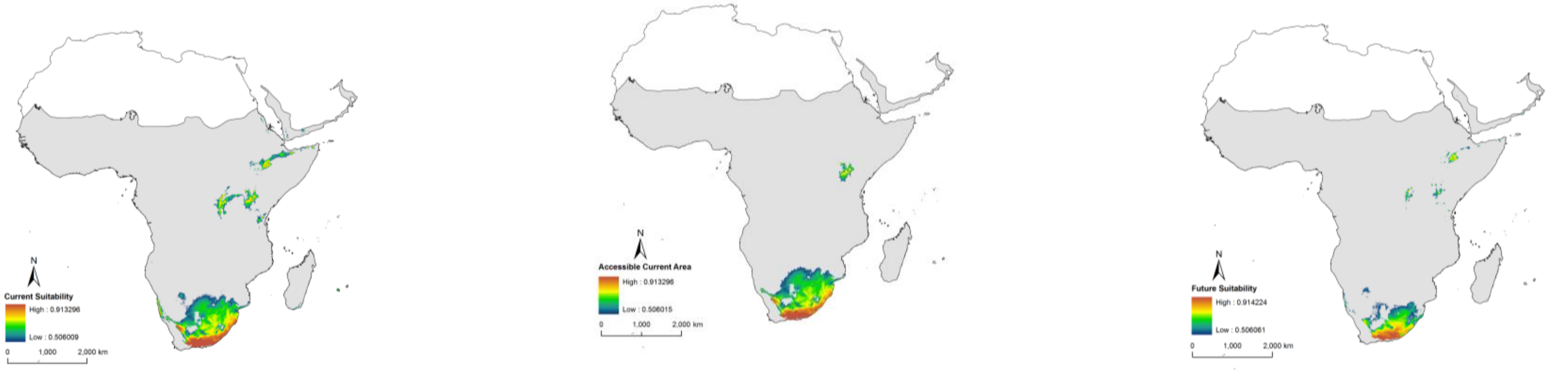


Figure 3. Continuation

Current with dispersal **Current no dispersal** **Future**

Rhinoceros unicornis

Dicerorhinus sumatrensis

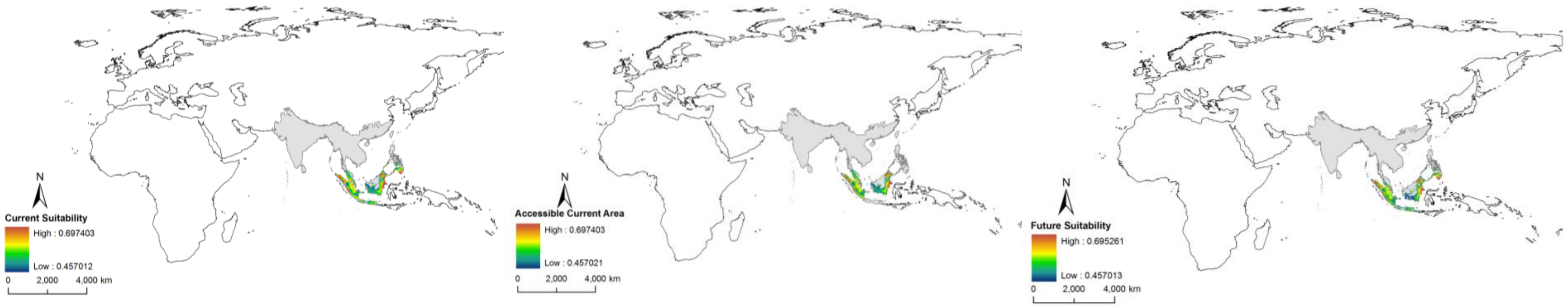
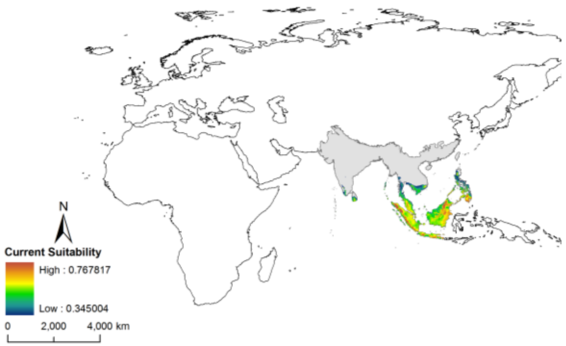
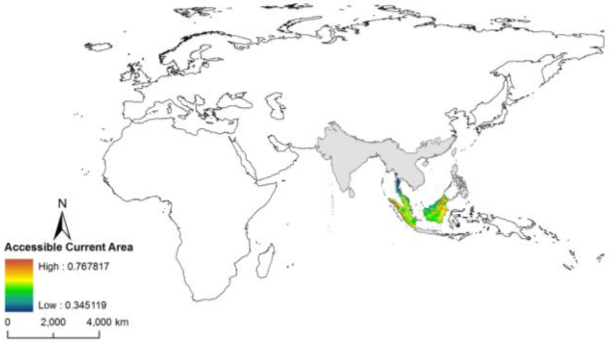


Figure 3. Continuation

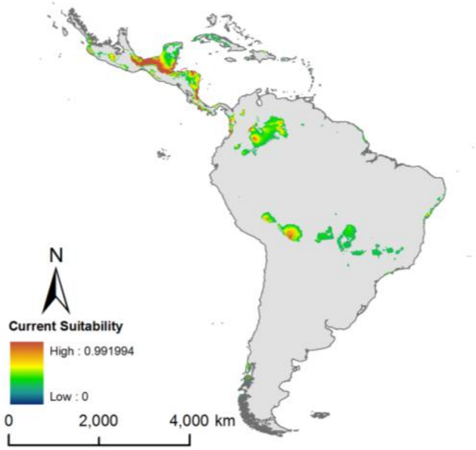
Current with dispersal **Current no dispersal** **Future**

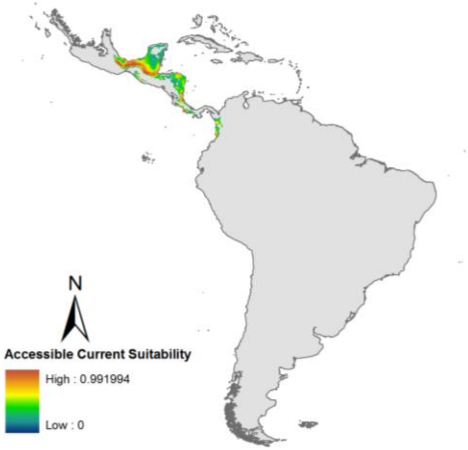
Tapirus indicus

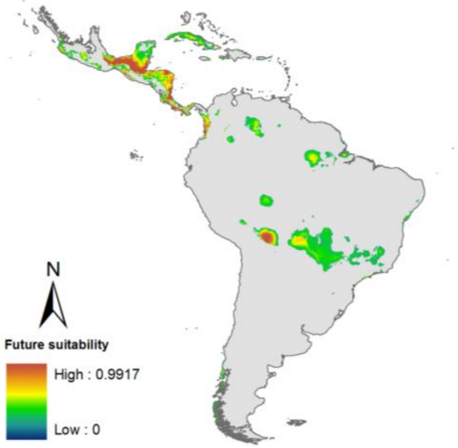




Tapirus bairdii

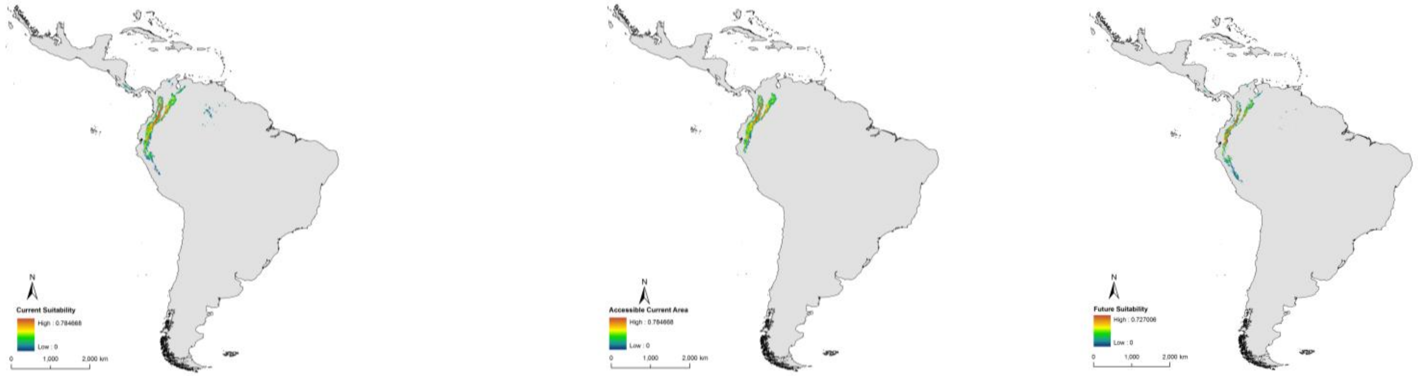






Current with dispersal **Current no dispersal** **Future**

Tapirus pinchaque



Tapirus terrestris

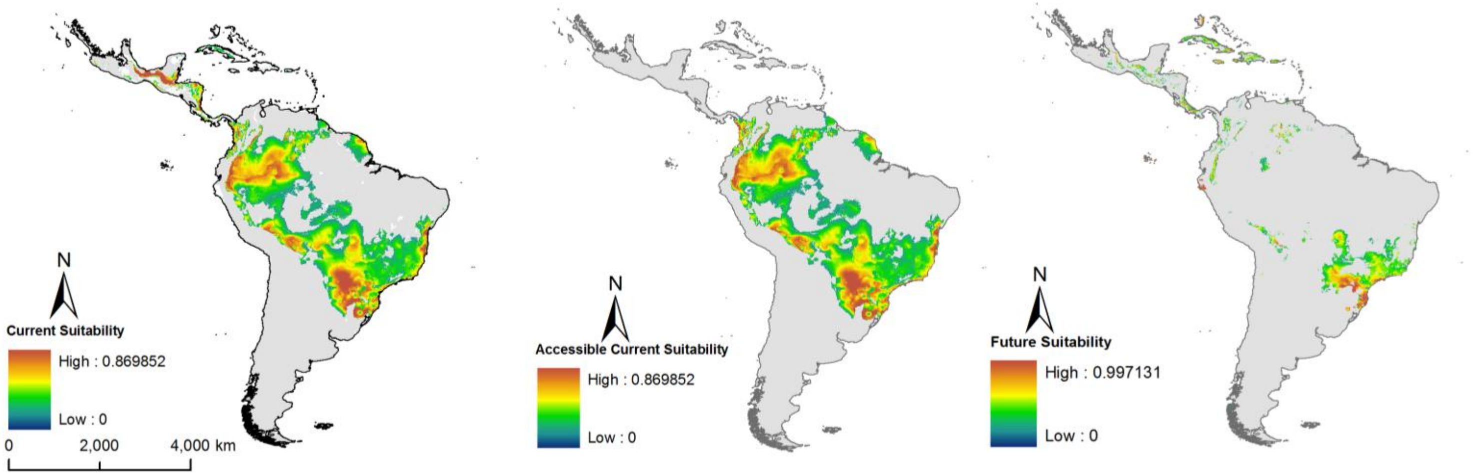
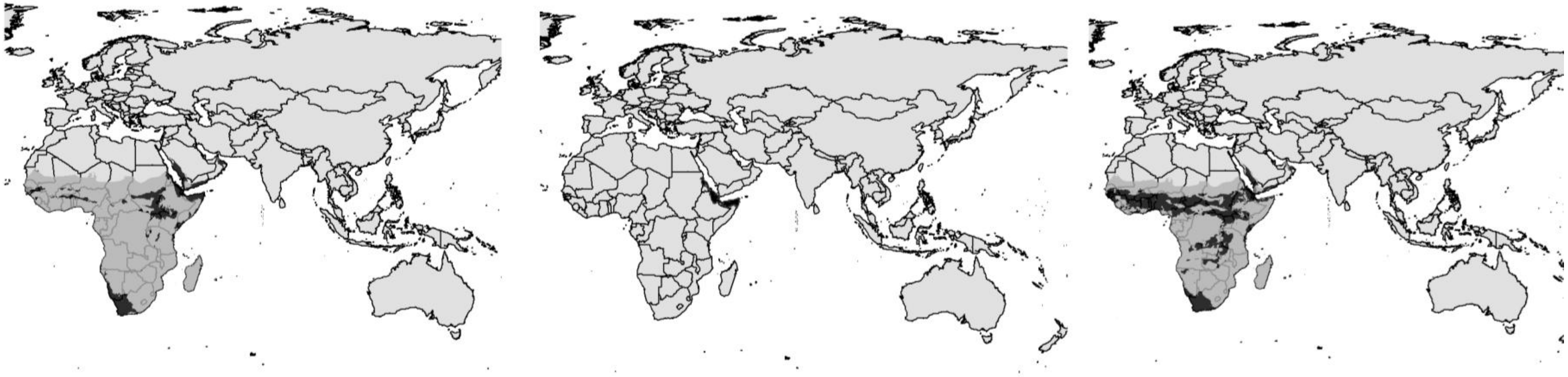


Figure 3. Continuation

SUPPORTING INFORMATION

Appendix S1 Binary maps of potential distribution of the species of Perissodactyla clade. The area of potential distribution in the future is the result of the intersection of GCMs.

