

UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA

**AS FAUNAS DE SERPENTES DA AMÉRICA DO SUL E
AUSTRÁLIA: ECOLOGIA, BIOGEOGRAFIA E EVOLUÇÃO**

Davi Lima Pantoja



TESE DE DOUTORADO

Brasília – DF

2013

UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA

**As Faunas de Serpentes da América do Sul e Austrália: Ecologia,
Biogeografia e Evolução**

Davi Lima Pantoja

Orientador: Guarino Rinaldi Colli, Ph.D.

Tese apresentada ao Programa de
Pós-Graduação em Ecologia,
Instituto de Ciências Biológicas,
Universidade de Brasília, como
parte dos requisitos para a obtenção
do título de Doutor em Ecologia

Brasília – DF
2013



UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Tese de Doutorado


DAVI LIMA PANTOJA LEITE


Título:

“As Faunas de Serpentes da América do Sul e Austrália: Ecologia,
Biogeografia e Evolução”.

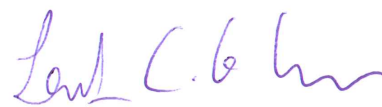
Banca Examinadora:


Prof. Dr. Ricardo Bonfim Machado
Presidente
ZOO/UnB


Prof. Dr. Ronaldo Fernandes
Membro Titular
UFRJ


Prof. Dr. Cristiano de Campos Nogueira
Membro Titular
USP


Profa. Dra. Lilian Gimenes Giugliano
Membro Titular
UnB


Prof. Dr. Ludgero Cardoso Galli Vieira
Membro Titular
FUP/UnB

Prof. Dr. Emerson Monteiro Vieira
Suplente
ECL/UnB

Brasília, 20 de dezembro de 2013.

À minha família

Agradecimentos

Agradeço a todos que direta ou indiretamente contribuíram para este trabalho, para minha formação, e para conclusão deste curso. Foram muitos anos de dedicação, muitos desafios, e muitas oportunidades de aprendizado. Não há como registrar minha gratidão em papel. Muitos agradecimentos já foram feitos pessoalmente, e tantos outros ainda serão, até que eu chegue a todos que estiveram comigo. Por ora agradeço especialmente:

À minha família, pelo apoio imenso, incondicional. Particularmente aos que conviveram em Brasília e compartilharam cada desafio, cada tropeço, cada descoberta, cada conquista e cada alegria, minha mãe Ana Cândida e meus irmãos Petra Raissa e João Álvaro.

À CAPES pelo suporte durante um ano e meio de bolsa doutoral no país, e um ano de Doutorado *Sanduiche* na University of Texas at Austin, USA (Processo BEX4911/10-05), através do Programa CAPES-UT e do projeto colaborativo ‘Evolução, Ecologia e Conservação da Herpetofauna do Cerrado’ (029/2008) coordenado pelos professores G. R. Colli (UnB), E. R. Pianka (UT).

Ao CNPq, pelo suporte durante um ano e meio de bolsa doutoral no país.

Ao Instituto de Ciências Biológicas da Universidade de Brasília, especialmente aos Diretores Sônia Bão e Jader Marinho-Filho, por viabilizarem a estrutura física de trabalho (*i.e.* sala, mesa, cadeira, e internet).

Ao Prof. Guarino R. Colli, pela orientação.

Ao Prof. Eric R. Pianka, pela co-orientação durante o estágio doutoral no exterior.

Ao Prof. David Cannatella (UT), pelo suporte durante o estágio doutoral no exterior.

Aos Profs. Frederico G. R. França, Gustavo, C. Vieira, e Daniel O. Mesquita, pelas contribuições conceituais e pelo suporte durante duas missões de estudos na Universidade Federal da Paraíba, João Pessoa.

Aos Profs. Cristiano C. Nogueira, Ronaldo Fernandes, Lilian G. Giugliano, Ludgero C. G. Vieira e Ricardo B. Machado, membros da banca examinadora, pela disponibilidade, críticas e contribuições.

Aos Profs. Cristiano C. Nogueira, Mário Almeida-Neto, Ronaldo Fernandes, e Ricardo B. Machado, pelas críticas durante o exame de qualificação, pelo material bibliográfico concedido, e apoio para o desenvolvimento do projeto.

Ao Prof. Luke R. Harmon, pelo suporte e sugestões durante visita técnica à University of Idaho, Moscow, USA.

À Dr^a. Alison M. Gainsbury, pela revisão do texto em inglês.

À Dr^a. Fernanda P. Werneck, pela revisão do capítulo 1.

À Silvia Rodrigues, pelo auxílio na compilação de dados.

Aos Profs. Ricardo B. Machado, Yuri Salmons e ao Dr. Pedro P. U. Aquino, pelo auxílio com mapas (capítulo 3).

À Dr^a. Ana Hermínia S. Bello, pelo auxílio na preparação da apresentação oral.

À todos os colegas do Laboratório de Herpetologia e do curso de Ecologia, pelas trocas de experiência.

A jornada para o doutoramento requer muitos mergulhos solitários, mas sempre há oportunidade para parceria. Lembro especialmente daqueles cuja amizade me trouxe força para enfrentar o que fosse preciso:

Isis Arantes, Pedro de Aquino, Cristiano Nogueira, Verônica Novaes, Tânia Queiroz, Bernardo Costa, Josué Anderson Azevedo, Roger Ledo, Guth Berger Falcon, Almir de Paula, André Barreto-Lima, Fernanda Werneck, Ana Hermínia Bello, Renan Bosque e Marcella Santos do Laboratório de Herpetologia da UnB;

Carlos Eduardo (Caê) Marinelli, Klécia Massi, Érica Barleto e Daniella Frensel do Programa de Pós-Graduação em Ecologia da UnB;

Fábio Borges e demais amigos da Associação dos Pós-Graduandos da UnB (APG), com os quais militamos arduamente por uma universidade melhor;

Frederico França, amigo de muitas vivências, pelas inúmeras contribuições, pelos ensinamentos, disponibilidade, apoio, incentivo, oportunidades, e grande generosidade.

Mariana Vasconcellos, Pamela Sertzen, Andrea Cavalcante, Renata Ponte, Alison Gainsbury, Stephen Goodyear, Jeanine Abrams, Sofia Rodriguez, Patricia Salerno, Carlos Guarnizo, Monica Guerra, André França, Bruno Marinone, e todos os “Gente Boa”, amigos em Austin que me apoiaram durante o *sanduíche*;

Maria do Carmo, Dom, Carlois e toda família Campelo, Darlan, Luiz Gustavo e demais amigos de Brasília, por terem viabilizado a chegada em Brasília, e por todo apoio desde então.

À lua do céu.

Sumário

The idea	1
Introdução	2
Material e métodos	7
Capítulo 1.....	13
Capítulo 2.....	15
Capítulo 3.....	16
Discussão	18
Referências bibliográficas	31
APÊNDICE 1. On the South America and Australia Connections: A Framework for Biological Comparisons	41
Abstract.....	42
Resumo	43
1. Introduction	44
2. Palaeogeography and Palaeoclimates: a general history of continental motion and its climatic and biogeographic consequences.....	51
3. Current features: present landscapes, environments, and biogeographic provinces.....	63
4. Conclusion.....	70
5. Acknowledgements	71
6. References	71
7. Legend of Figures.....	91
APÊNDICE 2. Biological Comparisons between South America and Australia: The State of the Art.....	97
Introduction	98
Shared biota	98
Comparative studies	100
Summary of comparative hypotheses on the biota formations ..	119
Acknowledgements	123
References	123
APÊNDICE 3. The Assembly of Continental Snake Faunas: A Comparative Study between South America and Australia	138
INTRODUCTION.....	140
METHODS.....	144

