Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Biologia Animal

Padrões ecológicos globais de dois clados de serpentes, Viperidae e Elapidae (Serpentes, Squamata)

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Tese de Doutorado

Levi Carina Terribile

Título:

"Padrões ecológicos globais de dois clados de serpentes, Viperiadae e Elapidae (*Serpentes, Squamata*)"

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Ao Marcelo...
por me ver chegar e partir tantas vezes...

APRESENTAÇÃO

A rápida ascensão da *macroecologia* como um novo programa de pesquisa em biologia tem levado ao desenvolvimento de novas ferramentas metodológicas, as quais, associadas à crescente disponibilidade de dados ecológicos em grandes escalas espaciais, tem contribuído ao desenvolvimento de arcabouços teóricos mais sólidos sobre os padrões ecológicos observados nas mais diferentes escalas geográficas. Contudo, há ainda uma carência de dados macroecológicos para vários grupos taxonômicos com características ecológicas e evolutivas distintas, o que tem limitado de certa forma a generalização dos mecanismos propostos para explicar esses padrões ecológicos. Da mesma forma, essa carência de dados tem prejudicado o desenvolvimento de programas mais eficientes de conservação da biodiversidade.

Nesse sentido, esta tese apresenta os resultados das análises realizadas com dois grupos de serpentes, Viperidae e Elapidae, as quais, de um modo geral, tem sido raramente incluídas nas pesquisas de padrões ecológicos em grandes escalas geográficas. A proposta de trabalhar com estes dois grupos tornou-se viável graças à parceria mantida entre os pesquisadores do Laboratório de Ecologia Teórica e Síntese da Universidade de Federal de Goiás e o Prof. Miguel Rodríguez do Laboratório de Ecologia da Universidad de Alcalá, Espanha. Durante o período de 4 meses em que realizei o meu estágio de doutorado (doutorado sanduíche financiado pela CAPES) junto ao laboratório do Prof. Miguel, foram reunidas todas as informações necessárias para a organização de uma base de dados global sobre a distribuição geográfica, tamanho corpóreo e variáveis ambientais usadas nas análises dos padrões ecológicos dos dois grupos de serpentes.

Essas análises consistiram na investigação do padrão global de riqueza e de tamanho do corpo e da identificação de prioridades globais para conservação das espécies terrestres continentais desses dois grupos. Os resultados desta investigação estão organizados em 4 artigos: o primeiro apresenta as análises do padrão global de riqueza de ambos os grupos (Apêndice 1); o segundo analisa a riqueza de espécies de Viperidae por meio de uma abordagem de desconstrução dos padrões (Apêndice 2); o terceiro discute a variação geográfica do tamanho corpóreo dessas serpentes (Apêndice 3); o quarto e último apresenta as análises de estratégias globais para a conservação da diversidade dessas espécies (Apêndice 4).

Para apresentar esses artigos, esta tese foi estruturada da seguinte maneira: a seção *1. INTRODUÇÃO E FUNDAMENTAÇÃO TEÓRICA* apresenta uma revisão geral dos padrões macroecológicos, incluindo os desenvolvimentos metodológicos e as principais hipóteses sugeridas, além de uma abordagem geral sobre conservação em grandes escalas geográficas. Além disso, essa seção também apresenta uma descrição geral dos dois grupos estudados, bem como uma revisão de estudos que abordam padrões macroecológicos de serpentes. A seção *2. OBJETIVOS* descreve os objetivos deste trabalho, relacionando cada um ao seu artigo específico. Na seção *3. METODOLOGIA* é apresenta um esboço geral das atividades envolvidas no trabalho; nesse caso, inicialmente estão descritos mais detalhadamente os procedimentos para obtenção dos dados e, posteriormente, é feita uma breve descrição das análises estatísticas envolvidas, uma vez que cada artigo e apresenta uma descrição detalhada de suas análises. Já a seção *4. RESULTADOS E DISCUSSÃO* apresenta um relato geral dos principais resultados de cada artigo, com a discussão interpretativa dos mesmos. Da mesma forma, as conclusões de cada artigo encontram-se resumidas na seção *5.CONCLUSÕES*. Finalmente, cada um dos artigos com descrição detalhada de hipóteses, metodologias, resultados e discussão foi anexado na parte final do trabalho, seção *7. APÊNDICES*, seguindo a ordem do desenvolvimento do trabalho apresentado acima.

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Acredito que o doutorado seja um dos passos mais importantes de todo um processo de amadurecimento acadêmico, e não estou me referindo apenas à dissertação de um trabalho final, mas de todo o período em que convivemos com outras pessoas em um ambiente, digamos, de trabalho, em que trocamos idéias e, principalmente, aprendemos muito. No que diz respeito à convivência, devo admitir que me considero privilegiada por ter tido a oportunidade de trabalhar nos últimos 4 anos no laboratório de Ecologia Teórica e Síntese (LETS) da UFG e, o mais importante, sob orientação do cientista mais brilhante que já conheci: o Prof. José Alexandre. A sua contribuição à minha formação acadêmica e pessoal, desde a época em que foi meu professor no mestrado, é simplesmente inestimável! Muito obrigada pela paciência, pelas discussões agradáveis dos artigos, pelo incentivo ao meu doutorado sanduíche e, pela sua serenidade e facilidade com que me ajudava a responder às "questões ecológicas" que resultaram neste trabalho.

Também tive o prazer de trabalhar com outro grande cientista, meu co-orientador, Prof. Miguel Rodríguez da Universidad de Alcalá, uma pessoa que admiro pela sua seriedade e obstinação em desenvolver um trabalho com melhor a qualidade possível. O Prof. Miguel é também, juntamente com o Prof. José Alexandre, o principal colaborador para desenvolvimento desta tese, porque foi durante o período de 4 meses de Doutorado Sanduíche na Universidad de Alcalá, na Espanha, que definitivamente delimitei este trabalho final. Para tanto, contei também com a ajuda inestimável de "mis compañeros" de laboratório. Destes, agradeço primeiramente ao Micky, que foi o grande responsável por me orientar na obtenção dos dados macroecológicos e também meu principal apoio quando da minha chegada a Madri; ao Nacho, por estar sempre disposto a georreferenciar mapas e mais mapas; também à Marta Rueda e Rosa Vidanes pelo mesmo motivo. À minha querida amiga Maria José e ao Fábio, pelas nossas conversas (em português) durante o café da tarde, pelo apoio durante os 4 meses e por me mostrarem um pouco mais da Espanha e seus castelos.

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Finalmente, gostaria de destacar que este trabalho foi desenvolvido pelo Programa de Pós-Graduação em Biologia Animal da Universidade de Brasília e recebeu o apoio financeiro integral da CAPES, por meio da concessão de uma bolsa de doutorado pelo Programa de Fomento à Pós-Graduação (PROF) e de uma bolsa de doutorado sanduíche pelo Programa de Doutorado no País com Estágio no Exterior (PDEE, processo 5142/06-7).

“He comenzado a vivir en tantos sitios y con tantas horas diferentes de nuestra época, que no sé por donde empezar: si por lo grande o lo pequeño, lo de adentro o lo de afuera, si por la chaqueta o por el corazón. Todo va fundido dentro de uno, fuera de uno, las vidas y los nacimientos, haciendo un círculo de hojas, de lágrimas, de fuego, de conocimiento, de recuerdos.

Trecho de “Viaje por las costas del mundo” de Pablo Neruda (Antologia Poética, 1984).

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RESUMO

O estudo dos padrões ecológicos em grandes escalas geográficas é de grande interesse atual para ecólogos e biogeógrafos. Em especial, o gradiente latitudinal de riqueza de espécies e a variação geográfica no tamanho do corpo dos organismos são os dois padrões emergentes que tem recebido bastante ênfase nos últimos anos dentro do programa de pesquisa de macroecologia. O conhecimento efetivo dos padrões de diversidade em grandes escalas e dos processos envolvidos em sua origem e manutenção é vital para estabelecer programas mais eficientes de conservação da biodiversidade. O presente trabalho propõe estudar o padrão global de riqueza e de tamanho corpóreo das espécies de serpentes das famílias Viperidae e Elapidae, além de propor estratégias globais para a conservação da diversidade de espécies de ambas as famílias. Para tanto, foram obtidos dados macroecológicos de extensão de ocorrência e de comprimento total máximo de 228 espécies de Viperidae e 224 espécies de Elapidae. As análises dos fatores ecológicos e evolutivos envolvidos nesses padrões mostraram que as variações geográficas na riqueza e tamanho do corpo de Viperidae são determinadas primeiramente por fatores climáticos contemporâneos, enquanto que para as espécies de Elapidae esses padrões estão mais associados a fatores histórico/evolutivos do grupo. Esses resultados também mostram a importância de se utilizar abordagens desconstrutivas, como é o caso do "princípio de desconstrução extrema" proposto no presente trabalho, para as análises dos padrões de diversidade. Finalmente, as análises mostraram a existência de estratégias viáveis para a conservação da diversidade de Viperidae e Elapidae em escala global.

ABSTRACT

The study of ecological patterns in large geographical scales is currently of great interest in ecology and biogeography. Particularly, the latitudinal gradient of species richness and the geographical variation in body size of organisms are the two emerging patterns that have received special attention in recent years within the research program of macroecology. It is clear that an effective knowledge of the processes involved in the origin and maintenance of biodiversity patterns in large scale is important to design efficient strategies for biodiversity conservation. The aim of this study is to evaluate the global pattern of richness and body size of the species of two snake families, Viperidae and Elapidae, and propose conservation strategies for both families. For this, macroecological data of occurrence and maximum total body length were obtained for 228 species of Viperidae and 224 species of Elapidae. The evaluation of the ecological and evolutionary factors involved in these patterns showed that geographical variations in richness and body size of Viperidae are mainly determined by contemporary climate, while for Elapidae these patterns are more related to the evolutionary history of this group. These results also showed the importance of using deconstructive approaches, such as the "principle of extreme deconstruction" proposed in this study for the analysis of diversity patterns. Finally, the analyses of conservation priorities indicated the existence of viable conservation opportunities to preserve Viperidae and Elapidae diversity in global scale.

1. INTRODUÇAO E FUNDAMENTAÇÃO TEÓRICA

1.1 Padrões macroecológicos

O estudo dos padrões espaciais observados em características ecológicas, tais como diversidade, abundância e distribuição dos organismos, e dos processos ecológicos e evolutivos envolvidos na origem e manutenção desses padrões, é um dos principais temas de interesse dos ecólogos e biogeógrafos. Questões como "por que algumas regiões possuem mais espécies que outras?" ou, "o que determina a variação na abundância, ou ainda, no tamanho do corpo das espécies?" são exemplos de temas que têm permeado grande parte da discussão acerca dos padrões ecológicos ao longo das décadas (e.g., Hutchinson, 1959; Klopfer & MacArthur, 1961; Atkinson & Sibly, 1997; Blanckenhorn, 2000). Em resposta a essas questões, diversos estudos foram desenvolvidos inicialmente dentro de uma abordagem reducionista e experimental (i.e., realização de experimentos em pequenas escalas de tempo e espaço e com algumas poucas espécies selecionadas em função da facilidade de manipulação experimental) que dominou a pesquisa em ecologia nos anos 70 e 80 (e.g., Rosenzweig, 1966; Levin & Paine, 1974; ver também Inchausti, 1994).

Mais recentemente, o interesse pelos padrões e processos ecológicos ressurgiu dentro da área de pesquisa da macroecologia (*sensu* Brown & Maurer, 1989), cujo objetivo é estudar as características emergentes de grandes grupos de organismos em grandes escalas espaciais e/ou evolutivas (Brown, 1995; Blackburn & Gaston, 1998). O número crescente de estudos em macroecologia tem levado a importantes avanços na compreensão dos padrões ecológicos em grande escala, embora suas causas ainda careçam de explicações plausíveis (Hawkins, 2004). Tais avanços têm sido impulsionados nos últimos anos principalmente pela maior disponibilidade de dados ecológicos (e.g., mapas de distribuição geográfica das espécies), evolutivos (estabelecimento de filogenias mais robustas e completas) e ambientais (principalmente provenientes de sensoriamento remoto e modelos climáticos gerais) em grandes escalas geográficas, assim como pela crescente ênfase em modelos teóricos que permitem diferenciar os mecanismos propostos para explicar esses padrões, desenvolvimento este associado a um aumento da capacidade computacional de processar e analisar dados (Hawkins, 2004).

Considerado como o mais antigo padrão a despertar o interesse de ecólogos e historiadores naturais (A. von Humboldt destacou a maior variedade de espécies em regiões tropicais em suas publicações do início do século XIX; ver Hawkins, 2001), o gradiente latitudinal de espécies é também uma das características ecológicas emergentes mais importantes que têm sido estudadas dentro da macroecologia (Rosenzweig, 1995; Brown & Lomolino, 1998; Willig *et al.*, 2003). Com notáveis exceções (e.g. Rabenold, 1979; Kouki *et al.*, 1994; Buckley, 2003; ver também a revisão de Hillebrand, 2004) esse gradiente de aumento da diversidade biológica dos pólos em direção ao equador tem sido confirmado para a maioria dos grupos taxonômicos (Hawkins *et al.*, 2003a).

Várias hipóteses foram propostas para explicar a variação latitudinal na riqueza de espécies (Pianka, 1966; Huston, 1979; Rohde, 1992; Colwell & Lees, 2000; Allen *et al.*, 2002; Wiens & Donogue, 2004), muitas das quais não são mutuamente exclusivas e outras diferem apenas no nível de explicação (Gaston, 2000). De modo geral, essas hipóteses podem ser separadas em 3 grupos (Mittelbach *et al.*, 2007): 1) hipóteses ecológico/ambientais, cuja ênfase são os mecanismos que permitem a coexistência e manutenção da diversidade de espécies (e.g., hipóteses de produtividade, energia, heterogeneidade espacial, predação, competição; ver revisão de Willig *et al.*, 2003); 2) hipóteses evolutivas, que associam o gradiente latitudinal às diferenças nas taxas de especiação e extinção entre regiões temperadas e tropicais (Jablonski *et al.*, 2006; Ricklefs, 2006) e; 3) hipóteses históricas associadas ao tempo de duração e a extensão geográfica dos ambientes tropicais ao longo da história do planeta (Mittelbach *et al.*, 2007).

Nos últimos anos, a maioria dos estudos sobre gradientes latitudinais de diversidade em grandes escalas espaciais focaram nas hipóteses ecológicas, por meio de análises das associações entre variáveis climático/ambientais e riqueza de espécies (e.g., Wright *et al.*, 1993; Francis & Currie, 2003; Hawkins *et al.*, 2003a). Esses modelos ecológicos partem do pressuposto de que os padrões observados são conseqüência direta (ou indireta) da influência do clima sobre as distribuições geográficas das espécies, independentemente de processos de longa duração, como especiação e extinção em escala regional. Desse modo, ocorre um acúmulo de espécies em climas mais propícios. Uma das hipóteses mais discutidas é a de energia ambiental. Variações espaciais na disponibilidade de energia podem afetar a riqueza de espécies de duas maneiras: diretamente, via requerimentos fisiológicos dos organismos, e indiretamente, via cadeias tróficas (Wright, 1983; Hawkins *et al.*, 2003a). No primeiro caso, a baixa riqueza de espécies em regiões temperadas estaria relacionada à intolerância dos organismos às baixas temperaturas. No segundo caso, a disponibilidade de água e energia ("dinâmica água-energia", *sensu* O'Brien, 1998) limita a produtividade primária de plantas, que por sua vez, limita a riqueza de herbívoros e assim sucessivamente ao longo da cadeia trófica.

Baseados em uma ampla revisão dos estudos envolvendo a hipótese de energia, Hawkins *et al.* (2003a) sugeriram que água e energia, tanto direta quanto indiretamente, fornecem uma explicação robusta para a variação da diversidade de plantas e animais em grandes escalas. Além disso, os autores observaram que, para a diversidade de animais, ocorre uma mudança na importância relativa de energia e água dos pólos em direção ao equador. Ou seja, em regiões temperadas, onde a água é abundante, a energia parece ser o fator limitante à diversidade. Por outro lado, em regiões tropicais com grande disponibilidade de energia, água (por si só ou em combinação com energia) é o fator mais importante (ver Hawkins *et al.*, 2003a). Estudos posteriores têm confirmado essas proposições (Rodríguez *et al.*, 2005; Whittaker *et al.*, 2007).

Mais recentemente, as hipóteses históricas e evolutivas vêm ganhando importância como explicação para os padrões de diversidade (e.g., Hawkins *et al.*, 2005, 2006, 2007; Wiens & Donogue, 2004; Wiens *et al.*, 2006; Donogue, 2008; Krug *et al.*, 2008). Uma dessas hipóteses sustenta que as regiões de clima tropical são mais antigas que as de clima temperado e, portanto, teriam tido um tempo efetivo maior para diversificação e acúmulo de espécies (hipótese do "tempo para especiação"; Stephens & Wiens, 2003). Suporte para tais proposições decorrem de estudos que mostram a ancestralidade tropical de muitos *taxa* com distribuição atual em regiões temperadas (e.g., Wiens *et al.*, 2006). Além disso, regiões tropicais foram historicamente mais extensas, especialmente durante o Cenozóico, o que pode ter levado a um aumento das taxas de diversificação devido a efeitos de área ou de maior produtividade e disponibilidade de energia sobres as taxas de especiação e extinção (Chown & Gaston, 2000; Mittelbach *et al.*, 2007).

Uma ênfase adicional aos processos evolutivos, causando gradientes de diversidade foi dada recentemente com a idéia de conservação do nicho ecológico das espécies (Wiens & Donoghue, 2004). De acordo com esse modelo, o padrão de resfriamento das regiões mais temperadas ao norte, iniciado há mais de 30 milhões de anos, causou uma retração das distribuições geográficas das espécies e ocorrência de processos mais fortes de extinção em escala regional. As espécies que permaneceram estariam, portanto, adaptadas a um ambiente tropical e assim continuariam seu processo de diversificação, e como os nichos tendem a se conservar no tempo evolutivo, essas regiões tropicais teriam acumulado mais espécies.

Não obstante as várias hipóteses, a compreensão dos mecanismos causadores dos padrões de diversidade ainda é incipiente. Segundo Marquet *et al.* (2004), as dificuldades em alcançar uma teoria unificada para tais padrões se devem, em parte, ao fato de que riqueza é uma variável heterogênea. Segundo esses autores, a riqueza de espécies é uma variável agregada, normalmente obtida por meio da sobreposição das extensões de ocorrência de diferentes espécies. Dessa forma, não são consideradas diferenças ecológicas nem as variações nas respostas às mudanças ambientais sob as quais as espécies estão sujeitas. Para tanto, Marquet *et al.* (2004) propõem que a análise dos padrões de riqueza de espécies seja feita por meio de uma abordagem "descontrutiva", na qual o padrão geral é "desmembrado" em grupos de espécies que compartilham determinadas características, como estrutura filogenética (espécies basais x espécies derivadas), tamanho da área de distribuição geográfica (espécies restritas x espécies amplamente distribuídas), tamanho do corpo (espécies pequenas x espécies grandes), e assim sucessivamente.

As vantagens dessa abordagem analítica foram evidenciadas recentemente em estudos de padrões de riqueza em grandes escalas. Por meio da "desconstrução filogenética" de espécies basais e derivadas, Hawkins *et al.* (2005, 2006 e 2007) mostraram que o padrão geral riqueza de aves está mais associado ao padrão de espécies basais do que de espécies derivadas. Esses resultados dão suporte aos mecanismos relacionados à conservação de nicho, conforme proposto por Wiens & Donoghue (2004). Adicionalmente, Jetz & Rahbek (2002) mostraram que o padrão de riqueza de espécies com distribuição ampla é diferente do padrão de espécies com distribuição restrita: enquanto que espécies com distribuição ampla demonstraram um padrão claro, determinado principalmente por fatores climáticos e ambientais, espécies com distribuição restrita distribuíam-se ao acaso no espaço geográfico. Ambos os exemplos sugerem que as causas subjacentes aos padrões de riqueza poderiam ser esclarecidas mais facilmente por meio da separação das espécies em grupos ecológica e historicamente distintos.

Pode-se perceber, entretanto, que esses dois exemplos (i.e. de desconstrução filogenética e geográfica), embora demonstrem a utilidade da idéia de desconstrução na compreensão dos processos ecológicos e evolutivos relacionados à diversidade, ainda possuem pontos de "truncamento" arbitrários. O problema geral está relacionado ao fato de que não é possível estabelecer de forma objetiva quais seriam as classes "naturais" de tamanho de distribuição geográfica, ou de "nível" filogenético, já que essas variáveis são, de fato, continuamente distribuídas ao longo das espécies. Assim, apesar dos importantes avanços teóricos e metodológicos na investigação dos padrões e processos macroecológicos de diversidade, ainda há a necessidade de se desenvolver métodos de análise que considerem variações individuais, como, por exemplo, a distribuição geográfica.

Quase tão antigo quanto a percepção de um gradiente de diversidade de espécies é a observação de que o corpo dos organismos varia latitudinalmente (Blackburn *et al.*, 1999). O tamanho do corpo é uma das características mais importantes dos organismos (Rodríguez *et al.*, 2006; Cushman *et al.*, 1993), com uma influência considerável na organização das comunidades ecológicas (Lawton, 1990; Brown & Nicoletto, 1991). Isso ocorre muito provavelmente porque muitos aspectos da vida dos organismos dependem dessa característica, tais como a interação com o ambiente abiótico, as taxas dos processos fisiológicos, ou ainda os resultados de suas interações com outros organismos (Cushman *et al.*, 1993).

O primeiro relato da variação geográfica do tamanho do corpo data de uma publicação de Carl Bergmann em 1847 (ver James, 1970), segundo o qual, dentro de um clado de organismos vertebrados endotérmicos, as espécies que vivem em regiões temperadas possuem tamanho de corpo maior quando comparadas aos seus parentes que vivem em regiões tropicais. Bergmann associou o padrão ao fato de que espécies maiores possuem menor razão superfície/volume, e, portanto, conseguem armazenar calor com maior eficiência que espécies pequenas em regiões frias.

O debate acerca do padrão de Bergmann (ou “regra de Bergmann”, como tem sido chamado) tem sido bastante controverso (e.g., Mayr, 1956; Lindsey, 1966; Geist, 1987; Paterson, 1987; Hawkins & Lawton, 1995) e se intensificou dentro da macroecologia na última década (e.g., Ashton & Feldman, 2003; Adams & Church, 2007). Autores divergem, por exemplo, quanto ao nível taxonômico em que o padrão deve ser observado (inter ou intra-específico). Embora Bergmann, em sua proposição original, tenha sugerido a ocorrência do padrão latitudinal no tamanho entre espécies aparentadas, Rensch (1938) e Mayr (1956) enfatizaram que o padrão de Bergmann é um fenômeno intra-específico e deve ser estudado como tal. Entretanto, Diniz-Filho *et al.* (2007) sugeriram que, dentro de uma perspectiva macroecológica, com uma maior disponibilidade de dados e métodos de análises em grande escala, é possível estudar os mecanismos evolutivos e biogeográficos envolvidos na origem dos padrões, como por exemplo, seleção em níveis elevados da hierarquia biológica, restrições energéticas à abundância e substituição de espécies mediada pela história de vida dos organismos ao longo do tempo (Webster *et al.*, 2004; Diniz-Filho *et al.*, 2007). Blackburn *et al.* (1999, p. 169) também sugeriram uma definição mais explicita para esse padrão: “tendência para uma associação positiva entre o tamanho do corpo das espécies em um grupo monofilético e a latitude ocupada por estas espécies”.

De um modo geral, o padrão de aumento do tamanho do corpo dos organismos das regiões tropicais em direção às regiões temperadas foi bastante estudado e geralmente confirmado para organismos endotérmicos (Blackburn & Gaston, 1996; Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006, 2008; Ramirez *et al.*, 2008). Esses estudos também concordam que tal variação ocorre em resposta ao clima, mediado pelo mecanismo proposto originalmente de conservação de calor. Ou seja, enquanto os organismos maiores são favorecidos em regiões de clima frio pela sua capacidade de conservar suas temperaturas corpóreas, para organismos pequenos o aumento da relação superfície/volume é vantajoso em regiões de clima quente porque facilita a dissipação de calor. Além disso, várias outras hipóteses foram sugeridas, com suporte variável. A hipótese de disponibilidade de recursos (alimento), por exemplo, está baseada no pressuposto de que espécies de tamanho grande são mais resistentes a longos períodos de escassez em regiões em que ocorre uma sazonalidade maior na abundância de recursos (como é o caso das regiões temperadas) (Blackburn *et al.*, 1999). A hipótese de disponibilidade de hábitat parece explicar uma exceção ao padrão de Bergmann em mamíferos da região Neotropical. Rodríguez *et al*. (2008) observaram que espécies neotropicais de montanhas eram menores que as espécies de planície. Razoavelmente, os autores sugerem que o gradiente climático altitudinal gera uma grande quantidade de habitats (i.e., zoneamento de hábitats). Esses hábitats, porém, são menores em extensão que aqueles de planície (Hawkins & Diniz-Filho, 2006) e, portanto, sustentam espécies também menores.

No que diz respeito aos organismos ectotérmicos, os estudos sobre a variação latitudinal do tamanho do corpo são menos concordantes. Enquanto alguns grupos confirmam a regra de Bergmann (e.g., formigas- Cushman, 1993; quelônios- Ashton & Feldman, 2003; lagartos- Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; e anuros- Olalla-Tárraga & Rodríguez, 2007), outros apresentam o padrão inverso (ou seja, espécies maiores em regiões tropicais e espécies menores em regiões temperadas), chamado de "padrão inverso de Bergmann" (e.g., serpentes- Ashton & Feldman, 2003; Olalla-Tárraga *et al.*, 2006). Independente disso, esses estudos sugerem que existe um efeito climático na variação do tamanho do corpo desses organismos, da mesma forma como referido acima para endotérmicos. Porém, essas discordâncias ressaltam a necessidade de se desenvolver hipóteses específicas que justifiquem essas variações nos padrões observados nos diferentes grupos.

Embora o mecanismo de conservação de calor seja razoável para explicar o padrão de Bergmann em determinados grupos de ectotermos (e.g., organismos com maior capacidade de termorregulação; Olalla-Tárraga & Rodríguez, 2007), explicações adicionais são necessárias para explicar o padrão inverso de Bergmann. Ashton & Feldman (2003) sugeriram que a ocorrência de organismos de tamanho pequeno em regiões de clima frio pode ser o resultado da pressão de seleção por uma maior razão superfície/volume que permita, assim, tanto ganhos quanto perdas rápidas de calor. Dessa forma, organismos menores teriam maior capacidade de controlar suas temperaturas por meio de comportamentos temorregulatórios e de se manterem ativos por longos períodos. Por outro lado, em regiões tropicais com maior disponibilidade de energia, as restrições termorregulatórias são menores, o que permitira aos organismos atingir um tamanho maior. Além disso, outra hipótese desenvolvida para explicar o padrão inverso de Bergmann é a de produtividade primária, segundo a qual, a baixa disponibilidade de alimento reduz as taxas de crescimento, e, conseqüentemente, o tamanho da fase adulta. Assim, regiões de baixa produtividade resultariam em espécies de tamanho menor.

Outro aspecto importante envolvido nas análises macroecológicas de determinados caracteres (como o tamanho do corpo) é que essas características são autocorrelacionadas filogeneticamente (Diniz-Filho, 2000). Consequentemente, os padrões ecogeográficos observados podem refletir não apenas efeitos ecológico/adaptativos “atuais”, mas também efeitos filogenéticos resultantes da substituição dos clados de níveis taxonômicos elevados ao longo do espaço geográfico

(Ramirez *et al.*, 2008). Atualmente existem vários métodos que permitem avaliar a variação ecológica em um contexto filogenético (e.g., método dos contrastes independentes, método de Monte Carlo, método de regressão de vetores filogenéticos; ver revisão de Garland *et al.*, 2005). Esses métodos buscam identificar a ocorrência e os efeitos de sinais filogenéticos em características ecológicas das espécies (Harvey & Pagel, 1991; Diniz-Filho, 2000).

Recentemente, Diniz-Filho *et al.* (2007) desenvolveram uma abordagem analítica que permite não apenas identificar esses efeitos mas, mais importante, separar os efeitos filogenéticos e ecológicos que estruturam os padrões macroecológicos no espaço geográfico. Esses desenvolvimentos teóricos e metodológicos, ao mesmo tempo em que permitem separar os diferentes mecanismos associados aos padrões macroecológicos (de diversidade e tamanho do corpo), fornecem uma base para a interpretação integrada de como esses mecanismos interagem (Diniz-Filho *et al.*, 2007). Dessa forma, a disponibilidade de novos conjuntos de dados em grande escala para os mais diversos grupos de organismos é de fundamental importância para investigar a generalidade desses padrões em si e dos mecanismos por trás dos mesmos.

1.2. Biogeografia da conservação

Na medida em que aumenta a disponibilidade de dados ecológicos (e.g., dados de biodiversidade) e ambientais (i.e., por meio dos sistemas de informação geográfica) para grandes escalas espaciais, torna-se evidente também a intensificação acelerada das alterações antrópicas sobre os padrões de biodiversidade (Gaston, 2005). Os efeitos do avanço das atividades humanas sobre áreas naturais têm causado níveis de extinção de espécies em escala global sem precedentes (Thomas *et al.*, 2004; Gaston, 2005), além da fragmentação de populações e destruição das áreas de dispersão (Ceballos & Ehrlich, 2002; Gaston *et al.*, 2003), que são tão severos quanto a perda de espécies *per se* (Gaston, 2005).

Com a eminência da crise global da biodiversidade, tem havido uma série de tentativas de utilizar padrões biogeográficos em estratégias de conservação aplicadas às escalas continentais e globais (Whittaker *et al.*, 2005) com o objetivo de identificar áreas de alto valor conservacionista, como é o caso dos "*Hotspots* de Biodiversidade" (Myers *et al.*, 2000), "Centros de Diversidade de Plantas" (WWF-IUCN, 1994–1997), e "Áreas Nativas de Alta Biodiversidade" (Mittermeier *et al.*, 2003). Muitos desses esquemas globais foram desenvolvidos por organizações não-governamentais (e.g., Conservação Internacional, WWF, etc.) e têm sido criticados por vários motivos, especialmente com relação à metodologia utilizada para identificar as áreas prioritárias (Mace *et al.*, 2000; Jepson & Canney, 2001; Whittaker *et al.*, 2005), por não incluírem importantes áreas de biodiversidade (Bates & Demos, 2001) e pelo fato de a maioria das instituições trabalharem isoladamente, gerando esforços redundantes e pouco efetivos em conservação (Mace *et al.*, 2000).

Mais recentemente, abordagens sistemáticas (Margules & Pressey, 2000) foram aplicadas com o objetivo de identificar prioridades para conservação "não-enviesadas" em grandes escalas espaciais, adaptando-se os principais métodos de planejamento sistemático em conservação (ver e.g., Ferrier *et al.*, 2000; Faith *et al.*, 2003). Essa nova abordagem passa a ser importante uma vez que há pouca disponibilidade de inventários biológicos detalhados para grandes escalas espaciais, de modo que utilizar dados macroecológicos (e.g., extensões de ocorrência) pode ser uma iniciativa eficiente em um contexto de biogeografia da conservação (Whittaker *et al*., 2005). É importante observar que essas análises em grande escala não têm por objetivo designar reservas ou unidades de planejamento diretamente (Moore *et al.*, 2003). Na realidade, parte-se do princípio de que análises em escalas espaciais amplas e baseadas em dados relativamente grosseiros podem ser úteis em um sistema hierárquico de tomada de decisões. Assim, a análise dos padrões de complementaridade nessas escalas permite identificar regiões potencialmente importantes, nas quais podem ser realizados estudos mais detalhados a fim de avaliar padrões de viabilidade populacional, fragmentação de hábitats, potenciais de manutenção da diversidade genética, etc. (Brooks *et al.*, 2001; Moore *et al.*, 2003).

Talvez uma das alternativas mais viáveis para se obter resultados eficientes seja a de integrar as abordagens de planejamento sistemático no contexto de biogeografia da conservação com as estratégias de priorização global desenvolvidos pelas instituições não-governamentais. Por exemplo, Brooks *et al.* (2006) combinou os esquemas globais de prioridades de conservação (um total de nove esquemas) gerados por meio de diferentes abordagens (i.e., vulnerabilidade e insubstitutibilidade), verificando que padrões gerais emergem dessa combinação (e.g., 79% da superfície terrestre é atendida por pelo menos um sistema de priorização) e que muitos desses sistemas se sobrepõem em seus objetivos conservacionistas. Iniciativas como a de Brooks *et al.* (2006) são importantes considerando, por exemplo, que muitas das áreas mais ameaçadas estão concentradas em regiões que também são as mais pobres economicamente. Dessa forma, a destinação dos recursos financeiros disponíveis para conservação poderia ser feita por meio da identificação das regiões consideradas as mais emergenciais entre todas as demais prioridades. Além disso, o panorama global gerado pela sobreposição desses sistemas globais poderá ser expandido pela inclusão de novos táxons, especialmente aqueles mais negligenciados em estudos de conservação, de modo a gerar um modelo comum a partir do qual estratégias em escala mais fina sejam direcionadas.

Finalmente, outro aspecto a ser considerado em conservação diz respeito aos estudos recentes que têm mostrado que as regiões do planeta com maior biodiversidade, ou seja, aquelas de grande importância para conservação são também áreas que favorecem o desenvolvimento de atividades econômicas, tais como agricultura e pecuária, o que as tornam áreas de interesses conflitantes (e.g., Balmford *et al.*, 2001; Chown *et al.*, 2003). Portanto, além de objetivar a representação máxima da biodiversidade, as análises de priorização devem também considerar fatores socioeconômicos, associados ao desenvolvimento das populações humanas em escalas locais e regionais (Abbit *et al.*, 2000), além de características que representem a disponibilidades de habitats para manutenção dessa diversidade (Cabeza & Moilanen, 2001).

1.3 Serpentes Viperidae e Elapidae

Viperidae e Elapidae constituem dois grupos monofiléticos de serpentes pertencentes ao grupo evolutivo Caenophidia (serpentes “avançadas”) (Mccarthy, 1985; Lukoschek & Keogh, 2006; Wüster *et al.*, 2008), cuja característica principal é a utilização de veneno, além da constrição, para subjugar suas presas (Kelly *et al.*, 2003;

Vidal *et al.*, 2007). As espécies viperídeas possuem um sistema inoculador de peçonha considerado o mais sofisticado dentre todas as serpentes venenosas, constituído de um par de dentes posicionados em um osso maxilar móvel, que permite que sejam projetados para fora no momento da inoculação (Jackson, 2003). Este mecanismo altamente especializado está diretamente associado aos seus hábitos de vida predominantemente sedentários (predação por "emboscada") e obtenção de presas relativamente grandes (Greene, 1992). De um modo geral, os viperídeos são encontrados desde em florestas tropicais, até em desertos e regiões de montanha, e incluem espécies arbóreas, terrestres e aquáticas (Campbell & Lamar, 2004).

A despeito de algumas controvérsias, estudos recentes sugerem que os viperídeos divergiram dos demais grupos caenofídeos há aproximadamente 60 milhões de anos (i.e., na transição do Cretáceo para o Terciário), muito provavelmente na Ásia (Lenk *et al.*, 2001; Sanders & Lee, 2008; Wüster *et al.*, 2008), o que coloca esse grupo como um dos mais basais dentro de Caenophidia (ver Vidal *et al.*, 2007). Irradiações posteriores ocorreram em direção à África (≈ 40 milhões de anos), Eurásia (≈ 30 milhões de anos) e Novo Mundo (≈ 22 milhões de anos) (Wüster *et al.*, 2008). A ausência de Viperidae na Austrália é justificada pelo fato de que esse continente já estava desconectado da América do Sul quando as primeiras linhagens de Caenophidia evoluíram no Cenozóico (Keogh, 1998). Isso também explica a ausência das linhagens mais antigas de Caenophidia nesse continente. Duas linhagens são reconhecidas dentro de Viperidae (≈ 260 espécies): Viperinae, amplamente distribuídos no Velho Mundo (Europa, Ásia e África), e Crotalinae, com espécies tanto no Hemisfério Ocidental ("víboras" do Novo Mundo) quanto no Hemisfério Oriental (Wüster *et al.*, 2008).

As serpentes elapídeas possuem um aparelho inoculador de peçonha constituído por dentes frontais pequenos e fixos em um maxilar imóvel (Jackson, 2003). É importante observar que, embora a presença de um sistema inoculador de peçonha seja comum aos dois grupos, esse sistema evoluiu independentemente e diversas vezes dentro de Caenophidia (Vidal, 2002; Kuch *et al.*, 2006).

Comparado com os viperídeos, a linhagem dos elapídeos é bem mais recente, divergindo das demais linhagens há aproximadamente 26 milhões de anos (entre o Oligoceno e o Mioceno) (mas ver também Scanlon *et al.*, 2003). Diferentes estudos oferecem suporte variável para a África e Ásia como o centro de origem deste grupo (Keogh, 1998; Wüster *et al.*, 2007). Irradiações posteriores ocorreram para o Novo Mundo (≈ 20-15 milhões de anos) e bem mais recentemente (≈ 10 milhões de anos) para a região da Australásia (Austrália, Nova Guiné e ilhas menores). Atualmente são reconhecidas 3 linhagens dentro de Elapidae (≈ 300 espécies): Elapinae, que inclui as espécies do Novo Mundo, da Ásia e da África, em sua maioria fossoriais e semi-fossoriais; Laticaudinae, que inclui as espécies anfíbias do Oceano Indo-Pácifico e Oxyuraninae, que inclui as espécies terrestres da Australásia e as serpentes marinhas (Sanders & Lee, 2008).

Exceto por alguns poucos estudos, as serpentes, de modo geral, bem como os demais grupos de répteis com exceção das aves (i.e., "répteis não-avianos", *sensu* Gauthier *et al.*, 1988), têm recebido pouca atenção por parte da literatura macroecológica. Isso se deve, muito provavelmente, à ausência de dados macroecológicos (e.g., mapas de extensão de ocorrência, dados de tamanho do corpo, dados de abundância) para essas espécies. Na revisão apresentada por Hawkins *et al.* (2003a) sobre os estudos dos padrões de diversidade em grande escalas para diversos grupos taxonômicos, apenas 6 estudos (de um total de 85 conjuntos de dados) haviam sido desenvolvidos com o objetivo de investigar as relações entre clima e riqueza de répteis: Terent'ev (1963) na antiga USSR; Pianka (1967) no oeste da América do Norte; Schall & Pianka (1977) na Península Ibérica; Schall & Pianka (1978) nos Estados Unidos e Austrália; Pianka & Shall (1981) e Scheibe (1987) nos Estados Unidos.