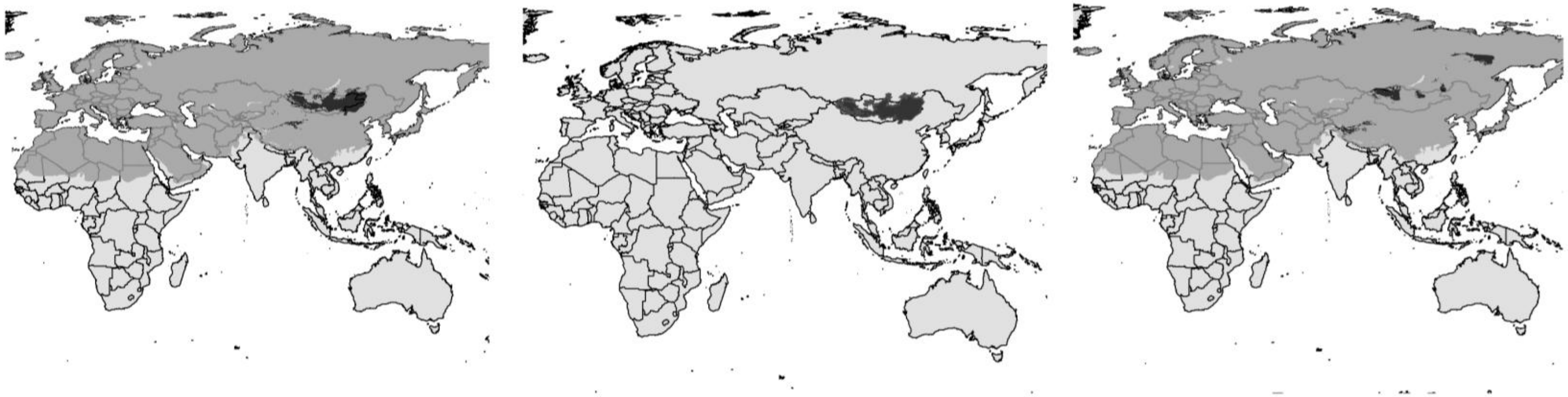


Current **Current no dispersal** **Future**

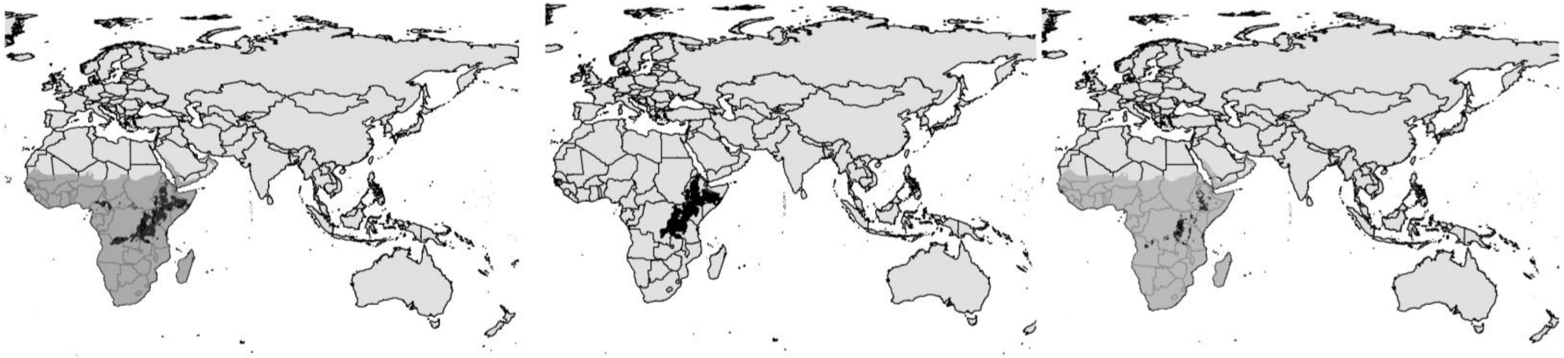
Equus africanus

Current **Current no dispersal** **Future**

Equus ferus

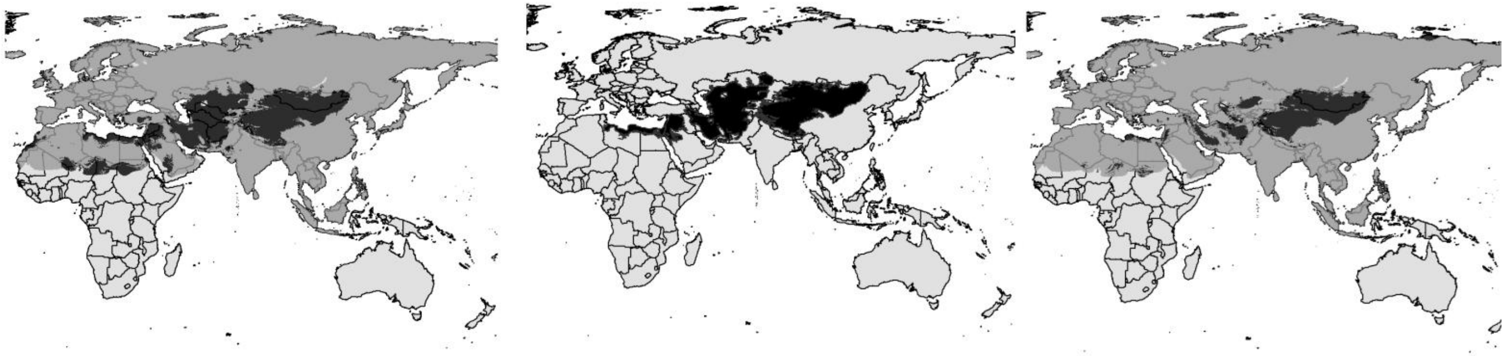


Equus grevyi

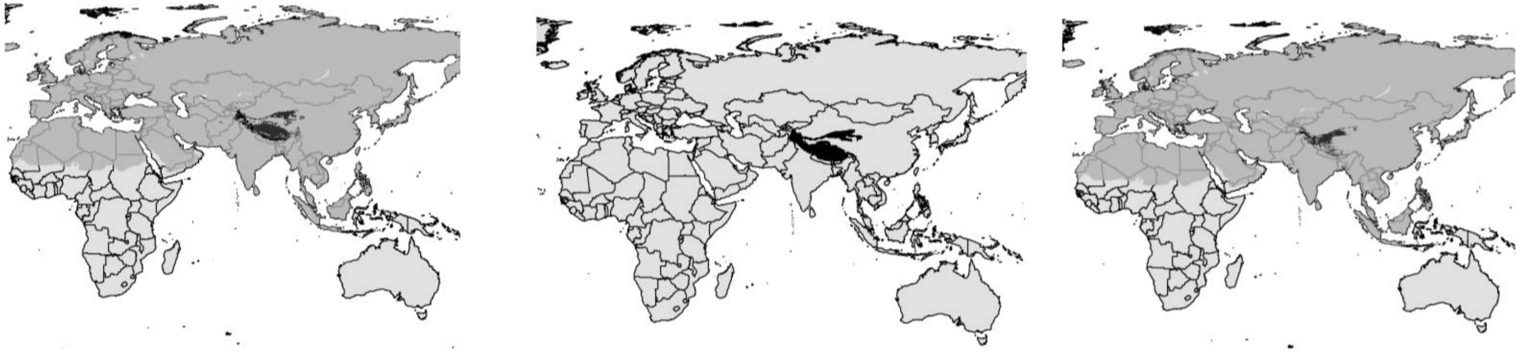


Current **Current no dispersal** **Future**

Equus hemionus

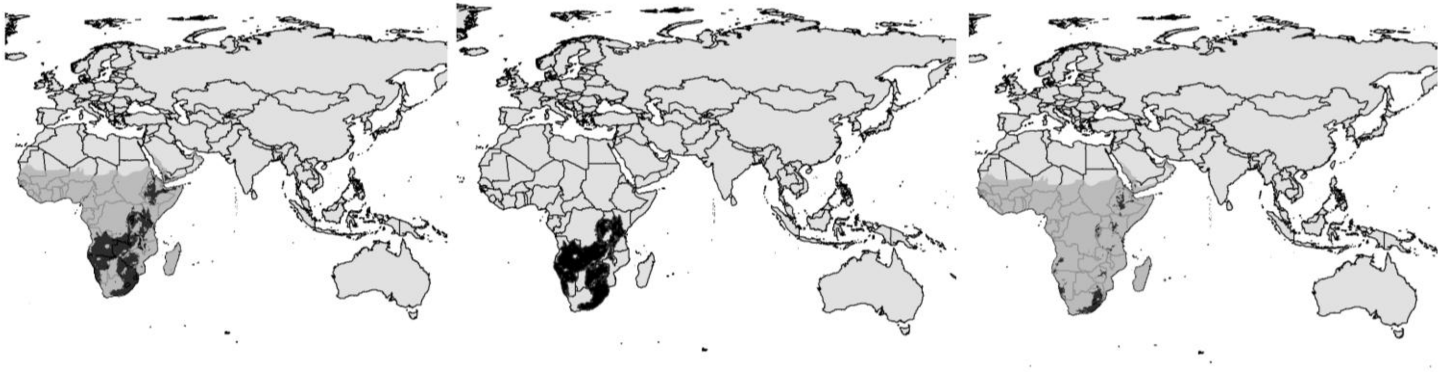


Equus grevyi

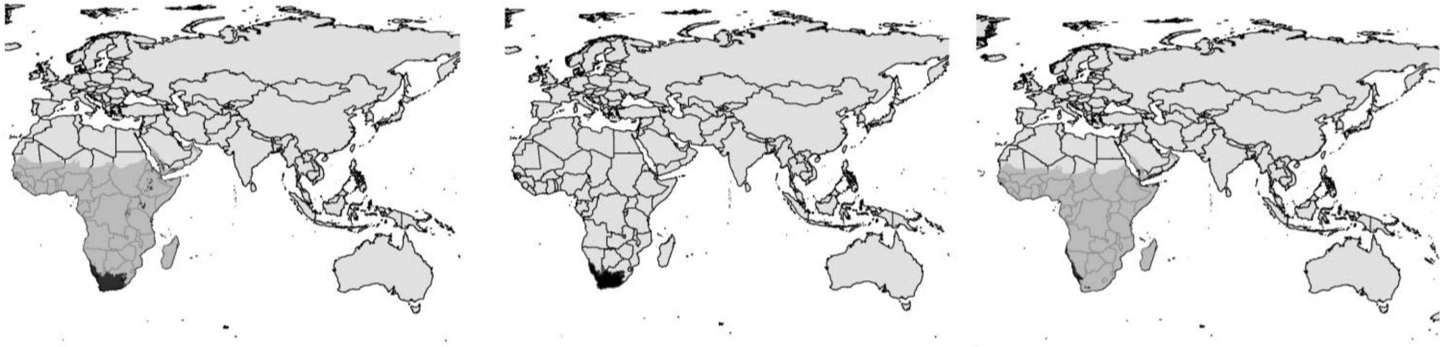


Current **Current no dispersal** **Future**

Equus quagga

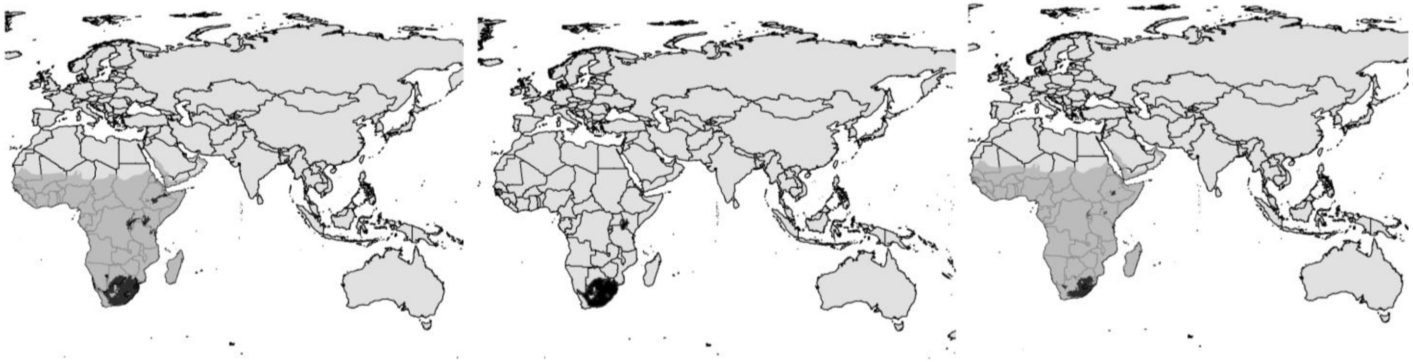


Equus zebra

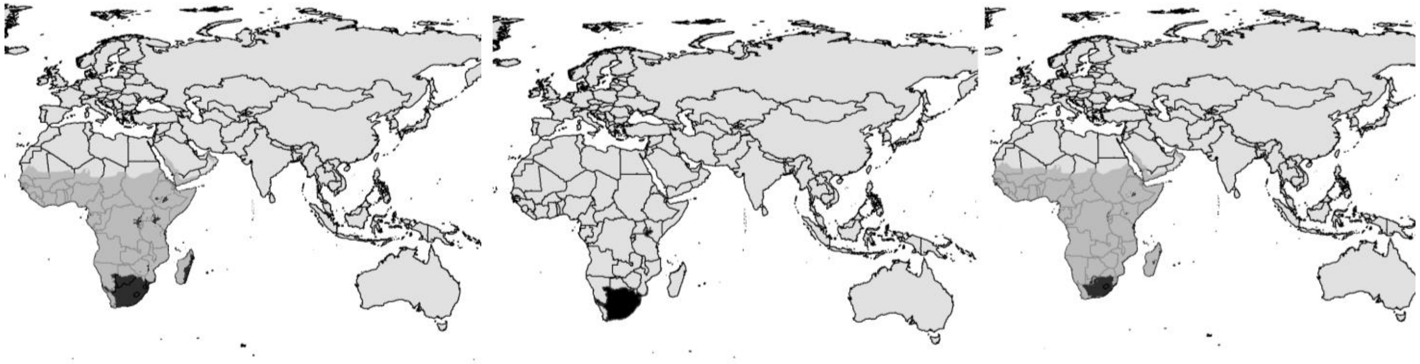


Current **Current no dispersal** **Future**

Diceros bicornis

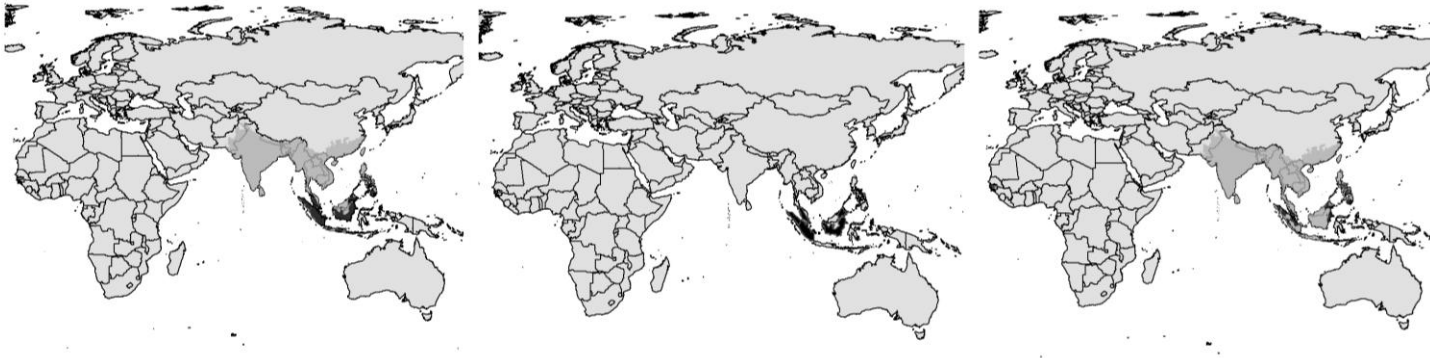


Cerathoterium simum

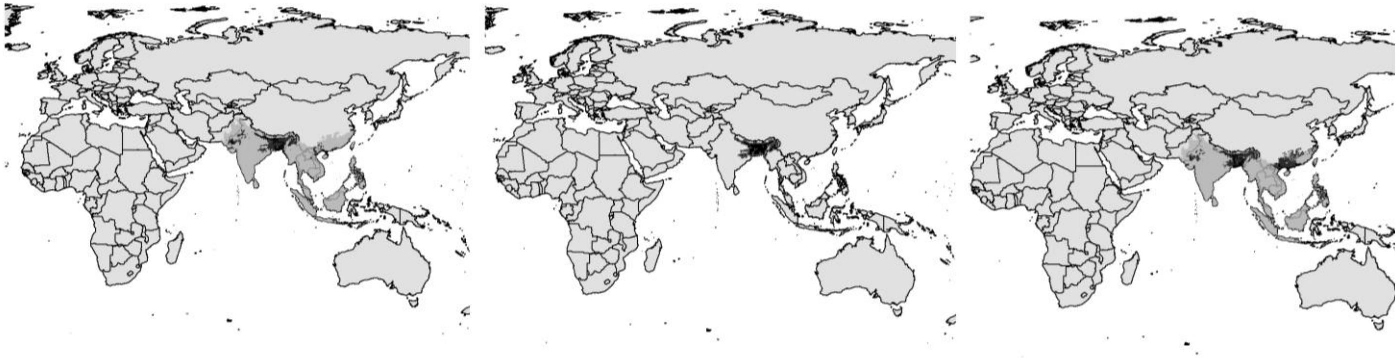


Current **Current no dispersal** **Future**

Dicerorhinus sumatrensis



Rhinoceros unicornis



Current **Current no dispersal** **Future**

Tapirus indicus

Tapirus bairdii

Current **Current no dispersal** **Future**

Tapirus pinchaque

Tapirus terrestris

CAPÍTULO 2

A ser submetido para: Jounal of Biogeography

Ecological niche models predict range expansion for *Tapirus terrestris* after last ice age

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Short Running Head *Tapirus terrestris*'s range expansion during the ice age

ABSTRACT

Aim We tested the hypothesis that environmental changes during the late Quaternary shaped the distribution of climatically suitable areas for lowland tapirs in the Neotropical region.

Location Neotropics

Methods We used Ecological Niche Modeling to simulate the paleoclimatic conditions from Last Interglacial, Last Glacial Maximum and Mid-Holocene, further pre-industrial climate condition. Climatic conditions for LGM, mid-Holocene and pre-industrial were compiled from five coupled Atmosphere-Ocean General Circulation Models (AOGCMs). The paleodistributions for lowland tapir were obtained using four algorithms.

Results Our results suggest that the most critical conditions that prevailed during the LGM reduced the geographical extent of areas climatically suitable for the tapir, expanding during the current interglacial period, with warmer temperatures. Furthermore, we identified a large area that was stable over time.

Main conclusions The paleodistribution modeling for the lowland tapir strongly supported the hypotheses proposed previously for phylogeographic and paleontological studies. Their wide environmental niche may have allowed lowland tapirs to rapidly expand its geographic distribution. The existence of a large stable area indicates that climate change effects may have been less significant for lowland tapirs when compared with other megafauna species. Although climate change does not appear to have been a serious problem for the species during its evolutionary history, the future should be different. Effects of climate change combined with other threats such as habitat loss can severely affect lowland tapir populations and their habitats.

Keywords: Climate change, hindcasting, lowland tapir, Neotropical, paleoclimate, Quaternary, range shift.

INTRODUCTION

The Quaternary was characterized by dramatic climatic oscillations between colder glacial and warmer interglacial climates (Jackson & Overpeck, 2000) and is considered to be one of the most dramatic periods of climatic change in Earth history. The transitions between glacial and interglacial climate promoted many evolutionary divergences and drastic alterations in ecosystems (Williams *et al*., 2004), causing several megafaunal extinctions worldwide (Nogués-Bravo *et al*., 2010). The late Quaternary was marked by a wave of extinctions in all continents and some islands (Koch & Barnosky, 2006), which affected many of the larger species of mammals (as well as birds and reptiles) (Nogués-Bravo *et al*., 2008; Lima-Ribeiro *et al*., 2012). Additionally, the megafauna extinction coincided with the appearance and expansion of humans in most continents (Barnosky *et al*., 2004). The debate about which stressor caused the extinction, or the synergy between them, is long-standing and has generated different discussions (Koch & Barnosky, 2006; Barnosky & Lindsey, 2010).

This paper focuses on the climate change hypothesis, which proposes that reductions in climatically suitable areas for species would have caused a reduction in their geographic ranges, thus increasing their vulnerability to extinction (Nogués-Bravo *et al*., 2010). Graham *et al.* (1996) showed that the geographic ranges of various species in the continental United States shifted at different times and directions in response to late Quaternary climatic changes. This species' range dynamics can be driven by the evolutionary and climatic history of the region in which the species occurs, as well as by their biological and ecological traits (Johnson, 2002; Thuiller *et al*., 2005; Heikkinen *et al*., 2006). For Davies *et al*. (2009), great climatic oscillations during the Quaternary may have favored species with wide distribution through the selection of generalist species. In addition, wide-ranging species may have survived climate change effects because they are inherently more climatically tolerant and, thus, can occupy a wider variety of environmental conditions (Owens & Bennett, 2000; Fisher & Owens, 2004; Thuiller *et al*., 2005).

Good models to test these assumptions are generalist species that survived these major environmental changes, especially throughout the Pleistocene period. A good example is the lowland tapir (*Tapirus terrestris*), one of the larger-bodied Neotropical herbivorous mammals of the order Perissodactyla, a generalist species (Tobler *et al*., 2010; Medici, 2011) and the last representative of the megafauna of Late Quaternary in South America. Although South America has lost most of its megafauna genera during late Quaternary extinctions (Koch & Barnosky, 2006, Barnosky *et al*., 2010), lowland tapirs survived and present today a wide geographic distribution throughout most of the South American continent (Medici, 2011; García *et al*., 2012).

The ancestral of *T. terrestris* dispersed from the Neartic to the Neotropical region together with other mammalian migrants from 3.1 to 2.7 million years ago, during the Great American Biotic Interchange (Marshall, 1988; Webb, 2006; Woodburne *et al*., 2006). Since then, the species has coped with various environmental alterations, especially in terms of vegetation. The earliest fossil records of lowland tapirs are reported in the southern range of the genus’ current distribution (Ferrero & Noriega, 2003; 2007). These fossil records indicate that the lowland tapir geographic range expansion occurred immediately after their diversification (Thoisy *et al*., 2010). Furthermore, the hypothesis proposed by Thoisy *et al.* (2010), based on phylogeographical analysis (nucleotide diversity), is that populations of lowland tapirs were drastically reduced during the Last Glacial Maximum (LGM – 21 kyr), with significant expansion during interglacial, occupying new environments. But how to do a retrospective analysis of what happened with the distribution of environmentally suitable areas for tapirs under the impacts of Quaternary climate oscillations?

The Ecological Niche Modeling (ENM) approach, coupled with paleoclimatic simulations, has been increasingly applied to predict species paleodistribution at regional and global scales (Nogués-Bravo, 2009; Varela *et al*., 2011; Svenning *et al*., 2011). In addition, it has been used to test biogeographical hypotheses, such as geographic range dynamics of extinct and extant species through the last glacial cycle (Martínez-Meyer & Peterson, 2006; Nogués-Bravo *et al*., 2008; Waltari & Guralnick, 2009; Varela *et al*., 2010; Colevatti *et al*., 2013). The main source of paleoclimatic data for ENM studies are past climatic reconstructions based on general circulation models (GCMs; or AOGCMs when the climatic simulations integrate an atmospheric-ocean coupled model). The mid- Holocene (6 kyr) and the LGM (21 kyr) are recognized as benchmark periods throughout the last glacial cycle (Otto-Bliesner, 2009), and have been the main focus for paleoclimatic simulations (see Paleoclimate Modelling Intercomparison Project – PMIP: http://pmip3.lsce.ipsl.fr).

In this paper, we address the hypothesis that environmental alterations during late Quaternary shaped the distribution of climatically suitable areas for lowland tapirs in the Neotropical region. Specifically, we used ENMs to test predictions made by previous phylogeographical and paleontological studies (Thoisy *et al*., 2010; Ruíz-Garcia, 2012): 1. The climatically suitable areas for *T. terrestris* were restricted during LGM, and 2. There was an expansion after the LGM. We used paleoclimate data from Last Interglacial (~125 kyr BP), LGM, Mid-Holocene, and Present (pre-industrial) conditions.

MATERIAL AND METHODS

The history of *Tapirus terrestris*

The family Tapiridae as a taxonomic entity is first recognizable in the Eocene of North America, nearly 50 Mya. Tapirs (Perissodactyla, Tapiridae, *Tapirus*) were distributed in nine genera and inhabited Europe, North America, and Southeast Asia (Colbert, 2007). Tapirs were part of a community of large Neotropical browsers that largely disappeared at the end of the Pleistocene and among the surviving Perissodactyla, tapirs are the most conservative (Kemp, 2005).

The current Tapiridae family (Gray 1821) is composed of a single genus, *Tapirus* (Brünnich 1772), which first appeared in the Miocene (25–5 Mya). Tapirs entered South America with the formation of the Isthmus of Panama between North and South America, during the Pliocene (7–2 Mya-- Ensenadan South American Land Mammal Age (SALMA)), late Pliocene to early Pleistocene (Cione & Tonni, 1996; Tonni *et al.*, 1999; Nabel *et al.*, 2000). Tapir species persist today in Southeast Asia, Central America, and South America. The lowland tapir (*Tapirus terrestris*) is one of four living species, presenting the widest geographic distribution throughout most of South America and found in a variety of habitats, from Venezuela to northern Argentina, and from the Brazilian Atlantic forest to the Ecuadorian sub-Andean foothills (Medici, 2011)

Occurrence data

Most of the records of current presence of lowland tapirs were obtained from data provided by experts from the IUCN/SSC Tapir Specialist Group (TSG). This database was complemented with data from literature, museum specimens deposited in online databases ((Global Biodiversity Information Facility, GBIF, www.gbif.org) and from records obtained from other research colleagues in Brazil. We used 312 spatially distinct occurrence points (from 525 compiled) to generate the distribution of lowland tapirs for both current and past climate conditions across the entire Neotropics.

Environmental Variables and Paleoclimatic simulations

To evaluate how the last glacial cycle affected the distribution of climatically suitable areas for *T. terrestris* we used paleoclimatic simulations from pre-industrial (representing current climate conditions), Last Glacial Maximum (LGM; ~21,000 years ago - 21 kyr BP) and Mid-Holocene (~6,000 years ago - 6 kyr BP). Because of relatively coarse resolution from native AOGCMs outputs, we used the standard change-factor approach (Wilby *et al*., 2004) to downscale the climatic layers to a 0.5^o spatial resolution (~55 km at the height of Ecuador), according to Collevatti *et al*. (2013). From the interpolated data of monthly precipitation and mean, maximum and minimum temperatures, we calculated 19 bioclimatic variables (see www.worldclim.org/bioclim). We used six variables (from a total of 19 available variables): annual mean temperature, temperature seasonality (coefficient of variation), mean temperature of the driest quarter, annual precipitation, precipitation seasonality (coefficient of variation) and precipitation during the warmest quarter.

Climatic conditions for LGM, mid-Holocene and pre-industrial were compiled from five coupled Atmosphere-Ocean General Circulation Models (AOGCMs) -- CCSM, CNRM, MIROC, MPI and MRI (Table 1) -- available in the databases CMIP5 (Coupled Model Intercomparison Project, Phase 5; http://cmip-pcmdi.llnl.gov) and PMIP3 (Paleoclimate Modelling Intercomparison Project, Phase 3; http://pmip3.lsce.ipsl.fr). LGM and mid-Holocene represent, respectively, the coldest and warmest phases through the last glacial cycle. In the second phase, we used the Last Interglacial (LIG; ~125,000 years ago - 125 kyr BP) climate data available only for CCSM (Otto-Bliesner *et al*., *in press*).

Paleodistributions modeling approach

The paleodistributions for lowland tapirs were obtained using four algorithms, including methods for presence-only data, which was selected based on its complexity in the following order: Envelope Score (ES), Mahalanobis Distance (MD), MaxEnt and Support Vector Machines (SVM). This complexity reflects directly on some properties of these models, such as over-fitting and transferability (Varela *et al*., 2011). Selected modeling procedures are based on two classes of methods: 1) The first class of models is only based on distances and therefore does not require adjustment to previously defined models, as Envelope Score and Mahalanobis Distance; 2) The second class uses presence/pseudo-absence data and requires some type of fit of the data to a model that represents the response to environmental conditions, as MaxEnt and SVM.

The Envelope Score is equivalent to the inclusive 'OR' implementation of Bioclim described in Piñeiro *et al*. (2007) and for each given environmental variable the algorithm finds the minimum and maximum at all occurrence sites. During the modeling process, the probability is determined by dividing between the layers within min-max threshold by number of layers. Mahalanobis Distance is a simpler model allowing for easier interpretation based on a geometric view of the Hutchinsonian niche -- this approach has been used as a multivariate index of environmental quality in studies examining species distribution (Farber & Kadmon, 2003). MD scores should be interpreted as a similarity index to climate conditions from sites where the species has been recorded.

The MaxEnt Software (version 3.3.3e) (Computer Sciences Department, Princeton University, 2004) is a general-purpose machine learning approach that uses a simple mathematical formulation for modeling geographic distribution of species with presence-only data (Phillips *et al.*, 2006). Absence data are generated by randomly selecting ‘‘pseudo-absence’’ points from regions where the species was not recorded (*i.e.*, the background of the area). The SVMs consist of a new group of learning algorithms used for classification and regression (Schlkopf & Smola, 2001) and are a class of non-probabilistic statistical pattern recognition algorithms for estimating, among other quantities, the boundary of the set from which a collection of observations is drawn (Drake *et al.*, 2006; Drake & Bossenbroek, 2009). These algorithms are typically designed for a two-class problem where the SVM seeks to define a hyperplane in predictor space that separates two classes, such as species presence/absence (Guo *et al.*, 2005).