RESULTS.....	151
DISCUSSION.....	158
CONCLUSION	173
ACKNOWLEDGEMENTS	174
REFERENCES	175
LEGEND OF FIGURES	196
SUPPOTING INFORMATION	202
Appendix S1a. Check list of inland South American snakes	202
Appendix S1b. Check list of inland Australian snakes	215
Appendix S2 – Taxonomy and Systematic	219
Appendix S3a (South America).....	225
Appendix S3b (Australia).....	228
Appendix S4a	230
Appendix S4b	231
Appendix S5a	233
Appendix S5b	235
Appendix S6a	236
Appendix S6b	241
Appendix S6c	244
Appendix S7a	245
Appendix S7b	248
Appendix S7c	250

THE IDEA

Present day characteristics of species and community structure are a consequence of historical-biogeographic events, past ecological relationships, and phylogenetic constraints, molded in response to present ecological interactions. A major challenge to explain traits of extant species and communities is to find a bridge between community ecology and biogeography. Intercontinental comparisons can be used as a pseudo-experiment to interpret how community ecology and biogeography interact in developing the structure of present communities. Both South America and Australia are similar in many ways, such as Gondwanan origin, present latitudes, general landscapes and ecosystems, among others. For instance, the South American Cerrado and Arid Australia are mostly covered by grassland and bush vegetation, very dry periods, poor, acidic, and aluminum-rich soils, frequent disturbance caused by fires, and abundant and diverse faunas of lizards and termites. Besides obvious particularities also observed in the extant biota of each continent, shared lineages and convergences may account for similarities between biotas. Lizards have been exploited in such intercontinental comparisons. Here I raise the following questions, by comparing snake faunas from both regions: are there recognizable morphological or ecological patterns for forested versus arid/savanna ecoregions? Do species and/or communities converge? Why were some lineages more successful in one continent than in the other? Does regional diversity affect local diversity in the same way in both continents? What is the relative importance of contemporary, historical, local, and regional processes in shaping community attributes?

INTRODUÇÃO

Semelhanças entre organismos podem ser consequências de sua proximidade filogenética (grau de parentesco) ou devido a evolução convergente. A evolução convergente entre organismos de diferentes áreas geográficas surge como uma resposta evolutiva às características físicas similares dos ambientes (i.e., forças seletivas similares devido a condições e disponibilidade de recursos similares) e interações biológicas que promovem padrões semelhantes de coevolução (Orians e Paine, 1983). Exemplos de convergência e paralelismo entre espécies são abundantes e bem conhecidos (e.g. Cody e Mooney, 1978; Chirat *et al.*, 2013; Archer *et al.*, 2011), mas não está claro se este fenômeno ocorre com frequência suficiente para induzir as comunidades a convergir (e.g. Lomolino, 1993; Kelt *et al.*, 1999). De fato, independente de semelhanças entre pares de espécies, a co-evolução em grupos independentes de espécies podem levá-los a desenvolver organizações e funções similares (Orians e Paine, 1983).

Para a maioria dos estudos disponíveis a expectativa tradicional de que ambientes similares contenham comunidades similares possui pouco suporte (Pianka, 1986; Schluter e Ricklefs, 1993b; Schluter e Ricklefs, 1993a), especialmente quando as comunidades compartilham pouco sua história. No entanto, fortes evidências sugerem a existência de convergências na estrutura das comunidades, incluindo a diversidade de espécies, características morfológicas e comportamentais, mesmo quando as características atuais das comunidades são oriundas de diferentes processos históricos (e.g. MacArthur *et al.*, 1962; Mooney, 1977; Orians e Solbrig, 1977; Losos *et al.*, 1998; Melville *et al.*, 2006; Fuentes, 1976; Stephens e Wiens, 2004; Winemiller *et al.*, 1995; Schluter e Ricklefs, 1993a; Simon *et al.*, 2009). A falta de consenso dos resultados dos testes de convergência no nível das comunidades revela a nossa

compreensão ainda pobre sobre os padrões macroecológicos de evolução das comunidades, abordagens inadequadas, ou simplesmente a falta de um padrão natural.

Características atuais das espécies e das comunidades são consequências de eventos histórico-biogeográficos, relações ecológicas do pretérito e restrições filogenéticas, moldadas pelas interações ecológicas atuais (Connell, 1980; Losos, 1996). Espécies relacionadas não são unidades evolutivas verdadeiramente independentes, dessa forma, as semelhanças atuais entre seus atributos não são evidências puras de processos recentes de seleção (Harvey e Pagel, 1998). Da mesma forma, a ausência de semelhanças não podem ser facilmente interpretada como consequência de fatores locais ou contemporâneos. Por exemplo, diferentes conjuntos de categorias tróficas podem ocorrer em comunidades de serpentes que ocupam habitats semelhantes, o que é explicado pelas restrições filogenéticas e biogeográficas das linhagens que compõem cada comunidade (Cadle e Greene, 1993). Estudos com os squamatas demonstraram que as características morfológicas e comportamentais podem permitir que algumas espécies explorem certos recursos atualmente disponíveis, mas os atributos das espécies têm raízes profundas na filogenia e portanto transcendem as comunidades atuais (Cadle e Greene, 1993; Vitt e Pianka, 2005; Colston *et al.*, 2010; Losos, 1994). Dessa forma, as comparações entre as comunidades modernas devem levar em conta as histórias filogenéticas e biogeográficas das linhagens que as compõem (Ricklefs, 2008; Webb *et al.*, 2002).

Comparações intercontinentais podem ser usadas como um experimento “natural” para interpretar como a ecologia de comunidades e a biogeografia interagem no desenvolvimento da estrutura das comunidades atuais. América do Sul e Austrália estão no hemisfério sul e apresentam semelhanças na estrutura geral do clima e ambientes existentes (veja Apêndice 1, Pantoja, *in review*). Os limites latitudinais

australianos se sobrepõem com a área core da América do Sul, e ambos são úmidos ao norte (tropical) e ao sul (temperado), preenchidos por regiões mais secas que podem agir como barreira para dispersão de algumas espécies (Nix, 1981; Haffer, 1987). A costa oriental de ambos os continentes é mais úmida do que o interior, e presumivelmente funciona como um corredor (Norte-Sul) para algumas espécies intolerantes à seca (Guedes *et al.*, 2011). Eles desenvolveram densas florestas em latitudes mais baixas, manguezais em regiões costeiras tropicais e grandes fisionomias abertas cobrem a maior parte do continente através das regiões centro-sul (Specht, 1981; Brown e Prance, 1987; Werneck, 2011). No entanto, a proporção de áreas florestais na América do Sul é maior do que na Austrália. As paisagens abertas e secas que cobrem a maior parte do continente australiano compartilham algumas características com Patagônia, Caatinga, e Cerrado, os maiores domínios de vegetação aberta da América do Sul. Embora não sejam propriamente desertos, tal qual na Austrália árida estes domínios vegetacionais sulamericanos são savânicos, na sua maioria cobertos por pastagens e vegetação arbustiva, e passam anualmente por períodos muito secos. O Cerrado em particular, se assemelha ainda por também possuir solos pobres em nutrientes, ácidos e ricos em alumínio, frequentes queimadas naturais, e faunas abundantes e diversificadas de lagartos e cupins (Colli *et al.*, 2006; Oliveira e Marquis, 2002; Pianka, 1989; Morton *et al.*, 2011). Essas características compartilhadas somado à longa independência entre os continentes no desenvolvimento de suas biotas tornam oportuna uma abordagem comparativa (Pantoja, *in review*; Pantoja, in prep. / consulte o Capítulo 1 e 2), e tem dado suporte a estudos utilizando vertebrados e invertebrados (e.g. Costa *et al.*, 2008a; Campos *et al.*, 2011; Costa *et al.*, 2013; Keast *et al.*, 1972).