Mais recentemente, estudos realizados em um contexto macroecológico encontraram associações positivas entre a riqueza de répteis Squamata e a quantidade de energia atmosférica disponível na América do Norte (Currie, 1991), Europa (Rodríguez *et al.*, 2005) e no Cerrado brasileiro (Costa *et al.,* 2007). Especificamente para serpentes, um estudo de Owen (1989 - não citado em Hawkins *et al.,* 2003a), verificou que 55% da variação na riqueza de serpentes do Texas é explicado pela variação na temperatura. Reed (2003) verificou que a riqueza de Viperidae e Elapidae é mais alta em direção ao Equador, porém a associação direta deste padrão com fatores ambientais não foi avaliada. Ainda, Couto *et al.* (2007) verificaram que 34% da variação na riqueza de serpentes do Cerrado brasileiro é explicada por variáveis ambientais.

Da mesma forma, os estudos sobre a variação geográfica no tamanho do corpo são escassos para os répteis Squamata, especialmente para as serpentes, e muitos desses estudos mostram padrões divergentes: enquanto alguns grupos seguem a regra de Bergmann, outros seguem aparentemente o padrão inverso (ver Lindsey, 1966; Ashton & Feldman, 2003; Reed, 2003; Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008). Em nível interespecífico, Lindsey (1966) mostrou que alguns grupos de serpentes mostram uma tendência de aumento do tamanho do corpo em altitudes elevadas, enquanto outros mostram uma tendência contrária. Reed (2003) não encontrou suporte para a regra de Bergmann nas espécies de Viperidae e Elapidae do Novo Mundo. Recentemente, Olalla-Tárraga *et al.* (2006) verificou que o tamanho do corpo das serpentes aumentava do norte para o sul na Europa (ou seja, o padrão inverso de Bergmann), embora o padrão não tenha sido muito claro na América do Norte. Em ambas as regiões, a variação latitudinal no tamanho do corpo foi explicada principalmente por temperatura, dando suporte para as hipóteses climáticas como determinantes desta variação.

Finalmente, a indisponibilidade de dados ecológicos tem dificultado também estudos mais abrangentes sobre a conservação das serpentes, agravado pelo fato de que as populações de muitas espécies estão declinando e outras já foram extintas (Dodd, 1987; Gibbons *et al.*, 2000). Além disso, vários estudos têm demonstrado que as serpentes, de modo geral, reúnem uma série de características que as tornam ainda mais suscetíveis à destruição de áreas nativas, como por exemplo, área de ocorrência limitada, baixas taxas de dispersão, menor freqüência reprodutiva e hábitos de vida especializado (Zamudio & Greene, 1997; Gibbons *et al.*, 2000; Reed & Shine, 2002; Webb *et al.*, 2002; Campbell & Lamar, 2004; Santos *et al.*, 2006; Terribile *et al.*, 2007). Estudos de prioridades para conservação de serpentes em escalas maiores foram conduzidos na África (Akani *et al.*, 1999; Brooks *et al.*, 2001; Moore *et al.*, 2003), Austrália (Cogger *et al.*, 2000); Canadá (Seburn & Seburn, 2000), China (Zhou & Jiang, 2005), Europa (Filippi & Luiselli, 2000) e no Brasil Central (França & Araújo, 2006; Couto *et al.*, 2007). Não obstante, mais que ações isoladas, fazem-se necessários estudos mais amplos dentro de um contexto de biogeografia da conservação, por meio de metodologias que permitam identificar as regiões mais importantes globalmente para representar a diversidade de serpentes. Além disso, a seleção de áreas para conservação de serpentes deve incorporar medidas de desenvolvimento humano e da disponibilidade de condições ambientais para sustentação de populações viáveis, de modo a minimizar conflitos e maximizar a preservação de sua diversidade.

Ao longo dessa revisão, pode-se constatar que são raros os estudos abordando padrões ecológicos para a fauna de serpentes em grande escala, e que nenhum estudo até o momento foi realizado em escala global. Portanto, a investigação da variação geográfica na riqueza e no tamanho do corpo de Viperidae e Elapidae poderá fornecer informações importantes sobre os mecanismos ecológicos e evolutivos que estruturam as comunidades de répteis em escalas mais amplas, ao mesmo tempo em que amplia nosso conhecimento sobre os padrões macroecológicos em outros grupos de organismos, além dos já bastante estudados para mamíferos e aves. Além disso, o conhecimento efetivo dos padrões ecológicos em grandes escalas e dos processos envolvidos em sua origem e manutenção é vital para estabelecer programas mais eficientes de conservação da biodiversidade.

2. OBJETIVOS

Este trabalho tem como objetivo geral avaliar comparativamente os padrões macroecológicos em escala global das espécies de serpentes das famílias Viperidae e Elapidae. Mais especificamente, este trabalho tem por objetivos:

- Avaliar o padrão global de riqueza de espécies de Viperidae e Elapidae em relação às hipóteses climáticas e históricas propostas para explicar os gradientes latitudinais de diversidade (ver Apêndice 1);

- Analisar o padrão de riqueza das espécies de Viperidae por meio da abordagem analítica de desconstrução da riqueza proposta por Market *et al.* (2004) e testar uma nova abordagem de desconstrução geográfica "extrema" (aqui denominada de "princípio de desconstrução extrema"), por meio da análise individual da área de distribuição de cada uma das espécies dessa família (ver Apêndice 2);

- Determinar os fatores ecológicos e filogenéticos associados à variação geográfica do tamanho do corpo das espécies viperídeas e elapídeas Apêndice 3) e;

- Gerar um cenário global de prioridades de conservação para as espécies de cada família e comparar esses cenários com os demais esquemas de priorização sumarizados em Brooks *et al.* (2006) (ver Apêndice 4).

3. METODOLOGIA

3.1 Dados das espécies: mapas de extensão de ocorrência, tamanho do corpo e filogenias

Para determinar as espécies incluídas no trabalho, inicialmente foi organizada uma lista geral de todas as espécies de serpentes das duas famílias tomando-se como base a lista atualizada da base de dados para répteis, fornecido pelo "Grupo de Estudos em Sistemática da Sociedade Germânica de Herpetologia" (*Systematics Working Group of the German Herpetological Society*), disponível no site http://www.reptile-database.org/ (ver também Uetz *et al.*, 2007). Essa base de dados disponibiliza informações acerca da taxonomia dos répteis atuais (com exceção das aves), incluindo nomes científicos, sinonímias e informações gerais sobre distribuição geográfica, além de fontes bibliográficas sobre as recentes atualizações taxonômicas. Essa fonte tem sido usada como a principal referência global em vários estudos que incluem répteis (e.g., Myers, *et al.*, 2000; Bisconti *et al.*, 2001; Brooks *et al.*, 2002; Szyndlar, 2008). A partir desta lista inicial, fez-se uma atualização por meio de fontes específicas sobre taxonomia e distribuição de cada grupo, disponíveis para os diferentes continentes (ver abaixo).

Considerando que o presente trabalho tem por interesse estudar os padrões ecológicos das espécies terrestres continentais, foram excluídas da lista as espécies insulares (com exceção da Grã Bretanha), cujos padrões podem ser afetados mais fortemente por características particulares das ilhas (como área e isolamento). Da mesma forma, foi excluído o grupo Laticaudinae e as espécies marinhas do grupo Oxyuraninae, da família Elapidae. Além disso, não foi possível incluir as espécies desses dois clados com distribuição para a Península Arábica, devido à ausência de dados. Portanto, o número final de espécies incluídas no trabalho foi de 228 viperídeas e 224 elapídeas (ver Apêndice 5).

Os mapas de extensão de ocorrência para as espécies do Novo Mundo foram obtidos de Campbell & Lamar (2004), além das espécies descritas em Renjifo & Lundberg (2003), Alvarado-Díaz & Campbell (2004) e Lavin-Murcio & Dixon (2004). Para as espécies da Europa foram utilizados os dados de Arnold (2002) e Arnold & Ovenden (2002). Para a África foram utilizadas as informações contidas em Branch (1988, 1998), Broadley & Doria (2003), Dobiey & Vogel (2007), Spawls *et al.* (2004). Os dados da Ásia são provenientes de Latifi (1991), Ananjeva *et al.* (2006), Vogel (2006) e Whitaker & Captain (2004), complementados por Cherlin (1981), Orlov & Tuniyev (1990), Tuniyev & Ostrovskikh (2001), Khan (2002), Mallow *et al.* (2003) e Geniez & Tynié (2005). Para as espécies de Elapidae da Austrália foram utilizados os mapas de Wilson & Swan (2003).

Esses mapas foram digitalizados e processados sobre grades de células de tamanho 110 x 110 km. A escolha dessa resolução foi baseada em recentes estudos que mostram que células de tamanho intermediário (i.e., maiores que 1^o e menores que 2^o de latitude x longitude) não são nem demasiadamente grosseiras a ponto de causar perda de informações ou falsas extrapolações, nem demasiadamente "finas" para causar descontinuidades nos padrões investigados, sendo, portanto, a resolução mais indicada para análises macroecólogicas (Rahbek & Graves, 2001; Hulbert & Jetz, 2007; ver também Apêndice 3). Para cada grade correspondente às diferentes regiões do globo foi utilizado um sistema de projeção equivalente ("área igual" – *Azimuthal Equal Area*). Esse sistema de projeção tem a propriedade de não deformar as áreas, de forma que a relação entre as células é constante. Além disso, células de regiões costeiras com menos de 50% de área continental foram excluídas das análises, evitando assim possíveis efeitos de área. A riqueza de espécies foi obtida somando-se as ocorrências em cada célula. Todos os mapas de extensão de ocorrência foram digitalizados no ArcGIS 9.2.

A medida de tamanho do corpo comumente usada em estudos de história de vida dos organismos é massa corpórea (Peters, 1983; Hedges, 1985). Porém, massa corpórea é uma característica que pode sofrer fortes variações intra-específicas, dependendo, por exemplo, da estação do ano ou do período reprodutivo (Gaston & Blackburn, 2000). Para serpentes, variações sazonais nos padrões de atividades (alimentação, reprodução) são bem conhecidas (ver e.g., Shine, 1977; Marques *et al*., 2006), o que afeta diretamente as medidas de massa corpórea. Além disso, a massa corpórea é uma medida raramente disponível para esses organismos. Por outro lado, medidas de comprimento, além de serem mais comuns, são consideradas mais apropriadas para organismos cuja forma do corpo é alongada, como é o caso das serpentes (Boback, 2003; Boback & Guyer, 2003). Assim, para este trabalho foi utilizado o comprimento total máximo (medido em mm) como uma medida geral do tamanho corpóreo (ver também Apêndice 3).

Os dados de comprimento total máximo foram obtidos nas mesmas fontes utilizadas para extrair os mapas. Esses dados foram transformados em Log10 e então mapeados sobre a mesma grade das espécies para calcular a média aritmética do tamanho do corpo em cada célula.

Nos últimos anos tem aumentado o número de estudos ocupados em investigar as relações filogenéticas entre as linhagens evolutivas dentro de cada um dos dois clados (i.e., Viperinae e Crotalinae, ou Elapinae, Laticaudinae e Oxyuraninae; e.g., Keogh, 1998; Lenk *et al.*, 1999; Slowinski & Keogh, 2000; Malhotra & Thorpe, 2004), porém não existe ainda um consenso quanto às relações filogenéticas entre todas as espécies que constituem cada uma das famílias. Por esse motivo, para realizar análises comparativas dos padrões macroecológicos (e.g., Apêndice 3) foi construída uma filogenia para cada família estabelecendo-se as relações filogenéticas em nível de gênero, a partir de filogenias disponibilizadas recentemente na literatura. Para Viperidae, foram utilizadas as filogenias de Lenk *et al.* (2001), Malhotra & Thorpe (2004) e Castoe & Parkinson (2006). Para Elapidae, essas relações foram estabelecidas por meio das filogenias de Scanlon & Lee (2004), Slowinski & Keogh (2000) e Castoe *et al.* (2007) (ver Apêndice 5). Os resultados gerados em nível de gênero foram posteriormente replicados para as espécies em cada família.

3.2 Dados climáticos, ambientais e de influência humana

Ao todo, foram geradas oito variáveis climático/ambientais, selecionadas a partir da associação de cada uma delas com as hipóteses propostas para explicar os padrões geográficos de riqueza e tamanho do corpo, as quais foram mapeadas sobre as grades de análise. A descrição detalhada de cada hipótese com as respectivas variáveis associadas encontram-se nos Apêndices 1 e 3. Foram utilizadas as seguintes variáveis:

- temperatura média anual (obtida a partir dos dados disponíveis em http://www.ngdc. noaa.gov/seg/eco/cdroms/gedii_a/datasets/a04/lw.htm#top), utilizada como uma medida da energia ambiental;

- Precipitação anual (obtida em http://www.grid.unep.ch/data/grid/gnv183.html), usada como uma medida da disponibilidade de água;

- Evapotranspiração potencial anual (PET) (calculada por meio da fórmula de Priestley-Taylor disponível em http://www.grid.unep.ch/data/grid/gnv183.htm), também utilizada como uma medida de energia ambiental;

- Evapotranspiração real anual (AET) (calculada por meio da fórmula de Thornthwaite disponível em http://www.grid.unep.ch/data/grid/gnv183.htm), que é uma estimativa do balanço entre a disponibilidade de água e energia, e muitas vezes utilizada para representar produtividade primária (Rosenzweig, 1968);

- Índice de vegetação global (GVI) (disponível em http://www.grid.unep.ch/data/data.php ?category=biosphere), utilizado como uma medida de biomassa das plantas;

- Variação topográfica (calculado como a diferença entre a altitude máxima e a altitude mínima dentro de cada célula, a partir do mapa de topografia disponível em http:// www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htm), usada como uma aproximação para a variabilidade climática (i.e., temperatura) ao longo do gradiente topográfico (ver Ruggiero & Hawkins, 2008);

- Interação clima-topografia (calculada como o produto da relação "temperatura média anual x variação topográfica"), usada como uma medida dos efeitos climáticos em mesoescala na formação de gradientes de habitats ao longo do gradiente topográfico (Hawkins & Diniz-Filho, 2006);

- Sazonalidade na produtividade primária – medida como o número de meses disponíveis para o crescimento vegetal. Para esse medida, inicialmente contou-se o número de meses em que a temperatura média (em ^{o}C) foi mais que o dobro da precipitação média (em mm) naquele mês. Assim foi obtida a duração da estação xerotérmica. Com esse cálculo, foram identificados os meses em que a baixa precipitação limita o crescimento vegetal. Assim, a duração da estação chuvosa foi calculada como 12 menos o número de meses com baixa precipitação. Em seguida, foi calculado também o número de meses em que o crescimento vegetal é limitado pelas baixas temperaturas. Para isso, foram identificados os meses cuja temperatura média é inferior a 5 ^{o}C (meses frios). Da mesma forma, o número de meses quentes foi obtido como 12 menos o número de meses frios. Finalmente, a variável de "sazonalidade" é soma dos meses da estação chuvosa com os meses quentes em cada célula (ver detalhes em Olalla-Tárraga, 2006).

Além dessas variáveis climáticas, foi mapeada também uma variável representando influência humana. Essa variável, denominada de *human footprint* (aqui traduzida como "influência humana" - HF) é um índice quantitativo da atividade humana em todos os biomas da superfície terrestre (Sanderson *et al.*, 2002). Essa variável foi gerada por meio da combinação de dados geográficos sobre densidade populacional humana, uso do solo, construção de estradas e infra-estrutura de energia elétrica (ver Sanderson *et al.*, 2002), e está disponível em http://www.ciesin.columbia.edu/download_data.html. No presente trabalho, a variável de influência humana foi utilizada para avaliar as prioridades globais de conservação para serpentes minimizando conflitos entre desenvolvimento humano e conservação (ver Apêndice 4).

3.3 Análises estatísticas

A associação entre os padrões de riqueza e de tamanho com as variáveis correspondentes às hipóteses foi inicialmente analisada por meio de correlação simples. Foram investigados também efeitos de multicolinearidade, por meio de diferentes combinações de variáveis nos modelos ambientais e por meio de uma matriz de correlação entre as variáveis (ver Apêndice 6), o que resultou na exclusão de algumas das variáveis descritas acima (ver Apêndices 1, 2 e 3). No caso das análises da desconstrução dos padrões de riqueza (Apêndice 2) e da variação geográfica no tamanho do corpo (Apêndice 3), o método de regressão múltipla de quadrados mínimos (OLS - *ordinary least-squares multiple regression*) foi usado para gerar modelos ambientais alternativos com diferentes combinações de variáveis climático/ambientais. A partir destes vários modelos gerados, foi aplicado um método de seleção de modelos baseado na teoria da informação para identificar os melhores modelos por meio do critério de Akaike (AIC, Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008) (ver detalhes nos Apêndices 2 e 3).

A investigação de efeitos históricos e evolutivos foi incorporada de diferentes formas nas análises dos padrões de riqueza e tamanho do corpo. Para o padrão de riqueza (Apêndice 1), essas análises foram feitas por meio da classificação dos dados de acordo com as regiões biogeográficas (RB) revisadas por Cox (2001): regiões Norte Americana, Sul Americana, Eurasiana, Africana, Oriental e Australiana (ver também exemplos de Hawkins *et al.*, 2003b; Buckley & Jetz, 2007). As regiões biogeográficas são caracterizadas pela exclusividade da fauna e flora que as compõem, o que sugere a existência de grandes barreiras inter-regionais à distribuição dos organismos, e, portanto, que as diferentes regiões devem conter um forte sinal histórico (Cox, 2001) (ver detalhes no Apêndice 1).

No caso das análises do padrão do tamanho do corpo, foi aplicada a abordagem analítica proposta por Diniz-Filho *et al.* (2007), baseada no método de regressão por autovetores filogenéticos, PVR (Diniz-Filho *et al.* 1998; Diniz-Filho, 2000) e recentemente aplicada aos estudos dos padrões ecológicos em grande escala (ver Diniz-Filho *et al.*, 2007; Ramirez *et al.*, 2008). O PVR (*phylogenetic eigenvector regression*) permite desdobrar a variação fenotípica em seus componentes filogenéticos e adaptativos, combinando procedimentos de análise multivariada e regressão múltipla. A idéia geral é transformar a matriz de distância filogenética em uma série de autovetores que expressam diferentes níveis hierárquicos da filogenia, que podem ser usados como preditores em um modelo linear. Assim, a regressão de uma característica (e.g., tamanho do corpo) contra esses vetores gera os valores esperados dessa característica em relação à estrutura filogenética, enquanto que os resíduos dessa regressão representam a parte da variação da característica que evoluiu independentemente dessa estrutura nas diferentes espécies (ver detalhes no Apêndice 3) (Diniz-Filho *et al.*, 2007). Similarmente, o método PVR foi utilizado para as análises de desconstrução dos padrões de riqueza (ver Apêndice 2).

Para as análises do princípio de desconstrução extrema (ver Apêndice 2), as distribuições geográficas das espécies foram modeladas por meio do método de regressão logística, e os parâmetros dos modelos de distribuição foram gerados por meio de um Modelo Linear Generalizado (GLM; McCullagh & Nelder, 1989).

Possíveis influências de autocorrelação espacial na interpretação dos resultados das análises dos padrões macroecológicos foram avaliados por meio dos valores do coeficiente *I* de Moran nos resíduos dos modelos de regressão (Diniz-Filho *et al.*, 2003) (ver detalhes nos Apêndices 1, 2 e 3) e por meio do modelo de regressão espacial SAR (*Simultaneous Autoregressive Model*; Cressie, 1993).

Finalmente, tendo como base os mapas de extensão de ocorrência das espécies, foram utilizados procedimentos de otimização para gerar redes de conservação em escala global com um número mínimo de células que representem pelo menos 25% da área de distribuição geográfica de todas as espécies (ver Polasky *et al.*,2000; Possingham et al., 2000; Cabeza & Moilanen, 2001). Além disso, foram geradas redes de conservação levando em consideração o grau de ocupação humana nas áreas prioritárias adicionando-se um custo de influência humana a cada célula. Esse custo é, na realidade, a variável de "influência humana" mapeada para cada célula das grades. Da mesma maneira, e baseado nas análises dos padrões de riqueza das serpentes, foram geradas redes de conservação considerando as áreas com maior "adequabilidade" ambiental para a ocorrência de altos valores de riqueza. Nesse segundo caso, utilizou-se a variável AET para representar adequabilidade ambiental.

Os modelos globais de prioridades de conservação estabelecidos para as duas famílias de serpentes foram a seguir comparados com os modelos de priorização global gerados sob os critérios de insubstitutibilidade e vulnerabilidade por meio de uma análise de variância (ANOVA), que comparou a diferença entre os valores médios de insubstitutibilidade para serpentes dentro e fora das prioridades globais (ver Brooks *et al.*, 2006). Os detalhes analíticos envolvidos na seleção de prioridades globais para a conservação de serpentes estão descritos no Apêndice 4.

Todas as análises relacionadas aos padrões de riqueza e tamanho do corpo foram realizadas por meio do programa de análise espacial em macroecologia SAM (*Spatial Analysis in Macroecology*), v.3.0 (Rangel *et al.*, 2006). As análises de prioridades globais para conservação foram realizadas no programa SITES v.1.0 (Andelman *et al.*, 1999).

4. RESULTADOS E DISCUSSÃO

4.1 Padrão global de riqueza de espécies (Apêndice 1)

De modo geral, o mapa global de riqueza de espécies de Viperidae é similar aos padrões geográficos de riqueza observados para outros grupos taxonômicos em escala global (e.g., Hawkins *et al.*, 2003b; Ceballos & Ehrlich, 2006), com tendência a um aumento da riqueza em direção as regiões tropicais (Figura 1a). Para Elapidae observa-se a mesma tendência, embora o padrão não seja tão claro, já que o grupo apresenta uma distribuição global restrita a regiões tropicais e subtropicais (Figura 1b). É importante notar, porém, o padrão "anômalo" de riqueza de elapídeos na Austrália, cujo valor de riqueza em uma única célula foi de até 25 espécies, em comparação com as demais regiões continentais.

Considerando que as variáveis ambientais são fortemente correlacionadas (ver matriz de correlação entre variáveis no Apêndice 6), optou-se por utilizar apenas AET (que mede simultaneamente a disponibilidade de água e energia) para representar a variação climática no modelo ecológico. Para Viperidae, 45.6% da variação na riqueza foi explicada por AET. Já o modelo de história, representado pela variação nas células da grade em regiões biogeográficas (RB), explicou 25.9% dessa variação. O modelo geral incluindo AET e RB explicou 48.3% da variância da riqueza. Os coeficientes de regressão parcial mostraram que o poder de explicação de AET foi três vezes maior (i.e., 22%) que de RB (7%), após controlar os efeitos de sobreposição entre essas variáveis (Figura 2a). Assim, o padrão observado para as espécies de Viperidae é coerente com as análises realizadas para diversos grupos de organismos e que mostram que uma combinação de disponibilidade de energia e água explica grande parte da variação nos padrões de riqueza de espécies (ver Hawkins *et al*., 2003a, b). Eventos históricos parecem ter um efeito secundário nesse caso.

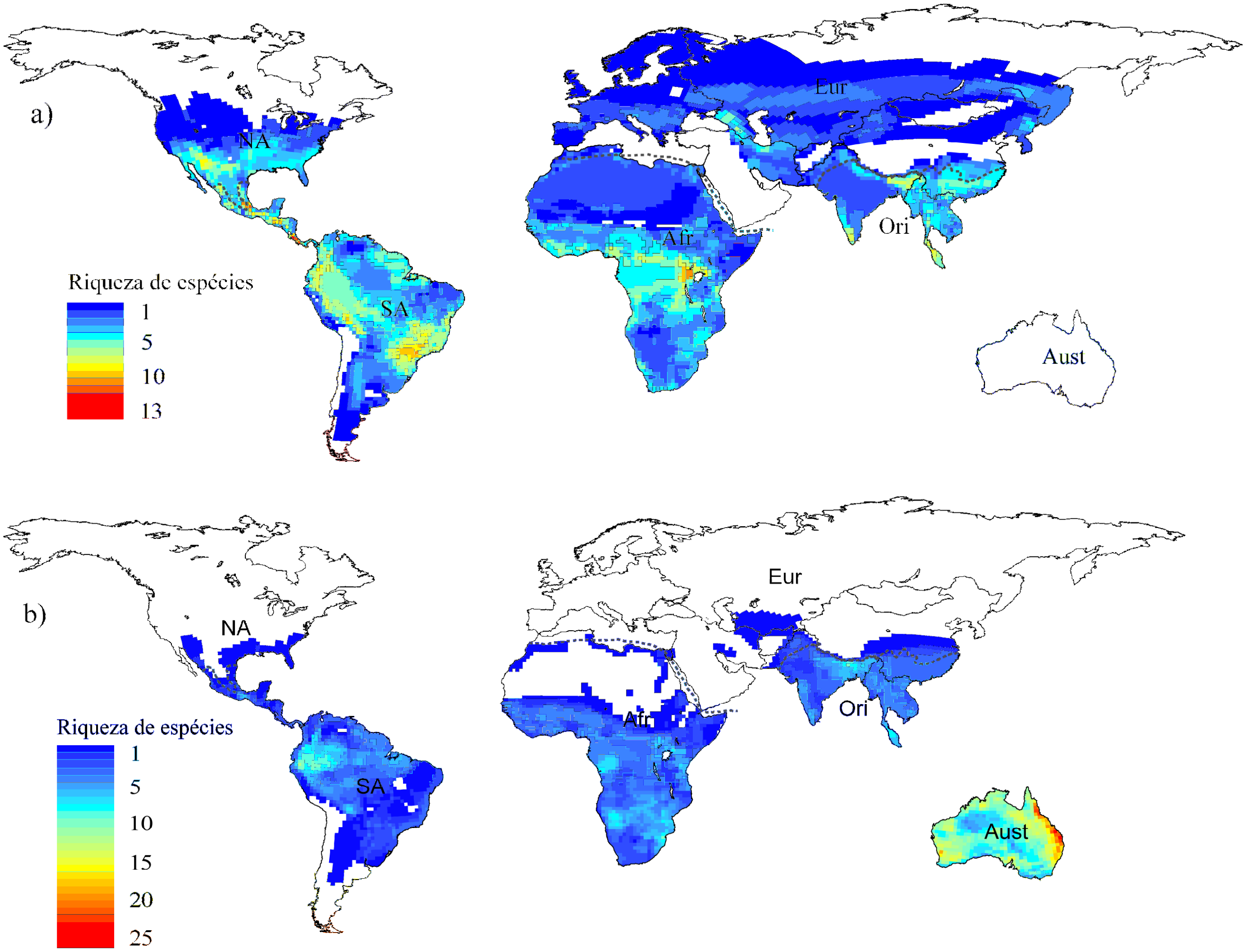

Figura 1. Padrão global de riqueza de espécies de Viperidae (a) e Elapidae (b). As linhas tracejadas delimitam as regiões biogeográficas de Cox (2001): NA – região Norte Americana; SA – região Sul Americana; Afr – região Africana; Eur – Região Eurasiana; Ori – região Oriental; Aust – região Australiana.

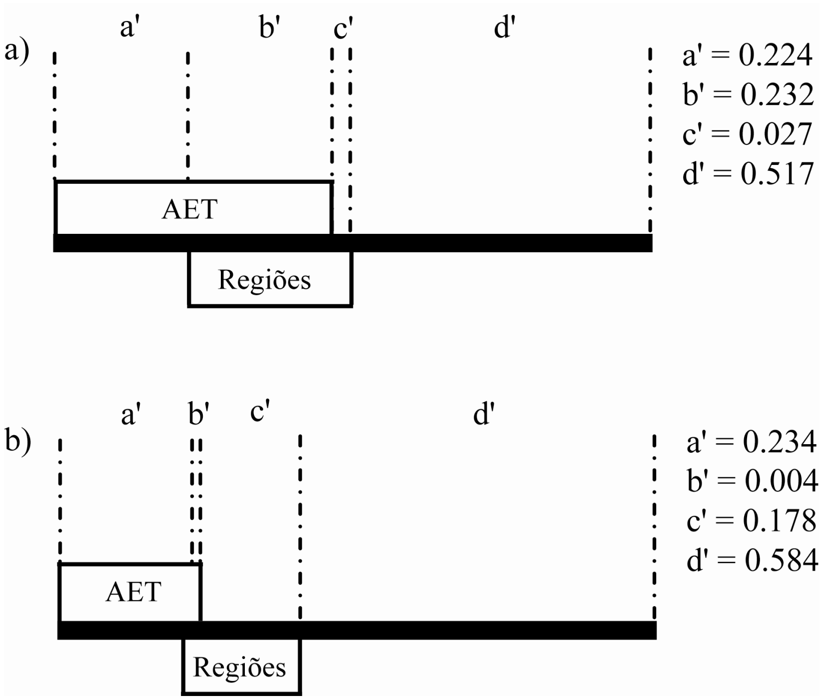

Figura 2. Resultados dos modelos de regressão parcial de riqueza de espécies com AET e regiões biogeográficas (RB); (a) – Viperidae e (b) – Elapidae (neste caso, Austrália foi excluída das análises devido ao efeito de interação com AET; ver detalhes no texto). A proporção de variância não explicada (*d'*) equivale a 1 – R^2 da OLS incluindo AET e RB, a qual corresponde a parte (*a'*+*b'*+*c'*); a sobreposição entre AET e RB (*b'*) equivale a (*a'*+*b'*) + (*b'*+*c'*) – (*a'*+*b'*+*c'*), onde (*a'*+*b'*) é o R^2 da regressão com AET, e (*b'*+*c'*) e o R^2 da regressão com RB. A variância explicada independentemente por cada variável após controlar o efeito de sobreposição entre elas é representado por *a'* no caso de AET, e por *c'* no caso de RB.

Vários estudos sobre padrões de riqueza de répteis não-avianos têm encontrado resultados similares de correlação entre medidas de energia ambiental e riqueza (e.g., Currie, 1991; Rodríguez *et al.*, 2005). De modo geral, essa associação tem sido atribuída à necessidade termorregulatória desses organismos ectotérmicos (ver e.g., Hawkins *et al.,* 2003a). Porém, no caso específico de serpentes, alguns estudos têm demonstrado que, embora certos aspectos da vida desses organismos dependam de um controle fisiológico-comportamental da temperatura corpórea (i.e., termorregulação, como é o caso de fêmeas grávidas), de modo geral elas conseguem manter temperaturas corpóreas relativamente constantes sem a necessidade de termorregular explicitamente (Shine & Madsen, 1996; Luiselli & Akani, 2002). Isso explicaria porque o padrão de riqueza de Viperidae não mostrou correlações fortes com medidas diretas de energia, ou seja, PET e temperatura (e.g., um modelo constituído de AET + temperatura explicou 48.9% da variação, $\Delta R^2 = 0.033$). Assim, parece razoável que a disponibilidade conjunta de água e energia, via efeitos na produtividade e disponibilidade de alimento, explique melhor a variação na riqueza de Viperidae.

Entretanto, qualquer generalização acerca desses padrões para serpentes seria precipitada, dados os resultados do modelo climático e histórico obtidos para Elapidae. Para esse grupo, as análises de riqueza revelaram padrões bem mais complexos. O modelo climático de AET explicou apenas 0.5% da variação, enquanto que o modelo de RB explicou 56.5%. O modelo total (AET + RB) explicou 68.3%. A variância explicada por RB controlando-se AET foi de 45.2%, ao passo que o efeito independente desta última na análise de regressão parcial foi nulo. Portanto, em uma primeira observação geral, pode-se concluir que a variação geográfica na riqueza de Elapidae é determinada por variações nas taxas de especiação, extinção e dispersão ao longo da história evolutiva do grupo, sem efeitos fortes do clima atual, como ocorre em Viperidae.

Essa diferença observada nos modelos de riqueza dos dois grupos pode ser interpretada dentro do contexto da história evolutiva de cada um. Conforme já citado anteriormente (ver seção 1.3), o clado Viperidae divergiu pelo menos 30 milhões de anos antes de Elapidae (Sanders & Lee, 2008; Wüster *et al.*, 2008; mas ver Scanlon *et al.*, 2003), e poder-se-ia presumir que o padrão de diversidade de Viperidae já "perdeu" o sinal histórico devido à dispersão em resposta a fatores climáticos contemporâneos. O padrão de Elapidae, entretanto, ainda estaria sob forte efeito histórico, dado que sua história evolutiva é mais recente.

É importante notar, porém, que o modelo total de AET + RB explicou muito mais variância (ou seja, 68.3%) de que seria esperado pela soma da quantidade de variância explicada puramente por RB (45.2%) com a quantidade de sobreposição entre as duas variáveis (11%). Isso se deve à diferença inter-regional que é observada no padrão de riqueza desse grupo (Figura 1a), ou seja, valores mais altos de riqueza na Austrália em comparação com outras regiões, e que gera efeitos não-lineares entre AET e RB. Devido a essa diferença, o padrão global de riqueza de Elapidae foi re-analisado excluindo-se a Austrália. É interessante observar que o efeito histórico foi reduzido de 54.2% para 17.8% controlando-se AET, após a exclusão dessa região biogeográfica. Já o efeito de AET aumentou para 23.4%, similar ao encontrado para Viperidae (Figura 2b).

Esses resultados mostram que o efeito histórico observado no padrão global de riqueza de Elapidae resulta primeiramente de processos históricos regionais ocorrendo na Austrália. Essas observações estão de acordo com as recentes hipóteses de que a irradiação de Elapidae para a Austrália ocorreu mais recentemente (Keogh, 1998; Sanders & Lee, 2008). Sanders & Lee (2008) estimaram que a divergência dos elapídeos da Australásia ocorreu há aproximadamente 10 milhões de anos (Mioceno Tardio), o que implica em um dos mais rápidos processos de diversificação e acúmulo de espécies de que se tem conhecimento dentro dos répteis. Muito provavelmente essa rápida diversificação foi favorecida pela disponibilidade de novas condições ambientais com relativamente pouca pressão de competição e predação no início da colonização dos ecossistemas marinho e terrestre da Australásia.

Deve-se notar ainda que, embora o processo de diversificação na Austrália explique o forte sinal histórico no padrão global de riqueza de Elapidae, esse sinal não desaparece totalmente quando a Austrália é excluída das análises (17.8% da variância na riqueza é explicada RB após controlar efeitos de AET), o que dá suporte à hipótese de que diferenças na idade evolutiva entre Viperidae e Elapidae expliquem as diferenças observadas nos modelos globais de riqueza.

4.2 Desconstrução dos padrões de riqueza de Viperidae (Apêndice 2)

Os resultados dos modelos de regressão logística revelaram que as distribuições geográficas de pelo menos metade das 228 espécies de Viperidae são determinadas por variações climático/ambientais (i.e., valores de ρ^2 *dos GLMs,* análogos ao coeficiente de determinação R^2 do OLS, variaram de 0 a 0.816; mediana = 0.269; ver Figura 3). Os mapas globais de riqueza de Viperidae estabelecidos para grupos de espécies com diferentes características macroecológicas (i.e., tamanho da área de distribuição geográfica, tamanho do corpo, estrutura filogenética, e ajuste ambiental da distribuição geográfica) apresentaram diferentes padrões de acordo com cada grupo (ver Apêndice 2).

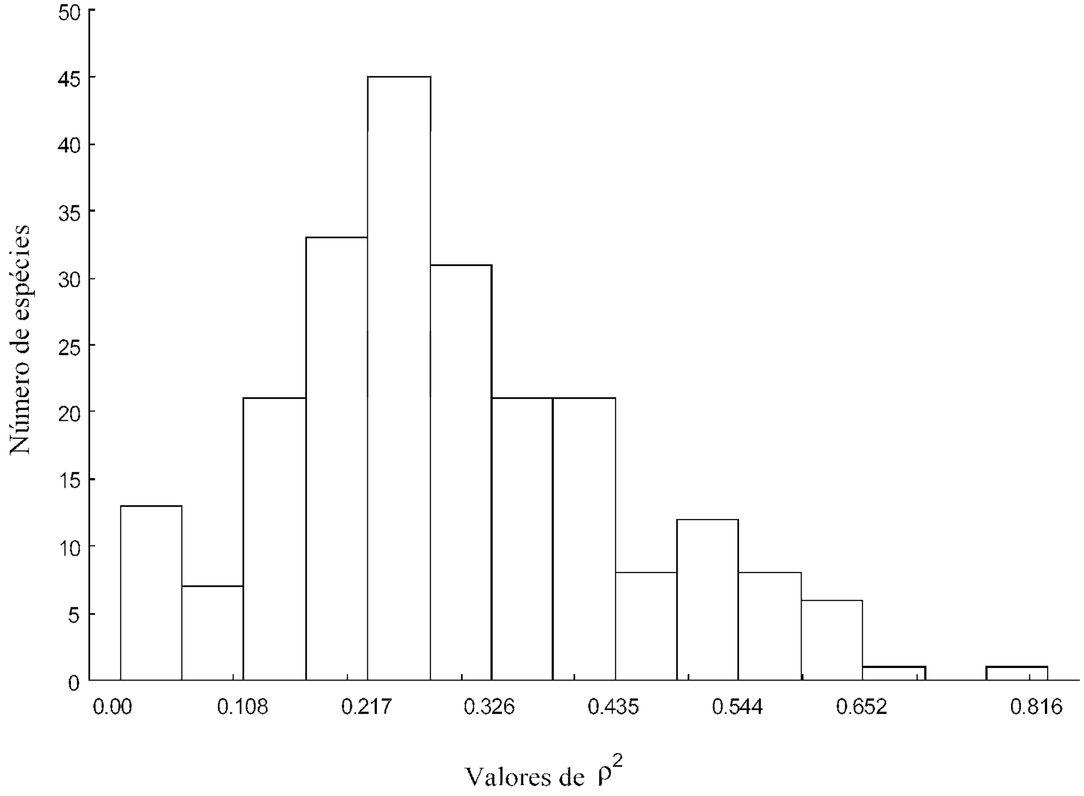

Figura 3. Distribuição de freqüência dos valores de ρ^2 (de 0 a 0.816) gerados a partir dos modelos de distribuição geográfica das 228 espécies de Viperidae por meio de GLM.