All models were fitted using current climate data (pre-industrial) and then back-projected (“hindcasting”) onto those relevant time periods in Pleistocene and Holocene (LIG, LGM and Mid-Holocene).

Model evaluation

Most modeling studies use AUC measure to evaluate generated models. The AUC is a threshold-independent measure that, for prediction from algorithms using presence-only or presence-absence data, can be interpreted as the ability of the algorithm to discriminate between a suitable climate condition and a random analysis pixel (Phillips *et al.*, 2006). AUC values range from 0 to 1, in which a score of 1 indicates perfect discrimination and a score of 0.5 or less implies discrimination that is no better than random (Elith *et al.*, 2006). Nevertheless, there is a series of concerns about its measure. Pearson *et al*. (2007) argue that the false-positive should not be considered for evaluating potential distribution models built only to reveal areas that can be occupied, and Lobo *et al*. (2008) list five reasons not to use AUC as a measure of evaluation (*e.g.*, AUC weights omission and commission errors equally). Thus, we used Liu *et al*. (2011) who suggested the use of AUC as a threshold independent general measure of fit, but added a threshold depended measure to evaluate the cases for which a binary prediction is needed.

We chose to use True Skill statistics (TSS) to evaluate model predictions because it performs well when compared to similar measures (Liu *et al*., 2011). This measure is also highly correlated with AUC, but it is not biased by prevalence (Allouche *et al*., 2006). TSS takes into account both omission and commission errors and ranges from −1 to +1, where +1 indicates perfect agreement, and values of zero or less indicate a performance that is no better than random predictions. TSS is a measure dependent on the threshold used to convert continuous species distributions model outputs in binary maps predicting potential presence/absence of each species. We adopted the lowest presence threshold (LPT) because it equals the minimum model prediction value for any of the training occurrence data. This approach can be interpreted ecologically as identifying pixels predicted as being at least as suitable as those where the species' presence has been recorded.

The potential paleodistributions were obtained by addint up the binary maps from five AOGCMs resulting from each algorithm, and considering two scenarios: 1. a more conservative scenario, in which only the areas predicted by the five common climatic models were considered; 2. a less conservative scenario, considering the area in which at least one climate model was predicted as climatically suitable for *T. terrestris.* Thus, the maps presented for each algorithm, in a time period was used as the single representative potential geographical prediction for the species.

Species range shift

To evaluate the range shifts of lowland tapirs throughout the last interglacial/glacial cycle (from Last Interglacial to current period), such as the expansions and contractions, we used the relative change (values >1 and <1 represent expanding and shrinking climate conditions, respectively) and proportional loss in potential distribution. These metrics have been used in other studies (Beaumont *et al.*, 2005; Thuiller *et al.*, 2005; Garcia *et al.*, 2012).

The relative change values were obtained by dividing the area occupied in a given period of time (*e.g.*, Last Interglacial) by the area occupied under climates on next time period (i.e., Last Glacial Maximum). The proportional loss was calculated by dividing the number of lost cells in a time slice by the potential distribution of basal time period (i.e., compared with the analyzed distribution). Thus, we evaluated the shifts in size of the climatically suitable areas in the following sequence: LIG to LGM; LGM to Mid-Holocene; Mid-Holocene to present-day. Furthermore, we defined areas of stability (regions in which the species were predicted to occupy irrespective of the time period) (Carnaval *et al.*, 2009), as a result of the intersection of the predicted suitable areas under current conditions and climatic extremes of the Late Quaternary (LGM and Mid-Holocene).

RESULTS

The AUC and TSS values for all models showed a relatively good fit (Table 2) and the ROC threshold choice was reinforced by TSS values, which were higher than TSS values from LPT in 16 of 20 models.

The combinations from AOGCMs and algorithms reveal that the climatically suitable areas available to lowland tapir increased from LGM (21 kyr BP) to mid-Holocene (6 kyr BP) (points above the reference line with 1:1 relationship; Fig. 1a). Only the models generated by SVM showed a decrease in potential distribution for this period (Table 3). From mid-Holocene to present-day (pre-industrial), the potential distribution of lowland tapir seems to have been stable, although slight variations were predicted (Fig. 1b; Table 4). The regression analyses showed that when a model predicts a high value for the size of the area in a given period, it also predicts for the other time period evaluated (Fig. 1a, b). The less complex algorithms, Envelope Score and Mahalanobis Distance, were those that least overpredicted the potential distribution in the three periods analyzed (Fig. 2).

When we analyzed the models through a more conservative approach, it was observed that the five AOGCMs indicated the same limits of distribution of climatically suitable areas and the central area of distribution for the species. Although the potential distribution of lowland tapirs increases through time, the models predicted loss of climatically suitable areas from the LGM to Mid-Holocene in some Neotropical regions, mainly in the Guiana Shield, portions of Eastern, Central and Western Amazonia, and in the northernmost region of the Brazilian Caatinga. Contrarily, portions of southern Brazil, northern Argentina and regions bordering the Andes in Bolivia and Peru became climatically suitable to the lowland tapir after LGM.

Therefore, our results strongly suggest that constraints on the distribution of climatically suitable areas for lowland tapirs throughout the last ice age occurred mainly during the LGM and expanded subsequently with small geographic alterations in the availability of climatically suitable areas after mid-Holocene.

However, we observed that there was also an increase in the potential distribution from the LIG (125 kyr BP) to LGM (Table 5). During the LIG, the three algorithms (ES, MD and MaxEnt) predicted unsuitable areas for lowland tapirs in a region that extends from eastern to western Brazil, including principally the Amazon River basin and central Amazonian lowlands. Furthermore, portions of Guiana and Brazilian Shields and a wide region of Argentina and Uruguay were also predicted as unsuitable. During the LGM, all these areas were predicted to become environmentally suitable.

The models predicted a wide refugium for lowland tapirs from LGM to present-day (areas climatically suitable in all time periods), which occurs particularly in the peripheral areas of the Amazon River basin, and in the central region of the South America. In addition, according with our models, most of central Amazonian lowlands along the Amazon River were unstable for *T. terrestris* through the last glacial cycle (Fig. 5).

DISCUSSION

Our results suggest that the coldest conditions prevailing during the LGM would have reduced the geographic extent of climatically suitable areas for the lowland tapir, expanding again during warmer current interglacial. Our findings from paleodistribution modeling strongly support predictions made by previous phylogeographic and paleontological studies (Ferrero & Noriega, 2003; 2007; Thoisy *et al*., 2010; Ruiz-García *et al*., 2012). As discussed by Colevatti *et al*. (2013), the demographic history of a species is more reliably described through time when both paleodistribution modeling, phylogeographic analysis, and fossil records provide convergent evidences (see also Svenning *et al*., 2011). This paper supports previous evidence that lowland tapirs experienced a clear historical population expansion after LGM (Thoisy *et al*., 2010; Ruiz-García *et al*., 2012), most probably becoming the most successful large herbivore in South America, surviving the late Quaternary extinctions. The fact that lowland tapirs occupy a broader environmental niche (García *et al*., 2012; see Chapter 1) most probably favored the species and allowed for a relatively rapid expansion of their geographic range after dramatic changes in their environment (*e.g.*, after the LGM). According to Dynesius & Jansson (2000), species with low specialization - such as the lowland tapir - are also more likely to survive while moving through heterogeneous environments.

It has often been stated that animal species survive environmental changes in two main ways: by evolving adaptations to new conditions or by shifting their geographic range, seeking a favored habitat (Lister, 2010). Thus, species may have responded to the Quaternary glaciations with large range shifts (Graham *et al*., 1996). In contrast, species with broader niches and flexible adaptations often stayed where they were (frequently over a wide area) or showed relatively minor expansions and contractions of their geographic range (see examples in Lyons *et al*., 2003, 2010). Although we are fully aware of the uncertainties inherent to the AOGCMs and ENM algorithms (Pearson *et al*., 2006), we identified a large stable area for lowland tapirs. The maintenance of this area indicates that the effect of climate change on lowland tapirs may have been much smaller than on the extinct megafaunal species. *Eremotherium,* for instance, an extinct giant ground sloth in South America, was predicted to have been narrowly distributed during early Holocene across scattered refugia, which most probably made it more prone to extinction under probable hunting by humans (Lima-Ribeiro & Diniz-Filho, 2013). Approximately 80% of climatically suitable areas for *Eremotherium* were lost from LGM to mid-Holocene (Lima-Ribeiro *et al*., 2012).

Negative effects of climate change were observed for different organisms worldwide. Contractions of climatically suitable areas during the last glacial cycle were recorded for frogs (Carnaval *et al.*, 2009), birds (Bonaccorso *et al*., 2006; Ribas *et al.*, 2011), mammals (Nogués-Bravo *et al*., 2008, Varela *et al*., 2010, Lima-Ribeiro & Diniz-Filho, 2012) and woody plants (Bonaccorso *et al*., 2006). However, each species responds differently to climate changes, as demonstrated by Lorenzen *et al*. (2011). Likewise, the evident contraction of climatically suitable areas for various extinct megafauna species at the end of the Pleistocene/earliest Holocene in South America (Lima-Ribeiro & Diniz-Filho, 2013) does not seem to have affected lowland tapirs. It is likely that lowland tapirs occupied new environments after the extinction of the Neotropical megafauna herbivores (Thoisy *et al*., 2010), which supports the idea that this widespread species presents high climate tolerance, principally in relation to average temperature, but not extreme cold as occurred during LGM (also in high altitudes, for example, Andean region).

Davies *et al*. (2009) suggest that large climate oscillations in the Quaternary may have shaped the distribution of geographic range size via the selective extinction of narrow-ranged species during glacial expansion or recolonization by species able to disperse after glacial retreats (Williams *et al*., 2004). The lowland tapir has the ability to disperse and occurred in a wide refuge in South America, allowing it to survive the last glacial cycle, as opposed to other megafauna species narrowly distributed in scattered refugia at the end of the Pleistocene.

However, our approach presents some issues. ENM-based predictions can be highly variable, given that both AOGCMs and modeling procedures can bring uncertainties to the predictions (Pearson *et al*., 2006; Thuiller *et al.*, 2008). Although different models predicted different distributions of climatically suitable areas for lowland tapirs, the combined use of various AOGCMs and ENM algorithms (the ensemble approach; see Araújo & New, 2007) indicated a relationship between them. The size of potential distribution was similar for all predictions between time periods, regardless of AOGCM or ENM algorithm used (Fig. 1).

Moreover, various assumptions can also affect the application of the ENM approach to test biogeographical hypotheses. A critical assumption of the ENMs for modeling past distributions is the climatic niche stability over the study period (Nogués-Bravo, 2009; Varela *et al*., 2011; Svenning *et al*., 2011). However, as stated by Peterson (2011), over relatively short periods, such as from LGM to present-day, evolutionary changes on species ecological niches are less likely than for longer time spans.

Lastly, it is well known that barriers to species dispersal and interspecific interactions may restrict the species distribution to narrower ranges than those predicted by ENMs (Soberón & Nakamura, 2009, Soberón, 2010). Rivers, mountains and vegetation can be considered as barriers, which was recently proposed by Barve *et al*. (2011) (see also De Marco *et al.*, 2008). However, the inclusion of barriers in paleodistribution modeling is a challenging issue. Given that the lowland tapir is a generalist herbivore which has the ability to move across heterogeneous environments, we did not incorporate barrier restrictions in our models. Our goal was not determine the true geographic distribution of lowland tapirs in the past, nor its exact geographic range size over time. Our aim was to determine how the species geographic distribution has changed since the last glacial cycle, which can be reliably tested from potential distributions.

Concluding Remarks

Although the ENM approach presents some methodological uncertainties, the evaluation of model predictions and assumptions, as well as the ecological traits of the studied species, indicate that our results are reliable to test the biogeographical hypotheses for the lowland tapir. Our results, coupled with previous phylogeographical and paleontological analyses, support a reduction of the lowland tapir geographic range during LGM, with subsequent expansion through current glacial. At the contrary of most megafauna species in South America, which did not recover from climate crisis during last glacial cycle, the lowland tapir was widely distributed on climatically suitable areas (refugial) throughout this time slice, surviving the late Quaternary extinctions.

A critical assumption for the distribution models based in hindcasting is the climatic niche stability over the study period. Peterson (2011) assumes that over relatively short periods, such as the LGM to recent period (21000 years), evolutionary niche changes are less likely than for longer time spans. Obviously, this is a Furthermore, we do not incorporated the restriction in species dispersion, considering that lowland tapir is able to move in heterogeneous environments, although the recent studies discuss the importance inserting dispersal scenarios into predictive models

(Barve *et al*., 2011). Nevertheless, it is possible to start thinking about the restriction of the dispersion over time considering rivers, mountains and vegetation as barriers which was recently proposed by Barve *et al*. (2011), but how to operationalize this approaches still an issue to be assessed. We consider that to overcome both problems – climatic uncertain and dispersal modeling -- it is needed the use of alternative paleoenvironmental reconstructions and several ENM algorithms, considering principally the species characteristics.

The resulting predictions can provide valuable information about the evolutionary history of the lowland tapir. Although climate change does not seem to have been a serious problem for the species during its evolutionary history, the challenges ahead can be serious. Climate change will most probably result in changes in environmental suitability throughout the lowland tapir distribution and affect particularly the vegetation, interfering with important ecological processes, such as seed dispersal. Furthermore, the combined effect of climate change with habitat loss and fragmentation, unsustainable hunting, road-kill and disease transmission could be drastic.

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REFERENCES

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

Barnosky, A., Koch, P., Feranec, R., Wing, S. & Shabel, A. (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science (New York, N.Y.)*, **306**, 70–75.

Barnosky, A.D. & Lindsey, E.L. (2010) Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International*, **217**, 10-29.

Beaumont, L., Hughes, L. & Pitman, A. (2008) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology letters*, **11**, 1135–1146.

Bonaccorso, E., Koch, I. & Peterson, A.T. (2006) Pleistocene fragmentation of Amazon species' ranges. *Diversity and Distributions*, **12**, 157–164.

Carnaval, A., Hickerson, M., Haddad, C., Rodrigues, M. & Moritz, C. (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science (New York, N.Y.)*, **323**, 785–789.

Cione, A.L. & Tonni, E.P. (2005). Bioestratigrafía basada em mamíferos del Cenozóico Superior de la Província de Buenos Aires, Argentina. Geología y recursos minerales de Província de Buenos Aires (ed. by E. Barrio, R.O. Etcheverry, M.F. Caballé and E. Llambias), pp. 183–200. Quick Press, La Plata, Argentina.

Cione, A.L. & Tonni, E.P. (2006) Central American provincialism and the Great American Biotic Interchange. *Advances in Late Tertiary Vertebrate Paleontology in Mexico and the Great American Biotic Interchange* (ed. by O. Carranza-Castañeda & E.H. Lindsay), pp. 10. Univ Nac Aut Mex. Inst Geol Centro Geoscien Publ Espec 4:73–100.

Colbert, M. (2007) New fossil discoveries and the history of *Tapirus*. *Tapir Conservation*, **16**, 12-14.

Collevatti, R. G., Terribile, L.C., Oliveira, G. de, Lima-Ribeiro, M., Nabout, J.C., Rangel, T.F. & Diniz-Filho, J.A.F. (2013) Drawbacks to palaeodistributions modelling: the case of South American seasonally dry forests. *Journal of Biogeography*, **40**, 345–358.

Davies, T., Purvis, A. & Gittleman, J. (2009) Quaternary climate change and the geographic ranges of mammals. *The American naturalist*, **174**, 297–307.

De Marco, P., Diniz-Filho, J.A.F. & Bini, L.M. (2008) Spatial analysis improves species distribution modelling during range expansion. *Biology Letters*, **4**, 577-580.

Drake, J.A., Randin, C. & Guisan, A. (2006) Modelling ecological niches with support vector machines. *Journal of Applied Ecology*, **43**, 424–432.

Drake, J.M. & Bossenbroek, J.M. (2009) Profiling ecosystem vulnerability to invasion by zebra mussels with support vector machines. *Theoretical Ecology*, **2**, 189-198.

Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 9115–9120.

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

Farber, O. & Kadmon, R. (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. *Ecological Modelling*, **160**, 115-130.

Ferrero, B.S. & Noriega, J.J. (2003) El registro fósil de los tapires (Perissodactyla: Tapiridae) en el Pleistoceno de Entre Ríos. *Ameghiniana*, **40**, 84R.

Ferrero, B.S. & Noriega, J.I. (2007) A new upper Pleistocene tapir from Argentina: remarks on the phylogenetics and diversification of neotropical Tapiridae. *Journal of Vertebrate Paleontology*, **27**, 504–511.

Fisher, D. & Owens, I. (2004) The comparative method in conservation biology. *Trends in Ecology & Evolution*, **19**, 391–398.

Garcia, R.A., Burgess, N.D., Cabeza, M., Rahbek, C. & Araújo, M.B. (2012) Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Global Change Biology*, **18**, 1253–1269.

García, M., Medici, E., Naranjo, E., Novarino, W. & Leonardo, R. (2012) Distribution, habitat and adaptability of the genus *Tapirus*. *Integrative Zoology*, **7**, 346–355.

Graham, R.W., Lundelius, E.L. Jr and Graham, M.A *et al*. (1996) Spatial response of mammals to late-Quaternary environmental fluctuations. *Science*, **272**, 1601–1606.

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

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, **30**, 1-27.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology,* **26**, 194–220.

Johnson, C.N. (2002) Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society B,* **269**, 2221-2227.

Kemp, T.S. (2005). The Origin and Evolution of Mammals. New York: Oxford University Press.

Koch, P.L. & Barnosky, A.D. (2006) Late Quaternary Extinctions: State of the Debate. *Annual Review of Ecology, Evolution, and Systematics,* **37**, 215-250.

Lima-Ribeiro, M.S., Varela, S., Nogués-Bravo, D. & Diniz-Filho, J.A.F. (2012) Potential suitable areas of giant ground sloths dropped before its extinction in South America: the evidences from bioclimatic envelope modeling. *Natureza & Conservação*, **10**, 145-151.

Lima-Ribeiro, M,S. & Diniz-Filho, J.A.F. (2012) Modelando a distribuição geográfica das espécies no passado: uma abordagem promissora em paleoecologia. *Revista Brasileira de Paleontologia*, **15**, 371-385.

Lima-Ribeiro, M.S. & Diniz-Filho, J.A.F. (2013). *Modelos Ecológicos e a Extinção da Megafauna: Clima e Homem na América do Sul.* Editora Cubo, São Paulo.

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

Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145-151.

Lorenzen, E., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., *et al.* (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature*, **479**, 359–364.

Lyons, S.K. (2003) A quantitative assessment of the range shifts of Pleistocene mammals. *Journal of Mammalogy*, **84**, 385-402.

Lyons, S.K., Wagner, P.J. & Dzikiewicz, K. (2010) Ecological correlates of range shifts of Late Pleistocene mammals. *Philosophical Transactions of the Royal Society B*, **365**, 3681-3693.

Marshall, L.G. (1988) Land Mammals and the Great American Interchange. *American Scientist*, **76**: 380-388.

Martínez-Meyer, E. & Peterson, A.T. (2006) Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography*, **33**, 1779–1789.

Medici, E.P. (2011). Family Tapiridae (Tapirs). *Handbook of the Mammals of the World, Volume 2: Hoofed Mammals* (ed. by D.E. Wilson, R.A. Mittermeier), pp. 182–204. Lynx Edicions, Spain.

Nabel, P.E., Cione, A. & Tonni, E. P. (2000) Environmental changes in the Pampean area of Argentina at the Matuyama– Brunhes (C1r–C1n) Chrons boundary. *Palaeogeography, Palaeo-climatology, Palaeoecology*, **162**, 403–412.

Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. & Araújo, M. (2008) Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biology*, **6**, e79.

Nogués-Bravo, D. (2009) Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, **18**, 521-531.

Nogués-Bravo, D., Ohlemüller, R., Batra, P. & Araújo, M. (2010) Climate predictors of late quaternary extinctions. *Evolution; International Journal of organic evolution*, **64**, 2442–2449.

Owens, I. & Bennett, P. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 12144–12148.

Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704–1711.

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

Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

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

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

Ribas, C., Aleixo, A., Nogueira, A., Miyaki, C. & Cracraft, J. (2011) A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proceedings. Biological sciences / The Royal Society*, **279**, 681–689.

Ruiz-García, M., Vásquez, C., Pinedo, M., Sandoval, S., Kaston, J., Thoisy, B., & Shostell, J. (2012) Phylogeography of the mountain tapir (*Tapirus pinchaque*) and the Central American tapir (*Tapirus bairdii*) and the molecular origins of the three South American tapirs. Current Topics in Phylogenetics and Phylogeography of Terrestrial and Aquatic Systems (ed. by K. Anamthawat-Jónsson). Rijeka, Croatia: In Tech.

Schölkopf, B. & Smola, A. (2001) *Learning with kernels: support vector machines, regularization, optimization and beyond*. MIT Press, Cambridge.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the Notional Academy of Sciences USA*, **106**, 19644–19650.

Soberón, J. (2010) Niche and area of distribution modeling: a population ecology perspective. *Ecography*, **33,** 159-167.

Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nógues-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews*, **30**, 2930–2947.

Thoisy, B. de, da Silva, A., Ruiz-García, M., Tapia, A., Ramirez, O., Arana, M., Quse, V., Paz-y-Miño, C., Tobler, M., Pedraza, C. & Lavergne, A. (2009) Population history, phylogeography, and conservation genetics of the last Neotropical mega-herbivore, the lowland tapir (Tapirus terrestris). *BMC Evolutionary Biology*, **10**, 278.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics,* **9**, 137-152.