Eventos biogeográficos semelhantes marcaram profundamente as biotas da América do Sul e Austrália (Apêndice 1, Pantoja, *in review*; Keast, 1971), e foram fundamentais na formação das características de suas herpetofaunas (Colli, 2005; Duellman, 1979; Tyler, 1979). Estes incluem: (1) origem comum no Gondwana (Mesozóico) (Sanmartín e Ronquist, 2004); (2) longo período de isolamento, durante a maior parte do Terciário, promovendo o desenvolvimento de um grande número de linhagens endêmicas (Westoby, 1988, Simpson, 1980); (3) aproximação e colisão contra continentes ao norte, permitindo a invasão e colonização de novos elementos bióticos, que iniciaram um novo universo de interações dentro das comunidades e promoveram extinção de elementos nativos (van Oosterzee, 1997; Stehli e Webb, 1985); (4) transgressões marinhas que promovem especiações vicariantes (Webb, 1995; McLoughlin e Kear, 2010); e (5) sucessivos ciclos climáticos, associados aos períodos glaciais e inter-glaciais, que promoveram especiação devido aos repetidos isolamentos e re-conexões de populações em refúgios (em áreas florestais nos períodos frios e secos, e áreas abertas nos períodos quentes e úmidos) (Brown e Ab'Sáber, 1979; Moritz *et al.*, 2009). Estes eventos históricos compartilhados afetam as comunidades biológicas influenciando a distribuição e diversificação das espécies, e a montagem das comunidades. Porque as respostas aos eventos biogeográficos são normalmente táxon-específicas, comunidades independentes provavelmente reagem distintamente aos mesmo tipo de evento histórico, no entanto, teoricamente, eles experimentaram influências potenciais semelhantes, o que é útil para compreender como as comunidades alcançaram suas características atuais.

As Serpentes formam um grupo monofilético dentro de Squamata e devido a plasticidade de suas características (tamanho do corpo, habitat, hábitos, alimentação, etc.) são um excelente modelo para estudos ecológicos (Mullin e Seigel, 2009; Shine

e Bonnet, 2000; Sites *et al.*, 2011). Como indicado acima, filogenia e biogeografia são componentes importantes de estudos sobre ecologia comparativa das comunidades (Brooks e McLennan, 1993; Moen *et al.*, 2009; Wiens, 2004), e têm sido amplamente aplicada na pesquisa com Squamata (e.g. Cadle e Greene, 1993; Colli, 2005). Os lagartos já foram usados comparando América do Sul e Austrália (Costa *et al.*, 2013; Pantoja *et al.*, in prep.; Costa *et al.*, 2008b; Costa *et al.*, 2008a; Colli *et al.*, 2006). Neste trabalho eu proponho comparar ambos os continentes usando Serpentes um clado avançado de Squamata. Apesar dos exemplos clássicos de convergência entre espécies de serpentes da América do Sul e Austrália (e.g. Shine, 1980; Shine, 1991; Greene, 1997) também existem diferenças marcantes, no entanto a característica e intensidade das similaridades e diferenças na estrutura organização das faunas ainda é desconhecida.

Neste trabalho investiga-se a existência de convergências entre as faunas de serpentes sul-americana e australiana, considerando que os atributos da comunidade são formados por processos históricos, contemporâneos, regionais e locais, e que ambientes similares oferecem forças seletivas similares. Convergências comunitárias têm sido tradicionalmente avaliada com base no fluxo de energia e materiais, estrutura física, e riqueza de espécies (Orians e Paine, 1983; Schluter e Ricklefs, 1993a). Eu utilizo a riqueza e densidade de espécies, história natural, tamanho do corpo, e filogenia para descrever faunas continentais, e testo a hipótese geral de que habitats de diferentes continentes com estruturas semelhantes (habitats fechados/florestais ou abertos/não-florestal) afetam similarmente a ecologia e evolução das faunas de serpentes. Além disso, se essas faunas convergem, suas comunidades (i.e. taxocenoses) de serpentes devem apresentar guildas ecológicas similares e proporções similares de espécies ocupando essas guildas. Globalmente,

espero que a estrutura da fauna em cada continente seja coerente com a proporção de habitats fechados e abertos, ou seja, América do Sul deve apresentar uma maior proporção de espécies ecologicamente e filogeneticamente associadas aos habitats fechados, enquanto o inverso deve ocorrer na Austrália com relação aos habitats abertos.

MATERIAL E MÉTODOS

Dados

O estudo abrange toda América do Sul e Austrália, excetuando-se as espécies de serpentes endêmicas dos territórios insulares associados, espécies marinhas ou exóticas. O conjunto de dados primários é uma compilação dos registros publicados de serpentes para América do Sul e Austrália, contendo uma lista de todas as espécies não-marinhas já descritas e com ocorrência conhecida em cada continente. A história natural de cada espécie foi descrita em seis dimensões biológicas, decompostas em 29 atributos biológicos, a partir de dados publicados e nossa própria experiência na América do Sul. 1) Habitat – refere-se à estrutura do habitat utilizado pelas pela espécie: habitat aberto (Op) inclui qualquer formação vegetacional estruturalmente aberta tais como savanas e desertos; habitat fechado (Cl) inclui apenas florestas efetivamente fechadas tais como florestas tropicais, matas de galeria, florestas temperadas úmidas, etc.; e ambos os habitats (Bo) para espécies cuja ocorrência inclui tanto ambientes fechados e abertos. 2) Hábito – refere-se à forma mais comum que uma determinada espécie utiliza para explorar espacialmente seu ambiente, também conhecido como uso do microhabitat: aquático (aq); semiaquático (saq); estritamente fossorial (fo); criptozóica+fossorial (cfo); estritamente criptozóica (cr); criptozóica+terrestre (cte); terrestre (te); semiarborícola (sar) e arborícola (ar). 3)

Período de atividade – refere-se ao principal período de atividade da espécie: diurno (D); noturno (N), e ambos os períodos (DN). 4) Reprodução – ovípara (O); vivípara (V), e ambas as estratégias reprodutivas (OV). 5) Dieta – inclui presas que correspondem aproximadamente a mais de 30 % da dieta das espécies: mamíferos (mam); aves (bir), répteis (rep); anfíbios (amp); peixes (fis), artrópodes (art) incluindo oncoforas, e invertebrados de corpo mole (goo) uma classe formada basicamente por minhocas e moluscos. 6) Comprimento do corpo – refere-se ao comprimento máximo total do corpo, da ponta do focinho à ponta da cauda, categorizado como: curto (S), até 500 mm; médio (M), entre 500 e 1000 mm; longo (L), entre 1000 e 2000 mm; e muito longo (VL), mais de 2000 mm.

As áreas continentais cobertas por habitats abertos ou fechados foram estimados e localizadas usando os dados do Global Land Cover Facility (<http://www.landcover.org/data/vcf/>). As imagens foram capturadas no ano 2000 pelo sensor MODIS a bordo do satélite Terra, da NASA, com 250 m de resolução espacial (DiMiceli *et al.*, 2011), e combinadas com as ferramentas Modis Reprojection Tools (http://gcmd.nasa.gov/records/MODIS_Reprojection_Tool.html). Pixels com índices de cobertura de vegetação menores de 60 foram usados pra identificar áreas com vegetação não-florestal, assumidos como habitat aberto; habitat fechados (florestas) corresponderam aos índices de 60 a 100. Áreas de interesse foram calculadas após vetorialização em projeção cilíndrica para o mundo, utilizando o ArcGIS.

Além da riqueza continental de espécies também utilizei a riqueza de espécies em habitats abertos e fechados como medidas de diversidade regional. A diversidade local média para cada tipo de habitat em cada continente foi calculado utilizando cinco localidades florestais e seis localidades em ambientes abertos, em cada continente. As localidades sulamericanas utilizadas estão posicionadas entre as

latitudes 03° e 24°S (florestas fechadas), e entre 07° e 24°S (habitats abertos), enquanto que na Austrália entre 12° e 20°S, e 17° e 28°S respectivamente.