Essas diferenças são bastante claras entre grupos de espécies separados de acordo com o tamanho da área de distribuição geográfica. Por exemplo, o modelo ambiental composto de variáveis climáticas e ambientais (i.e., temperatura média anual, precipitação, índice global de vegetação, variação topográfica e sazonalidade) não explica o padrão de riqueza de espécies com distribuição geográfica restrita ou intermediária

(Tabela 1). Porém, esse mesmo modelo explica 40% da variação na riqueza de espécies com área de distribuição geográfica ampla. Esses resultados confirmam os estudos de Jetz & Rahbek (2002) e Rahbek *et al*. (2007), que mostram que os modelos ambientais explicam melhor o padrão macroecológico de riqueza quando são analisadas espécies com distribuição ampla. Em contrapartida, espécies com distribuição restrita (com riqueza de espécies concentrada, por exemplo, na América Central, e ao longo das margens continentais da América do Sul, África e Índia; ver Apêndice 2), fatores não-climáticos, como é o caso dos efeitos de restrição geométrica (ver Jetz & Rahbek, 2001, 2002; Rangel & Diniz-Filho, 2005), ou ainda fatores que atual em escalas locais (competição e predação), podem ser mais importantes para explicar tal padrão de riqueza.

Tabela 1. Resultados dos modelos ambientais para a riqueza total e para os ‘grupos’ de riqueza gerados por desconstrução. A linha superior de cada modelo representa os resultados da seleção de modelos pelo critério de AIC: os coeficientes de determinação R^2 e os coeficientes padronizados de regressão do modelo médio resultantes da média de todos os modelos (i.e., 31) gerados com as cinco variáveis ambientais. As linhas inferiores (em negrito e itálico) representam a “primazia” de cada variável, ou seja, a freqüência de importância de cada uma nos modelos GLM de distribuição de cada espécie. A última coluna à direita (*r*) representa os índices de correlação de Pearson entre os coeficientes estandardizados (linha superior) e de “primazia” de cada modelo. O valor final de *r’* é a correlação entre os valores de R^2 e *r*.

Riqueza	R^2	***Temp***	***Prec***	***GVI***	***Elev***	***Sazonal***	***r***
TOTAL	0.476	0.318	0.204	0.149	0.211	0.223	0.675
		0.360	***0.219***	***0.167***	***0.048***	***0.140***	
Distribuiçao Geográfica							
Restrita	0.073	0.287	0.005	0.03	0.27	0.039	0.201
		0.35	***0.17***	***0.15***	***0.04***	***0.17***	
Restrita-Intermediária	0.003	-0.029	0.013	-0.025	<.001	0.045	-0.462
		0.389	***0.241***	***0.148***	***0.074***	***0.167***	
Intermediária-Ampla	0.100	0.171	0.129	0.081	0.191	0.010	0.239
		0.296	***0.259***	***0.185***	***0.074***	***0.111***	
Ampla	0.403	0.295	0.190	0.119	0.027	0.214	0.832
		0.481	***0.241***	***0.222***	***0.019***	***0.130***	
Tamanho do corpo							
Pequeno	0.233	0.252	-0.050	0.205	0.217	0.251	-0.227
		0.333	***0.237***	***0.202***	***0.053***	***0.079***	
Grande	0.224	-0.005	0.209	0.001	0.170	0.256	-0.385
		0.389	***0.204***	***0.133***	***0.044***	***0.195***	

Continua

Tabela 1. Continuação.

Riqueza	***R^2***	***Temp***	***Prec***	***GVI***	***Elev***	***Sazonal***	***r***
Filogenia							
Basal	0.491	0.427	0.141	0.224	0.142	0.188	0.830
		0.386	***0.210***	***0.210***	***0.017***	***0.070***	
Derivada	0.342	0.474	0.015	0.039	0.251	0.238	0.784
		0.350	***0.140***	***0.105***	***0.087***	***0.210***	
Modelo de Distribuição							
ρ^2 Baixo	0.448	0.197	0.379	0.032	0.08	0.216	0.524
		0.327	***0.274***	***0.159***	***0.035***	***0.080***	
ρ^2 Alto	0.463	0.231	0.351	0.323	-0.077	-0.07	0.352
		0.391	***0.165***	***0.174***	***0.061***	***0.200***	
					r' =		***0.734***

Temp (Temperatura média anual); Prec (precipitação anual); GVI (índice de vegetação global anual); Elev (variação topográfica); e sazonal (sazonalidade). AIC (Critério de Informação de Akaike); GLM (Modelo Linear Generalizado).

Embora as variações geográficas no padrão global de riqueza de espécies de tamanho pequeno e de tamanho grande tenham sido bem evidentes (ver mapas dos padrões no Apêndice 2), nenhum dos dois padrões foi bem explicado pelo modelo ambiental (Tabela 1). É possível que fatores ambientais atuem mais diretamente no balanço relativo entre espécies de diferentes tamanhos dentro das comunidades do que nos padrões de riqueza de espécies grandes ou pequenas separadamente.

Espécies basais e derivadas mostraram padrões de riqueza longitudinalmente opostos, com alta riqueza de espécies basais na África e Ásia, e de espécies derivadas nas Américas. Esse padrão parece claramente refletir a hipótese evolutiva de origem do clado no Velho Mundo e posterior diversificação para o Novo Mundo (Wüster *et al.*, 2008). Além disso, é interessante observar que o modelo ambiental explicou 49.1% da variação na riqueza de espécies basais, contra 34.2% para espécies derivadas, o que sugere que efeitos de conservação de nicho estão associados às variações geográficas na riqueza de espécies (*sensu* Wiens & Donoghue, 2004). Considerando que Viperidae tenha se originado em regiões de clima tropical, a tendência esperada quando do resfriamento das regiões mais temperadas ao norte é de que as espécies permanecessem em regiões com condições climáticas similares às tropicais, mantendo assim seus nichos ancestrais. Por outro lado, espécies mais recentes podem ter se adaptado a uma maior variedade de ambientes, levando a uma menor associação entre o padrão de riqueza de espécies derivadas com o modelo climático. Resultados similares para aves foram mostrados recentemente em Hawkins *et al.* (2007).

As análises realizadas para testar o princípio de desconstrução extrema proposto neste trabalho mostraram uma alta associação (r = 0.675) entre a importância de cada variável no modelo ambiental de riqueza (i.e., coeficientes estandardizados da OLS) e a importância de cada variável nos modelos de distribuição geográfica (dada pelos coeficientes de "primazia" dos modelos GLM; ver Tabela 1). Isso sugere que os fatores determinantes das distribuições geográficas das espécies são também, em último caso, responsáveis pelos padrões de riqueza que emergem da sobreposição destas distribuições.

Os diferentes padrões de riqueza gerados por meio da abordagem de desconstrução (i.e., para espécies com diferentes características macroecológicas) podem ser utilizados como replicações para os testes do princípio de desconstrução extrema. Sendo assim, as correlações entre os coeficientes do modelo OLS e do modelo GLM de cada replicação (ou seja, cada sub-conjunto de riqueza) variaram de -0.460 a 0.832 (Tabela 1). Esses resultados sugerem que determinados padrões podem, eventualmente, ser revelados em grandes escalas independente de processos que estejam atuando individualmente nas distribuições das espécies e de forma que nem sempre as causas são as mesmas.

Efeitos não-climáticos também podem determinar a área de ocupação de uma espécie, da mesma forma que podem gerar diferentes padrões na riqueza. Isso pode ocorrer se os padrões de riqueza são determinados por outros fatores emergentes nas assembléias (e.g., dispersão, competição, seleção [*sorting*] de espécies ou linhagens) além daqueles responsáveis por determinar a distribuição das espécies, o que também geraria variações nesses coeficientes de correlação. Outro exemplo são os fatores históricos, embora tais fatores sejam mais difíceis de mensurar, dificultando também interpretação de seus efeitos sobre a determinação das áreas de ocorrência das espécies.

Além disso, é importante observar que o modelo ambiental explicou a mesma quantidade de variação do padrão de riqueza de espécies cujas distribuições possuem alto ($R^2 = 0.463$) e baixo ($R^2 = 0.448$) ajuste aos fatores climáticos, embora essa explicação não tenha sido muito alta (Tabela 1). Esse resultado sugere que a falta de ajuste das distribuições geográficas aos fatores climáticos pode ser mais bem explicada por um processo histórico de não-equilíbrio com o ambiente (Araújo & Pearson, 2005; ver também De Marco *et al.*, 2008), e não devido à falta de alguma variável ambiental não incluída no modelo. Assim, a sobreposição das distribuições das espécies pode ser o resultado de fatores históricos (como por exemplo, conservação de nicho), de modo que correlações de riqueza com fatores climáticos pode ser uma conseqüência indireta de processos históricos relacionados à geografia e clima passado, e não devido às respostas individuais das espécies ao clima atual (ver Rangel *et al.,* 2007).

4.3 Padrão global de tamanho do corpo (Apêndice 3)

Os dois grupos de serpentes analisados mostraram um padrão espacialmente complexo de tamanho médio do corpo ao longo dos continentes (Figura 4). Para Viperidae, é possível observar uma tendência bastante clara do padrão inverso de Bergmann (i.e., aumento do tamanho médio das espécies em direção a baixas latitudes) na América do Sul e no Velho Mundo (Figura 4a). Para Elapidae, entretanto, não se observam tendências latitudinais no tamanho médio do corpo (Figura 4b). Vários outros estudos têm revelado padrões similarmente complexos ou inverso de Bergmann para serpentes (Lindsey, 1966; Ashton, 2001; Ashton & Feldman, 2003; Reed, 2003; Millien *et al.*, 2006; Olalla-Tárraga *et al.*, 2006), o que sugere que diferentes mecanismos podem estar associados às variações geográficas de tamanho nos diferentes grupos de organismos.

Tanto para Viperidae quanto para Elapidae, o melhor modelo ambiental OLS, selecionado de acordo com o critério de AIC, foi constituído por todas as variáveis climático/ambientais incluídas nas análises (i.e., temperatura média anual, precipitação, GVI e variação altitudinal). Esse modelo explicou 37.6% da variação no tamanho médio das espécies de Viperidae, sendo temperatura e GVI as variáveis mais importantes de acordo os coeficientes dessas variáveis no modelo médio (Tabela 2; ver detalhes das análises estatísticas no Apêndice 3). Esses resultados dão suporte às predições das hipóteses equilíbrio térmico e produtividade como prováveis mecanismos explicando as variações geográficas no tamanho do corpo das espécies viperídeas. Para Elapidae, entretanto, o modelo ambiental explicou apenas 4.5% da variação no tamanho do corpo, o que sugere que processos puramente ecológicos não são suficientes para explicar o padrão de tamanho médio do corpo dessas serpentes (Tabela 2).

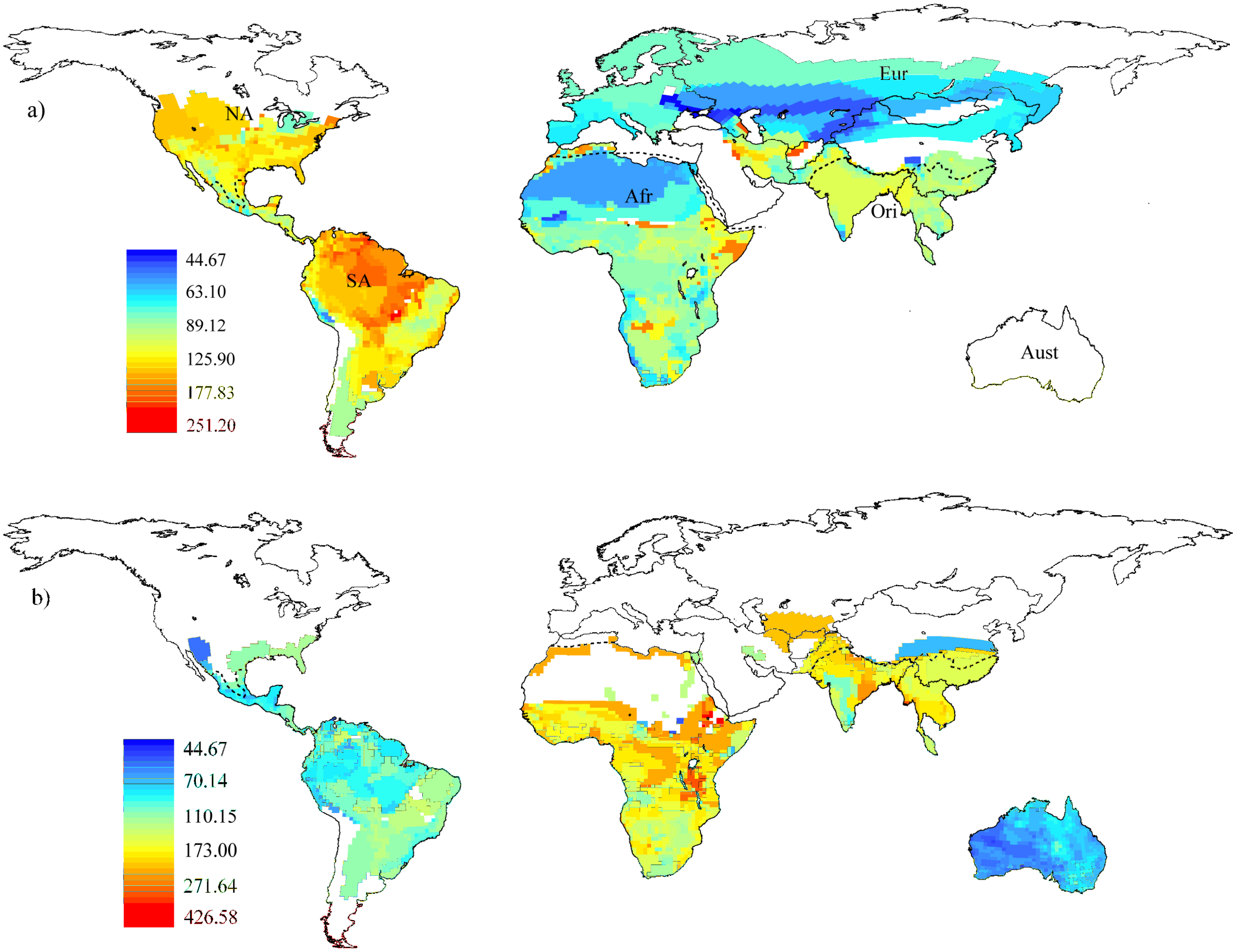

Figura 4. Padrão geográfico do tamanho médio do corpo das espécies de Viperidae (a) e Elapidae (b). As linhas tracejadas delimitam as regiões biogeográficas de Cox (2001): NA – região Norte Americana; SA – região Sul Americana; Afr – região Africana; Eur – Região Eurasiana; Ori – região Oriental; Aust – região Australiana.

Os resultados obtidos por meio da regressão do tamanho médio do corpo contra os autovetores extraído da matriz filogenética (ver detalhes das análises de PVR no Apêndice 3) revelaram resultados opostos aos observados no modelo ambiental. Ou seja, enquanto que para Viperidae o “modelo filogenético” explicou apenas 20% da variação no tamanho médio, para Elapidae esse modelo explicou 59%. Ao se separar a variação total do tamanho do corpo em dois componentes, filogenético (P) e adaptativo (S), observa-se um sinal adaptativo mais forte no tamanho do corpo dos viperídeos, dado que 32.1 % da variação no componente S foi explicada pelo modelo ambiental (Tabela 3). Para Elapidae, porém, embora se observe um aumento na variância explicada para cada componente em relação à variância total (ou seja, 8.1% para o componente P e 9.0% para o componente S, em comparação com 4.5% da variação total), esse resultado confirma que o tamanho médio do corpo de Elapidae não é determinado por fatores climático/ ambientais, mas sim pelas relações filogenéticas entre as espécies ao longo da evolução do grupo.

Tabela 2. Resultados dos modelos de regressão múltipla do tamanho médio do corpo de Viperidae e Elapidae. Na parte esquerda da tabela encontram-se os coeficientes padronizados do modelo médio ponderado resultante da média de todos os modelos (i.e., 15) gerados com as quatro variáveis ambientais: temperatura média anual (Temp), precipitação anual (Prec), índice de vegetação global anual (GVI), e variação topográfica (Elev). No lado direito encontram-se as variáveis incluídas nos melhores modelos AIC (i.e., os modelos com menores valores de AIC e com $\Delta AIC \leq 2$). Foram incluídos ainda o Akaike ponderado w_i (i.e., a probabilidade para cada modelo de ser o "melhor" modelo) e os coeficientes de determinação (R^2).

modelos médios			Melhor modelo AIC				
Variáveis	Viperidae	Elapidae	Modelo	AIC	ΔAIC	w_i	R^2
Temp	0.415	0.224	VIPERIDAE				
Prec	0.116	0.040	Temp, GVI, Prec, Elev	-11081.473	0.000	1.000	0.376
GVI	0.250	-0.127					
Elev	0.104	0.195	ELAPIDAE				
			Temp, Elev, GVI, Prec	-2780.738	0.000	0.750	0.045

Os resultados obtidos para Viperidae nos permitem interpretar a variação no tamanho médio do corpo desses organismos em relação às hipóteses ambientais baseadas em mecanismos adaptativos. Os coeficientes estandardizados do modelo ambiental médio, tanto para o tamanho do corpo total quanto para o componente S (Tabela 3), dão suporte às hipóteses de equilíbrio térmico (em primeiro lugar) e produtividade (em segundo lugar) como determinantes do padrão inverso de Bergmann observado para essas serpentes. A hipótese de equilíbrio térmico é baseada nas estratégias adotadas pelos organismos ectotérmicos para manutenção de temperaturas corpóreas ótimas (Pough, 1980). Estudos têm sugerido que as flutuações térmicas diárias (especialmente na temperatura e quantidade de energia solar) em latitudes maiores diminuem a quantidade de horas disponíveis para as atividades dos organismos, como termorregulação, forrageamento e atividades reprodutivas (e.g., Reed, 2003). Sob tais circunstâncias, organismos com tamanho menor, cuja área de superfície corpórea seja maior com relação ao volume, são favorecidos pelo fato de que conseguem controlar suas temperaturas corpóreas mais facilmente (e.g., aquecer mais rapidamente) e, portanto, teriam mais tempo disponível para outras atividades ecológicas (ver Shine *et al.*, 2000; Blouin-Demers & Weatherhead, 2002, Lourdais *et al.*, 2002; Shine, 2003). Por outro lado, conforme já explicado anteriormente, em regiões tropicais com maior disponibilidade de energia, as restrições termorregulatórias são menores, o que permitira aos organismos atingir um tamanho maior.

Tabela 3. Resultado dos modelos médios ponderados da análise global dos componentes filogenético (P) e adaptativo (S) do tamanho do corpo médio de Viperidae e Elapidae. Esses componentes P e S foram gerados para cada espécie por meio do PVR, e seus valores médios em cada célula foram obtidos considerando o número de espécies em cada uma. Para cada componente e também para o tamanho médio total (TT) são dados os coeficientes de regressão estandardizados do modelo médio (i.e., a partir dos 15 modelos gerados com quatro variáveis). Os valores de R^2 (itálico) correspondem ao melhor modelo (ver Apêndice 3 e Tabela 2 acima).

Variáveis *&* R^2 do melhor modelo	P médio	S médio	TT médio
VIPERIDAE			
Temperatura	-0.171	0.410	0.415
Precipitação	0.184	-0.001	0.116
GVI	0.238	0.306	0.250
Variação topográfica	0.171	-0.008	0.104
R^2	*0.183*	*0.321*	*0.376*
ELAPIDAE			
Temperatura	0.225	0.031	0.224
Precipitação	0.084	-0.095	0.040
GVI	-0.288	0.346	-0.127
Variação topográfica	0.208	-0.008	0.195
R^2	*0.081*	*0.090*	*0.045*

Além disso, baseado na associação do tamanho médio do corpo com GVI, é possível sugerir que a maior disponibilidade de alimento nas regiões tropicais permita às espécies viperídeas dessas regiões atingirem um tamanho maior que as espécies de regiões temperadas (ver e.g., Forsman, 1991; Madsen & Shine 2000; see also Blackburn *et al.*, 1999; Jones *et al.*, 2005; Yom-Tov & Geffen, 2006; Meiri *et al.*, 2007; ver também Apêndice 3). É importante considerar também que as variações morfológicas associadas a hábitos arborícolas resultaram em espécies de corpo mais alongado (Martins *et al.*, 2001), de modo que essa associação positiva entre tamanho do corpo e produtividade primária (GVI) pode refletir a abundância de espécies com hábitos semi-arbóreos e arbóreos em regiões tropicais (ver Parkinson, 1999; Martins *et al.*, 2001; Campbell & Lamar, 2004).

Com relação à Elapidae, entretanto, os resultados obtidos tanto para a variação total no tamanho do corpo quanto para os componentes P e S dessa variação não permitem inferir possíveis causas ambientais ao padrão global do tamanho do corpo. Uma primeira explicação para justificar pelo menos parte dessa falta de associação é que as espécies elapídeas terrestres, com poucas exceções, são em sua maioria fossoriais e semi-fossoriais e, portanto, passam boa parte do tempo sob condições microclimáticas favoráveis e relativamente constantes (How & Shine, 1999; Campbell & Lamar, 2004). Porém, deve-se observar que o modelo filogenético explicou quase 60% da variação no tamanho desses organismos. Esses resultados são similares aos obtidos para o padrão de riqueza desses organismos (ver seção 4.1), em que fatores históricos/evolutivos, em detrimento de fatores ambientais, explicam boa parte da variação. Dessa forma, pode-se supor que a mesma explicação baseada na diferença de idade evolutiva entre os dois clados tenha prevenido as serpentes elapídeas de gerar respostas adaptativas do tamanho do corpo frente às variações ambientais em determinadas regiões do globo. Além disso, algumas linhagens de Elapidae são consideradas morfologicamente conservativas (ver Silva & Sites, 2001; Campbell & Lamar, 2004; Castoe *et al.*, 2007), de modo que o padrão de variação no tamanho pode estar refletindo conservação de nicho (Wiens & Graham, 2005), no qual as espécies elapídeas teriam um tendência em conservar características ecológicas ancestrais.

Finalmente, é interessante observar que, na Austrália, a variação no tamanho do corpo de Elapidae mostrou um forte componente adaptativo ($R^2 = 0.561$ para o componente S do tamanho do corpo das espécies da Austrália; ver detalhes no Apêndice 3), da mesma forma que foi observado para o padrão de riqueza desse grupo naquela região. É provável que respostas adaptativas do tamanho do corpo à produtividade primária (considerando que GVI e precipitação foram as variáveis mais importantes nesse modelo) tenham evoluído paralelamente ao processo de grande diversificação desse grupo na Austrália, conforme descrito anteriormente nas análises de riqueza de espécies (ver seção 4.1 e Apêndice 1; ver também Sanders & Lee, 2008).

4.4 Prioridades globais para conservação (Apêndice 4)

Os dados macroecológicos de extensão de ocorrência das espécies de Viperidae e Elapidae foram utilizados para gerar redes de conservação em escala global que representassem pelo menos 25% da área de ocorrência de cada espécie dentro de regiões com menor influência humana (medido pela variável de influência humana) e com condições ambientais adequadas para sustentar altos valores de riqueza (medida por meio de AET; ver detalhes no Apêndice 4).

Para Viperidae, as soluções globais para essas metas foram alcançadas com um número mínimo de 1638 células considerando as áreas de menor influência humana, e 1527 células considerando áreas de alta adequabilidade ambiental (Figura 5a). Para Elapidae, foram necessárias 1089 células considerando as áreas de menor influência humana, e 986 células considerando áreas de alta adequabilidade ambiental (Figura 5b).

Essas redes globais nos fornecem informações gerais sobre quais são as áreas mais importantes para conservar a diversidade desses grupos dentro de uma expectativa de redução dos conflitos entre desenvolvimento e conservação, e ao mesmo tempo garantindo que as áreas selecionadas possuam as características ambientais adequadas para a ocorrência das espécies. Além disso, a sobreposição das duas soluções para cada grupo nos permitiu identificar as células importantes para os dois grupos, nas quais tanto a influência humana é minimizada quanto a adequabilidade ambiental é maximizada (Figura 5). Embora poucas células atendam a esses dois requisitos conjuntamente (458 células para Viperidae e 295 para Elapidae), essas áreas são potencialmente as mais importantes, nas quais podem ser realizados estudos mais detalhados a fim de avaliar padrões de viabilidade populacional, fragmentação de habitats, potenciais de manutenção da diversidade genética, etc., com o objetivo direto de estabelecer áreas de conservação.

A freqüência com que cada célula é selecionada para fazer parte das soluções de complementaridade ao longo das simulações fornece o seu valor de "insubstitutibilidade". De modo geral, poucas células apresentaram valores de insubstitutibilidade maiores que 0.5 (Figura 6a,b), as quais podem ser identificadas em todas as regiões ao longo das quais as espécies estão distribuídas. Esses padrões de insubstitutibilidade foram utilizados para avaliar o quão efetivos são os atuais esquemas globais de prioridades de conservação (ver Brooks *et al.*, 2006; ver Apêndice 4) para representar áreas prioritárias para as espécies de serpentes dessas duas famílias (Tabela 4).

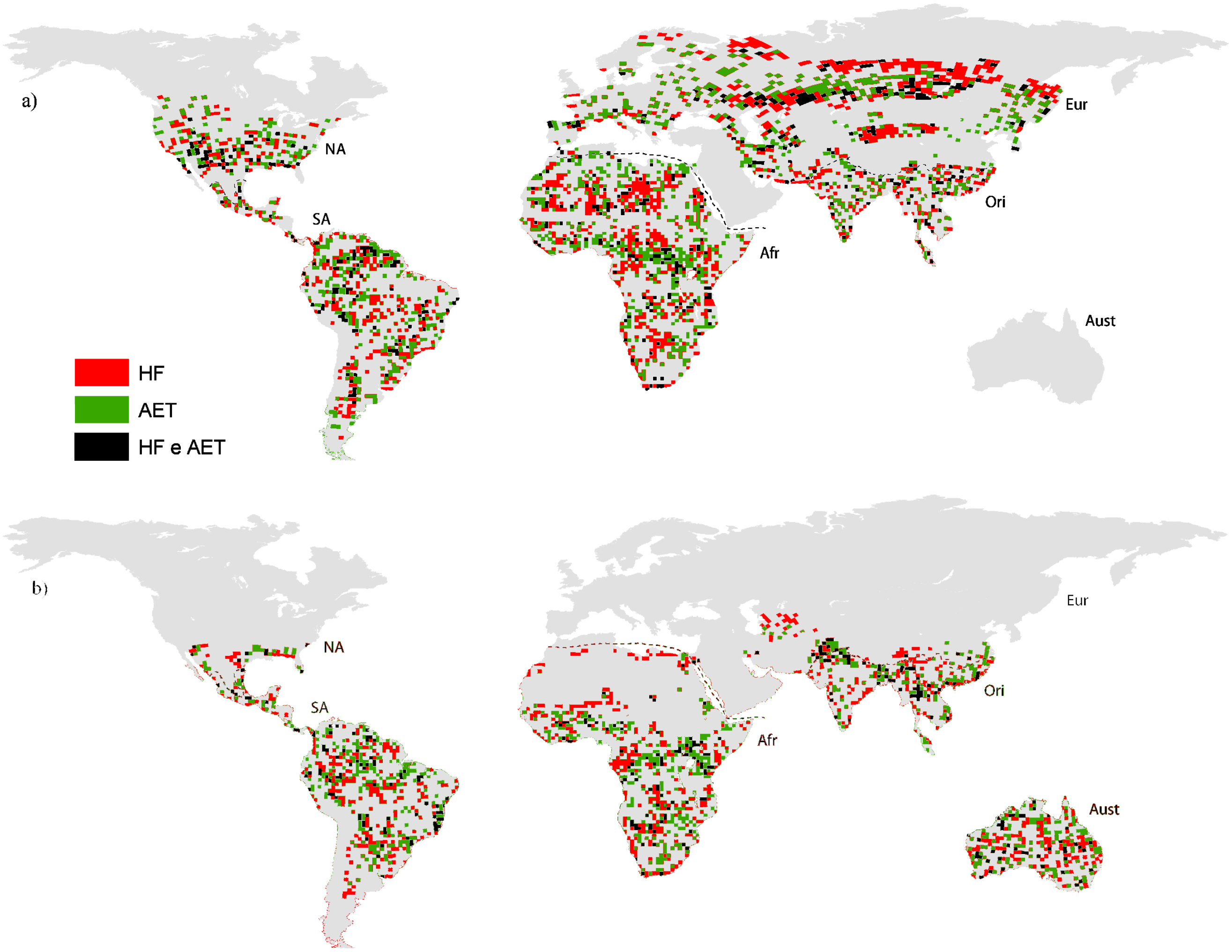

Figura 5. Padrão especial das células de 110 x 110 km selecionadas para compor as soluções de complementaridade considerando o mínimo de influência humana (i.e., “influência humana”; HF, células de cor vermelha) e o máximo de “adequabilidade ambiental” (AET, células de cor verde), para Viperidae (a) e Elapidae (b). As células de negro foram selecionadas em ambas as soluções. Regiões biogeográficas: NA – região Norte Americana; SA – região Sul Americana; Afr – região Africana; Eur – Região Eurasiana; Ori – região Oriental; Aust – região Australiana (ver detalhes no Apêndice 4).

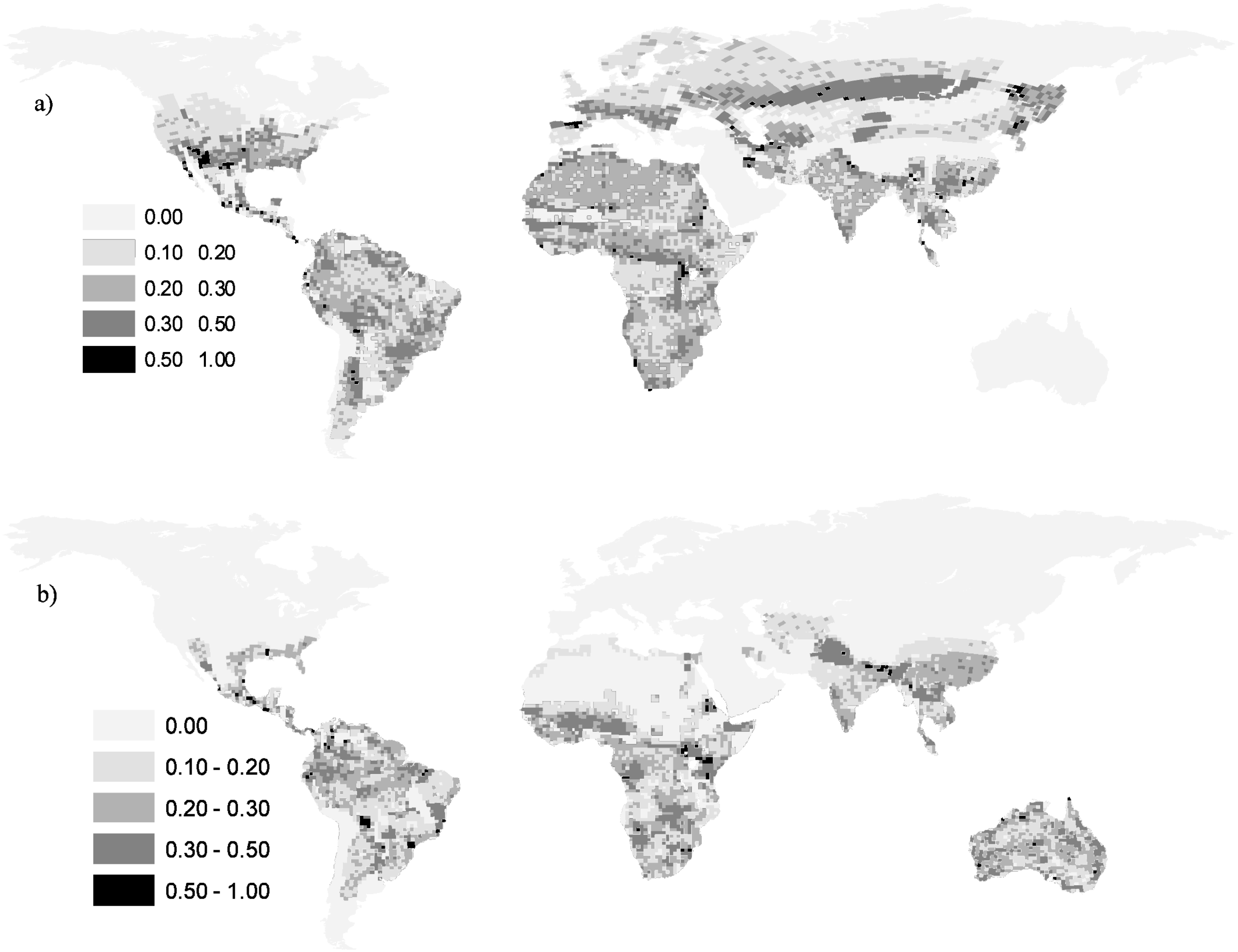

Figura 6. Padrão global de "insubstitutibilidade" para Viperidae (a) e Elapidae (b).

Com exceção das áreas denominadas "As Últimas Áreas Silvestres da Terra" (do inglês *Last of the Wild*; Sanderson *et al.*, 2002), todos os demais esquemas globais apresentaram uma diferença positiva de insubstitutibilidade, ou seja, a média de insubstitutibilidade das áreas compreendidas em cada esquema foi maior que das áreas não inseridas nesses modelos (Tabela 4). Para Viperidae, os maiores ganhos de insubstitutibilidade ocorreram nas "Áreas Endêmicas para Aves" (*Endemic Bird Areas*; Stattersfield *et al.*, 1998) e nas "Áreas Silvestres de Alta Biodiversidade" (*High-Biodiversity*

Wilderness Áreas; Mittermeier *et al*., 2003). Para Elapidae esse ganho também ocorreu nas "Áreas Endêmicas para Aves", porém as regiões incluídas em "As Últimas Áreas Silvestres da Terra" representaram uma perda de insubstitutibilidade para esse grupo.

Similarmente, os esquemas globais que incluem áreas com maior insubstitutibilidade para ambas as famílias também abrangem o maior número de células da solução de complementaridade baseada na maximização de AET (i.e., 25% das células da rede de conservação com AET máximo foram representadas nas "Áreas Endêmicas para Aves" e nas "Áreas Silvestres de Alta Biodiversidade"; ver Tabela 4). Por outro lado, as soluções geradas minimizando a influência humana tiveram maior representação nas "Últimas Áreas Silvestres da Terra". Embora isso seja esperado, considerando que essas regiões são caracterizadas como as de menor alteração antrópica, esse resultados não são necessariamente positivos porque eles representam também áreas de baixo valor (ou seja, baixa insubstitutibilidade) para conservação de serpentes elapídeas.

Tabela 4. Valores ajustados de insubstitutibilidade média (I_{aj}) calculados por meio da ANOVA entre os "grupos" de células abrangidas (1) e não-abrangidas (0) pelas áreas dos modelos globais de prioridades para conservação (ver Brooks *et al.*, 2006). O ganho proporcional de insubstitutibilidade para cada família em cada modelo foi calculado como a diferença entre a média de insubstitutibilidade em 0 e 1 dividido pela média em 0. Foi calculada também a porcentagem (%) de células das soluções globais de conservação envolvendo custos de AET e HF que coincidem com as áreas de cada um dos nove esquemas globais (ver Apêndice 4). Os valores destacados em negrito sublinhado indicam os modelos globais em que há um maior ganho de insubstitutibilidade; valores apenas em negrito indicam os modelos globais que contém a maior porcentagem de células de cada uma das soluções de AET e HF.

Modelos de prioridades globais			I_{aj}		Ganho proporcional de insubstitutibilidade	% de células	
Modelo & (abreviação)	Sistema de priorização Insubstitutibilidade	Vulnerabilidade	1	0		AET	HF
VIPERIDAE							
Biodiversity Hot-spots (BH)	alta	alta	0.233	0.221	0.054	22.4	20.4
Crisis Ecoregions (CE)	–	alta	0.228	0.221	0.031	21.9	18.3
Centers of Plant Diversity (CPD)	alta	–	0.237	0.221	0.072	23.5	22.3
Endemic Bird Areas (EBA)	alta	–	0.238	0.219	**0.086**	23.8	22.6
Frontier Forests (FF)	–	baixa	0.229	0.223	0.026	24.0	29.3
Global 200 ecoregions (G200)	alta	–	0.225	0.224	0.004	21.4	22.2
High-Biodiversity Wilderness Areas (HBWA)	alta	baixa	0.241	0.221	**0.090**	**25.1**	25.7
Last of the Wild (LW)	–	baixa	0.227	0.223	0.017	21.3	**30.3**
Megadiversity Countries (MC)	alta	–	0.231	0.219	0.054	22.3	21.4
ELAPIDAE							
Biodiversity Hot-spots (BH)	alta	alta	0.228	0.225	0.013	21.1	22.6
Crisis Ecoregions (CE)	–	alta	0.228	0.224	0.017	21.1	20.0
Centers of Plant Diversity (CPD)	alta	–	0.228	0.226	0.008	21.5	24.7
Endemic Bird Areas (EBA)	alta	–	0.245	0.215	**0.139**	**25.0**	23.1
Frontier Forests (FF)	–	baixa	0.237	0.223	0.062	**25.0**	27.0
Global 200 ecoregions (G200)	alta	–	0.228	0.222	0.027	21.0	23.5
High-Biodiversity Wilderness Areas (HBWA)	alta	baixa	0.229	0.225	0.017	22.0	25.1
Last of the Wild (LW)	–	baixa	0.216	0.231	**-0.064**	20.7	**29.4**
Megadiversity Countries (MC)	alta	–	0.234	0.214	**0.093**	22.7	22.5

Os autores de cada prioridade global são: BH, Myers *et al.* (2000); CE, Hoekstra *et al.* (2005); CPD, WWF-IUCN (1994–1997); EBA, Stattersfield *et al.* (1998); FF, Bryant *et al.* (1997); G200, Olson & Dinerstein (1998); HBWA, Mittermeier *et al.* (2003); LW, Sanderson *et al.* (2002); MC, Mittermeier *et al.* (1997).