Tobler, M.W., Janovec, J.P. & Cornejo, F. (2010) Frugivory and Seed Dispersal by the Lowland Tapir *Tapirus terrestris* in the Peruvian Amazon. *Biotropica*, **42**, 215–222.

Tonni, E.P., Cione, A.L. & Figini, A.J. (1999) Predominance of arid climates indicated by mammals in the pampas of Argentina during the Late Pleistocene and Holocene. *Palaeogeography Palaeoclimatology, Palaeocology,* **147**, 257-268.

Varela, S., Lobo, J.M., Rodríguez, J. & Batra, P. (2010) Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. *Quaternary Science Reviews***, 29,** 2027-2035.

Varela, S., Lobo, J.M. & Hortal, J. (2011) Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **310**, 451-463.

Waltari, E. & Guralnick, R.P. (2009) Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. *Journal of Biogeography*, **36**, 148–161.

Webb, S.D. (2006) The Great American Biotic Interchange: patterns and processes. *Annals of the Missouri Botanical Garden*, **93**, 245–257.

Wilby, R.L., Charles, S.P., Zorita, E., Timbal, B., Whetton, P. & Mearns, L.O. (2004) *Guidelines for use of climate scenarios developed from statistical downscaling methods: supporting material of the Intergovernmental Panel on Climate Change*. Task Group on Data and Scenario Support for Impacts and Climate Analysis, Rotherham.

Williams, J.W., Shuman, B.N., Webb, T., Bartlein, P.J. & Leduc, P. L. (2004) Late-quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecological Monographs*, **74**, 309–334.

TABLES

Table 1. Description of the five Atmosphere-Ocean coupled General Circulation Model (AOGCMs) used in species distribution models.

AOGCMs	**Research Center**	**Resolution**	**Source**	**Year**
CCSM3	University of Miami –RSMAS, USA	0.9° ×1.25°	CMIP5 PMIP3	2012
CNRM-CM5	Centre National de Recherches Meteorologiques / Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique, France	1.4° x 1.4°	CMIP5 PMIP3	2012
MIROC-ESM	Atmosphere and Ocean Research Institute (University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology, Japan	2.8° ×2.8°	CMIP5 PMIP3	2012
MPI-ESM-P	Max Planck Institute for Meteorology, Germany	1.9° ×1.9°	CMIP5 PMIP3	2011
MRI-CGCM3	Meteorological Research Institute, Japan	1.1° x 1.1°	CMIP5 PMIP3	2011

CMIP5 – Coupled Model IntercomparisonProject, Phase 5 (http://cmip-pcmdi.llnl.gov/)
PMIP3 –Paleoclimate Modelling Intercomparison Project, Phase 3 (http://pmip3.lsce.ipsl.fr/)

Table 2. AUC (training data) and TSS values for each algorithm and Atmosphere-Ocean coupled General Circulation Model (AOGCM).

AOGCM	Algorithm	AUC	TSS_LPT	TSS_ROC
CCSM	ES	1.00	0.40	0.40
CNRM	ES	1.00	0.40	0.40
MIROC	ES	1.00	0.23	0.43
MPI	ES	1.00	0.06	0.14
MRI	ES	1.00	0.17	0.17
CCSM	MD	0.67	0.17	0.26
CNRM	MD	0.64	0.23	0.20
MIROC	MD	0.71	0.10	0.42
MPI	MD	0.70	0.21	0.39
MRI	MD	0.71	0.27	0.39
CCSM	MaxEnt	0.73	0.25	0.36
CNRM	MaxEnt	0.76	0.31	0.37
MIROC	MaxEnt	0.84	0.12	0.54
MPI	MaxEnt	0.72	0.10	0.35
MRI	MaxEnt	0.77	0.12	0.42
CCSM	SVM	0.81	0.27	0.57
CNRM	SVM	0.81	0.19	0.48
MIROC	SVM	0.61	0.14	0.48
MPI	SVM	0.80	0.21	0.47
MRI	SVM	0.81	0.17	0.56

Table 3. Effects of climate changes on the proportion of remaining suitable areas for *T. terrestris* based on paleoclimate conditions (from the Last Maximum Glacial, 21 kyr BP, to 6 kyr BP (Mid-Holocene). The values presented are proportional to the suitable cell number for the various climate change scenarios (Loss and Relative change). The potential range size is expressed as the number of suitable cells (Resolution = ~55 km). AOGCMs = Atmosphere-Ocean coupled General Circulation Model.

Algorithm	AOGCM	Potential Range Size (21 kyr)	Potential Range Size (6 kyr)	Proportional Loss	Relative Change
ES	CCSM	4568	4831	0.07	1.06
MD	CCSM	4945	5394	0.00	1.09
MaxEnt	CCSM	4728	5132	0.04	1.09
SVM	CCSM	5478	5059	0.14	0.92
ES	CNRM	4419	4770	0.02	1.08
MD	CNRM	5020	5188	0.01	1.03
MaxEnt	CNRM	4992	5194	0.00	1.04
SVM	CNRM	5732	5607	0.05	0.98
ES	MIROC	4984	5288	0.02	1.06
MD	MIROC	5497	5665	0.04	1.03
MaxEnt	MIROC	5480	5760	0.02	1.05
SVM	MIROC	5002	5468	0.04	1.09
ES	MPI	5286	5510	0.01	1.04
MD	MPI	4970	4852	0.07	0.98
MaxEnt	MPI	5460	5587	0.02	1.02
SVM	MPI	5769	5715	0.04	0.99
ES	MRI	4139	4714	0.02	1.14
MD	MRI	5029	5319	0.02	1.06
MaxEnt	MRI	5436	5894	0.00	1.08
SVM	MRI	5867	5710	0.10	0.97

Table 4. Effects of climate changes on the proportion of remaining suitable areas for *T. terrestris* based on paleoclimate conditions (from the Mid-Holocene, 6 kyr BP, to Present Period (pre-industrial). The values presented are proportional to the suitable cell number for the various climate change scenarios (Loss and Relative change). The potential range size is expressed as the number of suitable cells (Resolution = ~55 km). AOGCMs = Atmosphere-Ocean coupled General Circulation Model. ES = Envelope Score. MD = Mahalanobis Distance. SVM = Support Vector Machines.

Algorithm	AOGCM	Potential Range Size (6 kyr)	Potential Range Size (Present)	Proportional Loss	Relative Change
ES	CCSM	4831	4915	0.03	1.02
MD	CCSM	5394	5367	0.02	0.99
MaxEnt	CCSM	5132	5192	0.02	1.01
SVM	CCSM	5059	5189	0.04	1.02
ES	CNRM	4770	4688	0.03	0.98
MD	CNRM	5188	5161	0.01	0.99
MaxEnt	CNRM	5194	5072	0.03	0.98
SVM	CNRM	5607	5556	0.02	0.99
ES	MIROC	5288	5214	0.02	0.99
MD	MIROC	5665	5716	0.02	1.01
MaxEnt	MIROC	5760	5757	0.01	1.00
SVM	MIROC	5468	5389	0.03	0.98
ES	MPI	5510	5517	0.01	1.00
MD	MPI	4852	5142	0.01	1.06
MaxEnt	MPI	5587	5757	0.04	1.03
SVM	MPI	5715	5742	0.02	1.00
ES	MRI	4714	4601	0.06	0.98
MD	MRI	5319	5391	0.01	1.01
MaxEnt	MRI	5894	5757	0.06	0.98
SVM	MRI	5710	5497	0.05	0.96

Table 5. Effects of climate changes on the proportion of remaining suitable areas for *T. terrestris* based on paleoclimate conditions (from the Last Interglacial, 125 kyr BP, to Last Maximum Glacial, 21 kyr BP. The values presented are proportional to the suitable cell number for the various climate change scenarios (Loss and Relative change). The potential range size is expressed as the number of suitable cells (Resolution = ~55 km). AOGCMs = Atmosphere-Ocean coupled General Circulation Model. ES = Envelope Score. MD = Mahalanobis Distance. SVM = Support Vector Machines.

Algorithm	AOGCM	Potential Range Size (125 kyr)	Potential Range Size (21 kyr)	Proportional Loss	Relative Change
ES	CCSM	4206	4568	0.10	1.09
MD	CCSM	3952	4945	0.07	1.25
MaxEnt	CCSM	4304	4728	0.09	1.10
SVM	CCSM	5469	5478	0.09	1.00

FIGURE LEGENDS

Figure 1. Points below of the black line indicate that there was loss of the suitable area resulting of a specific algorithm and points above the black line are predicted to gain suitability. The regression line is in red. (a) Change in range size from LGM to Mid LGM-Holocene; (b) Change in range size from Mid LGM-Holocene to Present climate condition (pre-industrial). ES = Envelope Score; MD = Mahalanobis Distance; SVM = Support Vector Machine. The points for each algorithm correspond to the five AOGCMs used (CCSM3, CNRM-M5, MPI-ESM-P, MIROC-ESM, MRI-CGCM3)

Figure 2. Binary maps of the distribution of environmental suitability for *T. terrestris* in Neotropical region, according with two modeling procedures (ES and MD) and five coupled atmosphere–ocean global circulation models for two paleoclimate conditions (LGM - ~21 yr BP and Mid-Holocene - ~6 kyr BP) and Present period (pre-industrial). The first column of each algorithm refers to the scenario more conservative (areas equally predicted by five AOGCMs) and the second column refers to the scenario less conservative (areas predicted by all AOGCMs).

Figure 3. Binary maps of the distribution of environmental suitability for *T. terrestris* in Neotropical region, according with two modeling procedures (MaxEnt and SVM) and five coupled atmosphere–ocean global circulation models for two paleoclimate conditions (LGM - ~21 yr BP and Mid-Holocene - ~6 kyr BP) and Present period (pre-industrial). The first column of each algorithm refers to the scenario more conservative (areas equally predicted by five AOGCMs) and the second column refers to the scenario less conservative (areas predicted by all AOGCMs).

Figure 4. Binary maps of the distribution of environmental suitability for *T. terrestris* in Neotropical region, according with four modeling procedures (ES, MD, MaxEnt and SVM) and one AOGCM (CCSM) for three paleoclimate conditions (LIG - ~125 kyr BP, LGM - ~21 yr BP and Mid-Holocene - ~6 kyr BP) and Present period (pre-industrial).

Figure 5. The map shows the areas environmentally predicted by four algorithms for lowland tapir (*Tapirus terrestris*). This map is the result of the intersection areas between all time periods (LGM, mid-Holocene and pre-industrial).

FIGURES

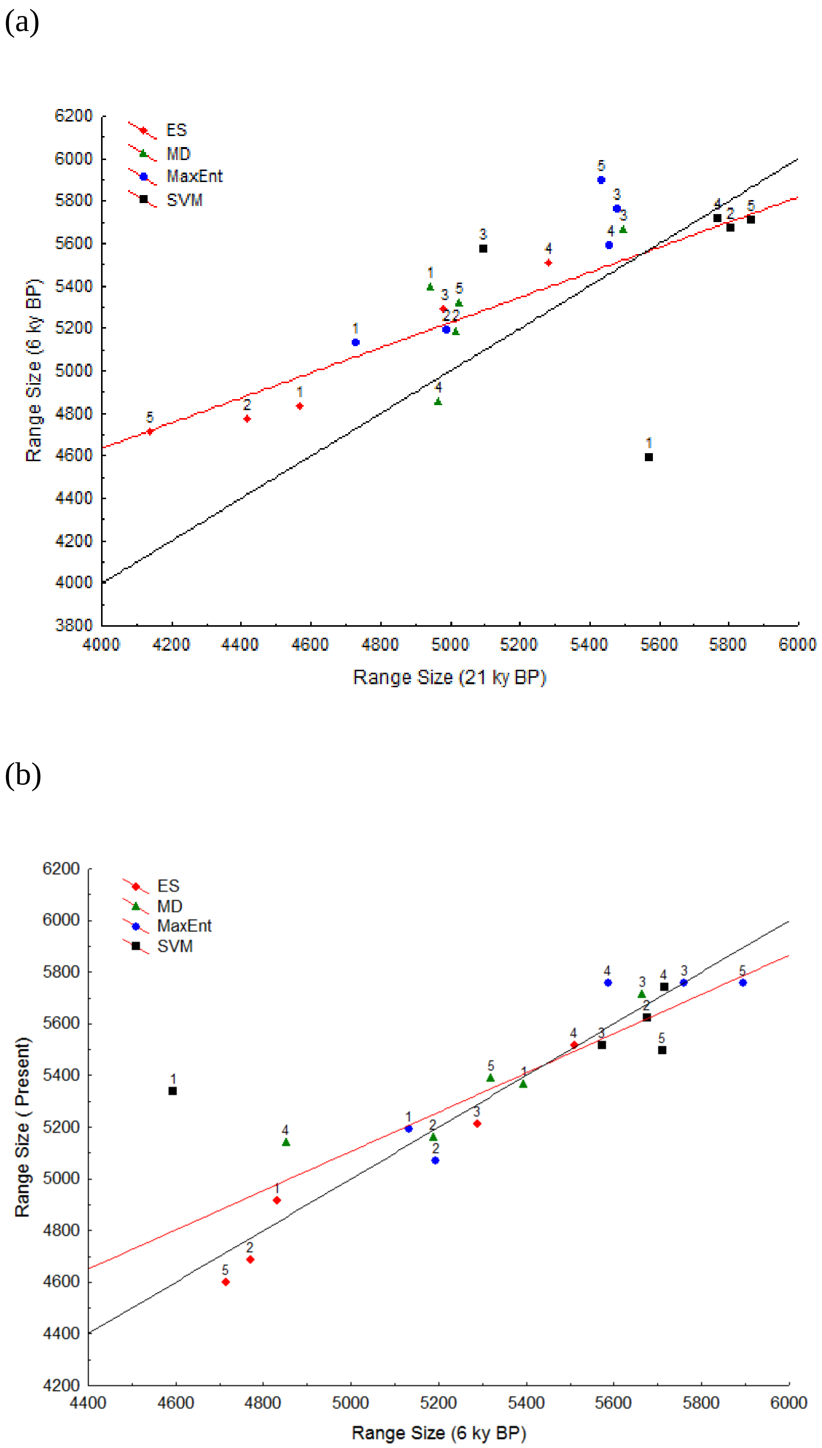
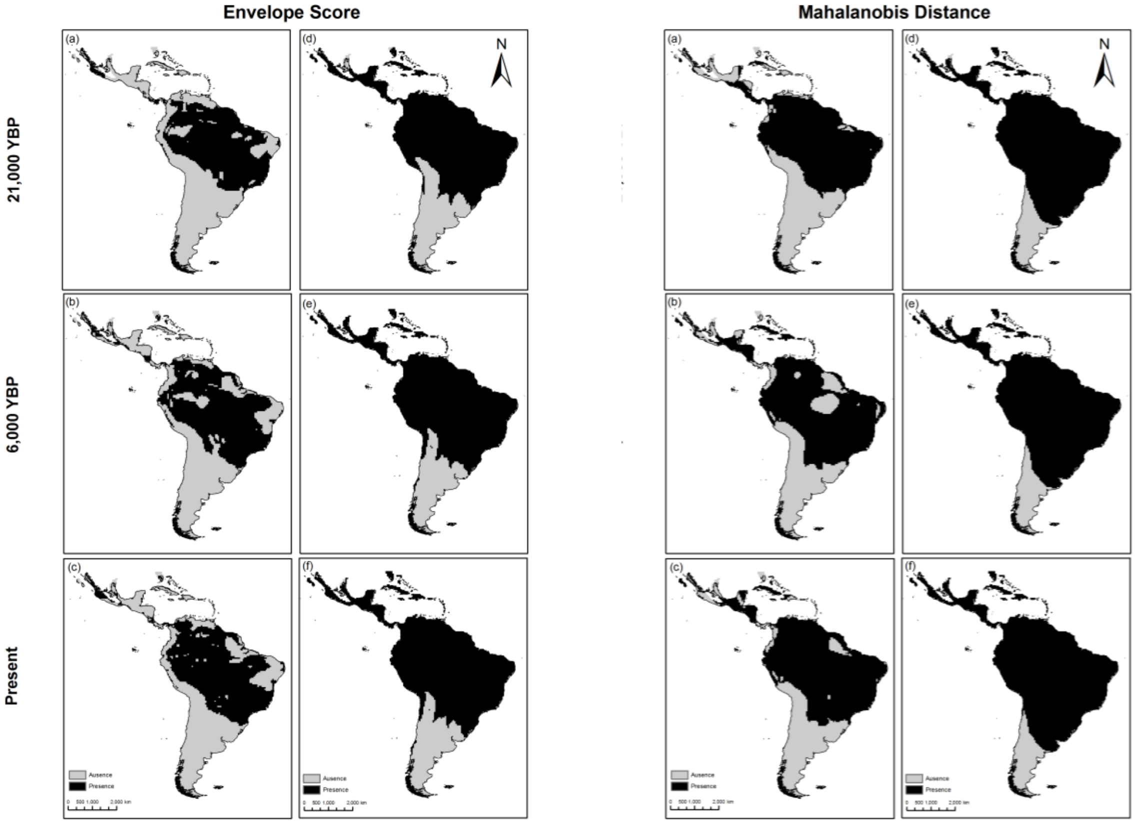


Figure 1.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6,000 YBP
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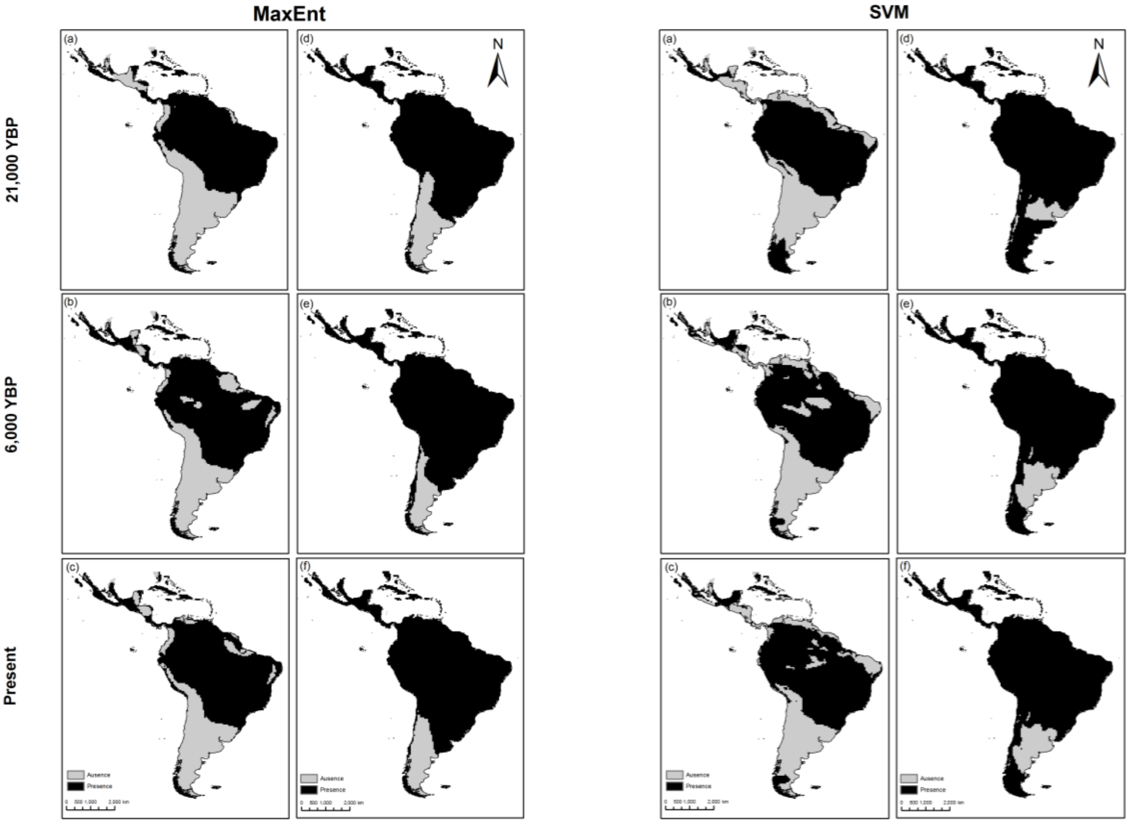
(f)
Ausence
Presence
0 500 1,000 2,000 km

Figure 2.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SVM
21,000 YBP
6,000 YBP
Present
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Presence
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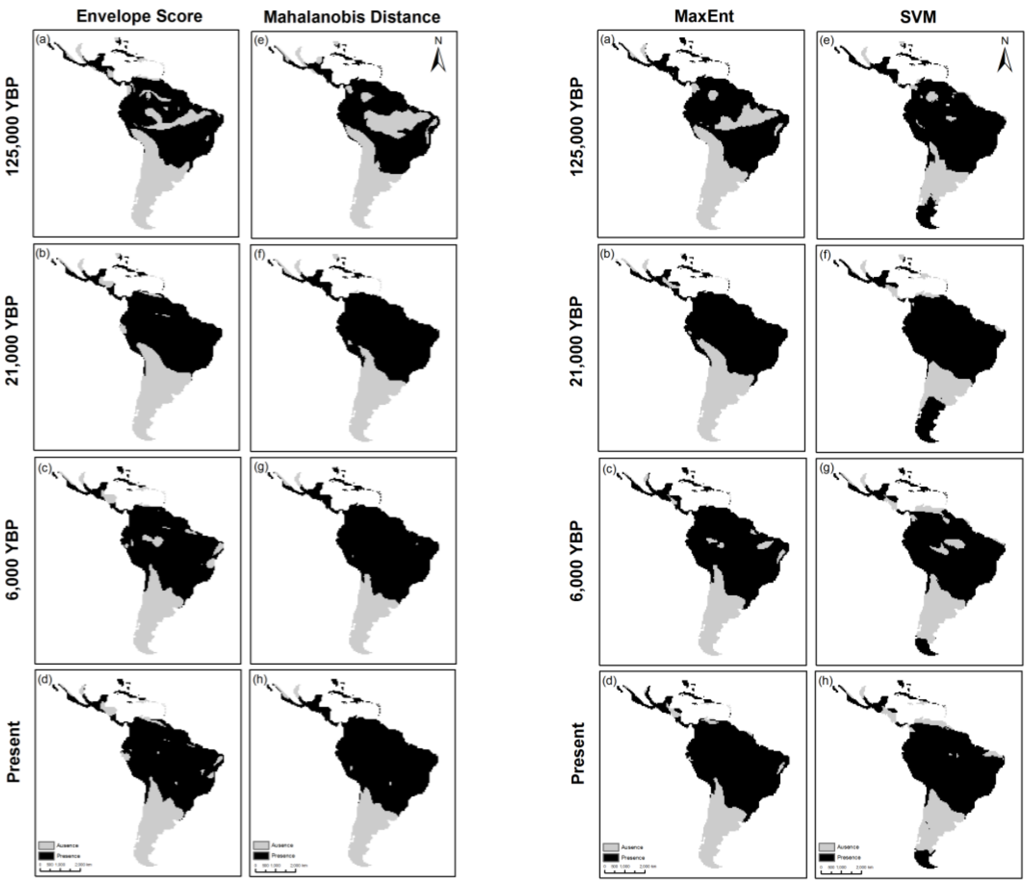
Figure 3.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Mahalanobis Distance
MaxEnt
SVM
125,000 YBP
21,000 YBP
6,000 YBP
Present
(a)
(b)
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(f)
(g)
(h)
N
Absence
Presence
0 500 1,000 2,000 km

Figure 4.

