

UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA



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**PRIORIZAÇÃO DE ECORREGIÕES PARA A
CONSERVAÇÃO DE VERTEBRADOS TERRESTRES**

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
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e aprovada pela Comissão Julgadora.
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Tese apresentada ao Instituto de
Biologia para obtenção do Título de
Doutor em Ecologia.

Orientador: Prof. Dr. Thomas Michael Lewinsohn

Campinas
2008

**FICHA CATALOGRÁFICA ELABORADA PELA
BIBLIOTECA DO INSTITUTO DE BIOLOGIA – UNICAMP**

L958p

Loyola, Rafael Dias

Priorização de ecorregiões para a conservação de vertebrados terrestres / Rafael Dias Loyola. – Campinas, SP: [s.n.], 2008.

Orientador: Thomas Michael Lewinsohn.

Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Biodiversidade. 2. Biogeografia. 3. Conservação. 4. Extinção (Biologia). 5. Vertebrados. I. Lewinsohn, Thomas Michael. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Título em inglês: Ecoregion prioritization for terrestrial vertebrate conservation.

Palavras-chave em inglês: Biodiversity; Conservation; Biogeography; Extinction (Biology); Vertebrates.

Área de concentração: Ecologia.

Titulação: Doutor em Ecologia.

Banca examinadora: Thomas Michael Lewinsohn, Célio Fernando Baptista Haddad, Eleonore Zulnara Freire Setz, Jean Paul Walter Metzger, José Alexandre Felizola Diniz Filho, André Victor Lucci Freitas, Luciano Martins Verdade, Denise de Alemar Gaspar.

Data da defesa: 05/12/2008.

Programa de Pós-Graduação: Ecologia.

Campinas, 05 de dezembro de 2008

BANCA EXAMINADORA

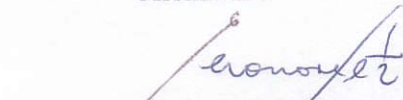
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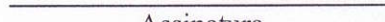
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Dedico essa tese à minha família – minha esposa Patrícia, meus pais Euler e Isabel, e minha irmã Viviane – pelo apoio e incentivo constantes.

*“There is no part of natural history more interesting or instructive,
than the study of the geographical distribution of animals.”*

Alfred Russel Wallace,
Travels on the Amazon and Rio Negro (1853).

Agradecimentos

Agradeço em primeiro lugar a Deus, quem me deu tudo o que tenho e me fez quem sou por sua graça e seu amor incondicional. Agradeço aos meus pais por todo investimento, apoio, carinho dedicados a minha formação, desde a pré-escola até a pós-graduação; e à minha irmã, quem primeiro despertou meu interesse pelo meio acadêmico, quando ainda cursava ela a faculdade.

Agradeço em especial a Patrícia, minha esposa e companheira, cujas palavras de incentivo sempre me impulsionaram mais e mais em direção à pesquisa científica e à busca do conhecimento – nobreza e privilégio concedido apenas ao ser humano. Pelo apoio nos momentos de crise e desânimo, assim como nos de euforia e imersão total em divagações ecológicas. Amo-te Patrícia! Tudo que eu faça será para você.

Ao meu orientador, Thomas Lewinsohn, não só pelo conhecimento que me passou durante esses anos na Unicamp, mas também pela coragem e confiança com as quais aceitou orientar essa tese, até certo ponto, distante de sua linha mestra de pesquisa e produção. Admiro sua capacidade Barão! Obrigado também pela parceria em inúmeros artigos, cuja qualidade, indiscutivelmente, tem sua marca.

Agradeço ao Rogério Parentoni, amigo que me despertou senão toda, muito da curiosidade por ciência em geral e por teorias ecológicas, em particular. Rogério é também responsável por minha incursão ao mundo do Jazz e dos vinhos.

Aos amigos e parceiros do Laboratório: Mário (por contribuir com minha maneira de pensar questões ecológicas e incentivar tanto a produção de bons artigos), Umberto (companheiro do início ao fim do doutorado, sempre disposto e prestativo – co-autor de trabalhos desenvolvidos com muito carinho), Marina, Paulinha (obrigado pelo carinho e ajuda de sempre), Denise, Rosane, Ricardo (pelos cafés, conversas, e interesse pelo que faço. Valeu pelo apoio Ricardinho!). Agradeço também ao amigo Paulo Guimarães Jr. (Miúdo) pelo exemplo, pelas conversas e incentivo para que pudesse enviar meus trabalhos a revistas competentes; ao Márcio e à Claudia, pela amizade, ajuda e bons momentos no México. A Jacy e ao Érico pelos bons momentos e conversas. Aos amigos da IBBG, pelo apoio em todos esses anos que Patrícia e eu vivemos aqui em Campinas – em especial a Natanael, Jesuína e Henrique, Bruno, Laura e Danilo. E a minha amiga Luciane Kern, por todas as oportunidades e por confiar sempre em meu trabalho.

Agradeço ainda a meus novos amigos do curso de campo no Pantanal, em especial à Nathália Machado e Souza, Liliane Piatti, Fernanda Cassemiro, Gustavo Santos, André Vargas e Pâmela Antunes. Vocês são nota dez!

Agradeço especialmente a José Alexandre Diniz-Filho – responsável direto pelo rumo tomado por esse trabalho – que leu e criticou toda a tese à medida que os artigos eram escritos; seu incentivo foi fundamental para que essa tese chegasse a esse ponto. A Célio Haddad, pela colaboração, empolgação e contribuição significativa à tese, em especial ao terceiro capítulo. E a Gustavo A. B. Fonseca, por suas contribuições e refinamento das idéias presentes no segundo capítulo.

Finalmente, agradeço ao CNPq pela bolsa concedida, a *Society for Conservation Biology* e a *Association for Tropical Biology and Conservation* pelo apoio financeiro de minha participação em reuniões científicas internacionais, e ao Programa de Pós-Graduação em Ecologia da Unicamp, pela oportunidade e formação concedida.

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Resumo

Procurei identificar prioridades de conservação para vertebrados terrestres em diferentes escalas geográficas (da regional/continental à global), usando ecorregiões como unidades geográficas. Mais especificamente, avaliei (1) a correlação entre riqueza e endemismo exibida por vertebrados terrestres que ocorrem em ecorregiões do Brasil e a eficiência de cada classe de vertebrados terrestres (anfíbios, répteis, aves e mamíferos) como grupos indicadores para a identificação de prioridades de conservação em ecorregiões brasileiras; (2) identifiquei ecorregiões prioritárias para a representação eficiente de todos os vertebrados terrestres, incluindo aqueles endêmicos e ameaçados de extinção, na região Neotropical, e o quanto essas ecorregiões representam da fauna existente nessa província biogeográfica; (3) identifiquei ecorregiões prioritárias para a representação eficiente de todos os anuros (Amphibia: Anura) ameaçados de extinção na região Neotropical e como a inclusão de características da história de vida (e.g. modo reprodutivo) desse grupo no processo de priorização pode auxiliar no delineamento dessas áreas prioritárias; (4) de maneira similar, assinalei ecorregiões prioritárias para a conservação de todos os carnívoros (Mammalia: Carnivora) na região Neotropical e no mundo, e como a inclusão de características ecológicas, evolutivas e da história de vida desse grupo - associadas a custos econômicos (US\$/km²) da aquisição de terras em ecorregiões - pode auxiliar no delineamento dessas áreas prioritária. Os resultados apontam, de maneira geral, ecorregiões localizadas no sul do México, América Central, Andes tropicais, sul da América do Sul, sudeste asiático e Filipinas, e a Mata Atlântica brasileira como áreas de extrema relevância, cuja conservação eficiente, por meio de redes de reservas cuidadosamente implementadas, poderia minimizar consideravelmente as ameaças atuais aos vertebrados terrestres. A identificação de áreas prioritárias para a conservação da biodiversidade que vão de uma escala regional/continental à global, é apenas um primeiro passo no estabelecimento de estratégias de conservação *in-situ* que garantirão a persistência de espécies por períodos ecológicos e evolutivos relevantes para sua existência. Os trabalhos incluídos nessa tese reforçam o arcabouço teórico e metodológico da avaliação de conservação e oferecem bases científicas para o delineamento de regiões prioritárias para a conservação de biodiversidade em um mundo em constante mudança.

Palavras-chave: Biodiversidade, Biogeografia da conservação, Complementaridade, Extinção, Planejamento sistemático de conservação, Priorização, Vertebrados.

Abstract

I aimed to identify conservation priorities for terrestrial vertebrates across different spatial scales (from regional/continental to global), using ecoregions as geographic units. I have evaluated, in particular, (1) the congruence between overall richness and endemism patterns among terrestrial vertebrates that occur in Brazil, and the effectiveness of each vertebrate class (amphibians, reptiles, birds, and mammals) as indicator groups for identifying conservation priorities among Brazilian ecoregions; (2) I have identified priority sets of ecoregions that are effective in representing terrestrial vertebrate diversity in the Neotropics, including those endemics and threatened of extinction; (3) I have also identified priority sets of ecoregions for the conservation of Neotropical threatened anurans, and have also evaluated how the inclusion of species life-history traits (e.g. reproductive modes) in the prioritization process may help to improve area-setting analysis; (4) similarly, I have highlighted Neotropical and Global priority sets of ecoregions for the conservation of all carnivores (Mammalia: Carnivora), and again, how the inclusion of biological traits – along with economic costs (US\$/km²) of land acquisition within ecoregions – may help in the delineation of these priority set of areas. In general, results highlighted ecoregions found in southern Mexico, Central America, tropical Andes, southern South America, southeast Asia and the Philippines, and the Brazilian Atlantic Forest as extreme-relevance areas. Their effective conservation, through the implementation of carefully designed reserve networks, could therefore minimize significantly current threats to terrestrial vertebrates. Identification of a comprehensive set of natural areas, as presented here, is a first step towards an *in-situ* biodiversity maintenance strategy, which only subtends a much more complex process of policy negotiation and implementation. The studies included in the thesis contribute to a joint framework for the development of national and continental strategies for biodiversity conservation, adding to burgeoning initiatives to plan the application of finite funds and efforts where they will be most effective.

Key words: Biodiversity, Complementarity, Conservation biogeography, Extinction, Prioritization, Vertebrates, Systematic conservation planning.

Introdução

Loyola RD & Lewinsohn TM (2008). **Diferentes abordagens para a seleção de prioridades de conservação em um contexto macrogeográfico.**
Megadiversidade, no prelo.

Diferentes abordagens para a seleção de prioridades de conservação em um contexto macro-geográfico

Rafael D. Loyola¹* & Thomas M. Lewinsohn¹

Resumo

Diante da crise atual de biodiversidade, exercícios que selecionam grupos de espécies e áreas prioritárias para a conservação tornaram-se imprescindíveis. Por essa razão, estratégias aplicadas de conservação têm progredido desde esforços direcionados a espécies particulares até a avaliação de grupos taxonômicos inteiros em grande escala geográfica. Tais avaliações, por sua vez, ajudam a direcionar ações e investimentos financeiros em conservação. Atualmente há diferentes abordagens para a seleção de prioridades de conservação que vão desde o uso de grupos indicadores até o uso de diferentes algoritmos que buscam conjuntos ótimos de áreas que compõem uma rede de reservas em escala regional, continental ou global. Todas elas assentam-se sobre o arcabouço conceitual e teórico proposto pela Biogeografia da Conservação e pelo Planejamento Sistemático de Conservação. Nesse artigo, revemos algumas dessas abordagens e discutimos os diferentes métodos pelos quais as mesmas podem ser aplicadas. Apresentamos sugestões sobre como melhorar os exercícios de priorização atuais por meio da inclusão de características biológicas das espécies a serem conservadas, fornecendo exemplos de aplicação. Discutimos ainda como é possível melhorar as avaliações de risco de extinção, considerando não só informações em nível específico, mas também populacional. Sustentadas pelo conhecimento teórico, o uso de diferentes abordagens para a seleção de prioridades fornece-nos uma base científica fundamental para o delineamento de estratégias de conservação eficientes que farão parte de um processo muito mais complexo e interdisciplinar de negociação política e implementação.

Palavras chave: biogeografia da conservação, extinção, modelagem, planejamento sistemático de conservação, priorização, vertebrados.

Abstract

We are on the verge of a major biodiversity crisis and therefore exercises that select particular species groups and areas for conservation became essential. For this reason, applied conservation strategies show a striking progression from endeavors targeted at single species or at individual sites, to the systematic assessment of entire taxa at large scales. These, in turn, inform wide-reaching conservation policies, strategies and financial investments. Today, there are different approaches for the selection of conservation priorities ranging from indicator groups to the use of several algorithms to find optimal sets of areas to be included in a reserve network at regional, continental and global scales. All of these approaches reside on the theoretical and conceptual framework proposed by the Conservation Biogeography and the Systematic Conservation Planning. In this paper, we review some of these approaches and discuss the different methods by which they are attained. We propose how to enhance prioritization exercises by the inclusion of species biological traits, providing examples of its application. We also discuss how to improve extinction risk assessments by using not only information at species level but also at the population level. Underpinned by theoretical knowledge, the use of distinct approaches to priority-selection exercises provide us a fundamental scientific basis for designing efficient conservation strategies, which can contribute to a much more complex and interdisciplinary process of policy negotiation and implementation.

Key words: conservation biogeography, extinction, modeling, systematic conservation planning, prioritization, vertebrates.

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Introdução

“O último exemplar selvagem de ararinha-azul (*Cyanopsitta spixii*) pode estar morto. Há 55 dias os pesquisadores do Projeto Ararinha Azul, na Bahia, não têm contato visual com o animal, um macho que habita a região de Curaçá, nordeste do Estado. E há quase um mês ninguém tem informação sobre a ave... o que pode significar a sua extinção na natureza”. Essa notícia foi divulgada em 28 de novembro de 2000 pelo jornal Folha de São Paulo (matéria completa disponível em <http://www1.folha.uol.com.br/folha/ciencia/ult306u1307.shtml>). Em 2007, a lista oficial de espécies ameaçadas de extinção, publicada pela União Mundial para a Conservação (IUCN), classificou esta espécie como “Criticamente em Perigo (CR)” (IUCN, 2007). Segundo a IUCN, embora se tenha conhecimento de populações da espécie mantidas em cativeiro, o último indivíduo existente na natureza (isto é, em liberdade) desapareceu no final do ano 2000, e a espécie pode muito bem ter sido extinta, principalmente por capturas para tráfico e por perda de habitat. Entretanto, não se pode pressupor que esta espécie esteja “Extinta na Natureza (EW)” a menos que todas as áreas com seus habitats potenciais sejam extensivamente inventariadas. Qualquer população ainda existente é provavelmente muito pequena, e por essa razão a espécie pode ser atualmente referida como “Possivelmente Extinta na Natureza” (IUCN, 2007). Ainda assim, a Lista Nacional das Espécies da Fauna Brasileira Ameaçadas de Extinção classifica *C. spixii* como “Extinta na Natureza” (Machado *et al.*, 2005).

Duas questões aqui são extremamente relevantes: (1) não podemos classificar a Ararinha Azul como oficialmente extinta na natureza, pois ainda não inventariamos todas as áreas nas quais os habitats potenciais da espécie podem ocorrer. Quando isso será feito (se é que será feito)? Ou seja, há um problema crucial proveniente de insuficiência amostral, falta de recursos financeiros e de pessoal que diz respeito à distribuição geográfica da espécie no Brasil e na América do Sul. (2) Por que existem duas listas oficiais de espécies ameaçadas, e por que as categorias de ameaça que estas listas empregam não são idênticas? Isso também será discutido no momento oportuno. Por agora, resta-nos avaliar o porquê de se encontrar taxas de extinção tão elevadas nos dias atuais e contextualizar tal situação frente a uma crise global de biodiversidade.

A crise atual de biodiversidade

Estamos em uma fase crucial do desenvolvimento de estratégias e teorias em conservação (Whittaker *et al.*, 2005). Reconhecemos que a diversidade de vida na Terra, incluindo a diversidade genética, específica e ecossistêmica, é uma herança inestimável e insubstituível, além de crucial para o bem-estar humano e para o desenvolvimento sustentável (Loreau *et al.*,

2006). Reconhecemos também que estamos diante de uma grande crise de biodiversidade e que esta vem sendo ameaçada em escala global: espécies vêm sendo extintas a taxas extremamente elevadas (Lawton & May, 1995). A diversidade, em suas distintas escalas, está em declínio acentuado e há um número imenso de populações e espécies que provavelmente serão extintas ainda este século (Loreau *et al.*, 2006).

Dentre os diversos propulsores desta crise atual, a destruição de habitats (especialmente em florestas tropicais, ecossistemas de água doce e costeiros), introdução de espécies exóticas, sobreexploração de espécies e recursos naturais (p. ex., sobrepesca marinha), poluição, e mudanças climáticas globais, que hoje estão no centro das atenções, são as maiores ameaças à biodiversidade. Tudo isso advém do crescimento insustentável da população humana mundial associada à produção, consumo e mercado financeiro necessários à manutenção de tal população (Loreau *et al.*, 2006). Como resultado destes fatores, aproximadamente 12% de todas as espécies de aves, 23% de todos os mamíferos, 32% de todos os anfíbios, e cerca de 50% de todas as plantas estão atualmente ameaçados de extinção (IUCN, 2007). Além disso, os efeitos esperados por mudanças climáticas devem colocar *ca.* 15 a 37% das espécies restantes à beira da extinção dentro dos próximos 50 anos (Thomas *et al.*, 2004).

A perda de biodiversidade é, portanto, um fenômeno global que atua em diferentes escalas e que demanda ações de conservação em nível internacional (Cardillo *et al.*, 2006). Conseqüentemente, análises voltadas para planejamento de conservação têm progredido de esforços centrados em espécies individuais (como o Mico-Leão Dourado) ou locais específicos (como a Mata Atlântica) para avaliações sistemáticas de grupos taxonômicos inteiros (p.ex. vertebrados terrestres) em escala regional ou global (Mace *et al.*, 2007). Durante a última década, diversas organizações não-governamentais (ONGs) internacionais desenvolveram exercícios de priorização de áreas em escala regionais ou continentais e, especialmente, na escala global (p. ex., Olson & Dinerstein, 2002; Mittermeier *et al.*, 2004) com o intuito de direcionar e priorizar a alocação de investimentos em conservação (Myers & Mittermeier, 2003). Tais exercícios resultam de análises de natureza essencialmente biogeográfica e vêm exercendo grande influência na organização e priorização de esforços de conservação (Myers & Mittermeier, 2003). Todavia, embora a biogeografia tenha exercido um papel fundamental junto com outros sub-campos da biologia como o da conservação da biodiversidade, sua aplicação na solução de problemas propostos pela Biologia da Conservação ainda é incipiente. Como passo fundamental em direção a uma aplicação mais proeminente, Whittaker *et al.* (2005) propuseram a definição do campo de conhecimento denominado Biogeografia da Conservação.

Biogeografia da Conservação: arcabouço conceitual e teórico

A Biogeografia da Conservação é definida como “a aplicação de princípios, teorias e análises biogeográficas concernentes à dinâmica de distribuição de grupos taxonômicos individuais ou combinados, para a solução de problemas da conservação da biodiversidade” (Whittaker *et al.*, 2005). Assim sendo, a Biogeografia da Conservação integra o arcabouço teórico e conceitual da Biogeografia com o da Biologia da Conservação.

A Biogeografia é o estudo, em todas as escalas de análise possíveis, da distribuição das espécies no espaço e como, ao longo do tempo, esta é/foi alterada. Uma de suas maiores preocupações têm sido a distribuição e dinâmica espacial da diversidade, normalmente abordada simplesmente por meio do número de espécies, ou proporção de espécies endêmicas (Lomolino *et al.*, 2004; Whittaker *et al.*, 2005).

A Biologia da Conservação, por outro lado, é um campo de pesquisa aplicado que pretende subsidiar decisões de manejo relacionadas à conservação da natureza. Como tal, suas raízes estão intimamente associadas ao desenvolvimento de análises e teorias de conservação do século XX. Trata-se de um campo extenso cuja fundamentação teórica pode ser dividida de acordo com a escala de aplicação de seus estudos (Whittaker *et al.*, 2005). Assim há (1) o desenvolvimento e a avaliação de teorias ecológicas diretamente relacionadas aos processos populacionais (sejam eles genéticos ou ecológicos), e que geraram estudos sobre populações minimamente viáveis, sobre a influência competitiva de espécies invasoras, depressão endogâmica em populações pequenas, espirais de extinção, ecologia comportamental, etc.; (2) teorias relacionadas a processos que ocorrem em escala local e de paisagem, incluindo todas as derivações provenientes da Teoria de Biogeografia de Ilhas como, por exemplo, a teoria de metapopulações, corredores de habitat, ou o debate sobre número e tamanho ideais de reservas naturais (conhecido como SLOSS); e, finalmente, (3) aplicações em uma escala ainda maior, associadas ao mapeamento e modelagem de padrões biogeográficos – o que necessariamente remete à biogeografia histórica e a explicações geográficas para os padrões de distribuição de espécies e especiação na natureza (Lomolino *et al.*, 2004, Whittaker *et al.*, 2005).

Portanto, a Biogeografia de Conservação, isto é, a aplicação da Biogeografia aos problemas enfrentados pela Biologia da Conservação, é um campo de conhecimento ainda em desenvolvimento, mas que oferece desafios intelectuais e é, ao mesmo tempo, de grande relevância social (Whittaker *et al.*, 2005) – na medida em que a sociedade deve fazer parte dos processos de implantação de medidas conservacionistas. A fundamentação teórica deste artigo tem como base o arcabouço teórico que abarca a Biogeografia da Conservação e, mais

especificamente, aquele relacionado ao planejamento de conservação e suas aplicações práticas como instrumento científico para a definição de prioridades de conservação em grande escala.

Priorização de espécies e áreas para a conservação

O principal objetivo das estratégias de conservação da biodiversidade em grande escala não é propriamente o de selecionar áreas para a criação de reservas, mas identificar áreas com alto valor de conservação que sejam significativas em um contexto global, continental ou regional (Moore *et al.*, 2003). Uma vez identificadas, avaliações de conservação mais detalhadas devem então ser direcionadas a estas áreas (Brooks *et al.*, 2001). Na verdade, a falta de informação sobre onde concentrar esforços de conservação é um dos maiores obstáculos a ser transposto pela conservação da biodiversidade tropical (Howard *et al.*, 1998, Loyola *et al.*, 2007).

O uso de grupos indicadores

Uma abordagem freqüentemente adotada para a identificação de áreas prioritárias para a conservação é o uso de subconjuntos de espécies como um indicador substitutivo da presença (*surrogates*) de todas as espécies (Gastón, 1996). Isto é, trata-se de concentrar as estratégias em grupos indicadores bem avaliados, os quais são constituídos por aquelas espécies pertencentes a grupos taxonômicos relativamente ricos, e que são capazes de representar a biodiversidade como um todo – portanto, sua distribuição geográfica prediz a importância geral da biodiversidade das áreas a serem conservadas (Loyola *et al.*, 2007). De maneira geral, grupos indicadores serão eficientes se o padrão de distribuição geográfica de outros subconjuntos de espécies for coincidente com o seu (Moore *et al.*, 2003). Em outras palavras, um bom grupo indicador é aquele cuja distribuição geográfica coincide espacialmente com distribuição dos demais grupos que compõem o *pool* de espécies de uma determinada região (Gastón, 1996; Flather *et al.*, 1997; Virolainen *et al.*, 2000).

Até o momento, poucos estudos realizados em grande escala avaliaram a qualidade da representação da biodiversidade baseada em grupos indicadores. Nos trópicos, a alta diversidade biológica, junto com a limitação de recursos financeiros para seu estudo, torna o uso de grupos indicadores uma abordagem ainda mais atraente (Howard *et al.*, 1998). Resultados de alguns estudos realizados em escala global ou continental sugerem uma forte correlação entre riqueza de espécies e endemismo (p. ex., Pearson & Carroll, 1999), ao passo que outros estudos não apóiam tal relação (Flather *et al.*, 1997; Orme *et al.*, 2005; Loyola *et al.*, 2007). Essa discrepância de resultados ocorre, em parte, devido aos padrões de diversidade beta exibido pelo

pool de espécies como um todo e por aquele composto apenas por espécies endêmicas (Loyola *et al.*, 2007).

Na verdade, a correlação entre a riqueza de espécies de diferentes grupos taxonômicos *per se* não é suficiente para determinar a eficiência de um único grupo (p.ex. aves) para apontar o valor de conservação de diferentes áreas – no entanto, este é a principal fundamentação atual para adotar ou propor determinados grupos como indicadores substitutos da diversidade biótica total (Gastón, 1996; Flather *et al.*, 1997). O valor de conservação pode ser medido, por exemplo, por meio da representação geral de espécies, insubstitutividade das áreas ou complementaridade de conjuntos de áreas (Loyola *et al.*, 2007). Portanto, uma avaliação mais apropriada é determinar em que medida conjuntos de regiões prioritárias selecionadas a partir de um único grupo indicador são capazes de representar também a diversidade de outros grupos taxonômicos (Howard *et al.*, 1998; Moore *et al.*, 2003; Mace *et al.*, 2007). A eficiência dos grupos indicadores pode ser avaliada observando a eficiência de representação da diversidade total em conjuntos prioritários, identificados com base nos grupos indicadores, em comparação com outros conjuntos prioritários gerados por meio de uma seleção aleatória de regiões (Moore *et al.*, 2003). Isso representa uma medida de sua utilidade em guiar decisões de conservação (Loyola *et al.*, 2007).

Para exemplificar a importância de avaliar a eficiência de diferentes grupos como indicadores substitutos, em um estudo realizado em Uganda, Howard *et al.* (1998) concluíram que diferentes grupos taxonômicos exibem padrões biogeográficos similares e, portanto, formações florestais que sejam prioritárias para um único grupo, representam coletivamente áreas importantes também para outros grupos. Tais resultados reforçam a necessidade de considerar as correlações entre *taxa* (e não somente a sua riqueza) ao avaliar indicadores potenciais para a seleção de reservas naturais. Em outro estudo feito em escala global, Lamoreux *et al.* (2006) demonstraram que os padrões espaciais de riqueza estão altamente correlacionados entre anfíbios, répteis, aves e mamíferos. O mesmo foi observado para os padrões de endemismo. Além disso, estes autores mostraram que, embora a correlação entre riqueza e endemismo de vertebrados terrestres seja baixa, regiões com alto endemismo ainda assim possuem significativamente mais espécies do que a mesma correlação em regiões aleatoriamente selecionadas. No Brasil, Loyola *et al.* (2007) demonstraram recentemente que utilizar vertebrados endêmicos (especialmente as aves endêmicas) como grupos indicadores substitutos para a conservação de outros *taxa* em escala regional ajuda a focar os esforços de conservação em regiões críticas (Howard *et al.*, 1998, Moore *et al.*, 2003). Ou seja, selecionar ecorregiões brasileiras fundamentado em grupos indicadores eficientes, fornece um ponto de partida para

avaliações mais rápidas sobre prioridades de conservação dentro de limites nacionais ou regionais (Loyola *et al.*, 2007).

O Planejamento de Conservação

Ao passarmos de uma abordagem baseada em grupos indicadores para procedimentos mais diretos na seleção de áreas prioritárias para a conservação, aproximamo-nos mais do que hoje se define como planejamento sistemático de conservação: o processo dedicado à identificação de novas áreas prioritárias para a conservação e a mensuração dos níveis de proteção existentes (Margules & Sarkar, 2007). O planejamento sistemático de conservação destaca-se entre muitas outras técnicas como uma ferramenta eficiente proposta para maximizar a conservação de elementos importantes em uma rede de áreas protegidas (Smith *et al.*, 2006). Trata-se de um processo guiado por alvos bem estabelecidos e utilizado para delinear (“design”) sistemas de reservas naturais. Essa abordagem envolve uma série de etapas que devem ser cumpridas a fim de que (1) se estabeleçam amplas metas de conservação para uma região específica, (2) sejam mapeados grupos de espécies ou regiões com alto valor de conservação, (3) sejam identificadas onde as áreas de conservação devem ser estabelecidas a fim de que se alcancem as metas propostas, e (4) desenvolva-se uma estratégia de implantação para que se alcancem os resultados esperados (Margules & Pressey, 2000).

Algoritmos para a identificação de áreas prioritárias

Estratégias de conservação baseada na seleção de regiões prioritárias geralmente incluem como um de seus critérios-alvo a minimização da área total de uma determinada rede de reservas, muito embora uma gama de outros critérios (tais como o nível de ameaça de espécies, ou a condição de conservação ou risco iminente das regiões avaliadas) possa também ser utilizada (Smith *et al.*, 2006). De qualquer maneira, o critério mais importante para identificar e delinear redes de reservas deve ser o de atingir uma representação máxima de biodiversidade com o menor custo possível (Pressey *et al.*, 1996; Margules & Pressey, 2000). Esse processo normalmente envolve o uso de programas específicos de computador que identificam soluções quase-ótimas (expressas como redes de reservas) que representam bem os alvos predefinidos, tais como o número de espécies desejadas a porcentagem de habitats nativos desejado (Smith *et al.*, 2007). Atualmente, tais técnicas de planejamento são consideradas as mais apropriadas para o desenho de redes de áreas protegidas (Pressey & Cowling, 2001; Margules & Sarkar, 2007).

Para trazer flexibilidade ao processo de seleção de áreas para a conservação é essencial que se identifique diferentes conjuntos de áreas importantes, isto é, que se crie alternativas aos

conjuntos de áreas prioritárias (Pressey *et al.*, 1996). Diversos métodos ou algoritmos foram desenvolvidos para criar um sistema de reservas que maximize a representação da biodiversidade em uma determinada região (para uma revisão, veja Cabeza & Moilanen, 2001). Hoje em dia, a maneira mais eficiente de decidir que conjunto de áreas engloba a representação mais inclusiva das espécies de uma região particular é utilizar algoritmos iterativos baseados em complementaridade de alguma medida de interesse, geralmente a riqueza total de espécies do táxon considerado (Pressey *et al.*, 1996; Reyers *et al.*, 2000). Tal abordagem é relativamente simples e maximiza o ganho de espécies na menor área possível (Csuti *et al.*, 1997; Reyers *et al.*, 2000). Embora se presuma que, *grosso modo*, áreas menores correspondem a custos menores, isto não é necessariamente verdadeiro (veja abaixo).

De forma resumida, os algoritmos de priorização de área podem ser divididos em dois tipos básicos: os heurísticos (mais simples) e os ótimos (mais complexos). Os heurísticos, como o bastante conhecido algoritmo “*greedy*” (“ganancioso”), levam em consideração apenas a representação de espécies, para um alvo de conservação predeterminado (p. ex., cada espécie deve ocorrer em pelo menos uma das áreas candidatas à prioritárias; ou então, pelo menos 80% de todas as espécies devem fazer parte das áreas mais importantes) (Cabeza & Moilanen, 2001, Sarkar *et al.*, 2006; Vanderkam *et al.*, 2007). O que este algoritmo faz é iniciar um conjunto prioritário com a região mais rica em espécies dentre todas as disponíveis. Em seguida, é acrescentada a região que contém o maior número de espécies não existentes na primeira. Logo, busca-se uma terceira região que contenha o maior número possível de espécies que não ocorrem no conjunto das duas primeiras regiões, e assim sucessivamente. Esse algoritmo incorpora, implicitamente, o princípio da complementaridade, por meio do qual se busca a máxima diversidade beta na menor área possível (Pressey *et al.*, 1996). A principal vantagem desse método de seleção de áreas é que sua lógica é muito simples. Além disto, ao se refazer a análise, deve-se chegar sempre ao mesmo conjunto prioritário, uma vez que por este algoritmo alcança-se o menor conjunto possível, isto é, uma única solução para o problema de se encontrar áreas mais importantes baseadas na representação de espécies. Isso torna o processo inteligível e facilmente explicável àqueles que não lidam diretamente com análises desse tipo, sendo, portanto, o método mais apropriado para uso em esferas externas ao meio acadêmico e à Biologia da Conservação: tomadores de decisão, políticos, gestores com outra formação técnica, etc.

Os algoritmos ótimos trabalham com uma lógica diferente para a identificação de áreas prioritárias. Esses algoritmos não chegam a uma só solução (um conjunto prioritário), mas simulam vários conjuntos “ótimos” e sobrepõem todos eles com o intuito de encontrar uma

solução consensual, e, portanto, realmente ótima (Sarkar *et al.*, 2006; Smith *et al.*, 2006; Vanderkam *et al.*, 2007; Margules & Sarkar, 2007). Isso é possível porque não se trabalha com uma só sequência de acréscimo de regiões; em vez disto, diversas possibilidades são geradas por meio de simulações computacionais. Essas análises, teoricamente, trazem mais confiança para o conjunto prioritário final (Vanderkam *et al.*, 2007). Outra vantagem importante desses algoritmos é a possibilidade de se incluir restrições (tais como custos) nas análises e, portanto, no delineamento dos conjuntos prioritários (Andelman *et al.*, 1999; Possingham *et al.*, 2000, Sarkar *et al.*, 2006). Por exemplo, é possível procurar conjuntos mínimos em que a extensão da área total funcione como uma “penalidade” aplicada a todas as soluções geradas. Dessa forma, soluções finais com área total muito extensa seriam mais caras em termos de implantação e, portanto, relegadas perante outros conjuntos com menor área total, e, por isso mesmo, com menor custo.

No exemplo acima, a área total é apenas uma das variáveis que pode ser usada como restrição; diversas outras (p. ex., nível de ameaça das espécies, grau de impacto humano das regiões, características ecológicas ou evolutivas das espécies) podem ser incluídas no modelo de priorização, embora isso raramente tenha sido feito por enquanto (mas veja, como exemplo, Strange *et al.*, 2006; Copeland *et al.*, 2007; Loyola *et al.*, 2008a, b). A grande desvantagem dos algoritmos ótimos é que eles são pouco intuitivos e são necessárias diversas etapas com escolhas até certo ponto arbitrárias de variáveis e dos valores que lhes são atribuídos, bem como dos alvos definidos em cada modelo. Esse problema foi chamado de “efeito caixa-preta” (Vanderkam *et al.*, 2007): após inserir diversos parâmetros em um modelo, o programa gera literalmente milhões de simulações e oferece um resultado ótimo – sacrificando, no processo, a transparência do processo de priorização (Sarkar *et al.*, 2006).

Alguns autores sugerem que algoritmos heurísticos não podem garantir resultados ótimos (maior representação na menor área possível) assim como também não são capazes de informar o grau de sub-otimização da solução, isto é, do conjunto prioritário identificado (Pressey *et al.*, 1996; Sarkar *et al.*, 2006; Vanderkam *et al.*, 2007). De qualquer forma, os algoritmos heurísticos parecem ser ainda eficientes, dado que suas soluções não parecem ser substancialmente piores que aquelas obtidas por algoritmos ótimos (Vanderkam *et al.*, 2007), embora alguns autores insistam nessa diferença (p. ex., Pressey *et al.*, 1996). Além disso, certo grau de sub-otimização parece não ser um problema real na prática, uma vez que outros fatores políticos e ecológicos influenciam nas decisões sobre a alocação real de reservas (Pressey *et al.*, 1996; Pressey & Cowling, 2001; Vanderkam *et al.*, 2007). Ainda assim, por sua maior rigorosidade e

possibilidade de inclusão de restrições importantes em práticas de conservação, os algoritmos ótimos tem sido mais amplamente usados no planejamento sistemático de conservação.

Uma questão de escala

Aparentemente, a eficiência de um ou outro método pode ser muito dependente da escala de trabalho envolvida. Quando as unidades geográficas de estudo estão em uma escala regional (na qual as unidades avaliadas são ecorregiões, ou tipos de vegetação) a diferença no número de regiões prioritárias em uma solução ótima ou sub-ótima pode ser, até certo ponto, relevada, pois essas regiões não funcionam como unidades de conservação a serem realmente implantadas. Em vez disto, essas soluções apenas indicam onde os esforços de conservação devem ser concentrados (Loyola *et al.*, 2007). Por outro lado, em escala ainda menor, como a utilizada no delineamento de reservas naturais, algoritmos mais complexos podem ser mais informativos e criteriosos, em função da incorporação outras variáveis econômicas ou socioambientais envolvidas (tais como uso de solo, preço de terra, ocupação humana, veja Whittaker *et al.*, 2005).

Ainda hoje, nosso conhecimento sobre a biodiversidade permanece inadequado, sendo afetado por problemas conhecidos como déficits Linneano e Wallaceano (Lomolino *et al.*, 2004, Whittaker *et al.*, 2005). O déficit Linneano refere-se ao fato de que da maioria das espécies encontradas no planeta ainda não está formalmente reconhecida e descrita, ao passo que o déficit Wallaceano sinaliza que, para a maioria dos grupos taxonômicos, as distribuições geográficas são pouco conhecidas e possuem inúmeras lacunas (Bini *et al.*, 2006). Ambos estes problemas são dependentes de escalas espaciais ou de tempo –tanto evolutiva, quanto ecológica – em que se realiza uma análise (Whittaker *et al.*, 2005). A propósito da questão da escala de estudo, deve-se destacar que, atualmente, a maioria das análises de priorização emprega como unidades geográficas padrão *grids* com área total padronizada (frequentemente, 1° latitude x 1° longitude). Diversas ferramentas de análise foram desenvolvidas com base nesse tipo de unidade, como os programas SITES (Andelman *et al.*, 1999; Possingham *et al.*, 2000), C-Plan (Anônimo, 2001), MARXAN (Ball & Possingham, 2000), CLUZ (Smith, 2004), entre outros. Estas ferramentas são especialmente úteis dentro de regiões com menor extensão, mas um de seus principais problemas é que requerem uma alta densidade e cobertura de registros de ocorrência de espécies nas células que compõem estes *grids* (Lamoreux *et al.*, 2006) e são extremamente sensíveis a deficiências na qualidade dos dados (Flather *et al.*, 1997; Araújo, 2004; Loyola *et al.*, 2008a). Isto se torna especialmente problemático na região Neotropical, pois registros de espécies nesta região são muito esparsos e altamente desiguais (Brooks *et al.*, 2006), com áreas muito bem

inventariadas e outras com grande deficiência de dados – um grande déficit Wallaceano. Nesse caso, análises baseadas em *grids* são menos eficientes, principalmente em escala continental (Kress *et al.*, 1998). Além disso, exercícios de priorização são também dependentes de escala (Brooks *et al.*, 2006).

Uma maneira de superar ou contornar a falta de dados de campo é sua substituição por distribuições geográficas esperadas das espécies, obtida por modelagem preditiva (Bini *et al.*, 2006). Mas isso, obviamente, é um paliativo à obtenção de dados reais de distribuição geográfica de espécies, porque expõe as análises de priorização de áreas, além de seus próprios problemas, aos pressupostos e erros potenciais dos métodos de modelagem de distribuição de espécies (Guisan *et al.*, 2006; Araújo & Guisan, 2006; Meynard & Quinn, 2007).

Ecorregiões como unidades geográficas

Outro problema associado à priorização de áreas baseadas em *grids* fixos (como as células de 1° de latitude e longitude) é que tais unidades geográficas não refletem nenhum tipo de característica ecológica ou divisão política das áreas. Assim, em um mesmo *grid* é possível encontrar comunidades ecológicas muito díspares (p. ex., formações vegetais distintas) e fronteiras políticas (limites entre estados ou países) nas quais a integração necessária a uma estratégia de conservação eficiente é inviável. O problema cresce à medida que as células unitárias são maiores, como as que têm de ser usadas para regiões com dados muito escassos. Esse problema não acontece quando se usa regiões delimitadas por critérios ecológicos, como as ecorregiões (Olson *et al.*, 2001). Ecorregiões são unidades geográficas delimitadas por similaridade de fauna e flora - suas fronteiras tentam refletir a distribuição real das comunidades no espaço geográfico (Olson *et al.*, 2001). Tais unidades geográficas são atualmente utilizadas em programas de conservação propostos pela *The Nature Conservancy* (Groves 2003), pelo Fundo Mundial para a Conservação da Natureza (WWF) em associação com o Banco Mundial (Olson *et al.*, 2001; Olson & Dinerstein, 2002; Olson *et al.*, 2002; WWF 2006), pelo *Global Environment Facility* (GEF), e no delineamento das áreas prioritárias (*Hotspots*) e das grandes áreas naturais (*Wilderness areas*) propostos pela Conservação Internacional (Mittermeier *et al.*, 2003, 2004). Ecorregiões têm também influenciado decisões governamentais relacionadas ao manejo de recursos naturais (veja Loyola *et al.*, 2007, 2008a, b).

Uma vez que a maioria das decisões em políticas públicas é tomada por países individualmente, ou seja, dentro de suas fronteiras nacionais, ecorregiões podem funcionar como as maiores unidades geográficas operacionais nas quais as decisões podem ser realmente

tomadas e implantadas. Não obstante, essas unidades apenas recentemente passaram a receber mais atenção em exercícios de avaliação (veja Lamoreux *et al.*, 2006, Loyola *et al.*, 2007).

Para além da contagem e representação de espécies

Programas e análises de priorização para a conservação de espécies normalmente enfatizam áreas com grande riqueza de espécies ou altos níveis de endemismo nas quais diversas espécies encontram-se sob risco iminente de extinção, ou onde a perda de habitat já ocorreu ou é intensa (Stattersfield *et al.*, 1998; Olson & Dinerstein, 2002; Mittermeier *et al.*, 2004; Cardillo *et al.*, 2006). Esta é, no entanto, uma abordagem paliativa que corresponde à necessidade de minimizar a perda de biodiversidade em regiões onde perturbações antrópicas severas dos habitats naturais já ocorreram ou estão ocorrendo (Cardillo *et al.*, 2006). Todavia, devido às altas taxas de perda e degradação de habitats e ao aumento dos impactos causados por populações humanas, torna-se igualmente importante a identificação de áreas nas quais os impactos humanos podem ser atualmente pequenos, mas o risco futuro de perda de espécies é alto (Loyola *et al.*, 2008b). A identificação dessas áreas pode ser feita por meio da inclusão – no processo de seleção de áreas – de outros atributos que vão além da contagem e da representação de espécies, sejam elas endêmicas ou ameaçadas. Tais atributos podem ser (1) características ecológicas das espécies (p. ex., densidade populacional, risco de extinção), características de história de vida (como modos reprodutivos, tempo de gestação, tamanho de ninhada), assim como características evolutivas (p. ex., diversidade filogenética, tamanho corporal, tamanho da área de distribuição geográfica) (Cardillo *et al.*, 2006, Loyola *et al.*, 2008a, b), ou (2) características inerentes às próprias regiões potencialmente prioritárias: nível de impacto humano, preço de terra, integridade da paisagem, padrão de uso de solo, custo de implementação de áreas, etc. (Strange *et al.*, 2006, Copeland *et al.*, 2007, Loyola *et al.*, 2008b).

Em um trabalho local, Copeland *et al.* (2007) utilizaram áreas de conservação já estabelecidas no estado do Wyoming (E.U.A.) para identificar áreas mais importantes para a conservação em relação a sua vulnerabilidade potencial, e, a partir daí, avaliaram os prováveis custos de conservação nestas áreas. Como medida de risco futuro, os autores utilizaram taxas de uso de terra que vêm gerando impactos na região. Assim, foi associado o custo de conservação à vulnerabilidade das áreas, de maneira que áreas mais vulneráveis fossem mais dispendiosas para a conservação na prática. Os autores mostraram que o custo monetário necessário para reverter os impactos associados a ameaças futuras em todas as áreas com baixa vulnerabilidade (~ 650.000 ha), cobriria apenas 5% da área total (~ 121.000 ha) necessária para a conservação eficiente de regiões altamente vulneráveis. Estudos como estes podem auxiliar na

implementação de ações conservacionistas, por propor uma metodologia que inclui estimativas de custo monetário associadas à urgência de intervenção nas áreas selecionadas. Isso, teoricamente, pode ser aplicado em qualquer escala espacial, inclusive por instituições que desenvolvem e implementam programas de conservação (Copeland *et al.* 2007).