Análises

Estrutura taxonômica

A estrutura taxonômica de cada fauna continental foi descrita com base no número de espécies e gêneros por família e clado superior, e pela dominância taxonômica entre clados dada em porcentagem. As diferenças entre dominâncias em cada continente foram avaliadas por “testes binomiais para comparar duas proporções”, com um nível de significância de 0,05. Este teste responde se a porcentagem de espécies em um determinado clado em um continente diferente da porcentagem de espécies no mesmo clado em outro continente, ou ainda, se este tipo de diferença pode surgir aleatoriamente (Crawley, 2007, p.301). Para controlar parcialmente o efeito de área eu também comparei as faunas com base na densidade (número de táxons por 1.000.000 km²).

Estrutura biológica

As estruturas biológicas foram descritas com base no número e proporção de espécies com cada atributo biológico. A representatividade da amostra para cada dimensão biológica foi avaliada pela porcentagem de espécies para as quais foram obtidos dados. Diferenças entre continentes foram testadas por meio de testes binomiais para comparação de proporções (Crawley, 2007). Guildas ecológicas em cada fauna foram reconhecidos através de métodos de agrupamento (UPGMA) com base em uma matriz de dissimilaridade de Jaccard. A entrada de dados foram matrizes de presença/ausência com os atributos biológicos nas colunas e as espécies como

linhas, apenas incluindo espécies para as quais todas as variáveis biológicas estavam disponíveis. Apesar de parcialmente restringir o conjunto de dados, estas análises foram baseadas em 337 espécies da América do Sul e 156 da Austrália, o que representa mais de 84% e 97 % da riqueza continental de gêneros respectivamente. A matriz de distancia foi calculada utilizando a função “vegdist” e para o agrupamento hierárquico “hclust”, ambos implementados pelo pacote “vegan” (Oksanen *et al.*, 2013) no ambiente estatístico R (R Core Team, 2013).

Guildas de espécies biologicamente similares foram sugeridas a partir do limite 0,70 de distância cofenética máxima dentro dos grupos de espécies. A contribuição relativa de cada atributo biológico foi dada pelos “valores indicadores” para cada atributo biológico em cada guilda (algoritmo indval, implementado pelo pacote “labdsv” Roberts, 2013; Dufrene e Legendre, 1997). Valores indicadores significativos foram utilizados para definir o perfil de cada guilda. A dominância entre guildas ecológicas em cada fauna de serpentes foi avaliada com base no percentual de espécies em cada guilda. Posteriormente, eu utilizei o mesmo método para verificar se há semelhanças qualitativas entre guildas ecológicas de diferentes continentes, tendo a matriz de valores indicadores como entrada de dados, com guildas de ambos os continentes como as linhas. Convergências faunísticas foram avaliadas com base no número de pares agrupados de guildas de diferentes continentes, e testando as diferenças entre as proporções de espécies dentro de pares de guildas.

Estrutura filogenética

As análises filogenéticas foram baseadas na mais completa hipótese molecular para os Squamata (ver Pyron *et al.*, 2013), contendo 235 espécies de serpentes não

marinhas da América do Sul e 82 da Austrália. Essa amostra representa cerca de 77% dos gêneros sulamericanos e 90% dos australianos. Para obter uma medida de história evolutiva eu calculei a diversidade filogenética (PD) pela soma de todos os comprimentos dos ramos da árvore filogenética da raiz aos ramos terminais em cada continente (Faith, 1992). A significância dos PD observados foram determinadas pela comparações com os valores de PD estimados por modelos nulos com base em 999 permutações utilizando as 1262 espécies de serpentes presentes na árvore de Pyron et al. (2013) (algoritmo *taxa.labels*, implementado pelo pacote “picante” Kembel *et al.*, 2010). Valores médios de PD foram padronizados para valores de Z e as faunas foram consideradas mais ou menos diversificadas do que o esperado ao acaso quando os valores eram maiores ou menores do que 1,96 e -1,96 respectivamente (Cavender-Bares *et al.*, 2004). A PD foi comparada entre faunas controlando-se o efeito da riqueza de espécies (Nipperess e Matsen, 2013) rarefazendo-se os valores de PD da fauna mais rica e comparando a PD média correspondente à mesma riqueza de espécies da fauna mais pobre, por meio do teste Z (sensu Gotelli e Colwell, 2001). Os modelos nulos foram gerados por 1000 iterações, sem reposição, com base no algoritmo *phylocurve.perm*, implementado pelo pacote de “ape” (R Core Team, 2013). Os mesmos procedimentos foram utilizados para comparar a PD e estrutura filogenética entre habitats abertos e fechados em ambos os continentes.

Diversidade de espécies

A riqueza local de espécies de cada continente foram comparadas pelo teste de Wilcoxon (Crawley, 2007, p.297). Diferenças entre riquezas locais de habitats fechados e abertos foram testadas por meio de comparações usando testes t pareados e valores de p ajustados pelo método de “holm” (Crawley, 2007, p.482). A relação

entre diversidades locais e regionais foi avaliada por uma adequação do método adotado por Westoby (1993). O comportamento desta relação é representado graficamente pela projeção da média das riquezas locais e da riqueza regional em um plano cartesiano log-espécies versus log-área, onde a inclinação da reta que une a riqueza local à regional é a “diferenciação de diversidade” (conforme Whittaker, 1977), e que por sua vez, trata-se de uma medida da substituição de espécies ao longo dos habitats (diversidade beta) e gradientes geográficos (diversidade delta) (Cody, 1993). Diversidades locais ou taxas de diferenciação de diversidade similares entre continentes foram tomado como evidência de convergência entre faunas. Três filtros foram utilizados para comparar continentes: entre as faunas totais, entre habitats fechados e entre habitats abertos. A riqueza de espécies que ocorrem em habitats fechados e habitats abertos foram tomadas como as medidas de diversidade regional.

CAPÍTULO 1

Sobre a conexão entre América do Sul e Austrália: um alicerce para comparações biológicas

Este capítulo avalia comparativamente os cenários físicos e ecológicos em que se formaram as comunidades biológicas da América do Sul e Austrália, e reúne os alicerces teóricos para comparações biológicas entre estes continentes: (1) fornecendo uma lista da bibliografia básica; (2) descrevendo a história geográfica e climática de ambos os continentes e seus ambientes atuais; e (3) destacando os elementos que dão suporte às comparações biológicas entre América do Sul e Austrália. A estrutura das biotas atuais é consequência de eventos histórico-biogeográficos, das relações ecológicas pretéritas, e das restrições filogenéticas de suas linhagens, que por fim, são moldadas pelas interações ecológicas atuais. Continentes com longo tempo de isolamento evoluem biotas sob significativa independência, funcionando como um experimento “natural” de longo prazo, útil para interpretar como ecologia de comunidades e biogeografia interagem no desenvolvimento das biotas atuais. América do Sul e Austrália se desmembraram de sua origem comum em Gondwana a mais de 30 milhões de anos atrás, e no presente são semelhantes em muitos aspectos, incluindo latitudes, e paisagens geral de seus ambientes. Ambos continentes são predominantemente cobertos por habitats estruturalmente abertos. Por exemplo, o Cerrado sulamericano e os desertos australianos são na sua maioria cobertos por pastagens e vegetação arbustiva, possuem períodos muito secos, solos pobres, ácidos e ricos em alumínio, frequentemente perturbados por incêndios, habitados faunas ricas e abundantes de lagartos e cupins. Além particularidades óbvias observados na

biota atual de cada continente, similaridade entre biotas podem ser atribuídas a presença de linhagens compartilhadas e convergências. Os cenários históricos e contemporâneos da América do Sul e Austrália, incluindo um conjunto de semelhanças entre os ambientes atuais, dão suporte às comparações biológicas entre estes continentes.