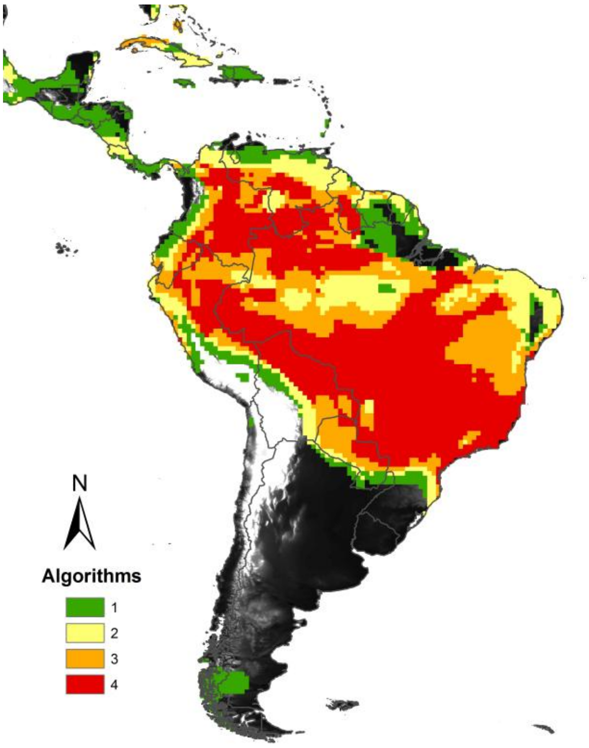

Figure 5.

CAPÍTULO 3

A ser submetido para: Biological Conservation

Present and future challenges for the conservation of *Tapirus terrestris* as revealed by ecological niche models

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Short Running Title *Tapirus terrestris* conservation revealed by ecological niche models

ABSTRACT

Climate change can potentially increase the susceptibility of species to extinction, particularly when a combination of modifications in climate suitability, life history and extrinsic threats occurs. Therefore, future losses of large mammals, such as the lowland tapir (*Tapirus terrestris*), could take place faster than expected. Through the use of species distribution models, we modeled the distribution of lowland tapirs in current and future climates, evaluating potential changes in suitable habitats of the species. In addition, we assessed existing Brazilian Protected Areas (≥ 500 km^2) and their effectiveness with regards to the distribution of suitable areas for *T. terrestris*. The models predicted a marked loss in environmental suitability, particularly in tropical moist broadleaf forests. Nevertheless, the total suitable area for lowland tapirs in protected areas should not change. We expect that areas with greater environmental suitability could sustain larger lowland tapir populations and could therefore be more resilient to various threats. This observation may suggest that simple comparisons in range limits may represent the potential negative effects of climate change on the species distribution very poorly. Thus examining changes in climatic suitability will provide important information regarding generalist species such as tapirs.

Keywords

Climate change, lowland tapir, protected areas, species distribution modeling, suitability, vulnerability.

1. Introduction

Climate change poses a major threat to biodiversity especially when complex interactions between life history and extrinsic threats (*e.g.*, habitat loss and fragmentation) increase the susceptibility of a species to extinction under future climate scenarios (Ackerly et al., 2010; Brook et al., 2009; Keith et al., 2008). As result of this combination, future losses of large mammals could be far more rapid than expected (Cardillo et al., 2005). The removal of large herbivores, such as the lowland tapir, from their natural habitats will most certainly impact the structure and composition of regenerating forests due to the tapirs'role as a long-distance seed disperser (Fragoso et al., 2003; Galetti et al., 2001; Tobler et al., 2010).

Climate change may modify the suitable areas for a specific species, driving these species to shift their geographic ranges, thus increasing their vulnerability to extinction (Nogués-Bravo et al., 2010; Root et al., 2003; Thomas et al., 2004). This process can affect the probability of species persistence in areas designated for conservation, forcing them into inadequate habitats or causing local extinctions (Araújo et al., 2004; Coetzee, 2008; Hannah et al., 2007; Parmesan and Yohe, 2003). Diverse climate change scenarios present an enormous challenge for the development of strategies for the protection and conservation of several species. Climate change presents a complex spatial problem for species conservation. Conservation requires finding future suitable places that are often restricted by current habitat fragmentation but are within the known range of the species. Moreover, evaluating the effectiveness of protected areas is problematic in conservation planning because these are immovable geographic areas which is hardly adequate under the dynamic scenarios of climate change (Dudley et al., 2008; Parmesan and Yohe, 2003; Root et al., 2003).

In recent years, the evaluation of species and reserve responses to global climate change has been possible through the application of different tools of conservation planning. One such tool, the Ecological Niche Model (ENM), has facilitated studies in basic and applied ecology, biogeography, conservation biology and wildlife management (Araújo et al., 2006; Coetzee et al., 2009; Guisan and Zimmermann, 2000; Rodríguez et al., 2007). The ENMs have become popular in predicting the suitability of the current habitat and future range shifts and particularly for estimating extinction risks induced by climatic changes (Araújo and Rahbek, 2006; Beever et al., 2011; Keith et al., 2008; Thomas et al., 2004). These models have also been used to evaluate the effectiveness of natural reserves in species protection (Hannah et al., 2005; Nóbrega and De Marco, 2011; Rodríguez-Soto et al., 2011; Urbina-Cardona and Loyola, 2008).

The availability of a set of global climate layers (climate grids) (Hijmans et al., 2005), along with the development of a large number of climate models, such as general circulation models (GCMs), by various meteorological research centers, has increased the predictive power of ENMs and has improved the evaluation of individual species responses to global climate change (Araújo et al., 2006; Beaumont et al., 2008; Peterson et al., 2002; Thuiller, 2003; Thuiller et al., 2005;). According to Beaumont *et al.* (2008), climate models are currently the best tools available for simulating future climate scenarios. However, ENMs present a certain level of uncertainty due to differences in alternated models, species characteristics and future scenarios (Thuiller et al., 2008). The crucial question is whether the models that predict current species distribution can also provide robust predictions for future distribution following climate change (Araújo and Rahbek, 2006; Elith and Leathwick, 2009). Additionally, whether the ENMs can predict the species' distribution in new or unsampled regions following predicted climate changes must be determined. Should these ENMs prove to be transferable (Heikkinen et al., 2012; Peterson et al., 2007; Randin et al., 2006), they could be used to manage anticipated climate conditions (Mbogga et al., 2010). Recent studies have addressed the errors, uncertainties and transferability of these models (Beaumont et al., 2008; Buisson et al., 2010; Heikkinen et al., 2012; Marmion et al., 2009). The identification and quantification of these uncertainties are crucial for improving the reliability of projected species range shifts in the future (Pearson et al., 2006; Thuiller, 2004). These projections are particularly important for completing risk-assessment exercises (Ormsby, 2005), making conservation management decisions (reintroduction programs (Hartley et al., 2006) and creating new or expanding protected areas.

The lowland tapir, *Tapirus terrestris*, is a suitable model for examining the impacts of climate change on the persistence of large mammal populations present at low densities. The last IUCN Red List assessment for tapirs has estimated that the number of lowland tapirs in the wild will continue to decline over the next three generations (33 years) (IUCN, 2012). Synergistic interactions between intrinsic biological traits, such as a slow reproductive cycle, delayed sexual maturity and long gestation period producing a single offspring (Barongi, 1993; Eisenberg, 1997), and extrinsic threats, including deforestation, hunting and road-kill, are driving the decline of lowland tapir populations (Medici et al., 2007). Consequently, tapir populations have become small and increasingly isolated throughout their geographic distribution, particularly in the Cerrado (Brazil), Atlantic Forest (Brazil) and Llanos (Venezuela/Colombia) biomes (Medici *et al.*, 2007; Medici *et al.*, 2012). Lowland tapir populations have become extinct in some regions of the Brazilian Atlantic Forest (Flesher and Gatti, 2010), in addition to the grasslands in Southern Brazil and the Caatinga (Brazil) (Medici *et al.*, 2012).

Considering the current distribution of lowland tapir populations, this paper presents a distribution model outlining suitable habitats under the present climate and under predicted climate scenarios for the future. Moreover, these predictions were used to evaluate current protected areas in Brazil with regards to their inclusion of suitable areas and predicted effectiveness under future climates.

2. **Material and methods**

2.1. Study species and Occurrence data

The first appearance of *Tapirus* in North America occurred in the late middle Miocene as a result of their immigration from Asia. In South America, the first records indicate that they appeared during the Plio-Pleistocene period (Cione and Tonni, 1996; Nabel et al., 2000) following migration from North America after the formation of the Isthmus of Panamá, during the Great American Biotic Interchange (Marshall et al., 1988; Webb, 2006). The lowland tapir, *Tapirus terrestris,* is a Neotropical mega-herbivore mammal (Hansen and Galetti, 2009). The species has expanded its distribution since it first appeared in the Pleistocene period (Thoisy et al., 2010), and has therefore become the most successful large herbivore in South America.

Tapirus terrestris occurs in Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, French Guyana, Paraguay, Peru, Suriname and Venezuela (Taber et al., 2008). Occurrence points were gathered and distributed over nearly the entire current geographic distribution of the lowland tapir. These data were provided by experts from the IUCN/SSC Tapir Specialist Group (TSG) in Bolivia, Brazil, Colombia, Ecuador and Paraguay and corresponded to approximately 70% of all records, including unpublished field data. To complement the data, we compiled information from the literature and from museum specimens deposited in online databases available within the Data Portal of the Global Biodiversity Information Facility (GBIF; www.gbif.org). We used 475 spatially distinct occurrence points (from 516 compiled) to generate the distribution of lowland tapirs for both current and future climate conditions throughout the Neotropics.

2.2. Climate layers

Environmental data were obtained from the WorldClim Database (www.worldclim.org) and included six variables (from 19 available): annual mean temperature, temperature seasonality (coefficient of variation), mean temperature of the driest quarter, annual precipitation, precipitation seasonality (coefficient of variation) and precipitation during the warmest quarter. These data were used at a 5’ spatial resolution (~9 km of cell-side size).

We used future climate datasets derived from three general circulation models (GCMs), for the year 2080 (www.ccafs-climate.org/data). These models included: 1) Canadian Centre for Climate Modelling and Analysis (CCCma) Coupled Global Climate Model (CGCM2), Second Version (Flato and Bôer, 2001); 2) CSIRO Atmospheric Research Mark 2b Climate Model (Hirst et al., 1996, 2000) and 3) HadCM3, which is the coupled ocean–atmosphere general circulation model developed by the Hadley Centre for Climate Prediction and Research (Gordon et al., 2000).

For each GCM described above, two emission scenarios for the year 2080 were selected. The first scenario, A2 was considered to be more severe and assumed 1% yr^{-1}

CO2 increase and did not take into account the effects of sulfate aerosols. The A2 model describes a heterogeneous world with a continuously increasing global population. The second scenario, B2, was more conservative and assumed 0.5%yr^{-1} CO2 increase and incorporated the effects of sulfate aerosols. The B2 scenario highlighted a world in which the emphasis is placed on local solutions to economic, social and environmental sustainability at a time when the global population is continuously expanding at a rate lower than that described in scenario A2 (Nakicenovic and Swart, 2000).

2.3. Modelling approach

To model the habitat suitability for *T. terrestris*, we used two different algorithms: Maximum Entropy (MaxEnt) and Mahalanobis Distance. A comparative analysis of these algorithms with other methods indicated that they have greater predictive accuracy (Elith et al., 2006; Elith and Graham, 2009; Farber and Kadmon, 2003; Johnson and Gillingham, 2005). Furthermore, we chose these two algorithms because they reflect distinct approaches. MaxEnt is a complex parameter-rich model that may produce less transferability estimates (Peterson et al., 2007; Phillips, 2008), especially for studies using large datasets. Mahalanobis Distance is a simpler model allowing for easier interpretation based on a geometric view of the Hutchinsonian niche (Farber and Kadmon, 2003). These distinct models helped us evaluate the uncertainties in our study.

MaxEnt Software (version 3.3.3e) (Computer Sciences Department, Princeton University, 2004) is a general-purpose machine learning approach that uses a simple mathematical formulation for modeling geographic distribution of species with presence-only data (Phillips et al., 2006). Absence data are generated by randomly selecting ‘‘pseudo-absence’’ points or the background of the area. MaxEnt models were built using 1000 iterations, logistic output format, and removal of all duplicates.

Recent studies have shown that MaxEnt models suffer from over-parameterization leading to transferability problems (Peterson et al., 2007) that may affect its predictions, particularly future climate (Elith et al., 2010). MaxEnt provides a number of features (linear, quadratic, hinges, logistic and product) representing the types of functions and combination of functions used during the process. The number of parameters in the model is directly (and sometimes exponentially) related to the number of features used in the model.

To control for over-parameterization, we developed the MaxEnt models using two distinct settings. The first used the “default” setting ("auto-features"), which allows for inclusion of six features (Phillips et al., 2006). The first set was called “complete” model. The second set was called “simple” setting and includes only two features: (i) linear, which constrains the output distribution for each species as having the same expectation for each of the continuous environmental variables and the sample locations for that species; and (ii) the quadratic feature, which models the tolerance of the species to variation from its optimal conditions (Phillips et al., 2006; Phillips and Dudík, 2008). Elith *et al.* (2010) argue that linear and quadratic features produce smoother models. Simple models with fewer parameters are expected to generate models with higher transferability.

The other approach used in this study was based on Mahalanobis Distance, a generalized squared distance statistic. This approach has been used as a multivariate index of environmental quality in studies examining species distribution. This generic algorithm was based on environmental dissimilarity metrics, which is an extension of the standardized Euclidian Distance and takes into account the covariance structure among the predictor variables. Mahalanobis Distance is more complex because the model considers the covariance matrix among environmental variables in the occurrence points (Farber and Kadmon, 2003).

2.4. Model evaluation

Recent advances in the evaluation procedures for species distribution models suggest that the use of both threshold-independent and threshold-dependent evaluation measures should be used to ensure that the methods are efficient both generally as well as with regards to the chosen threshold (Liu et al., 2011). In this paper we chose to use the True Skill Statistics (TSS), which performed well when compared to similar measures (Liu et al., 2011). This statistic is highly correlated with AUC (Area Under Curve) and is not biased by prevalence (Allouche et al., 2006). TSS takes into account both omission and commission errors and ranges from −1 to +1, where +1 indicates perfect agreement, and values of zero and less indicate a performance that is no better than random.

The AUC is a threshold-independent measure that can be interpreted as the ability of the algorithm to discriminate between a suitable environmental condition and a random analysis pixel (Phillips et al., 2006). AUC values range from 0 to 1, where 1 indicates perfect discrimination and a score of 0.5 implies discrimination that is no better than random (Elith et al., 2006). AUC was only used to determine the relative performance of the various models.

Thresholds are used to convert continuous species distributions model outputs in binary maps to predict the presence or absence of the species. Values smaller than the threshold were considered to be zero, while values higher than the threshold were considered to be 1. The low presence threshold (LPT) was used because it equals the minimum model prediction value for any of the training occurrence point data. Thus, the LPT minimizes omission errors in the models, which can be considered as an effective strategy for species conservation. This choice is especially appropriate for *T. terrestris* as the occurrence points are precise and contain no mis-identification or other common problems. Moreover, a comparison of the results using LPT with the threshold derived from the ROC curve showed extensive omission of known occurrences in the latter model (Supplementary material S1). Threshold was derived from the ROC curve representing the value with the lowest Euclidean distance from the zero point, the false positive and true positive (Elith et al., 2006).

The model transferability was quantified using the method proposed by Wenger and Olden (2012), which is based on a non-random division of the dataset and involves cross-validation. Thus, we initially separated the dataset into two spatially distinct subsets based on longitude, fitting the model with the first subset (denoted as the training dataset) and evaluating with the second subset (test dataset). Then, the reverse process was completed with the second subset. For each evaluation, we calculated the AUC and TSS values.

2.5. Species range shift and conservation under climate change

To evaluate the future range shifts of *T. terrestris,* such as expansions and contractions, we used relative changes in distribution (values >1 and <1 to represent expanding and shrinking climates, respectively) and the proportional distribution loss. The first metric was calculated by dividing the area occupied under future projections by the area occupied under current climate. The second metric was calculated by dividing the number of lost cells in future distribution by the number of cells in the current distribution. We also quantified the number of overlapping suitable cells in the present and the future, furthermore novel climates (absent now and present in the future); this was defined as a presently unsuitable habitat that was predicted to become suitable in the future (Thuiller et al., 2005; Williams et al., 2007). The differences in size of current and future distributions were tested using a t test for dependent samples.

To evaluate the effectiveness of existing protected areas (PAs) with respect to the distribution of suitable areas predicted under climate change scenarios, we assembled the geographical limits of Brazilian protected areas from ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade), the official Brazilian environmental agency. This dataset contains federal and state reserves implemented until 2012 including both strictly protected areas (equivalent to IUCN categories I and II) as well as sustainable use reserves (equivalent to IUCN category V).

Previous studies have estimated the size of the area required to maintain genetically viable populations (~200 individuals) of lowland tapirs in Atlantic Forest sites (Medici, 2010; Gatti et al., 2011; Medici and Desbiez, 2012). In this paper we used a conservative scenario and selected protected areas ≥ 500 km² regardless of the biome. We selected a total of 178 areas. In addition to these areas, we used the second scenario for all protected areas and placed no size restrictions on the analysis. In this group we included Private Natural Heritage Reserves (called Reserva Particular do Patrimônio Natural in Portuguese and denoted hereafter as “RPPN”), which are an official protected area category that allows private landowners to voluntarily turn their private forest into protected areas maintaining them in perpetuity. Furthermore, we categorized the CUs for five Brazilian biomes (Amazon, Atlantic Forest, Caatinga, Cerrado and Pantanal), calculated the mean climatic suitability for each conservation unit within the first group and evaluated whether there was a gain or loss in suitability in the future.

Conservation units were converted to a final resolution of 0.2º X 0.2º (approximately 22 X 22 km) independently of their size (Nóbrega and De Marco, 2011). For this analysis, we limited the resulting models of lowland tapir distribution to the Brazilian territory. The maps depicting predicted current and future suitable environments were compared to existing maps of protected areas in Brazil.

3. Results

3.1. Model evaluation

MaxEnt models produced higher AUC and TSS values compared to Mahalanobis Distance (Table 1). However, both yielded high transferability (Table 1, Figure 1), which is a desirable property for such models. Furthermore, the distribution areas predicted by Mahalanobis Distance indicated a potentially high rate of over-prediction, suggesting that the potential lowland tapir distribution could include areas where no records of tapir occurrence exist (*e.g.*, central region of Argentina) (Figure 1).

The complete MaxEnt models showed higher training AUC and TSS values (Table 1). However, the simple models demonstrated higher average transferability (0.46). Moreover, the distribution resulting from the complete models contained some gaps, particularly the model produced from the second data subset (Figure 1; Supplementary Material S2). These gaps occur in areas where tapirs are present and contribute to an increased model omission rate.

Considering the evaluation measure results (AUC and TSS) and the transferability of the models, we determined that the MaxEnt simple model was the most appropriate to describe potential tapir distributional areas. Specifically, we focused on the limited over-prediction by the MaxEnt models and the slightly higher transferability characteristic of the simple models.

3.2. Climate change and potential distribution shifts

The MaxEnt model predicts an average potential distribution of 15,322,662.00 km^2 for *T. terrestris* under current climate conditions; additionally, nearly 97% of the suitability cells were maintained in the future for all climate models and emission scenarios (Table 3). The values obtained for the relative change (>1) indicate that the suitable areas will expand in the future, increasing the potential distribution by 384,844.50 km^2 and 843,642.00 km^2 for new potentially suitable habitats (Table 2).

No significant difference was observed between the range size of the species in the present and in the future ($t = -1.346$, $df = 5$, $p = 0.236$). However, the models predict pronounced changes in the spatial distribution of suitable climates, with lost and gained habitats in various regions where lowland tapirs are currently distributed (Figure 2).