Outro exemplo instrutivo é o trabalho de Strange *et al.* (2006) realizado em escala regional, na Dinamarca. Usando dados da distribuição geográfica de 763 espécies em oito grupos taxonômicos distintos, estes autores compararam custos da inclusão de novas áreas na rede de áreas protegidas já existente, no país com vistas a conservação de todas as espécies. Eles concluíram que o custo do planejamento de conservação elaborado de maneira independente para cada estado do país é aproximadamente 20 vezes maior que uma estratégia traçada nacionalmente. Além disso, a substituição de uma variável direta, como o preço da terra, por outra indireta (a área total das localidades consideradas) aumenta em muito o custo esperado das áreas, sem necessariamente aumentar a representação das espécies. Resultados como esse sugerem que o uso de variáveis independentes das espécies per se são muito úteis na seleção de áreas prioritárias e na criação de cenários mais realistas para políticas públicas de conservação (Strange *et al.* 2006).

Em um estudo recente (Loyola *et al.*, 2008a) identificamos áreas prioritárias para a conservação de anuros ameaçados de extinção na região Neotropical. Todas as espécies de anuros foram separadas, segundo seu modo reprodutivo, em dois grupos: aquelas com fase larval aquática (isto é, cuja parte do ciclo de vida necessariamente se desenvolve em ambientes aquáticos como riachos, poças temporárias, etc.) e aquelas com desenvolvimento terrestre (incluindo espécies com desenvolvimento direto). Em seguida, identificamos conjuntos de ecorregiões prioritárias para a conservação de anuros ameaçados como um todo, e de espécies com larva aquática e desenvolvimento terrestre separadamente. O conjunto prioritário para a conservação de todas as espécies ameaçadas de extinção hoje em dia é composto por 66 ecorregiões. Entre estas, 30 são extremamente importantes para a conservação de espécies com ambos modos reprodutivos – tais regiões concentram-se na Mesoamérica e no Andes. Em contrapartida, 26 são prioritárias exclusivamente para a conservação de espécies com larva aquática, distribuindo-se amplamente ao longo da América Central e do Sul; e apenas 10 exclusivamente para espécies com desenvolvimento terrestre, a maioria concentrada nos Andes (Loyola *et al.*, 2008a). Os resultados esclarecem que, quando o modo reprodutivo das espécies não é incluído nas análises de seleção de áreas prioritárias, regiões extremamente importantes para espécies com larva aquática não são incluídas na solução (Fig. 1). Isto quer dizer que espécies com desenvolvimento terrestre são favorecidas e que a representação de espécies com

larva aquática é prejudicada (Fig. 2) – o que é extremamente grave, pois as espécies deste último grupo possuem os maiores índices de declínio populacional registrados hoje em dia (Becker & Loyola, 2007). Loyola *et al.* (2008a) mostraram como a inclusão de características da história de vida (no caso, o modo reprodutivo de indivíduos adultos) das espécies no processo de priorização pode gerar conjuntos prioritários mais abrangentes que, por sua vez, subsidiam estratégias de conservação mais eficientes para este grupo.

Para além destes resultados, exploramos a inclusão de diferentes características ecológicas (p. ex., risco de extinção e raridade) e evolutivas (p. ex., tamanho corporal e diversidade filogenética) nos exercícios de priorização de áreas (Loyola *et al.*, 2008b). Isto foi feito para um grupo específico e bastante vulnerável – os mamíferos da ordem Carnívora. Baseado nas espécies de carnívoros que ocorrem em cada uma das 179 ecorregiões Neotropicais, mapeamos os padrões de distribuição espacial de diversidade filogenética, tamanho do corpo, raridade e risco de extinção ao longo da região Neotropical (Fig. 3A-D). Combinamos então estes padrões com o objetivo de gerar uma restrição nas análises de priorização, de modo que os conjuntos prioritários não apenas representassem todas as espécies (como no estudo precedente), mas também favorecessem regiões com espécies que, simultaneamente, possuem alta diversidade filogenética, grande tamanho corporal, são raras e se encontram em categorias de ameaça elevada. Isto nos fornece um cenário de alta vulnerabilidade e que requer intervenção urgente para a conservação adequada das espécies. Esse cenário foi então sobreposto a outro derivado independentemente das espécies em questão, mas que visava minimizar os conflitos de conservação por meio da inclusão de ecorregiões menos impactadas por populações humanas (Fig. 3E). A conclusão é que algumas ecorregiões fazem parte de mais de um cenário de conservação e que, portanto, trariam um bom retorno de investimento a longo prazo, pois conservam regiões ainda pouco impactadas pela ação do homem (que possuem menores taxas de desmatamento e conversão de habitat, menores densidades populacionais humanas, etc.), mas em contrapartida, abrigam espécies extremamente vulneráveis e que necessitam uma intervenção urgente para que sejam salvas da extinção (ecorregiões em vermelho na Fig. 3E, ver também Loyola *et al.*, 2008b).

Melhorando as avaliações de risco de extinção: populações vs. espécies

Pesquisas sobre a extinção de populações e espécies têm revelado um declínio acelerado da biodiversidade nos dias atuais (Ceballos *et al.*, 2005). Isso foi mencionado anteriormente, contudo declínios e extinções populacionais parecem ser indicadores mais sensíveis da perda de biodiversidade que a extinção de espécies. Isso ocorre, pois diversas espécies que perderam uma

grande proporção de suas populações ainda serão provavelmente extintas regional ou globalmente, contribuindo para as estatísticas de extinção de espécies no futuro (Ceballos & Ehrlich 2002).

Um bom exemplo pode ser dado pelos anfíbios. Populações de anfíbios estão declinando em todo o mundo e isto tem causado grande preocupação (Stuart *et al.*, 2004, Loyola *et al.*, 2008a). Dentre os demais vertebrados, os anfíbios apresentam a maior proporção de espécies ameaçadas, assim como o maior número de registros de populações declinantes (IUCN *et al.*, 2006). Níveis tão altos de declínios em nível populacional e de espécies têm criado demandas por estratégias eficientes que maximizem os esforços de conservação para este grupo.

Recentemente, avaliamos a correlação entre avaliações de risco de extinção de anfíbios em nível populacional [desenvolvido pela Força Tarefa para o Declínio Global de Anfíbios (DAPTF), DAPTF 2007] e em nível específico [desenvolvido pela IUCN e a Avaliação Global de Anfíbios (GAA), IUCN *et al.*, 2006] (Becker & Loyola 2007). Tal correlação foi avaliada em escala global tanto para grandes províncias biogeográficas (Australiana, Neártica, Neotropical, Paleártica e Indo-Malaia) quanto para países que possuem registros numerosos e confiáveis sobre declínios de populações de anfíbios. A conclusão do estudo é que as avaliações de risco feitas em diferentes níveis (populacional e específico) não coincidem totalmente ao longo de diferentes regiões geográficas, isto é, o nível de congruência entre ambos os critérios de avaliação varia de acordo com as regiões estudadas.

Muitos anfíbios cujas populações encontram-se em declínio não estão incluídos nas listas de espécies ameaçadas de extinção publicadas pela IUCN. Nas regiões Paleártica e Indo-Malaia, menos de 25% das espécies com populações declinantes estão classificadas como oficialmente ameaçadas. Por outro lado, mais de 60% das espécies Australianas cujas populações estão em declínio, encontram-se listadas como ameaçadas de extinção segundo IUCN *et al.*, (2006) (Fig. 4). Entre as espécies ameaçadas, aquelas com desenvolvimento aquático são bastante mais frequentes, reforçando a necessidade da inclusão de modos reprodutivos nos exercícios de priorização de áreas para anfíbios. Como consequência, sugere-se que em diversas regiões do planeta, estratégias de conservação para anfíbios podem ser muito mais abrangentes e eficazes caso sejam utilizadas informações complementares sobre o risco de extinção baseadas em tendências populacionais coletadas ao longo de uma série temporal definida assim como aquelas provenientes de listas oficiais de espécies ameaçadas (Becker & Loyola 2007). Recomenda-se, portanto que a comunidade científica faça uso de todas as fontes de dados disponíveis para desenvolver estratégias integradas e abrangentes para a conservação da fauna. Não se sabe o quanto avaliações de extinção em diferentes níveis são coincidentes ou não para outros grupos

taxonômicos, especialmente invertebrados. Novos estudos precisam ser desenvolvidos nessa área por influenciarem no estabelecimento de prioridades de conservação desde a escala regional até a global. Isso será extremamente útil no direcionamento e na alocação de esforços de conservação onde eles realmente são necessários.

Conforme exposto acima, existem hoje diferentes abordagens para a identificação de prioridades de conservação, especialmente aquelas aplicadas a grandes escalas (Sarkar *et al.*, 2006, Mace *et al.*, 2007). Tais abordagens vão desde o uso de grupos indicadores e da congruência entre a riqueza de espécies e níveis de endemismo entre diferentes grupos taxonômicos, até a identificação de áreas prioritárias para a conservação de determinados grupos – o que pode ser melhorado tanto com a inclusão de características biológicas das espécies a serem conservadas e quanto por meio de avaliações de risco de extinção nos níveis populacionais e específicos. Independente de suas diferenças metodológicas, todas essas abordagens assentam-se sobre o arcabouço conceitual e teórico proposto pela Biogeografia da Conservação (Whittaker *et al.*, 2005) e pelo Planejamento Sistemático de Conservação (Margules & Pressey, 2000). O uso de diferentes abordagens sustentadas pelo conhecimento teórico fornece-nos uma base científica fundamental para o delineamento de estratégias de conservação cada vez mais bem definidas que farão parte de um processo de negociação muito mais complexo e interdisciplinar, porém imprescindível para a implementação política de reservas e outros meios para a conservação da biodiversidade em diferentes escalas geográficas.

Agradecimentos

Somos gratos a José Alexandre Felizola Diniz-Filho e José Maria Cardoso da Silva pelo convite e gentileza de incluir nosso artigo nesse volume especial. Agradecemos também a Gustavo A. B. Fonseca, José A. F. Diniz-Filho, Umberto Kubota, Célio F. B. Haddad, Carlos Guilherme Becker, Guilherme de Oliveira e Carlos R. Fonseca pelas inúmeras discussões e sugestões em nossos trabalhos sobre priorização de áreas para a conservação. Rafael D. Loyola é apoiado pelo CNPq (140267/2005-0). A pesquisa de Thomas M. Lewinsohn é financiada pelo CNPq (306049/2004-0) e FAPESP (04/15482-1).

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Legenda de figuras

Figura 1. Em A-C, mostram-se conjuntos mínimos de ecorregiões necessárias para a representação de espécies com diferentes modos reprodutivos: tanto aquelas com fase larval aquática (em amarelo) quanto as com desenvolvimento terrestre (em vermelho), sob diferentes níveis de corte de representação de espécies (95, 80 e 70%). Ecorregiões prioritárias para espécies com ambos os modos reprodutivos são representadas em cor de laranja. Em E-G, mostram-se conjuntos mínimos necessários para a representação de anuros sob diferentes níveis de corte de representação de espécies (95, 80 e 70%). Nesse caso, os modos reprodutivos não foram incluídos nas análises. Note a perda progressiva de regiões prioritárias para espécies cuja ontogenia inclui uma fase larval aquática. Adaptado de Loyola *et al.*, (2008a).

Figura 2. Porcentagem de representação de espécies de anuros ameaçados de extinção na região Neotropical atingida sob diferentes alvos de conservação. Note a sub-representação de espécies com fase larval aquática quando os modos reprodutivos não são considerados nas análises de priorização: o alvo original de representação não é sequer atingido.

Figura 3. Padrões espaciais de (A) diversidade filogenética, (B) tamanho corporal, (C) raridade e (D) risco de extinção, segundo a Lista de Espécies Ameaçadas de Extinção da IUCN 2007. O gradiente de cores exibido pela ecorregiões refletem valores baixos (amarelos) a altos (vermelhos) para essas características. Em (E), conjuntos mínimos para a representação de todas as espécies de carnívoros Neotropicais sob um cenário muito vulnerável e de intervenção urgente (ecorregiões em cor de laranja) combinado com aquele onde haverá possivelmente um menor conflito de conservação (ecorregiões em verde). Ecorregiões prioritárias compartilhadas por ambos cenários são mostradas em vermelho. Adaptado de Loyola *et al.*, (2008b).

Figura 4. Porcentagem de espécies com declínio registrado por província biogeográfica. Barras em preto representam espécies cujo desenvolvimento inclui uma fase larval aquática, barras em cinza representam espécies com desenvolvimento terrestre, barras brancas representam espécies não ameaçadas. Grau de ameaça obtido por meio da Lista de Espécies Ameaçadas de Extinção da IUCN 2007. Adaptado de Becker & Loyola (2007).

Figura 1

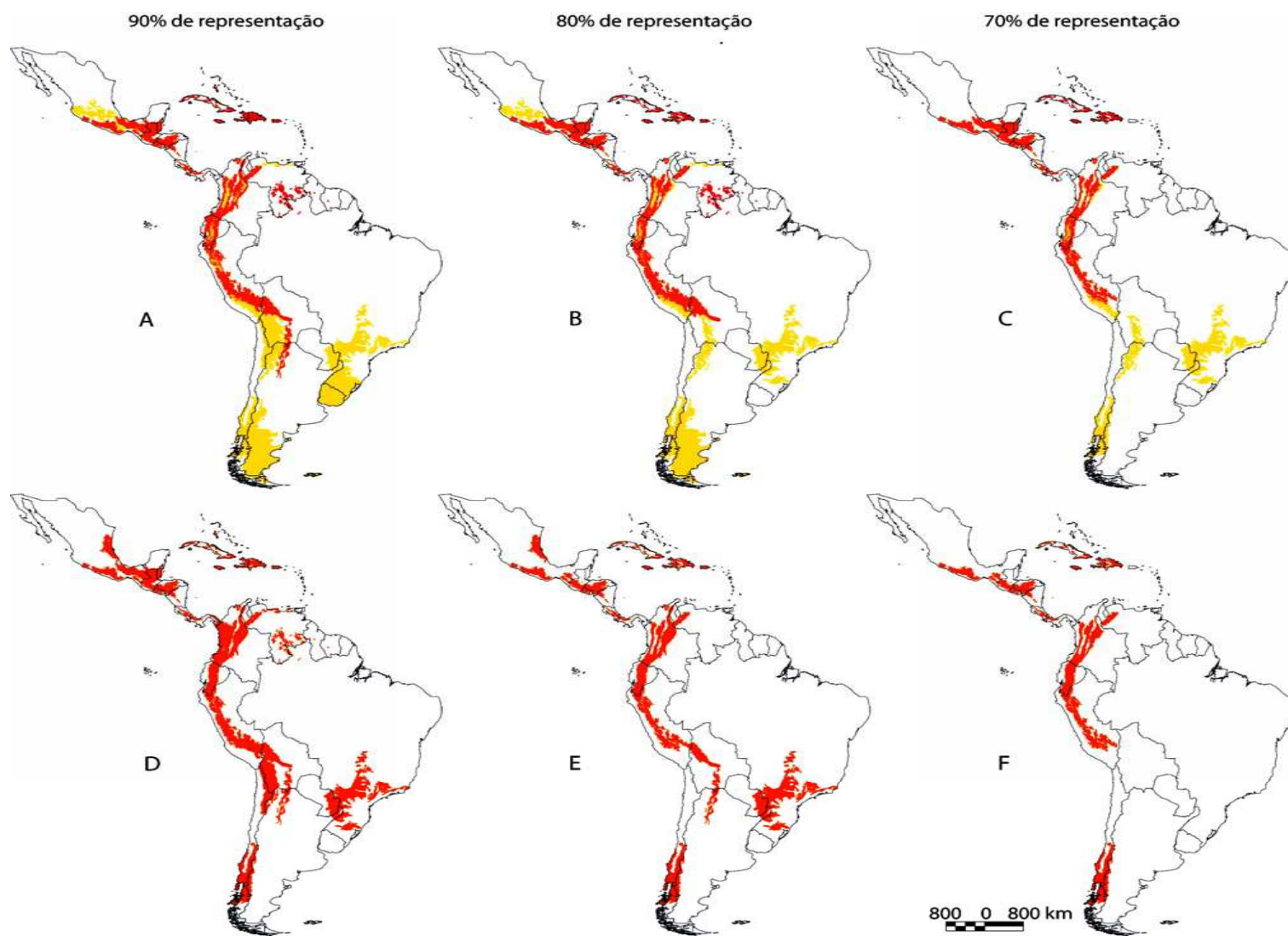


Figura 2

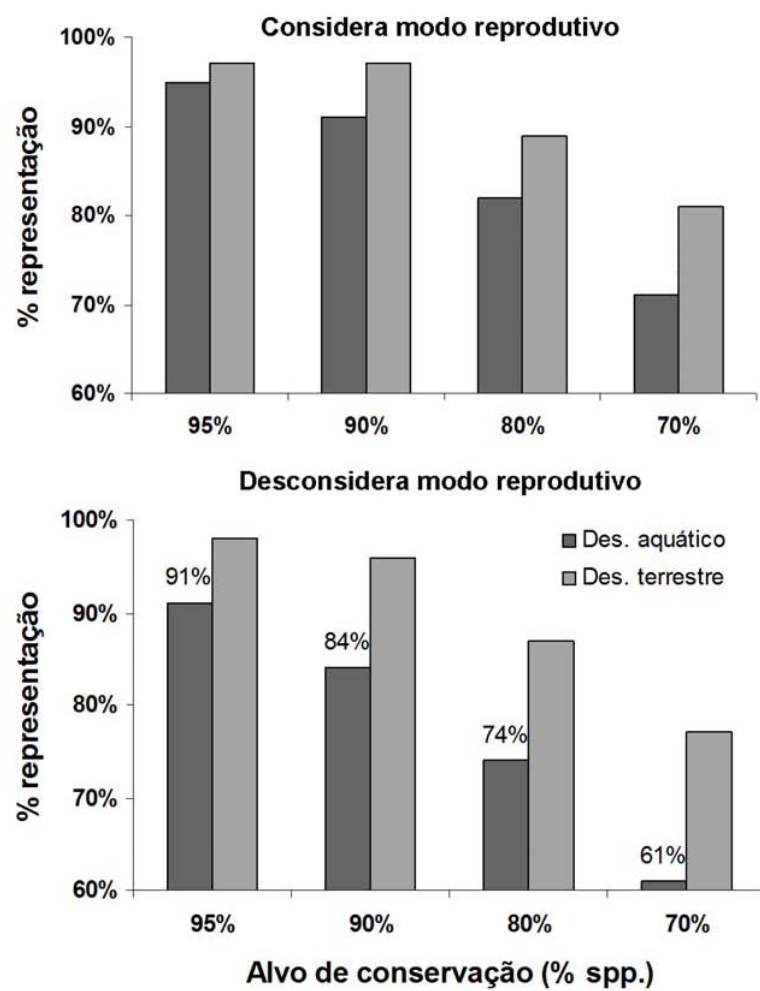


Figura 3

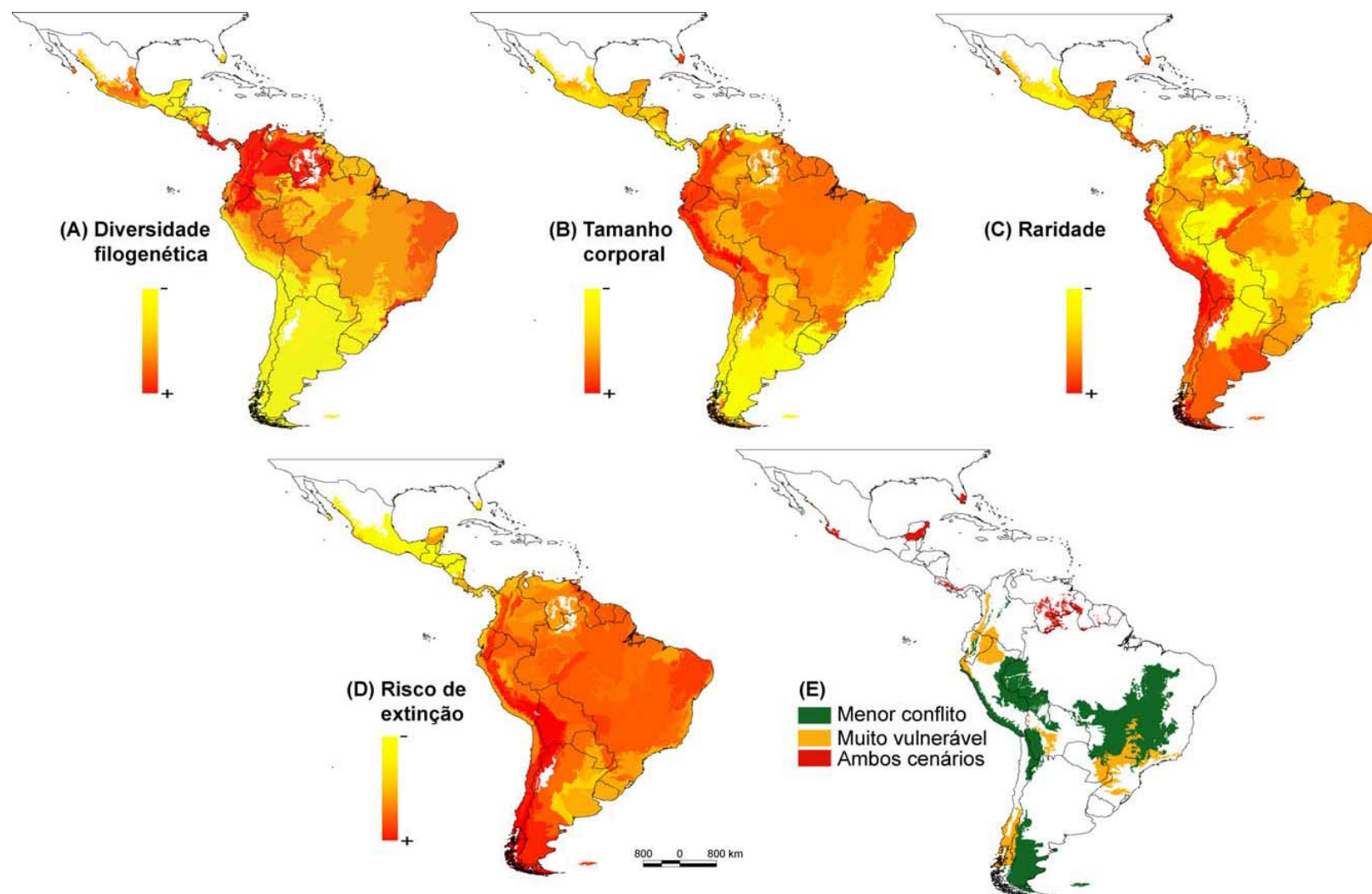
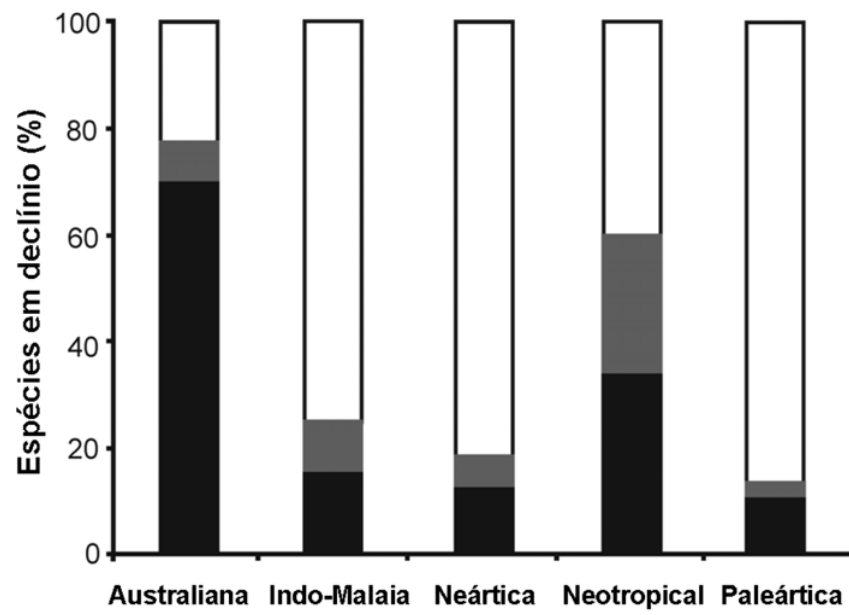


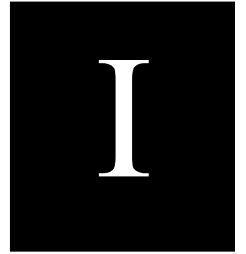
Figura 4



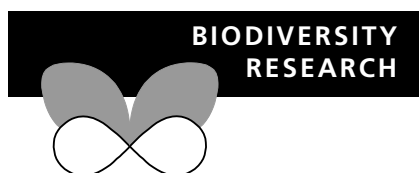
Objetivos

Conforme exposto na introdução geral da tese, existem hoje diferentes abordagens para a identificação de prioridades de conservação, especialmente aquelas aplicadas a grandes escalas geográficas. Tais abordagens vão desde o uso de grupos indicadores e da congruência entre a riqueza de espécies e níveis de endemismo entre diferentes grupos taxonômicos, até a identificação de áreas prioritárias para a conservação de determinados grupos. Independente de suas diferenças metodológicas, todas essas abordagens assentam-se sobre o arcabouço conceitual e teórico proposto pela Biogeografia da Conservação e pelo Planejamento Sistemático de Conservação. O conteúdo dessa tese perpassa por diferentes abordagens, tendo como alvo a identificação de prioridades de conservação para vertebrados terrestres em diferentes escalas geográficas, desde a regional até a global. Meus objetivos específicos nesse trabalho foram responder as seguintes questões:

1. Há uma alta correlação entre a riqueza e o endemismo exibido por vertebrados terrestres que ocorrem em ecorregiões do Brasil? Qual a eficiência de cada classe de vertebrados terrestres (anfíbios, répteis, aves e mamíferos) como grupos indicadores para a identificação de prioridades de conservação em ecorregiões brasileiras?
2. Quais ecorregiões são prioritárias para a representação eficiente de todos os vertebrados terrestres, incluindo aqueles endêmicos e ameaçados de extinção, na região Neotropical? O quanto essas ecorregiões representam da fauna existente nessa província biogeográfica?
3. Quais ecorregiões são prioritárias para a representação eficiente de todos os anuros (Amphibia: Anura) ameaçados de extinção na região Neotropical? Como a inclusão de características da história de vida (e.g. modo reprodutivo) desse grupo no processo de priorização pode auxiliar no delineamento dessas áreas prioritárias?
4. Quais ecorregiões são prioritárias para a representação eficiente de todos os carnívoros (Mammalia: Carnivora) na região Neotropical? Como a inclusão de características ecológicas e evolutivas desse grupo no processo de priorização pode auxiliar no delineamento dessas áreas prioritárias?
5. Quais ecorregiões são prioritárias para a representação eficiente de todos os carnívoros (Mammalia: Carnivora) em âmbito global? Como a inclusão de características biológicas (e.g. tamanho de corpo, densidade populacional, tamanho de ninhada) desse grupo, associadas a custos econômicos (US\$/km²) da aquisição de terras em ecorregiões pode melhorar o processo de priorização?



Loyola RD, Kubota U & Lewinsohn TM (2007). **Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions.** *Diversity and Distributions* 13: 389-396.



Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions

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ABSTRACT

Many studies have tested the performance of terrestrial vertebrates as surrogates for overall species diversity, because these are commonly used in priority-setting conservation appraisals. Using a database of 3663 vertebrate species in 38 Brazilian ecoregions, we evaluated the effectiveness of various subsets for representing diversity of the entire vertebrate assemblage. Because ecoregions are established incorporating information on biotic assemblages, they are potentially more amenable to regional comparison than are national or state lists. We used 10 potential indicator groups (all species; all mammals, birds, reptiles, or amphibians; all endemic species; and endemic species within each class) to find priority sets of ecoregions that best represent the entire terrestrial vertebrate fauna. This is the first time such tests are employed to assess the effectiveness of indicator groups at the ecoregion level in Brazil. We show that patterns of species richness are highly correlated among mammals, birds, amphibians, and reptiles. Furthermore, we demonstrate that ecoregion sets selected according to endemic species richness captured more vertebrate species per unit area than sets based on overall vertebrate richness itself, or than those selected at random. Ecoregion sets based on endemic bird, endemic reptile, or endemic amphibian richness also performed well, capturing more species overall than random sets, or than those selected based on species richness of one or all vertebrate classes within ecoregions. Our results highlight the importance of evaluating biodiversity concordance and the use of indicator groups as well as aggregate species richness. We conclude that priority sets based on indicator groups provide a basis for a first assessment of priorities for conservation at an infracontinental scale. Areas with high endemism have long been highlighted for conservation of species. Our findings provide evidence that endemism is not only a worthwhile conservation goal, but also an effective surrogate for the conservation of all terrestrial vertebrates in Brazil.

Keywords

Biodiversity concordance, complementarity, conservation, hotspots, indicator groups, species richness, vertebrates.

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INTRODUCTION

The foremost goal of large-scale strategies for conserving biodiversity is not to select areas for reserves, but to identify regions of high conservation value that are significant in a global or continental context (Moore *et al.*, 2003). Once identified, more detailed conservation assessments should be directed towards these areas (Brooks *et al.*, 2001). In fact, lack of information as to where conservation efforts should be concentrated is a major obstacle to conserving tropical biodiversity (Howard *et al.*, 1998).

One frequently adopted approach for identifying priority areas for conservation based on partial information has been to use a subset of species as surrogates for all species (Gaston, 1996), i.e. to focus on readily assessed indicator groups, which consist of those species in a relative speciose single taxon thought to represent biodiversity as a whole, whose distribution then predicts the overall importance of the biodiversity of candidate regions. In general, indicator groups will act as effective surrogates for other species subsets if patterns of distribution coincide across taxa (Moore *et al.*, 2003).

One possible way to identify indicator taxa is to quantify how far the spatial patterns of species richness coincide across different groups (Prendergast *et al.*, 1993; Gaston, 1996; Flather *et al.*, 1997; van Jaarsveld *et al.*, 1998; Virolainen *et al.*, 2000). Until now, few large-scale studies have evaluated the representation of non-target taxa in conservation priority sets based on indicator groups.

In the tropics, high biological diversity coupled with limited resources for its assessment means that the potential benefits of using indicators are substantial (Howard *et al.*, 1998). The results of some global or continental studies suggest congruence of species richness and endemism (e.g. Williams & Gaston, 1994; Pearson & Carroll, 1999; Lamoreux *et al.*, 2006), while other studies observed no such relationship (Ryti, 1992; Flather *et al.*, 1997; Robbins & Opler, 1997; Orme *et al.*, 2005).

Concordance in species richness with other taxa is not a sufficient test of a single taxon's ability to indicate the overall conservation value (measured as overall species representation, irreplaceability, or complementarity) of different sites (Saetersdal *et al.*, 1993; Gaston, 1996; Flather *et al.*, 1997). A more appropriate test is to ascertain to what extent the sets of priority regions based on a single candidate indicator taxon are able to capture diversity in other taxa as well (Balmford, 1998; Howard *et al.*, 1998; Moore *et al.*, 2003).

In this study, we used the effectiveness of indicators to represent other groups to evaluate the performance of priority sets based on indicators (Rodrigues *et al.*, 1999; Moore *et al.*, 2003). Effectiveness was also evaluated on how well a priority set represents total species richness compared to randomly assembled sets of ecoregions, which provide a measure of their usefulness in guiding decisions (Moore *et al.*, 2003). Finally, we asked how well the current data on putative indicator groups can robustly identify regions capable of conserving the entire terrestrial vertebrate biodiversity. Our study focuses on Brazil because the country ranks among the highest known diversity for most major groups (Mittermeier & Goettsch Mittermeier, 1997, 2004; Brandon *et al.*, 2005; Lewinsohn & Prado, 2005), and it includes several of the largest remaining wilderness areas (Mittermeier *et al.*, 2002). It thus is one of the very few countries worldwide where large-scale conservation decisions may still be of practical importance (Brandon *et al.*, 2005).

METHODS

The database used for the analyses [World Wildlife Fund (WWF), 2006] contains the current species list of mammals ($n = 620$), birds ($n = 1632$), reptiles ($n = 707$), and amphibians ($n = 704$) in Brazilian ecoregions. Lewinsohn & Prado (2005) present more recent countrywide counts, but differences are too slight to influence analyses and results presented here. We tallied the presence or absence of 3663 species recorded in each of 38 terrestrial ecoregions of Brazil. The number of species recorded extrapolates the total number of Brazilian known species because some ecoregions extend across national boundaries (see below).

Although there are many classifications of Latin America biogeographical regions, we follow the WWF's hierarchical classification of ecoregions (Olson *et al.*, 2001; WWF, 2006). We

used the data of all Brazilian ecoregions that are restricted to the country and included ecoregions shared with other countries whenever at least half of their area lies within Brazilian territory (Appendix 1).

Following Lamoreux *et al.* (2006), we tallied vertebrate class richness for each ecoregion and divided it by the total Brazilian species richness in the database for that class. This standardized species richness allowed us to compare taxa without a single species group overwhelming the others.

The values of standardized richness were also used to calculate a combined proportional richness index — an index that combines the other three remaining classes — as follows:

$$\text{Index}_{(e)} = \sum_{i=1}^n \frac{Gi_{(e)}}{Gi_{(t)}}$$

where $\text{Index}_{(e)}$ is the richness index for ecoregion e , $Gi_{(e)}$ is the number of species in taxon i per ecoregion, and $Gi_{(t)}$ is the total number of species of taxon i (Lamoreux *et al.*, 2006). Endemism indices were calculated in the same manner. An adjusted richness index was used for comparisons between overall richness and endemism; in that case, the richness totals included only non-endemic species so that endemics were not part of both comparative sets.

We regressed richness and endemism indices of each ecoregion against ecoregion land area (both variables were $\log_{10}$ -transformed) in order to reduce the influence of ecoregion size on the indices. We then used the residuals of each index for subsequent analyses. We correlated the corrected values of standardized richness and endemism among vertebrate taxa, and tested their statistical significance using a randomization procedure with 10 000 iterations (Manly, 1997). In accordance with Lamoreux *et al.* (2006), we used the following standards to evaluate correlation coefficients: large correlation coefficients were approximately 0.50 or higher, moderate correlations were around 0.30, and small correlations were about 0.10 (see also Cohen, 1988; Aron & Aron, 2003).

To evaluate the effectiveness of representation of non-target species taxa in priority sets based on each indicator group, we compared representation in these sets against that in (1) an all-vertebrate priority set using all species data and (2) randomly chosen priority sets for which ecoregions were drawn, without replacement, 1000 times. The species cumulative curve for each surrogate group (mammals, birds, reptiles, amphibians, and, respectively, endemic species) was constructed by arranging the ecoregions following the sequence of surrogate group richness, i.e. from the richest to the poorest one. Note that species richness of each group was used only for ecoregion ranking, whereas the effectiveness of a priority set was evaluated as the percentage of non-target species represented in that set. As pointed out by Moore *et al.* (2003), this measure assumes that the representation goal is at least a single representation of each species.

Finally, in order to show which indicator group was the most effective surrogate in general, i.e. which one presented the lowest deviations from the maximum complementarity curve, we constructed box plots and ordered them according to increasing median deviation values.

Table 1 Pearson correlation coefficients of Brazilian terrestrial vertebrates diversity measures.

	Amphibians	Reptiles	Birds	Mammals	Four classes
Richness†	0.479**	0.619**	0.569**	0.457**	
Endemism‡	0.187	0.668**	0.736**	0.478*	
Richness × endemism§	0.192	0.001	0.224	−0.030	0.179

* $P < 0.05$; ** $P < 0.01$.

†Correlation between class richness and a combined richness index of the three remaining classes.

‡Correlation between class endemism and a combined endemism index of the three remaining classes.

§Correlation between adjusted richness and endemism within each index, and the four classes combined.

RESULTS

Correlations of the area-adjusted species richness of any vertebrate class with the total richness of the remaining classes were strong, positive, and significant in all cases (Table 1). Likewise, correlations of the proportional endemism of each vertebrate class with the remaining ones were strong, positive, and significant for reptiles, birds, and mammals. Amphibians did not show any significant correlation with endemism of any other class (Table 1). Our analysis found no meaningful correlation of total richness with endemic richness within any of the vertebrate classes, or for vertebrates overall (Table 1). Given that regional and/or local rarity is often associated with endemism, this uncoupling of endemism from richness indicates that they are not both merely reflecting underlying differences in aggregate sampling effort among ecoregions.

Effectiveness, measured as the percentage of species present in all ecoregions, was highest for total endemic species, endemic birds, endemic reptiles, and endemic amphibians, with birds being least effective (Figs 1a & 2). When only endemic species of each vertebrate class were considered, the most effective indicator groups were: total endemic species, endemic birds, endemic reptiles, and endemic amphibians, in that order (Figs 1b & 2). In a similar way, sets of randomly selected ecoregions captured fewer species per unit area than sets of all other indicator groups, the total species set, or the total endemic species set (Fig. 1a,b).

Indicator groups differed in their deviation from the maximum complementarity curve. The total endemic species set presented the lowest deviation. Furthermore, endemic birds, endemic reptiles, and endemic amphibians also performed better than the 'all-species' set and the species richness of any vertebrate class (Fig. 2). However, neither total nor endemic mammal richness was effective predictors of overall vertebrate richness in Brazil, although both still performed better than total bird richness (Fig. 2).

DISCUSSION

We found that selecting ecoregions on the basis of their area-adjusted endemic species numbers is the most effective criterion for appraising the conservation of terrestrial vertebrates in Brazil.

Therefore, endemic vertebrate species are the most effective surrogate for ranking priority area sets for conservation in Brazil.

The ecoregion set used in our research is a uniquely comprehensive data set of terrestrial vertebrate distributions to evaluate Brazilian concordance in diversity patterns among the four classes, i.e. amphibians, reptiles, birds, and mammals. Moreover, these ecoregions as well as other world terrestrial ones, are currently adopted by the Nature Conservancy (Groves, 2003), the WWF in association with the World Bank (Dinerstein *et al.*, 1995; Olson & Dinerstein, 1998; WWF, 2006), and in the delineation of Conservation International's hotspots and high biodiversity wilderness areas (Mittermeier *et al.*, 2003, 2004). Ecoregions are also influential in governmental decisions on the management of natural resources (e.g. Soutullo & Gudynas, 2006).

Given that most conservation decisions and policies have to be met within national boundaries, ecoregions may stand for the largest operational units at which decisions can actually be taken and implemented. Nonetheless, they are only recently being given more consideration in evaluation exercises (e.g. Soutullo & Gudynas, 2006).

Our results confirm that the patterns of species richness among Brazilian terrestrial vertebrates are broadly concordant. This was also observed with global vertebrate patterns of diversity (Lamoreux *et al.*, 2006). Possible causes of coincident patterns of global biodiversity include a number of hypotheses that hinge on patterns of species geographical range, climate, or geological history; however, a combination of these factors seems the most likely explanation for this coincidence (Pimm & Brown, 2004).

Given the strong correlation between the proportional endemism of each class (except for amphibians) and the endemism of the other vertebrate classes, Brazilian terrestrial vertebrate endemism is useful and effective for guiding conservation decisions regarding overall endemism. However, the observed variance in endemism among ecoregions is only partially explained by correlations between classes, and therefore specific information for other groups has to be obtained for conservation strategies based on one taxon (Lamoreux *et al.*, 2006).

Endemic species are in themselves an important target of global conservation efforts (Myers *et al.*, 2000), since these species have small populations and, having few sites for conservation intervention, are inherently vulnerable to extinction (Gaston, 1998). Endemism patterns between taxa were correlated in this study, suggesting that an ecoregion set with relatively small total area might suffice to conserve most endemic vertebrates. This assumes great importance in the tropics where, faced with the continuing extinction crisis, conservation efforts must focus either on areas with high species richness to maximize the number of species covered, or on areas that contain large number of endemic species (Mittermeier *et al.*, 1997; Olson & Dinerstein, 1998; Myers *et al.*, 2000).

Global patterns of species richness and endemism tend to be spatially disjunct (Lamoreux *et al.*, 2006). Indeed, we found no significant correlation between richness and endemism within any of the four vertebrate classes or for vertebrates overall. This result indicates that possible priorities based on richness alone are likely to exclude many endemic species. Although no conservation

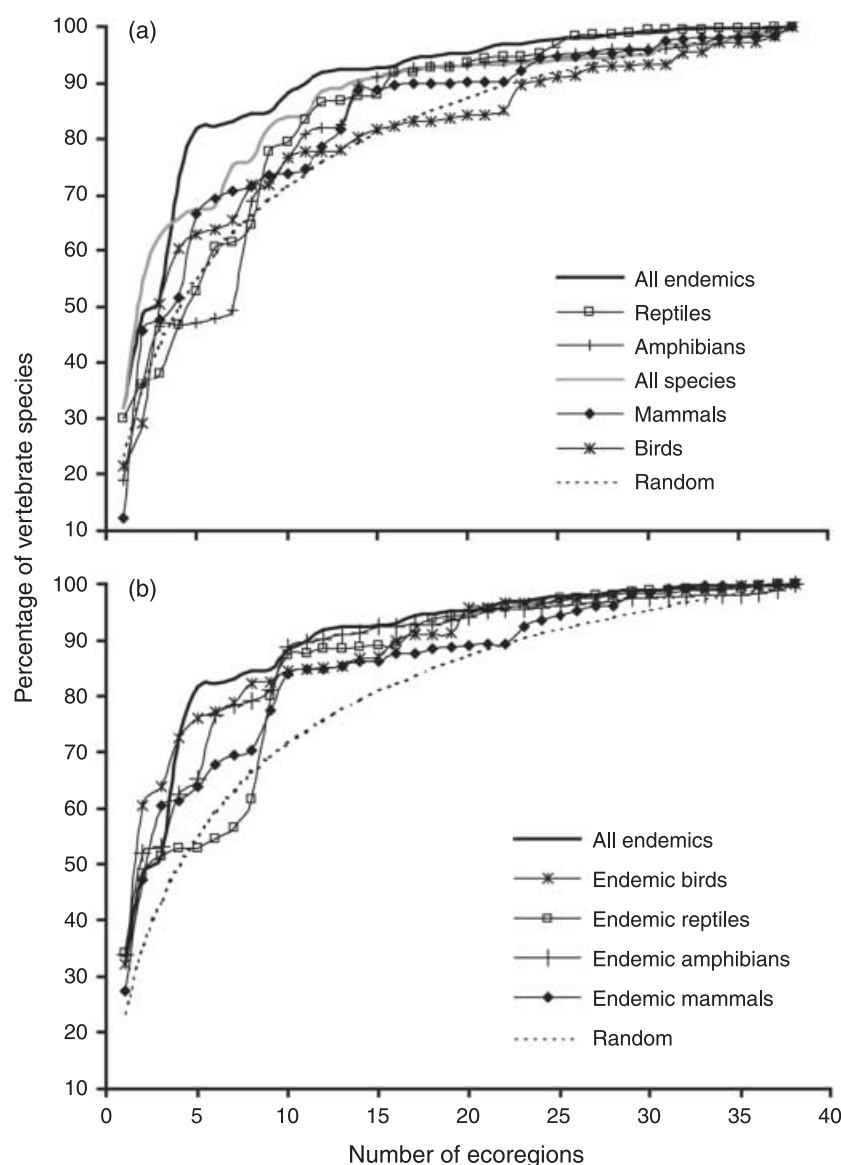


Figure 1 Cumulative representation of species across all four vertebrate classes (birds, mammals, amphibians, and reptiles) as a function of cumulative number of ecoregions, when ecoregions are selected on the basis of data on: (a) single taxa, on all species, on all endemic species, or at random; and (b) single endemic taxa, on all endemic species, or at random.

scientist or organization would propose such a procedure, it is important to note that among decision-makers, governmental or not, gross taxon richness figures often carry much weight.