O presente capítulo sintetizado no parágrafo acima foi redigido durante o Doutorado Sanduíche realizado na University of Texas at Austin (UT), EUA, durante o ano de 2011, e submetido para a revista *Biota Neotropica* em dezembro de 2013, sob o título “On the South America and Australia connections: a framework for biological comparisons”. O manuscrito encontra-se anexo, como Apêndice 1.

CAPÍTULO 2

Comparações biológicas entre América do Sul e Austrália: o estado da arte

Eu listei 35 estudos comparando diretamente organismos da América do Sul e Austrália. Os estudos focados primariamente na taxonomia e/ou sistemática não foram incluídos. Independente do número de linhagens compartilhadas entre continentes, a maior parte dos estudos comparativos utilizaram somente vertebrados como organismos modelo, representando mais da metade dos estudos. A maior parte dos demais estudos incluem invertebrados. Publicações comparando ecossistemas, plantas, ou microorganismos são menos frequentes. A maior parte dos estudos disponíveis abordam as relações biológicas entre continentes com base na ecologia (15) principalmente comparando os parâmetros comunitários (9). Oito publicações são primariamente focados em discussões biogeográficas, predominantemente utilizando animais (5). Estudos comparando faunas inteiras (10) ou floras (2) são particularmente relevantes para as comparações intercontinentais. Embora utilizem uma escala menos detalhada, estes estudos geralmente discutem a interação entre ecologia e biogeografia, e comparam conjuntos grandes de organismos sob uma escala geográfica mais ampla.

O presente capítulo sintetizado no parágrafo acima foi parcialmente redigido durante o Doutorado Sanduíche realizado na University of Texas at Austin (UT), EUA, durante o ano de 2011. O texto completo preparado como artigo encontra-se anexo (Apêndice 2) sob o título “Biological comparisons between South America and Australia: the state of the art”.

CAPÍTULO 3

A formação das faunas continentais de serpentes: um estudo comparativo entre América do Sul e Austrália

Descrevi e comparei as faunas de serpentes da América do Sul e Austrália utilizando a diversidade de espécies, história natural, tamanho do corpo e filogenia. Interpretei a estrutura e formação faunística com base em processos históricos, contemporâneos, regionais e locais, e avaliei as convergências faunísticas comparando a estruturas taxonômica, biológica, filogenética e a diversidade em escala continental. A estrutura faunística encontrada em cada continente é coerente com a sua proporção de habitats florestais/fechados e abertos, com América do Sul apresentando maior proporção de espécies ecologicamente e filogeneticamente associadas a ambientes fechados, e o inverso na Austrália com habitats abertos. Encontrei convergências em vários aspectos, embora diferenças marcantes também existam. América do Sul e Austrália apresentam proporção similar de espécies para vários atributos biológicos, e ambas as faunas são caracterizadas por um maior número de espécies terrestres, noturnas, ovíparas, que se alimentam de répteis, com comprimento do corpo curto ou médio. Para cada uma das principais guildas ecológicas sugeridas para Austrália há uma guilda semelhante na América do Sul. No entanto, a proporção de espécies em cada guilda varia consideravelmente. A estrutura do habitat tem um efeito significativo sobre a história natural das serpentes, com habitats fechados proporcionando maior diversidade de espécies do que habitat abertos. As diversidades locais refletem a diversidade regional semelhante em ambos os continentes, o que sugere um forte efeito histórico sobre a formação da diversidade

faunística observada, com resultados convergentes na escala continental. A maior “taxa de diferenciação diversidade” em habitats abertos australianos provavelmente equilibra o forte efeito de habitats fechados na América do Sul, permitindo a diversidade de espécies a convergir. Entre as diferenças faunísticas, as características ecológicas consistentemente associadas às linhagens mais diversificadas definem em grande parte as principais características de cada fauna, e são fortemente relacionadas com a maior proporção de habitats fechados ou abertos em cada continente. A maior diversidade de serpentes na América do Sul provavelmente reflete uma combinação de: maior área continental, extensão latitudinal, área dentro dos trópicos, proporção de áreas florestais, e a faixa altitudinal; maior pluviosidade; paisagem, clima e vegetação mais diversificados; mais oportunidades para “duplicação de faunas” em ambientes similares mas isolados; história mais antiga; maior estoque de linhagens autóctones; e colonização imigrante mais forte do que a Austrália. Como esperado, as faunas de serpentes da América do Sul e Austrália não são completamente convergentes ou completamente distintas.

O presente capítulo sintetizado no parágrafo acima é a principal contribuição desta tese. O texto completo preparado como artigo encontra-se anexo (Apêndice 3) sob o título “The assembly of continental snake faunas: a comparative study between South America and Australia”.

DISCUSSÃO

América do Sul tem maior riqueza do que a Austrália, em todos os níveis taxonômicos de Serpentes. A maior riqueza de espécies na América do Sul é explicada principalmente pelo efeito área, já que a América do Sul é mais de duas vezes maior do que a Austrália. No entanto, o tamanho da área *per se* não explica completamente as diferenças. América do Sul tem quase cinco vezes mais espécies do que Austrália, mas apenas duas vezes a densidade de espécies. Isto corrobora a maior riqueza de espécies na América do Sul controlando parcialmente o efeito direto de área. A menor diferença entre as densidades continentais de espécies do que entre as riquezas de espécies pode ser explicado pela presença de grandes áreas da América do Sul com pouca ou nenhuma ocorrência de serpentes. Poucas espécies podem sobreviver às altas e frias latitudes e altitudes disponíveis na América do Sul. Por exemplo, *Micrurus pyrhocryptus* é o elapideo mais meridional da América do Sul, chegando a 35°S (Roze, 1996) e nenhuma serpente ocorre mais ao sul do que o víperídeo *Bothrops ammodytoides*, chegando a 47°S (Carrasco *et al.*, 2010; Greene, 1997). América do Sul atinge sua extremidade cerca de 53°S, enquanto que o ponto mais meridional da Austrália está localizada a 39°S, quase 15° a menos. A riqueza de espécies de serpente diminui com a latitude em ambos os continentes, embora os padrões variam entre linhagens (Cadle e Greene, 1993; Shine, 1991; Darlington, 1965, p.20), e não há qualquer cadeia de montanhas Austrália que seja equiparável aos Andes (praticamente desabitados por serpentes em sua porção sudoeste e nas maiores elevações).

A diversidade de habitats reflete o efeito de área e extensão latitudinal e tem grande influência sobre a diversidade de espécies. América do Sul estende-se cerca de 68° de latitude atingindo 12°N (dentro da zona tropical). A Austrália não atravessa o

equador, estendendo-se cerca de 30° de latitude e atingindo 10°S em sua extremidade norte. A variação latitudinal afeta fortemente o clima e a vegetação, que definem as condições dos habitats utilizados pelas serpentes. Além disso, a América do Sul possui maior extensão altitudinal e maior variação entre suas principais províncias geomorfológicas. Os Andes promovem um enorme gradiente de altitude ao longo de toda a parte ocidental da América do Sul (Orme, 2007), sem nenhuma semelhança na Austrália. O Planalto Central Brasileiro cobrindo o centro-leste da América do Sul pode ser equiparável às montanhas do leste da Austrália (em sua maioria entre 600 e 2000 m de altitude), mas não há contrapartida australiana para o isolado Planalto das Guianas no extremo norte. Esses fatores contribuem para criar uma variedade de habitats, isolamentos geográficos, e consequentes diversificações da fauna (Rull, 2011; Antonelli *et al.*, 2009; Sawaya e Sazima, 2003; Passos *et al.*, 2009a; Passos e Lynch, 2010; Kok, 2010).