Considerando que as prioridade globais de “Áreas Silvestres de Alta Biodiversidade” e “Áreas Endêmicas para Aves” são consideradas “proativas” dentro de um eixo de vulnerabilidade x insubstitutibilidade (Brooks *et al.*, 2006; ver Tabela 4 e Apêndice 4), os resultados obtidos no presente trabalho são bastantes animadores porque mostram a existência de alternativas viáveis para a conservação de serpentes dentro dos principais esquemas globais, para os quais recursos financeiros e medidas conservacionistas mais direitas têm sido dirigidas (Brooks *et al.*, 2006). Por outro lado, deve observar que muitas das regiões com alta insubstitutibilidade, principalmente para espécies viperídeas, coincidem com algumas prioridades globais consideradas reativas e, portanto, de alta vulnerabilidade (como é o caso dos *Hotsposts* de Biodiversidade; Myers *et al.*, 2000) e alta insubstitutibilidade (como é o caso dos “Centros de Diversidade de Plantas”; WWF-IUCN, 1994–1997). Obviamente, esses resultados são mais preocupantes considerando que 70% das áreas dos *Hotspots* já foram destruídas, o que pode dificultar, ou até mesmo inviabilizar, estratégias mais locais para conservação dessas serpentes nessas áreas. Tornam-se necessários, portanto, estudos mais detalhados de viabilidade populacional (i.e., modelos de população mínima viável; dados sobre as áreas com condições ambientais adequadas dentro dos *Hotspots*) de modo avaliar a eficiência desses modelos reativos para esses grupos de organismos (ver e.g., Reed & Shine, 2002).

5. CONCLUSÕES

A crescente disponibilidade de conjuntos de dados para os diversos grupos de organismos e o desenvolvimento de novas abordagens metodológicas aplicadas às análises macroecológicas têm contribuído para o desenvolvimento de um arcabouço teórico consistente sobre os fatores determinantes dos padrões ecológicos em grande escala, bem como sobre suas conseqüências na estruturação de comunidades de espécies. Porém, a generalização desses fatores depende da avaliação de grupos de organismos com diferentes características ecológicas e evolutivas, como no caso das duas linhagens de serpentes abordadas neste trabalho. Ao longo das análises desenvolvidas, verificamos que:

- diferentes fatores estão associados ao padrão global de riqueza dos dois clados: enquanto o padrão de riqueza de Viperidae é primeiramente determinado por fatores climáticos e ambientais, uma combinação de fatores histórico/evolutivos e climáticos parece mais apropriada para explicar o padrão de riqueza de Elapidae. Isso mostra que modelos puramente ecológicos não são suficientes para explicar os gradientes latitudinais de riqueza;

- As diferenças observadas entre os clados dão ênfase à necessidade de se utilizar abordagens desconstrutivas para as análises dos padrões de diversidade. A desconstrução do padrão geral de riqueza de Viperidae evidenciou que diferentes fatores podem estar associados às variações geográficas de riqueza de espécies com características ecológicas e evolutivas distintas;

- Mais importante, parece provável que se a distribuição geográfica das espécies é fundamentalmente determinada por fatores climáticos, então esses mesmos fatores explicarão boa parte da variação no padrão de riqueza das mesmas, de modo que o “princípio de desconstrução extrema" é uma abordagem bastante útil para investigar esses padrões geográficos;

- O padrão global de tamanho médio do corpo dos dois clados também seguiu a tendência observada no padrão de riqueza, em que fatores climáticos explicam melhor a variação interespecífica no tamanho das espécies viperídeas, enquanto que os fatores evolutivos parecem regular essa variação para as espécies elapídeas;

- As diferentes respostas observadas no padrão global de tamanho do corpo dos dois clados sugerem que diferentes fatores governam a variação interespecífica de tamanho nos diversos grupos de organismos e descarta possibilidade de explicações singulares. Da mesma forma, os resultados observados reforçam a importância da aplicação de abordagens desconstrutivas quando da análise de padrões macroecológicos;

- Finalmente, foi possível definir estratégias eficientes para a conservação da diversidade de Viperidae e Elapidae em escala global, levando em consideração os conflitos entre interesses socioeconômicos e conservação, e a disponibilidade de áreas com condições ambientais adequadas para a ocorrência das espécies. Mais importante, essas estratégias se mostraram viáveis dentro dos atuais modelos globais de priorização, aumentando assim as chances de que estratégias desenvolvidas em escalas locais e regionais tenham sucesso na preservação da diversidade dessas serpentes.

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Apêndice 1. Padrão global de riqueza de espécies.

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COMMUNITY ECOLOGY - ORIGINAL PAPER

Global richness patterns of venomous snakes reveal contrasting influences of ecology and history in two different clades

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Abstract Recent studies addressing broad-scale species richness gradients have proposed two main primary drivers: contemporary climate and evolutionary processes (differential balance between speciation and extinction). Here, we analyze the global richness patterns of two venomous snake clades, Viperidae and Elapidae. We used ordinary least squares multiple regression (OLS) and partial regression analysis to investigate to what extent actual evapotranspiration (AET; summarizing current environmental conditions) and biogeographical regions (representing evolutionary effects) were associated with species richness. For viperids, AET explained 45.6% of the variance in richness whereas the effect of this variable for elapids was almost null (0.5%). On the other hand, biogeographic regions were the best predictors of elapid richness (56.5%), against its relatively small effect (25.9%) in viperid richness. Partial regressions also revealed similar patterns for independent effects of climate and history in both clades. However, the independent historical effect in Elapidae decreased from 45.2 to 17.8% when we excluded Australia from the analyses, indicating that the strong historical effect that had emerged for the global richness pattern was reflecting the historical process of elapid radiation into Australia. Even after excluding Australia, the historical signal in elapid richness in the rest of the globe was still significant and much higher than that observed in viperid richness at a global scale (2.7% after controlling for AET effects). Differences in the evolutionary age of these two clades can be invoked to explain these contrasting results, in that viperids probably had more time for diversification, generating richness responses to environmental gradients, whereas the pattern of distribution of elapid richness can be more directly interpreted in an evolutionary context. Moreover, these results show the importance of starting to adopt deconstructive approaches to species richness, since the driving factors of these patterns may vary from group to group according to their evolutionary history.

Keywords Evolutionary history · Latitudinal gradient · Snakes · Species richness · Water energy hypothesis

Introduction

As a result of the interest of ecologists in large-scale diversity gradients and their determinants over the last two centuries (von Humboldt 1808; Hutchinson 1959; Pianka 1966; Glazier 1987; Currie 1991; Hawkins et al. 2003a), there have been considerable advances in our knowledge about the most important drivers of global patterns in species richness (Hawkins et al. 2003a, b, 2007a; Ricklefs

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2003; Willig et al. 2003; Wiens and Donoghue 2004; Wiens et al. 2006a). Research on this subject has evolved into two well-founded frameworks: contemporary climate influences diversity gradients through energy inputs and/or water availability (Currie 1991; Francis and Currie 1998; Hawkins et al. 2003a; Rodríguez et al. 2005; Kreft and Jetz 2007; Buckley and Jetz 2007); and evolutionary history determines broad-scale richness patterns through a number of potential mechanisms such as niche conservatism, older age and stability of tropical regions, geographically structured variation in speciation and extinction rates, and differential species' dispersal capabilities of colonizing new areas (Latham and Ricklefs 1993; Ricklefs 2003; Hawkins et al. 2003b; Jablonski et al. 2006; Buckley and Jetz 2007; Mittelbach et al. 2007; Montoya et al. 2007; Svenning et al. 2008).

Ecological hypotheses based on the contemporary climate have been intensively tested over the past 50 years (see Hawkins et al. 2003a for a revision), and there is a consensus in that energy, through direct or indirect effects (via plant productivity), drives higher diversity in the tropics. However, it is also important to consider the evolutionary mechanisms underlying patterns in richness. In general, historical hypotheses assume that the tropics support more species due to two reasons: the tropics are older and historically larger than temperate regions, so they accumulated more species over time and/or; tropical regions have higher diversification rates due to higher speciation and lower extinction rates (see Mittelbach et al. 2007 for a recent review of hypotheses). Even so, we still lack good explanations for how environmental (or ecological) factors interact with evolutionary mechanisms to generate current geographic gradients in species richness, although recent studies have proposed hypotheses based on niche conservatism as a way of integrating ecology, evolution and historical biogeography to explain these gradients (see Wiens and Donoghue 2004; Wiens et al. 2006a; Ricklefs 2006; Hawkins et al. 2005, 2007a; Rangel et al. 2007). Moreover, the paucity of global datasets for a wide array of organisms prevents us from proposing a general explanation for all taxa as well as limiting our abilities to test the suggested ecological and evolutionary hypotheses underlying the patterns. Hence, if we are to understand the large-scale richness patterns and the causes underlying them, we need to consider the particular responses of different taxonomic groups.

For vertebrates, the available distributional databases and studies of gradients richness with a global coverage are those for fishes (Oberdoff et al. 1995), amphibians (IUCN 2006; Buckley and Jetz 2007), birds (Hawkins et al. 2003b, 2007a; Orme et al. 2005), and mammals (Ceballos and Ehrlich 2006). Overall, reptiles remain insufficiently documented in the macroecological and biogeographical literature and only a few studies have examined the existence of broad-scale richness gradients for this group (Schall and Pianka 1978; Owen 1989; Rodríguez et al. 2005; Costa et al. 2007). Furthermore, most of these studies have been geographically restricted to temperate regions, which limits the generalizability of their findings (e.g., Rodríguez et al. 2005). For snakes, the only investigation focused on macroecological patterns is the one by Reed (2003) and, as far as we know, there are neither global datasets nor global richness analyses for any group of reptiles (but see Lamoreux et al. 2006, for an analysis using species list on WWF ecoregions).

In this paper we present a global analysis of the richness patterns of two monophyletic clades within Caenophidia (the "advanced snakes"): Viperidae and Elapidae (Knight and Mindell 1994; Vidal and Hedges 2002; Kelly et al. 2003; Vidal et al. 2007). Although the snakes in these two families are similar in that they have front-fanged venom systems, they arose independently from non-venomous snake ancestors (Knight and Mindell 1994). Based on fossil venom fangs from the Lower Miocene, Kuch et al. (2006) dated the evolution of both Viperidae and Elapidae from the Early Cenozoic, thus stating that both clades evolved at the same time and before colubroid radiations of Miocene. However, studies inferring divergence times within snakes suggested that viperids diverged from colubroids between 60.9 and 43.0 million years ago (Rage et al. 1992; Wiens et al. 2006b). Recently, estimates of age clade provided by Sanders and Lee (2008) suggest that viperids evolved between 48.9 and 31.0 million years ago (mean divergence at 39.9 million years ago; see also Szyndlar and Rage 1999; Lenk et al. 2001 for similar conclusions), whereas elapids diverged between 32.2 and 21.1 million years ago (mean divergence at 26.2 million years ago). The study of Sanders and Lee (2008) is consistent with previous assertions of Heise et al. (1995), Keogh (1998), and Kelly et al. (2003), which proposed that Elapidae is a more recent clade in comparison with Viperidae. Taken into account the recent discussion about niche evolution and niche conservatism (see Peterson et al. 1999; Wiens and Donoghue 2004; Pearman et al. 2007), this evolutionary aspect is important if one consider that a "younger" clade had less time to disperse, diversify and adapt to new climatic conditions.

Here, we investigate whether current global richness patterns of Viperidae and Elapidae are associated with contemporary environmental variation or still reflect a signal of historical effects (barrier for dispersal, speciation, and extinction) considering the difference in evolutionary age between both lineages (i.e., the more recent origin of Elapidae). For this, we tested the relative importance of the current environment (present climate and primary productivity conditions) and history (biogeographical zooregion) to account for the global richness patterns of each clade. We also investigate the differences in historical and environmental effects across six zooregions, which allows us to identify a potential role for history in the current richness pattern of viperid and elapid snakes.

Materials and methods

Viperidae comprises around 256–260 species (Kelly et al. 2003; Castoe and Parkinson 2006) that are distributed across mainlands and islands of Asia, Africa, Europe and the New World, but are absent from Australia, possibly because the advanced caenophidians evolved during the Cenozoic (from 65.5 million years ago) when this region had already became a separated landmass (Keogh 1998). Elapidae comprises about 290–300 species (Keogh 1998; Castoe et al. 2007) of which around 60 are marine (sea snakes), and is distributed across Africa, Asia, Australia, the New World, and the Indian and Pacific Oceans. These two families represent around 20% of the caenophidians diversity (Kelly et al. 2003; Vidal et al. 2007), but are the only families within this large group for which distributional data is available at a global scale.

We generated a global checklist for both groups based on the updated Reptile Database, supported by the Systematics Working Group of the German Herpetological Society (Uetz 2007). Following this checklist, we used several sources of species distribution worldwide (see below) to obtain geographic distribution maps for all terrestrial species inhabiting large land masses; namely all continents and the well prospected island of Great Britain, which has enough extension and proximity to the mainland to warrant that richness patterns are not affected by island effects. Data scarcity for the Arabian Peninsula precluded the inclusion of this region in the analysis, and sea snakes were excluded because their distribution is likely to be conditioned by different environmental factors than terrestrial species. Thus, our final database comprised 228 viperids and 224 elapids (a full list of genera and number of species is provided in the Electronic supplementary material S1).

For the New World, species range maps were primarily obtained from Campbell and Lamar (2004), supplemented with the new species recently recognized by Renjifo and Lundberg (2003), Alvarado-Díaz and Campbell (2004) and Lavin-Murcio and Dixon (2004). For the Old World we used Branch (1988, 1998), Latifi (1991), Arnold (2002), Arnold and Ovenden (2002), Broadley and Doria (2003), Spawls et al. (2004), Ananjeva et al. (2006), Vogel (2006), Dobiey and Vogel (2007), supplemented by Cherlin (1981), Orlov and Tuniyev (1990), Tuniyev and Ostrovskikh (2001), Khan (2002), Mallow et al. (2003) and Geniez and Tynié (2005). For Australian elapids we used Wilson and Swan (2003). All maps were digitized and rasterized in ArcGIS 9.2 in grid systems of 110 × 110 km using region-specific equal area projections. Species richness was calculated directly from the raster files. Although used for representation purposes, those cells containing less than 50% of the land mass were not included in the analyses to avoid potential area effects in the results.

To examine the influence of environment on richness patterns, we first considered seven variables that have been commonly used to analyze broad-scale diversity gradients. These included the total annual sums of Thornthwaite's actual evapotranspiration (AET), precipitation, Priestley–Taylors's potential evapotranspiration, and the global vegetation index, as well as mean annual temperature, the number of months available for plant growth, and range in elevation (i.e., the difference between maximum and minimum elevation within each grid cell) (data sources and processing techniques can be seen in Olalla-Tárraga et al. 2006 and Rodríguez et al. 2008). However, these variables typically have strong collinearity, which may cause misinterpretations of environmental models involving multiple predictors. In fact, in our dataset, AET, which represents the joint availability of energy and water in the environment (see Currie 1991 and Hawkins et al. 2003a), was a linear combination of the remaining environmental predictors, with $R^2 = 0.882$. Thus, we used AET as a surrogate of current environmental variation in our environmental models of richness.

To take into account evolutionary (or historical) effects in a broad sense (see Hawkins et al. 2003b; Buckley and Jetz 2007; Hortal et al. 2008), we classified the dataset according to six biogeographic regions: North American, South American, Eurasian, African, Oriental and Australian (Cox 2001). These biogeographic regions are based on the historic distribution patterns of plants and animals and were used here as a surrogate of the evolutionary history of Viperidae and Elapidae. Even though the use of biogeographic regions can be considered a relatively crude measure of historical contingencies on geographical patterns of species richness, this has proved to be a successful proxy variable to represent differential speciation and extinction rates and interregional barriers to dispersal (Hawkins et al. 2003b; Buckley and Jetz 2007; Hortal et al. 2008).

We investigated to what extent AET (a continuous variable summarizing current environmental conditions) and region (a categorical variable) were associated with species richness using ordinary least squares multiple regression (OLS), coupled with variance partitioning using partial regression analysis (Legendre and Legendre 1998; Hawkins et al. 2003a). For each multiple regression model, influence of spatial autocorrelation in model residuals was assessed by Moran's I coefficients (Diniz-Filho et al. 2003), and since some autocorrelation coefficients were high, we repeated the partial regression analyses based on R^2 derived from a simultaneous autoregressive error model (SAR; see

Dormann et al. 2007; Kissling and Carl 2008; Araújo et al. 2008). However, because the sample size is too large for spatial modeling, we created ten subsamples with 1,000 randomly chosen cells (see Hawkins et al. 2007a) and ran SAR for each subsample, obtaining the partial regression for each one. Before all statistical analyses, cells containing zero species were excluded. For the remaining cells, richness was transformed to its square root because of the relatively low number of species in some cells, which tend to produce a strongly non-normal distribution of model residuals in the original (count) scale. All statistical analyses were performed using SAM 3.0 (Spatial Analysis in Macroecology; Rangel et al. 2006).

Results

Global viperid diversity increases towards the equator (Fig. 1a) and the map of richness is analogous to those published earlier for other vertebrates at a global scale (Hawkins et al. 2003b; Ceballos and Ehrlich 2006; Grenyer et al. 2006; Buckley and Jetz 2007). Regions with the highest richness include Central Africa, eastern and extreme southern parts of India and extreme southern Asia.

Elapidae has an almost exclusively tropical distribution (Fig. 1b). The group is most diverse on the east coast of Australia, where one cell (12,100 km^2) might reach 25 species. However, compared to Australia, elapid richness is very low in other regions, where the highest richness values do not reach more than ten species per cell.

Viperid species richness was more strongly associated with AET (which accounted for 45.6% of the variance, though this amount varied across regions, see Fig. 2a) than with biogeographic regions (25.9%) in simple regression models including only one of these variables, suggesting that history is less important than environment in determining the richness patterns of this clade. Consistent with this interpretation, a full model that included AET and regions, explained little more variance than AET alone (48.3%), with AET accounting for 22.4% variance after controlling for regional effects, and region for only 2.7% after controlling for AET effects (Fig. 3a). Still, the amount of variance that was explained by the overlap of AET and region was relatively high (23.2%; see Fig. 3a). So, although our data

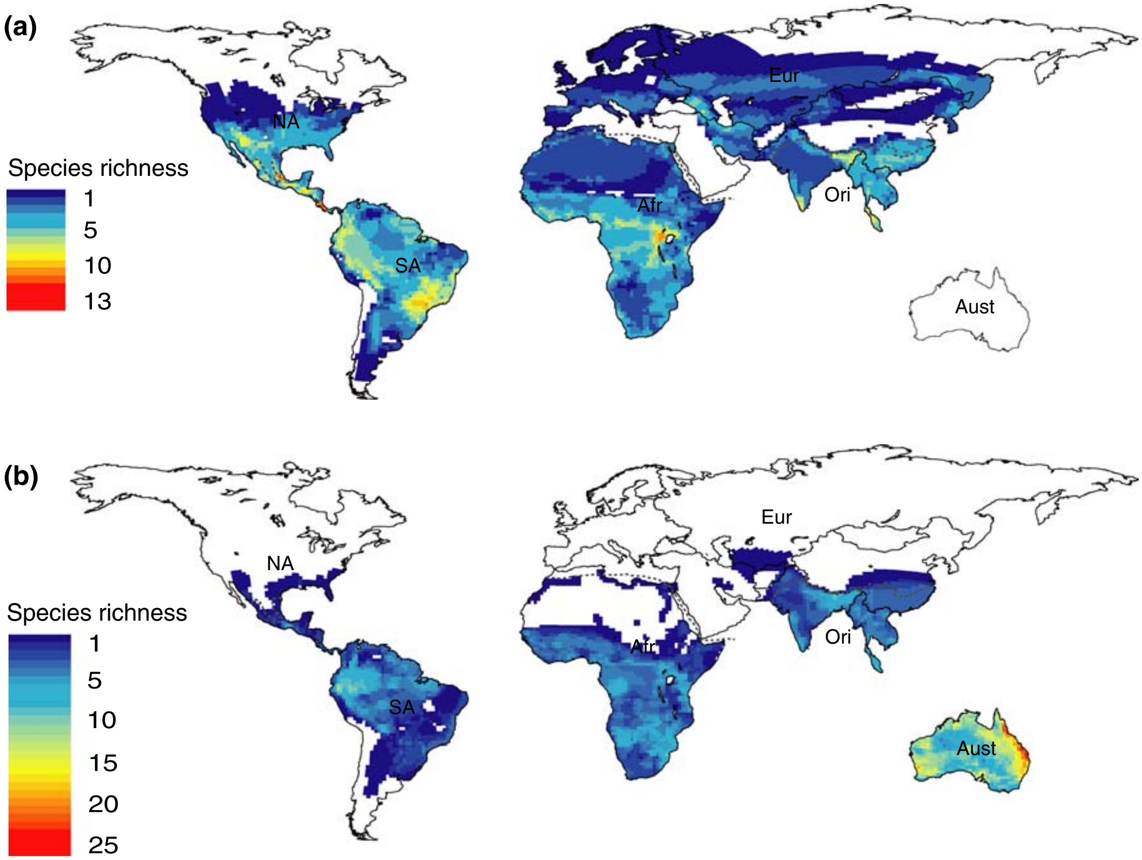

Fig. 1 Global biogeographical patterns of Viperidae (**a**) and Elapidae (**b**) species richness. The *dashed lines* identify the biogeographical limits of Cox (2001) used in our analyses. *NA* North American, *SA* South American, *Afr* African, *Eur* Eurasian, *Ori* Oriental, *Aust* Australian

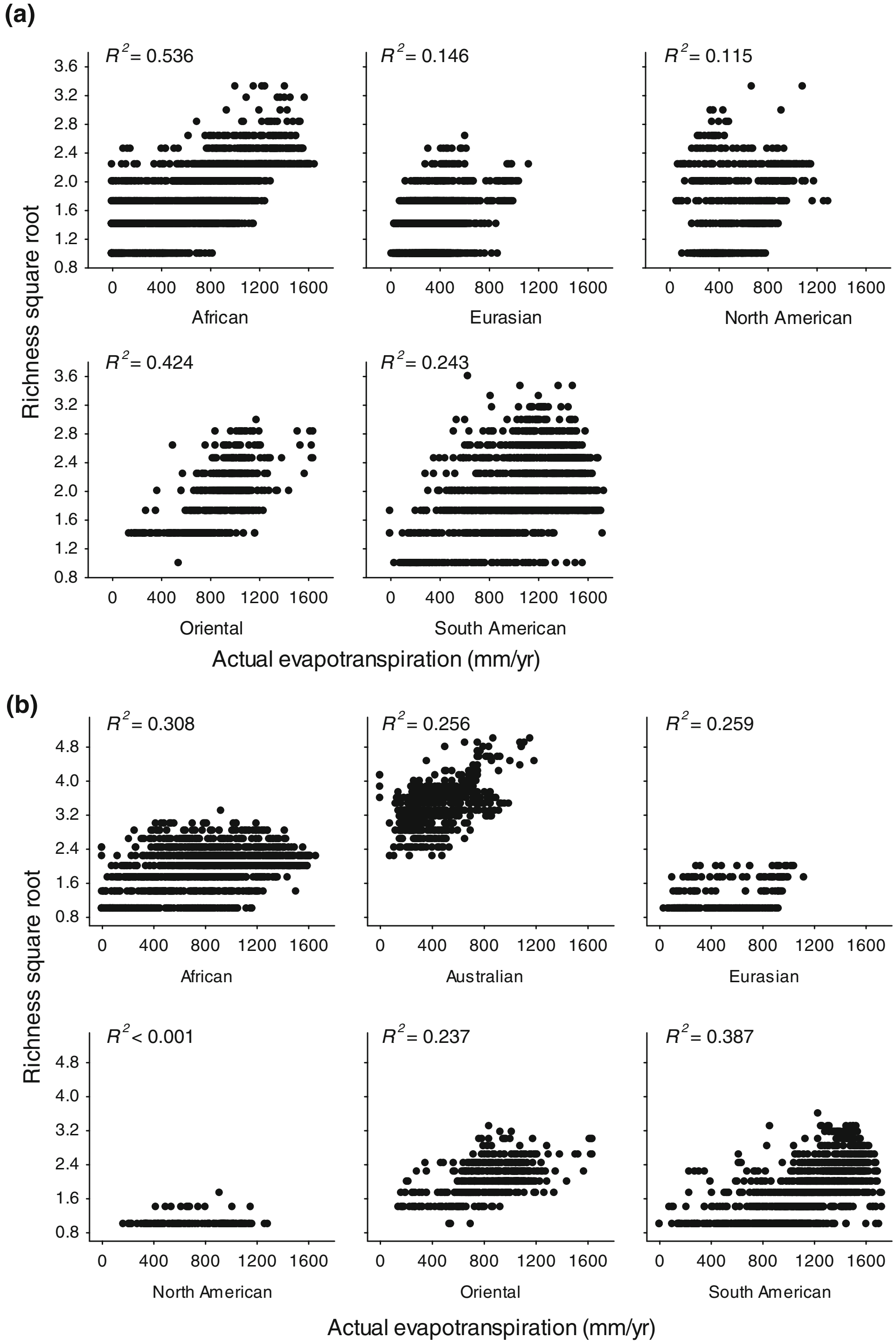

Fig. 2 Relationships between actual evapotranspiration (AET) and species richness of Viperidae (**a**) and Elapidae (**b**) in each biogeographic region. *yr* Year

support current water–energy dynamics as the primary determinant of viperid richness at the global scale, they also suggest some secondary role for history, the complete extent of which is uncertain given the amount of variance that is explained jointly by region and AET.

For elapids, the current environment model (i.e., including only AET) accounted for just 0.5% of the variance, and species richness values were almost evenly distributed across all AET values in all regions (Fig. 2b). In contrast, the historical model (i.e., including only regions) had a much higher coefficient of determination ($R^2 = 0.565$), suggesting that history is a considerable determinant of species richness of this group at the global scale. The full model, with AET and regions, explained 68.3% of the variance in richness, and partial regressions revealed that AET tend to a negative value (which indicates that AET had actually no

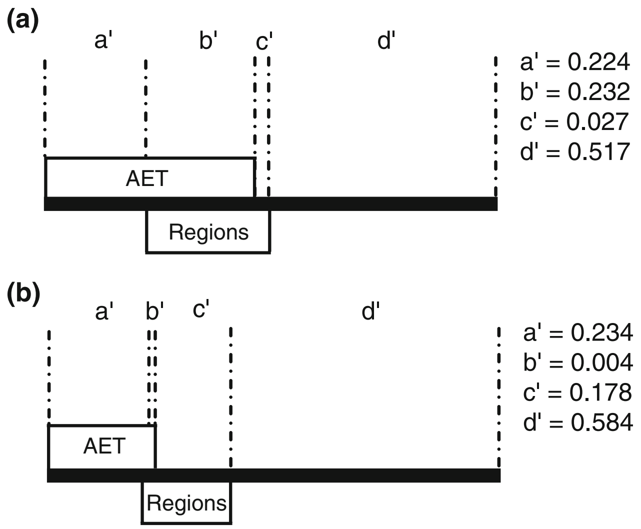

Fig. 3 Results of partial regression analyses using AET and biogeographic regions as predictors of global patterns in snake richness; **a** Viperidae and **b** Elapidae (in this case, Australia was excluded from the analyses of partial regression due to the strong interactive effect between this region and AET, see explanations in the text). The unexplained variance (d') is $1 - R^2$ of the ordinary least squares multiple regression including both AET and region, which corresponds to the portion ($a' + b' + c'$); the overlap between region and AET (b') is equal to ($a' + b'$) + ($b' + c'$) − ($a' + b' + c'$), where ($a' + b'$) is the R^2 of the regression using AET, and ($b' + c'$) is the R^2 of the regression using biogeographic region. a' Variance explained by AET only, c' variance explained by biogeographic regions only

independent effect), while region independently explained 45.2% of the variance. Overlapped effects of climate and history explained nearly 11%. So, in contrast to Viperidae, elapid species richness gradients appear primarily and strongly associated with history while the independent effects of current environment seem negligible.

It is important noting that the full model accounted for much more variance (68.3%) than the sum of regions independent effect (45.2%) and the overlapped variance (11%), and thus the effect of AET alone would provide a negative R^2-value in partial regression analysis. This is actually due to an interactive effect between AET and regions, and indeed the effect of an interaction term between AET and Australia increases the R^2 from 0.005 (AET alone) to 0.481 (AET × Australian region), although adding this term does not improve the overall model (i.e., the interaction between AET and all other regions do not increase the explanation power of AET alone). Thus, the higher sum of AET and region explaining global patterns is explained by a unique regional effect in Australia.

Because of this interaction, and due to the strong regional differences observed for Elapidae (i.e., Australia exhibits much higher diversity than the rest of the areas, see Fig. 1b), we reanalyzed the data excluding this region. We found that the independent effect of region decreased from 45.2 to 17.8% (see Fig. 3b), whereas the previously absent independent effect of AET was now 23.4%. This suggests that the strong historical effect that had emerged from the analysis involving all regions was reflecting historical processes of elapid radiation throughout Australia. Nonetheless, although the models are now similar with regard to their respective explanatory powers (i.e., 48.3% for Viperidae and 41.6% for Elapidae without Australia), there is still an independent effect of history on the richness patterns of Elapidae (17.8%) that is 6 times higher than the historical signal observed in Viperidae at the global scale (2.7%).

Finally, although some autocorrelation remains in model residuals (Moran's I in the first distance class = 0.21 in the full model for Viperidae, and 0.32 in the full model for Elapidae), this is unlikely to affect interpretation of the relative contribution of the main effects (contemporary climate and biogeographic region), based on coefficients of determination and partial regressions (see Hawkins et al. 2007b). Indeed, when repeating the analyses using the R^2 from a SAR model, no qualitatively differences appear (see Araújo et al. 2008). The average R^2 in the ten subsamples of AET alone was 0.224 for Viperidae and tends to 0.00 (actually a slightly negative value, as discussed above) for Elapidae. For history, the average R^2 was 0.024 for viperids and 0.438 for elapids.

Discussion

The most striking result from our analyses was the contrasting association of viperid and elapid species richness gradients with our indicators of current environmental conditions (AET, a measure of the water–energy balance in the environment) and history (biogeographical region). As indicated by partial regressions, the relative importance of AET in explaining Elapidae richness was lower in general, whereas history alone accounted for a considerable amount of variance. Conversely, global richness patterns of Viperidae were reasonably explained by AET, and supported that the gradients are more strongly determined by current conditions than by historical effects. Still, in this latter clade, there was a relatively large amount of explained variation that could not be independently attributed to either factor, for which we cannot discard some secondary role of history in determining its gradients.

The findings regarding viperid richness variation concur with previous studies that have identified water–energy inputs as the most emergent determinants of animal diversity, at different geographical scales (Hawkins et al. 2003a, 2007a; Hawkins and Porter 2003; Rodríguez et al. 2005). Also, previous large-scale (but not necessarily global) studies focused on reptile diversity have found similar results; where environmental energy alone or in combination with water availability was the best predictor (see Schall and Pianka 1978; Owen 1989; Currie 1991; Hawkins et al. 2003a; Rodríguez et al. 2005). Associated with these results, it is typically thought that the relationship between reptile richness and energy is due to the direct dependence of these organisms on solar energy to regulate and maintain their body temperatures (Owen 1989; Currie 1991; Hawkins et al. 2003a; Rodríguez et al. 2005; Whittaker et al. 2007).

However, in spite of the dependence on environmental energy to thermoregulate (which would suggest that energy inputs may restrict the distribution of Viperidae to some extent), Shine and Madsen (1996) showed that thermal constrains may influence snakes just in minor ways (e.g., some microhabitats may be too hot for long-term residence during daylight hours). This is because tropical species can maintain high and relatively stable body temperatures throughout the year (see Shine and Madsen 1996) and, in contrast with what happens with some lizards (Avery et al. 1982), snakes exhibit relatively little overt thermoregulatory behavior. In our analyses, viperid richness patterns were only weakly associated with pure environmental energy variables (i.e., potential evapotranspiration and temperature) after taking AET into account in multiple regression models (results not shown). This result suggests that the general explanation for reptiles' richness–energy association based on extreme energy dependence of these organisms might not be a rule and that viperid richness variation is mainly determined by combined influences of water and energy operating through effects of these variables on productivity and food supply (see Hawkins et al. 2003a, b; O'Brien 2006; see also Hawkins et al. 2007c for a recent global evaluation of energy hypothesis explaining richness patterns in the specific context of the metabolic theory of ecology).

In this regard, a study of Owen (1989), based on the patterns of herpetofaunal species richness in Texas, proposed that most snakes are habitat generalists and that greatest snake richness does not occur in areas of highest productivity. However, this is not a compelling proposition, since opposite reasoning for the primary productivity hypothesis has been proposed to explain species richness (Hawkins et al. 2003a; Rodríguez et al. 2005). In other words, areas with high productivity and, consequently, wide resource availability, could benefit both specialist and generalist species, either through the food supply or habitat availability.

Further, the weak support of the historical hypothesis tested here to explain the global pattern of viperid richness does not concur with the proposition of Reed (2003) for New World diversity of Viperidae. According to this author, the viperid richness peak in Central America and southern Mexico may be associated with the historical biogeography of these regions (i.e., the occurrence of several orogenic episodes), which could generate many opportunities for allopatric speciation. Apparently, and as shown above, this is not the main cause of the viperid richness pattern, even though the importance of climate or history to account for diversity can vary across different parts of world (Hawkins et al. 2003b), and historical biogeography could be important to some extent in explaining Viperidae richness. On the other hand, these biogeographic events appear to make sense when explaining the richness pattern of Elapidae.

In contrast to Viperidae, the global-scale variation of Elapidae richness seems to be primarily determined by the evolutionary history of the clade, as indicated by the strong explanatory power of the models including biogeographic regions. However, excluding Australia from the analysis led to the detection of a moderate effect of contemporary climate (indicated by AET) in the rest of the world, which lead us to suggest that the strong historical signal for this group is closely related to the particular evolutionary history in the Australian region. From a general perspective, the much stronger historical response of elapid richness suggests that a robust and unified explanation to global richness patterns of animals is a hard aim and points towards the need to adopt "deconstructive" approaches (sensu Marquet et al. 2004), in which richness is analyzed for groups that possess clear ecological or evolutionary unifying characteristics. In an evolutionary context, this is relevant if we consider that Viperidae is one of the most basal lineages of Caenophidia, which diverged prior to the separation of elapids from other colubroids (Heise et al. 1995; Kelly et al. 2003; Vidal et al. 2007). Thus, viperids probably had more time to diversify, generating richness responses to environmental gradients. In contrast, although the pattern of distribution of elapid richness responds to AET variation in some regions (Fig. 2b), it still reflects a recent history of colonization and diversification within tropical and subtropical regions (e.g., the Australian radiation), so that the frequently observed gradient of animal species richness may have not yet uniformly emerged in all regions.

Thus, the importance of the Australian region to an interpretation of the strong historical component in the richness pattern of Elapidae can be explained by the hypothesis of recent radiation of this clade into Australia (Keogh 1998; Scanlon and Lee 2004). This hypothesis was recently reaffirmed by Sanders and Lee (2008), whose divergence time estimation revealed that the terrestrial Australo-Papuan elapids (i.e., the Australian and Melanesian insular species) along with the sea snakes (both insular and marine species not included here) are a quite recent group, dating from the Late Miocene (~10 million years ago). This recent evolution implies that Australasian elapid radiation has undergone much more rapid species accumulation than previously assumed (Sanders and Lee 2008). This high and rapid diversification could had been favored by an early colonization of new environmental conditions available in the Australasian continental and marine ecosystems, since they were relatively free of both competition (in the absence of similar predatory competitors, such as viperids) and predation (due to the defensive capabilities including potent venom and fangs).

In sum, we conclude that both contemporary climate and evolutionary history must be taken into account to elucidate global richness patterns, thus giving support to the most recent attempts to integrate ecological and evolutionary phenomena as drivers of biodiversity. Moreover, these results showed the importance of analyzing each clade independently and starting to adopting richness deconstructive approaches (sensu Marquet et al. 2004) to investigate macroecology patterns, as the factors acting on richness may vary from group to group, according to their evolutionary history.

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Apêndice 2. Desconstrução dos padrões de riqueza de Viperidae.

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MACROECOLOGICAL METHODS

Richness patterns, species distributions and the principle of extreme deconstruction

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ABSTRACT

Aim To analyse the global patterns in species richness of Viperidae snakes through the deconstruction of richness into sets of species according to their distribution models, range size, body size and phylogenetic structure, and to test if environmental drivers explaining the geographical ranges of species are similar to those explaining richness patterns, something we called the extreme deconstruction principle.

Location Global.

Methods We generated a global dataset of 228 terrestrial viperid snakes, which included geographical ranges (mapped at 1° resolution, for a grid with 7331 cells world-wide), body sizes and phylogenetic relationships among species. We used logistic regression (generalized linear model; GLM) to model species geographical ranges with five environmental predictors. Sets of species richness were also generated for large and small-bodied species, for basal and derived species and for four classes of geographical range sizes. Richness patterns were also modelled against the five environmental variables through standard ordinary least squares (OLS) multiple regressions. These subsets are replications to test if environmental factors driving species geographical ranges can be directly associated with those explaining richness patterns.

Results Around 48% of the total variance in viperid richness was explained by the environmental model, but richness sets revealed different patterns across the world. The similarity between OLS coefficients and the primacy of variables across species geographical range GLMs was equal to 0.645 when analysing all viperid snakes. Thus, in general, when an environmental predictor it is important to model species geographical ranges, this predictor is also important when modelling richness, so that the extreme deconstruction principle holds. However, replicating this correlation using subsets of species within different categories in body size, range size and phylogenetic structure gave more variable results, with correlations between GLM and OLS coefficients varying from –0.46 up to 0.83. Despite this, there is a relatively high correspondence ($r = 0.73$) between the similarity of GLM-OLS coefficients and R^2 values of richness models, indicating that when richness is well explained by the environment, the relative importance of environmental drivers is similar in the richness OLS and its corresponding set of GLMs.

Main conclusions The deconstruction of species richness based on macroecological traits revealed that, at least for range size and phylogenetic level, the causes underlying patterns in viperid richness differ for the various sets of species. On the other hand, our analyses of extreme deconstruction using GLM for species geographical range support the idea that, if environmental drivers determine the geographical distribution of species by establishing niche boundaries, it is expected, at least in theory, that the overlap among ranges (i.e. richness) will reveal similar effects of these environmental drivers. Richness patterns may be indeed viewed as macroecological consequences of population-level processes acting on species geographical ranges.