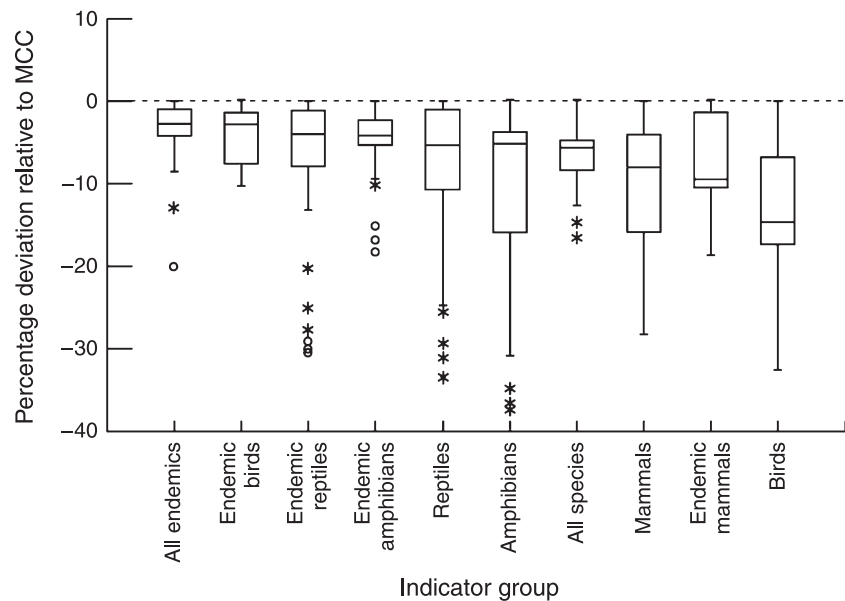
Perhaps the question most relevant to conservation decisions is whether a specific set of ecoregions selected according to one measure (e.g. bird species richness) will represent non-target species (Balmford, 1998; Howard *et al.*, 1998; Moore *et al.*, 2003). Our results suggest that the use of surrogates to select priority sets of ecoregions of conservation value will represent significantly more non-target richness than can be expected at random. The sets identified on the basis of all endemic species aggregated, endemic birds, endemic reptiles, or endemic amphibians would provide a useful initial basis for setting large-scale conservation priorities in a Brazilian reserve network. It is important to note, however, that although reptiles and amphibians were classified as effective indicator groups based on their median percentage deviation from the maximum complementarity curve, these groups showed higher deviation values. Hence, they present

fairly high deviations at some points, especially with few ecoregions accumulated (see Fig. 1a,b). Their effectiveness will thus depend on how many ecoregions are included in a given selection set.

The fact that priority sets based on endemic species contain large numbers of total species can be due to high turnover in species composition among areas of high endemism; that is, these areas are highly complementary in terms of endemic species in Brazil. Note, however, that the correlation of total richness with total endemic richness for vertebrates overall does not take into account this turnover and therefore this result is not significant.

The relative high representation of other taxa by reptiles and amphibians was unexpected, given the low number of species and the high degree of ecological specialization in these taxa. The distribution of many species of reptiles and amphibians is poorly known and it is possible that the geographical range of many species is underestimated; indeed, the number of newly described species has risen steadily in Brazil over the last decades (Pimenta *et al.*, 2005). In this case the number of ecoregions required to

Figure 2 Indicator group deviation relative to maximum complementarity curve (MCC). Box plots indicate the range of the data between brackets, the middle two quartiles within the box, the median value as the midline, outside (*) and far outside (o) values.



represent these groups would be overestimated, and hence inflate their representational power.

We cannot rule out the possibility that the high correlations among endemic richness of different taxa reflect differences in sampling coverage of different ecoregions. That is, if some ecoregions have been more comprehensively inventoried than others for several groups, the numbers of endemics would be expected to be correlated among these taxa. However, as pointed out above, one would likewise expect high correlations of species richness with endemic richness, contrary to what we found (Table 1). Hence we tend to view these correlations as a genuine pattern rather than a sampling artefact. A number of hypotheses, ecological or historical, could account for this pattern; a prominent example is the refugia hypothesis (see Prance, 1982) for which evidence is still controversial. To examine these hypotheses adequately requires further analysis of the composition and richness of endemics in each ecoregion.

This work furthers the understanding of how species diversity patterns can inform conservation priorities at a regional scale. However, we must note some important restrictions. First, the distribution patterns we report are only derived from vertebrate records and possibly may not hold for invertebrates or plants. Second, the number of species as a unit of measurement disregards other important aspects of vertebrate biodiversity, such as population and genetic differentiation. Whenever possible, as Lamoreux *et al.* (2006) point out, methods for setting conservation priorities should consider not only the number of endemics or total species present, but also the population viability (Groves, 2003), degree of threat (Myers *et al.*, 2000), ecological and evolutionary processes (Olson & Dinerstein, 1998; Groves, 2003), and economic costs and benefits of conservation (Balmford *et al.*, 2002). Third, the ecoregion classification in common usage, which we adopt here, is still fairly coarse and unevenly detailed among different Brazilian biomes. Of the 38 ecoregions included by our criterion, more than half (20) are Amazonian in broad

terms, and the remaining ones are spread among the rest of Brazil (Appendix 1). Thus, extensive biomes such as the Cerrado or the Pantanal are here treated as single units. However, additional subdivision of ecoregions will be useless unless combined with matching data on species distributions.

Some recent studies have demonstrated that global distribution and hotspots of species richness are not congruent with rare (endemic) or threatened vertebrates (Orme *et al.*, 2005; Grenyer *et al.*, 2006). Grenyer *et al.* (2006) suggested that cross-taxon congruence is highly scale-dependent, being particularly low at finer spatial resolutions. This is relevant because the ecoregion scale is coarse and therefore high congruence at the ecoregion scale does not guarantee that reserves within distinct ecoregions will show high congruence as well (Grenyer *et al.*, 2006). Hence, our findings should be viewed as a starting point with respect to applied conservation.

Factors that may contribute to the high degree of representation of non-target taxa achieved by indicator groups include: (1) close taxonomic and ecological similarities between indicator and non-target groups (Kremen, 1992; Caro & O'Doherty, 1999) and (2) species-rich indicator groups represent a large share of the total richness, geographical distribution, range size, and ecological adaptation of the entire target set (see Moore *et al.*, 2003). However, high representation does not guarantee correspondence between the identities of ecoregions in priority sets for different taxa. This is important because we measured numerical representation, rather than the coincidence of hotspots or similarity of the selected ecoregions among different priority sets (e.g. Orme *et al.*, 2005). Finally, the large scale of the study may have increased the overall efficiency of priority-setting exercises.

Conservation efforts must consider different spatial scales to be effective and strive to ensure the long-term survival of biodiversity in a region (Theobald *et al.*, 1997; Margules & Pressey, 2000; Groves, 2003). Using vertebrate groups as surrogates for conservation of other groups, along with other factors, to identify

regional priorities helps to focus these conservation efforts on critical regions (Howard *et al.*, 1998; Moore *et al.*, 2003; Diniz-Filho *et al.*, 2006). Selecting ecoregions based on effective surrogate groups provides a practical starting point for the short-term assessment of conservation priorities within national or regional boundaries.

ACKNOWLEDGEMENTS

We thank J.A.F. Diniz-Filho for his stimulating lectures and comments on the manuscript. Two reviewers helped us to improve the manuscript. This study was carried out in the Unicamp Graduate Program of Ecology. R.D.L. and UK were supported by CNPq (140267/2005-0) and CAPES, respectively. T.M.L. was funded by FAPESP (04/15482-1) and CNPq (306049/2004-0).

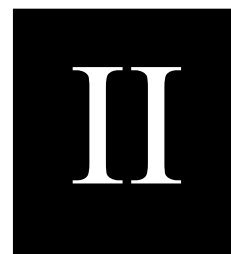
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Appendix 1 Brazilian ecoregions, number of total vertebrate species per class, and total area. The number of endemic species is shown in parentheses.

Code	Ecoregion name	Mammal richness	Bird richness	Amphibian richness	Reptile richness	Total Richness	Area (km ²)
NT0101	Araucaria moist forests	141 (0)	439 (0)	177 (1)	134 (3)	891 (4)	216,100
NT0102	Atlantic Coast restingas	196 (0)	257 (2)	195 (0)	46 (8)	694 (10)	7,900
NT0103	Bahia coastal forests	166 (5)	466 (30)	106 (0)	89 (15)	827 (50)	109,700
NT0104	Bahia interior forests	182 (6)	540 (39)	160 (1)	34 (5)	916 (51)	230,000
NT0125	Guianan moist forests	215 (2)	685 (3)	135 (20)	204 (11)	1239 (36)	512,900
NT0126	Gurupa varzea	174 (0)	558 (0)	32 (0)	27 (0)	791 (0)	9,900
NT0128	Iquitos varzea	255 (0)	624 (3)	131 (1)	164 (0)	1174 (4)	115,000
NT0132	Japurá-Solimoes-Negro moist forests	189 (0)	506 (8)	99 (4)	77 (2)	871 (14)	269,700
NT0133	Juruá-Purus moist forests	189 (0)	554 (0)	68 (0)	38 (0)	849 (0)	242,600
NT0135	Madeira-Tapajós moist forests	251 (15)	621 (6)	55 (0)	71 (2)	998 (23)	719,700
NT0138	Marajó varzea	184 (1)	540 (0)	53 (0)	86 (1)	863 (2)	88,700
NT0139	Maranhão Babaçu forests	133 (0)	268 (0)	26 (0)	112 (0)	539 (0)	142,300
NT0140	Mato Grosso seasonal forests	174 (0)	476 (3)	52 (0)	38 (0)	740 (3)	414,000
NT0141	Monte Alegre varzea	221 (0)	681 (2)	61 (0)	38 (0)	1001 (2)	66,800
NT0143	Negro-Branco moist forests	213 (0)	486 (2)	70 (3)	127 (3)	896 (8)	212,900
NT0144	North-eastern Brazil restingas	119 (0)	276 (1)	15 (0)	13 (0)	423 (1)	10,100
NT0150	Alto Paraná Atlantic forests	213 (1)	585 (0)	303 (0)	163 (1)	1264 (2)	483,800
NT0151	Pernambuco coastal forests	122 (0)	407 (6)	36 (0)	84 (2)	649 (8)	17,600
NT0152	Pernambuco interior forests	132 (0)	343 (0)	38 (0)	25 (0)	538 (0)	22,700
NT0156	Purus varzea	219 (2)	623 (2)	128 (3)	164 (2)	1134 (9)	177,500
NT0157	Purus-Madeira moist forests	183 (0)	572 (0)	72 (0)	36 (1)	863 (1)	174,000
NT0158	Rio Negro campinarana	216 (0)	358 (1)	65 (0)	25 (0)	664 (1)	80,900
NT0160	Serra do Mar coastal forests	175 (6)	628 (61)	247 (6)	123 (43)	1173 (116)	104,800
NT0163	Solimoes-Japurá moist forest	191 (0)	542 (0)	136 (0)	224 (1)	1093 (1)	167,700
NT0166	South-west Amazon moist forests	303 (3)	782 (13)	173 (14)	228 (11)	1486 (41)	749,700
NT0168	Tapajós-Xingu moist forests	179 (1)	556 (2)	58 (0)	113 (3)	906 (6)	336,600
NT0170	Tocantins/Pindare moist forests	164 (1)	517 (0)	35 (0)	152 (2)	868 (3)	193,600
NT0173	Uatuma-Trombetas moist forests	207 (2)	482 (0)	96 (2)	159 (3)	944 (7)	473,100
NT0180	Xingu-Tocantins-Araguaia moist forests	176 (0)	527 (1)	52 (0)	121 (2)	876 (3)	266,200
NT0202	Atlantic dry forests	147 (0)	311 (6)	41 (0)	26 (1)	525 (7)	115,100
NT0703	Campos Rupestres montane savanna	180 (2)	334 (5)	116 (0)	48 (1)	678 (8)	26,400
NT0704	Cerrado	254 (11)	571 (14)	205 (4)	219 (48)	1249 (77)	1 916,900
NT0707	Guianan savanna	225 (0)	444 (1)	94 (7)	68 (0)	831 (8)	104,400
NT0710	Uruguayan savanna	101 (1)	350 (9)	118 (6)	90 (4)	659 (20)	355,700
NT0907	Pantanal	172 (1)	423 (1)	54 (0)	101 (12)	750 (14)	171,100
NT1304	Caatinga	158 (5)	320 (12)	51 (0)	102 (37)	631 (54)	734,400
NT1401	Amazon-Orinoco-Southern Caribbean mangroves	271 (1)	113 (0)	14 (0)	53 (3)	451 (4)	4,500
NT1406	Southern Atlantic mangroves	187 (1)	75 (0)	61 (2)	24 (0)	347 (3)	200
Total		620 (59)	1632 (176)	704 (71)	707 (216)	3663 (522)	10,050,000



Loyola RD, Kubota U, da Fonseca GAB & Lewinsohn TM (2008). **Key Neotropical ecoregions for conservation of terrestrial vertebrates.**
Biodiversity and Conservation, aceito (em revisão).

Key Neotropical ecoregions for conservation of terrestrial vertebrates

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ABSTRACT

Conservation planning analyses show a striking progression from endeavors targeted at single species or at individual sites, to the systematic assessment of entire taxa at large scales. These, in turn, inform wide-reaching conservation policies and financial investments. The latter are epitomized by global-scale prioritization frameworks, such as the Biodiversity Hotspots. We examine the entire Neotropical region to identify sets of areas of high conservation priority according to terrestrial vertebrate distribution patterns. We identified a set of 49 ecoregions in which 90%, 82% and 83%, respectively of total, endemic and threatened vertebrates are represented. A core subset of 11 ecoregions captured 55%, 27% and 38% of these groups. The Neotropics hold the largest remaining wilderness areas in the world, and encompass most of the tropical ecosystems still offering significant options for successful broad-scale conservation action. Our analysis helps to pinpoint where conservation is likely to yield best returns at the ecoregion scale.

Key words: Brazil, biodiversity, conservation planning, ecoregions, extinction, hotspots, population declines, prioritization, protected areas, vertebrates.

INTRODUCTION

The Neotropics encompass six megadiversity countries and more than 10,000 vertebrate species. They are also one of the tropical regions in which mammal and amphibian population declines and species extinction are extremely elevated (Ceballos et al. 2005; Pounds et al. 2006). However, the global prominence of the entire Neotropics in biodiversity value does not inform where in this region lie the top conservation priorities.

Biodiversity loss is a well-recognized broad-scale phenomenon that forces conservation decisions to be taken not only within national boundaries but also at an international level (Cardillo et al. 2006). However, as global actions are extremely difficult, prioritization is unavoidable (Loyola et al. 2008a). For these reasons, a systematic conservation planning framework has been developed so as optimize the allocation of scarce conservation funding by prioritizing areas for protection (Margules and Pressey 2000).

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This approach has been increasingly applied at regional (Cowling et al. 2003; Smith et al. 2006), continental (Moore et al. 2003; Loyola et al. 2008a, b) and global scales (Mittermeier et al. 2004; Olson and Dinerstein 2002).

Priority-setting assessments usually emphasize areas with the highest species richness and endemism, where many species are thought to be at imminent risk of extinction (Olson and Dinerstein 2002; Mittermeier et al. 2004; Cardillo et al. 2006), and use either fixed-size units (such as one-degree latitude/longitude grids) or variable-sized geophysical or political units (such as countries) (Mace et al. 2007). Recently, some studies (Loyola et al. 2008a, b) have pointed out that the inclusion of species biological traits – such as life-history traits (e.g. reproductive modes) or evolutionary traits (for instance phylogenetic diversity or body size) – could improve the comprehensiveness and effectiveness of priority-setting analyses.

Many advanced approaches exist for identifying priority areas for conservation at a global scale. These approaches are based on a variety of algorithms that implement different criteria for prioritizing areas for conservation (Cabeza and Moilanen 2001). Among the most successful are complementarity-based algorithms, in which candidate areas are combined successively so as to maximize the number of species represented in the minimum total area. This has been applied at global (Ceballos and Ehrlich 2006) and regional scales (Howard et al. 1998; Reyers et al. 2000; Moore et al. 2003; Loyola et al. 2008a, b). These exercises, however, cannot be downscaled to specific areas and sites (Willis and Whittaker 2002).

For this study we plotted the distribution of 10,051 terrestrial vertebrates in all of the 175 Neotropical ecoregions in which they occur (Olson et al. 2001; WWF 2006) and evaluated them separately and in combination. Our assessments were targeted at the minimum ecoregion sets required to represent at least 80% of all species in these three attributes of vertebrate diversity, i.e., all species, endemic species and threatened species; as well as at the relative importance of each Neotropical ecoregion in representing terrestrial vertebrate diversity. Such priority sets were based on all taxa whose combination best represents each diversity attribute, an approach widely adopted in conservation assessments and planning (Balmford 1998; Howard et al. 1998; Moore et al. 2003; Lamoreux et al. 2006; Loyola et al. 2007; Mace et al. 2007).

METHODS

Scope of study. We centered our analyses on the entire set of 175 terrestrial ecoregions in the Neotropical region. Although there are several classifications of Latin America biogeographical regions, we follow the WWF hierarchical classification of ecoregions (Olson et al. 2001). Given that most conservation decisions and policies have to be met within national boundaries,

ecoregions may correspond roughly to the largest operational units at which decisions can actually be taken and implemented (Loyola et al. 2007, 2008b), although conservation areas must be established and implemented at smaller spatial scales, within states or counties. Moreover, we chose ecoregions because these broad areas are defined according to physiographic and biotic features, and therefore should reflect zoogeographic boundaries more closely. They are also less sensitive to heterogeneity in distribution data than grid-based analyses (Lamoreux et al. 2006). The richness of either total, endemic, or threatened species has often been used alternately as the key criterion for area selection (Howard et al. 1998; Olson and Dinerstein 2002; Moore et al. 2003; Mittermeier et al. 2004; Lamoreux et al. 2006; Rodrigues et al. 2006; Mace et al. 2007).

Data. The database used for the analyses (WWF 2006) contains the current species list of amphibians (n=2322), reptiles (n=2557), birds (n=3890) and mammals (n=1282) in Neotropical ecoregions. Threatened species were those classified by the 2006 IUCN Red List as “critically endangered”, “endangered” or “vulnerable”. Information on updates, detailed descriptions of the process, and complete lists of sources can be obtained from WWF (2006). Note that these datasets are periodically updated, and the files used in our analyses may differ from the most recent versions available from WWF (2006). We focused our analyses on threatened Neotropical vertebrates. The number of species in this group is not static, as new species continue to be discovered (Bini et al. 2006). However, the areas from which species are most often described tend to be the same and will likely accentuate the patterns we present (Bini et al. 2006). Systematic bias in the data may arise from differences in sampling efforts, as the distribution of certain groups (e.g., birds) or geographic areas (e.g., Central American ecoregions) for which sampling efforts have been more intense will be more reliable than those that are undersampled. To reduce the effect of such biases, we excluded from the analyses vertebrate species with an IUCN Red List category of “data deficient” because of the unreliability of their range maps, and therefore, of their occurrence in the studied ecoregions.

Analyses. We tallied the presence or absence of 10,051 terrestrial vertebrate species recorded in each of 175 terrestrial ecoregions of Latin America and the Caribbean. We then used an optimization procedure to select the minimum number of ecoregions necessary to represent all species at least once, based on the complementarity concept (Reyers et al. 2000; Sarkar et al. 2002). For each diversity attribute (i.e. overall richness, endemic species richness, and threatened species richness), we ran a simulated annealing procedure in the Site Selection Mode

(SSM) routine of the SITES software program (Andelman et al. 1999; Possingham et al. 2000) to find these combinations of ecoregions. We set the analyses parameters to 50 runs and 10 million iterations. We also set a relatively high penalty value for losing a species, so that every solution represented all species with a minimum number of ecoregions. Because there are frequently multiple combinations of ecoregions that satisfy this representation goal in each conservation scenario, we combined alternative solutions into a map in which the relative importance of each ecoregion is indicated by its rate of recurrence in optimal subsets. This is also an estimate of the irreplaceability of ecoregions, ranging from minimum irreplaceability (= 0.0) to maximum irreplaceability (= 1.0) (see Ferrier et al. 2000).

The algorithm we used is driven by patterns of beta-diversity and has been considered one of the most efficient approaches to define priority area sets for species conservation (Csuti et al. 1997; Balmford 1998; Reyers et al. 2000). The inclusion of patterns of beta-diversity in area selection algorithms captures variation in species communities, helping to maintain ecological and evolutionary processes together with the underlying environmental heterogeneity necessary for long-standing persistence (McKnight et al. 2007).

Representing all species is an ambitious conservation target which is often achieved with the inclusion of a high proportion of total area. Because the extent of coverage of priority areas will strongly affect the likelihood of implementation of conservation policies and strategies, we evaluated the proportion of area needed to represent species, as conservation target increases from 10% up to 100% of species representation. We found that both the number of ecoregions and the percentage of area coverage increase rapidly beyond the conservation target of 80% of species representation (see Fig. 1). Therefore we pooled all taxa searching for minimum sets that would represent at least 80% of all species in each attribute of vertebrate diversity (i.e., total richness, endemism, and threat). Priority sets obtained from these analyses were overlaid on a map of Neotropical ecoregions (Olson et al. 2001) using ArcView GIS 3.2 (ESRI, Redmond, California). Shapefiles and associated attribute tables were obtained from WWF (2006). Maps were combined to reveal the minimum set of ecoregions that should be included in a reserve system in order to protect at least 80% of all vertebrates within each attribute. As pointed out recently by Justus et al. (2008), high conservation targets, although ambitious, are valuable from a conservation standpoint because they select a larger share of the distribution of each biodiversity attribute for inclusion in a conservation-area network.

Finally, we tested the performance of these priority sets in representing each diversity attribute by comparing its species representation with those attained by 10,000 random-generated assortments. These random sets of ecoregions were obtained by resampling without

replacement sets of 49 (the minimum set of ecoregions capable of representing at least 80% of all vertebrate species) and 11 ecoregions (a core subset within the 49-ecoregion priority set, see Results). We employed an equal-area cylindrical projection in all maps.

RESULTS

Overall richness and irreplaceability patterns

Terrestrial vertebrate species richness is lower in the west coast and southern South America, and in the Caribbean Islands. Most Neotropical ecoregions concentrate a huge number of species, typically more than 600 species in each (Fig. 2A). Patterns of species endemism are somewhat different, because ecoregions with more endemic species are more scattered throughout the Neotropics (Fig. 2B). A similar scatter was observed in the spatial distribution of threatened species (Fig. 2C). Ecoregions with high endemism and/or threat levels are concentrated in Mexico, northern and western Amazon, in the Brazilian Atlantic forest, and in northern Argentina (Fig. 2B-C).

Due to the high number of species found in most Neotropical ecoregions and to the scattered distribution of endemic species throughout Latin America, most areas exhibited high irreplaceability values, so that almost all ecoregions were tagged as irreplaceable in strict area-setting analyses (Fig. 2D-E). Irreplaceability was better defined only with regard to threatened species richness, for which the least replaceable ecoregions were concentrated in the east coast and central regions of Brazil, southern Argentina, northern Amazon, and most of Mesoamerica (Fig. 2E).

Minimum sets for total, endemic and threatened species representation

For a conservation target of 80% of species representation within each diversity attribute, key ecoregions for each attribute of vertebrate diversity are found in Central Mexico, over a great part of Central America, in northern South America, the Andes, the Cerrado and the Atlantic Forest of Brazil, and in southern Chile and Argentina (Fig. 3).

We consolidated the three sets obtained by our analysis (Fig. 3) to produce the smallest combination of ecoregions that should be sufficiently covered in a reserve system in order to protect at least 80% of all vertebrates, as well as of endemic and of threatened species (Fig. 4). In this combined set, 49 ecoregions are able to retain 90%, 82% and 86% of total, endemic, and threatened species, respectively (Tables 1 and 2, Fig. 4). Ecoregions highlighted in this set are concentrated in southern Mexico, Central America and the Caribbean, the Andes, and in Brazil (Fig. 4). These levels of species representation exceed by far those achieved by selecting

ecoregions at random (Fig. 5A), but to attain this, the priority set spans almost 50% of the area of entire Neotropical region (Tables 1 and 2).

Within this combined set, a core subset of only 11 ecoregions included 55%, 27% and 38% of total, endemic and threatened vertebrate species, respectively (black areas in Fig. 4; Table 1 and 3). Such a subset is formed by ecoregions of highest importance, simultaneously, for overall richness, endemism and threat, i.e., by the coincidence of ecoregions highlighted for each attribute of diversity in Fig. 3. Ecoregions of this core subset are located in southeastern Mexico; the Andes; southern Argentina, and in the Cerrado and Atlantic Forest of Brazil (Fig. 4, Table 3). This subset has indeed an outstanding level of species representation, again exceeding the level of representation in random selections of ecoregions (Fig. 5B). Although comparatively small – 11 out of 179 regions, or about 17% of the Neotropical area – it includes more than half of all terrestrial vertebrates in the Neotropics and more than half of the threatened mammals or reptiles in the entire region (Table 1).

DISCUSSION

Our study explicitly included threatened species as a criterion of vulnerability in priority set delineation. This is particularly important (Mace et al. 2007; Rodrigues et al. 2006) because thousands of vertebrate species have declined, and hundreds are close to extinction or have already vanished in the Neotropics. Terrestrial vertebrate populations are declining worldwide (Gibbons et al. 2000; Stuart et al. 2004). For instance, nearly 34% of all Neotropical amphibian species and 17% of mammal species are currently listed as threatened (see Table 1).

Predictably, centers of threatened vertebrates cluster in regions with high-impact human activities, and also follow to a certain degree the patterns of species richness. Similar connections were found in other studies (Mittermeier et al. 2004; Ceballos and Ehrlich 2006; Loyola et al. 2008a). Therefore most ecoregions (*ca.* 72%) in our core subset are flagged at a critical/endangered or a vulnerable conservation status (Table 3).

The absence of Central Amazon ecoregions in these priority sets is explained by the area-selecting method we used. Tropical moist broadleaf forests in Peru, Venezuela and the Guyanas, which are included in our priority sets (see Fig. 3), share many of the species found in the Amazon basin, but fewer species among each other. Therefore, their complementarity is higher and they include most of the species found in the Central Amazon, which of course is of extremely high conservation value as the largest extant tropical wilderness area (Mittermeier et al. 2003).

Among ecoregions included in the core ecoregion set, *ca.* 73% are also considered as Biodiversity Hotspots and approximately 55% of them are also included in the Global 200 framework (Table 3). Note that neither the Biodiversity Hotspots nor the Global 200 approaches were used as filters or variables in our area-selecting algorithm. The independent convergence of high priority subsets selected by our systematic approach with the Biodiversity Hotspots reinforces the latter as an important ecoregion-level framework to direct priority conservation action, instead of multiplying the number of competing planning templates (Mace et al. 2000; Brooks et al. 2006). Hence, the priority sets identified in this study complement and lend support to priority setting frameworks derived independently. Congruence between our combined analysis and the Global 200 ecoregion set can be also ascribed to outstanding endemism levels in the Neotropics, together with the high value attributed to taxonomic uniqueness in that proposal (Olson and Dinerstein 2002).

Conservation assessments that examine larger biogeographical units are gaining support of major conservation organizations as well as of many government agencies (Olson et al. 2001; Mittermeier et al. 2003, 2004). The Global Environment Facility (GEF), the largest global biodiversity funding mechanism, has recently employed a resource allocation framework that was resolved at the scale of ecoregions, although adjusted to country boundaries to reflect government-led programs and priorities. However, it has yet to develop an allocation framework that introduces complementarity measures to its overall investment portfolio. The approach we have proposed in this study might help in this next step, reinforcing the suggestion that the scale of ecoregions might be better suited for designing networks of protected areas (Margules and Pressey 2000; Williams et al. 2000; Lamoreux et al. 2006).

Ecoregion-based analyses entail their own caveats. As in any classification, substantial differences within an ecoregion may remain undetected (Brooks et al. 2006). This risk increases in larger areas, such as the Cerrado ecoregion in Brazil (see Silva et al. 2006 for a recent spatial classification of the ecological diversity of the Cerrado), or the Patagonian Steppe in Argentina. Neotropical ecoregions range from 100 to 1,900,000 km² in area and, while this may reflect actual differences in their extent, some areas undoubtedly would warrant further subdivision, given additional knowledge (Loyola et al. 2007). Moreover, ecoregions cannot be conserved in their entirety. Broad-scale area assessments provide frameworks within which finer-scaled options for conservation setting and resource allocation have to be established and analyzed (Brooks et al. 2006; Mace et al. 2007). Because areas differ in quality, identification of a comprehensive set of natural areas, as presented here, is a first step towards an *in-situ*

biodiversity maintenance strategy, which only subtends a much more complex process of policy negotiation and implementation.

Conservation biologists and managers must carefully consider conservation priorities. At present, there are difficult questions not yet contemplated when efforts are focused on hotspots of species richness (Ceballos and Ehrlich 2006). Complementarity among ecoregions will be especially instrumental in making complex judgments about trade-offs between diversity and redundancy at the species level. Here we have analyzed patterns of vertebrate occurrence in Neotropical ecoregions to derive a set of areas that jointly prioritize the conservation of endemic and threatened species for all terrestrial taxa, as well as their total diversity. Most of these areas have critical or vulnerable conservation status and they are only partly congruent with those highlighted in previous analyses (Olson and Dinerstein 2002; Mittermeier et al. 2004). We do not see these results as conflicting. Rather, having been attained by different criteria and procedures, they contribute to a joint framework for the development of national and continental strategies for biodiversity conservation, adding to burgeoning initiatives to plan the application of finite funds and efforts where they will be most effective.

ACKNOWLEDGEMENTS

We thank J.F. Lamoreux, J.A.F. Diniz-Filho, and R. Dirzo for providing suggestions for this manuscript. J. Daltio wrote the computer program for complementarity analyses. R.D.L. and U.K. were supported by CNPq (140267/2005-0) and CAPES, respectively. T.M.L. was funded by FAPESP (04/15482-1) and CNPq (306049/2004-0).

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Table 1. Terrestrial vertebrate class richness, endemism and threat within all Neotropical ecoregions, and percentage of representation of those included in our priority set and its core subset (see Fig. 4).

	All ecoregions (n = 179)			Priority set (n = 49)			Core subset (n = 11)		
	Total	Endemic	Threatened	Total	Endemic	Threatened	Total	Endemic	Threatened
Amphibians	2322	943	780	93 %	89 %	91 %	44 %	23 %	32 %
Reptiles	2557	745	68	87 %	78 %	81 %	51 %	32 %	54 %
Birds	3890	503	380	91 %	77 %	76 %	62 %	29 %	39 %
Mammals	1282	113	209	91 %	63 %	89 %	65 %	29 %	55 %
Four classes	10051	2304	1427	90 %	82 %	86 %	55 %	27 %	38 %

Table 2. Key ecoregion set (n = 49) that should be considered in terrestrial vertebrate conservation strategies in the Neotropics. Ecoregion codes and names follow the WWF scheme (see WWF, 2006).

Ecoregion code	Ecoregion name	Conservation status	Area (Km²)
NT0103	Bahia coastal forests	Critical / Endangered	42,400
NT0105	Bolivian yungas	Vulnerable	34,900
NT0109	Cauca Valley montane forests	Critical / Endangered	12,400
NT0115	Chocó-Darién moist forests	Relatively stable / Intact	73,600
NT0117	Cordillera La Costa montane forests	Vulnerable	14,300
NT0118	Cordillera Oriental montane forests	Vulnerable	67,900
NT0119	Costa Rican seasonal moist forests	Critical / Endangered	10,700
NT0120	Cuban moist forests	Vulnerable	21,400
NT0121	Eastern Cordillera real montane forests	Vulnerable	102,500
NT0124	Guayanan Highlands moist forests	Relatively stable / Intact	337,600
NT0125	Guianan moist forests	Relatively stable / Intact	512,900
NT0127	Hispaniolan moist forests	Critical / Endangered	46,000
NT0129	Isthmian-Atlantic moist forests	Vulnerable	58,900
NT0130	Isthmian-Pacific moist forests	Critical / Endangered	29,300
NT0131	Jamaican moist forests	Critical / Endangered	8,300
NT0136	Magdalena Valley montane forests	Critical / Endangered	105,100
NT0142	Napo moist forests	Vulnerable	251,700
NT0145	Northwestern Andean montane forests	Vulnerable	81,200
NT0150	Paraná-Paraíba interior forests	Critical / Endangered	483,800
NT0153	Peruvian Yungas	Critical / Endangered	186,700
NT0154	Petén-Veracruz moist forests	Critical / Endangered	149,100
NT0159	Santa Marta montane forests	Vulnerable	4,800
NT0160	Serra do Mar coastal forests	Critical / Endangered	104,800
NT0165	Southern Andean Yungas	Vulnerable	61,100
NT0166	Southwest Amazon moist forests	Relatively stable / Intact	749,700

NT0167	Talamancan montane forests	Relatively stable / Intact	16,300
NT0168	Tapajós-Xingu moist forests	Vulnerable	336,600
NT0169	Tepuis	Relatively stable / Intact	48,800
NT0175	Venezuelan Andes montane forests	Vulnerable	29,400
NT0178	Western Ecuador moist forests	Critical / Endangered	34,100
NT0210	Chaco	Vulnerable	609,600
NT0228	Sinaloa dry forests	Critical / Endangered	77,500
NT0230	Southern Pacific dry forests	Critical / Endangered	42,000
NT0303	Central American pine-oak forests	Critical / Endangered	111,400
NT0309	Sierra Madre del Sur pine-oak forests	Critical / Endangered	61,200
NT0310	Trans-Mexican Volcanic Belt pine-oak forests	Critical / Endangered	91,800
NT0404	Valdivian temperate forests	Critical / Endangered	248,100
NT0704	Cerrado	Vulnerable	1,916,900
NT0710	Uruguayan savanna	Critical / Endangered	355,700
NT0805	Patagonian steppe	Critical / Endangered	487,200
NT1002	Central Andean puna	Vulnerable	161,400
NT1003	Central Andean wet puna	Vulnerable	117,300
NT1006	Northern Andean páramo	Relatively stable / Intact	30,000
NT1008	Southern Andean steppe	Relatively stable / Intact	178,200
NT1201	Chilean matorral	Critical / Endangered	148,500
NT1304	Caatinga	Vulnerable	734,400
NT1307	Galápagos Islands xeric scrub	Critical / Endangered	8,000
NT1315	Sechura desert	Vulnerable	184,900
NT1402	Amapá mangroves	Relatively stable / Intact	1,600

Table 3. Core subset of ecoregions (n = 11) that should be considered in terrestrial vertebrate conservation strategies in the Neotropics.

BH = Biodiversity Hotspots, G200 = Global 200.

Ecoregion code	Ecoregion name	Conservation status	BH?	G200?	Area (km²)
NT0115	Chocó-Darién moist forests	Relatively stable / Intact	Y	N	73,600
NT0117	Cordillera La Costa montane forests	Vulnerable	Y	N	14,300
NT0118	Cordillera Oriental montane forests	Vulnerable	Y	N	67,900
NT0153	Peruvian Yungas	Critical / Endangered	N	Y	186,700
NT0154	Petén-Veracruz moist forests	Critical / Endangered	Y	N	149,100
NT0160	Serra do Mar coastal forests	Critical / Endangered	Y	Y	104,800
NT0167	Talamancan montane forests	Relatively stable / Intact	Y	Y	16,300
NT0310	Trans-Mexican Volcanic Belt pine-oak forests	Critical / Endangered	Y	N	91,800
NT0704	Cerrado (Brazilian woodland savanna)	Vulnerable	Y	Y	1,916,900
NT0805	Patagonian steppe	Critical / Endangered	N	Y	487,200
NT1402	Amapá mangroves	Relatively stable / Intact	N	Y	1,600

FIGURE LEGENDS

Figure 1. Relation between conservation target (percent of terrestrial vertebrate species representation in the Neotropics) and the cumulative number of ecoregions and their associated area required to attain that representation target. The shape of the curve indicates the marginal value of altering the species representation threshold and hence requiring more area as a conservation priority. Note that beyond 80% of species representation, increasing the conservation target a major increase in total area coverage.

Figure 2. Spatial patterns of terrestrial vertebrate species richness across Neotropical ecoregions (A), and spatial patterns of irreplaceability estimated by the frequency of ecoregions in the 100 optimal solutions obtained with all terrestrial vertebrate species (B), endemic species (C), and threatened species (D) found in the Neotropics.

Figure 3. Priority ecoregion sets for each attribute of Neotropical terrestrial vertebrate diversity. A-C – minimum set necessary to represent at least 80% of all vertebrate species (blue, $n = 25$, A), all endemic species (yellow, $n = 37$, B), and all threatened species (red, $n = 29$, C).

Figure 4. Neotropical priority ecoregion set ($n = 49$) proposed for conserving at least 80% of all terrestrial vertebrates, including those endemics and threatened of extinction. Priority sets for total, endemic, and threatened species are represented respectively in blue, yellow and red. Combinations of priorities between aspects of vertebrate diversity are represented by intermediate colors (green fill for ecoregions of high importance both for total and endemic richness, orange for both endemic and threatened sets, and violet for both total and threatened sets). Congruence among all three diversity aspects - the core ecoregion subset ($n = 11$) - is represented in black.

Figure 5. Distribution of species-representation values obtained by 10,000 random sets of ecoregions resampled with (A) 49 ecoregions (mean value = 45%, highest value = 63%, value attained by our key ecoregion set = 86%), and (B) 11 ecoregions (mean value = 15%, highest value = 32%, value attained by our key ecoregion set = 38%).

Figure 1

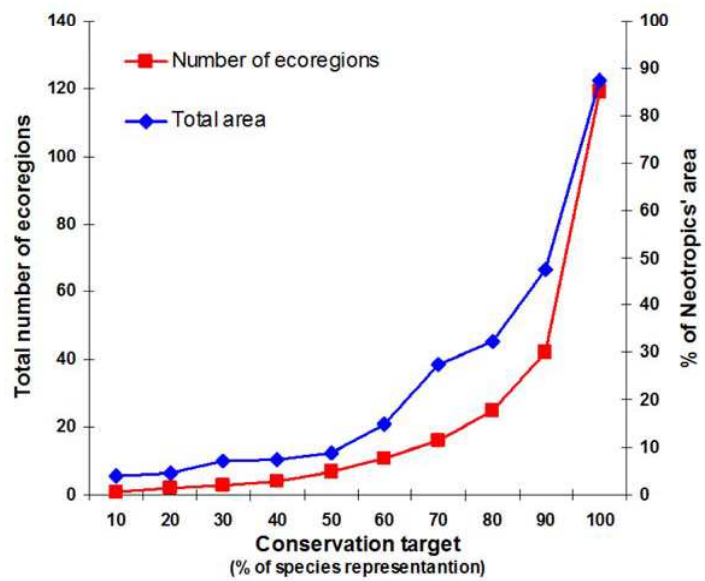


Figure 2

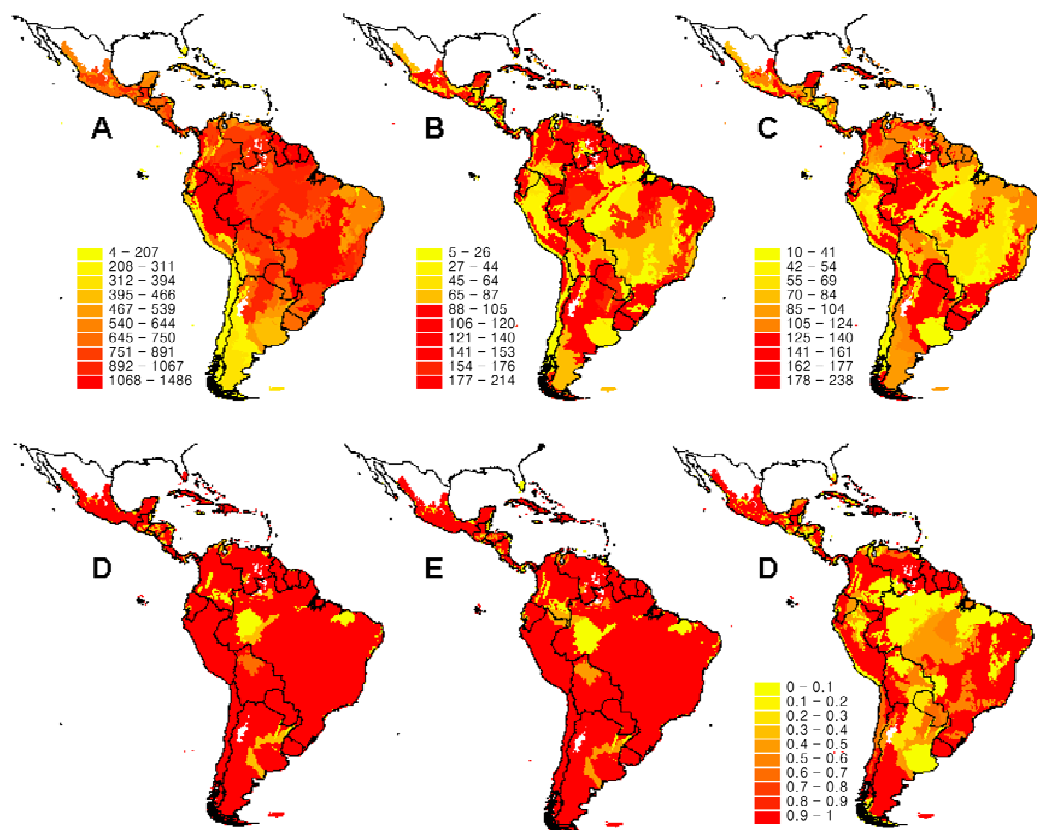


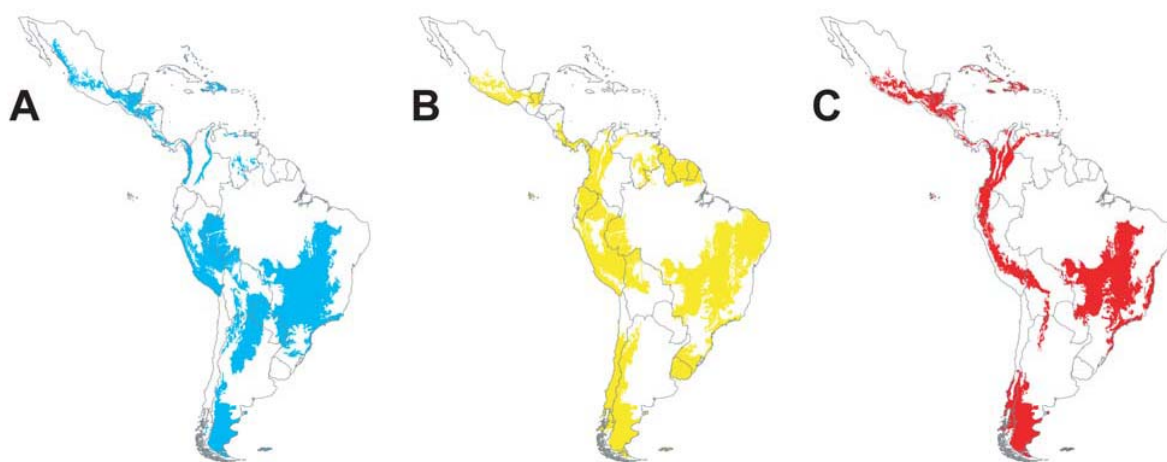
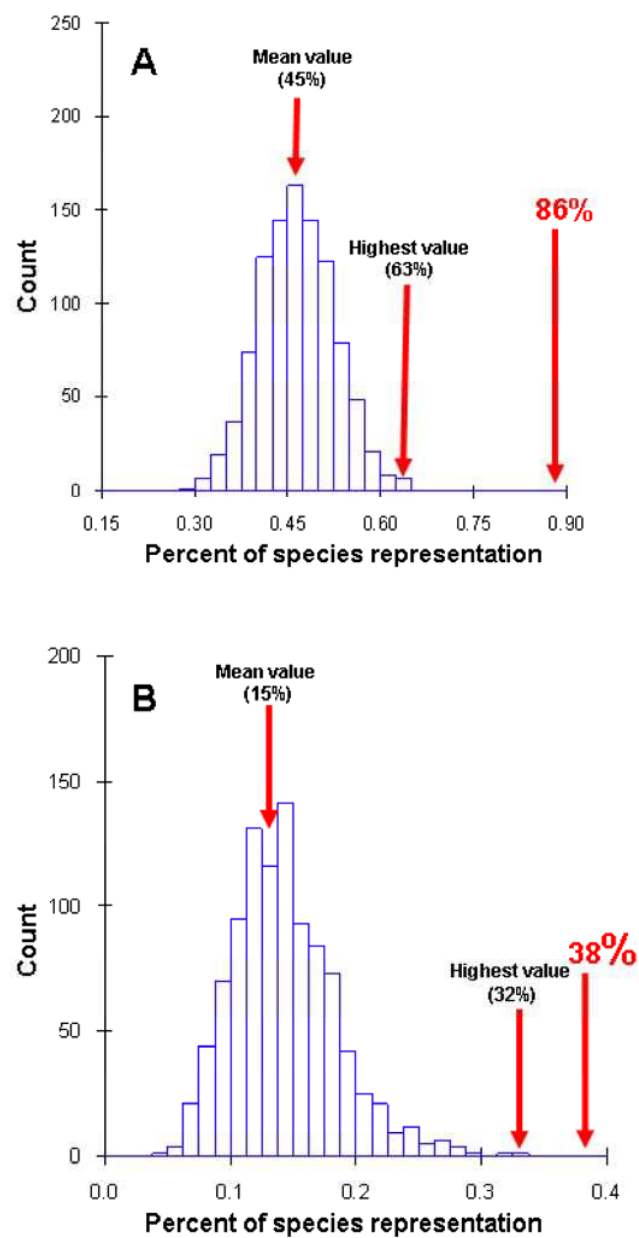
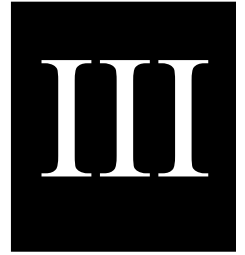
Figure 3

Figure 4

Figure 5





Loyola RD, Becker CG, Kubota U, Haddad CFB, Fonseca CR & Lewinsohn TM (2008). **Hung out to dry: choice of priority ecoregions for conserving threatened Neotropical anurans depends on life-history traits.** *PLoS ONE*, 3(5): e2120.