Results from different climate models follow the same pattern, but the Hadcm3 models (scenarios A2 and B2) yielded areas with greater losses than suggested by the other climate models. These models predict that a marked loss in environmental suitability will occur for the lowland tapir, especially in Tropical Moist Broadleaf Forests (Figure 2). The western Amazon (Brazil, Colombia and Peru) is predicted to suffer from the largest suitability losses when compared to other regions. Guianan moist forests are also predicted to be negatively affected by climate change.

The Cerrado and Pantanal biomes are predicted to undergo a considerable loss in suitability as well. Furthermore, other ecoregions such as Beni Savana (Bolivia), rainforests of Napo (Ecuador and a portion of Peru) and dry Chaco (portions of

Argentina, Bolivia and Paraguay) are expected to experience suitability shifts under climate change (Figure 2). The cells located in the Caatinga and the Atlantic Forest located above the Serra do Mar coastal forests will be affected by climate alterations as well, but these changes are likely to be less intense than those mentioned before.

Increases in the suitability are predicted to occur in areas where the species is not thought to be present, such as some regions in the Andes. Moreover, an increase in suitable grid cells may occur in the Brazilian Atlantic Forest, specifically in Araucaria moist forests, Alto Paraná Atlantic Forests and the Serra do Mar Coastal Forest (Figure 2).

3.3. Effectiveness of the Brazilian network of protected areas

As with the total distribution, there will be no change in the size of lowland tapir geographic distribution area under protection. Nevertheless, only 12% of the lowland tapir distribution will be within protected areas capable of supporting viable populations (≥ 500 km^2) (Table 3). When considering all Brazilian protected areas, approximately 15% of the potential lowland tapir distribution will be under some form of legal protection in the future.

Although there were no changes in the total distribution of tapirs, the models predicted pronounced changes in the spatial distribution of climatic suitability. All of the future climate models, using both emission scenarios, show similar qualitative patterns in changing environmental suitability, quantified in protected areas (PAs). However, the mean values for suitability are slightly different among the models (Table 2; Figure 3). The HadCM3 (A2 and B2) models are more pessimistic than the others, producing greater suitability losses (Table 2; Figure 3c, f). When evaluated by biome, the trend indicates a clear decrease in the environmental suitability of most of the PAs, especially in the Amazon, Cerrado, Caatinga and Pantanal biomes.

The protected areas in the Atlantic Forest include regions where the models predict a minimal increase in climatic suitability, with the exception of the Csiro (B2) model, which predicted an increase in these areas (B2) (Figure 3e). Furthermore, the suitability is stable over time based on the analysis of a small group (Figure 3). We note that the increase in suitability usually occurred in the same areas, principally in the Atlantic Forest regardless of the climate model; this observation minimizes the uncertainty among the models (Figure 3; Supplementary Material S3).

4. Discussion

4.1. Present and future challenges for lowland tapir conservation

The comparison between the current and the future distribution of lowland tapirs resulted in small changes in the overall species distribution. Nonetheless, model outcomes clearly show a strong shift in the average environmental suitability throughout the species distribution. This observation highlights the fact that simple comparisons of range limits do not fully describe the possible negative effects of climate change on species distribution. This reasoning is in line with recent advances in species distribution modeling, which is currently moving from strict estimation of species range to a more thoughtful evaluation of suitability distributions (Araújo et al., 2011; Diniz-Filho et al., 2010; Tôrres et al., 2012).

Predicted environmental suitability can be used to better understand the effects of environmental changes as these models represent how the physiological and ecological requirements of the species are met at a specific location (VanDerWal et al., 2009). For example, lowland tapirs have diverse behavioral strategies and physiological characteristics that can favor the occupation and use of the wide range of resources in extensive areas (García et al., 2012; Medici, 2010), and these characteristics may explain the large lowland tapir distribution size that the models predicted. Thus, a key element of this reasoning is that environmental suitability is at least monotonically related to actual population densities; therefore, environmental suitability has become an important surrogate for population survival and persistence.

Recent studies have tested whether environmental suitability, derived from species distribution modeling, could serve as a surrogate for species' performance and density. Tôrres et al. (2012) demonstrated that high jaguar densities were restricted to areas where the environmental suitability was the greatest. Low jaguar densities were observed in areas with low suitability. Recent studies (Montoya et al., 2009; Tôrres et al., 2012; VandDerWal et al., 2009) suggest that species distribution models provide valuable information on species abundance and on the effectiveness of conservation efforts for threatened species, such as the lowland tapir. These models are extremely valuable because it is usually difficult to obtain real species performance measures along environmental gradients (Thuiller et al., 2010).

The sensitivity of each species to climate change can vary with the life-history characteristics of the organism (Willians et al., 2008) and with their individual lifestyle. Low reproductive rates and low population density are usually associated with higher sensitivity to climate change. Therefore, the lowland tapir is a good model for ENM analyses given its very low reproductive rates and generally low population density (Medici et al., 2007; Medici, 2010; Novaro et al., 2000). These characteristics, combined with a decline in climatically suitable areas predicted by our models, could potentially influence the vulnerability of this species to extinction, similar to what has been predicted for other organisms (Araújo *et al.*, 2006; Beever *et al.*, 2011; Capinha *et al.*, 2012; Cardillo *et al.*, 2005; Diniz-Filho *et al.*, 2010; Ochoa-Ochoa *et al.*, 2012).

Specifically, climate change can introduce changes in vegetation, affecting the integrity of several biomes in South America (Leadley et al., 2010; Salazar et al., 2007) and consequently the survival of large herbivores such as tapirs (García et al., 2012). Climate change can prevent the species from maintaining a minimum viable population size (Willians et al., 2008), while small populations are extremely vulnerable to demographic stochasticity (Melbourne and Hastings, 2008). Additionally, if the patterns of rainfall and temperature change increasing the climate variability as predicted (IPCC, 2007; Schneider et al., 2007), tapirs may become even more dependent on water to regulate their body temperature (García et al., 2012).

Most of the areas predicted by the models to suffer moderate to high losses in future suitability are located in regions where tapir populations are currently declining at alarming rates, and local extinctions have also been reported(Flesher and Gatti, 2010; IUCN, 2012; Medici et al., 2012). Contrarily, some of the models have predicted that climate change will negatively impact areas where tapir populations are not considered to be threatened, such as the Brazilian Amazon, or in areas where the tapir is listed as Near Threatened, such as Pantanal (Medici et al., 2012).

These predictions are very serious, particularly if habitat loss and tapir hunting continue to take place (Medici et al., 2012). These threats could potentially have an overriding effect after drastic losses in climate suitability. Tapir populations in eastern and southern Amazonia -- the so-called "arc of deforestation" -- are rapidly declining due to extensive hunting and deforestation (Bodmer and Lozano, 2001; IUCN, 2012; Medici et al., 2007). In the Pantanal, the intensification of traditional cattle ranching practices threatens the medium-large frugivorous mammal community (Alho, 2011; Junk and Cunha, 2005). In fact, the Pantanal floodplains may be an appropriate model to study the potential impacts of climate change on Neotropical communities as extreme climate events such as droughts can significantly change local wildlife communities (Desbiez et al., 2010). Thus, the areas located in the Amazon and Pantanal biomes should be considered vulnerable to species survival in the future if no conservation strategy is implemented to minimize the predicted changes in climatic suitability and at the landscape level.

Recent studies have suggested that combinations of threats, including hunting, habitat loss, fire, invasive species and climate change, or feedback between threats can affect species survival and persistence and foster unpredictable interactions among plants, animals and microorganisms (Brook et al., 2008; Laurance and Useche, 2009; Thuiller, 2007). García et al. (2012) emphasized that the combination of environmental changes and threats including poaching, road-kill and infectious diseases strongly affects the likelihood of extinction of remaining tapir populations. Again, we expect that areas with higher environmental suitability could maintain larger populations and likely be more resilient to such threats.

Medici et al. (2012) assessed the conservation status of the *T. terrestris* in five Brazilian biomes (Amazon, Atlantic Forest, Caatinga, Cerrado and Pantanal). Tapir populations in the Atlantic Forest and Cerrado biomes were found to be seriously threatened. Our results indicated that the Cerrado biome as well as a portion of the Atlantic Forest above the Serra do Mar coastal forests, will be extremely threatened by the decline in environmental suitability. The Atlantic Forest is one of the most threatened tropical forests in the world and is highly fragmented as a consequence of a long history of degradation (Metzger, 2009; Myers et al., 2000; Ribeiro et al., 2009). It shelters many species that are threatened with extinction by anthropogenic pressures (Galetti et al., 2009).

Lowland tapirs were negatively impacted by habitat fragmentation in the Atlantic Forest and populations have been heavily hunted (Cullen et al., 2000; Flesher and Gatti, 2010). The Tabuleiro sand plain lowlands, located in southeastern Brazil, were drastically reduced and completely lost in some areas. Nevertheless, these areas still shelter the last lowland tapir populations in this forest type (Flesher and Gatti, 2010). Currently, 70% of tapir populations in the Atlantic Forest are considered to be at critical levels (Medici et al., 2012), meaning that they are below the minimum viable population size of 200 individuals (Gatti et al., 2011; Medici, 2010). The deleterious genetic effects of isolation are a long-term threat to small tapir populations (Gatti et al., 2011). A reduction in the genetic variability in tapir population is expected to affect the ability of the population to adapt to environmental fluctuations (Medici and Desbiez, 2012), such as those predicted to occur under climate change.

In the Cerrado biome, only 20% of tapir populations have long-term chance of survival, and populations will be restricted to protected areas (Medici et al., 2012). This is the second largest biome in the Neotropical region, but it has been transformed into one of the most important regions for cattle ranching and commodity crops in Brazil (Ferreira et al., 2012). Remaining natural patches within the Cerrado have been restricted to sloped areas (Carvalho et al., 2009). Recent studies have predicted severe landscape changes on the biome scale, and these changes are concentrated in the northern and northeastern regions of Brazil (Diniz-Filho et al., 2009; Ferreira et al., 2012). Habitat modifications and loss of environmental suitability in the Cerrado can affect small populations that are more susceptible to genetic, environmental and demographic constraints (Brito, 2009; Gatti et al., 2011; Lacy, 2000).

Tapir conservation efforts are also needed in areas that are predicted to experience decreases in environmental suitability in the future. These include regions in Argentina, Bolivia, Paraguay, Colombia, Ecuador and Peru. Many tapir populations in these regions are small and isolated due to an increase in agricultural and cattle ranching activities as well as overhunting (IUCN, 2012; Medici et al., 2007). In the Bolivian Chaco, lowland tapirs are an important food source for indigenous people (Brooks and Eisenberg, 1999) and are usually overexploited (Noss and Cuéllar, 2008).

In addition, our models predicted an increase in climatic suitability in areas located in the Atlantic Forest, such as the Serra do Mar Coastal Forests, which currently holds the largest lowland tapir population in the biome. Today, approximately 40% of the lowland tapir populations are found along the coast of São Paulo and Paraná States (Medici et al., 2012). The Serra do Mar is characterized by large forest fragments that extend into the Interior and Araucaria regions (Ribeiro et al., 2009). Medici and Desbiez (2012) presented the results of a population viability analysis (PVA) of a lowland tapir population in aprotected area (Morro do Diabo State Park) and surrounding forest fragments located in the Atlantic Forest of the Interior. Results of this PVA demonstrated that the effectiveness of tapir conservation efforts depends on promoting the functional connectivity of the landscape.

In southern Brazil, the species is locally extinct in several sites and is mostly found in protected areas (Fontana et al., 2003; Mikich and Bérnils, 2004; Rocha-Mendes et al., 2005). The Llanos in Venezuela has dwindling tapir populations due to subsistence hunting by indigenous people, peasants and settlers (Medici et al., 2007; Rodríguez and Rojas-Suárez, 2008). As discussed by Tôrres et al. (2012), extrinsic factors can limit species populations in regions with increased climate suitability values, contradicting what would be expected in regions where environmental conditions are favorable to persistence (Thuiller et al., 2010).

Although the models have predicted new suitable areas for lowland tapirs, it is very important to note that the dispersal to those areas could be limited (Hodgson et al., 2009). Brooker et al. (2007) observed that when the rates of climate change increase, decreased levels of long-distance dispersal drives mutualists to extinction. Ochoa-Ochoa et al. (2012) evaluated the dispersal of an amphibian species in Mexico and found that its low dispersal ability generates increased levels of extinction. Furthermore, species may not have sufficient time to adapt to new conditions (Loiselle et al., 2010). Despite a possible higher dispersal ability of tapirs in some regions, the increase of human-dominated landscapes, including pastures, agroecosystems and urban areas, may seriously limit the dispersal of existing populations in the future. Some studies provide a glimpse of hope and suggest that tapirs can use complex landscapes that include humans and populations could therefore persist in this new environments (Centoducatte et al., 2011; Medici, 2010; Noss et al., 2003). Furthermore, these new environments also have their own challenges, including hunting, road-kill, and the potential introduction of new infectious pathogenic agents into tapir habitat (Furtado et al., 2010; Mangini et al., 2012; Medici et al., 2007).

Many bionomic processes also affect local species distribution but may not have a measurable contribution at larger scales (global and regional, for example), in which the scenopoetics and biogeographical factors have a determinant effect (Hortal et al., 2010; Thuiller et al., 2004). Nevertheless, it is not possible to account for all of these factors in species distribution models (Kamino et al., 2011). An alternative approach is to compare the resulting habitat suitability models to characteristics of the habitats, including the presence, size and conservation state of forest remnants, connectivity between these remnants, presence of roads, existence of conservations units among others.

Currently, most lowland tapir populations are found in protected areas (Flesher and Gatti, 2010; IUCN, 2012; Medici et al., 2012). Unfortunately, only a small portion of the tapir's distribution in Brazil will remain protected in the future. Existing protected areas within the lowland tapir range are unevenly distributed between biomes. The PAs in the Amazon account for approximately 80% of the Brazilian PAs $\geq 500 km^2$, but these areas are expected to become less suitable for tapirs in the future. The effectiveness of protected areas in maintaining species and the predicted habitats following climate change have been discussed in previous studies (D'Amen et al., 2011; Marini et al., 2009). Although protected areas are geographically immovable (Wiens et al., 2011), and changes in environmental conditions can occur over time, as predicted by our models. Climate change will modify the conditions within protected areas worldwide, unleashing a cascade of changes within specific habitats (Wiens et al., 2011).

4.2.Methodological Issues

Species distribution modeling is still a growing science and any study focusing on the use of these methods should make contributions to the discussion of methodological issues. We observed that MaxEnt performed better than Mahalanobis Distance based on AUC and TSS values, a result that was also observed in other studies (Elith et al., 2006; Nabout et al., 2010; Rodríguez-Soto et al., 2011; Roura-Pascual et al., 2008). Farber and Kadmon (2003) found that Mahalanobis Distance model produced more accurate ENMs than other methods. However, we must emphasize that the values for predictive accuracy for both algorithms were relatively low; this finding indicates that tolerance negatively affects the predictive accuracy of our models, as discussed in previous studies (Brotons et al., 2004; Stockwell and Peterson, 2002; Tsoar et al., 2007). These authors discussed one possible explanation; they suggested that widespread and more general species, such as the lowland tapir, do not discriminate between slight differences in the environment and that the differences in ecological characteristics may be local or regional. Stockwell and Peterson (2002) also presented methodological justification to address the issue of presence data and background, which reduces the accuracy of these models.

Our data demonstrate the importance of model transferability in addition to model accuracy for model evaluation. In fact, the model developed in a specific region could be successfully used to predict changes in a different region. Peterson et al. (2007) also observed that the MaxEnt model was transferable only at very low thresholds, which reinforced our decision to use the low threshold presence (LTP) instead of the ROC threshold for our analyses.

5. Conclusion

Tapirs were part of a large community of Neotropical herbivores, whose habitat has undergone environmental fluctuations causing the extinction of the vast majority of these animals during the transition at the end of the Pleistocene-Holocene period (Lessa and Fariña, 1996). Tapirs have been successful for the last 3.5 million years of their diversification (Ruiz-García et al., 2012) and should be assumed to be able to find a way to cope with the spatial variation in climate conditions and future climate change. However, these large mammals may not be as successful in the future. The combination of lost climate suitability, habitat loss and fragmentation, hunting, road-kill, diseases and decreases in the overall population density can exacerbate the effects of climate change, consequently increasing the threats for its survival. We must define and prioritize critical habitats for the conservation of tapirs, planning future actions that consider the impacts of climate change.

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7. References

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft, N.J.B., 2010. The geography of climate change: implications for conservation biogeography. Diversity and Distributions 16, 476-487.

Alho, C., 2011. Concluding remarks: overall impacts on biodiversity and future perspectives for conservation in the Pantanal biome. Brazilian Journal of Biology 71, 337–341.

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

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10: 1618–1626.

Araújo, M.B., Thuiller, W, Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33, 1712–1728.

Araújo, M.B., Rahbek, C., 2006. How does climate change affect biodiversity? Science: 313, 1396–1397.

Araújo, M., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecology letters 14, 484–492.

Barongi, R.A., 1993. Husbandry and conservation of tapirs. International Zoo Yearbook 32, 7-15.

Beaumont, L.J., Hughes, L., Pitman, A.J., 2008. Why is the choice of future climate scenarios for species distribution modelling important? Ecology Letters 11, 1135–1146.

Beever, E.A., Ray, C., Wilkening, J.L., Brussard, P.F., Mote, P.W., 2011. Contemporary climate change alters the pace and drivers of extinction. Global Change Biology 17, 2054–2070.

Bodmer, R.E., Lozano, E.P., 2001. Rural development and sustainable wildlife use in Peru. Conservation Biology 15, 1163-1170.

Brito, D., 2009. Análise da viabilidade de populações: uma ferramenta para a conservação da biodiversidade no Brasil. Oecologia Brasiliensis 13(3), 452-469.

Brook, B., Sodhi, N., Bradshaw, C., 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23, 453–460.

Brook, B., Akçakaya, H., Keith, D., Mace, G., Pearson, R., Araújo, M., 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. Biology Letters 5, 723-725.

Brooker, R., Travis, J., Clark, E., Dytham, C., 2007. Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. Journal of Theoretical Biology 245, 59–65.

Brooks, D., Eisenberg, J.F., 1999. Estado y biología de los tapires neotropicales: perspectiva general, in: Fang, T.G., Montenegro, O.L., Bodmer, R.E. (Eds.). Manejo y conservación de la fauna silvestre en América Latina, Editorial-Instituto de Ecología. La Paz, Bolivia, pp. 409-414.

Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27, 437-448.

Buisson, L., Thuiller, W., Casajus, N., Sovan L., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. Global Change Biology 16, 1145–1157.

Capinha, C., Anastácio, P., Tenedório, J.A., 2012. Predicting the impact of climate change on the invasive decapods of the Iberian inland waters: an assessment of reliability. Biological Invasions 14, 1737-1751.

Cardillo, M., Mace, G., Jones, K., Bielby, J., Bininda-Emonds, O., Sechrest, W., Orme, C., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. Science (New York, N.Y.) 309, 1239–1241.

Carvalho, F.M.V., DeMarco, Jr. P., Ferreira, L.G., 2009. The cerrado into-pieces: habitat fragmentation as a function of landscape use in the savannas of central Brazil. Biological Conservation 142, 1392-1403.

Centoducatte, L., Moreira, D.O., Seibert, J.B., Gondim, M.F.N., Acosta, I.C.L., Gatti, A., 2011. Tapirus terrestris occurrence in a landscape mosaic of Atlantic Forest and Eucalyptus monoculture in southeast Brazil. Tapir Conservation 20, 16-19.

Cione A.L., Tonni E.P., 1996. Reassessment of the Pliocene-Pleistocene continental time scales of Southern South America. Correlations of the type Chapadmalalan with Bolivian sections. Journal of South American Earth Sciences 9, 221-236.

Coetzee, B.W.T., 2008. Conservation with caveats. Science 321, 340–341.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., Rensburg, B.J.van, Thuiller, W. 2009. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. Global Ecology and Biogeography 18, 701–710.

Cullen, L., Bodmer, R.E., Pádua, C.V., 2000. Effects of hunting in habitat fragments of the Atlantic forests, Brazil. Biological Conservation 95, 49-56.

D'Amen, M., Bombi, P., Pearman, P.B., Schmatz, D.R., Zimmermann, N.E., Bologna, M.A., 2011. Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? Biological Conservation 144, 989–997.

Desbiez, A.L.J., Bodmer, R.E., Tomas, W.M., 2010. Mammalian Densities in a Neotropical Wetland Subject to Extreme Climatic Events. Biotropica 42, 372-378.

Diniz-Filho, J.A.F., Oliveira, G. de, Lobo, F., Ferreira, L.G., Bini, L.M., Rangel, T.F.L.V.B., 2009. Agriculture, habitat loss and spatial patterns of human occupation in a biodiversity hotspot. Scientia Agricola 66, 764–771.

Diniz-Filho, J.A.F., Nabout, J.C., Bini, L.M., Loyola, R.D., Rangel, T.F., Nogues-Bravo, D., Araújo, M.B., 2010. Ensemble forecasting shifts in climatically suitable areas for *Tropidacris cristata* (Orthoptera: Acridoidea: Romaleidae). Insect Conservation and Diversity 3, 213–221.

Dudley, N., 2008. Guidelines for Applying Protected Area Management Categories. Gland, Switzerland: IUCN.

Eisenberg, J.F., 1997. Introduction, in: Brooks, D.M., Bodmer, R.E., Matola, S. (Eds.), Tapirs: Status Survey and Conservation Action Plan, IUCN/SSC Tapir Specialist Group (TSG), Gland, Switzerland, pp. 5-7.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R, Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 119-156.

Elith, J., Graham, C.H., 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. Ecography 32, 66-77.

Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.

Farber, O., Kadmon, R., 2003. Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecological Modelling 160, 115-130.