Keywords

Distribution modelling, extreme deconstruction, range size, snakes, species richness, Viperidae.

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INTRODUCTION

There is a consensus among ecologists that diversity is not randomly distributed at broad scales in geographical space. For instance, it has been recognized since the 18th century that tropics possess more species than temperate regions for most kinds of organisms (Hawkins, 2001), although the detailed ecological and evolutionary mechanisms that may be underlying the so-called latitudinal diversity gradient are still debated (Hawkins *et al.*, 2003; Willig *et al.*, 2003; Hillebrand, 2004; Ricklefs, 2006; Mittelbach *et al.*, 2007). Currently, a multicausal approach seems to be the most appropriate form of analysis for complex biological and ecological systems, as multiple causes can generate simultaneously the same patterns at different scales and for different groups of organisms (Elliot & Brook, 2007). In this type of approach, the relevant question is not if a given mechanism accounts for a given pattern, but rather what the relative importance of each one is to the overall patterns.

Marquet *et al.* (2004) also pointed out that part of the difficulty in finding overall explanations for broad-scale patterns of species richness is due to the fact that species richness is actually an 'aggregate' variable, usually obtained by overlapping geographical ranges (i.e. extents of occurrence) in macroecological studies. This overlap, in turn, may encompass groups of species with traits evolving in distinct ecological functions and under multiple evolutionary pathways, so that species and their overlap can present different geographical patterns and may respond in complex and different ways to environmental variation. Under niche conservatism, for example (see Wiens & Graham, 2005; Losos 2008a,b; Wiens, 2008), phylogenetically related species can have similar ecological requirements and environmental tolerances, and thus they should respond in more similar ways to environmental factors, creating as a consequence more similar patterns of geographical distribution that should overlap more frequently (increasing richness). Indeed, McPherson & Jetz (2007) showed that geographical range models vary among species with similar life-history characteristics.

Marquet *et al.* (2004) highlighted the advantages of partitioning richness patterns into sets of species that are defined according to particular traits (e.g. to be geographically restricted or widespread, small-bodied or large-bodied, exhibiting slow/short-dispersal or fast/long-dispersal). Under the assumption that these groups show more similar responses to intrinsic and extrinsic ecological processes, such as responses of abundance and distributions to environmental drivers, or extinction in the face of human pressures, it would be easier to interpret the factors driving species richness. Beyond other advantages, this 'deconstructive' approach can be used to clarify the causes underlying species richness patterns by framing questions concerning richness patterns in a clearer comparative way (see also Bini *et al.*, 2004).

The approach of defining sets of similar species has actually been used for a long time (e.g. Badgley & Fox, 2000; Bhattarai &Vetaas, 2003), but the work by Marquet *et al.* (2004) tried to formalize the use of deconstructive analyses and a priori thinking in planned comparisons of richness patterns. Two examples from recent macroecological literature reinforce the utility of deconstructing species richness to help understand the mechanisms underlying its geographical patterns. Hawkins *et al.* (2005, 2006, 2007) used a 'phylogenetic deconstruction' and calculated geographical patterns of richness separately for basal and derived groups. In all cases, overall richness was more related to richness calculated from basal species, which reinforces the idea that these patterns are related to a niche conservatism process, as proposed by Wiens & Donoghue (2004). Jetz & Rahbek (2002; see also Rahbek *et al.*, 2007) also showed that richness calculated using species with different geographical range sizes has different geographical patterns, so that richness from wide-ranging species clearly shows stronger correlations with environmental and climate variation than richness calculated for narrow-ranging species, which seem to be more randomly distributed in geographical space (see also Rahbek *et al.*, 2007; but see Hawkins & Diniz-Filho, 2006, and Ruggiero & Hawkins, 2008, for an alternative explanation related to mountain effects). Even though these studies did not explicitly used the term 'deconstruction', they clearly show that the causes underlying large-scale richness patterns can be better understood by decomposing richness into historical or ecologically distinguished groups of species.

In this context, we follow here the suggestion of Marquet *et al.* (2004) and use several criteria to deconstruct global patterns in species richness of Viperidae snakes (Serpentes). Our previous analyses (Terribile *et al.*, 2008) did not reveal strong evolutionary signals explaining richness patterns for this taxon and we found that present climate explains a reasonable amount of the variation in richness at global scales, as previously found for many other groups of organisms (see Hawkins *et al.*, 2003). Thus, we initially tested the hypothesis that sets of species with different ecological and evolutionary characteristics (range size, body size and phylogenetic structure) have different richness patterns that can be explained by different sets of environmental factors.

However, the richness deconstruction is in some sense subjective, since there is not a clear criterion (or actually there may be many alternatives) for establishing sets of species based on their ecological characteristics. In the limit, each species has its own and particular ecological niche that determines its response to environment, being thus a unique 'set'. Thus, here we have expanded and generalized the deconstructive approach to its theoretical limit by performing what can be called *extreme deconstruction*. The idea is to test if environmental predictors that are important to explain species geographical ranges are also important when modelling species richness. Thus, the 'extreme deconstruction' principle suggests that processes driving organism distributions in a lower hierarchical level (species geographical ranges) can be directly associated with environmental factors conditioning overlap of distributions at higher levels (species richness). There has been an increasing interest in techniques for modelling species geographical ranges (e.g. see Segurado & Araújo, 2004; Elith *et al.*, 2006; Philips *et al.*, 2006), but these techniques have been mainly used to estimate geographical ranges for conservation purposes or to predict shifts in geographical ranges or species richness after climate changes (Peterson & Vieglais, 2001; Araújo & Pearson, 2005; Thuiller *et al.*, 2005; Araújo *et al.*, 2006). Only a few papers have tried to relate the outputs of such models to the life history or ecological characteristics of species (e.g. see McPherson & Jetz, 2007).

Moreover, the logic of extreme deconstruction discussed here underlies recent simulation studies on richness patterns, in which environmental constraints are coupled with stochastic processes (dispersal) to define and establish limits for species geographical ranges. Although processes are established at range level, the analyses are performed to evaluate geographical patterns in species richness (Rangel & Diniz-Filho, 2005a; Storch *et al.*, 2006; Rahbek *et al.*, 2007; Rangel *et al.*, 2007; see Dormann *et al.*, 2007, and Kissling & Carl, 2008, for a completely different strategy of simulating patterns in species richness). Changing parameters of these simulations for limiting geographical ranges (environmental drivers or species tolerances to these drivers) generates different richness patterns (e.g. Rangel & Diniz-Filho, 2005b; Rangel *et al.*, 2007).

Additionally, it is worthwhile mentioning that Araújo & Pearson (2005) showed that the current distribution of each species can be due, at least in part, to historical effects, thus increasing the list of elements that question the 'equilibrium' with current climate postulate (see Guisan & Thuiller, 2005), a basic assumption of species range bioclimatic modelling. So, it is expected that, for sets of species with high levels of non-equilibrium, a low environmental component for species richness is also observed. Therefore, we also tested here if lack of fit between current species geographical distribution and environment (which can in principle be interpreted as non-equilibrium) is related to a lower environmental component in species richness and, thus, indicates a larger number of historical effects explaining geographical patterns in species richness.

MATERIALS AND METHODS

Data

We generated a global checklist of 228 terrestrial viperid snakes based on the updated Reptile Database, supported by the Systematic Working Group of the German Herpetological Society (Uetz, 2007). Except for the Arabian Peninsula, we were able to compile distribution maps for all these species in large land masses, namely all mainland continental areas to which viperids are native (i.e. Australia was excluded) and the well-surveyed island of Great Britain, which is of sufficient size and proximity to mainland Europe to warrant that macroecological patterns are not affected by island effects. Range maps were obtained from Campbell & Lamar (2004), Branch (1988, 1998), Latifi (1991), Broadley & Doria (2003), Spawls *et al.* (2004), Ananjeva *et al.* (2006), Vogel (2006) and Dobiey & Vogel (2007), and were mapped at 1° resolution for a grid with 7331 cells each containing at least one species. Species richness was obtained by overlaying these geographical ranges for each cell.

We also obtained macroecological data at the species level that were used in the deconstruction processes. Log_{10} of maximum total length (a standard size measure commonly reported for snakes) was used as an estimate of a species' overall body size (see Ashton & Feldman, 2003, Boback, 2003, and Boback & Guyer, 2003, for examples of use of body length as a measure of body size for snakes). These body size data were obtained from the same literature used for the geographical range data (see above; L.C. Terribile, unpublished data). A crude estimate of geographical range size was obtained by counting the number of cells in which each species occurs.

Phylogenetic relationships among species were established at genus level using a phylogenetic tree that was built by combining the phylogenies by Lenk *et al.* (2001), Malhotra & Thorpe (2004) and Castoe & Parkinson (2006). Sets of basal and derived species were identified, respectively, using the lower and upper quartiles of the count of number of nodes between each species and the root of the tree (see Hawkins *et al.*, 2005, 2006, 2007). We also used this same phylogeny in a phylogenetic eigenvector regression (PVR) (Diniz-Filho *et al.*, 1998) to summarize the relationships among taxa (see Diniz-Filho *et al.*, 2007, and Ramirez *et al.*, 2008, for recent applications in macroecology). The first 20 eigenvectors of the matrix among genera were retained for further analyses and used to evaluate the relative magnitude of phylogenetic effects on macroecological traits across the 228 species (body size, range size and fit of individual species' distribution models; see below), as well as to take into account the phylogenetic non-independence among species when testing relationships among these traits. The association of macroecological traits with the phylogenetic eigenvectors was established through multiple regression techniques in which minimum models where reached through a simplification process based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008).

Environmental data

Five environmental variables were used to model species distributions and to analyse richness patterns: (1) total annual precipitation; (2) mean annual temperature, (3) range in elevation (i.e. the difference between maximum and minimum elevation within each cell, which we used as a proxy for mesoscale climatic gradients); (4) primary productivity – measured as the annual global vegetation index (GVI); and (5) seasonality in primary productivity – measured as the number of months available for plant growth. For this measure (seasonality), we first calculated the xerothermic season length for each cell by counting the number of months in which the mean monthly temperature (in °C) was more than double the mean monthly precipitation (in mm). Based on this calculation, we identified hot dry months, i.e. those summer months for which low precipitation limits plant productivity. We then established the length of the rainy season as 12 minus the number of hot dry months. We also calculated the number of months in which plant growth is limited by low temperatures by counting the number of months having mean monthly temperatures lower than 5 °C (cold months). The number of hot months then was calculated as 12 minus the number of cold months. Finally, we defined our 'seasonality' variable as the sum of months in the rainy season and hot months in each cell. All data sources and processing techniques to obtain these variables are provided and discussed in detail in Olalla-Tárraga *et al.* (2006) and Rodríguez *et al.* (2008).

Primacy of variables across geographical range models

We estimated the effects of current environment on species geographical ranges using logistic regression to model the presence or absence of species in the cells with respect to the five environmental predictors. The parameters of each logistic regression were estimated by generating a saturated generalized linear model (GLM; i.e. a GLM including all five environmental variables) using a binomial distribution of error terms.

We evaluated the model fit in each range model using the McFadden's rho-squared (ρ^2), which is an attempt to approximate an ordinary least squares (OLS) standard coefficient of determination (R^2). It can be calculated by

$$\rho^2 = 1 - \left(\frac{\ln L_1}{\ln L_0}\right)$$

where ρ^2 is McFadden's rho-square, L_1 is the log-likelihood of the fitted model and L_0 is the log-likelihood of the null model (intercept-only model). ρ^2 has the desirable property of ranging between 0 and 1, which makes it analogous to R^2. However, estimates of ρ^2 and R^2 are not entirely equivalent, and we used a rule of thumb that ρ^2 values higher than 0.2 indicate good fits. Low ρ^2 can be interpreted as expressing high levels of non-equilibrium or indicating failure to model the correct environmental or ecological drivers for species distribution.

Finally, the importance of each environmental driver in each geographical range model was established according to its odds ratio, and the variable with the highest importance identified. The odds ratio for an independent variable represents the proportion by which the odds of species presence change when there is a one-unit change in the independent variable. The odds ratio of a coefficient b can be calculated by $\exp(b)$. If $\exp(b)$ is larger than 1, b increases the logit and therefore also increases the odds of species presence. If $\exp(b)$ equals 1, the independent variable has no effect on the presence of the modelled species. If $\exp(b)$ is less than 1, the independent variable decreases the logit and the odds of species presence.

Based on the odds ratio defined above, the 'primacy' (*sensu* Field *et al.*, 2008) for each predictor was then calculated as the frequency across GLM models at which this predictor is the most important factor in modelling geographical ranges. All models were generated with the new logistic regression module included in the latest version of the Spatial Analysis in Macroecology program (SAM 3.0; see Rangel *et al.*, 2006).

Richness models

Four criteria of similarity among species, based on GLM modelling, body size, geographical range size and phylogenetic structure, were used to obtain different sets of species and to calculate species richness: (1) species with geographical ranges having high and low fit in the GLM distribution models (above and below the median of McFadden's ρ^2, which also approximates the heuristic value of 0.2 suggested above); (2) basal and derived species; (3) large- and small-bodied species (above and below the median of maximum total length); and (4) four classes of geographical range size (defined by the quartiles of the range size frequency distribution, RSFD). Thus, by overlaying geographical ranges for species within these categories we generated 11 different variables of species richness. This allowed us to test whether separating species into sets according to different criteria reveals different species richness patterns.

We used a principal components analysis (PCA) (Legendre & Legendre, 1998) to represent similarity among the 11 richness patterns based on deconstruction. Eigenvectors were extracted from the correlation matrix among pairs of richness and the broken-stick criterion was used to define the number of axes necessary to represent the similarity patterns. Richness patterns were also modelled against the five environmental variables through standard OLS multiple regressions, processed within a multimodel framework (Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008). First, we generated all possible different models that could be obtained by combining five predictors (i.e. 31), and calculated the Akaike weight (w_i) of each model, an AIC-derived index that reflects the probability that model i is actually the best explanatory model among all possible models. Then we combined these regression models into a summary model in which the standardized regression coefficient of each variable (reflecting its relative importance as predictor of richness patterns) corresponded to the w_i-weighted average of its coefficients in all models. These average regression coefficients are estimates of the relative importance of the variables as drivers of richness variation, and were retained for further analyses involving comparisons with the GLM range distribution results previously generated (see below). Finally, levels of spatial autocorrelation in model residuals were determined using Moran's I calculated globally at 20 geographical distance classes (Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003). All these analyses were also performed in SAM 3.0 (Rangel *et al.,* 2006).

Correspondence between drivers of species ranges and drivers of richness patterns

Extreme deconstruction can be tested by evaluating the degree of correspondence between factors driving species geographical ranges and patterns of species richness. This was done by calculating a Pearson correlation between the average regression coefficients of environmental variables on richness with the primacy values across range model GLMs. However, in principle, a single correlation can be obtained when analysing richness and geographical ranges for a given group of organisms. Thus, to replicate this correlation and provide a more general test of extreme deconstruction, we used the different subsets of species previously defined and obtained 11 sets of regression slopes for richness and primacy for geographical ranges.

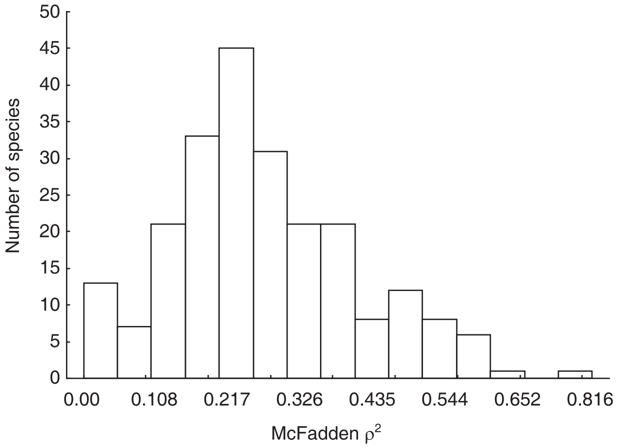

Figure 1 Frequency distribution of McFadden ρ^2 values (ranging from 0 to 0.816) from the 228 generalized linear modelling species distributions.

RESULTS

Modelling species geographical ranges

Values of McFadden's ρ^2 from the 228 GLMs modelling species distributions ranged from 0 to 0.816 (Fig. 1), with a median of 0.269. This indicates that about half of the viperid species have reasonable fit of their ranges to environmental variation. Notice that in our study McFadden's ρ^2 is not highly correlated with species geographical range ($r = 0.177$; $P = 0.05$ after taking into account the phylogenetic eigenvectors; see also Fig. 2a), so our conclusions will not be artefacts of prevalence (see Allouche *et al.*, 2006).

McFadden's ρ^2 is also not strongly phylogenetically structured ($R^2 = 0.125$ with 7 out of 20 eigenvectors selected by the AIC) nor can they be well predicted by log-transformed species body size ($r = 0.048$; $P = 0.02$ after taking phylogeny into account, see Fig. 2b). In general, McFadden's ρ^2 is not well predicted by simultaneous regression against phylogeny and any macroecological traits (body size and geographical range size) ($R^2 = 0.147$) across species.

Richness patterns

Overall, the richness of viperid snakes follows the well-known global diversity gradient, with high-richness cells concentrated in tropical regions (Fig. 3). The environmental model with five variables explained around 48% of the total variance in richness. Excepting a slightly higher effect of temperature and low effect of GVI, all environmental variables showed relatively homogeneous effects (Table 1).

Richness maps obtained by establishing sets of species according to different macroecological traits (i.e. geographical range size, body size, evolutionary level and environmental model fit of distributions) revealed different patterns across the world. The first component of the PCA used to represent similarity among the 11 sets of richness analysed explains only 38.8% of the variation and, according to the broken-stick criterion, it is the only important direction of correlation among these sets. Higher loadings for this first axis are found for total richness, richness for large-ranged species, richness for small-bodied species and for derived species.

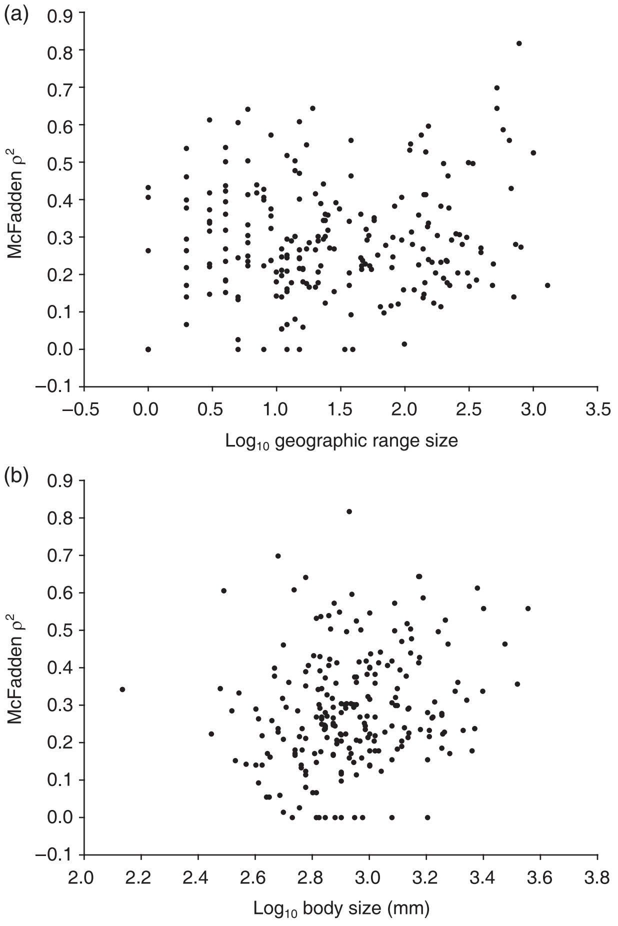

Figure 2 The relationships between McFadden ρ^2 values and Log$_{10}$-transformed geographical range size (a), and McFadden ρ^2 and Log$_{10}$-transformed body size (b) for the 228 viperid species. Geographical range size represents the number of occupied 1° cells by each species. Body size represents the maximum total length obtained for each species.

For geographical range size, maps showed that Central America and southern North America concentrate richness of small- and intermediate-ranged species (Fig. 4a,c), whereas South America and Central Africa hold high richness of large-ranged species (Fig. 4d). These differences were apparent in their environmental models as well. The R^2s of richness models increase when dealing with large-ranged species, as previously found by Jetz & Rahbek (2001) and Rahbek *et al.* (2007) (Table 1). The average environmental model for large-ranged species richness explained up to 40% of the variation, and temperature was the most important environmental driver, followed by seasonality. For species with very small ranges, richness was also explained by temperature, but not seasonality, although the R^2 of richness was quite low anyway (see Table 1).

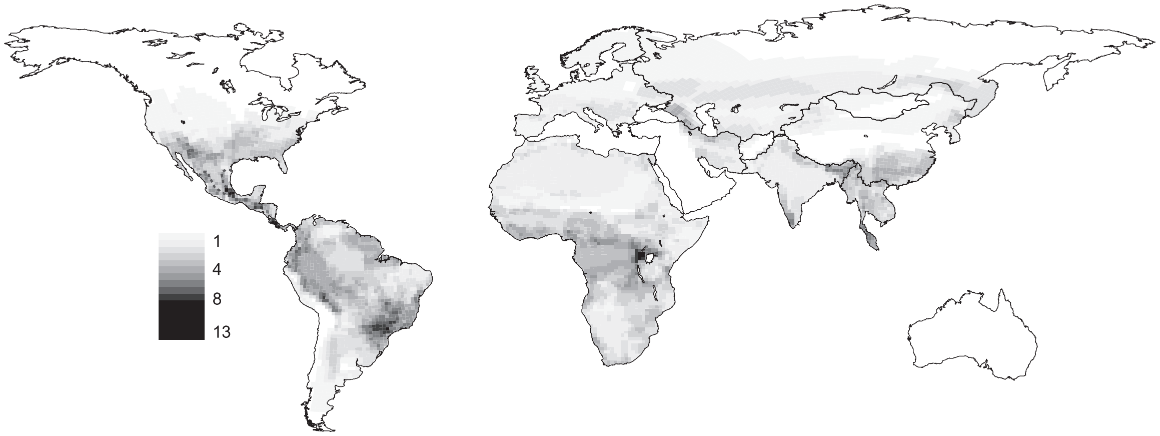

Figure 3 Global biogeographical patterns of Viperidae species richness.

For subsets of species distinguished according to body size (Fig. 5), high richness of small species occurs mainly in South America and Central Africa (Fig. 5a), whereas large species prevail in Central America and Southeast Asia (Fig. 5b). Environmental models, meanwhile, found no strong patterns of association between richness and environmental predictors for both species sets, as indicated by their relatively low explanatory power (around 20% in both cases), even though the importance of the variables in each model changed between them (Table 1).

Differences between the richness pattern for basal (Fig. 6a) and derived species (Fig. 6b) were quite strong (with all basal species occurring in the Old Word and derived species in the New Word), possibly reflecting the Afrotropical origin of Viperidae and their later expansion into New Word. The five environmental variables explained around 50% and 35% of richness variation for basal and derived species, respectively, and temperature emerged as the most important predictor in both cases.

Modelling richness patterns for species with low ($\rho^2 < 0.269$) and high ($\rho^2 > 0.269$) fit in GLM range models (see Fig. 7a,b) as described above, revealed a similar overall explanatory power of the environmental variables (i.e. around 45%, although using high-fit models gives slightly higher R^2) (Table 1). However, the coefficients of these models are slightly different, with a marked effect of temperature and precipitation in both richness models, but a high effect of GVI when modelling richness for species with high-fit range models and a high effect of seasonality when modelling richness for low-fit range models. It is also interesting to note that the predictor's odd ratios in low-fitted GLMs exhibited little variance, matching the 'concentration' of explanatory power in a single predictor for species richness (mainly in precipitation). On the other hand, OLS models of richness based on species with high-fit GLM exhibited less concentrated effects of precipitation, GVI and temperature, which is consistent with a larger variance in the standardized coefficients of GLM for each species.

Testing extreme deconstruction principle

The similarity between the environmental drivers of the richness models (i.e. the standardized OLS coefficients for each richness subset) and those on the GLM distribution models (i.e. the primacy of variables across species geographical range models) was equal to 0.645 when analysing all viperid snakes. Thus, in general, when an environmental predictor is important in modelling species geographical ranges, this predictor is also important when modelling richness.

However, replicating this correlation using subsets of species within different categories in body size, range size and phylogenetic structure gives more variable results, and correlations between GLM and OLS coefficients vary from –0.46 up to 0.83 (Table 1), depending on the dataset used. This variation in correlations would suggest problems with the extreme deconstruction and would eventually reveal that emergent properties are explaining richness patterns, independently of the processes acting at species geographical ranges. However, there is a relatively high correspondence ($r' = 0.73$; Table 1; see also Fig. 8) between the similarity of GLM-OLS coefficients (r values in Table 1) and R^2 values of richness models, which indicates that when richness is well-explained by the environment (high R^2), the relative importance of environmental drivers is similar in the richness OLS and its corresponding set of GLMs.

DISCUSSION

Richness deconstruction

The strong correspondence between environmental data and current patterns in species richness is well known (see Hawkins *et al.*, 2003). However, it is becoming clear that, independent of the ecological processes driving species richness, this high correspondence may appear because of common non-environmental components related to the geography and climate history of the Earth (Wiens & Donoghue, 2004; Rangel *et al.*, 2007). These non-environmental components create problems for interpreting richness patterns; thus it becomes important to find better approaches to evaluate mechanisms underlying the correlations between richness and environment, and one of the possibilities is to use species ecological characteristics to explain why these correlations arise.

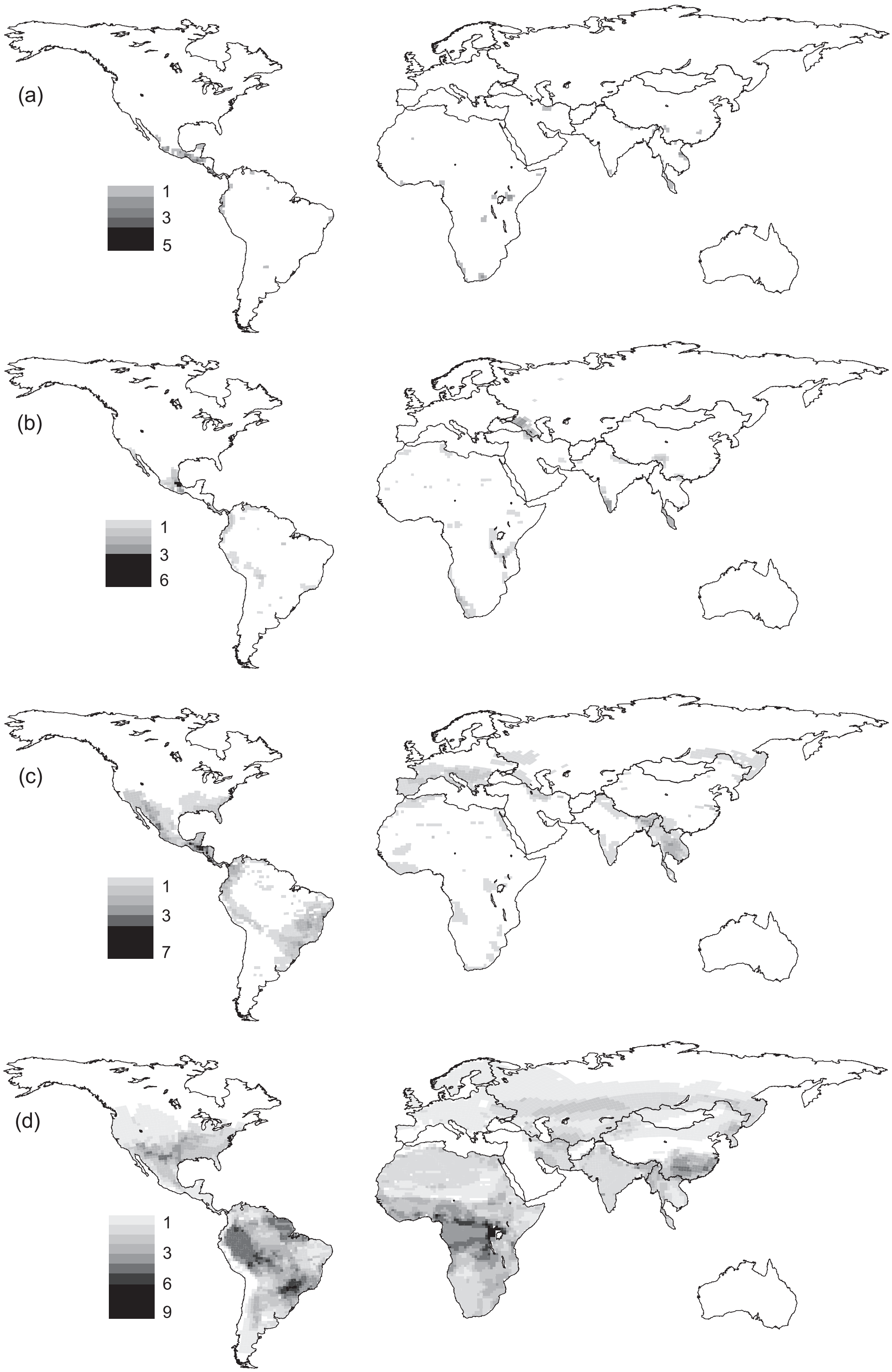

Figure 4 Global richness pattern of viperid species with: (a) small, (b) small to intermediate, (c) intermediate to large and (d) large range sizes. Range size was obtained by counting the number of cells in which each species occurs, and four classes of richness based on geographical range sizes were defined by the quartiles of the range size frequency distribution (RSFD).

Table 1 Summary of environmental models for total and deconstructed sets of richness. Upper rows in each model represent the results from the multimodel selection Akaike information criterion: R^2s and the w_i-weighted averaged standardized regression coefficients resulted from averaging the coefficients of all 31 possible models with five predictors. Lower rows (in bold and italics) represent the primacy of each predictor, i.e. the importance frequency of each predictor across individual species' generalized linear model distribution models. In the right-most column (r) are the Pearson correlation values between the standardized coefficients (upper line) and primacy (lower line) of each model. r' is the correlation between R^2 and r values.

Richness	R^2	Temp.	Precip.	GVI	Elev.	Season	r
Total	0.476	0.318	0.204	0.149	0.211	0.223	0.675
		0.360	***0.219***	***0.167***	***0.048***	***0.140***	
Geographical ranges							
Small	0.073	0.287	0.005	0.03	0.27	0.039	0.201
		0.35	***0.17***	***0.15***	***0.04***	***0.17***	
Small–intermediate	0.003	–0.029	0.013	–0.025	< 0.001	0.045	–0.462
		0.389	***0.241***	***0.148***	***0.074***	***0.167***	
Intermediate–large	0.100	0.171	0.129	0.081	0.191	0.010	0.239
		0.296	***0.259***	***0.185***	***0.074***	***0.111***	
Large	0.403	0.295	0.190	0.119	0.027	0.214	0.832
		0.481	***0.241***	***0.222***	***0.019***	***0.130***	
Body size							
Small	0.233	0.252	–0.050	0.205	0.217	0.251	–0.227
		0.333	***0.237***	***0.202***	***0.053***	***0.079***	
Large	0.224	–0.005	0.209	0.001	0.170	0.256	–0.385
		0.389	***0.204***	***0.133***	***0.044***	***0.195***	
Phylogeny							
Basal	0.491	0.427	0.141	0.224	0.142	0.188	0.830
		0.386	***0.210***	***0.210***	***0.017***	***0.070***	
Derived	0.342	0.474	0.015	0.039	0.251	0.238	0.784
		0.350	***0.140***	***0.105***	***0.087***	***0.210***	
Distribution model							
Low ρ^2	0.448	0.197	0.379	0.032	0.08	0.216	0.524
		0.327	***0.274***	***0.159***	***0.035***	***0.080***	
High ρ^2	0.463	0.231	0.351	0.323	–0.077	–0.07	0.352
		0.391	***0.165***	***0.174***	***0.061***	***0.200***	
				r′ =			***0.734***

Temp., mean annual temperature; Precip., annual precipitation; GVI, annual global vegetation index; Elev., range in elevation; season, seasonality.

Marquet *et al.* (2004) suggested that a promising strategy for associating ecological characteristics of species and their richness patterns would be the decomposition of richness into subsets of ecologically homogeneous groups prior to analysis. In our study, deconstruction of species richness based on macroecological traits revealed that, at least for range size and phylogenetic level, the causes underlying patterns in richness may be different across different subsets of richness. For range size, our results for viperid snakes in principle match those of Jetz & Rahbek (2002) and Rahbek's *et al.* (2007) for birds, as we also found that environmental models successfully explained large-scale richness patterns of wide-ranging species but not those of small-ranging ones (as measured by regression R^2). Viperid species with small (and small to intermediate) ranges are mainly concentrated in Central America and along the continental edges of South America, Africa and India, which could reinforce the idea that the area and geometric constraints effects in geographical or niche space (Jetz & Rahbek, 2001, 2002; Rangel & Diniz-Filho, 2005b) or even assembly-level processes (predation, competition) (see also Rahbek *et al.*, 2007) are also substantially important in determining species richness patterns.

On the other hand, Hawkins & Diniz-Filho (2006) showed, based on New World bird data, that differences in factors explaining richness for species with different range sizes may be related to mountain effects and, thus, may not reflect differences in factors *per se*, but only scale issues related to how effects are measured. Although this may be difficult to test directly, our results, at least in part, reinforce this alternative interpretation because the primacy for temperature is higher than all others and similar for all range size classes except for small to intermediate ones (although coefficients for richness vary in a more idiosyncratic way). Thus, differences in the explanatory power of environmental variables may be more related to scale issues and problems related to high measurement errors in small ranges than to historical or stochastic processes driving ranges with different sizes.

Patterns of richness deconstructed according to body size were weakly explained by the environmental models, for both small

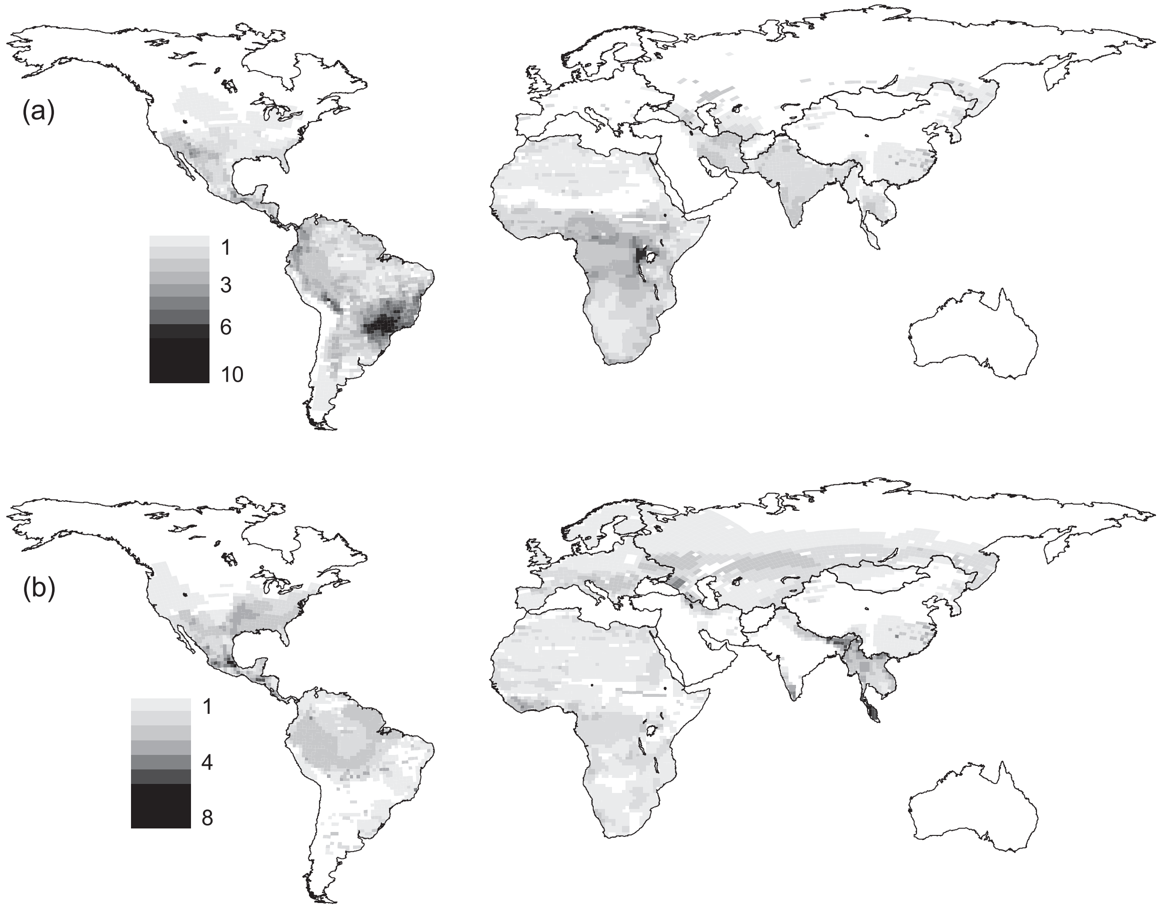

Figure 5 Global richness pattern of (a) small-bodied and (b) large-bodied viperid species. Maximum total length was used as a measure of body size, and two classes of richness (large- and small-bodied species) were obtained based on body sizes above and below the median of maximum total length.

and large-bodied viperids (R^2s around 20%). Although the coefficients of determination of the models for both size classes were relatively small, it is worth noting that the importance of the predictors (indicated by the regression coefficients) changed considerably between the two models (except for seasonality, which had similar importance in both cases). Large- and small-bodied species occur in different regions, so it is possible that other factors (e.g. historical effects, differences in extinction and dispersal rates) are unequally influencing richness in these two sets of species. Another possibility is that environmental drivers do not affect the richness of large-bodied and small-bodied species *per se* but instead affect the relative balance of species with different body sizes within assemblages. Therefore, it is difficult to decouple the environmental drivers based on richness and the historical events generating diversification of body sizes.