Hung Out to Dry: Choice of Priority Ecoregions for Conserving Threatened Neotropical Anurans Depends on Life-History Traits

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Abstract

Background: In the Neotropics, nearly 35% of amphibian species are threatened by habitat loss, habitat fragmentation, and habitat split; anuran species with different developmental modes respond to habitat disturbance in different ways. This entails broad-scale strategies for conserving biodiversity and advocates for the identification of high conservation-value regions that are significant in a global or continental context and that could underpin more detailed conservation assessments towards such areas.

Methodology/Principal Findings: We identified key ecoregion sets for anuran conservation using an algorithm that favors complementarity (beta-diversity) among ecoregions. Using the WWF's Wildfinder database, which encompasses 700 threatened anuran species in 119 Neotropical ecoregions, we separated species into those with aquatic larvae (AL) or terrestrial development (TD), as this life-history trait affects their response to habitat disturbance. The conservation target of 100% of species representation was attained with a set of 66 ecoregions. Among these, 30 were classified as priority both for species with AL and TD, 26 were priority exclusively for species with AL, and 10 for species with TD only. Priority ecoregions for both developmental modes are concentrated in the Andes and in Mesoamerica. Ecoregions important for conserving species with AL are widely distributed across the Neotropics. When anuran life histories were ignored, species with AL were always underrepresented in priority sets.

Conclusions/Significance: The inclusion of anuran developmental modes in prioritization analyses resulted in more comprehensive coverage of priority ecoregions—especially those essential for species that require an aquatic habitat for their reproduction—when compared to usual analyses that do not consider this life-history trait. This is the first appraisal of the most important regions for conservation of threatened Neotropical anurans. It is also a first endeavor including anuran life-history traits in priority area-selection for conservation, with a clear gain in comprehensiveness of the selection process.

Citation: Loyola RD, Becker CG, Kubota U, Haddad CFB, Fonseca CR, et al. (2008) Hung Out to Dry: Choice of Priority Ecoregions for Conserving Threatened Neotropical Anurans Depends on Life-History Traits. PLoS ONE 3(5): e2120. doi:10.1371/journal.pone.0002120

Editor: Wayne M. Getz, University of California, Berkeley, United States of America

Received: December 14, 2007; **Accepted:** April 7, 2008; **Published:** May 7, 2008

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Funding: RDL, CGB and UK were supported by CNPq (140267/2005-0), FAPESP (04/13132-3) and CAPES, respectively. CFBH thanks FAPESP and CNPq (302512/2005-5) for financial support. CRF is supported by CNPq (305428/2005-5). TML was funded by FAPESP (04/15482-1) and CNPq (306049/2004-0). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Amphibian populations are declining worldwide and this is causing growing concern [1,2]. As a group they are also extremely endangered. Of the 6,184 extant amphibian species [3], nearly one-third is globally threatened [4]. In the Neotropics, about 35% of anuran species were classified by The World Conservation Union (IUCN) as “critically endangered”, “endangered” or “vulnerable”. If we add species considered to be “near threatened” the percentage of threatened amphibians increases to 41%. Furthermore, relative to other animal groups, an outstandingly high proportion of amphibians are in higher threat categories [4]. These high threats at the population and species level demand effective strategies to devise conservation efforts for amphibians worldwide.

Among the leading factors that threaten amphibians, habitat loss, habitat fragmentation, and habitat split are the most important and, perhaps, the major causes of species' extinction in general [1,4–6]. Recently, many studies have focused on the widespread distribution of chytridiomycosis (an infection caused by the fungus *Batrachochytrium dendrobatidis*), currently considered to be the main cause of amphibian population declines in undisturbed areas [2,5,7–9]. In these studies, the pathogen primarily affected species with an aquatic larval stage such as stream- and pond-breeders, whereas most species with terrestrial development (i.e., species whose development can be completed outside water bodies) were less affected.

Anuran species with different developmental modes of reproduction respond to habitat disturbance in different ways [6,10–13]. Species with aquatic larvae are expected to suffer mainly with

habitat split, as the disconnection between suitable aquatic and terrestrial habitats forces this group to perform compulsory breeding migrations through unfamiliar hostile habitats [6]. On the other hand, species with terrestrial development are expected to suffer mainly with habitat loss and fragmentation, as their life cycle depends particularly on the integrity and connection of vegetation remnants. Therefore, the effect of habitat changes on species with different developmental modes depends on their particular life-history traits, such as migration patterns, habitat use and ability to cope with biotic and abiotic microhabitat changes caused by disturbances [6,14,15]. For this reason, species with different life-history traits require distinct conservation strategies to be effectively protected, and therefore, the inclusion of ecological traits (e.g. reproductive modes, extinction risk) in conservation assessments and planning helps to improve reserve networks and to increase the effectiveness of proposed priority sets see [16].

Insufficient information for targeting conservation efforts is a major obstacle to the conservation of tropical biodiversity [17,18]. As a result, the initial goal of large-scale strategies for conserving biodiversity is to identify regions of high conservation value that are significant in a global or continental context and then direct more detailed conservation assessments towards such areas [19,20]. The most important criterion for locating and designing reserve systems should be to achieve maximum representation of biodiversity with the smallest possible cost [21,22]. Several algorithms have been developed to create a reserve system that maximizes the representation of biodiversity in a region see [23]. Currently, one of the most efficient ways to decide which set of areas comprises the most inclusive representation of species for a particular region is through interactive site-selection heuristic or optimal algorithms based on complementarity [24–27].

In this paper we used the WWF's Wildfinder database [28], which encompasses 700 threatened anuran species in the 119 Neotropical Ecoregions, to identify minimum ecoregion sets that should be sufficiently covered in a reserve system to represent all threatened Neotropical anurans of each developmental mode (i.e. the aquatic larvae species and the terrestrial development species). We also compared the effectiveness of priority sets in representing species of different developmental modes when species subsets are treated separately according to this life-history trait, and when they are all considered together. Finally, we discuss how the inclusion of species biological traits such as life-history traits can enhance prioritization exercises for biodiversity conservation.

Results

Patterns of species richness and irreplaceability

Threatened anuran species are concentrated in southern Mexico, the tropical Andes, and rainforests of Colombia and Venezuela (Figure 1A). Other ecoregions with high levels of species threat are found in the Caribbean Islands (Figure 1A).

We found that 50 ecoregions were included in all 100 optimal sets necessary to represent each species with aquatic larvae at least once (Figure 1B). These areas of high irreplaceability are concentrated in Mexico, Central America, the Tropical Andes, southern South America, and eastern Brazil (Figure 1B). Some ecoregions—such as the Atlantic moist forests from Brazil, other areas in Mexico and the Caribbean Islands—figured in at least 50% of all optimal sets (Figure 1B). On the other hand, only 34 ecoregions were included in all 100 optimal sets necessary to represent each species with terrestrial development at least once (Figure 1C). These ecoregions are located in Mexico, Costa Rica (the Talamancan montane forests), the Tropical Andes, Chile and Brazil (Figure 1C).

Minimum sets of ecoregions for species representation in each developmental mode

The application of the simulated-annealing algorithm on the species occurrence matrix revealed that a key ecoregion set of 66 ecoregions must be sufficiently covered in a reserve system, in order to represent all threatened anuran species in the Neotropics (Figure 1D, Table S1). Among these ecoregions, 30 were classified as priority for all species, 26 ecoregions were of high priority exclusively for species with aquatic larvae, and 10 ecoregions only for species with terrestrial development (Figure 1D, Table S1). The total amount of land area covered by our combined priority set spans almost 33% of the entire Neotropical region, of which *ca.* 22%, 1%, and 11% correspond to key ecoregion sets for species with aquatic larvae, terrestrial development or both developmental modes, respectively (Table S1). Key ecoregions for both developmental modes or only for terrestrial development species are highly concentrated in the Andes and more widespread across Mesoamerica (Figures 1D and 2A–C). Conversely, ecoregions particularly important for preserving threatened aquatic larvae species are widely distributed across the Neotropics, including important southern non-forest areas such as the Patagonian steppe and the Argentine Espinal (see Figures 1 and 2A–C).

Analyses that separated anurans according to their developmental modes resulted in more comprehensive priority sets (Figure 2); with more species represented from either group (Table 1). Species with aquatic larvae are increasingly underrepresented when conservation targets are progressively lowered from 95 to 70% in analyses that do not discriminate developmental modes; moreover, species with aquatic larvae never attain the intended conservation target, and ecoregions excluded from priority sets were mainly those important for this species group (Tables 1 and S2; Figure 2D–F). When analyzed separately, the percentage of species with aquatic larvae represented is closer to those with terrestrial development, though always lower than the latter (Table 1; Figure 2D–F).

Priority ecoregions with conservation status defined as “critical/endangered” harbor the majority of threatened Neotropical anurans; however, threatened species which are endemic to a given ecoregion are mostly found in “vulnerable” ecoregions (Figure 3A, Table S1). Stable and vulnerable ecoregions have also greater variation in the number of threatened species when compared with critical ones (Figure 3B, Table S1).

Discussion

Optimal complementarity solutions based on biodiversity analyses have been successful in defining worldwide conservation networks [29], including those for anuran species [30]. Our analyses show that conservation efforts for threatened anurans in the Neotropics should be concentrated in a key set of 66 ecoregions, if all species with aquatic larvae or terrestrial development are meant to be represented. Patterns of geographic distribution of all amphibian species are not necessarily congruent with the distribution of threatened amphibian species [31]; hence our analysis cannot predict how effective the present priority sets will be in representing non-threatened anurans. This issue, although undoubtedly relevant, is beyond the scope of this paper—even though areas highlighted in this study are among the top β -diversity areas for amphibians in the Western Hemisphere [32].

Currently, most priority-setting assessments employ equal-area grids, and a number of effective tools have been developed for that purpose. These procedures are especially useful at smaller spatial scales, since they require a high density and coverage of records

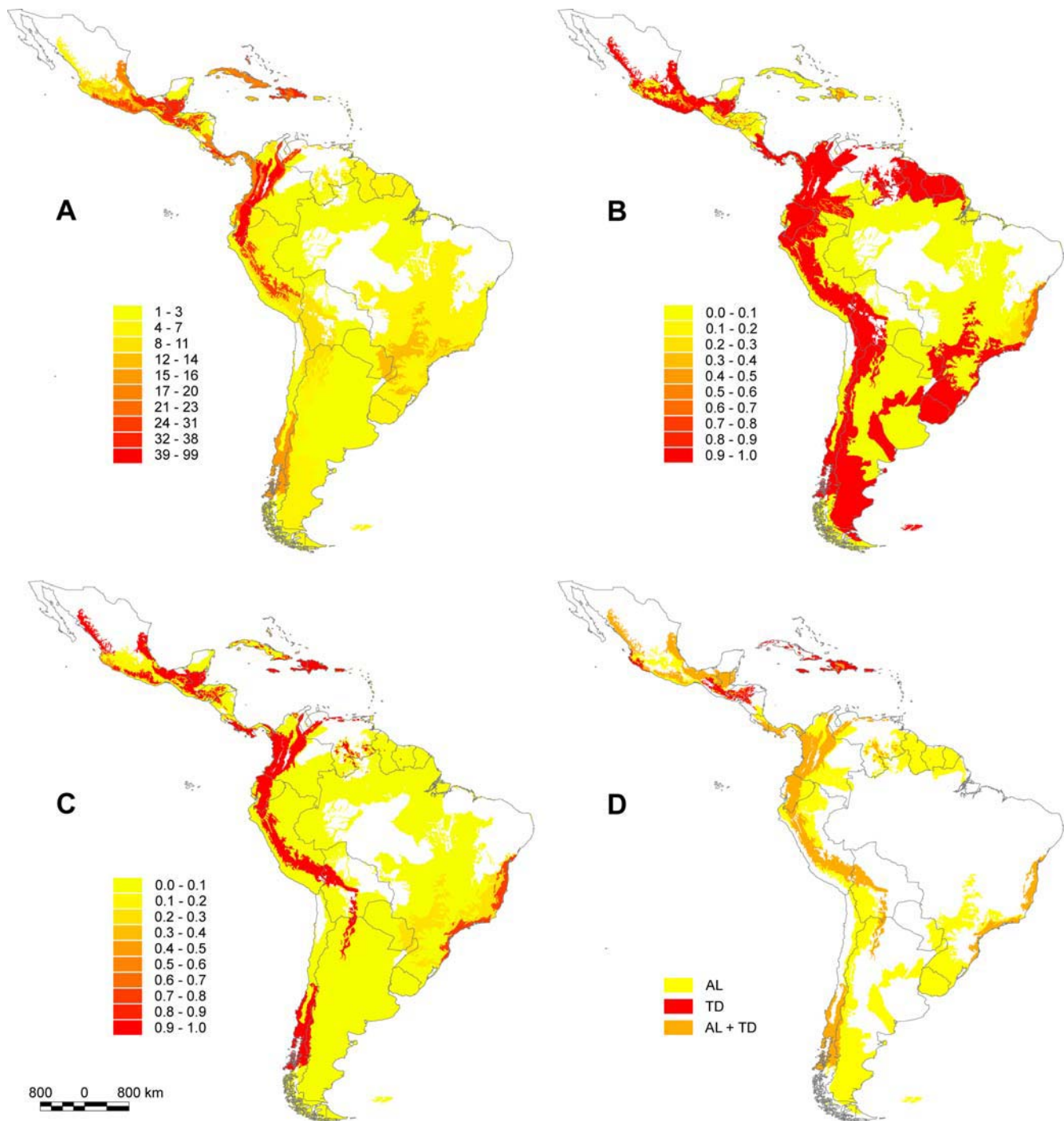


Figure 1. Pattern of species richness, irreplaceability and minimum ecoregion sets for representing threatened Neotropical anurans. Spatial patterns of threatened anuran species richness across Neotropical ecoregions (A) and spatial patterns of irreplaceability estimated by the frequency of ecoregions in the 100 optimal solutions obtained with all threatened anuran species with aquatic larvae (B) and terrestrial development (C) found in the Neotropics. Map showing minimum ecoregion sets ($n=66$ ecoregions) required for representation of all threatened anuran species with different developmental modes (D), both those with aquatic larvae (AL=yellow, $n=26$ ecoregions) and those with terrestrial development (TD=red, $n=10$ ecoregions). Ecoregions of high importance for species of both developmental modes (AL+TD, $n=50$ ecoregions) are represented in orange.

doi:10.1371/journal.pone.0002120.g001

across grid units [33]. However, species records in the Neotropical region are fairly sparse and highly uneven, so that common grid-based analyses are less effective at the continental scale [34]. To a certain extent, the lack of field records may be overcome by summing expected distributions of species obtained through

modeling [35]. Here, we chose to use ecoregions because these broad areas are defined according to physiographic and biotic features, and therefore should reflect zoogeographic boundaries more closely. They are also less sensitive to heterogeneity in distribution data than grid-based analyses [33] and are gaining

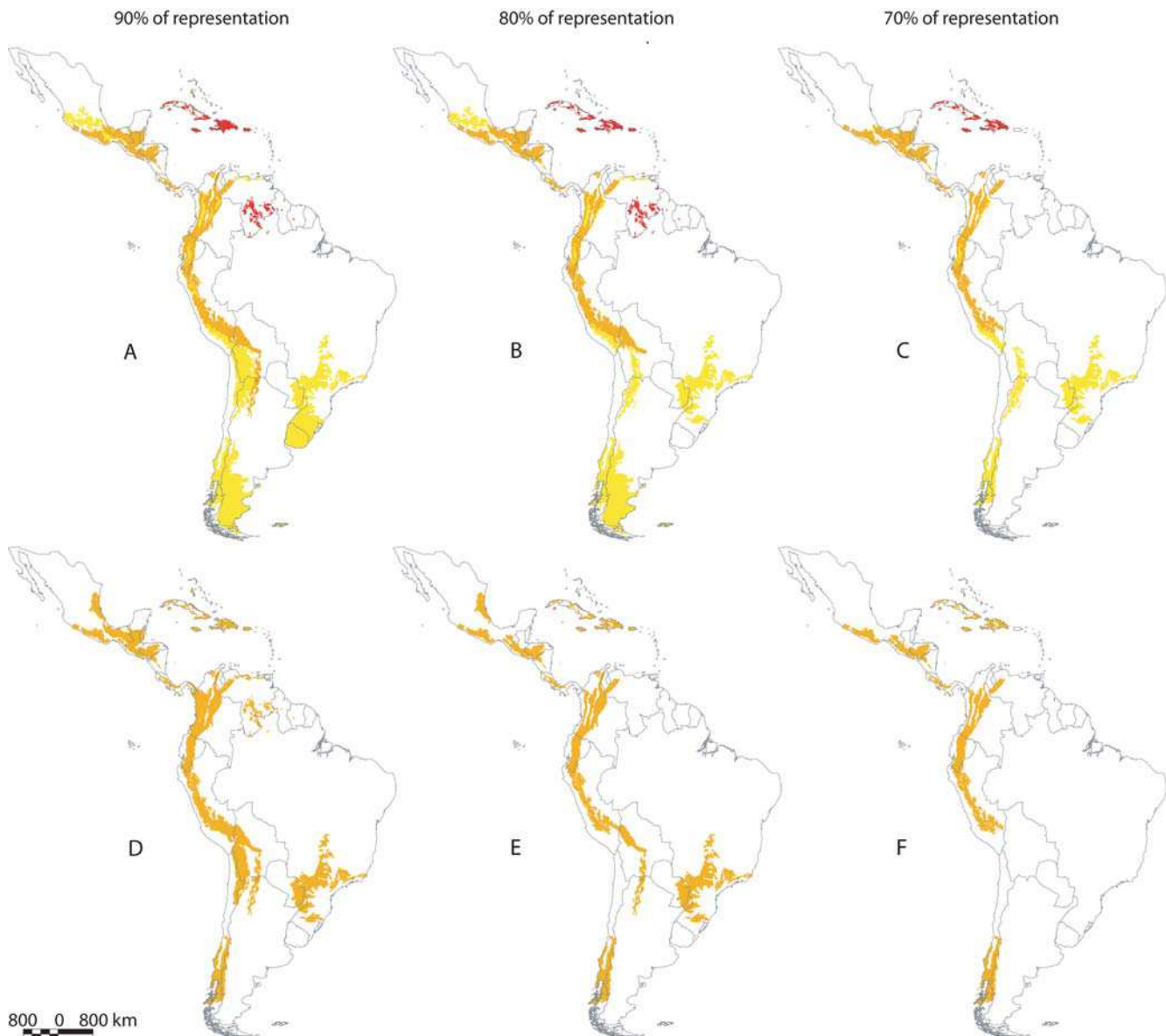


Figure 2. Key ecoregion sets for threatened Neotropical anurans obtained with or without discriminating species according to their developmental modes. (A–C) Maps showing the minimum ecoregion sets required for representation of species with different developmental modes, both those with aquatic larvae (AL = yellow) and those with terrestrial development (TD = red) at different cutoff levels of species representation (95, 80, and 70%). Ecoregions of high priority for species of both developmental modes (AL+TD) are represented in orange. (E–G) Maps show minimum ecoregion sets required for representation of anuran species at different cutoff levels of species representation (95, 80, and 70%).

doi:10.1371/journal.pone.0002120.g002

support of major conservation organizations as well as of many government agencies (see also Materials and Methods).

The incorporation of developmental modes improved the comprehensiveness of minimum ecoregion sets. The strong species turnover in the Andes and Mesoamerica is primarily related to their high habitat heterogeneity, corresponding to an exceptional topographic variability found in these regions [32]. This favored the representation of Andean and Mesoamerican ecoregions; since our algorithm is based on complementarity, ecoregions that share few species will always be more complementary [25]. In fact, the complex topography and variety of environments mostly resulting from early tectonic events and climatic fluctuations in the Pleistocene and continuing to the present provide an array of habitats for an Andean herpetofauna that is more diverse than one

might expect [36]. These geomorphological events probably are also responsible for generating high vertebrate β -diversity among ecoregions in Brazil [18], which harbors the richest amphibian fauna in the Neotropics [37].

Although the topographic history accounts for our priority set configuration, the high representation of threatened anurans in these regions can be further explained by other ecological phenomena. Wavy relief areas prevalent in Andean ecoregions have topographic features that favor the spatial separation between water sources and the remnants of natural vegetation cover. Natural remnants usually are concentrated in areas less suitable for agriculture, such as steeper slopes and hilltops [38,39]. Anuran life-history traits entails not only particular habitat requirements, but also influences the landscape habitat use by

Table 1. Representation of threatened Neotropical anurans in priority sets of ecoregions attained under different conservation targets.

Conservation target	Without discriminating anuran developmental modes			Discriminating anuran developmental modes		
	Number of ecoregions	AL	TD	Number of ecoregions	AL	TD
95% of representation	37	91%	98%	44	95%	97%
90% of representation	29	84%	96%	36	91%	97%
80% of representation	20	74%	87%	25	82%	89%
70% of representation	13	61%	77%	17	71%	81%

Number of ecoregions included in priority sets and percentage of representation of threatened Neotropical anuran species with different developmental modes attained in priority ecoregion-setting exercises, when species were discriminated according to this life-history trait (right columns) or not (left columns). Rows show progressively decreasing conservation targets. AL = species with aquatic larvae; TD = species with terrestrial development. Bold numbers show instances where the intended conservation target is not attained.

doi:10.1371/journal.pone.0002120.t001

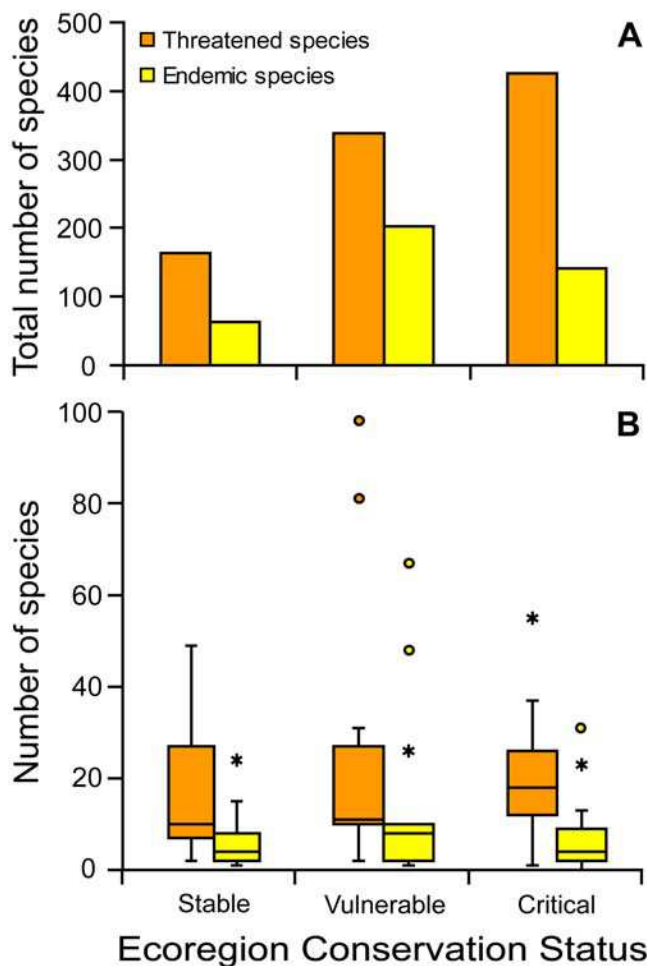


Figure 3. Conservation status of key ecoregions for the conservation of threatened Neotropical anurans. (A) Numbers of endemic and threatened species of Neotropical anurans found in ecoregions classified as Stable/Intact, Vulnerable or Critical/Endangered, according to [28]. (B) Distribution of the number of species found in ecoregions classified as Stable/Intact, Vulnerable or Critical/Endangered, according to [28]. Box plots indicate the range of the data between brackets, the middle two quartiles within the box, the median value as the midline, outside (+) and far outside (–) values.

doi:10.1371/journal.pone.0002120.g003

each group, making species with aquatic larvae more liable to disappear from ecoregions whose terrestrial and aquatic breeding sites are more disjunct [6,40–42]. It may be no coincidence that we observed higher counts of declining and threatened amphibians in these ecoregions [8], where the enforcement of laws that protect riparian vegetation thus becomes especially critical. Furthermore, high infection rates by chytridiomycosis in many Andean and Mesoamerican areas relatively protected from human influence strongly contribute to such a pattern [2,43]. Another factor which may account for this pattern is the distinct historical dispersal of anurans with aquatic larvae or terrestrial development [8,9,13]. Species with aquatic larvae disperse mainly through riverflows. Hence, these species could become widespread across many areas, suffering fewer chorographic restrictions than species with terrestrial development, which should tend to be confined in certain sites, increasing β -diversity at a regional scale. If so, this could also explain why Andean ecoregions, along with those found in tropical forests of Mesoamerica, were highly represented in our priority sets, and reinforces the separation of anurans according to their developmental modes [6,44]. Note, however, that geographic range (expressed as number of ecoregions) is not significantly different between species with aquatic larvae and terrestrial development.

Our priority sets are congruent with important areas indicated for the conservation of amphibians, as well as other vertebrates, derived from regional [45–47] and continental studies [5,32,48,49]. Such congruence is especially high in the Andes and in Mesoamerica, where altitudinal range seems to play the most important role in driving high levels of amphibian species richness, endemism and threat [32,47]. Our results suggest that, for the most part, ecoregions valuable for conserving species with terrestrial development have experienced severe habitat reduction, mainly driven by livestock grazing and agricultural expansion [28]. On the other hand, the priority set for conserving species with aquatic larvae includes ecoregions whose water sources are severely impacted (e.g. large parts of the Andes, Central America, and some dry lands [28]). These ecoregions have lost their natural habitats especially in the most accessible and irrigated areas for agriculture, whereas drier ecoregions, such as savannas and open formations, are threatened by the introduction of exotic species and agriculture expansion, especially along rivers [28].

Conclusions

To sum up, our results highlight sets of areas of particular interest for the conservation of threatened Neotropical anurans. The inclusion of anuran developmental modes in prioritization analyses resulted in a more comprehensive coverage of priority

ecoregions—especially those essential for species that require an aquatic habitat for their reproduction—when compared to usual analyses that do not factor in life-history traits. Moreover, if such life-history traits are not taken into consideration, priority area-setting exercises tend to favor species with terrestrial development. This result is particularly important because several recent reports of population declines worldwide pointed to higher suppression rates in populations of species with aquatic larvae [6,8,9,44]. We propose that, whenever feasible, conservation assessments should include key life-history traits in order to improve reserve networks and thus to increase the effectiveness of proposed priority sets see [16]. Because areas differ in quality, identification of a comprehensive set of natural areas, as presented here, is a first step towards an *in-situ* biodiversity maintenance strategy, which only subtends a much more complex process of policy negotiation and implementation. Complementarity among ecoregions will be especially instrumental in making complex judgments about trade-offs between diversity and redundancy at the anuran species level.

Materials and Methods

Study site

We focused our analyses to all the 119 terrestrial ecoregions of the Neotropics because it harbors a highly diverse amphibian fauna, representing half of the world's total species richness [5], and is one of the tropical regions in which amphibian population declines and species extinction are extremely elevated [4,5,44]. Although there are several classifications of Latin America biogeographical regions, we follow the WWF hierarchical classification of ecoregions [28,50]. Conservation assessments within the framework of larger biogeographical units are gaining support of major conservation organizations as well as of many government agencies see [50]. Given that most conservation decisions and policies have to be met within national boundaries, ecoregions may correspond roughly to the largest operational units at which decisions can actually be taken and implemented [18], although the implementation of Conservation Area Network must be produced at smaller spatial scales such as State or Municipality.

Data

The database used for the analyses contains the current species list of 1,970 anurans in the 179 Neotropical ecoregions [28]. We tallied the presence or absence of 700 threatened anuran species which occur in 119 terrestrial ecoregions of the Neotropics. Threatened species were those classified by the 2006 IUCN Red List as “critically endangered”, “endangered” or “vulnerable”. We had to exclude 208 threatened species from the analyses because they were not assigned to ecoregions in the available database. Information on updates, detailed descriptions of the process, and complete lists of sources can be obtained from the Web site indicated by [28]. Note that these datasets are periodically updated, and the files used in our analyses may differ from the most recent versions available from [4,28]. We focused our analyses on threatened Neotropical anurans. The number of species in this vertebrate group is not static, as new species continue to be discovered [37,51]. However, the areas from which species are most often described tend to be the same and will likely accentuate the patterns we present [51]. Systematic bias in the data may arise from differences in sampling efforts, as the distribution of amphibians or geographic areas (e.g. Central American ecoregions) for which sampling efforts have been more intense will be more reliable than those that are undersampled. As a safety measure against such biases, we excluded from the analyses anuran species with an IUCN Red List category of “data

deficient” [4] because of the unreliability of their range maps, and therefore, their occurrence in the studied ecoregions.

Analyses

In order to identify key ecoregion sets for anuran conservation, we grouped species by their developmental mode, either with aquatic larvae ($n = 336$ species) or terrestrial development ($n = 364$ species). The determination of each developmental mode was based on the 31 reproductive modes of Neotropical anurans recognized by [52]. Species with reproductive modes that do not require aquatic habitats for their development were classified as species with terrestrial development, whereas species that do require an aquatic habitat for larval development were classified as species with aquatic larvae.

We used an optimization procedure to select the minimum number of ecoregions necessary to represent all species at least once, based on the complementarity concept [24–27]. For each anuran subset (i.e. species with aquatic larvae or terrestrial development), we ran a simulated annealing procedure in the Site Selection Mode (SSM) routine of the SITES software program [53–54] to find these combinations of ecoregions. We set the analyses parameters to 100 runs and 20 million iterations. We also set a relatively high penalty value for losing a species, so that every solution represented all species with a minimum number of ecoregions. Because there are frequently multiple combinations of ecoregions that satisfy this representation goal in each conservation scenario, we combined alternative solutions into a map in which the relative importance of each ecoregion is indicated by its rate of recurrence in optimal subsets (see Fig. 1B–C). This is also an estimate of the irreplaceability of ecoregions [55], ranging from 0.0 (minimum irreplaceability) to 1.0 (maximum irreplaceability) see [56].

This algorithm represents one possible solution to a problem known as the reserve site selection problem [29], which can be represented formally as follows:

maximize

$$\sum_{i \in I} i^y_i \quad (1)$$

subject to

$$\sum_{j \in N_i} x_j \geq y_i \quad \text{for all } i \in I \quad (2)$$

$$\sum_{j \in J} x_j \leq k \quad (3)$$

$$y_i = (0,1) \quad \text{for all } i \in I \quad (4)$$

$$x_j = (0,1) \quad \text{for all } j \in J, \quad (5)$$

where $J = \{j | j = 1, \dots, n\}$ denotes the index set of candidate ecoregions from which to select, and $I = \{i | i = 1, \dots, m\}$ denotes the set of the species to be covered. The set N_i , a subset of J , is the set of candidate ecoregions that contain species i . The variable $x_j = 1$ if ecoregion j is selected, 0 if ecoregion j is not selected. Constraint (3) limits the total number of ecoregions selected to no more than k . The variable y_i will be 1 except when $x_j = 0$ for all j in N_i (since constraint (2) will force $y_i = 0$ in that case)—i.e., constraint (2) enforces that the species not be counted as preserved if none of its ecoregions is selected [29].

The algorithm we used—which is driven by patterns of β -diversity—has been considered one of the most efficient approaches to define priority area sets for species conservation [24–27,29], because including patterns of β -diversity in area selection algorithms captures variation in species communities, helping to maintain ecological and evolutionary processes in addition to underlying environmental heterogeneity necessary for long-standing persistence [32].

Ecoregions highlighted in our analyses were designated as the highest priority set. Minimum sets obtained from these analyses were drawn on a map of Neotropical ecoregions, as defined by [50], using ArcView GIS 3.2 (ESRI, Redmond, California). Shapefiles and associated attribute tables were obtained from [28]. Maps were combined to reveal the minimum set of ecoregions that should be included in a reserve system in order to represent all of anurans with aquatic larvae and of those with terrestrial development. We employed an equal-area cylindrical projection in all maps.

Finally, we compared the total coverage of species with aquatic larvae or terrestrial development in priority sets produced with different conservation targets (95, 90, 80 and 70% of threatened anuran representation). The analyses were repeated with and without discrimination for anuran developmental modes. Maps showing the minimum set of ecoregions obtained in each of these conservation targets were also produced as described above.

Supporting Information

Table S1 Priority ecoregion sets for threatened Neotropical anurans with terrestrial development and aquatic larvae. Key

ecoregion set ($n = 66$) proposed for representing all threatened Neotropical anuran species with different developmental modes (AL = aquatic larvae, TD = terrestrial development). Numbers in parentheses represent endemic species. Ecoregion conservation status obtained from [28]; threatened species combine those classified in the 2006 IUCN Red List as critically endangered, endangered or vulnerable.

Found at: doi:10.1371/journal.pone.0002120.s001 (0.15 MB DOC)

Table S2 Priority ecoregions included (indicated by x) in priority sets attained with or without discriminating anuran developmental modes under different targets of species representation (90, 80 and 70%). For threatened species richness, numbers in parentheses represent endemic species. Threatened species combine those classified in the IUCN 2006 Red List as critically endangered, endangered or vulnerable.

Found at: doi:10.1371/journal.pone.0002120.s002 (0.12 MB DOC)

Acknowledgments

We thank J. A. F. Diniz-Filho, K. Lips, N. Urbina-Cardona, T. Halliday, D. Green, and two anonymous referees for their comments on the manuscript. Jaude Daltio helped with complementarity analyses.

Author Contributions

Conceived and designed the experiments: RL CB. Analyzed the data: RL UK. Wrote the paper: CH RL TL CB UK CF.

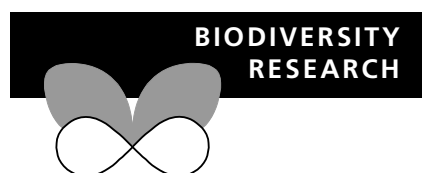
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Loyola RD, Oliveira G, Diniz-Filho JAF & Lewinsohn TM (2008). **Conservation of Neotropical carnivores under different prioritization scenarios: mapping species traits to minimize conservation conflicts.** *Diversity and Distributions*, 14: 949-960.



Conservation of Neotropical carnivores under different prioritization scenarios: mapping species traits to minimize conservation conflicts

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ABSTRACT

Aim To define priority sets of ecoregions that should be sufficiently covered in a reserve system to represent all Neotropical carnivores (Mammalia: Carnivora) under three distinct conservation scenarios.

Location The Neotropical region.

Methods We used broad-scale biogeographical data of species distribution to define priority sets of ecoregions for conservation of carnivores and mapped four species traits (phylogenetic diversity, body size, rarity and extinction risk), which were used as constraints in prioritization analyses, based on the complementarity concept. We proposed three scenarios: a very vulnerable one, one of species persistence and another of lower human impact. We used the simulated annealing algorithm to generate ecoregion-irreplaceability pattern and to find the combinations of ecoregions in each conservation scenario.

Results We found that only 8% of Neotropical ecoregions are needed to represent all 64 carnivore species at least once. Rain forest ecoregions harbour a greater amount of carnivore phylogenetic diversity, whereas the tropical Andes hold large-bodied carnivores. Western and southern Neotropical ecoregions have more rare species as well as higher threat levels. In the lower human-impact set, 12 ecoregions were needed to represent all species. These coincide only partially with those attained by other prioritization scenarios. In the very vulnerable and in the species persistence scenario, 14 and 12 ecoregions were represented, respectively, and the congruence between either one and the lower human-impact set was fairly low. Shared ecoregions are located in Mexico, Costa Rica, northern Amazon and western Chile.

Main conclusions Our results highlight areas of particular interest for the conservation of Neotropical carnivores. The inclusion of evolutionary and ecological traits in conservation assessments and planning helps to improve reserve networks and therefore to increase the effectiveness of proposed priority sets. We suggest that conservation action in the highlighted areas is likely to yield the best return of investments at the ecoregion scale.

Keywords

Complementarity, conservation planning, ecoregions, irreplaceability, phylogenetic diversity, prioritization.

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INTRODUCTION

Biodiversity loss is a well-recognized broad-scale phenomenon that forces conservation decisions to be taken at an international level (Cardillo *et al.*, 2006). However, as global actions are

extremely difficult, prioritization is unavoidable. Given this need, conservation assessment and planning aim to optimize the allocation of scarce conservation funding by prioritizing areas for protection (Margules & Pressey, 2000). This approach has been increasingly applied at regional (e.g. Cowling *et al.*, 2003;

Kerley *et al.*, 2003; Smith *et al.*, 2006), continental (e.g. Dinerstein, 1995; Moore *et al.*, 2003; Burges, 2004; Loyola *et al.*, 2008) and global scales (e.g. Mittermeier *et al.*, 2004; Olson & Dinerstein, 2002; Grenyer *et al.*, 2006). Prioritization exercises for species conservation usually emphasize areas with the highest species richness and endemism where many species are thought to be at imminent risk of extinction, or where habitat loss has already occurred (Stattersfield *et al.*, 1998; Olson & Dinerstein, 2002; Mittermeier *et al.*, 2004; Cardillo *et al.*, 2006; Grenyer *et al.*, 2006). This is a remedial approach, responding to the need to minimize biodiversity loss in regions where severe human disturbance to natural habitats has already occurred or is taking place (Cardillo *et al.*, 2006). However, because of the high rates of habitat degradation and increase in human impacts, it is equally important to identify areas where disturbances may currently be low, but where the risk of future species loss is high. This can be achieved by including other attributes in the prioritization process such as species ecological traits (e.g. reproductive modes, extinction risk, gestation length) as well as evolutionary traits (e.g. phylogenetic diversity, body size, geographical range size) (Cardillo *et al.*, 2006; Loyola *et al.*, 2008).

Currently, few studies aimed at defining regional or continental priorities for mammals or for a particular subset of species within this group (but see Noss *et al.*, 1996; Ferguson & Larivière, 2002; Ceballos *et al.*, 2005; Valenzuela-Galván *et al.*, 2008). Mammals are an extremely endangered group: around a quarter of extant species are considered to be threatened (Ceballos & Ehrlich, 2002; IUCN, 2007), and such a high level of threat clearly indicates that these vertebrates have been severely affected by the contemporary extinction crisis (Ceballos & Ehrlich, 2002). Among mammals, carnivores are one of the most endangered groups (Valenzuela-Galván *et al.*, 2008). Moreover, they are an excellent group for developing conservation strategies as their biology and phylogeny are well studied, they have a widespread distribution, and they include species at all levels of extinction risk (Cardillo *et al.*, 2004). Carnivores include several major conservation icons, such as the tigers, jaguars and the giant pandas, and many others are considered flagship, umbrella, keystone, and indicator species (Gittleman, 2001). However, the charismatic status of so many mammals and carnivores in particular, entails its own problems. As highlighted by Gittleman *et al.* (2001), carnivore conservation would be more effective if conservation strategies were focused on the prioritization of geographical areas or entire ecological communities, rather than addressing individual species separately. In fact, there has been a shift in the conservation literature from single-species conservation planning toward multispecies or ecosystem conservation planning (e.g. Nicholson & Possingham, 2006; Rodríguez *et al.*, 2007).