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

Ferreira, M.E., Ferreira, L.G., Miziara, F., Soares-Filho, B.S., 2012. Modeling landscape dynamics in the central Brazilian savanna biome: future scenarios and perspectives for conservation. Journal of Land Use Science, 1-19.

Flato, G.M., Boer, G.J., 2001. Warming asymmetry in climate change simulations. Geophysical Research Letters 28, 195-198.

Flesher, K.M., Gatti, A., 2010. *Tapirus terrestris* in Espírito Santo, Brazil. Tapir Conservation 19/1(26), 16-23.

Fontana, C.S., Bencke, G.A., Reis, R.E., 2003. Livro vermelho da fauna ameaçada de extinção no Rio Grande do Sul. EDIPUCRS.

Fragoso, J.M.V., Silvius, K.M., Correa, J.A., 2003. Long-Distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84(8), 1998–2006.

Furtado, M., Jácomo, A., Kashivakura, C., Tôrres, N., Marvulo, M., Ragozo, A., de Souza, S., Neto, J., Vasconcellos, S., Morais, Z., Cortez, A., Richtzenhain, L., Silva, J., Silveira, L., 2010. Serologic survey for selected infectious diseases in free-ranging Brazilian tapirs (*Tapirus terrestris*) in the cerrado of central Brazil. Journal of zoo and wildlife medicine : official publication of the American Association of Zoo Veterinarians 41, 133–6.Galetti, M., Keuroghlian, A., Hanada, L., Morato, M.I., 2001.Frugivory and Seed Dispersal by the Lowland Tapir (*Tapirus terrestris*) in Southeast Brazil. Biotropica 33(4), 723–726.

Galetti, M., Giacomini, H.C., Bueno, R.S., Bernardo, C.S.S., Marques, R.M., Bovendorp, R.S., Steffler, C.E., Rubim, P., Gobbo, S.K., Donatti, C.I., Begotti, R.A., Meirelles, F., Nobre, R.deA., Chiarello, A.G., Peres, C.A., 2009. Priority areas for the conservation of Atlantic forest large mammals. Biological Conservation 142, 1229-1241.

García, M., Medici, E., Naranjo, E., Novarino, W., Leonardo, R., 2012. Distribution, habitat and adaptability of the genus *Tapirus*. Integrative Zoology 7, 346–355.

Gatti, A., Brito, D., Mendes, S.L., 2011. How many lowland tapirs (*Tapirus terrestris*) are needed in Atlantic Forest fragments to ensure long-term persistence? Studies on Neotropical Fauna and Environment 46(2), 77-84.

Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B., Wood, R.A., 2000. The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. Climate Dynamics 16, 147-168.

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

Hannah, L., Midgley, G., Hughes, G., Bomhard, B. 2005. The View from the Cape: Extinction Risk, Protected Areas, and Climate Change (55) 3, 231-242.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Front Ecol Environ 5(3), 131–138.

Hansen, D., Galetti, M., 2009. Ecology. The forgotten megafauna. Science (New York, N.Y.) 324, 42–43.

Hartley, S., Harris, R., Lester, P.J., 2006. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. Ecology Letters 9, 1068–1079.

Heikkinen, R.K., Marmion, M., Luoto, M., 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography 35, 276-288.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965-1978.

Hirst, A.C., Gordon, H.B., OFarrell, S.P., 1996. Global warming in a coupled climate model including oceanic eddy-induced advection. Geophysical Research Letters 23, 3361-3364.

Hirst, A.C., OFarrell, S.P., Gordon, H.B., 2000. Comparison of a Coupled Ocean-Atmosphere Model with and without Oceanic Eddy-Induced Advection. Part I: Ocean Spinup and Control Integrations. Journal of Climate 13, 139-163.

Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46, 964-969.

Hortal, J., Roura-Pascual, N., Sanders, N.J., Rahbek, C., 2010. Understanding (insect) species distributions across spatial scales. Ecography 33, 51-53.

Johnson, C.J., Gillingham, M.P., 2005. An evaluation of mapped species distribution models used for conservation planning. Environmental Conservation 32, 117-128.

Junk, W.J., Cunha, C.N., 2005. Pantanal: A large South American wetland at a crossroads. Ecological Engineering 24, 391-401.

Kamino, L., Stehmann, J., Amaral, S., De Marco, P., Rangel, T., de Siqueira, M., De Giovanni, R., Hortal, J., 2012. Challenges and perspectives for species distribution modelling in the neotropics. Biology Letters 8, 324–326.

Keith, D., Akçakaya, H., Thuiller, W., Midgley, G., Pearson, R., Phillips, S., Regan, H., Araújo, M., Rebelo, T., 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology letters 4, 560-563.

Lacy, R.C., 2000. Considering threats to the viability of small populations using individual-based models. Ecological Bulletin 48, 39-51.

Laurance, W., Useche, D., 2009. Environmental synergisms and extinctions of tropical species. Conservation biology: the journal of the Society for Conservation Biology 23, 1427–1437.

Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarres, J.F., Proenca, V., Scharlemann, J.P.W., 2010. Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. In: Secretariat of the Convention on Biological Diversity (ed. Diversity SotCoB). Published by the Secretariat of the Convention on Biological Diversity, Montreal, pp. 1–132. Technical Series no. 50.

Lessa, E.P., Farina, R.A., 1996. Reassessment of extinction patterns among the late Pleistocene mammals of South America. Palaeontology 39, 651-662.

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

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17,145-151.

Loiselle, B.A., Graham, C.H., Goerck, J.M., Ribeiro, M.C., 2010. Assessing the impact of deforestation and climate change on the range size and environmental niche of bird species in the Atlantic forests, Brazil. Journal of Biogeography 37, 1288–1301.

Mangini, P., Medici, E.P., Fernandes-Santos, R., 2012. Tapir health and conservation medicine. Integrative Zoology 7, 331–345.

Marini, M.Â., Barbet-Massin, M., Lopes, L.E., Jiguet, F., 2009. Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. Biological Conservation 142, 3039–3050.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller. W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions 15, 59–69.

Marshall, L.G., 1988. Land mammals and the great American interchange. American Scientist 76, 380-388.

Mbogga, M.S., Wang, X., Hamann, A., 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. Journal of Applied Ecology 47, 731–740.

Medici, E.P., Desbiez, A.L.J., Gonçalves da Silva, A., Jerusalinsky, L., Chassot, O., Montenegro, O.L., Rodríguez, J.O., Mendoza, A., Quse, V.B., Pedraza, C., Gatti, A., Oliveira-Santos, L.G.R., Tortato, M.A., Ramos, Jr. V., Reis, M.L., Landau-Remy, G., Tapia, A., Morais, A.A., 2007. Lowland Tapir (*Tapirus terrestris*) Conservation Action Plan. IUCN/SSC Tapir Specialist Group (TSG) & IUCN/SSC Conservation Breeding Specialist Group (CBSG), Brasil.

Medici, E.P., Flesher, K., Beisiegel, B.M., Keuroghlian, A., Desbiez, A.L.J., Gatti, A., Pontes, A.R.M., Campos, C.B., Tófoli, C.F., Moraes, E.A., Azevedo, F.C., Pinho, G.M., Cordeiro, J.L.P., Santos, T.S.Jr., Morais, A.A., Mangini, P.R., Rodrigues, L.F., Almeida, L.B., 2012. Avaliação do Risco de Extinção da Anta brasileira *Tapirus terrestris* Linnaeus, 1758, no Brasil. Biodiversidade Brasileira Ano II, 3, 103-116.

Medici, E., Desbiez, A., 2012. Population viability analysis: using a modeling tool to assess the viability of tapir populations in fragmented landscapes. Integrative Zoology 7, 356–372.

Melbourne, B., Hastings, A., 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature 454, 100–103.

Metzger, J.P., 2009. Conservation issues in the Brazilian Atlantic forest. Biological Conservation 142, 1138-1140.

Mikich, S.B., Bérnils, R.S., 2004. Livro vermelho da fauna ameaçada no Estado do Paraná. Instituto Ambiental do Paraná.

Montoya, D., Purves, D.W., Urbieta, I.R., Zavala, M.A., 2009. Do species distribution models explain spatial structure within tree species ranges? Global Ecology and Biogeography 18, 662-673.

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

Nabel, P.E., Cione, A., Tonni, E.P., 2000. Environmental changes in the Pampean area of Argentina at the Matuyama-Brumbes (C1r-C1n) Chrons boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 162, 403-412.

Nabout, J., Soares, T., Diniz-Filho, J., De Marco Júnior, P., Telles, M., Naves, R., Chaves, L., 2010. Combining multiple models to predict the geographical distribution of the Baru tree (*Dipteryx alata* Vogel) in the Brazilian Cerrado. Revista Brasileira de Biologia 70, 911–919.

Nakicenovic, N., Swart, R., 2000. Emissions scenarios. 2000 Special Report of the Intergovernmental Panel on Climate Change. Cambridge CB2 2RU ENGLAND, Cambridge University Press, The Edinburgh Building Shaftesbury Road.

Nóbrega, C.C., Marco, P.D., 2011. Unprotecting the rare species: a niche-based gap analysis for odonates in a core Cerrado area. Diversity and Distributions 17, 1-15.

Nogués-Bravo, D., Ohlemüller, R., Batra, P., Araújo, M., 2010. Climate predictors of late quaternary extinctions. Evolution; international journal of organic evolution 64, 2442–2449.

Noss, A.J., Cuéllar, R.L., Barrientos, J., Maffei, L., Cuéllar, E., Arispe, R., Rúmiz D., Rivero K., 2003. A camera trapping and radio telemetry study of lowland tapir (*Tapirus terrestris*) in Bolivian dry forests. Tapir Conservation 12, 24–32.

Noss, A.J, Cuéllar, R.L., 2008. La sostenibilidad de la cacería de *Tapirus terrestris* y de *Tayassu pecari* en la tierra comunitaria de origen isoso: el modelo de cosecha unificado. Mastozoología Neotropical 15(2), 241-252.

Ochoa-Ochoa, L.M., Rodríguez, P., Mora, F., Flores-Villela, O., Whittaker, R.J., 2012. Climate change and amphibian diversity patterns in Mexico. Biological Conservation 150, 94-102.

Parmesan, C., Yohe, G., 2003 A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(2), 37-42.

Pearson R.G., Thuiller W., Araujo M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P., Lees, D.C., 2006. Model-based uncertainty in species range prediction.Journal of Biogeography 33, 1704–1711.

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

Phillips, S.J., 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography 31, 272-278.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161-175.

Ormsby, M.,2005. Risk analysis for biosecurity in New Zealand. Biosecurity 64: 24–25.

Peterson, A.T., Ball, L.G., Cohoon, K.C., 2002. Predicting distributions of Mexican birds using ecological niche modelling methods. Ibis 144, 27–32.

Peterson, A.T., Papeş, M., Eaton, M., 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30, 550-560.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33, 1689–1703.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142, 1141-1153.

Rocha-Mendes, F., Mikich, S.B., Bianconi, G.V., Pedro, W.A., 2005. Mamíferos do município de Fênix, Paraná, Brasil: Etnozoologia e Conservação. Revista Brasileira de Zoologia 22(4), 991-1002.

Rodríguez, J.P., Brotons, L., Bustamante, J., Seoane, J., 2007. The application of predictive modelling of species distribution to biodiversity conservation. Diversity and Distributions 13, 243-251.

Rodríguez, J., Rojas-Suárez, F., 2008. Libro rojo de la fauna venezolana. Provita and Shell of Venezuela, Caracas, Venezuela.

Rodríguez-Soto, C., Monroy-Vilchis, O., Maiorano, L., Boitani, L., Faller, J.C., Briones, M.Á., Núñez, R., Rosas-Rosas, O., Ceballos, G., Falcucci, A., 2011. Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: identification of priority areas for conservation. Diversity and Distributions 17, 350–361.

Root, T., Price, J., Hall, K., Schneider, S., Rosenzweig, C., Pounds, J., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.

Roura-Pascual, N., Brotons, L., Peterson, A.T., Thuiller, W., 2008. Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. Biological Invasions 11, 1017–1023.

Ruiz-García, M. Vásquez, C., Pinedo-Castro, M., Sandoval, S., Castellanos, A., Kaston, F., Thoisy, B. de, Shostell, J. 2012. Phylogeography of the Mountain Tapir (*Tapirus pinchaque*) and the Central American Tapir (*Tapirus bairdii*) and the Origins of the Three Latin-American Tapirs by Means of mtCyt-B Sequences, in: Current Topics in Phylogenetics and Phylogeography of Terrestrial and Aquatic Systems, pp. 83-116.

Salazar, L.F., Nobre, C.A., Oyama, M.D., 2007. Climate change consequences on the biome distribution in tropical South America. Geophysical Research Letters 34, 1-6.

Schneider, S.H., Semenov, S., Patwardhan, A., Burton, I., Magadza, C.H.D., Oppenheimer, M., Pittock, A.B., Rahman, A., Smith, J.B., Suarez, A., Yamin, F., 2007. Assessing key vulnerabilities and the risk from climate change, in: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, , Cambridge University Press, Cambridge, UK, pp. 779-810.

Schloss, C., Nuñez, T., Lawler, J., 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences of the United States of America 109, 8606–8611.

Stockwell, D., Peterson, A., 2002. Effects of sample size on accuracy of species distribution models. Ecological Modelling 148, 1–13.

Taber, A., Chalukian, S.C., Altrichter, M., Minkowski, K., Lizárraga, L., Sanderson, E., Rumiz, D., Edsel, A.M., de Angelo, C., Antúnez, M., Ayala, G., Beck, H., Bodmer, R., Salvador, B.B., Cartes, J.L., de Bustos, S., Eaton, D., Emmons, L., Estrada, N., Flamarion, L., Fragoso, J., Garcia, R., Gomez, C., Gómez, H., Keuroghlian, A., Ledesma, K., Lizcano, D., Lozano, C., Montenegro, O., Neris, N., Noss, A., Palacio, V. J.A., Paviolo, A., Perovic, P., Portillo, H., Radachowsky, J., Reyna-Hurtado, R., Rodriguez, O.J., Salas, L., Sarmiento, D. A., Sarria, P.J.A., Schiaffino, K., Thoisy, B., Tobler, M., Utreras, V., Varela, D., Wallace, R., Zapata, R.G., 2008. El Destino de los Arquitectos de los Bosques Neotropicales: Evaluación de la Distribución y el Estado de Conservación de los Pecaríes Labiados y los Tapires de Tierras Bajas.Pigs, Peccaries and Hippos Specialist Group (IUCN/SSC); Tapir Specalist Group (IUCN/SSC); Wildlife Conservation Society and Wildlife Trust.

Thoisy, B. da Silva, A., Ruiz-García, M., Tapia, A., Ramirez, O., Arana, M., Quse, V., Paz-y-Miño, C., Tobler, M., Pedraza, C., Lavergne, A., 2009. Population history, phylogeography, and conservation genetics of the last Neotropical mega-herbivore, the lowland tapir (*Tapirus terrestris*). BMC Evolutionary Biology 10, 278-295.

Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., Erasmus, B., De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A., Midgley, G., Miles, L., Ortega-Huerta, M., Peterson, A., Phillips, O., Williams, S., 2004. Extinction risk from climate change. Nature 427, 145–148.

Thuiller, W., 2003. BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9, 1353–1362.

Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10, 2020–2027.

Thuiller, W., Araújo, M.B., Lavorel, S., 2004. Do we need land-cover data to model species distributions in Europe? Journal of Biogeography 31, 353–361.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences USA 102, 8245–8250.

Thuiller, W., 2007. Climate change and the ecologist. Nature 448(2), 550-552.

Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., Zimmermann, N.E., 2008. Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9, 137–152.

Thuiller, W., Albert, C., Dubuis, A., Randin, C., Guisan, A., 2010. Variation in habitat suitability does not always relate to variation in species' plant functional traits. Biology letters 6, 120–123.

Tobler, M.W., Janovec, J.P., Cornejo, F., 2010. Frugivory and seed dispersal by the Lowland Tapir *Tapirus terrestris* in the Peruvian Amazon. Biotropica 42(2), 215–222.

Tôrres, N.M., Marco, P.D., Santos, T., Silveira, L., Jácomo, A.T. de A, Diniz-Filho, J.A.F., 2012. Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. Diversity and Distributions 18, 615–627.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R., 2007. A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distributions 13, 397–405.

Urbina-Cardona, J.N., Loyola, R.D., 2008. Applying niche-based models to predict endangered-hylid potential distributions: are neotropical protected areas effective enough? Tropical Conservation Science 1(4), 417-445.

VanDerWal, J., Shoo, L., Johnson, C., Williams, S., 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. The American Naturalist 174, 282–291.

Wallace, R., Ayala, G., Viscarra, M., 2012. Lowland tapir (*Tapirus terrestris*) distribution, activity patterns and relative abundance in the Greater Madidi-Tambopata Landscape. Integrative Zoology 7, 407-419.

Webb, D.S., 2006. The great American biotic interchange: patterns and processes. Annals of the Missouri Botanical Garden 93, 245-257.

Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3, 260-267.

Wiens, J.A., Seavy, N.E., Jongsomjit, D., 2011. Protected areas in climate space: What will the future bring? Biological Conservation 144, 2119-2125.

Williams. J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. PNAS 104(14), 5738-5742.

Williams, S., Shoo, L., Isaac, J., Hoffmann, A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biology 6, 2621–2626.

Table

Table 1. AUC (training data) values, TSS and the proportion of correctly identified transferability values for each of the thresholds (ROC and LPT) determined by the MaxEnt (complete model), MaxEnt (simple model) and Mahalanobis Distance algorithms. Two data subsets were used to produce the models for lowland tapir distributions.

Data subset	Algorithm	AUC	TSS_LPT	Transferability ROC	Transferability LPT
1º	MaxEnt (complete)	0.86	0.37	0.07	0.55
2º	MaxEnt (complete)	0.92	0.46	0.05	0.32
1º	MaxEnt (simple)	0.85	0.25	0.04	0.50
2º	MaxEnt (simple)	0.89	0.35	0.03	0.41
1º	Mahalanobis Distance	0.83	0.42	0.15	1.000
2º	Mahalanobis Distance	0.74	0.15	0.36	0.996

Table 2. Statistical analysis (t-test) of protected area suitability under current and future climatic conditions. Selected protected areas were ≥ 500 km^2 in size

ESs	GCMs	Current Suitability		Future Suitability		Values (df= 177)	
		Mean	St. Dev.	Mean	St. Dev	t	p
A2	CCCma	0.38	0.113	0.19	0.160	20.363	<0.05
A2	CSIRO	0.38	0.116	0.20	0.148	31.952	<0.05
A2	HadCM3	0.38	0.114	0.09	0.173	30.202	<0.05
B2	CCCma	0.38	0.115	0.24	0.151	21.589	<0.05
B2	CSIRO	0.38	0.117	0.19	0.124	20.373	<0.05
B2	HadCM3	0.38	0.116	0.12	0.182	27.851	<0.05

Table 3. Effects of future climate changes on the proportion of remaining suitable areas for *T. terrestris* based on current climate conditions. The values presented are proportional to the suitable cell number for the various climate change scenarios (Overlap, Loss and Relative change) and for the number of cells gained with respect to the future distribution (Gain). The future distribution is expressed as the number of suitable cells (Resolution = ~9 km). GCMs = General Circulation Models; ESs = Emission Scenarios. The predictions are derived from a simple model MaxEnt.

Algorithm	ESs	GCMs	Proportional overlap	Proportional gain	Proportional loss	Relative change	Current distribution	Future distribution
MaxEnt	A2	CCCma	0.98	0.05	0.0	1.03	188 189	193 330
MaxEnt	B2	CCCma	0.99	0.03	0.0	1.03	188 365	193 862
MaxEnt	A2	CSIRO	1.00	0.07	0.0	1.07	189 551	203 717
MaxEnt	B2	CSIRO	1.00	0.06	0.0	1.07	190 440	203 358
MaxEnt	A2	HadCM3	0.89	0.06	0.1	0.95	189 034	179 813
MaxEnt	B2	HadCM3	0.96	0.04	0.0	1.00	189 433	189 439

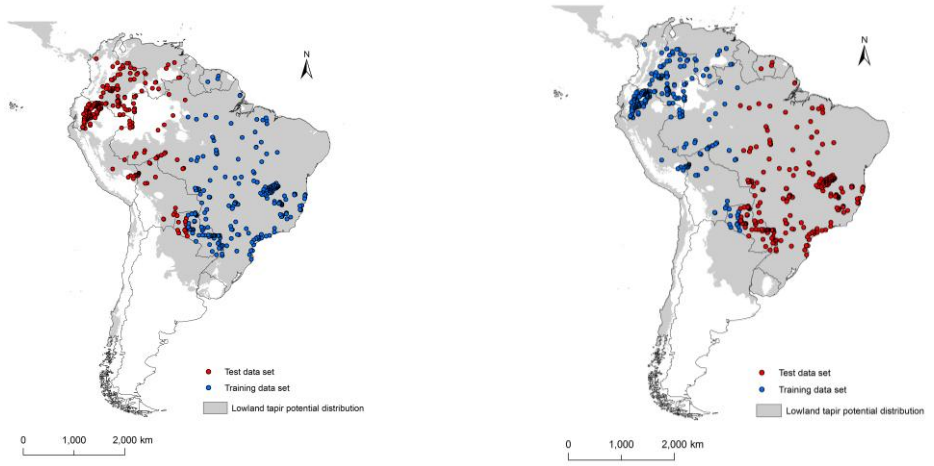
Figure Legends

Figure 1 Transferability predicted by the MaxEnt simple model (a, b), the MaxEnt complete model (c, d) and by Mahalanobis Distance (e, f). The lowland tapir distributions were divided into two spatially independent regions: eastern and western. The blue points were used to train the models, and the models were then tested using the red points for both data subsets.