Disposição dos principais elementos fisiográficos da América do Sul formam um relevante cenário para a especiação por promoverem a “duplicação de faunas” isoladas em ambientes similares (Keast, 1972). Os principais pares de blocos isolados são: (1) a floresta tropical a oeste vs. leste dos Andes; (2) a Amazônia ao norte vs. Mata Atlântica a leste, interrompidas pela diagonal de vegetação seca/aberta (Vanzolini, 1963; Werneck, 2011); e (3) o Planalto Central Brasileiro vs. Planalto das Guianas, largamente correspondendo às vegetações do Cerrado no Brasil e as planícies isoladas do Llanos venezuelanos. O alto nível de endemismo associado a estes blocos fornece evidência para o efeito de duplicação (Nogueira *et al.*, 2011; Passos *et al.*, 2009b; Passos *et al.*, 2010; Hoogmoed, 1982). Por outro lado, não há reais duplicações faunas no continente australiano (Keast, 1972).

O desenvolvimento da fauna de serpentes na América do Sul claramente começou mais cedo do que na Austrália, refletindo a seu maior número de linhagens antigas e radiações autóctones. Este alicerce inicial de linhagens distintas teve profundas consequências para as diferenças atuais na riqueza continental de táxons. O clado Serpentes surgiu em Gondwana na transição Juarássico-Cretáceo e diversificou-se principalmente durante o Cenozóico (Vidal *et al.*, 2009; Vitt e Caldwell, 2009; Pyron e Burbrink, 2012). Os Aniliidae (Estes e Báez, 1985), Boidae (Estes e Báez, 1985; Albino, 1996), Tropidophiidae (Vitt e Caldwell, 2009), e Scolecophidia [Anomalepididae (Vitt e Caldwell, 2009), Leptotyphlopidae e Typhlopidae (Vanzolini e Heyer, 1985)] formam o estoque autóctone sulamericano, com origem gonduânica (Tabela 9) (Duellman, 1979; Colli, 2005). Colubroidea (Viperidae, Elapidae e Colubridae) contém os elementos septentrionais, relativamente recentes (Estes e Báez, 1985; Vanzolini e Heyer, 1985; Kelly *et al.*, 2009; Cadle, 1987). Por outro lado, todas as linhagens viventes de serpentes australianas são relativamente recentes, derivadas de ancestrais orientais (Tyler, 1979; Hutchinson e Donnellan, 1993; Greer, 1997; Keogh, 1998; Kelly *et al.*, 2009; Scanlon, 2003). As invasões e colonizações orientais foram presumivelmente facilitadas quando a placa australiana colidiu com o sudeste asiático durante o Mioceno Médio (Raven e Axelrod, 1972; Hall, 2001). O último remanescente de uma fauna de serpentes gonduânica compartilhada entre a América do Sul e Austrália foi a família Madtsoiidae (Buffetaut e Rage, 1993; Greer, 1997; Scanlon, 2005a), difundida em Gondwana durante o Cretáceo e Paleogeno. Os matdsoiids estão relacionados com os atuais Henophidia (que inclui as jibóias e pítons), extinguiu-se na América do Sul durante o Eoceno mas sobreviveram na Austrália até o Pleistoceno (LaDuke *et al.*, 2010; Scanlon, 2005b). Acrochordidae é a mais antiga dentre as linhagem australianas viventes, é a linhagem mais basal dos

Caenophidia e se divergiram no Cretáceo Superior (Pyron e Burbrink, 2012). Entretanto, as evidências fósseis e a distribuição das espécies viventes de Acrochordidae sugerem origem asiática para o grupo ao invés de gonduânica (Sanders *et al.*, 2010; Tyler, 1979). Assim, imigrantes colonizadores formam o alicerce da fauna de serpentes australianas. No entanto, as imigrações para América do Sul foram ainda mais frequentes. A formação de uma conexão terrestre entre as Américas durante o Plioceno Superior-Pleistoceno Inferior (Webb, 2006; Iturralde-Vinent, 2006; Simpson, 1980; Stehli e Webb, 1985; Coates e Obando, 1996) intensificou notavelmente o intercâmbio faunístico que já havia se iniciado durante o Neogeno (Vanzolini e Heyer, 1985; Estes e Báez, 1985) e desempenhou um importante papel na formação da fauna de serpentes da América do Sul (Head *et al.*, 2012; Cadle, 1985). O continente australiano nunca experimentou invasão faunística tão intensa, embora uma conexão terrestre com Nova Guiné ocorrida no Quaternário permitiu intercâmbio de espécies de serpentes (Shine, 1991, p.52).

Estrutura taxonômica

Em ambas as faunas Alethinophidia prevalece sobre Scolecophidia, embora em menor proporção na Austrália. América do Sul possui maior número de famílias, gêneros e espécies Scolecophidia, porém a maior proporção de espécies na Austrália é devido a altíssima riqueza do gênero *Ramphotyphlops* (Typhlopidae) na Austrália, que ainda engloba significativa diversidade críptica (Marin *et al.*, 2013). A família Typhlopidae é cosmopolita e ocorre em ambos os continentes estudados, porém, representa menor proporção da fauna sulamericana.

Os Caenophidia (chamados serpentes avançadas) prevalecem sobre os demais Afrophidia (i.e., Henophidia), com o maior número de espécies em ambas as faunas,

embora em menor proporção na Austrália. Mesmo em maior número (subfamílias, gêneros e espécies) os Boidae representam uma fração menor da fauna sulamericana do que os Pythonidae da australiana. No entanto, ambos representam baixas percentagens de suas respectivas fauna (menos de 10 %). A diversidade de serpentes avançadas é distribuída ao longo de três famílias na América do Sul e quatro na Austrália. Colubridae e Elapidae são compartilhadas entre os continentes, a primeira predomina na América do Sul e a segunda na Austrália. Além de Colubridae, as linhagens de Caenophidia restantes na América do Sul representam 14,4% de toda a fauna, enquanto os caenophídios não elapídeos na fauna australiana correspondem a cerca de metade deste valor (7,3%). Estas diferenças devem-se principalmente a uma proporção relativamente maior de espécies de jararacas (Viperidae) e cobras-corais (Elapidae) na América do Sul em comparação com a soma dos acrocordídeos (Acrochordidae), colubrídeos (Colubridae) e cobras-de-mangue (Homalopsidae). Portanto, as serpentes avançadas encontram-se em maior proporção na América do Sul em comparação com a Austrália. Colubridae na América do Sul é taxonomicamente bem estruturada em comparação com as famílias australianas, com quatro subfamílias e várias tribos, ao passo que os poucos colubrídeos australianos são divididos em apenas duas subfamílias. Os Elapídeos australianos pertencem a uma única subfamília, Hydrophiinae. Elapidae e Colubridae (incluindo Colubrinae) têm distribuições cosmopolitas (Vitt e Caldwell, 2009).

América do Sul possui um clado superior exclusivo e seis famílias exclusivas comparando com Austrália, que possui três famílias exclusivas. Os Amerophidia e Anomalepididae não ocorrem fora da região Neotropical (Vidal *et al.*, 2009; Freire *et al.*, 2007), Leptotyphlopidae ocorre nas porções ocidentais de Gondwana, principalmente na região Neotropical e África (Adalsteinsson *et al.*, 2009). A família

Boidae tem uma distribuição ampla, ocorrendo em todo o Novo Mundo, da África central ao sul da Ásia, Madagascar e ilhas do Pacífico (sudoeste), mas não na Austrália (Noonan e Chippindale, 2006; Vitt e Caldwell, 2009). A família Viperidae é distribuída por todo o mundo, exceto pela região papua-australiana, ilhas oceânicas, e os pólos (Greene, 1997; Wüster *et al.*, 2008). Acrochordidae e Homalopsidae têm distribuições similares, em toda a costa da Ásia meridional da Índia até a China, e no norte da Austrália (Murphy, 2011; Sanders *et al.*, 2010). A Família Pythonidae ocorre em toda África ao sul do Sahara, e do sul e sudeste da Ásia até a Austrália (Rawlings *et al.*, 2008). Quantitativamente, as contribuições dessas famílias exclusivas para as relações de dominância entre os clados na Austrália são mais relevantes do que na América do Sul, com efeito mais forte sobre estrutura taxonômica da fauna na Austrália. O padrão geral observado de riqueza de espécies entre os clados está de acordo com o padrão global de diversidade de serpentes, com várias linhagens jovens e muito especiosas (Pyrone e Burbrink, 2012). Apesar das semelhanças históricas e atuais, América do Sul e Austrália desenvolveram faunas de serpentes com características particulares. O desafio consiste em quantificar a contribuição relativa da filogenia, biogeografia e ecologia, na formação da estrutura da fauna existente.