The Neotropics harbours a highly diverse vertebrate fauna, and is one of the tropical regions in which mammal population declines and species extinction are extremely elevated (Ceballos *et al.*, 2005; IUCN, 2007). Identifying broad-scale priorities for this realm could represent a significant contribution to carnivore conservation as the establishment of priorities on a regional scale acts as a coarse filter to help to allocate scarce resources for animal conservation (Ginsberg, 2001; Loyola *et al.*, 2007).

In this paper we used broad-scale biogeographical data of carnivore species distribution – occurrence in Neotropical ecoregions, according to WWF (World Wildlife Fund, 2006) – to define priority sets of ecoregions that should be sufficiently covered in a reserve system to represent all Neotropical carnivores. To this end, we developed three scenarios based on the joint mapping of four ecological and evolutionary species traits, which successively (1) identify priority sets of ecoregions that are very vulnerable and need urgent intervention for safeguarding each Neotropical carnivore in at least one ecoregion; (2) establish priority sets that can maximize species persistence; and (3) define priority sets that minimize conservation conflicts by favouring areas with lower levels of human impact. Our conservation goal was to represent every Neotropical carnivore in at least one ecoregion in each of these conservation-planning scenarios – this means that the three scenarios should harbour independently all species found in the Neotropics. These prioritization scenarios were combined to pinpoint where conservation is likely to yield the best return for the investment at the ecoregion scale.

METHODS

Study site

We focused our analyses on the Neotropical region. Although there are several classifications of Latin American biogeographical regions, we follow here the WWF hierarchical classification of ecoregions (Olson *et al.*, 2001; WWF, 2006). Conservation assessments within the framework of larger biogeographical units are gaining support of major conservation organizations as well as of many government agencies (see Olson *et al.*, 2001 and references therein). Given that most conservation decisions and policies have to be met within national boundaries, ecoregions may correspond roughly to the largest operational units at which decisions can actually be taken and applied (Loyola *et al.*, 2007).

Data

The data base used for the analyses (WWF, 2006) contains the current species list of mammals ($n = 1282$) in Neotropical ecoregions. We focused our analyses on the 64 Neotropical carnivore species that occur in this realm (see Table 1), whose occurrence ranges were obtained from Wilson & Reeder (2005). Information on updates, detailed descriptions of the data base, and complete lists of sources can be obtained from the web site indicated by WWF (2006). Note that these data sets are periodically updated, and the files used in our analyses may differ from the most recent versions available from the WWF (2006) and IUCN (2007). For each species, we obtained four variables. First, the relative amount of independent evolutionary history given by the branch length from a species to its most recent common ancestor (hereafter, MRCA). This is a measure of phylogenetic diversity, i.e. a biodiversity index that measures the length of evolutionary pathways that connect a given set of

Table 1 Terrestrial carnivore species found in Neotropical ecoregions, their common name, phylogenetic diversity (mean evolutionary branch length to their most recent common ancestor – MRCA), body size, 'rarity' level (endemism), threat category, and version of the criteria (i.e. last time in which species conservation status was assessed). Carnivore taxonomy based on Wilson & Reeder (2005). Phylogenetic information obtained from Bininda-Emonds *et al.* (1999), body size data from Smith *et al.* (2004), and threat category and criteria version from IUCN (2007). IUCN threat categories shown here are DD, data deficient; LC, lower concern; NT, near threatened; VU, vulnerable; EN, endangered. See Material and Methods for further explanations.

Family	Species	Common name	MRCA (my)	Body size (g)	Ecoregion endemic	Threat category (IUCN 2007)	Criteria version
Canidae	<i>Atelocynus microtis</i>	Short-eared dog	7.6	8360	No	DD	ver3.1 (2001)
	<i>Canis latrans</i>	Coyote	2.5	12,000	No	LC	ver3.1 (2001)
	<i>Cerdocyon thous</i>	Crab-eating fox	7.6	5740	No	LC	ver3.1 (2001)
	<i>Chrysocyon brachyurus</i>	Maned wolf	7.6	23,300	No	NT	ver3.1 (2001)
	<i>Lycalopex culpaeus</i>	Culpeo	0.8	8620	No	LC	ver3.1 (2001)
	<i>Lycalopex griseus</i>	South American gray fox	0.8	6340	No	LC	ver3.1 (2001)
	<i>Lycalopex gymnocercus</i>	Pampas fox	0.8	4540	No	LC	ver3.1 (2001)
	<i>Lycalopex sechurae</i>	Sechuran fox	0.8	4230	No	DD	ver3.1 (2001)
	<i>Lycalopex vetulus</i>	Hoary fox	2.5	4230	No	DD	ver3.1 (2001)
	<i>Speothos venaticus</i>	Bush dog	7.6	6320	No	VU	ver3.1 (2001)
	<i>Urocyon cinereoargenteus</i>	Grey fox	4.7	3830	No	LC	ver3.1 (2001)
	<i>Vulpes macrotis</i>	Kit fox	1.1	2140	No	LC	ver3.1 (2001)
	<i>Vulpes vulpes</i>	Red Fox	1.1	4840	No	LC	ver3.1 (2001)
Felidae	<i>Leopardus braccatus</i>	Pantanal cat	1.9	4400	No	NT	ver3.1 (2001)
	<i>Leopardus colocolo</i>	Colocolo	1.9	4400	No	NT	ver3.1 (2001)
	<i>Leopardus geoffroyi</i>	Geoffroy's cat	3.2	2730	No	NT	ver3.1 (2001)
	<i>Leopardus guigna</i>	Kodkod	3.2	2500	No	VU	ver3.1 (2001)
	<i>Leopardus jacobitus</i>	Andean mountain cat	1.9	8130	No	EN	ver3.1 (2001)
	<i>Leopardus pajeros</i>	Pampas cat	1.9	4400	No	NT	ver3.1 (2001)
	<i>Leopardus pardalis</i>	Ocelot	0.3	11,900	No	LC	ver3.1 (2001)
	<i>Leopardus tigrinus</i>	Little spotted cat	3.2	2210	No	NT	ver3.1 (2001)
	<i>Leopardus wiedii</i>	Margay	0.3	3270	No	LC	ver3.1 (2001)
	<i>Lynx rufus</i>	Bobcat	3.1	6390	No	LC	ver3.1 (2001)
	<i>Panthera onca</i>	Jaguar	2.1	84,900	No	NT	ver3.1 (2001)
	<i>Puma concolor</i>	Mountain lion	3.1	53,900	No	NT	ver3.1 (2001)
	<i>Puma yaguaroundi</i>	Jaguarundi	3.1	6880	No	LC	ver3.1 (2001)
Mustelidae	<i>Conepatus chinga</i>	Molina's hog-nosed skunk	4	1920	No	LC	ver2.3 (1994)
	<i>Conepatus humboldtii</i>	Humboldt's hog-nosed skunk	1.1	1100	No	LC	ver2.3 (1994)
	<i>Conepatus leuconotus</i>	Eastern hog-nosed skunk	4	3450	No	LC	ver2.3 (1994)
	<i>Conepatus semistriatus</i>	Striped hog-nosed skunk	1.1	2020	No	LC	ver2.3 (1994)
	<i>Eira barbara</i>	Tayra	8.2	4140	No	LC	ver2.3 (1994)
	<i>Galictis cuja</i>	Lesser grison	1.8	1000	No	LC	ver2.3 (1994)
	<i>Galictis vittata</i>	Grater grison	1.8	2790	No	LC	ver2.3 (1994)
	<i>Lontra canadensis</i>	Northern river otter	1.2	8090	No	LC	ver3.1 (2001)
	<i>Lontra longicaudis</i>	Neotropical river otter	1	6550	No	DD	ver3.1 (2001)
	<i>Lontra provocax</i>	Southern river otter	0.6	7500	No	EN	ver3.1 (2001)
	<i>Lyncodon patagonicus</i>	Patagonian weasel	8.2	225	No	LC	ver2.3 (1994)
	<i>Mephitis macroura</i>	Hooded skunk	5	1100	No	LC	ver2.3 (1994)
	<i>Mephitis mephitis</i>	Striped skunk	5	2400	No	LC	ver2.3 (1994)
	<i>Mustela africana</i>	Amazon weasel	1.1	622	No	DD	ver2.3 (1994)
	<i>Mustela felipei</i>	Colombian weasel	1.1	211	No	EN	ver2.3 (1994)
	<i>Mustela frenata</i>	Long-tailed weasel	2.6	191	No	LC	ver2.3 (1994)
	<i>Mustela vison</i>	American mink	10.4	904	No	LC	ver2.3 (1994)
	<i>Pteronura brasiliensis</i>	Giant otter	0.3	26,000	No	EN	ver3.1 (2001)
	<i>Spilogale putorius</i>	Eastern spotted skunk	2.1	569	No	LC	ver2.3 (1994)
	<i>Spilogale pygmaea</i>	Pygmy spotted skunk	2.1	365	No	LC	ver2.3 (1994)
	<i>Taxidea taxus</i>	Badger	20.8	7840	No	LC	ver2.3 (1994)

Table 1 *Continued*

Family	Species	Common name	MRCA (my)	Body size (g)	Ecoregion endemic	Threat category (IUCN 2007)	Criteria version
Procyonidae	<i>Bassaricyon alleni</i>	Allen's olingo	17.1	1240	No	LC	ver2.3 (1994)
	<i>Bassaricyon beddardi</i>	Beddard's olingo	17.1	1240	No	LC	ver2.3 (1994)
	<i>Bassaricyon gabbii</i>	Bushy-tailed olingo	17.1	1250	No	LC	ver2.3 (1994)
	<i>Bassaricyon lasius</i>	Harris' olingo	17.1	1200	No	EN	ver2.3 (1994)
	<i>Bassariscus astutus</i>	Ringtail	0.3	1020	No	LC	ver2.3 (1994)
	<i>Bassariscus pauli</i>	Chiriqui olingo	17.1	1200	No	EN	ver2.3 (1994)
	<i>Bassariscus sumichrasti</i>	Cacomistle	0.3	906	No	LC	ver2.3 (1994)
	<i>Nasua narica</i>	White-nosed coati	2.3	4580	No	LC	ver2.3 (1994)
	<i>Nasua nasua</i>	South American Coati	2.3	3790	No	LC	ver2.3 (1994)
	<i>Nasuella olivacea</i>	Mountain coati	3.7	1340	No	DD	ver2.3 (1994)
	<i>Potos flavus</i>	Kinkajou	19	2480	No	LC	ver2.3 (1994)
	<i>Procyon cancrivorus</i>	Crab-eating raccoon	1.2	6950	No	LC	ver2.3 (1994)
	<i>Procyon insularis</i>	Raccoon	1.2	5426	Yes	EN	ver2.3 (1994)
	<i>Procyon lotor</i>	Northern raccoon	1.2	6370	No	LC	ver2.3 (1994)
	<i>Procyon pygmaeus</i>	Cozumel raccoon	1.2	2960	Yes	EN	ver2.3 (1994)
Ursidae	<i>Ursus americanus</i>	Black bear	5.7	111,000	No	LC	ver2.3 (1994)
	<i>Tremarctos ornatus</i>	Spectacled bear	14.5	123,000	No	VU	ver2.3 (1994)

species (Faith, 1992). In fact, MRCA was also called species-phylogenetic diversity by Sechrest *et al.* (2002). This was determined by the complete phylogeny (supertree) of extant carnivores available in Bininda-Emonds *et al.* (1999). Second, species body sizes (body mass in grams) were obtained from Smith *et al.* (2004). Third, species extinction risks were extracted from the 2007 IUCN Red List (IUCN, 2007). We followed Purvis *et al.* (2000) in converting the IUCN Red List categories to a continuous index as follows: data deficient and least concern = 0, near threatened = 1, vulnerable = 2, endangered = 3. None of the Neotropical carnivores are currently classified as critically endangered (= 4). Last, rarity for each species was defined as 1/geographical range (km²) (as in Gaston, 2003). Each of these traits have been proposed as surrogates of species threats, and have actually been used, alone or in combination, to predict extinction risks. In particular, the rationale for the phylogenetic diversity measure is that species with higher amounts of independent evolution be assigned a higher priority ranking because they 'retain' more genetic/evolutionary information, maximizing the accumulation of 'feature diversity' (Crozier, 1997; Sechrest *et al.*, 2002; Forest *et al.*, 2007). We followed Wilson & Reeder (2005) for the taxonomy of Neotropical carnivore species. General conservation status at the ecoregion level was extracted from Dinerstein (1995) and WWF (2006). The conservation status of ecoregions was determined by weighting the numerical values assigned to five key landscape-level variables: loss of original habitat, number and size of large blocks of original habitat, degree of fragmentation and degradation, rate of conversion of remaining habitat and degree of protection (Dinerstein, 1995). In weighting these variables, the loss of original habitat and the number of large blocks of intact habitat received much greater prominence. The reasoning for this is that these variables – reflecting historical and current levels of human impact – are the

best indicators of the probability of persistence of species and ecological processes within ecoregions (Dinerstein, 1995).

Analyses

Given the occurrence of all 64 carnivore species in 148 Neotropical ecoregions, we used an optimization procedure to select the minimum number of ecoregions necessary to represent all species at least once, based on the complementarity concept (Church *et al.*, 1996; Pressey *et al.*, 1997; Margules & Pressey, 2000; Williams *et al.*, 2000; Cabeza & Moilanen, 2001; see also Fig. 1). A simulated annealing procedure in the site selection mode (SSM) routine of SITES software (Andelman *et al.*, 1999; Possingham *et al.*, 2000) was used to find these combinations of ecoregions, by performing 150 runs with 10 million iterations. We set a relatively high penalty value for losing a species, so that every solution represented all species with a minimum number of ecoregions. Because frequently there are multiple combinations of ecoregions that satisfy this representation goal, we combined alternative solutions into a map in which the relative importance of each ecoregion is indicated by its rate of recurrence in optimal subsets. This is also an estimate of the irreplaceability of ecoregions (Meir *et al.*, 2004), ranging from 0.0 (minimum irreplaceability) to 1.0 (maximum irreplaceability) (see Ferrier *et al.*, 2000).

We also added to SSM a cost for each ecoregion, which was estimated by a set of variables expressing human impact levels in ecoregions (based on ecoregion conservation status; from stable/intact to critical/endangered; WWF, 2006) (Fig. 1) and the species' traits previously defined: phylogenetic diversity (MRCA), body size, rarity and extinction risk for each carnivore species (Table 1, Fig. 1). We calculated mean values for these traits within each ecoregion and identified, by a randomization procedure,

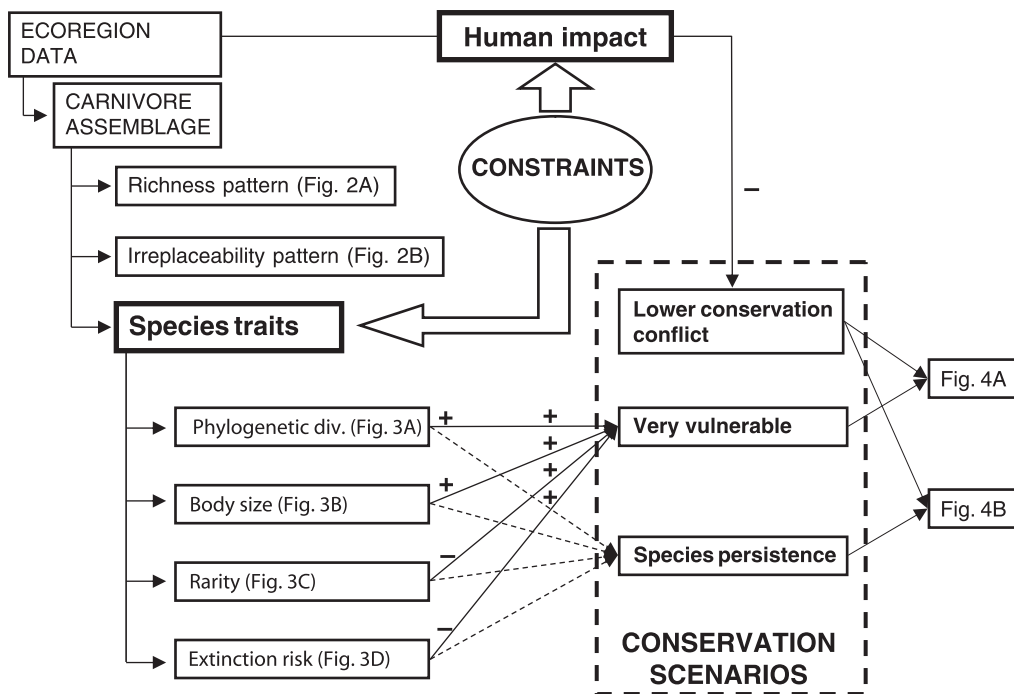


Figure 1 Flow outline of the prioritization evaluation procedure for conserving Neotropical carnivores. Human-impact levels in ecoregions and species ecological and evolutionary traits were used as constraints to produce optimal sets of ecoregions under three distinct prioritization scenarios. 'Very vulnerable' and 'species persistence' scenarios were derived from intrinsic traits of the carnivore assemblage, whereas the 'lower conservation conflict' scenario was derived exclusively from the ecoregion conservation status. These scenarios were then combined to show their congruence, as a heuristic device to ascertain ecoregion sets for effective conservation action. See Figs 2–4 and Materials and Methods for further details.

ecoregions in which trait values were higher or lower than expected by a null-model of equiprobable species occurrence in all ecoregions, given a fixed (observed) richness found in an ecoregion. Randomizations were performed in BootRMD software written by one of us (JAFDF) in Basic language for IBM-PC compatibles and available from the authors upon request.

We evaluated three distinct prioritization scenarios: (1) a very vulnerable one in which mean values of phylogenetic diversity (MRCA), body size and rarity, as well as threat levels are higher than expected, i.e. a priority set that focuses on ecoregions with high carnivore phylogenetic diversity containing simultaneously rare, highly threatened and large-bodied species; (2) another scenario that maximizes species persistence, in which mean values of MRCA and body size are higher than expected, but threat levels and rarity are lower than expected. This results in a priority set containing ecoregions with high carnivore phylogenetic diversity and large-bodied species, but with relatively few threatened or endemic ones; and (3) a third scenario in which optimal sets minimize conservation conflicts by favouring areas with lower levels of human impact (i.e. having a relatively stable conservation status, according to Dinerstein (1995) and WWF (2006)). These scenarios were then combined to reveal their overall congruence (Fig. 1). In prioritization scenarios, we used the SSM routine to find optimal combinations of ecoregions, by performing 50 runs with 20 million iterations.

Standardized values of species traits, as well as priority sets of ecoregions obtained from our analyses, were overlaid in a map of Neotropical ecoregions (Olson *et al.*, 2001) using ArcView GIS 3.2 (ESRI, Redmond, California). Shapefiles and associated attribute tables were obtained from WWF (2006). We employed an equal-area cylindrical projection in all maps.

RESULTS

Patterns of species richness and irreplaceability

Carnivore species richness is concentrated in southern Mexico, tropical Andes, rain forests of Colombia and Venezuela, Bolivian dry forests, the Brazilian Cerrado and large wetlands such as the Pantanal and the Chaco (Fig. 2a). Other rich ecoregions are located all over Central America and Brazil. Southern ecoregions (e.g. the Patagonian steppe) as well as those found in the west coast of South America have fewer species (Fig. 2a).

We found that only 12–14 ecoregions (c. 8% of all 148 ecoregions considered) are needed to represent all 64 carnivore species at least once (Table 2). Only four ecoregions occurred in all of the 150 optimal sets necessary to represent each species at least once (Fig. 2b). These irreplaceable areas are concentrated in Mexico (the Yucatán moist forests and the Jalisco dry forests), United States (the Everglades, in Florida), and Costa Rica (the Talamancan montane forests). Among ecoregions that were included in at

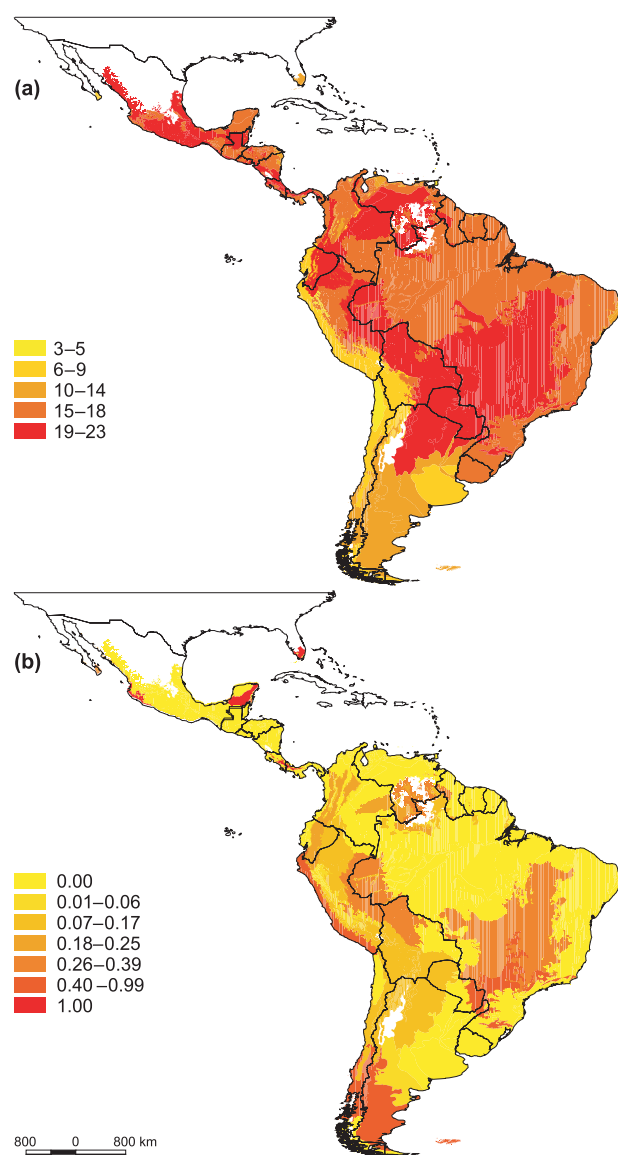


Figure 2 Spatial patterns of carnivore species richness across Neotropical ecoregions (a), and spatial patterns of irreplaceability estimated by the frequency of ecoregions in the 150 optimal solutions obtained with the 64 species of carnivores found in the Neotropics (b). (Colour version of figure available online.)

least 70% of optimal complementary sets are the Argentinean Patagonian steppe, and the Peruvian Sechura desert. Several ecoregions from Brazil – such as the Cerrado, the Atlantic moist forests and other areas in western and northern Amazon – and from Colombia and Venezuela figured in more than 50% of all optimal sets (Fig. 2b).

Spatial patterns of carnivore phylogenetic diversity, body size, rarity and threat

Rain forest ecoregions found in Costa Rica, Panama, Colombia and Venezuela harbour a greater amount of carnivore phylogenetic diversity given that species within these areas had higher values

of MRCA (Fig. 3a). Conversely, several other ecoregions from Central America and southern South America had lower aggregated phylogenetic diversity than the average in random species sets. These include the Patagonian steppe and the Argentine Espinal, the Uruguayan savanna, the Chaco and the Valdivian temperate forests in Chile (Fig. 3a).

The tropical Andes harbours carnivores with larger mean body sizes than expected compared to random samples of the regional species pool (Fig. 3b). The Atlantic forest of Brazil, as well as ecoregions found in southern South America, had species with body sizes smaller than expected (Fig. 3b). A very distinctive pattern of geographical distribution is found for carnivore species rarity in the Neotropics, western and southern ecoregions in South America having more rare species than expected in random assortments (Fig. 3c). Conversely, many ecoregions in Mesoamerica, the Amazon and wetlands in the entire Neotropics hold species with large geographical ranges. Perhaps it is no coincidence that an equivalent pattern was found in the distribution of carnivore threat levels (Fig. 3d). Ecoregions containing many highly threatened species are also concentrated in southern South America and southern Andes. On the other hand, in some Mexican ecoregions the number of carnivores classified at a low extinction risk is higher than expected (Fig. 3d).

Prioritization scenarios

In the scenario that favoured the inclusion of ecoregions less impacted by human activities (a lower conservation-conflict set), 12 ecoregions were needed to represent all 64 species at least once (Table 2, Fig. 4). These ecoregions coincide only partially with those selected under the other two prioritization scenarios. In the very vulnerable scenario 14 ecoregions were represented, and the congruence between this scenario and the lower conservation-conflict set was very low – only five ecoregions were shared (Table 2), two of which in Mexico and one each in Costa Rica, the northern Amazon, and the Florida Everglades (Fig. 4a). The congruence between the 12 ecoregions comprised in the optimal set under the species persistence scenario, and the lower conservation-conflict set was a little higher, with seven ecoregions in common of which five are identical to the ones identified above (Table 2, Fig. 4b). Two further areas were shared, namely the Sechura desert in Peru and the Central Andean dry puna; there are also four ecoregions that need urgent intervention and have high irreplaceability, all of which occur in both aforementioned scenarios.

DISCUSSION

Our analyses showed that conservation efforts for carnivores in the Neotropics should be concentrated in priority sets of 12–14 ecoregions if all species are intended to be represented. These results provide a coarse-scale initial framework for focusing conservation efforts in the Neotropical region. The most important ecoregions are those that occur in the optimal sets that minimize conservation conflicts as well as those that are very vulnerable and call for urgent intervention. We suggest that conservation

Table 2 Priority ecoregions for Neotropical carnivore conservation included (indicated by 'x') in optimal sets under a very vulnerable scenario, a species persistence scenario, a lower conservation conflict scenario, and in the high-irreplaceability set. Ecoregion conservation status and area obtained from WWF (2006).

Code	Name	Very vulnerable	Species persistence	Lower conflict	High irreplaceability	Conservation status	Area (km ²)
NT0121	Eastern Cordillera real montane forests	x	x			Vulnerable	10,2500
NT0124	Guianan Highlands moist forests	x	x	x	x	Intact	337,600
NT0128	Iquitos várzea		x			Vulnerable	115,000
NT0142	Napo moist forests	x				Vulnerable	251,700
NT0143	Negro-Branco moist forests	x				Vulnerable	212,900
NT0150	Alto Paraná Atlantic forests		x			Critical	483,800
NT0166	Southwest Amazon moist forests			x	x	Intact	749,700
NT0167	Talamancan montane forests	x	x	x	x	Intact	16,300
NT0181	Yucatán moist forests	x	x	x	x	Vulnerable	69,700
NT0202	Atlantic dry forests	x				Vulnerable	115,100
NT0205	Balsas dry forests				x	Critical	62,400
NT0212	Chiquitano dry forests	x				Critical	230,600
NT0214	Ecuadorian dry forests				x	Critical	21,300
NT0217	Jalisco dry forests	x	x	x	x	Critical	26,100
NT0227	Sierra de la Laguna dry forests	x				Vulnerable	4000
NT0232	Tumbes-Piura dry forests	x				Critical	41,300
NT0306	Miskito pine forests				x	Vulnerable	18,900
NT0307	Sierra de la Laguna pine-oak forests			x		Vulnerable	1100
NT0404	Valdivian temperate forests	x	x			Critical	248,100
NT0703	Campes Rupestres montane savanna				x	Intact	26,400
NT0704	Cerrado			x	x	Vulnerable	1,916,900
NT0803	Humid Pampas				x	Critical	240,800
NT0805	Patagonian steppe			x	x	Critical	487,200
NT0904	Everglades	x	x	x		Vulnerable	20,100
NT1001	Central Andean dry puna		x	x		Intact	307,400
NT1003	Central Andean wet puna	x				Vulnerable	117,300
NT1005	Cordillera de Merida páramo				x	Intact	2800
NT1006	Northern Andean páramo			x		Intact	30,000
NT1313	Paraguana xeric scrub				x	Critical	16,000
NT1315	Sechura desert		x	x		Vulnerable	18,4900
NT1404	Northern Mesoamerican Pacific mangroves		x			Critical	2100

action in these areas is likely to yield the best return for the investment at the ecoregion scale, given that they contain species that tend to carry high phylogenetic diversity, have larger body sizes, and are rare and/or threatened of extinction; at the same time, these ecoregions have been less impacted by human activities till now. Conservation of carnivore biodiversity is important everywhere. However, in those ecoregions, which have suffered widespread habitat destruction, the cost and level of effort to conserve carnivores will be far higher than in less impacted ecoregions (see Dinerstein, 1995). Very vulnerable scenarios also are the primary goal of effective conservation strategies (Margules & Pressey, 2000; Mittermeier *et al.*, 2004) and optimal complementarity solutions based on biodiversity analyses have been successful in defining conservation networks (Csuti *et al.*, 1997), including those for carnivore species (Valenzuela-Galván *et al.*, 2008).

Even when a lower conservation-conflict scenario was evaluated, some critical and vulnerable ecoregions were represented in the

optimal set. This occurs because we set a high penalty value for losing a species, so that all species must be included at least in one ecoregion. This means that ecoregions harbouring endemic species were always included, regardless of their conservation status. In consequence, a challenge posed by our analyses is that several priority ecoregions needed for carnivore conservation have a vulnerable conservation status. These represent areas that, although demanding the implementation of efficient carnivore conservation strategies, have already suffered detrimental human impacts. For such settings, new conservation approaches are required (see Valenzuela-Galván *et al.*, 2008 and references therein).

The incorporation of species evolutionary and ecological traits generated more ecologically supported priority sets and this has important implications for reserve network design. The scale at which priority analysis is conducted is a crucial consideration when conservation strategies are planned (Valenzuela-Galván *et al.*, 2008). Large-bodied carnivores, for instance, tend to have larger home ranges; hence protected areas should be extensive

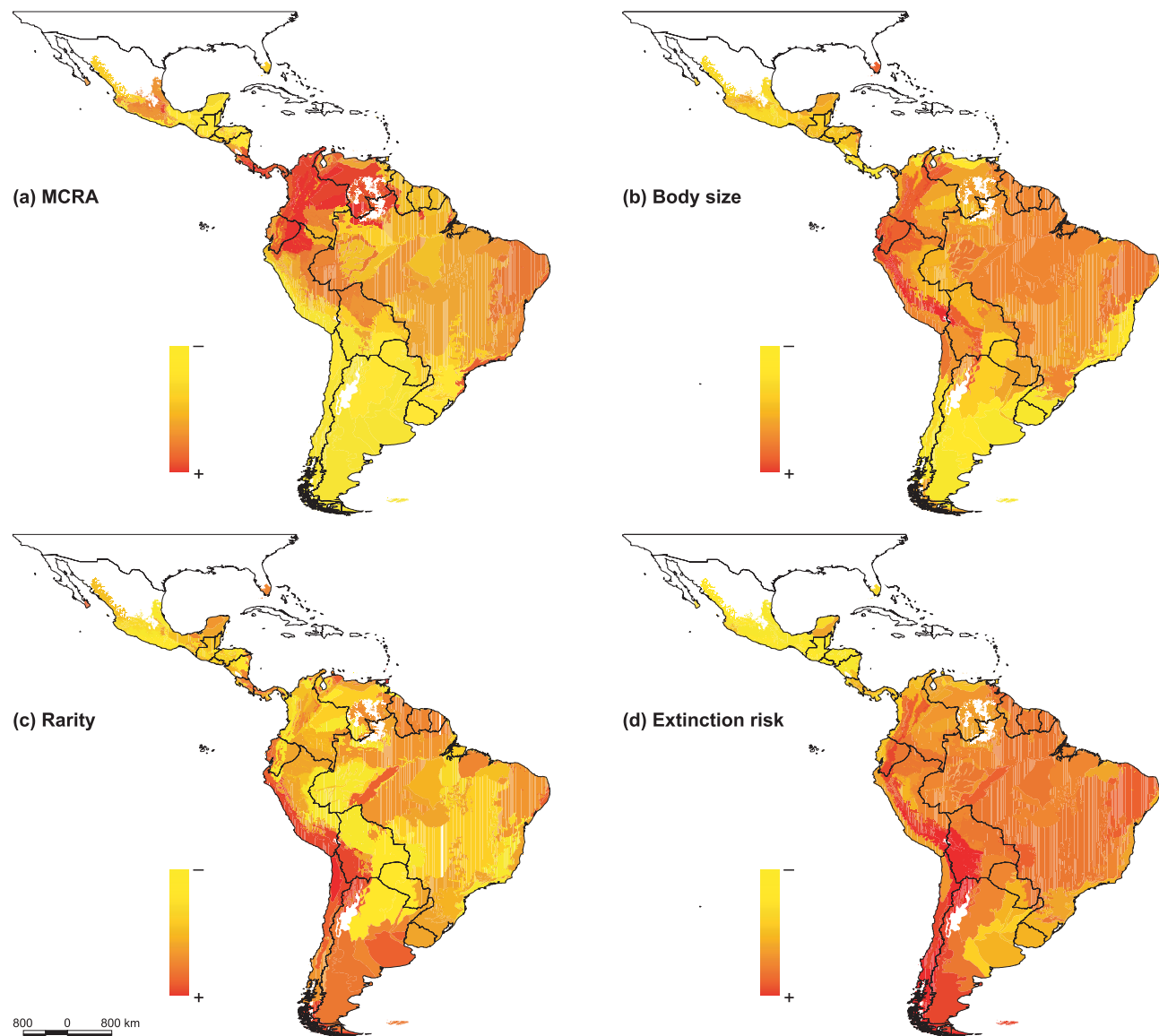


Figure 3 Spatial patterns of species mean evolutionary branch length to its most recent common ancestor – MRCA (a), body size (b), rarity (c), and (d) extinction risk level, according to the 2007 IUCN Red List. The gradient of fill colours/shading for ecoregions reflects values ranging from lower (yellow/light grey) to higher (red/dark grey) than expected by a null-model of equiprobable species occurrence in all ecoregions, given the observed richness of an ecoregion (see also Material and Methods). (Colour version of figure available online.)

enough to ensure these requirements. This means, for instance, that we need large reserves in the tropical Andes – an area whose ecoregions harbour carnivores with mean body size higher than expected in a chance assortment (see Fig. 3b). Perhaps these protected areas should be large enough to be designated as megareserves, as suggested by Peres (2005) for the Amazon region. Large-bodied carnivores have also an above-average risk of extinction. This is not only a result from the way that species traits associated with vulnerability are scaled with body size (Cardillo *et al.*, 2005). In a broad-scale analysis of extinction risk in mammals, Cardillo *et al.* (2005) found that impacts of both intrinsic and environmental factors increase sharply above a threshold body mass of *c.* three kilograms. Prioritizing ecoregions

in those species that tend to have larger body size values is therefore a fundamental criterion for developing effective conservation strategies for this group.

The evolutionary history of species residing within ecoregions is a yet unknown component of Neotropical biodiversity, although this may prove a more inclusive measure of biodiversity than species numbers (Purvis & Hector, 2000; Sechrest *et al.*, 2002). The inclusion of evolutionary measures such as phylogenetic diversity in prioritization exercises, as performed in this study, can be used to determine areas with greater evolutionary diversity and greater importance for the conservation of evolutionary processes (Tôrres & Diniz-Filho, 2004). Some academic papers have suggested ways to maximize the conservation of phylogenetic

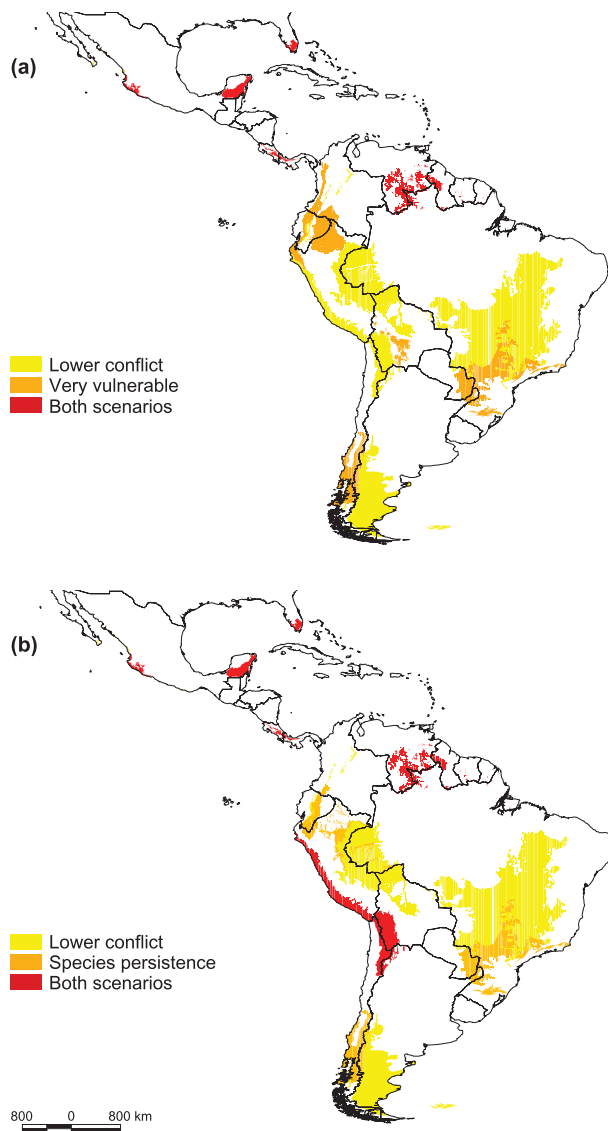


Figure 4 Priority ecoregion sets for conserving Neotropical carnivore species. In (a), the map shows minimum ecoregion sets required for representation of all carnivores at least once under a very vulnerable scenario (orange/mid-grey ecoregions) combined with those included in a scenario of lower conservation conflict (yellow/light grey ecoregions). Priority ecoregions shared by both prioritization scenarios are shown in red/dark grey. In (b), the map shows the combination of a species persistence scenario and the lower conservation conflict scenario. Ecoregion colour/shading codes as above. See also Table 2 for ecoregion information. (Colour version of figure available online.)

diversity (e.g. Faith, 1992; Crozier, 1997; Nee & May, 1997), but these have rarely been incorporated into conservation strategies before (Isaac *et al.*, 2007; but see Forest *et al.*, 2007). Sechrest *et al.* (2002) showed that hotspots for conservation priorities (Mittermeier *et al.*, 2004) are not only crucial areas of species-level endemism, but also unique reservoirs of evolutionary history. Forest *et al.* (2007) revealed that selection of priority areas based

only on conventional taxon complementarity tends to miss localities that would provide larger gains in phylogenetic diversity of plants in a biodiversity hotspot – the Cape of South Africa. In this context, our optimal sets, by taking species evolutionary history into account, also contribute to strengthen a framework for the development of effective strategies for carnivore conservation. The implicit recommendation here is to ensure that phylogenetic diversity be maximized, through the inclusion of suitable areas into conservation schemes for a given group. Arguably, one should also preserve recently radiated groups that may have high evolutionary potential, rather than focusing solely on the preservation of evolutionary unique organisms (i.e. high amount of phylogenetic diversity). However, along with other authors, we feel that prioritizing species that show little change over long periods is particularly important, because the extinction of species in an old, monotypic or species-poor clade would entail a greater loss of biodiversity than that of a young species with many close relatives (Sechrest *et al.*, 2002; Mace *et al.*, 2003; Forest *et al.*, 2007; Isaac *et al.*, 2007).

The five priority ecoregions common to all prioritization scenarios (see Table 2) exhibit several promising attributes: most have an intact conservation status, they have species with medium to low values of rarity (Fig. 3c), which are at below-average extinction risk (Figs 3d and 4). It is known that among other mammals, carnivores are more likely to come into conflict with humans and consequently suffer population declines or go extinct (Ginsberg, 2001). Cardillo *et al.* (2004) assert that the ultimate driving force of almost all recent and ongoing declines in mammal populations and their immediate causes (e.g. habitat loss, hunting, and species invasion) is the growth of human populations; hence species inhabiting more heavily impacted regions are at higher extinction risks (Forester & Machlis, 1996; Brashares *et al.*, 2001; McKinney, 2001; Ceballos & Ehrlich, 2002; Parks & Harcourt, 2002; Becker & Loyola, 2007; Loyola *et al.*, 2008).

Ecoregion-based analyses entail their own caveats. As in any *a priori* classification, substantial differences within an ecoregion may remain undetected (Brooks *et al.*, 2006). This risk increases in larger areas, such as the Cerrado ecoregion in Brazil (see Silva *et al.* (2006) for a recent spatial classification of the ecological diversity of the Cerrado), or the Patagonian Steppe in Argentina. Neotropical ecoregions range from 100 to 1,900,000 km² in area and, although this may reflect actual differences in their extent, some areas undoubtedly would warrant further subdivision, given additional knowledge (Loyola *et al.*, 2007). Moreover, ecoregions cannot be conserved in their entirety. Broad-scale area assessments provide frameworks within which finer-scaled options for conservation setting and resource allocation have to be established and analysed (Brooks *et al.*, 2006; but see Rouget, 2003).

To sum up, our results highlight areas of particular interest for the conservation of Neotropical carnivores. The inclusion of evolutionary or ecological traits in conservation assessments and planning helps to improve reserve networks and therefore to increase the effectiveness of proposed priority sets. Because areas differ in quality, identification of a comprehensive set of natural

areas, as presented here, is a step towards an *in situ* biodiversity maintenance strategy, which only subtends a much more complex process of policy negotiation and implementation. Although our scenarios are no substitute for this negotiation process, they are part of a wide-ranging effort to strengthen the scientific basis for conservation decisions (Mittermeier *et al.*, 2004; Soutullo *et al.*, 2007). Complementarity among ecoregions will be especially instrumental in making complex judgements about trade-offs between diversity and redundancy at the carnivore species level. In fact, ecoregions characterized by high beta diversity may require more protected areas that are well distributed across the landscape to conserve the full complement of endemic carnivores. Our analyses contribute to a joint framework for the development of national and continental strategies for carnivore biodiversity conservation, adding to growing efforts to establish action plans to apply finite funds and efforts where they will be most effective.

ACKNOWLEDGEMENTS

We thank two anonymous referees for their comments on the manuscript. RDL was supported by CNPq (140267/2005-0). GO was supported by a CAPES MSc fellowship. JAFDF research has been supported by grants from CNPq (301259/2005-4 and 470918/2006-3) and FUNAPE-UFG. TML was funded by FAPESP (04/15482-1) and CNPq (306049/2004-0). Umberto Kubota helped prepare Figs 1–4.

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Editor: Jon Paul Rodriguez



Loyola RD, Oliveira-Santos LGR, Almeida-Neto M, Nogueira D, Kubota U, Diniz-Filho JAF & Lewinsohn TM (2008). **Integrating economic costs and biological traits into global conservation priorities for carnivores.** *PLoS ONE*, aceito (em revisão).

Integrating economic costs and species biological traits into global conservation priorities for carnivores

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Abstract

Prioritization schemes usually call attention to species-rich areas, where many species are thought to be at imminent risk of extinction. To be more ecologically-supported these schemes should also include species biological traits into area-setting methods. Furthermore, in a world of limited conservation funds, prioritization is limited to land acquisition. Hence, including the economic costs of conservation into conservation priorities can lead to substantially larger biological gains. We examined three global conservation scenarios for carnivores based on the joint mapping of economic costs and species biological traits, which successively identify the most cost-effective priority sets of ecoregions, indicating best returns or opportunities for investments for safeguarding each carnivore species, and establish priority sets that can maximize species representation in areas needing an urgent intervention for carnivore conservation – these areas harbor species with higher extinction risks. We compared these results with another scenario that only minimizes the total number of ecoregions. We found that cost-effective conservation investments should focus on 44 ecoregions which are highly concentrated in Africa and more widespread across the New World and southeast Asia, coinciding partially with those selected under the urgency scenario (37 shared ecoregions). These ecoregions should yield best returns of investments since they harbor species with high extinction risk and have lower mean land cost per ecoregion. Our results draw attention to ecoregions of particular importance for the conservation of the World's carnivores, and are the first to define global conservation priorities for these species considering socioeconomic factors. We acknowledge that the identification of a comprehensive priority-set of areas is a first step towards an *in-situ* biodiversity maintenance strategy, which subtends a much more complex process of policy negotiation.