For phylogeny, the clear longitudinal difference in the richness patterns of basal species (with higher richness values concentrated in Africa and, to a lesser extent, in Eurasia) and derived species (higher richness across the New World) is consistent with the evolutionary hypothesis of an Old World origin of the viperid ancestor, and subsequent expansion into the New World (see Parkinson, 1999; Lenk *et al.*, 2001). Additionally, the different importance of the current environment for basal and derived clades (R^2 of average models is 0.491 and 0.342, respectively; difference in $R^2 = 0.149$) suggests some component of niche conservatism (*sensu* Wiens & Donoghue, 2004) in geographical richness patterns of viperids, with the most recent species being less determined by current environment than basal species. A possible explanation for these differences is that the group originated in environments more similar to current tropical habitats (see Lenk *et al.*, 2001), and that subsequent global changes that created temperate regions also caused rearrangements in the geographical distribution of the basal taxa, thus generating a trend for species to accumulate towards areas showing more similar conditions (i.e. tropical regions) to those prevailing in their ancestral niches (see Hawkins *et al.*, 2005, for similar trends and niche conservatism explanations in Australian birds). In contrast, most newly derived species may have appeared in, and adapted to, different and varied environments, which may explain why they show weaker relationships with current environmental gradients. Interestingly, differences of nearly identical magnitude between basal and derived clades in terms of predictive power of current environment models were found by Hawkins *et al.* (2007) for global patterns in terrestrial bird richness (basal bird richness $R^2 = 0.717$; derived bird richness $R^2 = 0.545$; difference in $R^2 = 0.172$), thus supporting

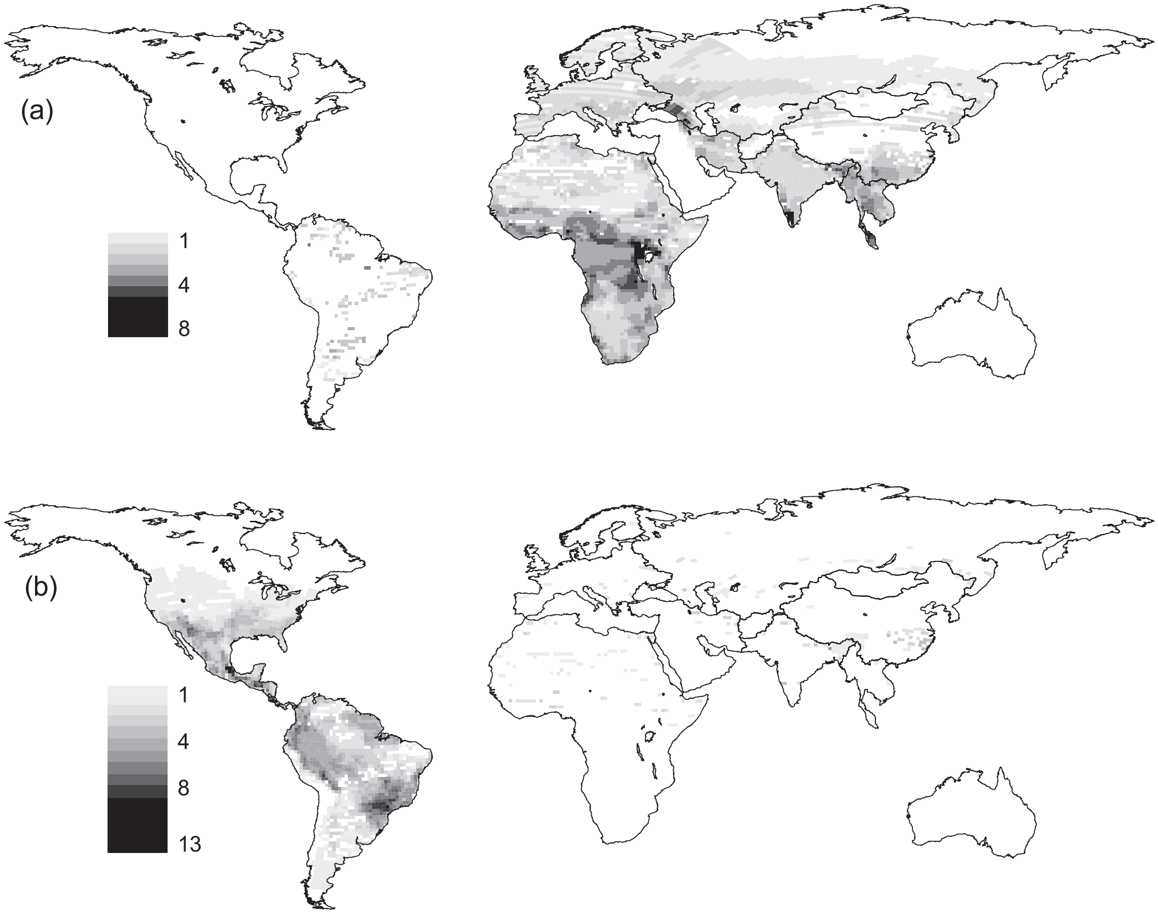

Figure 6 Global richness pattern of (a) basal and (b) derived viperid species. Sets of basal and derived species were identified, respectively, using the lower and upper quartiles of the count of number of nodes between each species and the root of the phylogenetic tree. Phylogenetic relationships among species were established at genus level using a phylogenetic tree that was built by combining the phylogenies by Lenk *et al.* (2001), Malhotra & Thorpe (2004) and Castoe & Parkinson (2006).

the prediction of these authors that niche conservatism would be shown to influence many groups.

Thus, the results of the 'standard' deconstruction approach described above furnish some insights about richness patterns and are in agreement with previous findings in the literature. The next step is then to think whether this idea can be pushed more so that ecological drivers of each species' geographical range can also be associated with the drivers explaining species richness.

Extreme deconstruction

Our analysis shows that, across all viperid species, environmental predictors that are important to explain species geographical ranges are also important when modelling species richness, so that the extreme deconstruction principle applies. Moreover, the 'standard' deconstruction approach described above provides 'replications' for supporting our extreme deconstruction principle, and shows that, because richness results from the overlap of geographical ranges, drivers of species distributions must also create patterns in species richness. Thus, our analyses support the idea that richness patterns may indeed be viewed as macroecological consequences of population-level processes acting on species geographical ranges (see Gaston, 2003, for an overview, and Colwell *et al.*, 2004, and Rangel & Diniz-Filho, 2005b, for related discussions on mechanisms underlying mid-domain patterns). In other words, if environmental drivers determine the geographical distribution of species through the establishment of niche boundaries, it is expected, at least in theory, that the overlap among ranges will reveal similar effects of these environmental drivers.

However, it is clear that the causes driving species ranges will not always be responsible for their overlap pattern (i.e. richness), mainly because amounts of range overlap and the shape, location and size of these ranges might also arise due to non-environmental effects of different sorts. Non-environmental effects can affect species ranges just as much as they affect range overlap. For example, apparent differences in drivers will appear if richness is partially determined by additional components to those that determine species distributions, such as assemblage rules for communities. These effects will not cause differences in drivers for individual species and richness *per se*, but they weaken the correlation between GLM and OLS coefficients, and perhaps

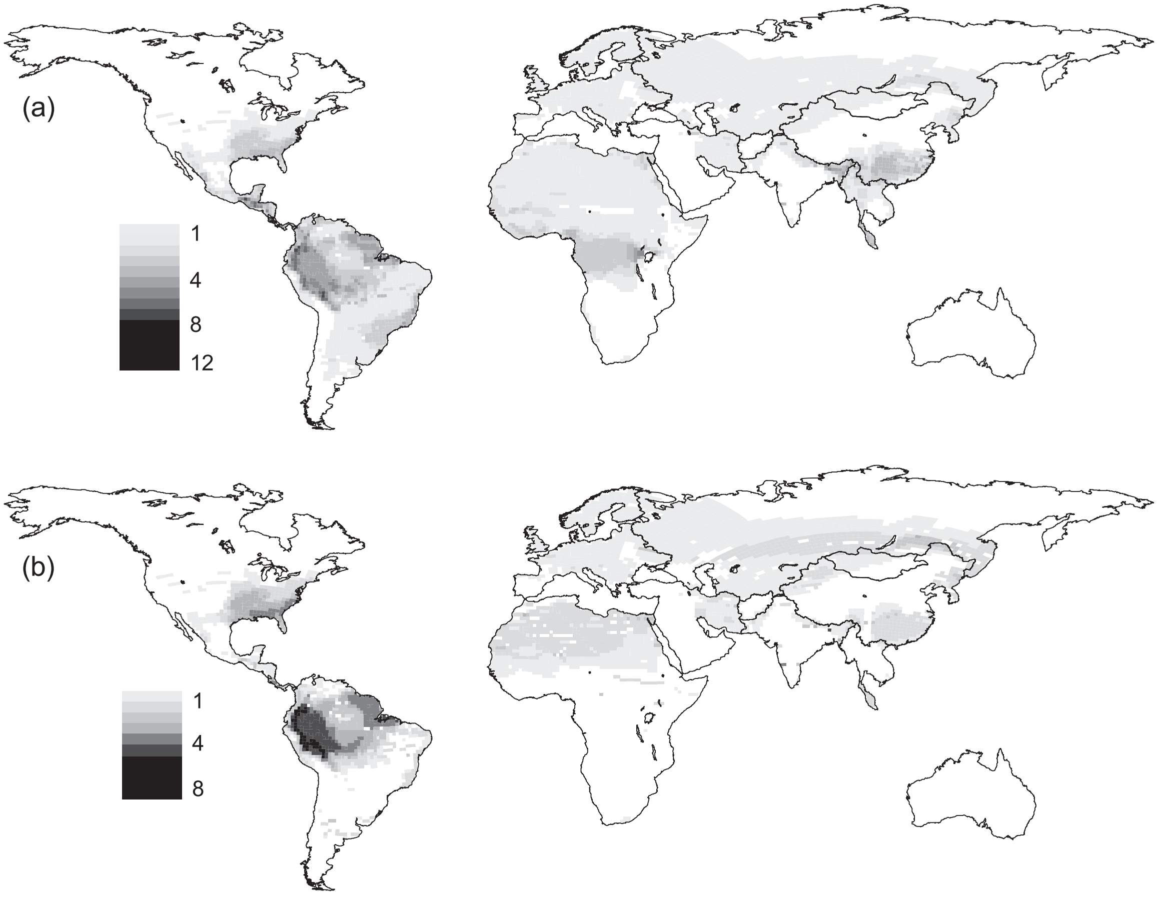

Figure 7 Global richness pattern of viperid species that have (a) low and (b) high fit of their ranges to environmental variation (i.e. species with lowest and higher McFadden ρ^2 in the generalized linear models ranges, respectively).

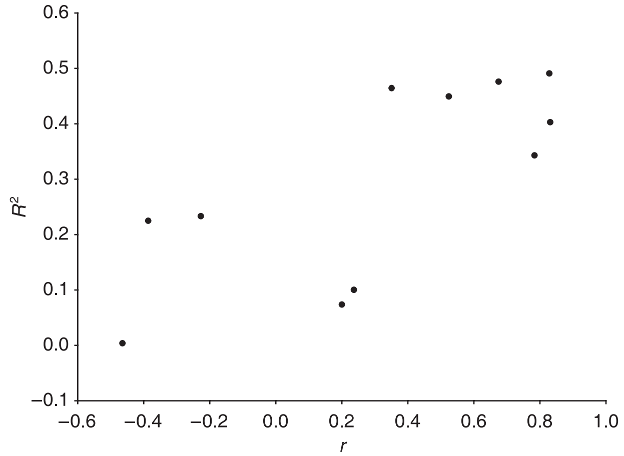

Figure 8 The relationship between R^2 values from each richness model and the similarity r values (r values are the correlation between the w_i-weighted averaged standardized regression coefficients of the five environmental predictors and the primacy of each predictor, i.e. their importance frequency across individual species' generalized linear model distribution models).

explain residual variation in the relationship between similarity GLM-OLS and the magnitude of environmental effects on richness (see Fig. 8).

In a general sense, historical processes are usually used to explain these deviations, but it is difficult to establish exactly how to define (and measure) 'history' in different time-scales. De Marco *et al.* (2008) recently showed that, for example, even when ranges are fully determined by environmental variation, a colonization lag will appear as non-equilibrium when modelling geographical distribution using niche models (i.e. Maxent), and this is actually a form of historical process causing a lack of high environmental effects. Indeed, our analysis also shows that although correlations between GLM-OLS results vary, they are at the same time correlated to the amount of environmental signal in richness (Fig. 8). Although it is not possible, as previously discussed, to establish if lack of fit is due to historical effects or a lack of relevant environmental predictors, this reinforces that, when models are well defined for both species richness and geographical ranges, the important predictors tend to be the same.

But it is important to realize that richness patterns in sets of species with low and high GLM fit are explained to more or less the same extent by environmental factors, reinforcing that a lack of fit in GLM can be better explained by historical non-equilibrium and not due to missing crucial environmental predictors. The idea is that overlap of range can be due to historical factors (such as niche conservatism, also supported by our analyses based on derived and basal sets of species), so that correlations of richness appear at least in part purely as an indirect consequence of historical processes related to the geography and climate history, and not due to responses of each species to current environment (see Rangel *et al.*, 2007).

In a more methodological sense, some studies of species richness–environment relationships (e.g. Wisz *et al.*, 2007; Costa *et al.*, 2007; Terribile & Diniz-Filho, 2008) have started by using niche models (based on environmental variables) to generate predicted geographical ranges of species and, by overlapping them, the species richness values that were later related with the same (or similar) drivers to look for explanations of the patterns found. This sounds tautological in principle, and may actually inflate the effects of some drivers, but the logic underlying this discussion relies on the idea that both range patterns and their overlap (richness) may reflect the same processes appearing at different scales. Actually, any definition of a geographical range, independently of using a niche-based model (or other form of species distribution modelling), will generate bounds and patterns in environmental space because of spatial autocorrelation in the environment.

In summary, our study showed that using deconstructive analyses of richness may be useful to unveil different processes acting at different scales on present-day patterns of species richness. More importantly, taking this idea to an extreme, it is clear that if environmental factors strongly determined the distribution of individual species, it is likely that species overlap (richness) is associated with the same factors. Of course, deeper studies are necessary to improve the methods to be used in extreme deconstruction, especially methodological developments which are needed to better link richness models and species distribution (or niche) models in terms of parameter estimates of environmental factors. Also, it is important to better establish the conceptual relationships between deep-time historical processes explaining richness and term processes creating non-equilibrium species distribution. In this way, our analysis is a first step, showing that more dialogue is needed between ecologists interested in modelling species richness and those interested in modelling species distributions, a separation that is actually more due to alternative traditions in geographical ecology than to real differences in methods and theoretical issues.

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BIOSKETCHE

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Apêndice 3. Padrão global de tamanho do corpo.

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Ecological and evolutionary components of body size geographic variation of venomous snakes at global scale

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Short title: Snakes body size variation

Abstract

Biogeographical patterns of animal body size and the environmental and evolutionary mechanisms that may be driving them have been broadly investigated in macroecology, although just barely in ectotherms. We separately studied two snake clades, Viperidae and Elapidae, and used Phylogenetic eigenVector Regression (PVR) and Ordinary Least Squares multiple regression methods (OLS) to perform a global grid-based analysis of the extent at which the patterns of body size (measured for each species as its $\log_{10}$-transformed maximum body length) of these groups are phylogenetically structured or driven by current environment trends. Phylogenetic relatedness explained 20% of the across-species size variation in Viperidae, and 59% of that of Elapidae, a more recent clade. Conversely, when we analyzed spatial trends in mean body size values (calculated for each grid-cell as the average size of its extant species), an environmental model including temperature, precipitation, primary productivity (as indicated by the global vegetation index) and topography (range in elevation) explained 37.6% of the variation of Viperidae, but only 4.5% of that of Elapidae. These contrasted responses of body size patterns to current environment gradients were discussed taking into consideration the dissimilar evolutionary histories of these closely related groups. Additionally, these results emphasize the importance to start adopting deconstructive approaches in macroecology.

Additional Keywords: Bergmann's rule – ectotherms – interspecific variation – niche conservatism – model selection – phylogenetic eigenvector regression – snakes.

Introduction

The trend of body sizes to increase towards cold macroclimates has been termed Bergmann's rule in honor of its propositor Carl Bergmann, in 1847, and has been broadly reported in macroecology (e.g., Lindsey, 1966; Miller, 1991; Hawkins, 1995; Hawkins & Lawton, 1995, Arnett & Gotelli, 1999; Ashton, 2001; Ashton & Feldman, 2003; Jones *et al.*, 2005; Olalla-Tárraga, Rodríguez & Hawkins*,* 2006; Olalla-Tárraga & Rodríguez, 2007; Ramirez, Diniz-Filho & Hawkins, 2008; Rodríguez, Olalla-Tárraga & Hawkins, 2008; see also Meiri & Dayan, 2003 for a review). The interest in this ecogeographic rule, along with other well-known rules in geographical ecology and biogeography (e.g. Allen's rule, Rensch's rule or Rapoport's rule), has grown in recent years (Lomolino *et al.*, 2006; Gaston, Chown & Evans, 2008). It is also worth mentioning the intense debate around several aspects of Bergmann's rule, including the taxonomic level at which the rule should be considered to act (e.g., Rensch, 1938; Mayr, 1956; Blackburn, Gaston & Loder, 1999), the mechanisms (or hypotheses) explaining body size gradients (e.g., James, 1970; Van Voorhies, 1996; Blackburn *et al.*, 1999; Yom-Tov & Geffen, 2006; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007) and even the degree of generality of these gradients across taxa (e.g., Willemsen & Hailey, 1999; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007).

To some extent, these discussions have been fuelled by an increased recent trend to test the rule in its original, interspecific formulation (Blackburn *et al.*, 1999). In general, recent studies have found support for the rule and its original explanation for endotherms – including mammals: Blackburn & Hawkins (2004), Rodríguez, López-Sañudo & Hawkins (2006), Rodríguez *et al.* (2008); and birds: Blackburn & Gaston (1996), Ramirez *et al.* (2008)– based on the heat conservation mechanism. That is, larger endotherms take advantage of living in colder regions because their lower surface area-to-volume ratio facilitates heat retention (Meiri, Yom-Tov & Geffen, 2007; Meiri & Thomas, 2007).

For ectotherms, broad-scale patterns of body size have not yet been studied as intensely as in endotherms. Perhaps the most controversial point regarding body size gradients in this case is that while some ectothermic groups exhibit Bergmann's trends – e.g. ants in Europe (Cushman, Lawton & Manly, 1993), lizards in Argentina (Cruz *et al.*, 2005) and Europe (Olalla-Tárraga *et al.*, 2006), and anurans in Europe and North America (Olalla-Tárraga & Rodríguez, 2007)–; others either display the converse trend, or do not show clear patterns of variation –e.g. bees in the United States (Hawkins, 1995); snakes in the New World (Reed, 2003); urodeles and snakes in Europe and North America (Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007; Adams & Church, 2008) (see also Lindsey, 1966) and lizards in South America (Pincheira-Danoso, Hodgson & Tregenza, 2008). Hawkins & Lawton (1995) also found that gradients in butterfly body sizes were inconsistent across different geographical regions (North America, Europe, Australia and Afrotropics) and families. These inconsistencies lead to two possible alternatives. Firstly, generalizations about the patterns and associated mechanisms of body size variation cannot be done for these groups. And, secondly, a general explanation for the observed patterns is difficult to be attained across all taxa, because even if the mechanisms driving body size trends were the same for all groups, these mechanisms may have given rise to different geographical gradients in each case (see Angilletta *et al.*, 2004; Ashton & Feldman, 2003).

Assemblage level studies addressing the interspecific variation in body size of ectothermic vertebrates have tested, or at least suggested, a wide range of environmental hypotheses –e.g. the heat conservation, heat balance, primary productivity, climatic variability, migration abilities, starvation resistance, size dependence, and water availability (see e.g., Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006, 2009; and Olalla-Tárraga & Rodríguez, 2007). The relative support for each of these potential explanations has varied in different groups of fishes (Garvey & Maschall, 2003), amphibians (Lindsey, 1966; Olalla-Tárraga & Rodrígues, 2007; Adams & Church, 2008), and nonavian reptiles (e.g., Cruz *et al.*, 2005; and Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008). However, these studies often did not consider the effect of evolutionary history in constraining body size variation, independently of environmental variation. Omitting evolutionary aspects when analyzing macroecological patterns, especially those of body size, can bring about some limitations in interpreting the mechanisms associated with these patterns (Ruggiero & Hawkins, 2006). To solve this problem, Diniz-Filho *et al.* (2007) and Ramirez *et al.* (2008) recently developed a deconstructive approach to incorporate phylogenetics into assemblage-based interspecific analyses of body size variation. This approach allows the partition of the interspecific variation of body size into phylogenetic, or niche conservatism, and ecological components. It has been applied to interpret how much body size variation in European Carnivora (Diniz-Filho *et al.*, 2007) or New World birds (Ramirez *et al.*, 2008) could be attributed to unique and independent adaptive responses of each species to contemporary environmental conditions (e.g. such as Bergmann's *per se* effects).

In relation to squamate reptiles, contrasting body size gradients have been documented in several intra- and inter-specific studies (e.g., Lindsey, 1966; Ashton & Feldman, 2003; Reed, 2003; Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008). For instance, in a recent interspecific assemblage-based analysis, Olalla-Tárraga *et al.* (2006) found that lizard and snake mean body sizes show opposite trends and associations with environmental energy predictors (potential evapotranspiration and temperature) in Europe, with the mean sizes of lizards increasing and those of snakes decreasing towards the cold, northern areas. Moreover, similar associations with environmental energy were also evident in North America, although the patterns of mean size variation were less clear in this region. These results reinforce that, at least in temperate regions, the body size patterns of each particular group might be determined by a unique and specific set of factors and processes (Olalla-Tárraga *et al.*, 2006).

Along these lines, it is important to note that the above mentioned studies virtually represent the only ones that have documented mean body size patterns in these reptiles, possibly because of the greater scarcity of data regarding the distribution of squamate species at broad geographical scales. Also, few studies (see e.g. Ashton & Feldman, 2003; Pincheira-Donoso *et al.*, 2008) have explored the extent to which macroecological patterns for squamates are structured phylogenetically (and therefore reflect historical legacies) or are driven by contemporary gradients of environmental variation. Here we addressed these issues in two venomous snake families, Viperidae and Elapidae, following the analytical framework proposed by Diniz-Filho *et al.* (2007). Recently, Terribile *et al.*, (*in press*) found that the global patterns of species richness in these two families were differently linked with current climate variation and history (as represented by the distribution of these clades across biogeographic regions): current climate was more associated with the gradients of viperid richness, and history with the variation in elapid richness. Similarly, here we investigate to what extent patterns in body size variation of these groups support explanations based on current environment effects or reflect the presence of historic (i.e. phylogenetic) legacies. Also, we evaluate whether trends observed at the global scale are reproduced within biogeographical regions.

Along with this, we also tested four environmental hypotheses for body size variation of viperids and elapids:

1. *Heat balance*: this hypothesis has been recently developed for ectotherms as an expansion of the classical heat conservation mechanism for endotherms (Olalla-Tárraga & Rodríguez, 2007). For larger thermoregulating ectothermic groups such as snakes, this hypothesis predicts a converse Bergmann pattern as the low surface area-to-volume ratio of these organisms increases heating times in colder regions and limits the time available for other activities such as feeding (see e.g., Shine & Lambeck, 1990; Ayers & Shine, 1997; Blouin-Demers & Weatherhead, 2002; Shine *et al.*, 2002; see also Huey & Slatkin, 1976) and reproduction (Shine *et al.*, 2000; Gregory, Crampton & Skebo, 1999). Thus, small-bodied snakes in cooler climates have benefit of more rapid heating (Bogert, 1949; Stevenson, 1985) and greater ability to control their body temperatures (Ashton & Feldman, 2003), thus allowing them to spend more time to other activities than thermoregulation (Blouin-Demers & Weatherhead, 2002).

2. *Habitat availability*: this hypothesis was proposed recently by Rodríguez *et al.*, (2008) to explain the effects of topography in driving converse patterns of Bergamnn in mammals from south Neartic and Neotropic (i.e., the occurrence of small species in mountains and large species in lowlands; see Rodríguez *et al.*, 2008). It was based on the proposition that strong climatic variation across topical and subtropical mountains generates greater habitat zonation, which in turn reduces habitat areas (see Janzen, 1967; Hawkins & Diniz-Filho, 2006) and consequently limits the occurrence of large species (Rodríguez *et al.*, 2008). Given that temperate regions have less habitat zonation and montane habitats tend to be are more similar to lowlands habitats, it is expected that habitat availability would not limit the occurrence of large species across mountains in these regions. Reed (2003) found positive association between range size and body size in New World snakes species. He also found that species with small geographic range and small

body size occurred not randomly at higher elevations, which may suggest possible effects of habitat availability constraining body size of these organisms. Thus, the importance of this hypothesis to explain broad-scale variation in snake body sizes deserves further investigation.

3. *Primary productivity*: this hypothesis states that, for some species, geographical trends in body size may be better explained in terms of food availability than of temperature (see Rosenzweig, 1968; Blackburn *et al.*, 1999). According to this hypothesis, decreased food availability reduces growth rate and size at maturity, so that low productivity regions tend to harbour more small bodied-species. For snakes, intraspecific studies have found that the individual growth rate is more positively associated with food availability than with other environmental variables (e.g., temperature; see Lindell, 1997; see also Bronikowski & Arnold, 1999; Madsen & Shine, 2000). Thus, the effect of food availability, if any, on interspecific body size variation at broad-scale in these ectotherms warrants examination.

4. *Seasonality* (or *starvation resistance*): this hypothesis suggests that larger organisms can take advantage in highly seasonal climates because they are more resistant to starvation when availability of resources fluctuates seasonally (Lindsey, 1966; Murphy, 1985; Blackburn *et al.*, 1999; Gaston & Blackburn, 2000). However, Mousseau (1997), Blanckenhorn *et al.* (2006) and Olalla-Tárraga *et al.* (2006) emphasized that the length of growing season is a more plausible mechanism to explain body size variation in ectotherms than starvation resistance (see Geist, 1987), due to the interaction between season length and the time available for physiological development. This may explain the converse Bergmann's rule frequently observed in these organisms (Mousseau, 1997; Blanckenhorn *et al.*, 2006).

Methods

Species data

Viperids are distributed across Asian, African, European and New World mainlands and islands and comprise around 256 to 260 species (Kelly, Barker & Villet, 2003; Castoe & Parkinson, 2006). This group is absent from Australia, possibly because it evolved during the Cenozoic when this region had already become a separated landmass (Keogh, 1998). Elapids are distributed across Africa, Asia, Australia, the New World, and the Indic and Pacific Oceans and comprise about 290 to 300 species of which around 60 are marine (Keogh, 1998; Castoe *et al.*, 2007). However, we did not analyze sea snakes because their distribution is likely to be conditioned by different environmental factors than terrestrial species.

We generated a global checklist for both groups based on the updated Reptile Database, supported by the Systematics Working Group of the German Herpetological Society (Uetz, 2007). Except for the Arabian Peninsula, we were able to compile distribution maps for all terrestrial species inhabiting large land masses; namely all continents and the well prospected island of Great Britain, which has enough extension and proximity to mainland Europe to warrant that body size patterns are not affected by insularity. Thus, our final database included 228 viperids and 224 elapids, i.e., around 90% and 75% of the overall diversity of these groups, respectively. For New World species, the species distribution maps were obtained from Campbell & Lamar (2004) supplemented with Renjifo & Lundberg (2003), Alvarado-Díaz & Campbell (2004) and Lavin-Murcio & Dixon (2004). For the Old World we used Branch (1988, 1998), Latifi (1991), Arnold (2002), Arnold & Ovenden (2002), Broadley & Doria (2003), Spawls *et al.* (2004), Ananjeva *et al.* (2006), Vogel (2006), Dobiey & Vogel (2007), Whitaker & Captain (2004), supplemented with Cherlin (1981), Orlov & Tuniyev (1990), Tuniyev & Ostrovskikh (2001), Khan (2002), Mallow, Ludwig & Nilson (2003) and Geniez & Tynié (2005). For Australian elapids we used Wilson & Swan (2003).

It is known that the interpretation of macroecological patterns and their underlying mechanisms are subjected to scale effects (Rahbek & Graves, 2001; Willis & Whittaker, 2002; Rahbek, 2005). Thus, choosing an appropriate scale of analysis is the first important step in examining such patterns. Some studies have suggested that the most appropriate scale to evaluate continental-to-global patterns generated through range maps is at 1° or 2 ° (≈ 100 and 200 km, respectively; see Rahbek & Graves, 2001; Hulbert & Jetz, 2007) of resolution. Therefore, following previous studies of Olalla-Tárraga *et al*. (2006) and Olalla-Tárraga & Rodríguez (2007) here we used grid systems of 110 km x 110 km cells, which we consider as being not too coarse to result in an excessive loss of information or to cause spurious extrapolation, neither too fine to generate spatial discontinuities in the global body size patterns (Rahbek & Graves, 2001; Hulbert & Jetz, 2007). We also used region-specific equal area projections, and those cells containing less than 50% of the land mass were excluded. Thus, area was held as constant as possible and was not included explicitly in the analyses. All range maps were digitized and rasterized using ArcGIS 9.2.

Some authors have suggested body mass as the best estimate of body size (e.g., Hedges, 1985; Gaston & Blackburn 2000) mainly because body mass is a measure that allows comparison among several different taxa with different basic body shapes (see e.g., Olalla-Tárraga *et al*., 2006). However, body mass can be highly variable among individuals, and depend on such factors as season, breeding condition, health and individual history (Gaston & Blackburn, 2000). For snakes, individual variation in body mass may be strongly influenced by seasonal activities on feeding and reproduction, which is well known for most species (see e.g., Shine, 1977; Marques *et al.*, 2006), and by other seasonal changes in body conditions (see e.g., McCue, 2007). On the other hand, for these elongate organisms body length has been proposed to be less sensitive to seasonal variation (Boback, 2003; Boback & Guyer, 2003), and therefore, more appropriate to compare closely related species (Gaston & Blackburn 2000). Furthermore, most previous studies have stated that the trends observed in broad-scale patterns of body length are very similar to those observed using body size (see e.g., Kaufman & Gibbons, 1975; Ashton & Feldman, 2003; Brown, 1995). Therefore, for these organisms that grow indeterminately (Partridge & Coyne, 1997; Olalla-Tárraga *et al.*, 2006) we used maximum total length (a standard size measure commonly reported for snakes) of each species as a surrogate of its overall body size.

The data on maximum total length were obtained from Branch (1988), Orlov & Tuniyev (1990), Latifi (1991), Tuniyev & Ostrovskikh (2001), Arnold (2002), Arnold & Ovenden (2002), Khan (2002), Mallow *et al.* (2003), Campbell & Lamar (2004), Spawls *et al.* (2004), Whitaker & Captain (2004), Geniez & Teynié (2005), Vogel (2006), Dobiey & Vogel (2007) and Wilson & Swan (2003). To correct for allometric effects and heterocedasticity, as well as normalizing statistical distributions, all maximum total lengths were $\log_{10}$-transformed before calculating mean body size values (see Peters, 1983; see also Brown, 1995), which consisted in arithmetic means obtained separately for each family in each grid cell.

Environmental hypotheses

We firstly investigate the multiple environment-based hypotheses as potential mechanisms driving body size variation at broad scales based on different predictor variables, as follows: (1) *Heat conservation*: this hypothesis can be tested by two environmental energy variables –mean annual temperature, and Priestley-Taylors's potential evapotranspiration (PET, see Lu *et al.*, 2005). (2) *Habitat availability*: two indirect indicators of mesoscale climatic variation –range in elevation (i.e., the difference between maximum and minimum elevation within each cell), and 'interaction' (i.e., the standardized values of mean annual temperature multiplied by the standardized values of range in elevation in each cell)– have been used to test this hypothesis (see Hawinks & Diniz-Filho, 2006; Rodríguez *et al.*, 2008). (3) *Primary productivity*: the global vegetation index (GVI), and total annual precipitation (or annual actual evapotranspiration, AET), are normally used as proxies for plant productivity (see e.g., Hawkins, Porter & Diniz-Filho, 2003). (4) *Seasonality* (or *starvation resistance*): measured as the number of months available for plant growth. For this measure (seasonality), we first calculated the xerothermic season length for each cell by counting the number of months in which the mean monthly temperature (in° C) was more than double the mean monthly precipitation (in mm) (see Gaussen, 1945). Based on this calculation, we identified hot dry months, i.e. those summer months for which low precipitation limits plant productivity. We then established the length of the rainy season as 12 minus the number of hot dry months. We also calculated the number of months in which plant growth is limited by low temperatures by counting the number of months having mean monthly temperatures lower than 5° C (cold months). The number of hot months then was calculated as 12 minus the number of cold months. Finally, we defined our 'seasonality' variable as the sum of months in the rainy season and hot months in each cell. All data sources and processing techniques to obtain these variables are provided and discussed in detail in Rodríguez, Belmontes & Hawkins (2005), Olalla-Tárraga *et al.* (2006), Hawkins *et al.* (2007) and Rodríguez *et al.* (2008).

Environmental modelling of mean body size variation

We analyzed separately the patterns of mean body size for Viperidae and Elapidae. We first looked for relationships between mean body size (i.e. calculated for each cell as the arithmetic mean of the $\log_{10}$-trasformed maximum lengths of its extant species) and the eight environmental predictors above mentioned through Pearson's correlations. Since the variables used to generate these environmental models include some "compounded" variables (e.g., AET, PET, interaction, seasonality), the multicollinearity among them and other "primary" explanatory variables (i.e., mean temperature, precipitation, GVI and range in elevation) could lead to a tangled interpretation of the importance of these predictors expressed on the regression coefficients (Graham, 2003). Indeed, the Pearson's correlation (r) matrix performed across all variables revealed values higher than 0.8 between the "compounded" and "primary" variables (correlation matrix provided as Supplementary Material). To avoid this problem, we only used the four "primary" predictors for modelling. Then, the environmental hypotheses were investigated by using ordinary least squares multiple regression (OLS), in which body size was regressed against multiple environmental predictors.

We used an Akaike's-based approach (AIC) (see Burnham & Anderson, 2004; Diniz-Filho, Rangel & Bini, 2008) for model selection. Specifically, for each snake family, besides calculating the AIC of each model, we also computed its ΔAIC_i value (i.e. $\Delta AIC_i = AIC_i - minAIC$; where $\Delta AICs > 10$ represent poor fits, and $\Delta AICs \leq 2$ correspond to models equivalent to the best model (Burnham & Anderson, 2004)) and Akaike's weighting (w_i), an index representing the probability that model i is actually the best explanatory model among all possible models with four variables (i.e. 15 models). The use of these indexes has become common in geographical ecology analyses (e.g., Olalla-Tárraga & Rodríguez, 2007; Ramirez *et al.*, 2008; Kissling & Carl, 2008), mainly as an alternative to deal with multi-inferential uncertainty generated by spatial autocorrelation in ecological data (Diniz-Filho *et al.*, 2008). However, as stressed by Diniz-Filho *et al.* (2008), using an AIC approach in OLS does not avoid all potential autocorrelation problems, since AIC-derived values are related to residual variance of the models, which can be in turn affected by the spatial structure of the data. Additionally, although the best AIC models selected using spatial methods (e.g. autoregressive models and spatial eigenvector mapping; see Diniz-Filho *et al.*, 2008 for details) have no spatial autocorrelation in the residuals, they are often unstable regarding the variables included in the models and have different uncertainty levels. To avoid these problems, Diniz-Filho *et al.* (2008) proposed that, instead of using the best non-spatial OLS (due to spatial autocorrelation) or the best spatial model (due to their uncertainty), a suitable approach is to interpret the averaged model, as it generates consistent and robust results across different methods and may be the best approach for understanding of macroecological patterns. In these averaged models, coefficient estimates from spatial and non-spatial models tend to converge (see Diniz-Filho *et al.*, 2008). Based on this, the relative importance for body size variation of the four predictors selected for modelling were established taking into account the standardized regression coefficients of best model (i.e. the one with lowest AIC value), as well as those resulting from calculating w_i-weighted averages of the coefficients of all 15 possible models.

This analytical framework was applied to the data at the global extent and also separately to each Cox's (2001) zoogeographical region (African, Australian, Eurasian, North American, Oriental, and South American). However, it is noteworthy that elapids are mainly tropical and absent from Europe and most parts of North America and extratropical Asia. Also, though viperids are more globally distributed (but absent from Australia), they are scarcely represented northward Russia (species richness maps for Viperidae and Elapidae are provided as Supplementary Material, and in Terribile *et al.*, *in press*). Taking this into account, and that low cell occupancies may strongly affect analyses of mean body size variation (Olalla-Tárraga *et al.*, 2006), we did not analyzed the body size pattern of the Eurasian and North American zoogeographic regions separately. Even so, the data corresponding to these two regions were used to give a global picture of the patterns (moreover, excluding these data did not qualitatively change our global analyses).

After excluding grid cells containing zero species, global analyses were performed with a total of 7331 cells for Viperidae and 4698 cells for Elapidae.

Analysis of phylogenetic and ecological components of body size

We followed the procedure described in Diniz-Filho *et al.* (2007) to partition the variation in snakes body size into phylogenetic and adaptive responses with Phylogenetic eigenVector Regression (PVR) (see also Diniz-Filho, Sant'ana & Bini, 1998, for the original proposition of PVR). Phylogenies for the two groups were built based on different sources, which were combined to generate a single phylogenetic tree. For Viperidae, we combined phylogenies provided in Lenk *et al.* (2001), Malhotra & Thorpe (2004), and Castoe & Parkinson (2006), including 36 genera. For Elapidae, we used the phylogeny generated by Scanlon & Lee (2004) for the Australian monophyletic group, and combined it with those by Slowinski & Keogh (2000) and Castoe *et al.* (2007) to include all 41 genera. All these phylogenies were analyzed at the generic level, since detailed information for relationships at the species level are not available for all known species.