Estrutura biológica

As espécies podem convergir em algumas dimensões biológicas, mas não em outras (Orians e Paine, 1983). Meus resultados sugerem que este fenômeno ocorre com a fauna de serpentes australianas e sul-americanas. Similaridades biológicas e discrepâncias entre faunas podem ser explicadas tanto por suas contingências histórico-filogenéticas quanto pelas proporções atuais de habitats fechados vs. abertos disponíveis em cada continente afetando a ecologia. As faunas de ambos os

continentes são constituídas principalmente por espécies terrestres, noturnas, ovíparas, com dieta baseada em répteis, e corpo de comprimento curto ou médio. Além disso, as faunas não diferem na proporção de espécies que usam ambos os habitats (fechados e abertos); com habito aquático, semiaquático, criptozóico+terrestre, estritamente terrestre, ou semiarborícola; dieta baseada em peixes, aves e/ou mamíferos; nem entre qualquer classe de comprimento do corpo. Estas semelhanças sugerem níveis significativos de convergência entre faunas.

Por outro lado, a maior proporção de espécies na América do Sul que utilizam habitats estritamente fechados, com hábitos arborícolas, diurnas ou com ambos os períodos de atividade, e que se alimentam principalmente de anfíbios ou invertebrados de corpo mole deve estar refletindo a maior proporção de áreas fechadas/florestais na América do Sul. Além da óbvia disponibilidade maior de árvores viabilizando o desenvolvimento de hábitos arborícolas, habitats fechados oferecem mais oportunidades do que habitats abertos para a diurnalidade, porque os indivíduos usufruem de menor exposição à predadores, mesmo durante o dia. A precipitação na América do Sul é muito maior do que na Austrália, o que viabilizou ao continente desenvolver uma fauna diversificada e abundante de anfíbios e invertebrados de corpo mole. América do Sul é o continente com maior diversidade de anfíbios do mundo (Duellman, 1979). América do Sul possui densidade de espécies de anfíbios do que o esperado, também atribuído à sua maior proporção de florestas tropicais úmidas e menos sazonais (Duellman e Pianka, 1990; Duellman, 1979). Além disso, as linhagens sul-americanas mais especiosas, Xenodontinae e Dipsadinae, alimentam-se principalmente de anfíbios e invertebrados de corpo mole respectivamente, sugerindo forte efeito filogenético sobre a estrutura biológica da fauna sulamericana (Cadle e Greene, 1993). É importante mencionar que a área total

de habitats fechados na América do Sul é aproximadamente metade do tamanho da área de habitats abertos, mas contém número maior de espécies, o que demonstra fortemente a capacidade das florestas em manter maior diversidade de espécies de serpentes (veja a discussão abaixo, na seção diversidade espécies). A maior proporção de espécies ovíparas na América do Sul é parcialmente explicada pela predominância de espécies ovíparas nas famílias mais especiosas, Colubridae e Elapidae.

A maior proporção de espécies na Austrália utilizando habitats estritamente abertos, com hábitos estritamente fossoriais, atividade noturna, e alimentando-se principalmente de répteis ou artrópodes reflete a maior proporção de áreas abertas na Austrália. Hábitos fossoriais e atividade noturna são provavelmente associados ao uso de habitats abertos, especialmente considerando o alto nível de exposição a predadores e intempéries climáticos nos ambientes abertos. Hábitos noturnos são favorecidos sob maior sazonalidade climática (Duellman e Pianka, 1990). Austrália abriga uma das mais diversas faunas de répteis do mundo, com mais de 920 espécies descritas (Wilson e Swan, 2010; Cogger, 2000), lagartos apresentam a maior riqueza conhecida, densidade e abundância de espécies (Pianka, 1989; Pianka, 1996), que é atribuído à maior proporção de áreas abertas e secas na Austrália (Duellman e Pianka, 1990; Duellman, 1979). Além disso, o efeito filogenético sobre a estrutura biológica é muito evidente. As linhagens australianas mais especiosas, Elapidae e Typhlopidae, se alimentam principalmente de répteis e artrópodes respectivamente, sendo Typhlopidae estritamente fossorial e noturna. A fossorialidade é difundida através dos elapídeos de todo o mundo. Ainda, a viviparidade é comumente encontrada associada ao hábito aquático. A Austrália tem duas famílias vivíparas inteiramente aquáticas, Acrochordidae e Homalopsidae, representando uma pequena percentagem da fauna; os elapídeos australianos desenvolveram uma tribo vivípara inteiramente marinha,

Hidrophini (Sanders *et al.*, 2013), tão diversa quanto seus parentes continentais. No entanto, os elapídeos vivíparos não-marinhas nunca adquiriram hábitos aquáticos. Portanto, o hábito aquático na Austrália não parece estar relacionado com a alta proporção de espécies vivíparas. Por outro lado, embora a oviparidade seja a condição reprodutiva ancestral de elapídeos australianos (Keogh *et al.*, 1998), a viviparidade aparece em quase metade das espécies não-marinhas. A radiação dos elapídeos vivíparos na Austrália começou logo depois da invasão pelos primeiros colonizadores e está fortemente associada as oscilações climáticas e baixas temperaturas (Shine, 1991; Keogh *et al.*, 1998). América do Sul tem quatro famílias vivíparas Aniliidae, Tropicophiidae, Boidae e Viperidae (exceto *Lachesis*), apenas Viperidae proporcionalmente representando quantidade significativa de espécies. Os Colubridae altamente diversificados na América do Sul são predominantemente ovíparos e também evoluíram a viviparidade, mas em baixa proporção de espécies.

América do Sul e Austrália apresentam diferentes números de guildas ecológicas. O maior número na América do Sul aparentemente reflete sua maior densidade de espécies e maior pressão para desenvolver combinações ecológicas peculiares em habitats estruturalmente fechados (i.e. florestas). Guildas ecológicas podem ser consideradas como “macro zonas adaptativas” (Keast, 1972) que evoluem provavelmente relaxando a competição inter-específica. Evidentemente, as espécies em uma guilda não são ecologicamente uniformes, mas as diferenças ecológicas entre as espécies de uma mesma guilda são menores do que entre diferentes guildas, o que implica maior competição dentro de uma guilda do que entre guildas. Além disso, as diferenças ecológicas entre guildas são maiores dentro de continentes do que entre continentes, sugerindo que para cada guilda australiana exista uma guilda equivalente

na América do Sul. Essas correspondências entre guildas serve como evidência qualitativa de convergência entre faunas.

Certas combinações entre atributos biológicos provavelmente contribuem mais para o valor adaptativo (fitness) das espécies do que outras combinações, o que deve favorecer a similaridade entre guildas. Por exemplo, pares de guildas similares corroboram a consistência entre hábito e dieta, especificamente entre o hábito fossorial e dieta baseada artrópodes; hábito arborícola e dieta baseada endotérmicos; hábito terrestre e dieta baseada ectotérmicos; e entre hábito aquático e dieta baseada em peixes. Correspondências fortes entre atributos biológicos das serpentes já foram sugeridas anteriormente, especialmente entre hábito e forma do corpo (Cadle e Greene, 1993; Vitt, 1987; França *et al.*, 2008). Estas combinações potencialmente “ótimas” provavelmente contribuem para o padrão observado em que a maioria das espécies estão em um pequeno número de guildas. A falta de correspondência entre a proporção de espécies em guildas similares reflete a alta proporção de espécies da América do Sul em guildas caracterizadas pelo uso de habitats fechados e uma alta proporção de espécies australianas em guildas caracterizadas pelo uso de habitats abertos.