Key words: conservation biogeography, conservation planning, endemism, extinction, prioritization, vertebrates.

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Introduction

Conservation assessment and planning aim to optimize the allocation of scarce conservation funding by prioritizing areas for protection (Margules & Pressey, 2000; Margules & Sarkar, 2007). This approach has been increasingly applied at regional (e.g. Cowling *et al.*, 2003, Smith *et al.*, 2006; Loyola *et al.*, 2007), continental (e.g. Dinerstein *et al.*, 1995; Burgess *et al.*, 2004; Loyola *et al.*, 2008a, b) and global scales (e.g. Mittermeier *et al.*, 2004; Olson & Dinerstein, 2002; Grenyer *et al.*, 2006). Especially in the later, several major templates of global prioritization for biodiversity conservation were published over the past decades (Brooks *et al.*, 2006), including the biodiversity hotspots and the high-biodiversity wilderness areas (Mittermeier *et al.*, 2003, 2004), the Global 200 ecoregions (Olson & Dinerstein, 2002), and the endemic bird areas (Stattersfield *et al.*, 1998). All these templates fit within a central piece to conservation planning theory, i.e. the conceptual framework that considers irreplaceable and/or vulnerable areas (see Margules & Pressey, 2000). They have, however, portrayed significantly different priorities onto the framework: some prioritize highly irreplaceable or vulnerable areas while others, conversely, favor areas with low levels of vulnerability (see Brooks *et al.*, 2006).

Regardless of the emphasis on template's irreplaceability or vulnerability, all these prioritization schemes usually call attention to areas with the highest species richness and endemism, where many species are thought to be at imminent risk of extinction, or where habitat loss has already occurred (Stattersfield *et al.*, 1998; Olson & Dinerstein, 2002; Mittermeier *et al.*, 2004; Cardillo *et al.*, 2006; Grenyer *et al.*, 2006). Such approach is directed towards the necessity of minimizing biodiversity loss in regions where severe human disturbance to natural habitats has already occurred or is taking place (Cardillo *et al.*, 2006). However, species respond differently to threats (e.g. Becker & Loyola, 2007; Loyola *et al.* 2008a) and several factors can influence such responses. Cardillo *et al.* (2005, 2006) showed that extinction risk in mammals can be driven both by environmental factors (e.g. habitat loss, climate change) and intrinsic biological traits of the species (e.g. gestation length, body size, population density). Furthermore, they revealed that small and large species have different probabilities of extinction given that smaller ones are more affected by environmental factors while larger species may suffer from a combination of environmental factors and intrinsic traits. Specifically for carnivores, Cardillo *et al.* (2004) demonstrated that some species are likely to move more rapidly towards extinction than others, by predicting extinction risks from their biology and combining it with projected human population density. They argued that a preventive approach to species conservation is required for protecting species that may not be threatened to date but may become so in a foreseeable future. Recently, Loyola *et al.* (2008b) included species

evolutionary and ecological traits in different prioritization scenarios for Neotropical mammals and were able to find regions that are less impacted today due to human activities while harboring most very vulnerable species. These regions should, therefore, provide the best return of conservation efforts.

Among mammals, the carnivores are one of the most endangered groups (Valenzuela-Galván *et al.*, 2008, Valenzuela-Galván & Vázquez, 2008), including several major conservation icons, such as the tiger and the giant panda, and many other considered flagship, umbrella, keystone, and indicator species (Gittleman *et al.*, 2001). Some well known species of carnivores, such as the Jaguar in South America, also take part in human-wildlife conflicts, when – as consequence of diet, home range and habitat resource requirements of many species – they prey upon sheep, horses, and cattle, which, in turn, leads to human illegal actions (e.g. hunting, poaching, poisoning) that adversely affect their viability (Rodinini & Boitani, 2007). Beyond the charismatic appeal of many carnivores, protection for the entire group would be more effective if conservation strategies were focused on the prioritization of geographical areas or entire ecological communities, rather than addressing individual species separately (Gittleman *et al.*, 2001).

On the other hand, in a world of limited conservation funds, prioritization of areas for conservation has often been limited to land acquisition (Rodinini & Boitani, 2007). Recently, Underwood *et al.* (2008) argued that efficiency in prioritization would be better measured in terms of conservation returns on financial investment. It also has been progressively more accepted that including the economic costs of conservation into conservation priorities can lead to substantially larger biological gains (Naidoo *et al.*, 2006; Underwood *et al.*, 2008). Therefore, under a systematic conservation planning framework, scenarios that try to minimize the cost for land acquisition should be closer to optimal (Davis *et al.*, 2006).

In this paper, we used broad-scale biogeographical data of carnivore species distribution - occurrence in World ecoregions, according to WWF (World Wide Fund for Nature, 2006) - to define priority sets of ecoregions that should be sufficiently covered in a reserve system to represent all the World's carnivores. To this end, we examined three conservation scenarios based on the joint mapping of economic costs and species biological traits, which successively (1) identify the most cost-effective priority sets of ecoregions, indicating best returns or opportunities for investments for safeguarding each carnivore species, and (2) establish priority sets that can maximize species representation in areas needing an urgent intervention for carnivore conservation – these areas harbor species with higher extinction risks. We compared these results with another planning scenario that minimizes the total number of ecoregions in the

final solution regardless to variation on threats and costs (socioeconomic factors). Finally, we also evaluated these scenarios relative to their amount of area already protected, their available area for conservation and their estimated human population density in 2015. Evaluating the congruencies among these conservation plans allowed us to pinpoint where conservation is likely to yield the best return for investment at the ecoregion scale.

Material and Methods

Data. We followed the WWF hierarchical classification of ecoregions (Olson *et al.*, 2001; WWF, 2006). The database used for the analyses contains the current species list of mammals in the terrestrial ecoregions. We focused our analyses on all 236 World's carnivore species, whose occurrence ranges were obtained from Wilson & Reeder (2005). We also followed the later for the taxonomy of carnivore species. Information on updates, detailed descriptions of the database, and complete lists of sources can be obtained from the Web site indicated by WWF (2006). Note that these datasets are periodically updated, and the files used in our analyses may differ from the most recent versions available from the WWF (2006).

For each species, we obtained five biological variables used by Purvis *et al.* (2000) and update from Cardillo *et al.* (2004), to include more recently published information. These variables were species' body size, interbirth interval, litter size, gestation length, and population density. Continuous variables were log-transformed before analysis.

Following Underwood *et al.* (2008), we calculated the cost of acquiring land for protection by first applying an equation for the regular cost of annual management – originally proposed by Balmford *et al.* (2003) – and then multiplying the values found by a correction factor (50.6, see Underwood *et al.* 2008) to estimate the cost of land acquisition in each ecoregion. According to Balmford *et al.* (2003), the regular cost of annual management in US\$ km⁻² can be estimated by:

$$\log(\text{Cost US\$}) = 1.61 + 0.57 * \log(\text{GNI US\$ km}^{-2}) - 0.7 * \log(\text{PPP}) - 0.46 * \log(\text{Area, km}^2) \quad (1)$$

However, the area term in the equation, which is related to the influence of reserve size on annual management cost, was not considered here. Given that ecoregions cannot be conserved in their entirety (Loyola *et al.* 2007, Loyola *et al.* 2008a) and that our objective was to merely pinpoint priority sets among diverse possible sets of ecoregions, a relative monetary value per unit area per ecoregion was used for comparison, which allowed for the variable reserve size to be excluded from the equation. Therefore, the resulting equation for this study is:

$$\log(\text{Cost US\$}) = [1.61 + 0.57 * \log(\text{GNI US\$ km}^{-2}) - 0.7 * \log(\text{PPP})] * 50.6 \quad (2)$$

We obtained Gross National Income (GNI) from the International Monetary Fund's International Financial Statistics (2004) and compiled Purchasing Power Parity (PPP) and GDP deflators from the World Bank (<http://devdata.worldbank.org/wdi2006/contents/Section4.htm>). As the PPP term is the PPP conversion factor divided by the exchange rate, we calculated the area-weighted average after determining the costs for each country to allow the inclusion of ecoregions that span multiple countries.

Finally, we obtained the following data for each ecoregion from WWF (2006): total area (in km²), proportion of area protected (area under IUCN category I-VI), proportion of land-use area (area under agricultural lands and urbanization) and proportion of land available for conservation [calculated as the total area – (land-use area + protected area)]. For our measures of Human Population Density (HPD), we used the Gridded Population of the World (CIESIN *et al.*, 2005), a spatially explicit global database of predicted HPD for 2015, coarsened to a resolution of 0.5 x 0.5°. Values of HPD for a given country were then assigned for each ecoregion within its political limits.

Analyses. We set up three different conservation-planning scenarios: one of minimum planning units (i.e. ecoregions), one of minimum cost (i.e. US\$ km⁻² for land acquisition), and another of high urgency for carnivore species. The minimum-ecoregion (1) was a reference “null” scenario aimed at the conservation of all species in the minimum number of ecoregions in the World; variation in species threat and economic cost of each ecoregion (i.e. socioeconomic factors) were not considered. As we had several solutions with the same number of ecoregions, we used that whose ecoregion summed area was the smallest. This scenario minimizes the number of ecoregions and the area where the conservation plan was applied.

In the cost-effective scenario (2), all species were represented while the cost of each ecoregion was equaled to the calculated cost (US\$ km⁻²) of land acquisition. This scenario minimizes the mean costs per unit area for land acquisition in the ecoregion set where the conservation plan was applied.

Finally, in the urgency scenario (3), the aim was to find a minimum set of areas that represent all species, but favoring ecoregions in which species are endangered or at imminent threat. To find these ecoregions, we attributed an urgency-cost for each one of them based on the biological variables mentioned above. We calculated mean values for these species' traits within

each ecoregion and identified (by the standardized z-scores provided by a randomization procedure) ecoregions in which trait values were higher or lower than expected from a null-model of equiprobable species occurrence in all ecoregions, given a fixed (observed) richness found in an ecoregion. Randomizations were performed in BootRMD software written by one of us (JAFDF) in Basic language for IBM-PC compatibles and available from the authors upon request. The z-scores representing each variable within ecoregions were summed in a way that an urgent ecoregion for carnivore conservation was that tending to aggregate large-bodied species as well as with high interbirth interval, high gestation length, low litter size, and low local population density (see also Loyola *et al.*, 2008b). This scenario represented all species, maximizing species extinction risk where the conservation plan was applied.

Given the occurrence of the 236 carnivore species in 661 ecoregions, we used an optimization procedure to select the minimum number of ecoregions necessary to represent all species at least once, based on the complementarity concept (Pressey *et al.*, 1997; Margules & Pressey, 2000). A simulated annealing procedure in the Site Selection Mode (SSM) routine of SITES software (Andelman *et al.*, 1999; Possingham *et al.*, 2000) was used to find these combinations of ecoregions. We set the analyses parameters as follow: 100 runs and 20,000,000 iterations. We also set a relatively high penalty value for losing a species, so that every solution represented all species with a minimum number of ecoregions. Because there are frequently multiple combinations of ecoregions that satisfy this representation goal in each conservation scenario, we combined alternative solutions into a map in which the relative importance of each ecoregion is indicated by its rate of recurrence in optimal subsets (see Fig. 1B-D). This is also an estimate of the irreplaceability of ecoregions, ranging from 0.0 (minimum irreplaceability) to 1.0 (maximum irreplaceability).

The summary results of each systematic planning scenario were evaluated according to their total amount of area (in km²), total number of ecoregions, mean land acquisition costs, proportion of protected area, proportion of land-use area, and proportion of available area for conservation, as well as their predicted HDP in 2015 [a measure of indirect conservation conflict *sensu* Cardillo *et al.* (2004)].

The spatial pattern in carnivore species richness as well as the priority sets of ecoregions obtained from our analyses, were overlaid in a map of World ecoregions (Olson *et al.*, 2001) using ArcView GIS 3.2 (ESRI, Redmond, California). Shapefiles and associated attribute tables were obtained from WWF (2006). We employed an equal-area cylindrical projection in all maps.

Results

Species richness pattern and ecoregion irreplaceability

Carnivore species richness is highly concentrated in southeast Asia, the Philippines, central and southeast Africa (Fig. 1A). Other species-rich ecoregions are located all over Central America and the tropical Andes, as well in western U.S.A., southern Africa, central Asia and Middle East (Fig. 1A). Ecoregions of southern South America, those found in the east coast of the U.S.A., and those belonging to the Sahara and Arctic realms have few carnivore species.

Under the minimum-ecoregion scenario, only 14 ecoregions occurred in all of the 100 optimal sets necessary to represent each species at least once (Fig. 1B). These areas with high-irreplaceability values are concentrated in Africa, forming an ecoregion belt in the center of the continent, but including also ecoregions in the south and in Madagascar; in southeast Asia, ecoregions near to Himalayan Mountains have also high-irreplaceability values (Fig. 1B). Among ecoregions that were included in at least 70% of optimal complementary sets are the Argentinean Patagonian steppe, and Brazilian Cerrado, as well as some ecoregions from southeast Africa.

Irreplaceability patterns in the cost-effective scenario were partially similar to those found in the minimum-ecoregion plan. Sixteen ecoregions occurred in all optimal solutions ran for this scenario: some located at central Africa, and some found in particular Neotropical regions, such as the Valdivian Temperate forests in Chile, the Yucatán Moist Forests in Mexico and the Everglades in Florida, U.S.A. (Fig. 1C). Ecoregions included in more than 70% of optimal solutions are located again in Africa and southeast Asia.

Finally, only 13 ecoregions were included in all optimal solutions found within the urgency scenario for global carnivore conservation (Fig. 1D). These ecoregions occur in North America (e.g. the South Central Rockie Forests, the Californian Chaparral, the Trans-Mexican Volnic Belt pine-oak forests, and the Yucatán Moist Forests), Central America (the Talamancan Montane Forests) and Africa (e.g. the North Saharan steppe and woodlands, the East Sudanian savanna, the Northeastern Congolian forests, and the Madagascar lowland forests) (see Fig. 1D).

Conservation planning scenarios

The minimum-ecoregion scenarios needed 41 ecoregions to represent all carnivore species. These areas are mainly concentrated in Africa (Fig. 2A). In the cost-effective set, 44 ecoregions were able to represent all 236 species at least once (Table 1 and S1, Fig. 2B). These ecoregions are also highly concentrated in Africa and more widespread across the New World and southeast Asia, coinciding only partially with those selected under the urgency scenario and with those

found in the minimum-area scenario (Table 1 and S1, Fig. 2B, Fig. 3). The urgency scenario harbors 43 ecoregions, which are clustered primary in Africa and more widely distributed across South America and southern Asia. The congruence between this scenario and the minimum-ecoregion set, exclusively, was very low – only 5 ecoregions were shared (Table 1 and S1, Fig. 3).

As expected, the mean land cost per ecoregion was lower in the cost-effective scenario than in any other, and the mean predicted population density in 2015 was higher in the urgency conservation scenario (Table 1). The minimum-ecoregion set had a much larger total area than other scenarios. Relative to the mean proportion of protected and available area, the three scenarios were very similar (Table 1). The cost-effective setting presented a higher mean value of land use than the others, albeit the difference being very small. Finally, the combination of cost-effective and urgency scenario revealed a key set of 60 ecoregions, from which 16 have high-irreplaceability values (Table 1). These two scenarios shared 37 ecoregions, which are concentrated in Africa, but there are other important ecoregions in the northwestern U.S.A., Mexico, Chile and Brazil, as well as in the Philippines (Table 1 and S1, Fig. 2B, Fig. 3).

Discussion

Recently, several studies have defined geographic priorities for the conservation of distinct taxonomic groups at different spatial scales (e.g. Rondinini *et al.*, 2005, Das *et al.*, 2006, Rondinini & Boitani, 2007, Bode *et al.*, 2008, Loyola *et al.* 2008a). However, just few were focused on carnivores (but see Loyola *et al.*, 2008b, Valenzuela-Galván & Vázquez, 2008, Valenzuela-Galván *et al.*, 2008). Our results draw attention to ecoregions of particular importance for the conservation of the World's carnivores, and are the first to define global conservation priorities for these species considering socioeconomic factors, especially variation in extinction risk (based on their biological traits), but also in economic costs across ecoregions. The attained flexibility of our optimal procedure gives several options for areas where conservation of carnivores should be focused.

A growing body of evidence indicates that species that are large-bodied, have sizeable home range, occur at low densities, and feed at higher trophic levels are more likely to become locally extinct in habitat fragments (Laurance *et al.*, 2002, Cardillo *et al.*, 2005, 2006, Boyd *et al.*, 2008). This seems to be the case for most carnivores. As pointed out by Cardillo *et al.* (2004), small geographic ranges and low population densities (along with low litter size) are traits that limit the maximum population size a species can attain; gestation length and interbirth period (other biological traits used in this study) are effective indicators of life-history speed,

determining how quickly populations can recover from low levels (Gittleman, 1993); moreover, their need for large foraging areas coupled with their dependence on prey species that may themselves be in jeopardy (Carbone & Gittleman, 2002) put carnivores in danger across the Globe, particularly in regions in which a high human population density is found (Cardillo *et al.*, 2004). This enhances the necessity of including species biological traits into conservation planning analyses, as done recently by Loyola *et al.* (2008a, b). In these studies, we showed how the inclusion of evolutionary and ecological traits, along with those inherent to species life-history, can generate more ecologically-supported priority sets, having important implications for reserve network design. Therefore, the conservation value of our urgency scenario is further strengthened.

Very vulnerable scenarios are the primary goal of conservation strategies (Margules & Pressey, 2000; Mittermeier *et al.*, 2004), and some area-demanding species, such as large carnivores, merit conservation action at the landscape scale to address localized declines even though they are not themselves globally threatened (Boyd *et al.*, 2008). Large-bodied carnivores tend to have also larger home ranges; hence, protected areas should be extensive enough to ensure these requirements (Loyola *et al.*, 2008b). This means that we need large reserves in the Tropical Andes, central Africa and southeast Asia. The good news here is that these regions also concentrate several ecoregions included in our cost-effective scenario, meaning that cost-effective conservation investments in these regions are still an available option.

The disparity in economic cost found among ecoregions means that there is potential for great benefit in seeking efficient financial investments (Underwood *et al.*, 2008). Area-setting analyses that neglect cost, implicitly assume that this factor is homogeneously distributed across the geographic space, possibly reducing priority-set efficiency. Note that our results clearly indicate that a minimum-ecoregion set was less efficient (in terms of total area and economic costs) than all others (see Table 1). Furthermore, in their recent paper, Bode *et al.* (2008) concluded that the inclusion of socioeconomic factors (threat and cost) is crucial for determining priorities for biodiversity conservation. They created efficient global funding schedules using information about costs, species-endemism level of seven different taxonomic groups, and predicted habitat loss rates in the biodiversity hotspots proposed by Conservation International (Mittermeier *et al.*, 2004). They found that funding allocations were less sensitive to variation in taxon assessed than to variation in cost and threat. Moreover, they highlighted that we can be more confident about global-scale decisions guided by single taxonomic groups (Bode *et al.*, 2008). This places the combination of our urgency and cost-effective scenarios at the center of effective conservation strategies for the World's carnivores, given that they have a high overall

congruence and therefore indicate areas that, if sufficiently covered in a global network of protected areas, would safeguard most carnivores with minimum economic cost.

The priority sets identified in this study complement and lend support to priority setting frameworks derived independently (see Brooks *et al.*, 2006). Concordance among important areas indicated as priority for carnivores reside mainly in the U.S.A. (Valenzuela-Glaván *et al.*, 2008), Mexico (Loyola *et al.*, 2008b, Valenzuela-Galván & Vázquez, 2008), Tropical Andes, Brazilian Atlantic forest, and southern South America (Loyola *et al.*, 2008b). Other congruencies were also observed among priority areas proposed for other taxonomic groups such as mammals and amphibians in Africa (Rondinini *et al.*, 2005), threatened anurans in the Neotropics (Loyola *et al.*, 2008a), and endemic plants as well as terrestrial vertebrates worldwide (Olson & Dinerstein, 2002, Mittermeier *et al.*, 2004). The independent convergence of high priority sets selected by our systematic approach with other ones reinforces our exercise as an important ecoregion-level framework to direct priority conservation action, instead of multiplying the number of competing planning templates (Mace *et al.*, 2000; Brooks *et al.*, 2006).

The necessity of developing conservation action at the landscape level – sometimes combined with broad-scale actions (Boyd *et al.*, 2008) – supports the use of ecoregions as fundamental geographic units. We chose to use ecoregions because these broad areas are defined according to physiographic and biotic features and, therefore, should reflect zoogeographic boundaries more closely. They are also less sensitive to heterogeneity in distribution data than grid-based analyses (Lamoreux *et al.*, 2006) and are gaining support of major conservation organizations as well as of many government agencies (Olson *et al.*, 2001, Loyola *et al.*, 2007, 2008a, b) – although an ecoregion approach entails its own caveats (Loyola *et al.*, 2007, 2008a).

Protected area remains as the cornerstone of conservation strategies. Our results showed that mean percentage of area protected in different conservation scenarios vary between 14 to 17%. However, there is also a great variation in the coverage of area protection, some ecoregions having *ca.* 38% of protection whereas others have no protection at all. We should notice the relative high proportion (> 0.55) of area still available for conservation in the combined set of urgency and cost-effective ecoregions – which offers a unique opportunity to review carefully a possible implementation of protected areas especially in Africa, Tropical Andes and southeast Asia.

Loucks *et al.* (2008) have demonstrated that, globally, species endemism, species richness, and to a lesser extent threatened species explained better the global pattern of protected area coverage. Indeed, endemism level has long been highlighted for conservation of species

(Lamoreux *et al.*, 2006, Loyola *et al.*, 2007), however in the Indo-Malayan realm (a combination of continental and insular ecoregions), protected areas are inversely related to endemism (Loucks *et al.*, 2008). Although this appears to be an exception to the global pattern, it is of concern given that ecoregions situated in this realm figure as high priority and irreplaceable in our conservation scenarios for carnivores. Finally, while our urgency scenario harbors the highest predicted human population density for 2015, the cost-effective scenario exhibits the lowest. As high human population density is the ultimate cause driving species extinction risk (Cardillo *et al.*, 2004), and acts in synergy with species biological traits, the resulting scenario from the combination of urgency and cost-effective would, arguably, yield best return of investments at ecoregion scale. Minimizing economic costs while maximizing the conservation of species needing an urgent intervention could help to reduce the current “knowing-doing gap” that exists in conservation assessment science (Pfeffer & Sutton, 1999).

At last, we must acknowledge that a prioritization analysis like the one presented here should be considered more indicative than prescriptive. It should be considered by conservation planners as a quick and coarse grain view of potential costs in achieving a particular conservation goal (Valenzuela-Galván & Vázquez, 2008). The identification of a comprehensive set of natural areas is only a first step towards an *in-situ* biodiversity maintenance strategy, which subtends a much more complex process of policy negotiation and implementation (Loyola *et al.*, 2008a). Final decisions should ideally be based on comparing alternatives and involving different institutions (Pressey *et al.*, 1997). While our scenarios are no substitute for this negotiation process, they are part of a wide-ranging effort to strengthen the scientific basis for conservation decisions (Mittermeier *et al.*, 2004; Soutullo *et al.*, 2007), which will be most enlightened if conservation research focuses on socioeconomic factors such as the economic costs of conservation action (Bode *et al.*, 2008), and the extinction risk of species driven by their biological traits.

Acknowledgements

RDL was supported by CNPq (140267/2005-0). LGROS was supported by a CAPES MSc fellowship. MAN and UK were funded by FAPESP (06/56889-2) and CAPES, respectively. JAFDF research has been supported by grants from CNPq (301259/2005-4 and 470918/2006-3) and FUNAPE-UFG. TML was funded by FAPESP (04/15482-1) and CNPq (306049/2004-0).

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Table 1. Summary results for the three systematic planning scenarios for conservation of the World's carnivores

Conservation goal	Conservation scenario			
	Minimum ecoregion	Cost-effective	Urgency	Cost-effective + Urgency
N° ecoregions	41	44	43	60
N° highly irreplaceable ecoregions	14	16	13	16
Mean land cost (x1000 US\$ km ⁻²)	980.12 (± 2039.69)	782.28 (± 2039.69)	962.41 (± 2033.11)	725.01 (± 1965.30)
Mean proportion protected area	0.17 (±0. 21)	0.15 (±0. 21)	0.16 (±0. 21)	0.14 (± 0.19)
Mean proportion land-use area	0.31 (± 0.26)	0.36 (± 0.27)	0.31 (± 0.27)	0.34 (± 0.28)
Mean proportion available area	0.53 (± 0.28)	0.50 (± 0.28)	0.55 (± 0.28)	0.53 (± 0.27)
Mean pop. density 2015 (peoples km ⁻²)	6.28 (± 17.61)	5.72 (± 16.94)	6.54 (± 17.36)	6.05 (± 16.05)
Total area (x10,000 km ²)	1,026.75	903.09	867.10	1,091.90

Figure legends

Figure 1. Pattern in species richness (A), and spatial patterns of irreplaceability in the three different conservation planning scenarios: minimum ecoregion (B), cost-effective (C), and urgency (D). Irreplaceability was estimated by the frequency of ecoregions in the 100 optimal solutions obtained with the 236 species of carnivores found in 661 ecoregions of the World.

Figure 2. Minimum sets of ecoregions for representation of the World's carnivores in the three different conservation planning scenarios: minimum ecoregion (A), and cost-effective + urgency (B).

Figure 3. Congruence of ecoregions in the three different conservation planning scenarios. Note the relatively high number of ecoregions shared by all conservation plans and by the cost-effective and urgency ones. Percentages are of total number of ecoregions represented in three conservation planning scenarios (see Material and Methods).

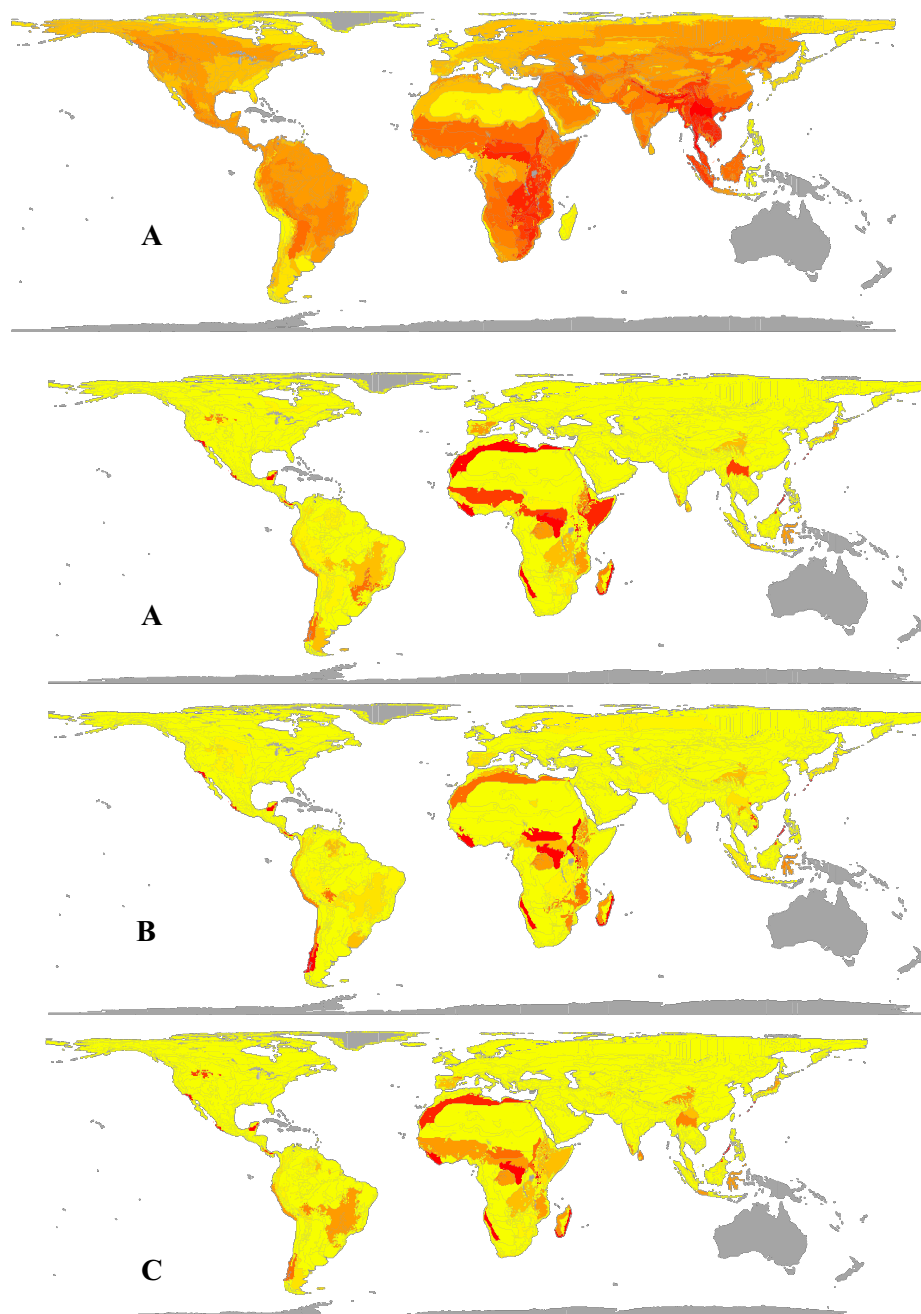
Figure 1

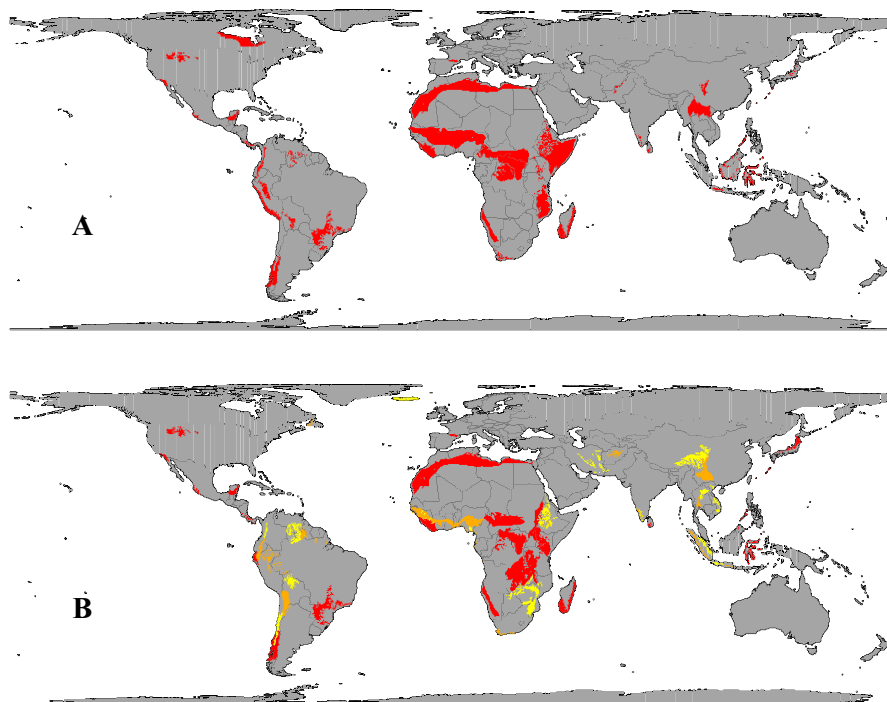
Figure 2

Figure 3

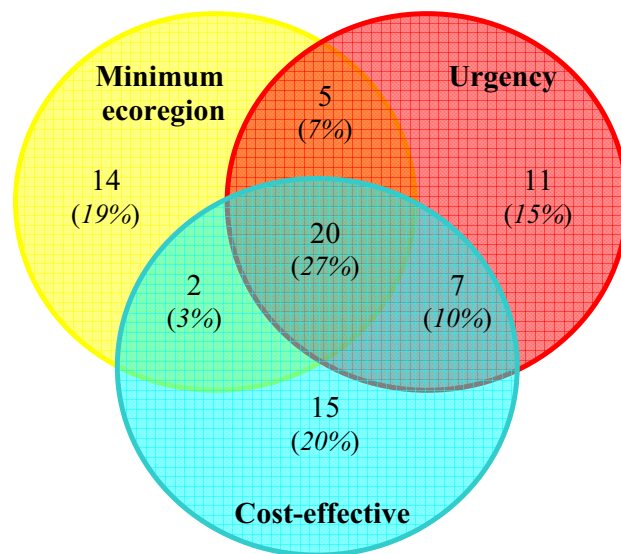


Table S1. Priority ecoregions for conserving the World’s carnivores included (indicated by “x”) in optimal sets under a minimum-ecoregion scenario, a cost-effective scenario, and a urgency scenario – along with their irreplaceability values. Ecoregion area obtained from WWF (2006).

Code	Name	Área (km ²)	Irreplaceability value in the scenario			Presence in the scenario		
			Minimum ecoregion	Cost effective	Urgency	Minimum ecoregion	Cost effective	Urgency
AA0123	Sulawesi lowland rain forests	115,810	0.50	0.48	0.50	1	1	1
AA0124	Sulawesi montane rain forests	75,472	0.50	0.52	0.50	0	0	0
AA0201	Lesser Sunda deciduous forests	39,281	0.00	0.00	0.00	0	0	0
AT0101	Albertine Rift montane forests	103,404	0.00	0.00	0.00	0	0	0
AT0102	Atlantic Equatorial coastal forests	188,821	0.00	0.00	0.00	0	0	0
AT0103	Cameroonian Highlands forests	37,879	0.04	0.00	0.07	0	0	0
AT0104	Central Congolian lowland forests	412,882	0.47	0.45	0.41	1	0	0
AT0106	Cross-Niger transition forests	20,629	0.01	0.21	0.13	0	1	0
AT0107	Cross-Sanaga-Bioko coastal forests	51,840	0.04	0.00	0.09	0	0	0
AT0108	East African montane forests	65,199	1.00	1.00	1.00	1	1	1
AT0109	Eastern Arc forests	23,556	0.00	0.00	0.00	0	0	0
AT0110	Eastern Congolian swamp forests	92,315	0.53	0.55	0.59	0	1	1
AT0111	Eastern Guinean forests	188,895	0.00	0.00	0.00	0	0	0
AT0112	Ethiopian montane forests	247,734	0.01	0.00	0.03	0	0	0
AT0114	Guinean montane forests	30,924	0.06	1.00	0.13	0	1	0
AT0115	Knysna-Amatole montane forests	3,061	0.07	0.00	0.00	0	0	0
AT0116	KwaZulu-Cape coastal forest mosaic	17,779	0.04	0.00	0.00	0	0	0
AT0117	Madagascar lowland forests	111,760	1.00	1.00	1.00	1	1	1
AT0118	Madagascar subhumid forests	198,972	0.00	0.00	0.00	0	0	0
AT0119	Maputaland coastal forest mosaic	30,146	0.09	0.45	0.07	0	0	0

AT0121	Mount Cameroon and Bioko montane forests	1,141	0.07	0.00	0.07	0	0	0
AT0122	Niger Delta swamp forests	14,343	0.01	0.00	0.03	0	0	0
AT0123	Nigerian lowland forests	67,043	0.00	0.00	0.00	0	0	0
AT0124	Northeastern Congolian lowland forests	531,067	1.00	1.00	1.00	1	1	1
AT0125	Northern Zanzibar-Inhambane coastal forest mosaic	112,151	0.00	0.00	0.00	0	0	0
AT0126	Northwestern Congolian lowland forests	432,190	0.02	0.00	0.07	0	0	0
AT0128	Southern Zanzibar-Inhambane coastal forest mosaic	146,463	0.00	0.00	0.02	0	0	0
AT0129	Western Congolian swamp forests	128,060	0.00	0.00	0.00	0	0	0
AT0130	Western Guinean lowland forests	204,226	1.00	1.00	1.00	1	1	1
AT0202	Madagascar dry deciduous forests	151,564	0.51	0.46	0.42	0	0	0
AT0203	Zambezian <i>Cryptosepalum</i> dry forests	38,085	0.00	0.00	0.00	0	0	0
AT0701	Angolan Miombo woodlands	657,515	0.03	0.00	0.03	0	0	0
AT0702	Angolan Mopane woodlands	133,028	0.00	0.00	0.00	0	0	0
AT0704	Central Zambezian Miombo woodlands	1,179,319	0.32	0.11	0.34	0	1	1
AT0705	East Sudanian savanna	913,702	0.20	1.00	0.66	0	1	1
AT0706	Eastern Miombo woodlands	482,013	0.42	0.70	0.45	1	0	0
AT0707	Guinean forest-savanna mosaic	670,790	0.14	0.00	0.43	0	0	1
AT0708	Itigi-Sumbu thicket	7,809	0.12	0.11	0.05	0	0	0
AT0709	Kalahari Acacia-Baikiaea woodlands	334,545	0.00	0.00	0.00	0	0	0
AT0710	Mandara Plateau mosaic	7,479	0.00	0.00	0.00	0	0	0
AT0711	Northern Acacia-Commiphora bushlands and thickets	324,482	0.08	0.43	0.25	0	1	1
AT0712	Northern Congolian forest-savanna mosaic	705,006	0.79	0.31	0.41	1	0	0
AT0713	Sahelian Acacia savanna	3,042,451	0.04	0.00	0.02	0	0	0
AT0714	Serengeti volcanic grasslands	17,948	0.00	0.00	0.00	0	0	0
AT0715	Somali Acacia-Commiphora bushlands and thickets	1,049,301	0.83	0.00	0.40	1	0	0
AT0716	Southern Acacia-Commiphora bushlands and thickets	226,770	0.03	0.08	0.03	0	0	0

AT0717	Southern Africa bushveld	222,541	0.18	0.00	0.16	0	0	0
AT0718	Southern Congolian forest-savanna mosaic	567,187	0.00	0.00	0.00	0	0	0
AT0719	Southern Miombo woodlands	406,913	0.00	0.00	0.01	0	0	0
AT0721	Victoria Basin forest-savanna mosaic	165,042	0.04	0.00	0.05	0	0	0
AT0722	West Sudanian savanna	1,631,860	0.80	0.00	0.44	1	0	0
AT0723	Western Congolian forest-savanna mosaic	411,615	0.00	0.00	0.00	0	0	0
AT0724	Western Zambezian grasslands	33,890	0.00	0.00	0.00	0	0	0
AT0725	Zambezian and Mopane woodlands	471,874	0.25	0.55	0.19	0	1	0
AT0726	Zambezian Baikiaea woodlands	263,554	0.05	0.00	0.03	0	0	0
AT0801	Al Hajar montane woodlands	25,485	0.00	0.00	0.00	0	0	0
AT0901	East African halophytics	2,626	0.00	0.00	0.00	0	0	0
AT0902	Etosha Pan halophytics	7,208	0.00	0.00	0.00	0	0	0
AT0903	Inner Niger Delta flooded savanna	45,868	0.00	0.00	0.00	0	0	0
AT0904	Lake Chad flooded savanna	18,761	0.00	0.00	0.00	0	0	0
AT0905	Saharan flooded grasslands	178,952	0.00	0.00	0.00	0	0	0
AT0906	Zambezian coastal flooded savanna	19,484	0.00	0.00	0.00	0	0	0
AT0907	Zambezian flooded grasslands	152,878	0.00	0.00	0.00	0	0	0
AT0908	Zambezian halophytics	30,289	0.00	0.00	0.00	0	0	0
AT1001	Angolan montane forest-grassland mosaic	25,418	0.03	0.00	0.07	0	0	0
AT1002	Angolan scarp savanna and woodlands	74,055	0.00	0.00	0.00	0	0	0
AT1003	Drakensberg alti-montane grasslands and woodlands	11,894	0.00	0.00	0.00	0	0	0
AT1004	Drakensberg montane grasslands, woodlands and forests	201,962	0.06	0.00	0.00	0	0	0
AT1005	East African montane moorlands	3,273	0.00	0.00	0.00	0	0	0
AT1006	Eastern Zimbabwe montane forest-grassland mosaic	7,804	0.00	0.00	0.00	0	0	0
AT1007	Ethiopian montane grasslands and woodlands	244,349	0.51	0.48	0.31	1	1	0
AT1008	Ethiopian montane moorlands	25,049	0.49	0.52	0.69	0	0	1

AT1009	Highveld grasslands	185,863	0.00	0.00	0.00	0	0	0
AT1010	Jos Plateau forest-grassland mosaic	13,281	0.00	0.00	0.00	0	0	0
AT1011	Madagascar ericoid thickets	1,273	0.00	0.00	0.00	0	0	0
AT1012	Maputaland-Pondoland bushland and thickets	19,515	0.10	0.00	0.15	0	0	0
AT1013	Rwenzori-Virunga montane moorlands	2,661	0.00	0.00	0.00	0	0	0
AT1014	South Malawi montane forest-grassland mosaic	10,191	0.00	0.00	0.00	0	0	0
AT1015	Southern Rift montane forest-grassland mosaic	33,360	0.00	0.00	0.00	0	0	0
AT1201	Albany thickets	17,084	0.05	0.00	0.11	0	0	0
AT1202	Lowland fynbos and renosterveld	32,744	0.10	0.00	0.22	0	0	1
AT1203	Montane fynbos and renosterveld	45,780	0.06	0.00	0.10	1	0	0
AT1302	Arabian Peninsula coastal fog desert	82,689	0.00	0.00	0.01	0	0	0
AT1303	East Saharan montane xeric woodlands	27,775	0.01	0.00	0.00	0	0	0
AT1304	Eritrean coastal desert	4,577	0.03	0.00	0.03	0	0	0
AT1305	Ethiopian xeric grasslands and shrublands	151,869	0.02	0.00	0.02	0	0	0
AT1306	Gulf of Oman desert and semi-desert	62,297	0.00	0.00	0.00	0	0	0
AT1307	Hobyos grasslands and shrublands	25,454	0.00	0.00	0.00	0	0	0
AT1309	Kalahari xeric savanna	586,846	0.00	0.00	0.00	0	0	0
AT1310	Kaokoveld desert	45,585	0.00	0.00	0.00	0	0	0
AT1311	Madagascar spiny thickets	43,294	1.00	1.00	1.00	1	1	1
AT1312	Madagascar succulent woodlands	79,496	0.49	0.54	0.58	1	1	1
AT1313	Masai xeric grasslands and shrublands	100,505	0.09	0.57	0.35	0	0	0
AT1314	Nama Karoo	350,726	0.00	0.00	0.00	0	0	0
AT1315	Namib desert	80,689	0.00	0.00	0.00	0	0	0
AT1316	Namibian savanna woodlands	224,903	1.00	1.00	1.00	1	1	1
AT1319	Somali montane xeric woodlands	62,375	0.00	0.00	0.00	0	0	0
AT1320	Southwestern Arabian foothills savanna	273,758	0.00	0.00	0.00	0	0	0