The idea of PVR is that the phylogenetic relationships among a set of species (or higher taxa) can be expressed as a set of orthogonal vectors obtained by an eigenanalysis (we used Principal Coordinates Analysis; PCoA) of the phylogenetic distance matrix (Legendre & Legendre, 1998). These eigenvectors can then be used as predictors of the trait (i.e., body size) measured in the analyzed species (see Diniz-Filho *et al.*, 2007 for a detailed explanation). We extracted eigenvectors at the generic level from the phylogenetic distance matrix of each group, so that our PVR analyses expressed the amount of deviation of each species' body size from the expected phylogenetic mean of its genus (see Ramirez *et al.*, 2008 for a similar approach at the family level). Specifically, for each clade, species' body sizes were regressed against the eigenvectors to obtain an estimate of the family's overall amount of phylogenetic signal (the PVR`s R^2) in body size. For this analysis, we took into account that, when eigenvectors are successively added to the model, based on their associated eigenvalues, there is a curvilinear relationship between the magnitude of the phylogenetic signal and the number of eigenvectors added. Thus, for each snake family, we used the first 15 eigenvectors and an AIC-based model selection procedure to detect the best “phylogenetic model” (i.e., formed by the selected eigenvectors) among the 32,767 possible models (2^{15} models minus the model with intercept only). On the other hand, the value estimated by PVR for each genus can be interpreted as the expected body size of its species in an explicitly phylogenetic context (i.e. for each species this value measures the phylogenetic component–P of its body size, *sensu* Diniz-Filho *et al.*, 1998, 2007), whereas the model residual corresponding to each species expresses the deviation of its body size from the expected phylogenetic value (its adaptive component–S, *sensu* Cheverud, Dow & Leutenegger, 1985; Diniz-Filho *et al.*, 1998).

The P and S components from PVR are components of total body size variation across species, and following Diniz-Filho *et al.* (2007) we took into account the P and S values corresponding to the species present in each cell to generate cell averages for each component. Then, these cell mean-P and mean-S values were subjected to the same multiple regression-based analyses we used for mean body size (see above) to investigate their association with environmental variation.

All statistical analyses were performed using Spatial Analyses in Macroecology (SAM) software, v. 3.0 (Rangel, Diniz-Filho & Bini, 2006).

Results

The global patterns of mean body size variation of Viperidae and Elapidae do not show simple latitudinal trends, as would otherwise be expected by Bergmann's rule or its converse, although they vary longitudinally with their mean body sizes tending to be larger and smaller towards the New World, respectively (Fig. 1). The patterns vary within different parts of the world too. Viperids show the converse of Bergmann's rule across South America and in the Old World, while in North America there are no clear trends. For Elapidae, however, there are no clear clines except in Australia, where a west-to-east longitudinal trend of increasing mean body sizes is detected.

The best environmental OLS models for the mean body sizes of both families (i.e. the model with lowest AIC value in each case) included all variables- mean annual temperature, precipitation, GVI, and range in elevation- and the evidence in favour of these models as being the best ones (as indicated by their respective Akaike's weightings: w_i) was of 100% for Viperidae and 75% for Elapidae (Table 1). The percentage of variance in mean body size explained by the best environmental models was 37.6% for Viperidae, but only 4.5% for Elapidae, which indicates that current environment is poorly associated with mean body size variation in the latter family. On the other hand, focusing on the standardized coefficients of the averaged model for viperid body size, mean annual temperature showed the highest value while GVI rated second, both with positive signs. These results lend support to the mechanisms described in the heat balance and productivity hypotheses as being the main and secondary potential driving forces, respectively, of mean body size variation in this group. In the case of Elapidae, mean temperature followed by range in elevation were the most important variables in the averaged model (Table 1), but the low fit of the best environmental models makes it difficult to interpret the influence of these variables on mean body size variation.

PVR analyses showed that, for Viperidae, less than 20% of the among species variation in body size was explained by phylogenetic relatedness. In contrast, for Elapidae, this figure raised to 59%, a high value that is similar to those observed in other vertebrate taxa (see Diniz-Filho *et al.*, 2007 and Ramirez *et al.*, 2008), and that indicates that the body sizes of elapid species are strongly determined by the phylogeny.

Taking into account the phylogenetic (P) and adaptive (S) components generated by PVR for each species, as well as the species presences in the grid cells, we calculated mean-P and mean-S cell values for each family, which we related with the environmental predictors the same way as we did for mean cell body sizes. For Viperidae, the percentages of variance described by the best environmental models were 18.3% for mean-P, but 32.1% for mean-S (Table 2, see also Supplementary Material for AIC selected models), suggesting a moderate phylogenetically structured environmental variation of body size (see Diniz-Filho *et al.*, 2007), and a stronger adaptive response of this trait to environmental predictors, respectively. As for the environmental drivers of mean-S variation, the data suggest a leading role of environmental energy and a secondary one of primary productivity, as indicated by the regression coefficients of mean annual temperature and GVI, which rated first and second in the averaged model of S component (see Table 2). GVI was also the best predictor for the P component in this group.

Compared with Viperidae, the best models for Elapidae mean-P and mean-S accounted for much less variance: 8.1% and 9.0%, respectively (see Table 2 and Supplementary Material for AIC selected models). These low figures are consistent with the findings described above regarding both the low dependence shown by elapid mean body size on environmental drivers (see Table 1), and the strong influence of phylogenetic relationships on the across-species variation of this trait. Still, the slightly higher percentage of described variance corresponding to the mean-S component (which is also higher than the that described by the models for mean body size; i.e. 4.5%) suggests an adaptive response of size to environment, which would be mostly related with gradients of primary productivity, as indicated by the higher regression coefficient of GVI in the averaged model (see Table 2).

Regional scale results were consistent in general with those observed at the global extent. For Viperidae, the regional environmental models explained from 14.2 % (Oriental region) to 42.5% (South America) of body size trends, and temperature (in Oriental and South American regions) and GVI (in African and South American regions), emerged again as the most important predictors (Table 3). Similarly, the regional environmental models for the mean values of the phylogenetic and adaptive components of body size had low explanatory power in all instances (described variance < 20%) except for mean-S in South America (41.2%). In this regard, it is interesting that mean-S variation was again primarily and positively associated with temperature and GVI in this and the Oriental region, and with GVI in the African region (see Table 3). These results support the adaptive nature of the relationships of viperid body size with temperature and primary productivity we found at the global extent (see above).

Finally, for the case of elapids, body size gradients across regions were poorly supported by the respective environmental models, as indicated by the generally lower proportions of variance they described (see Table 3). However, there was a notable exception in the case of the mean-S variation in Australia, where the environmental model accounted for 55.8% of the variance, and two predictors of primary productivity (i.e., GVI and precipitation) emerged as the most important ones. This suggests that regional adaptive responses have emerged in Australia; that is, in the region where Elapidae exhibits a greater diversification (see Elapidae species richness map in Supplementary Material and in Terribile *et al.*, *in press*).

Discussion

The spatial variation in body size of Viperidae and Elapidae was idiosyncratic in general in our global analysis, both across the two clades and biogeographical regions. Elapidae showed no clear patterns, whereas Viperidae displayed a clinal variation tending to a Bergmann's converse at least in the Old World and South America. Many other studies have also found no trend or converse Bergmann's patterns in ectotherms (e.g., Masaki, 1967; Mousseau, 1997; Garvey & Marschall, 2003; Olalla-Tárraga & Rodríguez, 2007; Adams & Church, 2008; Pincheira-Donoso *et al.*, 2008), and more specifically in snakes (Ashton, 2001; Ashton & Feldman, 2003; Reed, 2003; and Olalla-Tárraga *et al.*, 2006). Also, in a recent review of ecogeographical patterns, Millien *et al.* (2006) found that, among all vertebrate groups with a significant positive relationship between latitude and across-populations body size variation, snakes presented the lowest percentage of agreement with Bergmann's rule. Moreover, incongruent patterns among cold-blooded vertebrate groups, such as those reported here, are not surprising, and have been commonly found in studies of ectotherm body size gradients (e.g., Lindsey, 1966; Ashton & Feldman, 2003; Reed, 2003; Olalla-Tárraga *et al.*, 2006, Olalla-Tárraga & Rodríguez, 2007). Given these results, it is reasonably to think that the same mechanisms may not be influencing body size variation across different ectothermic groups.

On the other hand, our global scale analysis of mean body size trends and of those of its phylogenetic and adaptive components still revealed interesting gradients and relationships with environmental factors. In the case of viperids, the data lent support to the heat balance and primary productivity hypotheses, as the environmental models did find positive associations of mean body size with temperature (firstly) and GVI (secondarily), respectively. Additionally, our analyses of phylogenetic and specific (adaptive or ecological) components of body size indicated both that phylogeny has a low influence in the across-species variation of viperid body size (<20%), and that species' adaptive responses within this clade may be behind the observed relationships of mean body size with temperature and primary productivity. Indeed, this was indicated by the fact that, similar to what was observed for mean body size, positive associations with temperature and primary productivity were also evident in the environmental models obtained for the mean adaptive component of viperid body size (i.e., mean-S), both at global scale and for each biogeographic region (see Tables 2 and 3).

Selection for maintenance of preferred body temperatures in ectotherms constitutes the basis of the heat balance hypothesis, and provides a straightforward explanation to the trend of mean viperid body size to increase with warmth. In cooler regions, larger temperature and energy inputs fluctuations restrict snakes to reduced daily sunlight hours and low annual energy budgets necessary for their daily or seasonal activities, such as heating, growth, maintenance, and reproduction (Reed, 2003). Under these circumstances, the increased surface area-to-volume ratios of small-bodied snakes may result advantageous, as it allows for faster basking and cooling rates and, hence, for a more effective thermoregulation (Ashton & Feldman, 2003). Moreover, by spending less time heating, small snakes may spend more time foraging for food and partners (Shine *et al.*, 2000; Blouin-Demers & Weatherhead, 2002, resulting in more frequent breeding and potentially higher lifetime fitness (Lourdais *et al.*, 2002; Shine, 2003). In contrast, for larger snakes, the energy inputs necessary to attain minimum energetic thresholds for successful reproduction may result in lower breeding frequencies in cooler areas (Brown, 1991), thus disfavouring them. In warmer regions, however, thermoregulation is less a limiting factor for larger snakes (Shine & Madsen, 1996; Ashton & Feldman, 2003), which may explain why viperid body sizes increased with temperature. Even though these explanations were thought for variation in body sizes at the intraspecific (i.e. across-populations) level, it is reasonable to think that analogous adaptive pressures are behind the interspecific trends observed here. This was also supported by our data, particularly by the observation that temperature was as an important factor in our global and regional environmental models for the mean adaptive (mean-S) component of viperid body size. Moreover, a similar positive association between mean body size and energy was found by Olalla-Tárraga & Rodríguez (2007) for the amphibian faunas of Europe and North America, and the authors also suggested the trade-off between increased surface area-to-volume ratio and rapid heating (i.e. the heat balance hypothesis) as a likely explanation for these interspecific patterns.

Alternatively, positive size-temperature associations observed in ectotherms have been explained by invoking season length effects on growth and development of organisms (see Ray, 1960; Mousseau, 1997; Blanckenhorn & Demont, 2004 and Olalla-Tárraga *et al*., 2006). However, when we added a variable expressing 'seasonality' to our environmental model (i.e., the model included temperature, precipitation, GVI, range in elevation and seasonality), virtually no increment in the proportion of variance described was noticed ($\Delta R^2 = 0.011$). So it seems unlikely that seasonality was behind the observed relationship with temperature.

Primary productivity (GVI) was a secondary, positive predictor of viperid mean body size, and was also detected as an important determinant of the mean adaptive component of viperid body size at global and regional scales, thus supporting the adaptive nature of this relationship (Tables 2 and 3). A potential explanation (i.e. the primary productivity hypothesis) is that the more productive tropics offer a greater stock of prey (see Campbell & Lamar, 2004) thus enabling tropical viperids to attain larger sizes than those living in cooler regions, where seasonal and more limited food availability could constrain body sizes (see e.g., Forsman, 1991; Madsen & Shine 2000; see also Blackburn *et al.*, 1999; Jones *et al*., 2005; Yom-Tov & Geffen, 2006; Meiri *et al*., 2007). Also, bearing in mind that morphological traits associated with arboreality typically result in more elongated bodies (Martins *et al*., 2001), this positive association with primary productivity could reflect the abundance of semi-arboreal and arboreal species in tropical forests (e.g. the Neotropical *Bothrops* and the Asiatic *Trimeresurus*) (see Parkinson, 1999; Martins *et al*., 2001; Campbell & Lamar, 2004). Similar indirect (i.e. habitat-mediated) influences of primary productivity on biogeographical gradients have been proposed to explain amphibian species richness patterns in Europe (Rodríguez *et al*., 2005).

Regarding elapids, the environmental model for global mean body size variation had virtually no explanatory power (see Table 1), suggesting either that environmental variables not included in our study may be driving the patterns or, more likely, that they are weakly climatically determined at the global extent. Indeed, it should be noted that many terrestrial elapids are fossorial or semi-fossorial (How & Shine, 1999; Campbell & Lamar, 2004) and therefore spend most of the time in favourable and relatively constant microclimatic conditions (How & Shine, 1999; Campbell & Lamar, 2004). This may explain why mean body size was not affected by environmental gradients in this group (see Rodríguez *et al.*, 2006 for similar trends and explanations in other vertebrate groups). Complementarily, this lack of association with environmental factors may also reflect that elapids have had not enough time to diversify and generate adaptive responses of body size to environmental gradients in most areas (see below). Bearing in mind that, in an evolutionary context, Elapidae is a more recent clade than Viperidae (Vidal *et al.*, 2007), this seems a plausible possibility, which in turn may explain why we found that the across-species body size variation of elapids was strongly phylogenetically determined. Moreover, our regional models for the mean adaptive (mean-S) component of elapid body size also support this explanation, as they had low explanatory power in all areas except for Australia (see Table 3); that is, for the region where this family has experienced a greater diversification. Notably, in this region, the mean adaptive component of elapid body size was mostly associated with primary productivity predictors (GVI and precipitation), which can be interpreted the same way as we did above for the relationships of primary productivity and viperid body size.

On the other hand, some authors have pointed out that some elapids are morphologically conservative (see Silva & Sites, 2001; Campbell & Lamar, 2004; Castoe *et* *al.*, 2007), which suggests that the patterns of body size variation in this group may be reflecting niche conservatism (Wiens & Graham, 2005), so that elapid species would posses a stronger tendency to retain ancestral ecological characteristics. This interpretation is supported by the global environmental models generated for the mean adaptive component of both groups, as the model corresponding to Viperidae had an explanatory power that was almost three times higher than the model for Elapidae (see Table 2). However, the above mentioned results for this adaptive component in Australia weaken the plausibility of such an interpretation, as the model obtained for this region had an explanatory power (55.8%) that had no parallel either at global or regional scales, or considering the models obtained for viperids. In other words, if niche conservatism was behind the stronger phylogenetic inertia of elapid body size, then Australian elapids should be considered an exception to this general trend.

To conclude, we would like to summarize two general conclusions based on our extensive analyses. Firstly, it is unlikely that a general interspecific pattern of body size variation exists across different snake groups at very broad scales, even in closely related taxa as showed here. Secondly, the mechanisms constraining body size spatial distributions can vary across groups and according to differences in the evolutionary history of each clade. Viperidae and Elapidae constitute a good example, as they showed distinct body size trends which were differently associated with environmental gradients and evolutionary history. This reinforces the importance of starting to adopting deconstructive approaches (as provided by Diniz-Filho *et al.*, 2007) if we are to gain a better understanding of macroecological patterns.

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Figure Legend

Figure 1. Geographical patterns of Viperidae (A) and Elapidae (B) mean body size. The maps were built using cell averages of $\log_{10}$-transformed maximum length values, while the numbers included in the legends have been recalculated by antilog transformation of the original values to reflect geometric means of maximum length in millimetres. Dashed lines separate ecogeographical regions as described by Cox (2001): North American (NA), South American (SA), African (Afr), Eurasian (Eur), Oriental (Ori), and Australian (Aust).

Table 1. Multiple regression models for the global analysis of viperid and elapid mean body sizes. Left panel includes w_i-weighted averaged standardized regression coefficients resulting from averaging the coefficients of all possible (15) models with four predictors; namely, mean annual temperature (Mean Temp), annual precipitation (Prec), annual global vegetation index (GVI), and range in elevation (Range). Right panel presents the variables included in the "best" model (i.e., with lowest AIC values and ΔAIC ≤ 2) ranked from the most to the least important variable according to their respective regression coefficients. The Akaike's weighting or probability of each model of being actually the best model (w_i), and the models' coefficients of determination (R^2) are also included.

w_i-weighted averaged models			AIC best model				
Variables	Viperids	Elapids	Model	AIC	ΔAIC	w_i	R^2
Mean Temp	0.415	0.224	VIPERIDAE				
Prec	0.116	0.040	Mean Temp, GVI, Prec, Range	-11081.473	0.000	1.000	0.376
GVI	0.250	-0.127					
Range	0.104	0.195	ELAPIDAE				
			Mean Temp, Range, GVI, Prec	-2780.738	0.000	0.750	0.045

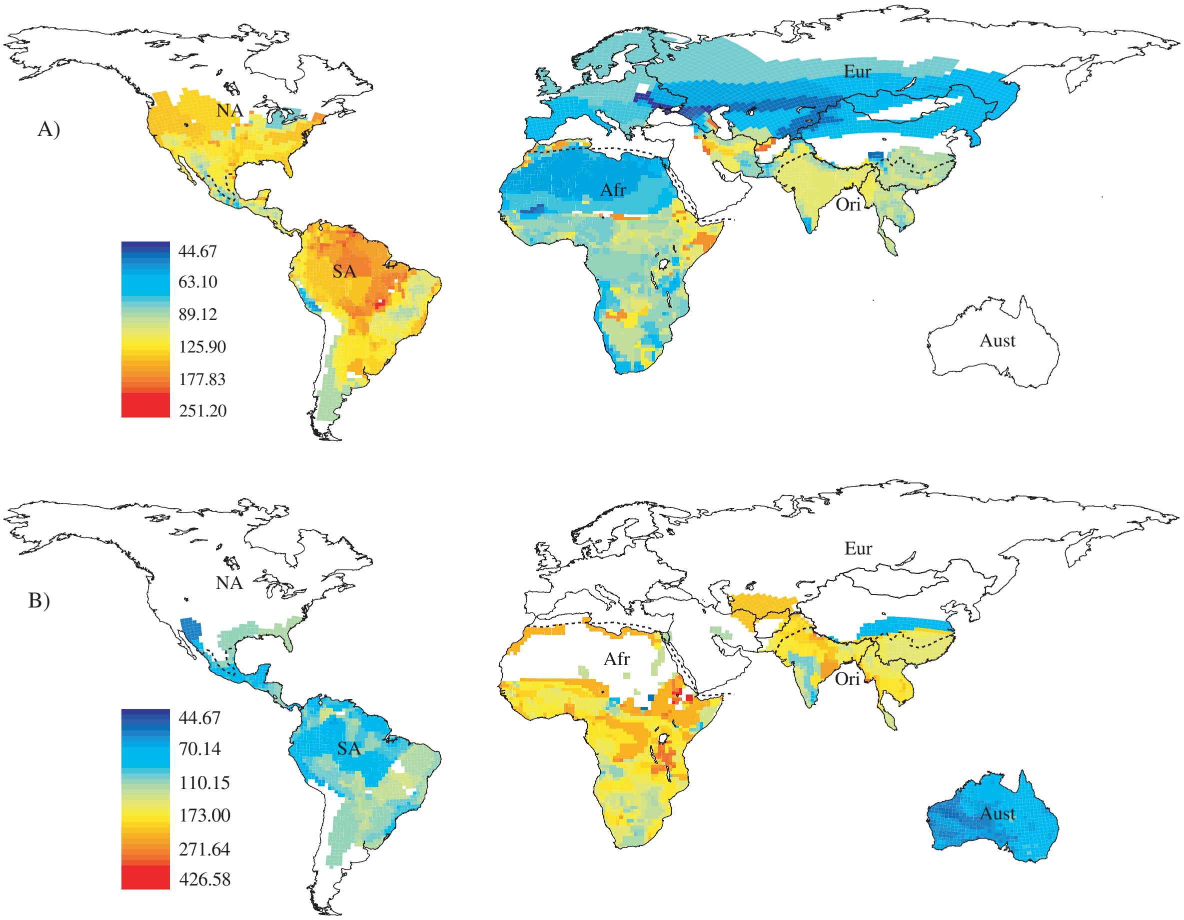
Table 2. Multiple regression w_i-weighted averaged models for the global analysis of the phylogenetic (mean-P) and adaptive (mean-S) components of viperid and elapid mean body sizes. P- and S-component values were generated for each species through Phylogenetic eigenVector Regression (PVR) and their mean values were obtained for each cell by taking into account its extant species. To facilitate comparison with the w_i-weighted averaged models for mean body sizes presented in Table 1, these models (mean-BS) are also included. The numbers reflect w_i-weighted averages of the standardized regression coefficients of all possible (15) models with four predictors. The R^2s (italics) correspond to those of the best models (see Supplementary Material) and are provided to reflect the strength of the relationships of the variables of body size with current environment variation.

Variables & "best" model-R^2	mean-P	mean-S	mean-BS
VIPERIDAE			
Temperature	-0.171	0.410	0.415
Precipitation	0.184	-0.001	0.116
GVI	0.238	0.306	0.250
Range in elevation	0.171	-0.008	0.104
R^2	*0.183*	*0.321*	*0.376*
ELAPIDAE			
Temperature	0.225	0.031	0.224
Precipitation	0.084	-0.095	0.040
GVI	-0.288	0.346	-0.127
Range in elevation	0.208	-0.008	0.195
R^2	*0.081*	*0.090*	*0.045*

Table 3. Multiple regression w_i-weighted averaged models for the regional analyses of the viperid and elapid mean body sizes (mean-BS), and of their phylogenetic (mean-P) and adaptive (mean-S) components. The numbers reflect w_i-weighted averages of the standardized regression coefficients of all possible (15) models with four predictors. As in Table 2, the R^2s (italics) correspond to those of the best models (see Supplementary Material). Although used for mapping mean body size patterns (see Figure 1), the North American and Eurasian regions were not included in our analyses due to low richness values of both families in these areas (Methods).

Variables & "best" model-R^2	African			Australian			Oriental			S. American		
	mean-BS	mean-P	mean-S	mean-BS	mean-P	mean-S	mean-BS	mean-P	mean-S	mean-BS	mean-P	mean-S
VIPERIDAE												
Temperature	0.091	-0.109	0.1	-	-	-	0.313	<.001	0.32	0.318	0.554	0.257
Precipitation	0.060	-0.204	0.083	-	-	-	-0.142	-0.151	0.03	0.126	-0.249	0.157
GVI	0.404	0.286	0.357	-	-	-	-0.056	-0.302	0.283	0.227	0.051	0.227
Range in elevation	0.127	0.041	0.12	-	-	-	-0.032	-0.124	0.111	-0.126	0.259	-0.162
R^2	*0.207*	*0.051*	*0.191*	-	-	-	*0.143*	*0.200*	*0.150*	*0.426*	*0.186*	*0.413*
ELAPIDAE												
Temperature	0.144	0.147	0.055	0.050	0.259	-0.198	0.037	-0.177	0.183	-0.076	-0.033	-0.073
Precipitation	0.141	0.15	0.093	0.300	-0.014	0.385	0.085	0.055	0.109	-0.341	0.029	-0.344
GVI	-0.056	-0.176	0.149	0.245	-0.123	0.507	0.11	0.146	0.064	-0.116	0.009	-0.117
Range in elevation	0.141	0.176	-0.002	-0.267	-0.159	-0.206	-0.015	-0.104	0.080	-0.401	-0.052	-0.397
R^2	*0.044*	*0.049*	*0.051*	*0.171*	*0.172*	*0.561*	*0.020*	*0.047*	*0.034*	*0.217*	*0.002*	*0.217*

Figure 1.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Supplementary material

Appendix 2. ‘Best’ environmental models (i.e., with ΔAIC ≤ 2) for the cell mean values of the phylogenetic (mean-*P)* and adaptive (mean-*S*) components from PVR, for Viperidae and Elapidae at global scale.

Model	**AIC**	**ΔAIC**	w_i	R^2
Viperidae				
Phylogenetic (mean-P)				
MeanTemp, GVI, Range, Prec	-15703.604	0.000	1.000	0.183
Adaptive (mean-S)				
MeanTemp, GVI	-12566.355	0.000	0.488	0.321
MeanTemp, GVI, Range	-12564.964	1.391	0.243	0.321
MeanTemp, GVI, Prec	-12564.359	1.996	0.180	0.321
Elapidae				
Phylogenetic (mean-P)				
MeanTemp, GVI, Range, Prec	-3672.465	0.000	1.000	0.081
Adaptive mean- (S)				
MeanTemp, GVI, Prec	-11834.914	0.000	0.539	0.090
MeanTemp, GVI, Range, Prec	-11832.917	1.997	0.199	0.090

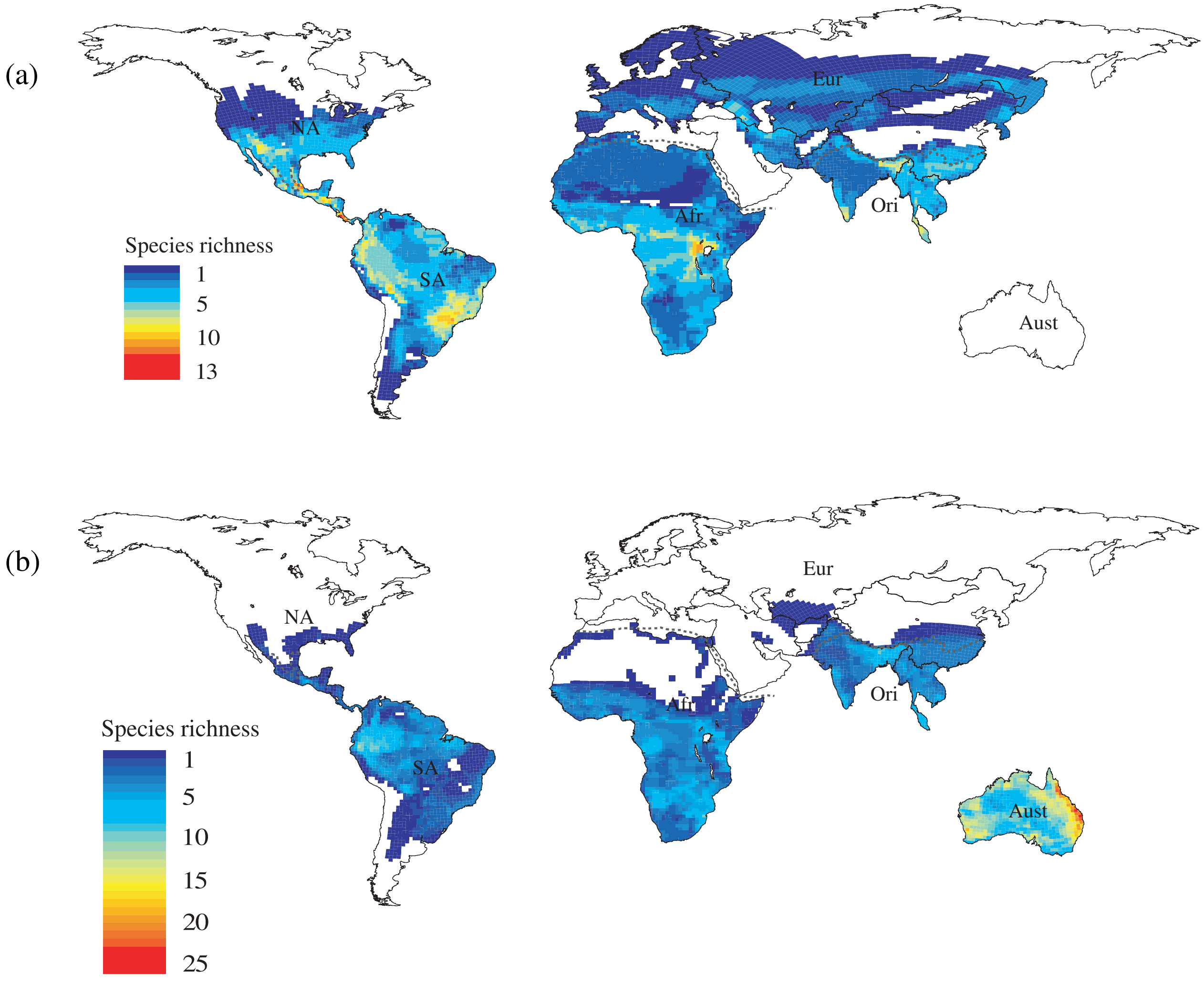
Supplementary material

Appendix 3. Regional 'best' environmental models (i.e., with ΔAIC ≤ 2) for the cell mean values of Viperidae and Elapidae mean body sizes (mean-BS) and for their phylogenetic (mean-*P)* and adaptive (mean-*S*) components.

	Models	**AIC**	**ΔAIC**	w_i	R^2
VIPERIDAE					
	Total (mean-BS)				
	MeanTemp, GVI, Prec, Range	-4315.791	0.000	0.587	0.207
	MeanTemp, GVI, Range	-4315.081	0.709	0.412	0.206
	Phylogenetic (mean-P)				
African	MeanTemp, GVI, Prec, Range	-14516.373	0.000	0.642	0.051
	MeanTemp, GVI, Prec	-14515.203	1.169	0.358	0.050
	Adaptive (mean-S)				
	MeanTemp, GVI, Prec, Range	-4127.973	0.000	0.830	0.191
	Total (mean-BS)				
	MeanTemp, Prec	-2042.723	0.000	0.385	0.143
	MeanTemp, GVI, Prec	-2042.301	0.422	0.311	0.146
	MeanTemp, Prec, Range	-2041.055	1.668	0.167	0.144
	Phylogenetic (mean-P)				
Oriental	GVI, Prec, Range	-2022.517	0.000	0.661	0.200
	MeanTemp, GVI, Prec, Range	-2020.589	1.927	0.252	0.200
	Adaptive (mean-S)				
	MeanTemp, GVI, Range	-2170.027	0.000	0.439	0.150
	MeanTemp, GVI	-2168.86	1.167	0.245	0.146
	MeanTemp, GVI, Prec, Range	-2168.336	1.691	0.189	0.151
	Total (mean-BS)				
	MeanTemp, GVI, Prec, Range	-3409.974	0.000	1.000	0.426
	Phylogenetic (mean-P)				
S. American	MeanTemp, GVI, Prec, Range	-9129.107	0.000	0.555	0.186
	MeanTemp, Prec, Range	-9128.666	0.441	0.445	0.184
	Adaptive (mean-S)				
	MeanTemp, GVI, Prec, Range	-3455.987	0.000	1.000	0.413
ELAPIDAE					
	Total (mean-BS)				
	MeanTemp, GVI, Prec, Range	-2563.567	0.000	0.509	0.044
	MeanTemp, Prec, Range	-2563.496	0.070	0.491	0.042
	Phylogenetic (mean-P)				

African	MeanTemp, GVI, Prec, Range	-3424.959	0.000	0.998	0.049
	Adaptive (mean-S)				
	MeanTemp, GVI, Prec	-4481.496	0.000	0.435	0.051
	GVI, Prec	-4479.537	1.959	0.163	0.048
	MeanTemp, GVI, Prec, Range	-4479.509	1.987	0.161	0.051
Australian	*Total (mean-BS)*				
	GVI, Prec, Range	-1834.164	0.000	0.614	0.171
	MeanTemp, GVI, Prec, Range	-1833.235	0.929	0.386	0.172
	Phylogenetic (mean-P)				
	MeanTemp, GVI, Range	-2192.732	0.000	0.600	0.172
	Adaptive (mean-S)				
	MeanTemp, GVI, Prec, Range	-2655.714	0.000	1.000	0.561
Oriental	*Total (mean-BS)*				
	GVI, Prec	-1062.658	0.000	0.207	0.020
	GVI	-1062.376	0.282	0.180	0.016
	MeanTemp, GVI, Prec	-1061.519	1.139	0.117	0.021
	GVI, Prec, Range	-1061.207	1.451	0.100	0.021
	MeanTemp, GVI	-1060.872	1.787	0.085	0.017
	Phylogenetic (mean-P)				
	MeanTemp, GVI Range	-1912.946	0.000	0.307	0.047
	MeanTemp, GVI	-1912.655	0.292	0.265	0.043
	MeanTemp, GVI, Prec, Range	-1912.423	0.524	0.236	0.049
	MeanTemp, GVI, Prec	-1911.602	1.345	0.157	0.045
	Adaptive (mean-S)				
	MeanTemp, Prec	-1643.675	0.000	0.276	0.034
	MeanTemp, Prec, Range	-1643.244	0.431	0.223	0.036
	MeanTemp, GVI, Prec	-1643.170	0.504	0.215	0.036
	MeanTemp, GVI, Prec, Range	-1642.184	1.491	0.131	0.038
S. American	*Total (mean-BS)*				
	MeanTemp, GVI, Prec, Range	-3646.353	0.000	0.870	0.217
	Phylogenetic (mean-P)				
	Range	-10962.649	0.000	0.185	0.002
	MeanTemp, Range	-10961.889	0.760	0.127	0.003
	MeanTemp, Prec, Range	-10961.298	1.351	0.094	0.004
	GVI, Prec	-10961.235	1.414	0.091	0.002
	Prec	-10961.194	1.455	0.089	<0.001
	Adaptive (mean-S)				
	MeanTemp, GVI, Prec, Range	-3650.826	0.000	0.842	0.217

Appendix 4. Global biogeographical patterns of Viperidae (a) and Elapidae (b) species richness. The dashed lines identify the biogeographical limits of Cox (2001): North American (NA), South American (SA), African (Afr), Eurasian (Eur), Oriental (Ori), and Australian (Aust).



Apêndice 4. Prioridades globais para conservação.

For: *Diversity and Distributions*

GLOBAL STRATEGIES FOR SNAKE CONSERVATION: PUTTING EFFORTS TOGETHER

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Short title: *Global strategies for snake conservation*

ABSTRACT

Aim We present the first attempt of mapping global conservation priorities for two snake clade: Viperidae and Elapidae. We compared the global conservation priorities of each clade with the nine global conservation schemes synthesized by Brooks *et al*. (2006), in order to evaluate how effective these schemes are in ensuring the preservation of viperid and elapid biodiversity.

Location Global

Methods Based on range maps of 228 species of Viperidae and 224 species of Elapidae, we used systematic conservation planning methods of complementarity and irreplaceability to identify areas of high conservation value and to generate a set of conservation networks under two cost scenarios: (1) minimizing conservation-human development conflicts and (2) maximizing environmental suitability for high snake richness. Analysis of variance was used to investigate whether the mean irreplaceability of cells matching the areas covered by each of the nine global prioritization schemes in Brooks *et al*. (2006) was higher than the mean irreplaceability of cells located outside these areas.

Results Overall, few areas showed irreplaceability higher than 0.5. The conservation networks generated in expectation of low conflicts between human development and conservation were quite different of those networks of high environmental suitability. Areas with higher irreplaceability coincided with the regions covered by global schemes of Endemic Bird Areas (for Viperidae and Elapidae) and High-Biodiversity Wilderness (for Elapidae).

Main conclusions Our findings indicated the existence of viable conservation opportunities for these two snake groups. This study can be viewed as an alternative approach to the recent criticism concerning the independent development of several global conservation priorities which have led to a considerable redundancy in the results. More than simply determining priorities for snake's conservation, our analyses showed that the development of parallel priority-setting initiatives can be reconciled with those strategies for which financial resources are already being designed.

Keywords: complementarity, biodiversity, global conservation priorities, reserve network, snakes.

INTRODUCTION

The accelerated expansion of human activities in detriment of natural environments has caused irreversible biodiversity losses worldwide (Ehrlich, 1994; Pimm *et al.*, 1995). In response to an imminent crisis in biodiversity, several global schemes of prioritization have been developed in recent years, particularly by non-governmental organizations, aimed at identifying regions of high conservation value (e.g., Bryant *et al.*, 1997; Stattersfield *et al.*, 1998; Myers *et al.*, 2000; see Brooks *et al.*, 2006 for a recent review). However, such global schemes differ in respect to the nature of the conservation target, where or how conservation should be done, as well as in the principles underlying each approach (Redford *et al.*, 2003). In this sense, they can be conceptually distinguished in two main groups: those that prioritize regions of high threat and high irreplaceability and those that prioritize regions of low threat but high irreplaceability (i.e., the "purely reactive" and the "purely proactive" approaches, respectively; *sensu* Brooks *et al.*, 2006).

Reactive approaches focus on pressing regions where human disturbance to natural habitats has been harsh and for which conservation actions are most urgent to prevent more biodiversity loss –e.g., the Biodiversity Hotspots and the Crisis Ecoregions defined by Myers *et al.* (2000), and Hoekstra *et al.* (2005), respectively. Conversely, the proactive approaches focus on regions of high conservation value where the current exploitation, although low, may result in a severe species loss in the future –e.g., the High-Biodiversity Wilderness Areas and the Frontier Forests of Mittermeier *et al.* (2003) and Bryant *et al.* (1997), respectively. Other global schemes may still be ranked between these two frameworks, which actually represent the extreme of a continuous axis, in the extension to which they prioritize irreplaceability or vulnerability (see Brooks *et al.*, 2006).

Most of the global schemes have emphasized the conservation of plants (WWF & IUCN, 1994-1997; Bryant *et al.*, 1997), and birds (Stattersfield *et al.*, 1998), and other global priorities have been mapped for amphibians (IUCN *et al.*, 2006), and mammals (Ceballos *et al.*, 2005; Carwardine *et al.*, 2008). These organisms have benefited from the accumulation of biodiversity data applied for conservation purposes at large scale and, consequently, have attracted substantial research efforts and conservation funding (Fonseca, 2000). Unfortunately, the availability of datasets and conservation plans in broad scale for other groups such as non-avian reptiles (*sensu* Gauthier *et al.*, 1988), especially for snakes, are scarce.

Population declines and geographic range contractions have been documented for several snake species around the world (e.g., Jaggi & Baur, 1999; Nilson *et al.*, 1999; Gibbons *et al.*, 2000; Terribile *et al.*, 2007). Forest degradation and habitat loss associated to some characteristics, such as habitat specialization, small home-range size, low dispersal rate, low reproductive frequency, and the small range of prey species used in their feeding habitats (Zamudio & Greene, 1997; Gibbons *et al.*, 2000; Reed & Shine, 2002; Webb *et al.*, 2002; Campbell & Lamar, 2004; Santos *et al.*, 2006; Terribile *et al.*, 2007) make most of snake species particularly susceptible to habitat changes and, ultimately, highly vulnerable to extinction (Santos *et al.*, 2006). It stands to reason that, though these organisms have been less studied than other groups, considerable efforts have been registered in order to indentify snake conservation priorities (e.g., Akani *et al.*, 1999; Filippi & Luiselli, 2000; Cogger *et al.*, 2000; Brooks *et al.*, 2001; Moore *et al.*, 2003; Zhou & Jiang, 2005; Couto *et al.*, 2007; Cagle, 2008). Nevertheless, overall these studies were based on small samples of the snake's diversity (but see Cogger *et al.*, 2000 and Reed & Shine, 2002), and the unavailability of data has prevented the development of global-scale conservation strategies.