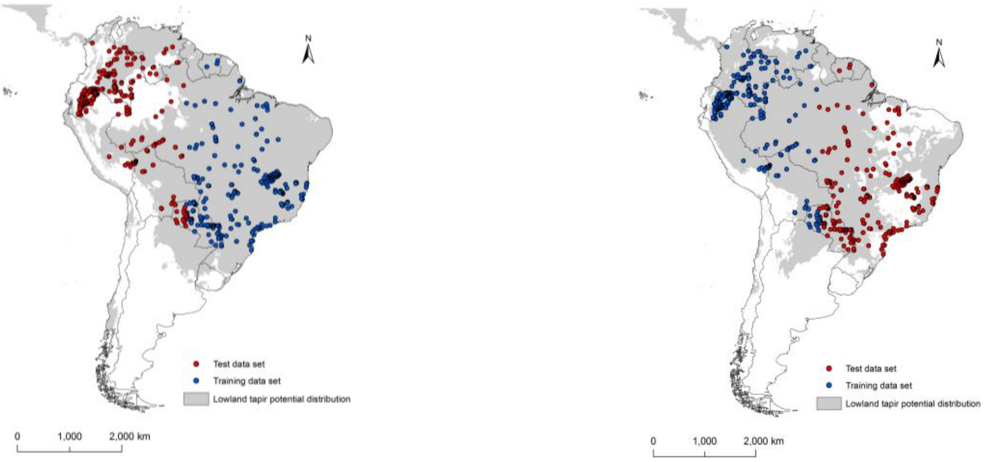
Figure 2 Maps depicting differences in the environmental suitability for lowland tapir distributions. Maps are shown for the three climate models (CCCma, HadCM3 and Csiro) and for the current climate using both emission scenarios.

Figure 3 Mean climatic suitability for each Brazilian protected area (≥ 500 km^2) located in five biomes and the lowland tapir distribution (localized in Brazil only). Points below the line indicate the CUs that are predicted to lose climatic suitability, and points above the line are predicted to gain suitability.

(a) MaxEnt (simple) – 1º subset (b) MaxEnt (simple) – 2º subset



(c) MaxEnt (complete) – 1º subset (d) MaxEnt (complete) – 2º subset



(e) Mahalanobis Distance – 1º subset (f) Mahalanobis Distance – 2º subset

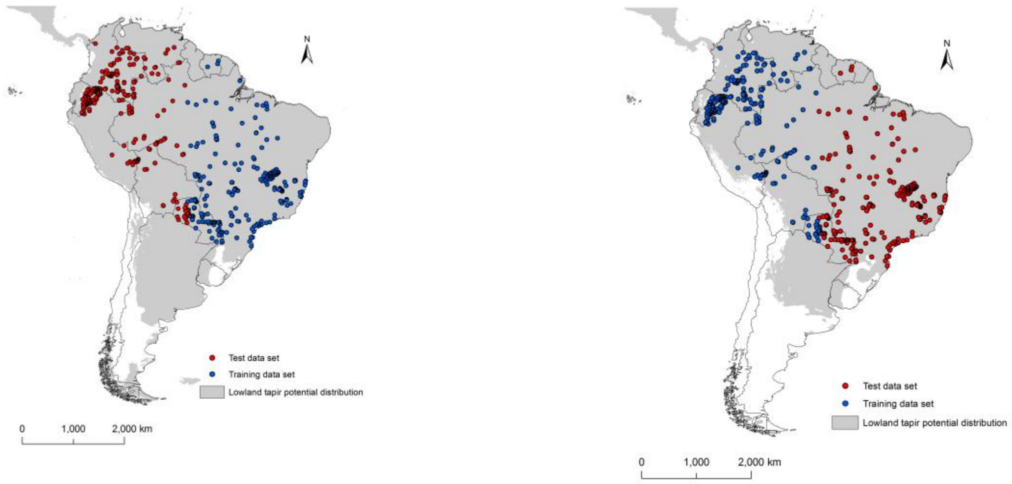


Figure 1

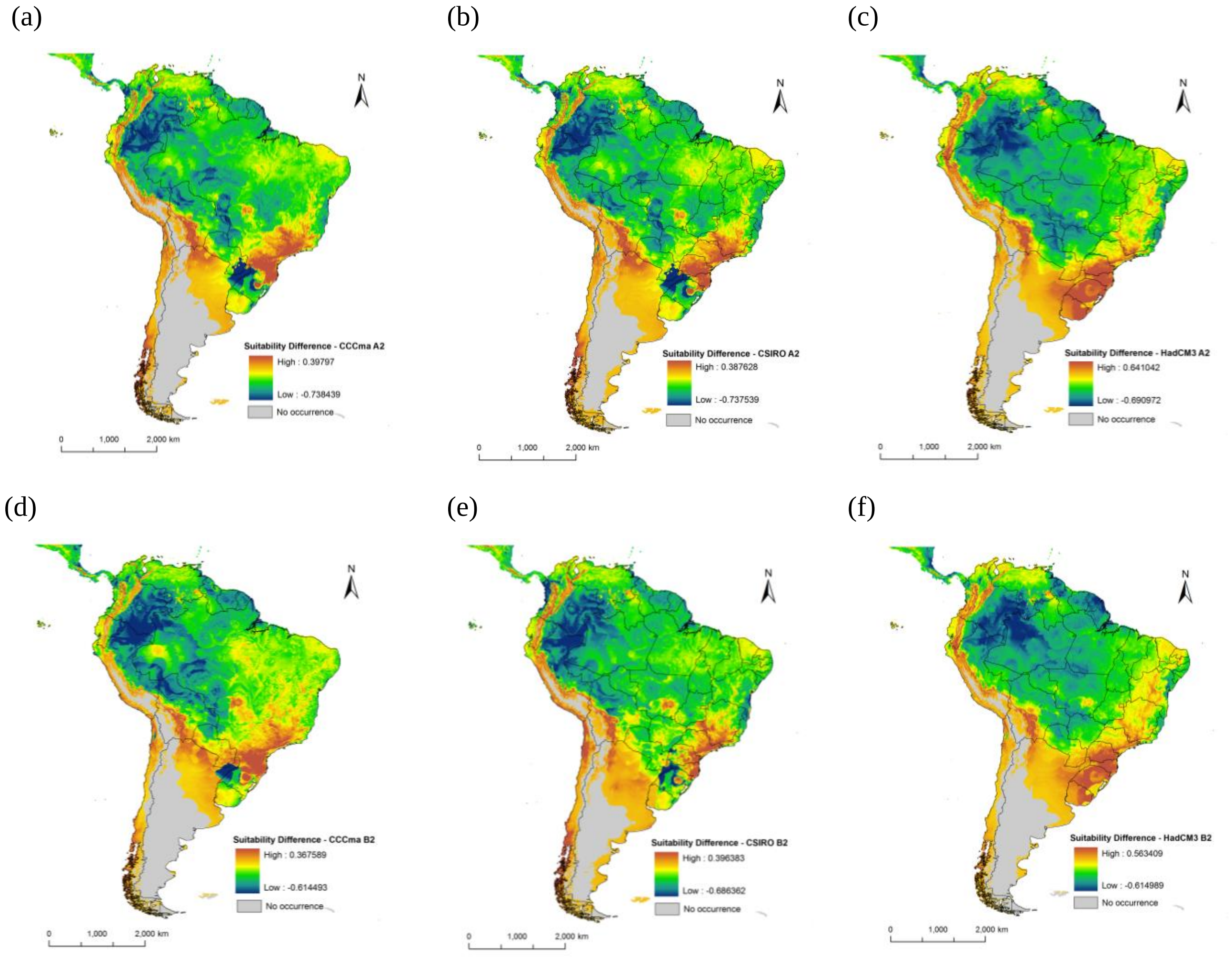

(a)
N
Suitability Difference - CCCma A2
High : 0.39797
Low : -0.738439
No occurrence
0
1,000
2,000 km
(b)
N
Suitability Difference - CSIRO A2
High : 0.387628
Low : -0.737539
No occurrence
0
1,000
2,000 km
(c)
N
Suitability Difference - HadCM3 A2
High : 0.641042
Low : -0.690972
No occurrence
0
1,000
2,000 km
(d)
N
Suitability Difference - CCCma B2
High : 0.367589
Low : -0.614493
No occurrence
0
1,000
2,000 km
(e)
N
Suitability Difference - CSIRO B2
High : 0.396383
Low : -0.686362
No occurrence
0
1,000
2,000 km
(f)
N
Suitability Difference - HadCM3 B2
High : 0.563409
Low : -0.614989
No occurrence
0
1,000
2,000 km

Figure2

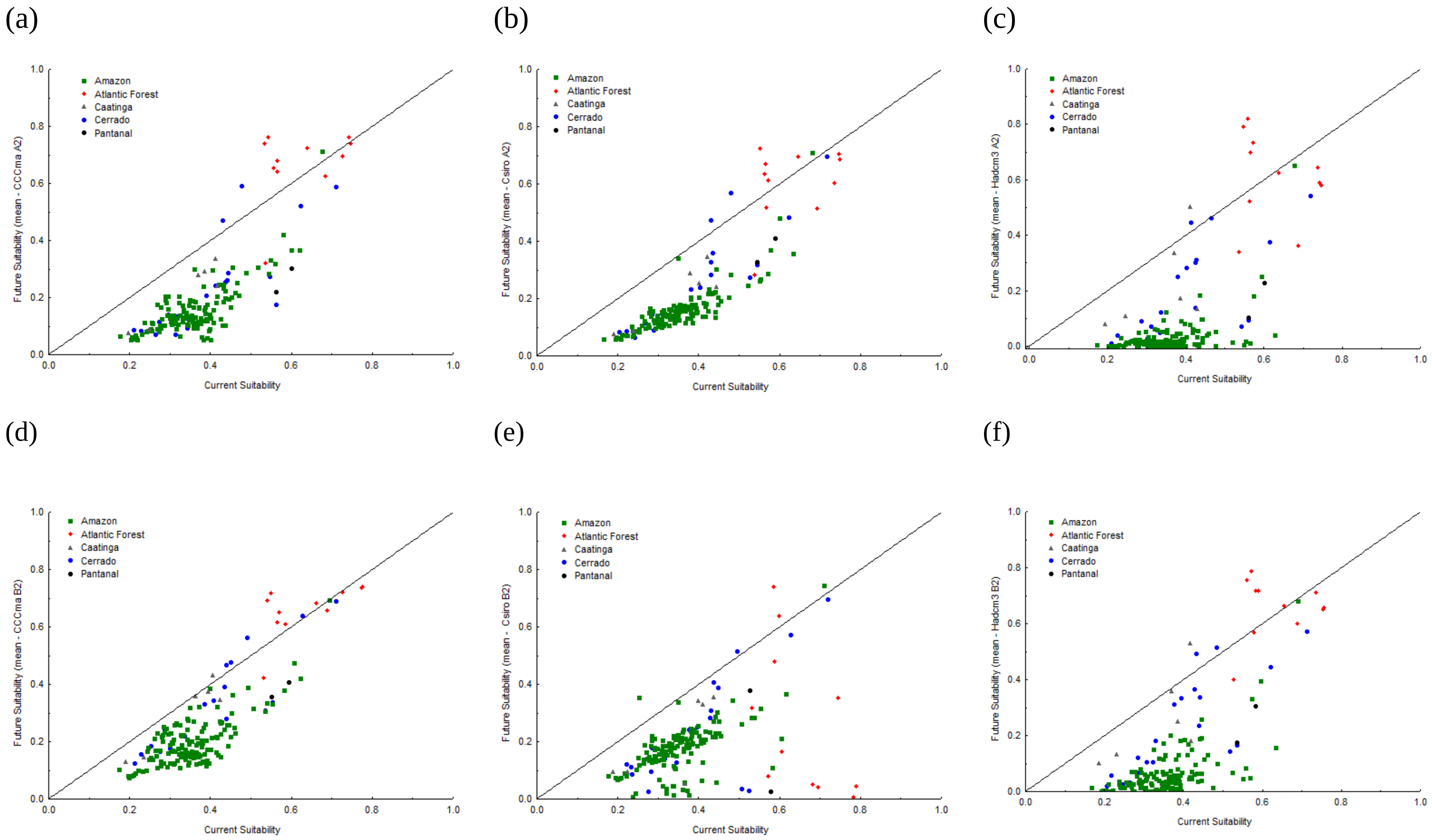

(a)
(b)
(c)
(d)
(e)
(f)
Amazon
Atlantic Forest
Caatinga
Cerrado
Pantanal
Future Suitability (mean - CCCma A2)
Future Suitability (mean - Csiro A2)
Future Suitability (mean - Hadcm3 A2)
Future Suitability (mean - CCCma B2)
Future Suitability (mean - Csiro B2)
Future Suitability (mean - Hadcm3 B2)
Current Suitability
0.0
0.2
0.4
0.6
0.8
1.0

Figure 3.

Material Supplementary

S1

The ROC threshold, by increasing the omission, tends to produce a distribution model with low cohesion range, especially for species with high density of occurrence records in particular sites.

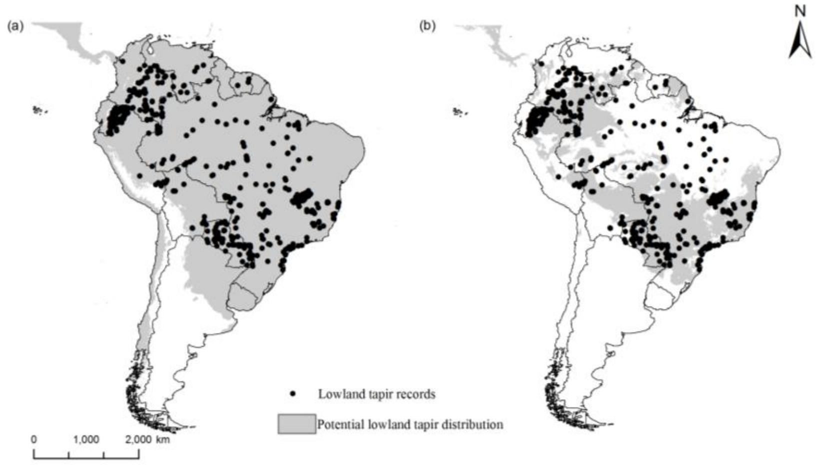


Figure S1 Records of lowland tapir presence (*Tapirus terrestris*) in South America (N = 516). Dark gray shows the potential distribution according with the thresholds: (a) LPT (low presence training) e (b) ROC (receiver operating characteristic).

S2

The complete models MaxEnt suffer from over-parameterization leading to transferability problems and may have a strong effect on its predictions, especially for future climates, produced distribution models less smooth.

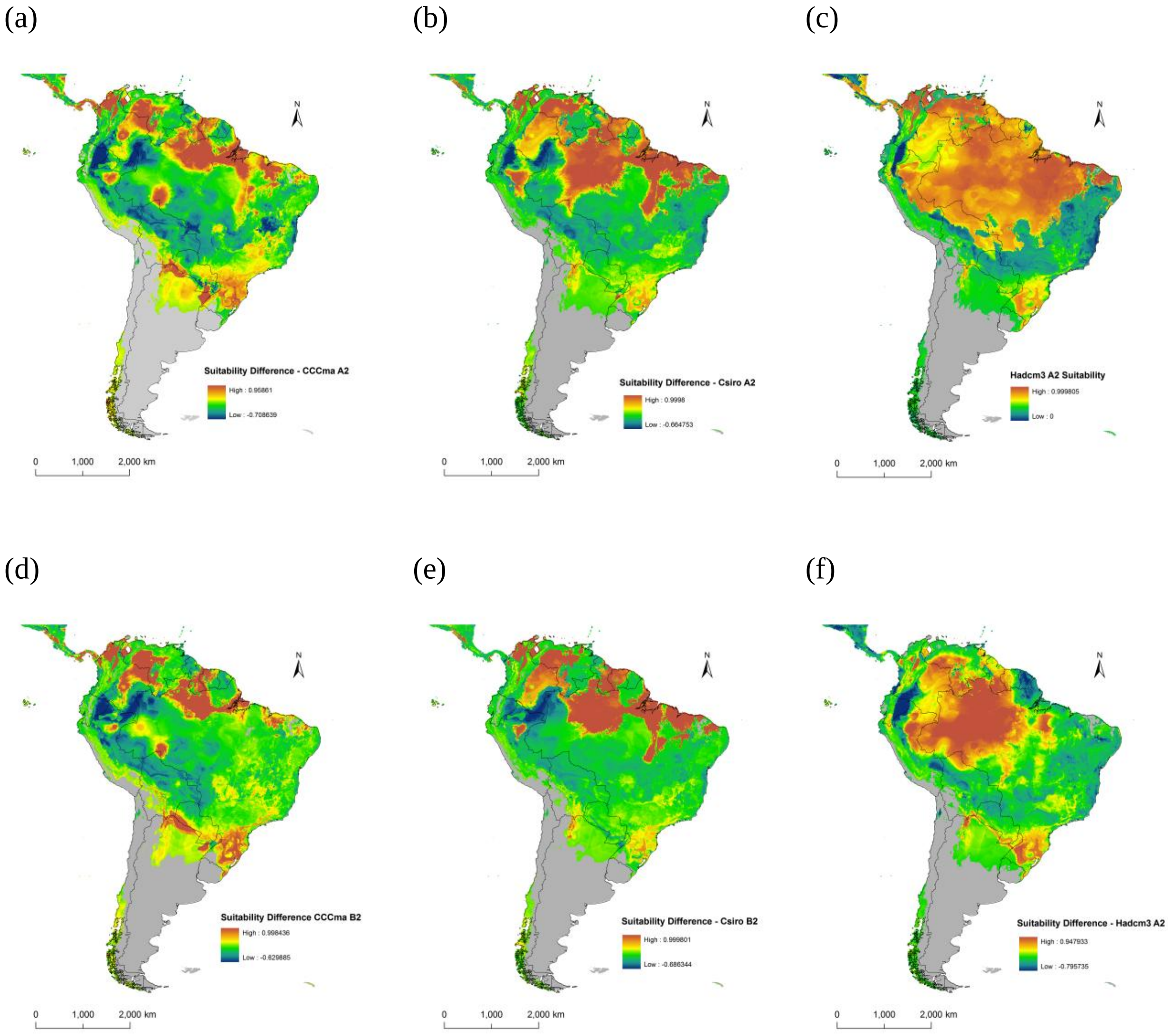


Figura S2 The maps showing the differences in the suitability, in lowland tapir distribution, between the three climate models (CCCMA, HadCM3 and CSIRO) and current climate, for both emission scenarios. The resulting models were produced by complete models MaxEnt.

S3

Groups of protected areas in three Brazilian biomes showing similar patterns in gain climatic suitability, in all climate models for lowland tapirs in the future. ES

Biome	**Conservation Unit**	**ES A2**			**ES B2**		
		CCCma	**Csiro**	**HadCM3**	**CCCma**	**Csiro**	**HadCM3**
Amazon	Juréia-Itatins ES	**X**	**X**	**-**	**-**	**X**	**-**
Amazon	Serra do Aracá SP	**-**	**-**	**-**	**-**	**X**	**-**
Atlantic Forest	Jacupiranga SP	**X**	**X**	**-**	**X**	**-**	**X**
Atlantic Forest	Serra do Tabuleiro SP	**X**	**X**	**X**	**X**	**-**	**X**
Atlantic Forest	Serra do Mar SP	**X**		**-**	**-**	**-**	**-**
Atlantic Forest	Serra do Mar SP	**X**	**X**	**-**	**X**	**-**	**X**
Atlantic Forest	Iguaçu NP	**X**	**-**	**X**	**X**	**-**	**X**
Atlantic Forest	Serra da Bocaina NP	**X**	**X**	**-**	**X**	**X**	**-**
Atlantic Forest	Serra do Itajaí NP	**X**	**X**	**X**	**X**	**X**	**X**
Cerrado	Chapada Diamantina NP	**-**	**-**	**X**	**-**	**-**	**X**
Cerrado	Chapada dos Veadeiros NP	**-**	**-**	**-**	**X**	**-**	**-**
Cerrado	Emas NP	**-**	**-**	**-**	**X**	**-**	**-**
Cerrado	Sempre-Vivas NP	**X**	**X**	**-**	**-**	**-**	**X**
Cerrado	Serra da Canastra NP	**X**	**X**	**X**	**X**	**X**	**X**

CONSIDERAÇÕES FINAIS

Em um cenário que inclui todos os Perissodactyla, é evidente que cada espécie apresenta características de nicho distintas, e que não só as espécies especialistas podem sofrer negativamente com os efeitos das mudanças climáticas. Outro ponto que deve ser considerado é que as barreiras podem limitar a dispersão dessas espécies para novas áreas ambientalmente adequadas. Dentre os Perissodactyla, a anta sul-americana *T. terrestris*, se mostrou a espécie mais climaticamente generalista. Contudo, a avaliação da resposta da espécie em relação às diferentes mudanças climáticas sugere que as condições mais críticas, que prevaleceram durante o Último Máximo Glacial, reduziram a extensão geográfica das áreas climaticamente adequadas, com uma subsequente expansão.

Apesar do clima não ter sido um problema muito sério na história evolutiva da espécie, os desafios para a sua conservação na atualidade e no futuro podem ser bem maiores. Além disso, a combinação da perda da adequabilidade ambiental, perda de habitat e fragmentação, caça, atropelamentos, doenças e decréscimo na população total pode intensificar os efeitos das mudanças climáticas e, consequentemente, diminuir a sobrevivência da espécie. Dessa forma, a emergência de novas áreas ambientalmente adequadas deve ser considerada em planos de manejo futuros, especialmente na criação de novas unidades de conservação tanto para *T. terrestris* quanto para as demais espécies do clado Perissodactyla, sejam elas ameaçadas ou não.