AT1321	Southwestern Arabian montane woodlands	86,632	0.01	0.00	0.00	0	0	0
AT1322	Succulent Karoo	102,585	0.00	0.00	0.00	0	0	0
AT1401	Central African mangroves	30,791	0.02	0.48	0.13	0	0	1
AT1402	East African mangroves	16,013	0.00	0.00	0.00	0	0	0
AT1403	Guinean mangroves	23,419	0.00	0.00	0.00	0	0	0
AT1404	Madagascar mangroves	5,188	0.00	0.00	0.00	0	0	0
AT1405	Southern Africa mangroves	993	0.00	0.00	0.00	0	0	0
IM0102	Borneo lowland rain forests	425,583	0.09	0.09	0.04	0	0	0
IM0103	Borneo montane rain forests	115,078	0.08	0.03	0.12	0	0	0
IM0104	Borneo peat swamp forests	67,172	0.11	0.00	0.02	1	0	0
IM0105	Brahmaputra Valley semi-evergreen forests	56,613	0.00	0.00	0.00	0	0	0
IM0106	Cardamom Mountains rain forests	44,074	0.00	0.00	0.00	0	0	0
IM0107	Chao Phraya freshwater swamp forests	38,858	0.03	0.00	0.03	0	0	1
IM0108	Chao Phraya lowland moist deciduous forests	20,337	0.00	0.00	0.01	0	0	0
IM0109	Chin Hills-Arakan Yoma montane forests	29,617	0.00	0.00	0.00	0	0	0
IM0111	Eastern highlands moist deciduous forests	340,171	0.00	0.00	0.00	0	0	0
IM0112	Eastern Java-Bali montane rain forests	15,829	0.08	0.08	0.06	0	0	1
IM0113	Eastern Java-Bali rain forests	53,666	0.06	0.11	0.03	0	0	0
IM0114	Greater Negros-Panay rain forests	34,856	0.00	0.00	0.00	0	0	0
IM0115	Himalayan subtropical broadleaf forests	38,125	0.00	0.00	0.00	0	0	0
IM0116	Irrawaddy freshwater swamp forests	15,107	0.00	0.00	0.03	0	0	0
IM0117	Irrawaddy moist deciduous forests	137,910	0.01	0.00	0.01	0	0	0
IM0118	Jian Nan subtropical evergreen forests	662,292	0.00	0.00	0.00	0	0	0
IM0119	Kayah-Karen montane rain forests	119,158	0.06	0.00	0.03	0	0	0
IM0120	Lower Gangetic Plains moist deciduous forests	253,509	0.00	0.00	0.00	0	0	0
IM0121	Luang Prabang montane rain forests	71,585	0.00	0.50	0.01	0	1	0

IM0122	Luzon montane rain forests	8,273	0.00	0.00	0.00	0	0	0
IM0123	Luzon rain forests	94,877	0.00	0.00	0.00	0	0	0
IM0124	Malabar Coast moist forests	35,331	0.00	0.00	0.00	0	0	0
IM0126	Meghalaya subtropical forests	41,629	0.00	0.00	0.00	0	0	0
IM0127	Mentawai Islands rain forests	6,470	0.00	0.00	0.00	0	0	0
IM0128	Mindanao montane rain forests	18,120	0.00	0.00	0.00	0	0	0
IM0129	Mindanao-Eastern Visayas rain forests	104,667	0.00	0.00	0.00	0	0	0
IM0131	Mizoram-Manipur-Kachin rain forests	135,245	0.01	0.00	0.02	0	0	0
IM0132	Myanmar coastal rain forests	66,332	0.00	0.00	0.03	0	0	0
IM0134	North Western Ghats moist deciduous forests	48,044	0.00	0.00	0.00	0	0	0
IM0135	North Western Ghats montane rain forests	30,825	0.00	0.00	0.00	0	0	0
IM0136	Northern Annamites rain forests	47,053	0.00	0.27	0.00	0	0	0
IM0137	Northern Indochina subtropical forests	435,869	0.79	0.23	0.59	1	0	0
IM0138	Northern Khorat Plateau moist deciduous forests	16,794	0.00	0.00	0.00	0	0	0
IM0139	Northern Thailand-Laos moist deciduous forests	42,010	0.00	0.00	0.02	0	0	0
IM0140	Northern Triangle subtropical forests	53,774	0.00	0.00	0.00	0	0	0
IM0141	Northern Vietnam lowland rain forests	22,522	0.00	0.00	0.00	0	0	0
IM0142	Orissa semi-evergreen forests	22,228	0.00	0.00	0.00	0	0	0
IM0143	Palawan rain forests	14,278	1.00	1.00	1.00	1	1	1
IM0144	Peninsular Malaysian montane rain forests	17,097	0.11	0.00	0.09	0	0	0
IM0145	Peninsular Malaysian peat swamp forests	3,610	0.00	0.00	0.00	0	0	0
IM0146	Peninsular Malaysian rain forests	124,944	0.05	0.00	0.15	0	0	0
IM0147	Red River freshwater swamp forests	10,724	0.02	0.77	0.05	0	1	0
IM0149	South China-Vietnam subtropical evergreen forests	223,724	0.00	0.00	0.00	0	0	0
IM0150	South Western Ghats moist deciduous forests	23,676	0.51	0.46	0.42	1	1	0
IM0151	South Western Ghats montane rain forests	22,545	0.49	0.54	0.58	0	0	1

IM0152	Southern Annamites montane rain forests	46,314	0.00	0.77	0.01	0	1	0
IM0153	Southwest Borneo freshwater swamp forests	36,603	0.07	0.13	0.07	0	0	0
IM0154	Sri Lanka lowland rain forests	12,500	0.46	0.25	0.24	1	1	1
IM0155	Sri Lanka montane rain forests	3,066	0.31	0.39	0.24	0	0	0
IM0156	Sulu Archipelago rain forests	2,326	0.00	0.00	0.00	0	0	0
IM0157	Sumatran freshwater swamp forests	17,995	0.02	0.11	0.08	0	0	0
IM0158	Sumatran lowland rain forests	258,288	0.17	0.17	0.09	0	0	0
IM0159	Sumatran montane rain forests	72,618	0.10	0.21	0.08	0	0	1
IM0160	Sumatran peat swamp forests	87,120	0.06	0.12	0.11	0	1	0
IM0161	Sundaland heath forests	76,205	0.08	0.05	0.07	0	0	0
IM0162	Sundarbans freshwater swamp forests	14,525	0.00	0.00	0.00	0	0	0
IM0163	Tenasserim-South Thailand semi-evergreen rain forests	96,930	0.03	0.00	0.01	0	0	0
IM0164	Tonle Sap freshwater swamp forests	25,926	0.01	0.00	0.02	0	0	0
IM0165	Tonle Sap-Mekong peat swamp forests	29,262	0.00	0.00	0.04	0	0	0
IM0166	Upper Gangetic Plains moist deciduous forests	262,643	0.00	0.00	0.00	0	0	0
IM0167	Western Java montane rain forests	26,171	0.39	0.40	0.45	1	1	0
IM0168	Western Java rain forests	41,481	0.47	0.41	0.46	0	0	0
IM0169	Hainan Island monsoon rain forests	15,489	0.00	0.00	0.00	0	0	0
IM0170	Nansei Islands subtropical evergreen forests	4,064	1.00	1.00	1.00	1	1	1
IM0171	South Taiwan monsoon rain forests	2,570	0.00	0.00	0.00	0	0	0
IM0172	Taiwan subtropical evergreen forests	33,322	0.00	0.00	0.00	0	0	0
IM0201	Central Deccan Plateau dry deciduous forests	239,409	0.00	0.00	0.00	0	0	0
IM0202	Central Indochina dry forests	318,937	0.01	0.00	0.04	0	0	0
IM0203	Chhota-Nagpur dry deciduous forests	122,134	0.00	0.00	0.00	0	0	0
IM0204	East Deccan dry-evergreen forests	25,432	0.00	0.00	0.00	0	0	0
IM0205	Irrawaddy dry forests	34,987	0.01	0.00	0.01	0	0	0

IM0206	Khathiar-Gir dry deciduous forests	266,386	0.00	0.00	0.00	0	0	0
IM0207	Narmada Valley dry deciduous forests	169,458	0.00	0.00	0.00	0	0	0
IM0208	Northern dry deciduous forests	58,154	0.00	0.00	0.00	0	0	0
IM0209	South Deccan Plateau dry deciduous forests	81,925	0.00	0.00	0.00	0	0	0
IM0210	Southeastern Indochina dry evergreen forests	123,784	0.00	0.00	0.00	0	0	0
IM0211	Southern Vietnam lowland dry forests	34,905	0.00	0.00	0.03	0	0	0
IM0212	Sri Lanka dry-zone dry evergreen forests	48,213	0.23	0.36	0.52	0	0	0
IM0301	Himalayan subtropical pine forests	76,125	0.01	0.00	0.00	0	0	0
IM0303	Northeast India-Myanmar pine forests	9,685	0.00	0.00	0.00	0	0	0
IM0304	Sumatran tropical pine forests	2,748	0.00	0.00	0.00	0	0	0
IM0401	Eastern Himalayan broadleaf forests	82,916	0.01	0.00	0.02	0	0	0
IM0402	Northern Triangle temperate forests	10,709	0.00	0.00	0.00	0	0	0
IM0403	Western Himalayan broadleaf forests	55,825	0.00	0.00	0.00	0	0	0
IM0501	Eastern Himalayan subalpine conifer forests	27,436	0.00	0.00	0.00	0	0	0
IM0502	Western Himalayan subalpine conifer forests	39,650	0.00	0.00	0.00	0	0	0
IM0701	Terai-Duar savanna and grasslands	34,524	0.00	0.00	0.02	0	0	0
IM0901	Rann of Kutch seasonal salt marsh	27,839	0.00	0.00	0.00	0	0	0
IM1001	Kinabalu montane alpine meadows	4,320	1.00	1.00	1.00	1	1	1
IM1301	Deccan thorn scrub forests	339,068	0.00	0.00	0.00	0	0	0
IM1302	Indus Valley desert	19,479	0.00	0.00	0.00	0	0	0
IM1303	Northwestern thorn scrub forests	487,535	0.00	0.00	0.00	0	0	0
IM1304	Thar desert	238,254	0.00	0.00	0.00	0	0	0
IM1401	Goadavari-Krishna mangroves	6,980	0.00	0.00	0.00	0	0	0
IM1402	Indochina mangroves	26,762	0.01	0.00	0.01	0	0	0
IM1403	Indus River Delta-Arabian Sea mangroves	5,779	0.00	0.00	0.00	0	0	0
IM1404	Myanmar Coast mangroves	21,238	0.01	0.00	0.02	0	0	0

IM1405	Sunda Shelf mangroves	37,280	0.06	0.09	0.08	0	0	0
IM1406	Sundarbans mangroves	20,383	0.00	0.00	0.00	0	0	0
NA0201	Sonoran-Sinaloa transition subtropical dry forest	50,903	0.00	0.00	0.00	0	0	0
NA0302	Sierra Madre Occidental pine-oak forests	222,334	0.00	0.00	0.00	0	0	0
NA0303	Sierra Madre Oriental pine-oak forests	65,496	0.00	0.00	0.00	0	0	0
NA0401	Allegheny Highlands forests	84,011	0.00	0.00	0.00	0	0	0
NA0402	Appalachian mixed mesophytic forests	192,264	0.00	0.00	0.00	0	0	0
NA0403	Appalachian-Blue Ridge forests	159,343	0.00	0.00	0.00	0	0	0
NA0404	Central U.S. hardwood forests	296,135	0.00	0.00	0.00	0	0	0
NA0405	East Central Texas forests	52,583	0.00	0.00	0.00	0	0	0
NA0406	Eastern forest-boreal transition	348,614	0.00	0.05	0.00	0	0	0
NA0407	Eastern Great Lakes lowland forests	116,673	0.00	0.02	0.00	0	0	0
NA0408	Gulf of St. Lawrence lowland forests	39,516	0.00	0.00	0.00	0	0	0
NA0409	Mississippi lowland forests	112,240	0.00	0.00	0.00	0	0	0
NA0410	New England-Acadian forests	238,153	0.00	0.00	0.01	0	0	0
NA0411	Northeastern coastal forests	89,778	0.00	0.00	0.00	0	0	0
NA0412	Ozark Mountain forests	62,008	0.00	0.00	0.00	0	0	0
NA0413	Southeastern mixed forests	347,724	0.00	0.00	0.00	0	0	0
NA0414	Southern Great Lakes forests	244,828	0.00	0.00	0.00	0	0	0
NA0415	Upper Midwest forest-savanna transition	166,477	0.00	0.00	0.00	0	0	0
NA0416	Western Great Lakes forests	274,721	0.00	0.00	0.00	0	0	0
NA0417	Willamette Valley forests	14,883	0.00	0.00	0.00	0	0	0
NA0501	Alberta Mountain forests	39,933	0.01	0.00	0.00	0	0	0
NA0502	Alberta-British Columbia foothills forests	121,017	0.02	0.07	0.01	0	0	0
NA0503	Arizona Mountains forests	109,052	0.00	0.00	0.00	0	0	0
NA0504	Atlantic coastal pine barrens	8,975	0.00	0.00	0.00	0	0	0

NA0505	Blue Mountains forests	64,844	0.00	0.00	0.01	0	0	0
NA0506	British Columbia mainland coastal forests	137,750	0.00	0.08	0.00	0	0	0
NA0507	Cascade Mountains leeward forests	46,451	0.00	0.06	0.00	0	0	0
NA0508	Central and Southern Cascades forests	44,950	0.00	0.00	0.00	0	0	0
NA0509	Central British Columbia Mountain forests	72,090	0.00	0.04	0.02	0	0	0
NA0510	Central Pacific coastal forests	73,863	0.00	0.00	0.00	0	0	0
NA0511	Colorado Rockies forests	132,841	0.07	0.10	0.04	0	0	0
NA0512	Eastern Cascades forests	55,299	0.00	0.00	0.00	0	0	0
NA0513	Florida sand pine scrub	3,879	0.00	0.00	0.00	0	0	0
NA0514	Fraser Plateau and Basin complex	137,636	0.00	0.06	0.00	0	0	0
NA0515	Great Basin montane forests	5,788	0.00	0.00	0.00	0	0	0
NA0516	Klamath-Siskiyou forests	50,370	0.00	0.00	0.01	0	0	0
NA0517	Middle Atlantic coastal forests	133,597	0.00	0.00	0.00	0	0	0
NA0518	North Central Rockies forests	246,515	0.00	0.04	0.00	0	0	0
NA0519	Northern California coastal forests	13,287	0.00	0.00	0.00	0	0	0
NA0520	Northern Pacific coastal forests	60,755	0.01	0.06	0.00	0	0	0
NA0521	Northern transitional alpine forests	25,783	0.00	0.02	0.00	0	0	0
NA0522	Okanagan dry forests	53,496	0.01	0.06	0.00	0	0	0
NA0523	Piney Woods forests	140,797	0.00	0.00	0.00	0	0	0
NA0524	Puget lowland forests	22,605	0.00	0.00	0.00	0	0	0
NA0525	Queen Charlotte Islands	9,999	0.00	0.00	0.00	0	0	0
NA0526	Sierra Juarez and San Pedro Martir pine-oak forests	4,002	0.00	0.00	0.00	0	0	0
NA0527	Sierra Nevada forests	52,872	0.00	0.00	0.00	0	0	0
NA0528	South Central Rockies forests	159,693	0.56	0.21	0.76	1	1	1
NA0529	Southeastern conifer forests	236,352	0.00	0.00	0.00	0	0	0
NA0530	Wasatch and Uinta montane forests	41,509	0.00	0.00	0.00	0	0	0

NA0601	Alaska Peninsula montane taiga	48,043	0.00	0.00	0.00	0	0	0
NA0602	Central Canadian Shield forests	463,345	0.13	0.02	0.01	0	0	0
NA0603	Cook Inlet taiga	28,015	0.00	0.00	0.03	0	0	0
NA0604	Copper Plateau taiga	17,275	0.00	0.00	0.00	0	0	0
NA0605	Eastern Canadian forests	488,587	0.06	0.01	0.02	0	0	0
NA0606	Eastern Canadian Shield taiga	757,250	0.01	0.00	0.00	0	0	0
NA0607	Interior Alaska-Yukon lowland taiga	446,261	0.00	0.00	0.04	0	0	0
NA0608	Mid-Continental Canadian forests	369,628	0.00	0.02	0.01	0	0	0
NA0609	Midwestern Canadian Shield forests	548,394	0.05	0.02	0.02	0	0	0
NA0610	Muskwa-Slave Lake forests	263,806	0.00	0.01	0.00	0	0	0
NA0611	Newfoundland Highland forests	16,391	0.01	0.00	0.03	0	0	1
NA0612	Northern Canadian Shield taiga	617,319	0.02	0.00	0.05	0	0	0
NA0613	Northern Cordillera forests	264,234	0.00	0.03	0.01	0	0	0
NA0614	Northwest Territories taiga	348,147	0.01	0.00	0.00	0	0	0
NA0615	South Avalon-Burin oceanic barrens	2,035	0.00	0.00	0.00	0	0	0
NA0616	Southern Hudson Bay taiga	375,339	0.10	0.07	0.02	1	0	0
NA0617	Yukon Interior dry forests	62,742	0.00	0.00	0.00	0	0	0
NA0701	Western Gulf coastal grasslands	80,515	0.00	0.00	0.00	0	0	0
NA0801	California Central Valley grasslands	55,084	0.00	0.00	0.00	0	0	0
NA0802	Canadian Aspen forests and parklands	399,039	0.00	0.02	0.02	0	0	0
NA0803	Central and Southern mixed grasslands	282,267	0.04	0.08	0.01	0	0	0
NA0804	Central forest-grasslands transition	407,235	0.00	0.00	0.00	0	0	0
NA0805	Central tall grasslands	248,867	0.00	0.00	0.00	0	0	0
NA0806	Edwards Plateau savanna	61,734	0.00	0.00	0.00	0	0	0
NA0807	Flint Hills tall grasslands	29,632	0.00	0.00	0.00	0	0	0
NA0808	Montana Valley and Foothill grasslands	81,929	0.00	0.00	0.00	0	0	0

NA0809	Nebraska Sand Hills mixed grasslands	61,212	0.05	0.12	0.05	0	0	0
NA0810	Northern mixed grasslands	219,614	0.00	0.00	0.00	0	0	0
NA0811	Northern short grasslands	640,109	0.08	0.15	0.02	0	0	0
NA0812	Northern tall grasslands	76,259	0.01	0.01	0.00	0	0	0
NA0813	Palouse grasslands	46,993	0.00	0.01	0.00	0	0	0
NA0814	Texas blackland prairies	50,215	0.00	0.00	0.00	0	0	0
NA0815	Western short grasslands	435,313	0.04	0.11	0.03	0	0	0
NA1101	Alaska-St. Elias Range tundra	152,718	0.00	0.00	0.02	0	0	0
NA1103	Arctic coastal tundra	98,909	0.00	0.00	0.02	0	0	0
NA1104	Arctic foothills tundra	130,032	0.02	0.00	0.04	0	0	0
NA1105	Baffin coastal tundra	9,172	0.00	0.00	0.02	0	0	0
NA1106	Beringia lowland tundra	151,820	0.01	0.00	0.05	0	0	0
NA1107	Beringia upland tundra	97,953	0.00	0.00	0.00	0	0	0
NA1108	Brooks-British Range tundra	160,646	0.01	0.00	0.06	0	0	0
NA1109	Davis Highlands tundra	88,523	0.00	0.00	0.00	0	0	0
NA1110	High Arctic tundra	467,509	0.03	0.00	0.00	0	0	0
NA1111	Interior Yukon-Alaska alpine tundra	234,132	0.01	0.00	0.01	0	0	0
NA1112	Kalaallit Nunaat high arctic tundra	306,129	0.00	0.00	0.02	0	0	0
NA1113	Kalaallit Nunaat low arctic tundra	172,182	0.02	0.00	0.05	0	0	0
NA1114	Low Arctic tundra	801,765	0.00	0.00	0.03	0	0	0
NA1115	Middle Arctic tundra	1,040,236	0.02	0.00	0.00	0	0	0
NA1116	Ogilvie-MacKenzie alpine tundra	209,808	0.01	0.00	0.04	0	0	0
NA1117	Pacific Coastal Mountain icefields and tundra	107,362	0.10	0.01	0.07	0	0	0
NA1118	Torngat Mountain tundra	32,463	0.00	0.00	0.06	0	0	0
NA1201	California coastal sage and chaparral	36,249	1.00	1.00	1.00	1	1	1
NA1202	California interior chaparral and woodlands	64,627	0.00	0.00	0.00	0	0	0

NA1203	California montane chaparral and woodlands	20,407	0.00	0.00	0.00	0	0	0
NA1301	Baja California desert	77,590	0.00	0.00	0.00	0	0	0
NA1302	Central Mexican matorral	59,195	0.00	0.00	0.00	0	0	0
NA1303	Chihuahuan desert	508,892	0.00	0.00	0.00	0	0	0
NA1304	Colorado Plateau shrublands	326,501	0.05	0.11	0.04	0	0	0
NA1305	Great Basin shrub steppe	336,212	0.00	0.00	0.00	0	0	0
NA1306	Gulf of California xeric scrub	23,537	0.00	0.00	0.00	0	0	0
NA1307	Meseta Central matorral	124,975	0.00	0.00	0.00	0	0	0
NA1308	Mojave desert	130,647	0.00	0.00	0.00	0	0	0
NA1309	Snake-Columbia shrub steppe	218,533	0.00	0.00	0.01	0	0	0
NA1310	Sonoran desert	222,843	0.00	0.00	0.00	0	0	0
NA1311	Tamaulipan matorral	16,237	0.00	0.00	0.00	0	0	0
NA1312	Tamaulipan mezquital	141,231	0.00	0.00	0.00	0	0	0
NA1313	Wyoming Basin shrub steppe	132,577	0.11	0.12	0.05	0	0	0
NT0101	Araucaria moist forests	215,673	0.00	0.00	0.00	0	0	0
NT0102	Atlantic Coast restingas	7,850	0.01	0.00	0.02	0	0	0
NT0103	Bahia coastal forests	109,305	0.00	0.00	0.00	0	0	0
NT0104	Bahia interior forests	229,241	0.00	0.10	0.04	0	0	0
NT0105	Bolivian Yungas	90,229	0.09	0.15	0.24	0	0	0
NT0106	Caatinga Enclaves moist forests	4,776	0.00	0.00	0.00	0	0	0
NT0107	Caqueta moist forests	183,358	0.00	0.00	0.00	0	0	0
NT0108	Catatumbo moist forests	22,753	0.00	0.00	0.00	0	0	0
NT0109	Cauca Valley montane forests	31,915	0.18	0.22	0.20	0	1	0
NT0111	Central American Atlantic moist forests	89,450	0.00	0.00	0.00	0	0	0
NT0112	Central American montane forests	13,251	0.00	0.00	0.00	0	0	0
NT0113	Chiapas montane forests	5,759	0.00	0.00	0.00	0	0	0

NT0114	Chimalapas montane forests	2,077	0.00	0.00	0.00	0	0	0
NT0115	Chocó-Darién moist forests	73,305	0.00	0.00	0.00	0	0	0
NT0117	Cordillera La Costa montane forests	14,282	0.00	0.00	0.00	0	0	0
NT0118	Cordillera Oriental montane forests	67,577	0.00	0.00	0.00	0	0	0
NT0119	Costa Rican seasonal moist forests	10,653	0.02	0.00	0.02	0	0	0
NT0121	Eastern Cordillera real montane forests	102,062	0.19	0.00	0.29	0	0	1
NT0122	Eastern Panamanian montane forests	3,031	0.00	0.00	0.00	0	0	0
NT0124	Guianan Highlands moist forests	145,958	0.19	0.32	0.07	0	0	0
NT0125	Guianan moist forests	476,136	0.00	0.00	0.00	0	0	0
NT0126	Gurupa varzeß	9,881	0.00	0.00	0.00	0	0	0
NT0128	Iquitos varzeß	114,506	0.13	0.10	0.11	0	0	1
NT0129	Isthmian-Atlantic moist forests	58,359	0.00	0.00	0.05	0	0	0
NT0130	Isthmian-Pacific moist forests	29,176	0.02	0.00	0.07	0	0	0
NT0132	Japurá-Solimões-Negro moist forests	268,444	0.00	0.00	0.00	0	0	0
NT0133	Juruá-Purus moist forests	241,493	0.00	0.00	0.00	0	0	0
NT0135	Madeira-Tapajós moist forests	716,682	0.00	0.00	0.00	0	0	0
NT0136	Magdalena Valley montane forests	104,598	0.23	0.24	0.19	0	0	0
NT0137	Magdalena-Urabá moist forests	76,440	0.00	0.00	0.00	0	0	0
NT0138	Marajó varzeß	88,305	0.00	0.00	0.00	0	0	0
NT0139	Maranhão Babatu forests	141,635	0.00	0.00	0.00	0	0	0
NT0140	Mato Grosso seasonal forests	412,314	0.01	0.20	0.02	0	0	0
NT0141	Monte Alegre varzeß	66,506	0.00	0.00	0.00	0	0	0
NT0142	Napo moist forests	250,591	0.16	0.06	0.10	0	0	0
NT0143	Negro-Branco moist forests	200,932	0.12	0.00	0.10	0	0	0
NT0144	Northeastern Brazil restingas	10,011	0.00	0.00	0.00	0	0	0
NT0145	Northwestern Andean montane forests	80,806	0.19	0.32	0.22	1	0	0

NT0146	Oaxacan montane forests	7,577	0.00	0.00	0.00	0	0	0
NT0147	Orinoco Delta swamp forests	28,028	0.00	0.00	0.00	0	0	0
NT0148	Pantanos de Centla	17,153	0.00	0.00	0.00	0	0	0
NT0149	Guianan freshwater swamp forests	7,690	0.00	0.00	0.00	0	0	0
NT0150	Alto Paran� Atlantic forests	482,879	0.64	0.13	0.42	1	1	1
NT0151	Pernambuco coastal forests	17,502	0.00	0.00	0.00	0	0	0
NT0152	Pernambuco interior forests	22,597	0.00	0.00	0.00	0	0	0
NT0153	Peruvian Yungas	185,961	0.05	0.00	0.08	0	0	0
NT0154	Pet�n-Veracruz moist forests	148,595	0.00	0.00	0.00	0	0	0
NT0156	Purus varze�	176,760	0.00	0.00	0.00	0	0	0
NT0157	Purus-Madeira moist forests	173,261	0.00	0.00	0.00	0	0	0
NT0158	Rio Negro campinarana	95,986	0.17	0.00	0.11	0	0	0
NT0159	Santa Marta montane forests	4,766	0.00	0.00	0.00	0	0	0
NT0160	Serra do Mar coastal forests	104,610	0.01	0.00	0.00	0	0	0
NT0161	Sierra de los Tuxtlas	3,890	0.00	0.00	0.00	0	0	0
NT0162	Sierra Madre de Chiapas moist forests	11,218	0.00	0.00	0.00	0	0	0
NT0163	Solim�es-Japur� moist forests	166,931	0.00	0.00	0.00	0	0	0
NT0164	South Florida rocklands	2,071	0.00	0.00	0.00	0	0	0
NT0165	Southern Andean Yungas	75,150	0.07	0.00	0.09	0	0	0
NT0166	Southwest Amazon moist forests	746,653	0.17	0.12	0.08	0	0	0
NT0167	Talamancan montane forests	16,274	0.98	1.00	0.93	1	1	1
NT0168	Tapaj�s-Xingu moist forests	335,099	0.00	0.00	0.00	0	0	0
NT0169	Pantepui	50,675	0.20	0.39	0.22	1	0	0
NT0170	Tocantins/Pindare moist forests	192,766	0.00	0.00	0.00	0	0	0
NT0171	Trinidad and Tobago moist forests	4,722	0.00	0.00	0.00	0	0	0
NT0173	Uatuma-Trombetas moist forests	470,048	0.00	0.00	0.00	0	0	0

NT0174	Ucayali moist forests	114,443	0.23	0.06	0.11	1	0	0
NT0175	Venezuelan Andes montane forests	29,269	0.00	0.00	0.00	0	0	0
NT0176	Veracruz moist forests	68,946	0.00	0.00	0.00	0	0	0
NT0177	Veracruz montane forests	4,942	0.00	0.00	0.00	0	0	0
NT0178	Western Ecuador moist forests	33,954	0.00	0.00	0.00	0	0	0
NT0180	Xingu-Tocantins-Araguaia moist forests	265,072	0.00	0.00	0.00	0	0	0
NT0181	Yucatán moist forests	69,482	1.00	1.00	1.00	1	1	1
NT0182	Guianan piedmont and lowland moist forests	229,836	0.20	0.29	0.18	0	1	0
NT0201	Apure-Villavicencio dry forests	68,245	0.00	0.00	0.00	0	0	0
NT0202	Atlantic dry forests	114,660	0.01	0.14	0.02	0	0	0
NT0204	Bajío dry forests	37,384	0.00	0.00	0.00	0	0	0
NT0205	Balsas dry forests	62,247	0.00	0.00	0.00	0	0	0
NT0206	Bolivian montane dry forests	72,780	0.11	0.16	0.14	1	0	0
NT0207	Cauca Valley dry forests	7,313	0.00	0.00	0.00	0	0	0
NT0209	Central American dry forests	67,773	0.00	0.00	0.00	0	0	0
NT0210	Dry Chaco	786,790	0.17	0.00	0.06	0	0	0
NT0211	Chiapas Depression dry forests	13,974	0.00	0.00	0.00	0	0	0
NT0212	Chiquitano dry forests	229,767	0.01	0.28	0.01	0	0	0
NT0214	Ecuadorian dry forests	21,187	0.00	0.00	0.00	0	0	0
NT0217	Jalisco dry forests	26,050	1.00	1.00	1.00	1	1	1
NT0219	Lara-Falcón dry forests	16,870	0.00	0.00	0.00	0	0	0
NT0220	Lesser Antillean dry forests	907	0.00	0.00	0.00	0	0	0
NT0221	Magdalena Valley dry forests	19,549	0.00	0.00	0.00	0	0	0
NT0222	Maracaibo dry forests	30,085	0.00	0.00	0.00	0	0	0
NT0223	Maracaibo dry forests	11,322	0.00	0.00	0.00	0	0	0
NT0224	Panamanian dry forests	5,087	0.00	0.00	0.00	0	0	0

NT0225	Patpa Valley dry forests	2,261	0.00	0.00	0.00	0	0	0
NT0227	Sierra de la Laguna dry forests	3,975	0.00	0.00	0.00	0	0	0
NT0228	Sinaloa dry forests	77,362	0.00	0.00	0.00	0	0	0
NT0229	Sin. Valley dry forests	24,879	0.00	0.00	0.00	0	0	0
NT0230	Southern Pacific dry forests	42,282	0.00	0.00	0.00	0	0	0
NT0232	Tumbes-Piura dry forests	41,100	0.40	0.43	0.50	0	1	1
NT0233	Veracruz dry forests	6,616	0.00	0.00	0.00	0	0	0
NT0235	Yucatán dry forests	49,623	0.00	0.00	0.00	0	0	0
NT0302	Belizian pine forests	2,822	0.00	0.00	0.00	0	0	0
NT0303	Central American pine-oak forests	110,942	0.00	0.00	0.00	0	0	0
NT0306	Miskito pine forests	18,854	0.00	0.00	0.00	0	0	0
NT0307	Sierra de la Laguna pine-oak forests	1,061	0.00	0.00	0.00	0	0	0
NT0308	Sierra Madre de Oaxaca pine-oak forests	14,298	0.00	0.00	0.00	0	0	0
NT0309	Sierra Madre del Sur pine-oak forests	60,973	0.00	0.00	0.00	0	0	0
NT0310	Trans-Mexican Volcanic Belt pine-oak forests	92,026	0.00	0.00	0.00	0	0	0
NT0402	Magellanic subpolar forests	164,642	0.01	0.00	0.00	0	0	0
NT0404	Valdivian temperate forests	248,398	0.62	1.00	0.70	1	1	1
NT0702	Beni savanna	125,589	0.31	0.66	0.60	0	1	0
NT0703	Campos Rupestres montane savanna	26,313	0.01	0.05	0.00	0	0	0
NT0704	Cerrado	1,910,038	0.32	0.24	0.49	0	0	0
NT0707	Guianan savanna	104,494	0.12	0.00	0.32	0	0	1
NT0708	Humid Chaco	291,590	0.02	0.01	0.04	0	0	0
NT0709	Llanos	375,787	0.00	0.00	0.00	0	0	0
NT0710	Uruguayan savanna	352,496	0.00	0.34	0.02	0	0	0
NT0801	Espinal	298,735	0.00	0.00	0.00	0	0	0
NT0802	Low Monte	353,640	0.02	0.00	0.03	0	0	0

NT0803	Humid Pampas	398,555	0.00	0.00	0.01	0	0	0
NT0805	Patagonian steppe	576,599	0.35	0.00	0.27	0	0	0
NT0904	Everglades	20,028	0.00	0.00	0.00	0	0	0
NT0905	Guayaquil flooded grasslands	2,924	0.00	0.00	0.00	0	0	0
NT0906	Orinoco wetlands	5,988	0.00	0.00	0.00	0	0	0
NT0907	Pantanal	170,501	0.00	0.00	0.02	0	0	0
NT0908	Paraná flooded savanna	37,099	0.00	0.00	0.00	0	0	0
NT0909	Southern Cone Mesopotamian savanna	26,867	0.00	0.00	0.01	0	0	0
NT1001	Central Andean dry puna	254,929	0.12	0.10	0.07	0	0	1
NT1002	Central Andean puna	211,478	0.12	0.00	0.07	0	0	0
NT1003	Central Andean wet puna	116,874	0.02	0.00	0.10	0	0	0
NT1004	Cordillera Central páramo	12,120	0.00	0.00	0.00	0	0	0
NT1005	Cordillera de Merida páramo	2,798	0.00	0.00	0.00	0	0	0
NT1006	Northern Andean páramo	29,810	0.21	0.22	0.10	0	0	0
NT1007	Santa Marta páramo	1,239	0.00	0.00	0.00	0	0	0
NT1008	Southern Andean steppe	124,779	0.08	0.00	0.09	0	0	0
NT1010	High Monte	116,569	0.07	0.00	0.03	0	0	0
NT1201	Chilean matorral	148,381	0.11	0.59	0.03	0	1	0
NT1301	Araya and Paria xeric scrub	5,260	0.00	0.00	0.00	0	0	0
NT1303	Atacama desert	104,903	0.00	0.00	0.01	0	0	0
NT1304	Caatinga	731,320	0.01	0.14	0.01	0	0	0
NT1308	Guajira-Barranquilla xeric scrub	31,477	0.00	0.00	0.00	0	0	0
NT1309	La Costa xeric shrublands	68,181	0.00	0.00	0.00	0	0	0
NT1312	Motagua Valley thornscrub	2,328	0.00	0.00	0.00	0	0	0
NT1313	Paraguana xeric scrub	15,909	0.00	0.00	0.00	0	0	0
NT1314	San Lucan xeric scrub	3,867	0.00	0.00	0.00	0	0	0

NT1315	Sechura desert	184,213	0.60	0.57	0.50	1	0	0
NT1316	Tehuac�n Valley matorral	9,862	0.00	0.00	0.00	0	0	0
NT1401	Amazon-Orinoco-Southern Caribbean mangroves	40,894	0.00	0.00	0.00	0	0	0
NT1403	Mesoamerican Gulf-Caribbean mangroves	26,658	0.00	0.00	0.00	0	0	0
NT1404	Northern Mesoamerican Pacific mangroves	8,174	0.00	0.00	0.00	0	0	0
NT1405	South American Pacific mangroves	13,461	0.00	0.00	0.00	0	0	0
NT1406	Southern Atlantic mangroves	10,025	0.00	0.00	0.00	0	0	0
NT1407	Southern Mesoamerican Pacific mangroves	7,827	0.00	0.00	0.00	0	0	0
PA0101	Guizhou Plateau broadleaf and mixed forests	269,132	0.00	0.00	0.00	0	0	0
PA0102	Yunnan Plateau subtropical evergreen forests	239,854	0.19	0.00	0.36	0	0	1
PA0401	Appenine deciduous montane forests	16,147	0.00	0.00	0.00	0	0	0
PA0402	Atlantic mixed forests	400,447	0.00	0.00	0.00	0	0	0
PA0404	Balkan mixed forests	224,768	0.00	0.00	0.00	0	0	0
PA0405	Baltic mixed forests	117,107	0.01	0.00	0.00	0	0	0
PA0406	Cantabrian mixed forests	79,846	0.00	0.00	0.00	0	0	0
PA0407	Caspian Hyrcanian mixed forests	55,132	0.01	0.05	0.00	0	0	0
PA0408	Caucasus mixed forests	170,538	0.02	0.00	0.06	0	0	0
PA0409	Celtic broadleaf forests	210,027	0.00	0.00	0.00	0	0	0
PA0410	Central Anatolian steppe and woodlands	101,493	0.02	0.00	0.00	0	0	0
PA0411	Central China loess plateau mixed forests	359,867	0.00	0.00	0.00	0	0	0
PA0412	Central European mixed forests	733,978	0.00	0.00	0.01	0	0	0
PA0413	Central Korean deciduous forests	104,602	0.00	0.12	0.00	0	0	0
PA0414	Changbai Mountains mixed forests	93,438	0.00	0.00	0.00	0	0	0
PA0415	Changjiang Plain evergreen forests	437,582	0.00	0.00	0.00	0	0	0
PA0416	Crimean Submediterranean forest complex	30,215	0.00	0.00	0.00	0	0	0
PA0417	Daba Mountains evergreen forests	168,170	0.00	0.01	0.00	0	0	0

PA0418	Dinaric Mountains mixed forests	58,286	0.00	0.00	0.00	0	0	0
PA0419	East European forest steppe	730,128	0.00	0.01	0.02	0	0	0
PA0420	Eastern Anatolian deciduous forests	81,628	0.02	0.00	0.00	0	0	0
PA0421	English Lowlands beech forests	45,770	0.00	0.00	0.00	0	0	0
PA0422	Euxine-Colchic broadleaf forests	74,513	0.02	0.00	0.00	0	0	0
PA0423	Hokkaido deciduous forests	25,583	0.00	0.04	0.00	0	0	0
PA0424	Huang He Plain mixed forests	434,240	0.00	0.00	0.00	0	0	0
PA0426	Manchurian mixed forests	505,287	0.00	0.00	0.02	0	0	0
PA0427	Nihonkai evergreen forests	21,637	0.09	0.16	0.05	0	0	0
PA0428	Nihonkai montane deciduous forests	82,360	0.43	0.22	0.50	0	1	1
PA0429	North Atlantic moist mixed forests	38,835	0.00	0.00	0.00	0	0	0
PA0430	Northeast China Plain deciduous forests	232,909	0.00	0.00	0.00	0	0	0
PA0431	Pannonian mixed forests	307,716	0.00	0.00	0.01	0	0	0
PA0432	Po Basin mixed forests	42,461	0.00	0.00	0.00	0	0	0
PA0433	Pyrenees conifer and mixed forests	25,930	0.50	0.22	0.56	1	1	1
PA0434	Qin Ling Mountains deciduous forests	123,278	0.13	0.28	0.10	0	0	0
PA0435	Rodope montane mixed forests	31,685	0.00	0.00	0.00	0	0	0
PA0436	Sarmatic mixed forests	850,317	0.01	0.13	0.00	0	0	0
PA0437	Sichuan Basin evergreen broadleaf forests	98,009	0.00	0.00	0.00	0	0	0
PA0438	South Sakhalin-Kurile mixed forests	12,563	0.00	0.00	0.00	0	0	0
PA0439	Southern Korea evergreen forests	14,724	0.00	0.06	0.00	0	0	0
PA0440	Taiheiyo evergreen forests	138,266	0.07	0.19	0.05	0	0	0
PA0441	Taiheiyo montane deciduous forests	41,913	0.07	0.13	0.06	0	0	0
PA0442	Tarim Basin deciduous forests and steppe	54,533	0.00	0.00	0.00	0	0	0
PA0443	Ussuri broadleaf and mixed forests	197,954	0.00	0.00	0.00	0	0	0
PA0444	Western Siberian hemiboreal forests	224,488	0.00	0.00	0.00	0	0	0

PA0445	Western European broadleaf forests	493,836	0.02	0.00	0.00	0	0	0
PA0446	Zagros Mountains forest steppe	397,569	0.02	0.04	0.00	0	0	0
PA0501	Alps conifer and mixed forests	149,871	0.00	0.00	0.00	0	0	0
PA0502	Altai montane forest and forest steppe	142,875	0.02	0.03	0.01	0	0	0
PA0503	Caledon conifer forests	22,112	0.00	0.00	0.00	0	0	0
PA0504	Carpathian montane forests	125,335	0.00	0.00	0.01	0	0	0
PA0505	Da Hinggan-Dzhagdy Mountains conifer forests	249,275	0.00	0.00	0.00	0	0	0
PA0506	East Afghan montane conifer forests	20,071	0.00	0.01	0.01	0	0	0
PA0507	Elburz Range forest steppe	63,287	0.04	0.02	0.00	0	0	0
PA0508	Helanshan montane conifer forests	24,704	0.01	0.00	0.00	0	0	0
PA0509	Hengduan Mountains subalpine conifer forests	99,291	0.01	0.02	0.00	0	0	0
PA0510	Hokkaido montane conifer forests	45,853	0.00	0.14	0.01	0	0	0
PA0511	Honshu alpine conifer forests	11,505	0.34	0.12	0.33	1	0	0
PA0512	Khangai Mountains conifer forests	2,902	0.00	0.00	0.00	0	0	0
PA0513	Mediterranean conifer and mixed forests	23,091	0.00	0.00	0.00	0	0	0
PA0514	Northeastern Himalayan subalpine conifer forests	46,220	0.00	0.00	0.00	0	0	0
PA0515	Northern Anatolian conifer and deciduous forests	101,410	0.01	0.00	0.00	0	0	0
PA0516	Nujiang Langcang Gorge alpine conifer and mixed forests	82,699	0.00	0.00	0.00	0	0	0
PA0517	Qilian Mountains conifer forests	16,653	0.02	0.00	0.03	0	0	0
PA0518	Qionglai-Minshan conifer forests	80,134	0.37	0.36	0.22	1	0	1
PA0519	Sayan montane conifer forests	358,833	0.00	0.00	0.00	0	0	0
PA0520	Scandinavian coastal conifer forests	19,401	0.02	0.00	0.04	0	0	0
PA0521	Tian Shan montane conifer forests	27,568	0.01	0.00	0.00	0	0	0
PA0601	East Siberian taiga	3,922,555	0.06	0.02	0.02	0	0	0
PA0602	Iceland boreal birch forests and alpine tundra	92,077	0.00	0.10	0.00	0	1	0
PA0603	Kamchatka-Kurile meadows and sparse forests	147,064	0.00	0.00	0.00	0	0	0