In this paper, we used a global dataset of Viperidae and Elapidae species distributions to generate the first global model of snake conservation priorities based on systematic conservation planning methods (i.e., complementarity and irreplaceability) (Margules & Pressey, 2000). Although complementarity approaches may give us an efficient answer to the question of what locations should be included in a representative conservation network (Brooks *et al.*, 2001), conservationists have insisted that effective conservation planning must deal not only with the representation of species, but also with potential conflicts between biodiversity conservation and human development (Margules & Pressey, 2000; Balmford *et al.*, 2001, 2003; Chown *et al.*, 2003; Diniz-Filho *et al.*, 2006). Moreover, defining strategies for broad-scale conservation planning based on species richness should be done by taking into account the environmental factors that are associated with biodiversity patterns in these scales (Bini *et al.*, 2006). Consequently, effectiveness of systematic conservation planning results in part from its efficiency in preserving environmentally important regions for maintenance of species richness without overlapping with economically important areas. Based on these two premises we also generated conservation networks that represent the total species richness of each group with a minimum of human influence and a maximum of environmental suitability.

Additionally, we compared the global pattern of irreplaceability and conservation networks obtained for each snake family with the nine global conservation priorities recently synthesized by Brooks *et al.* (2006), in order to evaluate how effective these schemes are in ensuring the preservation of viperid and elapid biodiversity. Thus, the combination of the global priority maps (generated by these authors under the criteria of reactive and proactive approaches) with the global picture of irreplaceability built for snakes will give us a general perspective of the current threat level of the most important areas to preserve snake biodiversity.

METHODS

Data

We generated a global checklist of Viperidae and Elapidae species based on the updated Reptile Database supported by the Systematics Working Group of the German Herpetological Society (Uetz, 2007). Given that our conservation planning analyses focused on continental species, we excluded insular and sea snake species, aside from the well prospected island of Great Britain. Data scarcity for the Arabian Peninsula also precluded including this region in the analysis. Our final dataset comprised 228 viperids and 224 elapids (see Terribile *et al.*, *in press*, for a full list of genera and number of species), for which maps of geographic distribution were compiled from several sources of species distribution worldwide.

For the New World, species range maps were primarily obtained from Campbell & Lamar (2004), supplemented with the new species recently recognized by Renjifo & Lundberg (2003), Alvarado-Díaz & Campbell (2004) and Lavin-Murcio & Dixon (2004). For the Old World we used Branch (1988, 1998), Latifi (1991), Arnold (2002), Arnold & Ovenden (2002), Broadley & Doria (2003), Spawls *et al.* (2004), Ananjeva *et al.* (2006), Vogel (2006), Dobiey & Vogel (2007), supplemented by Cherlin (1981), Orlov & Tuniyev (1990), Tuniyev & Ostrovskikh (2001), Khan (2002), Mallow *et al*. (2003) and Geniez & Tynié (2005). For Australian elapids we used Wilson & Swan (2003).

All distribution maps were digitized and rasterized in ArcGIS 9.2 in grid systems of 110 km x 110 km (i.e. equaling 1° latitude by 1° longitude at the equator) using region-specific equal area projections. For comparative purposes, the nine global scenarios analyzed by Brooks *et al*. (2006; see Appendix 1) were also processed in the same grid of 110 km x 110 km, denoting presence (1) or absence (0) in each grid cell. Cells containing less than 50% of the land mass were not included in the analyses to avoid potential area effects in the results.

Conservation planning analyses and comparisons with global priorities

To identify specific patches or cells representing optimum (or near-optimum) conservation networks for snakes across the world, we used methods based on biodiversity complementarity (Faith *et al*., 2003). These methods are used to estimate the gain in species representation when adding an area (i.e., a cell) to a set of pre-selected areas (Williams, 1998; Faith *et al*., 2003), so that certain areas would be selected because they have the most species between them, but not necessarily the most species richness individually. The resulting pattern is a combination of areas (cells) that have the highest representation of species (Williams, 1998).

Based on the occurrence of the viperid and elapid species in the grid cells across de globe (i.e., a total of 9563 cells for viperid and 9627 cells for elapid species), we used the simulated annealing algorithm implemented on Site Selection Mode (SSM) of SITES

V. 1.0 software program (Andelman *et al*., 1999) to select the minimum number of cells necessary to represent at least 25% of each species' geographical range. This strict conservation goal was used to ensure that all species would be conserved in most solutions within a minimal area needed to support viable populations. These analyses were performed for both snake family with $1x10^7$ interactions and 150 repeated runs.

The frequency of each cell in the various optimized networks indicates its relative importance for the complementary solutions, and was used here to estimate and map the irreplaceability of cells (Ferrier *et al*., 2000; Meir *et al*., 2004). The irreplaceability values vary between 0 and 1, so that cells with values of 1 (i.e., completely irreplaceable cells) are essential for achieving one or more conservation goals, whereas cells with decreasing values have increasing numbers of potential replacements to preserve the targets and achieve the established goals (Ferrier *et al*., 2000; Carwardine *et al*., 2007).

Several studies have shown that water and energy availability are among the most important drivers of species richness at large scales (e.g., Currie, 1991; Hawkins *et al*., 2003a; Currie *et al*., 2004; O'Brien, 2006), and this was also recently confirmed for viperid and elapid richness (see Terribile *et al*., *in press*). To take into account the influence of environmental variables on determining macroscale species richness variation, we defined a cost value to each grid cell as the inverse of Actual Evapotranspiration (AET, available in http://www.grid.unep.ch/data/data.php?category=atmosphere), which represents the joint availability of energy and water in the environment (see Currie, 1991 and Hawkins *et al*., 2003a). The purpose is to generate a global network that represents all species in a set of areas having suitable environmental conditions to support high snake richness.

Possible conflicts between biodiversity conservation and human development were taken into account by adding a cost variable of 'human footprint' (available in http://www.ciesin.columbia.edu/download_data.html) representing human influence to each grid cell. Human footprint (hereafter HF) is a quantitative index of human activity in every biome on the land surface, built by combining geographic data on human population density, land transformation, access, and electrical power infrastructure (see details Sanderson *et al*., 2002).

Thus, we generated a set of four reserve networks (i.e., two for each snake clade) that preserve all species at least once under two cost scenarios: a) maximizing AET by finding a combination of cells whose sum of the inverse of AET is lowest in the set of selected cells; and b) minimizing human influence by finding a combination of cells with the lower human footprint value in each grid cell. In both cases was used the same SSM protocol described above by performing optimization routines of 50 runs and 2×10^7 interactions. The two networks for each snake group were then overlapped and the Sorensen similarity coefficient (Krebs, 1998) was used to compare how concordant the complementary solutions with different costs are. Sorensen coefficient near to 1 (high similarity) would indicate that cells selected in the optimum reserve network of low human influence were also selected in the optimum reserve network of high AET. For comparative purposes, we also calculate the amount of area (in number of 110 x 110 km cells) of the reserve networks in each biogeographical region as defined by Cox (2001): African, Australian, Eurasian, North American, Oriental, and South American.

Finally, the irreplaceability of cells was used to evaluate which of the global systems summarized by Brooks *et al*. (2006) (see Table 2 and Brooks's *et al*., 2006

Supporting Online Material in www.sciencemag.org/cgi/content/full/313/5783/58/DC1 for details) supports the most irreplaceable areas for Viperidae and Elapidae. By setting irreplaceability as our dependent variable, we used Analysis of Variance (ANOVA; Sokal & Rohlf, 1995) to investigate whether the mean irreplaceability of cells matching the areas covered by each of the nine global prioritization schemes (our independent variable of presence [1] and absence [0]) is higher than the mean irreplaceability of cells located outside these areas. Thus, we were able to identify which global scheme best represents the areas of high conservation value for snake biodiversity. Before the ANOVA, grid cells containing zero species were excluded from analyses.

RESULTS

Overall, few cells showed irreplaceability higher than 0.5, which indicates that the combinations of cells were highly variable in each one of the 150 optimized solutions. Cells with high irreplaceability for both groups are evident across Central and North America, and Central Africa (Fig. 1a, b), although irreplaceable areas of viperids were more scattered across continents than those of elapids (excepted in Australia where viperids are absent). This is expected given the wider coverage of Viperidae distributions worldwide.

For Viperidae, the global networks that collectively met the established conservation goals (i.e., to represent at least 25% of species ranges) with a minimum cost were achieved with a total of 1527 cells for AET (i.e., cells with highest AET values) and 1638 cells for human influence (i.e., cells with lowest HF values) (respectively, 15.9% and 17.1% of the total of cells analyzed for this taxon; Table 1, Fig. 2a). For Elapidae, these goals were represented in two networks, one with 986 cells for AET and the other with 1089 cells for HF (respectively, 10.2% and 11.3% of the total of cells analyzed for this taxon; Fig. 2b). Oriental and Australian were the two biogeographic regions with the largest number of cells included in the reserve networks, respectively, for Viperidae and Elapidae (Table 1; see also Fig.2).

Sorensen coefficient was low for both taxa (0.30 for Viperidae and 0.28 for Elapidae), indicating that conservation management plans based on the strategies of low conservation-human development conflicts could not ensure the preservation of those areas of high snake richness (Fig. 2, see also Table 1). Indeed, the overlapping of the two types of networks indicated that only 458 cells (4.7%) for viperids, and 295 cells (3.0%) for elapids, were represented in both solutions.

Analyses of variance showed that the regions covered by the nine global conservation priorities summarized by Brooks *et al.* (2006), except Last of the Wild areas (Sanderson *et al*., 2002), represent a gain in irreplaceability in comparison with regions not covered by them (Table 2). For viperids, areas with higher irreplaceability coincided with the regions covered by Endemic Bird Areas and High-Biodiversity Wilderness Areas. For elapids, considerable gain in irreplaceability was also found in Endemic Bird Areas, but the areas falling within the Last of the Wild regions represent a loss of irreplaceability in comparison with the cells outside of this priority.

For both Viperidae and Elapidae, the same global models for which a gain in irreplaceability was previously defined were also the most efficient ones in representing high proportion of complementary areas selected by solutions maximizing AET (i.e., 25% of cells in the AET cost solutions were represented in Endemic Bird Areas and

High-Biodiversity Wilderness Areas, see Table 2). Conversely, for the solution minimizing human influence, a highest percentage of cells were represented in Last of the Wild areas. This is expected given that Last of the Wild zones represent the least influenced areas of each biome across the world (Sanderson *et al.*, 2002). It is also important to note that, although the Last of the Wild areas comprise almost 30% of the cells from the HF lower cost solution for elapids, they also represented a loss of irreplaceability for this group given that the areas encompassed by this scheme have lower irreplaceably values.

DISCUSSION

In general, cells required to meet the goal of preserving at least 25% of each snake species' geographical range presented low irreplaceability values, although relatively highly irreplaceable areas were registered virtually in all continents. Moreover, it is important to consider that we did not include species from islands, many of which are endemic (e.g., Melanesian elapids). An increase of irreplaceability towards the areas encompassing these island endemics would likely be observed if they were included in the analyses (see Ferrier *et al.*, 2000), but the absence of island species do not prevent us from a comprehensive assessment of the conservation status of snakes across the continental mainland areas of the world.

The accelerated human development and the crescent demand for food production require the reconciliation of conflicts between areas of high values for biodiversity conservation and human needs (Margules & Pressey, 2000). Our analyses showed where it is possible to establish conservation priorities that represent the targets according to the established goals and, at the same time, minimize undesirable impacts caused by high human footprint. These networks give an initial picture of the most important areas to preserve viperid and elapid biodiversity in expectation of low conflicts between human development and conservation. However, our analyses also reveals that it may be problematic that few areas minimizing conflicts with human footprint were common to those areas of high environmental suitability. Also, when considering the nine global conservation schemes defined by Brooks *et al.* (2006), though around 30% of cells of the lowest human influence reserve networks are contained in Last of the Wild areas, these areas have low conservation value for both Viperidae and Elapidae as showed by the irreplaceability analyses (see Table 1).

On the other hand, a quarter of cells of the reserve networks with highest AET match with areas whose conservation value is high for both groups (e.g., Endemic Bird Areas and High-Biodiversity Wilderness Areas). It seems plausible, therefore, that conservation strategies to preserve viperid and elapid biodiversity are focused mainly in those areas of high environmental suitability despite not minimizing conservation-human development conflicts, given that areas with low potential conflicts have lower irreplaceability values. Anyway, it is still possible to find overlapping areas that satisfy both low conflicts (i.e., low human influence) and high AET. In practice, these areas are the most appropriate to implement conservation actions to warrant snake species preservation.

Efforts to identify conservation priorities at large scales have been criticized mainly because the priorities defined for some groups have failed to reflect diversity and rarity patterns for other groups (e.g., Mace, 2000; Rodriguez *et al*., 2004; Grenyer *et al*., 2006). It has been recommended, for instance, that conservation strategies should be developed with independent datasets from several taxa (Mace, 2000). It is clear that considerable results would be achieved if we were able to include the largest amount of biodiversity data as possible in these global priority analyses. The problem is that complete information on species distributions and other data in large scales are often scarce (Raven & Wilson, 1992; Lamoureux *et al*., 2006) and, in face of the dramatic loss of species, conservationists cannot afford waiting for comprehensive biodiversity data sets to be available (Balmford & Gaston, 1999; Bini *et al*., 2006). In this sense, the initiative of Brooks *et al*. (2006) is of great importance because it enables us to compare the effectiveness of the current global conservation systems in representing conservation strategies for others groups of organisms, as long as additional biodiversity datasets at broad scales become available. Also, the elucidation of proactive and reactive schemes can be used to interpret the level of threat for particular taxa, because if their most irreplaceable areas overlap with the reactive priorities, we can expect that they are under risk unless immediate conservation action is taken within these priorities (Brooks *et al*., 2006).

Our analyses showed that the priorities for which a gain in both irreplaceability and proportion of cells of the cost networks occurred were those designed as proactive. These findings are quite encouraging because they indicate the existence of viable conservation opportunities for these two snake groups. Viperids can benefit from the establishment of protected areas within the High-Biodiversity Wilderness Areas (e.g. Amazonia forest and African tropical forests) and Endemic Bird Areas (e.g., Brazilian

Atlantic forest). The latter is also important to preserve elapid biodiversity, as well as the areas encompassed by the Megadiversity Countries.

However, it is important to note that, at least for viperids, regions of high irreplaceability matched also with the reactive priorities, whose areas are highly threatened (i.e., Centers of Plant Diversity) and vulnerable (i.e., Biodiversity Hotspots) (see Brooks *et al*., 2006). This is problematic given that more than 70% of the primary habitat from Biodiversity Hotspots has already been lost (Myers *et al*., 2000), and several studies have shown that habitat destruction is a serious threat to viperid (e.g., Zamudio & Greene, 1997; Parkinson *et al*., 2001; Santos *et al*., 2006; Pleguezuelos *et al*., 2007) as well as elapid species (e.g., Shine & Fitzgerald, 1989; Terribile *et al*., 2007) throughout their ranges. It is important that more detailed data at population level (i.e., minimum viable population models and data on area available with suitable habitats within hotspots) are obtained, so that overall efficiency of reactive schemes is evaluated for these particular groups of organisms (see e.g., Reed & Shine, 2002).

Additionally, analogous to other groups of organisms (e.g., Hawkins *et al*., 2003b; Ceballos & Ehrlich, 2006; Buckley & Jetz, 2007), the peaks of Viperidae and Elapidae species richness occur at tropical regions (Terribile *et al*., *in press*; see also Pauwels *et al*., 2008), which are often the most threatened and poorest economically (Gaston, 2000, 2007; Brooks *et al*., 2006). Thus, conservation strategies even within those areas threatened by high human densities are still necessary to preserve natural areas and refuges in order to protect rare and endemic snake species.

Finally, the analyses performed in this study can be viewed as an alternative approach to the recent criticism concerning the independent development of several global conservation priorities by different non-governmental organizations, which have led to a considerable redundancy in the results and few effective actions (Mace, 2000; Fonseca, 2000). Instead of simply evaluating the match of diversity patterns to an unique scheme (e.g., hotspots) and identifying matching problems (Grenyer *et al.*, 2006), it is possible to compare the fit of different schemes, and understand the reasons behind this. In the long run, accumulation of these analyses may reveal which one is most adequate, in general or for a set of particular groups of organisms. Thus, more than simply determining priorities for snake's conservation, our analyses showed that the development of parallel priority-setting initiatives can be reconciled with those strategies for which financial resources are already being designed.

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Figure captions

Fig. 1. Global pattern of irreplaceability for Viperidae (a) and Elapidae (b).

Fig. 2. Spatial configuration of 110 x 110 cells chosen to represent the Viperidae (a) and Elapidae (b) biodiversity in a set with minimum human influence (red cells) and maximum AET (green cells). Black cells represent the ones that were chosen in both solutions. HF – human footprint; AET – actual evapotranspiration. Dashed lines separate biogeographical regions as described by Cox (2001): North American (NA), South American (SA), African (Afr), Eurasian (Eur), Oriental (Ori), and Australian (Aust).

Table 1. Number of 110 x 110 km cells of the reserve networks obtained with a cost of high actual evapotranspiration (AET) and low human footprint (HF) in each Cox's (2001) biogeographic region (see also Fig. 2). Values in parentheses represent the percentage of reserve network cells in each biogeographic region calculated from the total of cells analyzed for each group (i.e., 9563 for viperids and 9627 for elapids). AET+HF column represents the number of cells (and percentage) that are common in both reserve networks.

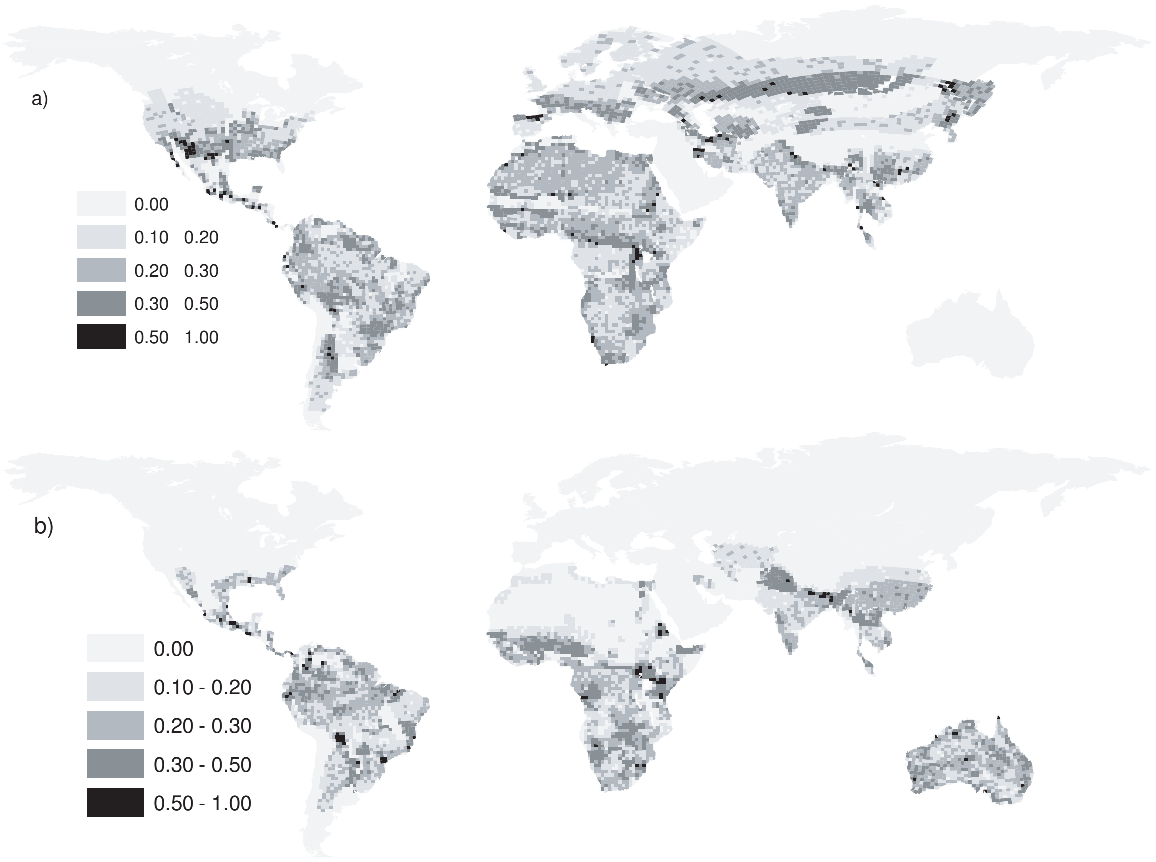
Biogeographic region/family (total cell number)	**Viperidae (9563)**			**Elapidae (9627)**		
	AET	HF	AET+HF	AET	HF	AET+HF
African	504 (21.3)	561 (23.7)	133 (5.6)	325 (13.7)	384 (16.2)	91 (3.8)
Australian	-	-	-	156 (25.0)	161 (25.8)	45 (7.2)
Eurasian	421 (12.0)	469 (13.4)	132 (3.7)	49 (1.4)	56 (1.6)	16 (0.4)
North American	134 (8.7)	137 (8.9)	48 (3.1)	29 (1.9)	32 (2.1)	8 (0.5)
Oriental	144 (24.5)	135 (22.9)	45 (7.6)	136 (23.1)	149 (25.3)	49 (8.3)
South American	324 (20.3)	336 (21.1)	100 (6.2)	291 (18.3)	307 (19.3)	86 (5.4)
Total	**1527 (15.9)**	**1638 (17.1)**	**458 (4.7)**	**986 (10.2)**	**1089 (11.3)**	**295 (3.0)**

Table 2. Values of adjusted mean irreplaceability (I_{aj}) from ANOVA calculated between 'groups' of cells coinciding (1) and not coinciding (0) with the areas of each global conservation priority scheme fitted within the conceptual framework of irreplaceability relative to vulnerability (see Brooks *et al.*, 2006). Proportional gains in irreplaceability for each family in each global conservation scheme were calculated as the difference between mean adjusted irreplaceability in 0 and 1 divided by the mean adjusted irreplaceability in 0. Cell percentages for cost solutions involving actual evapotranspiration (AET) and human footprint (HF) that match the areas covered by each of the nine global prioritization schemes are also given (Cell %) (see Methods). Bold underlined values represent those global schemes for which there was a gain in irreplaceability; bold values represent the global schemes that hold higher percentage of cells from the reserve networks with the lowest AET and the highest HF.

Global conservation priority scheme			I_{aj}		Proportional gain in irreplaceability	Cell %	
Scheme denomination & (abbreviation)	Scheme prioritization		1	0		AET	HF
	Irreplaceability	Vulnerability					
VIPERIDAE							
Biodiversity Hot-spots (BH)	high	high	0.233	0.221	0.054	22.4	20.4
Crisis Ecoregions (CE)	–	high	0.228	0.221	0.031	21.9	18.3
Centers of Plant Diversity (CPD)	high	–	0.237	0.221	0.072	23.5	22.3
Endemic Bird Areas (EBA)	high	–	0.238	0.219	**0.086**	23.8	22.6
Frontier Forests (FF)	–	low	0.229	0.223	0.026	24.0	29.3
Global 200 ecoregions (G200)	high	–	0.225	0.224	0.004	21.4	22.2
High-Biodiversity Wilderness Areas (HBWA)	high	low	0.241	0.221	**0.090**	**25.1**	25.7
Last of the Wild (LW)	–	low	0.227	0.223	0.017	21.3	**30.3**
Megadiversity Countries (MC)	high	–	0.231	0.219	0.054	22.3	21.4
ELAPIDAE							
Biodiversity Hot-spots (BH)	high	high	0.228	0.225	0.013	21.1	22.6
Crisis Ecoregions (CE)	–	high	0.228	0.224	0.017	21.1	20.0
Centers of Plant Diversity (CPD)	high	–	0.228	0.226	0.008	21.5	24.7
Endemic Bird Areas (EBA)	high	–	0.245	0.215	**0.139**	**25.0**	23.1
Frontier Forests (FF)	–	low	0.237	0.223	0.062	**25.0**	27.0
Global 200 ecoregions (G200)	high	–	0.228	0.222	0.027	21.0	23.5
High-Biodiversity Wilderness Areas (HBWA)	high	low	0.229	0.225	0.017	22.0	25.1
Last of the Wild (LW)	–	low	0.216	0.231	**-0.064**	20.7	**29.4**
Megadiversity Countries (MC)	high	–	0.234	0.214	**0.093**	22.7	22.5

Authors of global conservation priority schemes are as follows: BH, Myers *et al*. (2000); CE, Hoekstra *et al*. (2005); CPD, WWF-IUCN (1994–1997); EBA, Stattersfield *et al*. (1998); FF, Bryant *et al*. (1997); G200, Olson & Dinerstein (1998); HBWA, Mittermeier *et al*. (2003); LW, Sanderson *et al*. (2002); MC, Mittermeier *et al*. (1997).

Figure 1.


a)
0.00
0.10 0.20
0.20 0.30
0.30 0.50
0.50 1.00
b)
0.00
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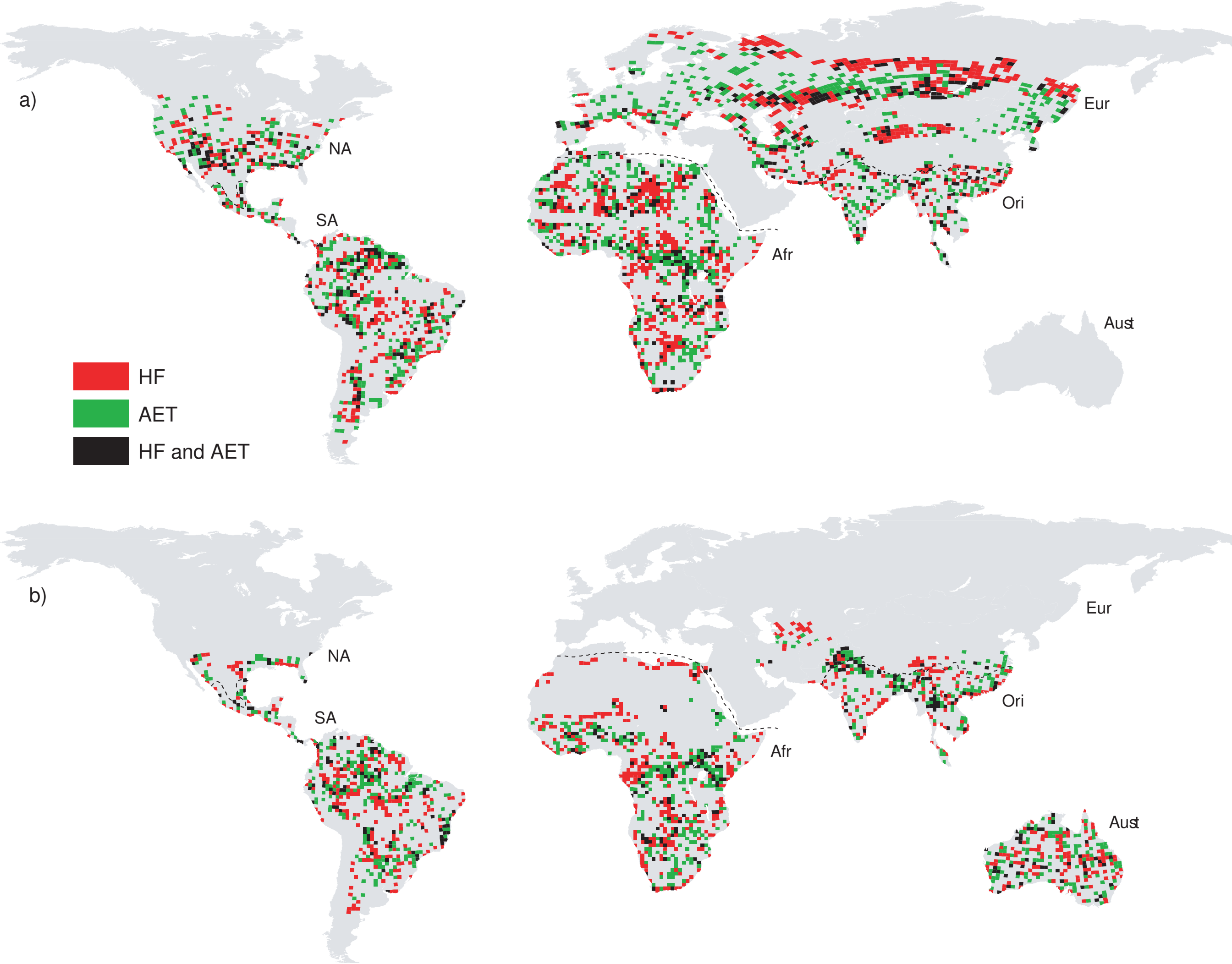
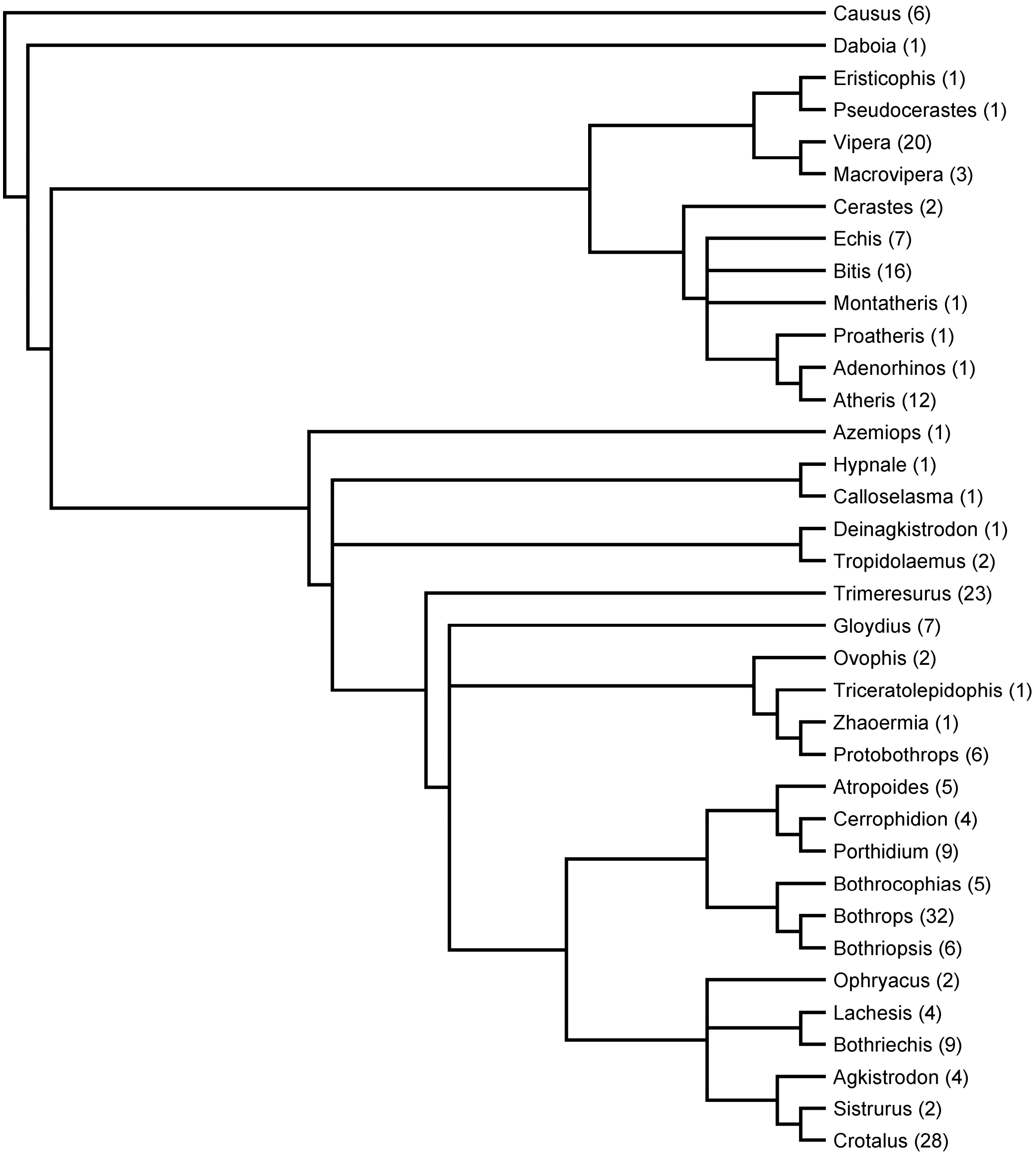
0.20 - 0.30
0.30 - 0.50
0.50 - 1.00

Figure 2.

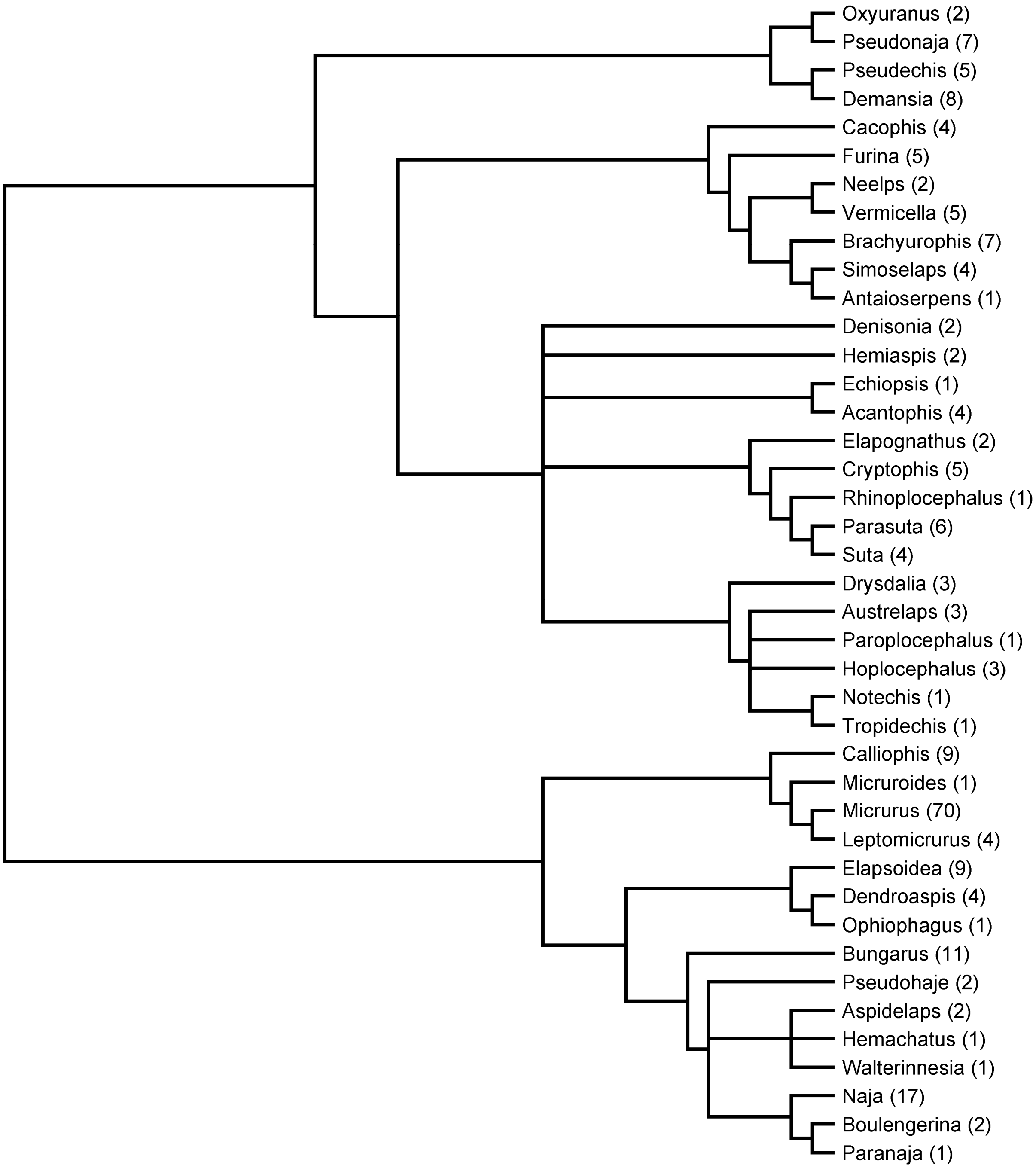


Apêndice 5. Filogenias dos gêneros de Viperidae (a) e Elapidae (b), e número de espécies (entre parênteses).

a)



b)



Oxyuranus (2)
Pseudonaja (7)
Pseudechis (5)
Demansia (8)
Cacophis (4)
Furina (5)
Neelps (2)
Vermicella (5)
Brachyurophis (7)
Simoselaps (4)
Antaioserpens (1)
Denisonia (2)
Hemiaspis (2)
Echiopsis (1)
Acantophis (4)
Elapognathus (2)
Cryptophis (5)
Rhinoplocephalus (1)
Parasuta (6)
Suta (4)
Drysdalia (3)
Austrelaps (3)
Paroplocephalus (1)
Hoplocephalus (3)
Notechis (1)
Tropidechis (1)
Calliophis (9)
Micruroides (1)
Micrurus (70)
Leptomicrurus (4)
Elapsoidea (9)
Dendroaspis (4)
Ophiophagus (1)
Bungarus (11)
Pseudohaje (2)
Aspidelaps (2)
Hemachatus (1)
Walterinnesia (1)
Naja (17)
Boulengerina (2)
Paranaja (1)

Apêndice 6. Matriz de correlação de Pearson entre as variáveis ambientais.

Variáveis	Temp	PREC	PET	AET	GVI	Elev	Inter
PREC	0.348						
PET	0.897	0.439					
AET	0.457	0.851	0.586				
GVI	0.296	0.741	0.395	0.868			
Elev	-0.224	0.032	-0.065	-0.026	-0.081		
Inter	0.641	0.308	0.651	0.361	0.197	0.565	
Sazonal	0.285	0.780	0.226	0.857	0.835	0.049	0.233

Temp – temperatura média anual; Prec – precipitação anual; PET – evapotranspiração potencial; AET – evapotranspiração atual; GVI – índice de vegetação global; Elev – variação topográfica; Inter – interação clima-topografia; Sazonal – sazonalidade.