PA0604	Kamchatka-Kurile taiga	15,294	0.00	0.00	0.00	0	0	0
PA0605	Northeast Siberian taiga	1,133,262	0.02	0.04	0.06	0	0	0
PA0606	Okhotsk-Manchurian taiga	403,504	0.00	0.00	0.00	0	0	0
PA0607	Sakhalin Island taiga	68,944	0.00	0.00	0.00	0	0	0
PA0608	Scandinavian and Russian taiga	2,170,288	0.05	0.16	0.02	0	0	0
PA0609	Trans-Baikal conifer forests	201,186	0.00	0.00	0.00	0	0	0
PA0610	Ural montane forests and tundra	175,548	0.01	0.14	0.01	0	0	0
PA0611	West Siberian taiga	1,680,245	0.03	0.17	0.00	0	0	0
PA0801	Alai-Western Tian Shan steppe	127,683	0.00	0.00	0.00	0	0	0
PA0802	Altai steppe and semi-desert	83,192	0.00	0.00	0.00	0	0	0
PA0803	Central Anatolian steppe	24,934	0.01	0.00	0.01	0	0	0
PA0804	Daurian forest steppe	209,634	0.00	0.00	0.00	0	0	0
PA0805	Eastern Anatolian montane steppe	168,382	0.01	0.00	0.01	0	0	0
PA0806	Emin Valley steppe	65,135	0.00	0.00	0.00	0	0	0
PA0808	Gissaro-Alai open woodlands	168,156	0.02	0.00	0.00	0	0	0
PA0809	Kazakh forest steppe	422,308	0.01	0.00	0.01	0	0	0
PA0810	Kazakh steppe	807,557	0.00	0.00	0.00	0	0	0
PA0811	Kazakh upland	72,199	0.00	0.00	0.00	0	0	0
PA0812	Middle East steppe	132,288	0.00	0.00	0.00	0	0	0
PA0813	Mongolian-Manchurian grassland	889,460	0.00	0.00	0.00	0	0	0
PA0814	Pontic steppe	997,073	0.00	0.01	0.00	0	0	0
PA0815	Sayan Intermontane steppe	34,057	0.00	0.00	0.00	0	0	0
PA0816	Selenge-Orkhon forest steppe	228,369	0.01	0.04	0.01	0	0	0
PA0817	South Siberian forest steppe	162,600	0.02	0.04	0.00	0	0	0
PA0818	Tian Shan foothill arid steppe	129,231	0.00	0.00	0.00	0	0	0
PA0901	Amur meadow steppe	123,622	0.00	0.00	0.00	0	0	0

PA0902	Bohai Sea saline meadow	11,565	0.00	0.00	0.00	0	0	0
PA0903	Nenjiang River grassland	23,260	0.00	0.00	0.00	0	0	0
PA0904	Nile Delta flooded savanna	50,953	0.01	0.00	0.07	0	0	0
PA0905	Saharan halophytics	53,854	0.00	0.00	0.03	0	0	0
PA0906	Tigris-Euphrates alluvial salt marsh	35,573	0.00	0.00	0.00	0	0	0
PA0907	Suiphun-Khanka meadows and forest meadows	33,836	0.00	0.00	0.00	0	0	0
PA0908	Yellow Sea saline meadow	5,320	0.00	0.00	0.00	0	0	0
PA1001	Altai alpine meadow and tundra	90,434	0.01	0.09	0.00	0	0	0
PA1002	Central Tibetan Plateau alpine steppe	629,190	0.05	0.01	0.03	0	0	0
PA1003	Eastern Himalayan alpine shrub and meadows	121,014	0.00	0.00	0.00	0	0	0
PA1004	Ghorat-Hazarajat alpine meadow	66,482	0.14	0.19	0.36	0	0	1
PA1005	Hindu Kush alpine meadow	28,268	0.00	0.02	0.00	0	0	0
PA1006	Karakoram-West Tibetan Plateau alpine steppe	143,265	0.01	0.00	0.01	0	0	0
PA1007	Khangai Mountains alpine meadow	37,168	0.00	0.01	0.00	0	0	0
PA1008	Kopet Dag woodlands and forest steppe	58,319	0.04	0.17	0.03	0	0	0
PA1009	Kuh Rud and Eastern Iran montane woodlands	126,224	0.09	0.11	0.01	0	1	0
PA1010	Mediterranean High Atlas juniper steppe	6,328	0.00	0.00	0.00	0	0	0
PA1011	North Tibetan Plateau-Kunlun Mountains alpine desert	374,494	0.00	0.00	0.00	0	0	0
PA1012	Northwestern Himalayan alpine shrub and meadows	49,390	0.00	0.00	0.00	0	0	0
PA1013	Ordos Plateau steppe	215,604	0.00	0.00	0.00	0	0	0
PA1014	Pamir alpine desert and tundra	118,025	0.01	0.00	0.01	0	0	0
PA1015	Qilian Mountains subalpine meadows	73,285	0.05	0.01	0.04	0	0	0
PA1016	Sayan Alpine meadows and tundra	81,213	0.00	0.00	0.00	0	0	0
PA1017	Southeast Tibet shrublands and meadows	460,542	0.35	0.33	0.46	0	1	0
PA1018	Sulaiman Range alpine meadows	23,850	0.10	0.00	0.07	1	0	0
PA1019	Tian Shan montane steppe and meadows	280,611	0.01	0.00	0.00	0	0	0

PA1020	Tibetan Plateau alpine shrublands and meadows	271,999	0.01	0.00	0.02	0	0	0
PA1021	Western Himalayan alpine shrub and Meadows	70,090	0.00	0.00	0.00	0	0	0
PA1022	Yarlung Tsangpo arid steppe	59,381	0.00	0.00	0.00	0	0	0
PA1101	Arctic desert	162,810	0.01	0.00	0.00	0	0	0
PA1102	Bering tundra	477,269	0.00	0.00	0.00	0	0	0
PA1103	Cherskii-Kolyma mountain tundra	560,461	0.02	0.02	0.03	0	0	0
PA1104	Chukchi Peninsula tundra	300,485	0.00	0.04	0.02	0	0	0
PA1105	Kamchatka Mountain tundra and forest tundra	119,889	0.00	0.00	0.00	0	0	0
PA1106	Kola Peninsula tundra	59,185	0.01	0.00	0.00	0	0	0
PA1107	Northeast Siberian coastal tundra	224,278	0.00	0.00	0.01	0	0	0
PA1108	Northwest Russian-Novaya Zemlya tundra	286,282	0.01	0.03	0.00	0	0	0
PA1110	Scandinavian Montane Birch forest and grasslands	244,865	0.02	0.00	0.03	0	0	0
PA1111	Taimyr-Central Siberian tundra	962,154	0.02	0.01	0.00	0	0	0
PA1112	Trans-Baikal Bald Mountain tundra	218,608	0.07	0.01	0.00	0	0	0
PA1113	Wrangel Island arctic desert	7,600	0.00	0.00	0.00	0	0	0
PA1114	Yamal-Gydan tundra	415,131	0.00	0.02	0.05	0	0	0
PA1201	Aegean and Western Turkey sclerophyllous and mixed forests	133,558	0.00	0.00	0.00	0	0	0
PA1202	Anatolian conifer and deciduous mixed forests	86,393	0.01	0.00	0.04	0	0	0
PA1204	Corsican montane broadleaf and mixed forests	3,634	0.00	0.00	0.00	0	0	0
PA1205	Crete Mediterranean forests	8,192	0.00	0.00	0.00	0	0	0
PA1207	Eastern Mediterranean conifer-sclerophyllous-broadleaf forests	143,853	0.01	0.00	0.00	0	0	0
PA1208	Iberian conifer forests	34,461	0.00	0.00	0.00	0	0	0
PA1209	Iberian sclerophyllous and semi-deciduous forests	297,956	0.42	0.27	0.34	0	0	0
PA1210	Illyrian deciduous forests	40,639	0.00	0.00	0.00	0	0	0
PA1211	Italian sclerophyllous and semi-deciduous forests	102,225	0.00	0.00	0.00	0	0	0
PA1212	Mediterranean acacia-argania dry woodlands and succulent thickets	99,975	0.00	0.00	0.00	0	0	0

PA1213	Mediterranean dry woodlands and steppe	292,082	0.03	0.33	0.08	0	0	0
PA1214	Mediterranean woodlands and forests	358,243	0.00	0.00	0.00	0	0	0
PA1215	Northeastern Spain and Southern France Mediterranean forests	90,851	0.00	0.00	0.00	0	0	0
PA1216	Northwest Iberian montane forests	57,406	0.04	0.21	0.05	0	0	0
PA1217	Pindus Mountains mixed forests	39,584	0.00	0.00	0.00	0	0	0
PA1218	South Appenine mixed montane forests	13,095	0.00	0.00	0.00	0	0	0
PA1219	Southeastern Iberian shrubs and woodlands	2,868	0.00	0.00	0.00	0	0	0
PA1220	Southern Anatolian montane conifer and deciduous forests	76,475	0.01	0.00	0.00	0	0	0
PA1221	Southwest Iberian Mediterranean sclerophyllous and mixed forests	71,123	0.04	0.30	0.05	0	0	0
PA1222	Tyrrhenian-Adriatic Sclerophyllous and mixed forests	85,084	0.00	0.00	0.00	0	0	0
PA1301	Afghan Mountains semi-desert	13,682	0.00	0.01	0.00	0	0	0
PA1302	Alashan Plateau semi-desert	674,352	0.04	0.01	0.10	0	0	0
PA1303	Arabian Desert and East Sahero-Arabian xeric shrublands	1,847,461	0.02	0.00	0.00	0	0	0
PA1304	Atlantic coastal desert	39,887	0.00	0.00	0.00	0	0	0
PA1305	Azerbaijan shrub desert and steppe	64,089	0.00	0.00	0.03	0	0	0
PA1306	Badghyz and Karabil semi-desert	133,647	0.00	0.01	0.00	0	0	0
PA1307	Baluchistan xeric woodlands	288,424	0.09	0.00	0.04	0	0	0
PA1308	Caspian lowland desert	267,976	0.00	0.00	0.00	0	0	0
PA1309	Central Afghan Mountains xeric woodlands	139,333	0.10	0.18	0.16	0	0	0
PA1310	Central Asian northern desert	663,853	0.00	0.00	0.00	0	0	0
PA1311	Central Asian riparian woodlands	88,800	0.02	0.00	0.00	0	0	0
PA1312	Central Asian southern desert	567,376	0.00	0.00	0.01	0	0	0
PA1313	Central Persian desert basins	580,655	0.07	0.05	0.06	0	0	0
PA1314	Eastern Gobi desert steppe	282,368	0.00	0.02	0.01	0	0	0
PA1315	Gobi Lakes Valley desert steppe	139,714	0.01	0.01	0.00	0	0	0
PA1316	Great Lakes Basin desert steppe	157,706	0.01	0.03	0.01	0	0	0

PA1317	Junggar Basin semi-desert	304,938	0.00	0.00	0.00	0	0	0
PA1318	Kazakh semi-desert	680,441	0.00	0.00	0.00	0	0	0
PA1319	Kopet Dag semi-desert	26,286	0.00	0.00	0.00	0	0	0
PA1320	Mesopotamian shrub desert	210,908	0.01	0.00	0.00	0	0	0
PA1321	North Saharan steppe and woodlands	1,673,776	0.96	0.67	0.85	1	1	1
PA1322	Paropamisus xeric woodlands	92,609	0.00	0.03	0.00	0	0	0
PA1323	Persian Gulf desert and semi-desert	72,518	0.00	0.00	0.00	0	0	0
PA1324	Qaidam Basin semi-desert	192,147	0.00	0.00	0.00	0	0	0
PA1325	Red Sea Nubo-Sindian tropical desert and semi-desert	649,658	0.04	0.00	0.01	0	0	0
PA1326	Registan-North Pakistan sandy desert	276,999	0.05	0.14	0.10	0	0	0
PA1327	Sahara desert	4,629,416	0.00	0.00	0.03	0	0	0
PA1328	South Iran Nubo-Sindian desert and semi-desert	350,889	0.01	0.05	0.00	0	0	0
PA1329	South Saharan steppe and woodlands	1,098,254	0.00	0.09	0.01	0	0	0
PA1330	Taklimakan desert	742,657	0.02	0.00	0.00	0	0	0
PA1331	Tibesti-Jebel Uweinat montane xeric woodlands	82,009	0.00	0.24	0.00	0	0	0
PA1332	West Saharan montane xeric woodlands	257,450	0.00	0.00	0.07	0	0	0
PA1333	Red Sea coastal desert	59,197	0.02	0.00	0.03	0	0	0

Apêndice I

Becker CG & Loyola RD (2008). **Extinction risk assessments at the population and species level: implications for amphibian conservation.**
Biodiversity and Conservation, 17: 2297-2304.

Extinction risk assessments at the population and species level: implications for amphibian conservation

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Received: 31 May 2007 / Accepted: 24 October 2007 / Published online: 5 December 2007
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Abstract Amphibian populations are declining worldwide and this is causing growing concern. High levels of population declines followed by the expansion of red lists are creating demands for effective strategies to maximize conservation efforts for amphibians. Ideally, integrated and comprehensive strategies should be based on complementary information of population and species extinction risk. Here we evaluate the congruence between amphibian extinction risk assessments at the population level (Declining Amphibian Database—DAPTF) and at species level (GAA—IUCN Red List). We used the Declining Amphibian Database—DAPTF that covers 967 time-series records of amphibian population declines assigned into four levels of declines. We assigned each of its corresponding species into GAA—IUCN red list status, discriminated each species developmental mode, and obtained their geographic range size as well. Extinction risk assessments at the population and species level do not fully coincide across geographic realms or countries. In Palearctic, Nearctic and Indo-Malayan realms less than 25% of species with reported population declines are formally classified as threatened. In contrast, more than 60% of all species with reported population declines that occur in Australasia and the Neotropics are indeed threatened according to the GAA—IUCN Red List. Species with aquatic development presented proportionally higher extinction risks at both population and species level than those with terrestrial development, being this pattern more prominent at Australasia, Palearctic, and Nearctic realms. Central American countries, Venezuela, Mexico and Australia presented the highest congruence between both population and species risk. We address that amphibian conservation strategies could be improved by using complementary information on time-series population trends and species threat. Whenever feasible, conservation assessments should also include life-history traits in order to improve its effectiveness.

Keywords Biodiversity · Extinction · Management · Policy · Population declines · Threat

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Introduction

Research on population and species extinctions shows an accelerating decay of contemporary biodiversity (Ceballos et al. 2005). Population declines and population extinctions are a more sensitive indicator of the loss of biological diversity than species extinctions, mainly because several species that have lost a great portion of their populations are likely to go regionally or globally extinct, entering in the species extinction statistics in the future (Brown and Lomolino 1998; Ceballos and Ehrlich 2002). Actually, the majority of analyses of the current biodiversity loss emphasize patterns of population declines (see Channell and Lomolino 2000).

Amphibian populations are declining worldwide (Alford and Richards 1999; Collins and Storfer 2003; Stuart et al. 2004; Whiles et al. 2006). Among other vertebrates, amphibians present the higher proportion of formally threatened species as well as records of population declines (IUCN et al. 2006). These high levels of declines at population and species level are creating demands for effective strategies to maximize conservation efforts for amphibians.

Here we evaluate the congruence between amphibian extinction risk assessment at the population level (DAPTF 2007—Declining Amphibian Database) and extinction risk assessment at species level (IUCN et al. 2006—GAA). We assessed the concordance between these two types of information both for large biogeographic realms (Australasia, Nearctic, Neotropic, Indo-Malay, and Palearctic) and for countries that present numerous records of amphibian population declines.

Materials and methods

Extinction risk assessment at the population level came from Declining Amphibian Database (DAPTF 2007), which encompasses 967 time-series records of amphibian population declines assigned into four declining levels (Low, Medium, High, and High-absent in resurveys). Extinction risk assessments at species level, in terms of IUCN Red List status, came from Global Amphibian Assessment—GAA (IUCN et al. 2006). We assigned each species with record of population decline into one of the six categories of IUCN Red List status (Lower concern, Near threatened, Vulnerable, Endangered, Critically endangered, and Extinct).

Since we support that conservation strategies can be refined by using data on species life-history traits, we reported the general results discriminating amphibian developmental modes. As amphibian species with different developmental modes respond to habitat disturbances in different ways (see Gascon et al. 1999; Tocher et al. 2001; Bell and Donnelly 2006; Urbina-Cardona et al. 2006), using this life-history trait as additional information could improve the effectiveness of amphibian conservation strategies. Hence, we discriminated each species developmental mode in (i) terrestrial development, and (ii) aquatic development. We determined each developmental mode following all amphibian reproductive modes (Duellman and Trueb 1986; Haddad and Prado 2005). Species that do not require aquatic habitats to complete their development were classified as species with terrestrial development, whereas species that indeed require an aquatic habitat were classified as species with aquatic development.

Finally, we obtained each species geographic range size (measured in km²) from GAA (IUCN et al. 2006) and tested its correlation with the DAPTF levels of population

declines, as well as with the GAA—IUCN Red List status by means of Spearman correlation coefficients.

Results

Extinction risk assessments at the population level and at species level do not fully coincide across all geographic realms, i.e., the level of concordance between both risks vary with zoogeographic regions. Many amphibian species with reported population declines are not included in the IUCN Red List, as expected given the criteria of inclusion in the Red List applied by the GAA—IUCN. In Palearctic, Nearctic and Indo-Malayan realms less than 25% of species with reported population declines are formally classified as threatened. In contrast, more than 60% of all species with reported population declines that occur in Australasia and the Neotropics are indeed threatened according to the GAA—IUCN Red List (Fig. 1).

Among threatened species with records of population declines, species with aquatic development were more frequent than species with terrestrial development, being this pattern more prominent at Australasia, Palearctic, and Nearctic realms (Fig. 1). Along with those species with aquatic development, stream- and pond-breeders accounted for 96.6% of records. In Nearctic and Neotropics, terrestrial development species with declining populations were essentially Pletodontids and Brachycephalids, respectively. The only countries with higher records of terrestrial development species were Honduras and Puerto Rico; leveraged by leaf-litter species of the Eleutherodactylinae subfamily.

Most species with reported population declines have medium to large geographic range sizes (Fig. 2a). Geographic range size was negatively correlated with DAPTF levels of population declines ($R_s = -0.150$, $P < 0.05$; Fig. 2b), being species with smaller ranges assigned in higher levels of population declines. As expected by the GAA—IUCN Red List criteria of inclusion, the range of species with declining populations was negatively correlated to their threat status ($R_s = -0.786$, $P < 0.001$); while species with smaller ranges were found in higher threat categories (Fig. 2c).

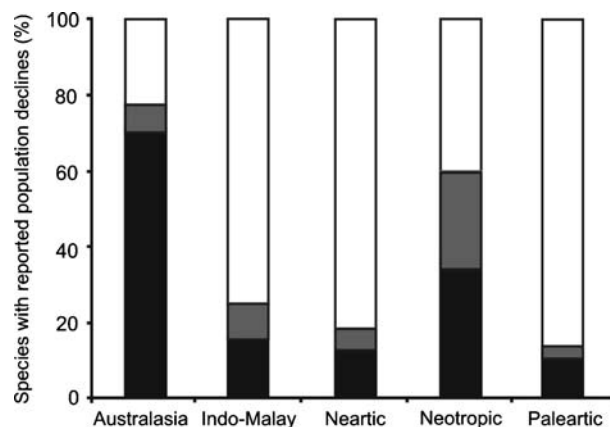


Fig. 1 Species with reported population declines (%) per biogeographic realm. Black fill represents threatened species with aquatic development; grey fill stands for threatened species with terrestrial development; empty fill represents non-threatened species. Threatened species were those classified as “critical”, “endangered” and “vulnerable” by the GAA—IUCN Red List. African realm was not included due low records of population declines

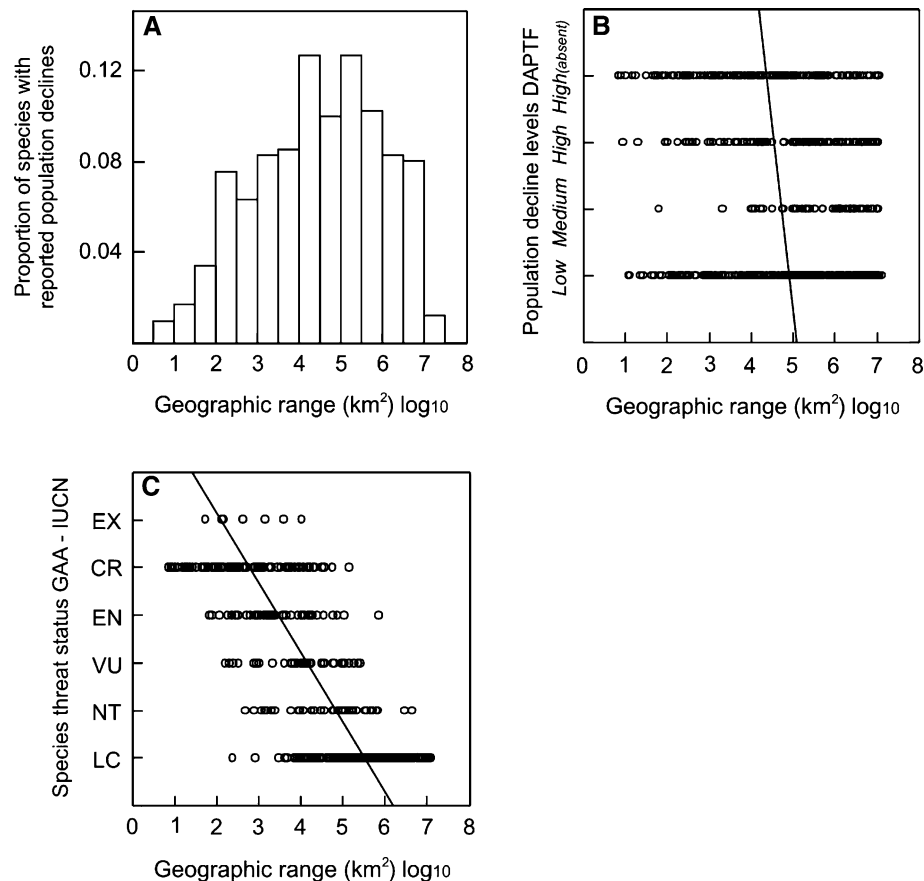


Fig. 2 (a) Proportion of species with reported population declines per geographic range class (measured in km^2 and Log_{10} transformed), (b) correlation between geographic range size of species with reported population declines and the DAPFT population decline levels ($R_s = -0.150$, $P < 0.05$ —Low decline level; Medium decline level; High decline level; High decline level—absent in re-surveys), (c) correlation between geographic range size of species with reported population declines and GAA—IUCN Red List status ($R_s = -0.786$, $P < 0.001$ —LC, lower concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; EX, extinct). The plotted line represents only a tendency without any model adjustment

Central American countries, Venezuela, Mexico and Australia had the highest congruence between both population and species risk, this pattern being influenced by the smaller species geographic range size. Countries harboring species with higher geographic ranges, such as the European ones, have much less threatened species, according to the GAA—IUCN Red List (Fig. 3).

Discussion

We address that, in many regions, amphibian conservation strategies could be much more comprehensive by using complementary information of extinction risk based on time-series population trends and official threatened species lists. Complementing the status of each

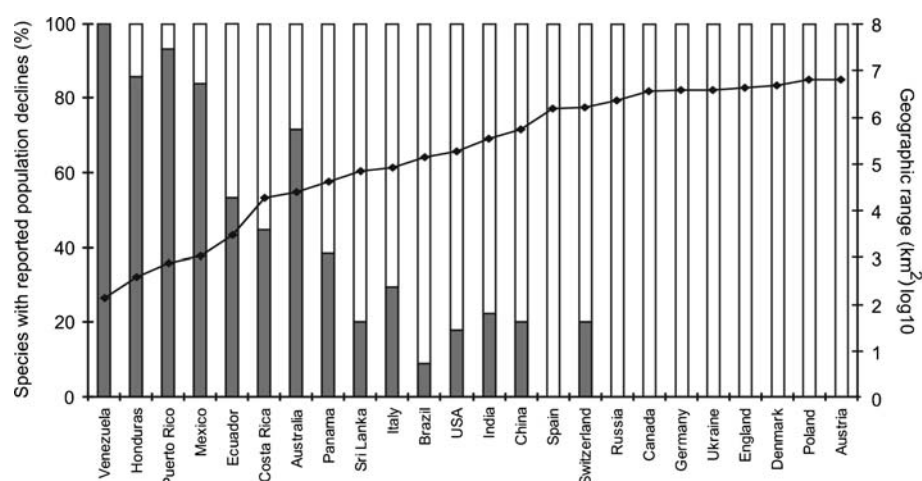


Fig. 3 Species with reported population declines (%) per country (bars); grey fill represents threatened species and empty fill stands for non-threatened species. Species geographic range size was measured in km² and Log₁₀ transformed (line). Countries with less than five records of amphibian population declines were not included

species (GAA—IUCN Red List), Declining Amphibian Database—DAPTF provides additional information on status and trends of individual amphibian populations worldwide. Population-level information is much more inclusive than species-level information, which needs at least a 50% decline (or 30% if the reason of decline is unknown) for its least threatened category (VU) to be listed (Lamoreux et al. 2003; Rodrigues et al. 2006). Actually, the choice between a 30% and a 50% rate of decline for deciding whether or not a species is globally threatened depends on whether the causes of decline are known, and, at the same time, reversible and ceased (Rodrigues et al. 2006). However, conservation scientists have not yet found amphibian species for which the decline is understood and, simultaneously, reversible and ceased. Hence, GAA—IUCN have always used the 30% decline over 10 years or three generations (whichever is the longer) as the trigger for inclusion in the Vulnerable category under criterion A in the Red List (IUCN 2001).

It is also relevant to note that the absence of concordance between the population-level and species-level risk was not influenced by the degree of knowledge on amphibian fauna found among countries. Indeed, countries with little overlap of both information sources also presented high variability in the proportion of species with deficient data (which reflects a poorer knowledge about species status caused by reasons such as very large countries with many remote or unexplored regions, few scientific experts to collect, identify, or study species, among others).

Several global conservation assessments highlight endemic species as a worthwhile conservation goal, e.g., the Endemic Bird Areas (Stattersfield et al. 1998), the Global 200 ecoregions (Olson and Disnerstein 2002), and Biodiversity Hotspots (Mittermeier et al. 2004). Some studies also point out that endemic species also provide a useful guideline for identifying conservation priorities at a global or regional scale (Lamoreux et al. 2006; Loyola et al. 2007).

Among many factors that can lead to amphibian population declines and species threat, the greatest ones are, by far, habitat loss and degradation (IUCN et al. 2006). Recently, many studies have also called attention to the widespread distribution of chytridiomycosis (an infectious disease caused by the chytrid fungus *Batrachochytrium dendrobatidis*), recognized as the important cause of amphibian population declines (especially for

endemic species) in relatively undisturbed areas of Central America and Australia (Pounds et al. 1999, 2006; Lips et al. 2003a; Hero et al. 2005). Such factors could help to explain the higher correlation observed among records of population declines and the GAA—IUCN threat status in the Neotropics and Australasia; regions in which chytridiomycosis has presumably higher impacts than Neartic, Palearctic, and Indo-Malay.

Another hypothesis to explain the observed concordance is that in some regions—especially in Eastern Australia, Tropical Andes, and Central America—species geographic ranges are smaller and/or disrupted (IUCN et al. 2006). This pattern is mainly generated by geographic restrictions imposed by the landscape, which is composed primarily of mountainous regions. Areas like the ones found in these regions have high topographic variation and features that favor the human occupation on wet valleys, being the natural remnants usually concentrated in less suitable areas for agriculture, such as steeper slopes and dry hilltops (Viana et al. 1997; Silvano et al. 2005; Silva et al. 2007). In this scenario of disturbed breeding sites (streams and ponds), many amphibian species (especially those with aquatic larval stage) are expected to suffer. Perhaps, not coincidentally, we observed higher counts of threatened species with reported declining populations for Australasia and the Neotropics, mainly aquatic larvae species. Actually, most local studies of population declines revealed that species with aquatic larvae (such as stream and pond-breeders) were primarily affected, whereas most species with terrestrial development or species reproducing in foam nests floating on water accumulated on the axils of terrestrial bromeliads were less affected (Lips et al. 2003b; Hero and Morrison 2004; Hero et al. 2005; Bustamante et al. 2005; Eterovick et al. 2005). In fact, a similar situation exists in other tropical regions (i.e. India, Sri Lanka, China and Southeast Asia), but in such places, amphibian declines have generally been less severe—presumably because of the lower impacts of chytridiomycosis.

Implications for amphibian conservation

Conservation strategies focused on species level such as GAA—IUCN Red List can be more inclusive if considered further information of population extinction risk. This seems to be appropriate for Neotropical countries such as Brazil, which ranks among the highest known diversity for most major vertebrate groups (Mittermeier and Mittermeier 1997; Mittermeier et al. 2004; Brandon et al. 2005; Lewinsohn and Prado 2005), houses the richest amphibian fauna in the world (Pimenta et al. 2005), two biodiversity hotspots (the Atlantic Forest and the Cerrado, Mittermeier et al. 2004), and includes several of the largest remaining wilderness areas (Mittermeier et al. 2003). It thus is one of the very few countries worldwide still offering significant options for successful broad-scale conservation action (Brandon et al. 2005; Loyola et al. 2007).

Declining populations can be used as rough surrogates for threatened species in the foreseeable future (Brown and Lomolino 1998). This seems to be especially true for species with small or disrupted geographic ranges, which are more vulnerable to human impacts (Ceballos et al. 2005). It is well known that the fauna of certain countries, having rapid rates of human disturbances, can be identified as being most at risk. For this reason, and because resources for conservation are limited, the scientific community must provide managers and politicians with a solid basis for establishing conservation priorities (Ceballos and Ehrlich 2002; Ceballos et al. 2005) to minimize amphibian population declines and subsequently species threat. Time-series records of population declines coupled with information on life history traits could help to improve the conservation planning.

Both extinction risk assessments (Declining Amphibian Database—DAPFT and the GAA—IUCN Red List) pointed to the importance of habitat loss as the primary cause of

threat, and therefore, to habitat protection as the main strategy for conserving species. In the case of amphibians, the complicating factor resides also with the chytrid fungus that seems to operate independently from habitat loss or species ranges, although the probability of a highly restricted species to be affected to the point of extinction by the fungus will be much higher by definition than for wider ranging species. In regions that have been experiencing severe habitat loss, especially where there is a large number of species with aquatic larvae suffering with population declines, specific laws regarding the restoration of riparian forest should be reinforced. To conclude, we recommend that the conservation community should use all available sources to derive integrated and comprehensive strategies for amphibian conservation. This will be extremely helpful in guiding and allocating conservation efforts where they are really needed.

Acknowledgements The authors are grateful to T. Halliday, J. Kauffman (Declining Amphibian Populations Task Force—DAPFT), S. Stuart and J. Chanson (Global Amphibian Assessment) for providing an early version of their databases. We thank T. Halliday, J. Kauffman, S. Stuart, J. Chanson, C. R. Fonseca, J. A. F. Diniz-Filho, P. C. Eterovick, S. Pawar, and two anonymous referees for their helpful comments on the manuscript. This study was carried out in the UNICAMP Graduate Program of Ecology. Carlos Guilherme Becker and Rafael Dias Loyola were respectively supported by FAPESP (04/13132-3) and CNPq (140267/2005-0).

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Conclusões

Como visto na introdução geral dessa tese, existem hoje diferentes abordagens para a identificação de prioridades de conservação, especialmente aquelas aplicadas a grandes escalas. Tais abordagens vão desde o uso de grupos indicadores e a congruência entre a riqueza de espécies e níveis de endemismo entre diferentes grupos taxonômicos, até a identificação de áreas prioritárias para a conservação de determinados grupos. Independente de suas diferenças metodológicas, todas essas abordagens assentam-se sobre o arcabouço conceitual e teórico proposto pela Biogeografia da Conservação e pelo Planejamento Sistemático de Conservação.

O conteúdo dessa tese fundamentou-se no uso de tais abordagens de priorização, tendo como alvo a identificação de prioridades de conservação para vertebrados terrestres na região Neotropical e no mundo. Assim, no primeiro capítulo, “*Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions*”, encontra-se a análise da eficiência de vertebrados terrestres como grupos indicadores para o estabelecimento de prioridades de conservação no Brasil. O método de seleção de ecorregiões para avaliação da eficiência desses grupos indicadores não seguiu, como nos outros capítulos, o princípio de complementaridade. Isso se deve, basicamente, a duas razões. Inicialmente, naquele momento, não estava familiarizado com boa parte da literatura, e não dei a devida atenção aos benefícios (medidos como o acúmulo de espécies em um menor número de regiões) e objetivo ecologicamente fundamentado de maximizar a diversidade beta em um conjunto de regiões prioritárias. Em segundo lugar, embora isso seja desejável e tenha sido aplicado nos capítulos subsequentes, o primeiro ensaio dessa tese não tinha como objetivo a seleção de áreas *per se*, mas a verificação da eficiência de alguns grupos em representar a diversidade total de vertebrados no Brasil. Assim, o não uso de uma análise de complementaridade não invalida os resultados obtidos no capítulo 1.

O segundo capítulo “*Key Neotropical ecoregions for terrestrial vertebrate conservation*” tratou da seleção de áreas (ecorregiões prioritárias) para a conservação de vertebrados terrestres em toda a região Neotropical. Os conjuntos mínimos de ecorregiões necessárias para tal objetivo são prioritários também para espécies endêmicas e ameaçadas de extinção.

O terceiro capítulo, intitulado “*Hung out to dry: choice of ecoregions for conservation of threatened Neotropical anurans depends on life-history traits*”, mostra como a inclusão de características da história de vida (no caso, o modo reprodutivo de indivíduos adultos) de anuros ameaçados de extinção pode gerar conjuntos prioritários mais abrangentes que, por sua vez, subsidiam estratégias de conservação mais eficientes para este grupo.

O quarto capítulo revelou que é possível incluir características ecológicas (e.g. risco de extinção e raridade) e evolutivas (e.g. tamanho corporal e história evolutiva – filogenia) nos

exercícios de priorização de áreas. Isto foi feito para um grupo específico e bastante vulnerável, a saber, os mamíferos da ordem Carnívora. Neste estudo, comparamos a sobreposição de conjuntos prioritários incluídos em diferentes cenários de conservação com outro derivado independentemente das espécies em questão, mas que visa minimizar os conflitos de conservação por meio da inclusão de ecorregiões menos impactadas por populações humanas. Este capítulo intitula-se “*Conservation of Neotropical carnivores under different prioritization scenarios: mapping species traits to minimize conservation conflicts*”.

O último capítulo da tese revela claramente minha preocupação com a inclusão de características biológicas (ecológicas, evolutivas e de história de vida) no processo de identificações de áreas prioritárias para a conservação da biodiversidade. Nesse capítulo, “*Integrating economic costs and species biological traits into global conservation priorities for carnivores*”, incluímos cinco características biológicas de mamíferos carnívoros na busca de um cenário de conservação que necessitasse uma intervenção urgente por congregarem espécies em altos níveis de risco de extinção. A grande novidade apresentada nesse capítulo, além de uma ampliação do âmbito do estudo, dessa vez feito em escala global, é a inclusão de custos monetários (dólares por km² para a aquisição de terras em ecorregiões) no delineamento de áreas prioritárias. Isto é certamente uma tendência clara observada nos estudos de planejamento de conservação, como foi destacado no capítulo.

A tese contou ainda com um apêndice “*Conservation assessments at the population and species level: implications for amphibian conservation*” no qual discutimos como estratégias de conservação devem se valer de todos os dados disponíveis e que possam indicar futuras ameaças, não só em nível específico, mas também populacional.

É interessante observar alguns pontos particulares: (1) embora as análises tenham sido feitas em escala continental e global e para diferentes grupos de vertebrados – por vezes, todas as espécies, por outra, anuros ou mamíferos carnívoros – existe certa congruência entre ecorregiões apontadas como prioritárias em todos esses exercícios. Isso é extremamente satisfatório e mostra que talvez, abordagens focadas em alguns grupos particulares como carnívoros (para os quais existem dados de melhor qualidade disponíveis para uso em pesquisa e conservação) podem oferecer boas indicações de prioridades para outros grupos. Um exemplo claro disso foi discutido no último capítulo da tese. Ecorregiões em comum concentram-se no sul do México, América Central, Andes Tropicais, sul da América do Sul (Patagônia e florestas temperadas do sul do Chile) e na Mata Atlântica brasileira; (2) parece-me bastante claro que a inclusão de características biológicas de espécies em processos de seleção de área, além de terem se mostrado bastante úteis para a identificação de cenários urgentes do ponto de vista das

espécies em questão, é fundamental e deveria ser incorporado sempre que possível em análises desse tipo por oferecer conjuntos prioritários menos arbitrários ou que simplesmente salientem áreas com alta diversidade e/ou endemismo. Embora isso me pareça fundamental, nunca havia sido proposto na literatura até então; (3) a inclusão de custos monetários traz clareza e objetividade ainda maior às estratégias de conservação. Ficou claro, por exemplo, no último capítulo, que a redução do número total de ecorregiões no conjunto final de áreas prioritárias não parece ser uma estratégia eficiente de alocação de recursos, uma vez que, é possível incluir um maior número de ecorregiões por meio de um custo total (em US\$/km²) ainda mais barato. Isso é de total relevância para que abordagens como essa migrem do ideal acadêmico e passem a ser consideradas em estratégias de conservação reais e aplicáveis – embora isso exija, claramente, uma longa política de discussão, negociação e implementação – na maioria das vezes (e desejavelmente) multidisciplinar; (4) dos sete textos apresentados nessa tese, cinco encontram-se publicados ou no prelo em revistas científicas internacionais. Isso garante que as idéias e proposições do trabalho já foram, até certo ponto, avaliadas por pesquisadores de instituições internacionais e estão à disposição para consulta, críticas e uso – como indicado por algumas citações, também em periódicos internacionais, já recebidas por alguns dos artigos incluídos nessa tese.

Preciso fazer, contudo, duas críticas passíveis de discussão. A primeira é focada no uso *per se* de ecorregiões como unidades geográficas. Embora existam inúmeras vantagens no uso dessas unidades (como descrito na introdução geral e em alguns dos capítulos), ele também apresenta algumas restrições: (1) conforme exposto em alguns capítulos, há uma discrepância na área total de algumas dessas unidades geográficas. Ora, ao passo que isso reflete, de certa, forma uma diferença intrínseca entre as comunidades de plantas e animais de uma ecorregião; em contrapartida, há dados disponíveis e passíveis de serem utilizados no refinamento dos limites de algumas áreas. O Cerrado brasileiro, por exemplo, é considerado uma única ecorregião, embora o mesmo possa ser subdividido em inúmeras outras regiões com similaridade de fauna e flora locais mais bem delimitadas. Isso foi apresentado em alguns dos capítulos; (2) a lista de espécies por ecorregião – banco de dados básico usado em todas as análises da tese – foram obviamente desenvolvidas com base em mapas de extensão de ocorrência de espécies de vertebrados terrestres. Isso implica na existência clara de certos problemas tais como erros de omissão e comissão, invariavelmente associados ao problema recorrente conhecido com déficit Wallaceano. Dados sobre a distribuição de espécies no interior de cada uma dessas ecorregiões não estão disponíveis, e precisam ser necessariamente modelados com base em teorias de conservação de nicho e modelagem computacional.

A segunda crítica é, na verdade, um aspecto que tem chamado minha atenção e direcionado minha curiosidade, é que não se sabe o grau de coincidência entre os conjuntos prioritários delineados com base em vertebrados terrestres e seus subconjuntos com outros grupos taxonômicos, especialmente invertebrados e plantas. A verificação de tal congruência, embora não tenha feito parte do escopo dessa tese, é sem dúvida um objetivo a ser cumprido, uma vez que além de extremamente desejável, tal congruência facilitaria o trabalho de tomadores de decisão, favorecendo a implementação de áreas de conservação em alguma das ecorregiões apresentadas nessa tese. Alguns dados, como a ocorrência de plantas endêmicas em ecorregiões podem ser obtidos para que isso comece a ser desenvolvido. Ainda assim, e conforme apontado em todos os capítulos da tese, a identificação de áreas prioritárias para a conservação da biodiversidade que vão de uma escala regional/continental à global, é apenas um primeiro passo no estabelecimento de estratégias de conservação *in-situ* que garantirão a persistência de espécies por períodos ecológicos e evolutivos relevantes para sua existência. Os trabalhos incluídos nessa tese reforçam o arcabouço teórico e metodológico da avaliação de conservação e oferecem bases científicas para o delineamento de regiões prioritárias para a conservação de biodiversidade em um mundo em constante mudança.

ANEXO 1 – a



Figura 1. Mapa das 179 ecorregiões delimitadas por Olson et al. (2001) na região Neotropical.

ANEXO 1 – b

Algumas considerações sobre os dados de distribuição geográfica de espécies utilizados nesta tese

Os recursos disponíveis para análises de priorização em escala macrogeográfica são escassos, especialmente na região Neotropical. A associação de espécies à ecorregiões foi feita com base nos mapas de extensão de ocorrência das espécies de vertebrados terrestres que ocorrem na região. Espécies introduzidas, vagais ou migratórias não foram consideradas. As listas de distribuição geográfica de espécies provieram de fontes arbitradas, a saber: dados sobre anfíbios, *The American Museum of Natural History* (<http://research.amnh.org/herpetology/amphibia/index.php>); dados sobre répteis *The European Molecular Biology Laboratory at Heidelberg* (banco de dados atualmente administrado por <http://www.reptile-database.org>); dados sobre aves *Sibley and Monroe World List of Bird Names* (<http://www.ornitaxa.com/SM/SMOrg/sm.html>); dados sobre mamíferos, Wilson & Reeder (2005). Algumas modificações foram feitas nessas listas sob sugestão e consulta à especialistas (ver WWF 2006).

Sempre que disponível, distribuições geográficas históricas foram utilizadas ao invés das atuais porque (1) a inclusão de distribuições geográficas históricas é consistente com o conceito de ecorregiões, refletindo sua cobertura vegetal original ou potencial (Olson et al. 2001), (2) o uso de distribuições geográficas históricas torna as comparações entre grupos mais uniforme e (3) a inclusão de distribuições geográficas históricas é importante por indicar regiões adequadas para possíveis re-introduções. Note que espécies globalmente extintas foram excluídas do banco de dados.

Embora a inclusão de distribuições geográficas históricas pudesse gerar algum viés em análises biogeográficas, WWF (2006) ressaltou que, de maneira geral, o uso de tais distribuições não deve afetar de maneira significativa análises realizadas em macroescala, uma vez que os mapas históricos são disponíveis apenas para 200 espécies, de um total de 26.000.

Como relatado acima, os dados de distribuição de espécies foram obtidos a partir de diversos

trabalhos, incluindo guias de campo, ou diretamente com especialistas (WWF 2006). Embora certo grau de subjetividade seja esperado na compilação de listas dessa natureza, WWF (2006) teve por objetivo ser mais inclusiva que arriscar-se a perder espécies em uma ecorregião particular. O resultado é um aumento inevitável de erros de comissão (falsas presenças), os quais tendem a superestimar a distribuição geográfica das espécies. Portanto, todos os nossos resultados devem ser interpretados, levando isso em consideração.

De qualquer maneira, a opção pelo favorecimento da inclusão de espécies no caso de dúvida foi guiada pelo objetivo de fornecer a conservacionistas e tomadores de decisão com listas abrangentes de espécies que precisam ser consideradas em programas de conservação e manejo (WWF 2006). Tais listas podem e devem ser posteriormente confirmadas com dados coletados em escala local e regional, especialmente para aquelas espécies endêmicas ou consideradas ameaçadas de extinção, segundo a IUCN. Nesta tese usamos o banco de dados elaborado pela WWF porque o enxergamos como um conjunto de dados abrangente e único, permitindo avaliar a concordância em padrões de biodiversidade entre vertebrados terrestres (Loyola et al. 2007).