Estrutura filogenética e o efeito do habitat

As relações filogenéticas não estão distribuídas aleatoriamente na fauna sulamericana nem australianas, indicando a presença de estrutura filogenética. No entanto as espécies em cada fauna são mais aparentadas do que o esperado ao acaso. Este resultado sugere que a formação de ambas as faunas foi significativamente marcada por eventos recentes de diversificação e/ou colonização (Wiens e Donoghue, 2004; Webb *et al.*, 2002). A combinação entre a diversidade de espécies e as métricas

de diversidade filogenética são úteis para entender os efeitos históricos sobre a estrutura da fauna (Pavoine e Bonsall, 2011). A comparação dentro da América do Sul demonstrou maior riqueza de espécies e maior PD em habitats fechados do que abertos, sugerindo um tempo longo de diversificação (Wiens e Donoghue, 2004), enquanto que a menor riqueza e PD em habitats abertos sugerem colonização mais recente e menor tempo para a diversificação. Este padrão corrobora a hipótese de que a maior parte das espécies de serpentes da América do Sul são representantes de famílias de imigrantes do norte (Cadle e Greene, 1993; Colli, 2005) que provavelmente colonizaram os habitats das florestas tropicais antes de alcançarem as savanas sulamericanas. O padrão oposto é observado na Austrália com baixa riqueza de espécies e PD em habitats fechados, sugerindo eventos recentes de colonização e um tempo mais curto para a diversificação. No entanto, a alta riqueza de espécies e baixa PD em habitats abertos australianos sugerem eventos recentes de radiação adaptativa (Slingsby e Verboom, 2006). A radiação rápida e recente dos elapídeos australianos esta associada com o aumento da aridificação no continente (Kuch *et al.*, 2005; Sanders *et al.*, 2008; Byrne *et al.*, 2008). Os maior PD na América do Sul comparado com Austrália reflete o maior número de espécies, linhagens mais antigas, e história mais antiga da América do Sul (ver também as discussões acima).

Diversidade de espécies

A discussão acima destaca uma combinação de padrões convergentes e divergentes comparando a fauna de serpentes australiana e sul-americana. Convergência entre comunidades é esperada quando o número e tipos de espécies co-existentes são determinadas localmente (Schluter e Ricklefs, 1993a). A despeito do maior tamanho da América do Sul em comparação com a Austrália ambos os

continentes têm áreas maiores cobertas por habitats estruturalmente abertos do que habitats fechados/florestais. Entretanto, as comparações utilizando habitats fechados vs. abertos sugerem que os habitats fechados são melhores do que os habitats abertos em promovendo a diversidade de serpentes, com maiores densidades de espécies e maiores diversidades locais em ambos os continentes. Este padrão compartilhado suporta a importância de processos locais e contemporâneos na formação de comunidades presentes.

É possível que histórias independentes tenham consequências similares em diferentes regiões biogeográficas, levando biotas a convergir (Westoby, 1993; Orians e Paine, 1983; Schluter e Ricklefs, 1993a). Um outro padrão compartilhado pode ser observado por meio das relações entre diversidades locais e continentais. América do Sul e Austrália possuem diferentes diversidades locais, mas refletem de forma semelhante a diversidade regional, o que implica um forte efeito histórico sobre a estrutura da diversidade faunística (Westoby, 1993). Um consistente efeito área associado a “taxas de diferenciação da diversidade” similares sugere que a diversidade de espécies foi alcançada através de processos similares operando em ambos os continentes. Este padrão compartilhado dá suporte à hipótese de convergência entre faunas. É esperado que habitats similares possam ter efeitos similares sobre o número de espécies que coexistem (Orians e Paine, 1983; Schluter e Ricklefs, 1993a). América do Sul e Austrália têm áreas maiores cobertas por habitats abertos do que por habitats fechados, essa semelhança potencialmente molda a estrutura da diversidade de forma similar entre os continentes. No entanto, vimos acima que a maior proporção de habitats fechados na América do Sul em comparação com a Austrália tem grandes consequências diferenciando os patamares de riqueza em cada continente. A riqueza de espécies em habitats fechados da América do Sul

(diversidade regional) é maior do que em habitats abertos, embora cubra uma área menor. Como poderia então as faunas convergirem em diversidade de espécies, considerando a área relativamente pequena que na Austrália é coberta por habitats fechados?

Possíveis explicações emergem se comparamos a taxa de “diferenciação da diversidade” entre habitats similares de continentes mas de continentes opostos. Os resultados sugerem que os habitats abertos da Austrália possuem maior taxa de diferenciação da diversidade do que habitats abertos da América do Sul, provavelmente equilibrar o forte efeito dos habitats fechados na América do Sul, e levando a diversidade de espécies a convergir na escala continental. Esse contraste entre os continentes é provavelmente devido a particularidades de cada região biogeográfica, e não devido a restrições na escala local, embora mantém-se o efeito regional sobre a diversidade local. Esta hipótese evoca fortemente a importância dos processos históricos moldando a estrutura continental das faunas (Westoby, 1993).

Semelhanças evidentes entre paisagens abertas da América do Sul e Austrália dão suporte aos estudos intercontinentais (ver Colli *et al.*, 2006; Campos *et al.*, 2011; Pantoja, *in review*; Pantoja, *in prep.*), contudo, as similaridades aparentemente não sobrepujam as diferenças. A maior taxa de diferenciação da diversidade em habitats abertos da Austrália em relação a América do Sul é potencialmente explicada por: 1) paisagens abertas são provavelmente mais heterogênea na Austrália do que na América do Sul, com maior número de fitofisionomias, e consequentemente maior complexidade habitat (Cochrane, 1963; Oliveira e Marquis, 2002; Specht, 1981; Brown e Prance, 1987; Werneck, 2011); 2) a complexidade de habitat pode ser aumentada por incêndios naturais, um fenômeno provavelmente mais eficaz na Austrália (Costa *et al.*, 2013; Pantoja, 2007; Morton *et al.*, 2011; Pianka, 1996;

Pelegrin e Bucher, 2010; Miranda *et al.*, 2002); e 3) flutuações climáticas do Neogeno Médio e do Quaternário promoveram ciclos repetidos de aridez e umidade (associados com períodos glaciais), o que permitiu a diversificação em refúgios (e.g. montanhas isoladas na zona árida Pepper *et al.*, 2011; Couper *et al.*, 2008; Moritz *et al.*, 2009; Byrne *et al.*, 2008; Twidale, 1972). Estes eventos histórico-climáticos desempenharam papéis importantes na diversificação das serpentes das paisagens abertas australianas (Shine, 1991) e também na diversificação da biota sulamericana (Haffer, 1969; Brown e Ab'Sáber, 1979; Vanzolini e Williams, 1970; Vanzolini e Williams, 1981), no entanto, provavelmente com um efeito menor sobre as serpentes da América do Sul (Bush e Oliveira, 2006; Colli, 2005).

A discussão apresentada perpassa os principais resultados desta tese. O conteúdo completo encontra-se distribuído nos três apêndices anexos.

REFERÊNCIAS BIBLIOGRÁFICAS

- ADALSTEINSSON, S. A., W. R. BRANCH, S. TRAPE, L. J. VITT, e S. B. HEDGES. 2009. Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). *Zootaxa*:1-50.
- ALBINO, A. M. 1996. The South American fossil Squamata (Reptilia: Lepidosauria). *Münchener Geowiss Abh. (A)* 30:185-202.
- ANTONELLI, A., J. A. A. NYLANDER, C. PERSSON, e I. SANMARTIN. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences of the United States of America*. 106:9749-9754.
- ARCHER, M., R. BECK, M. GOTT, S. HAND, H. GODTHELP, e K. BLACK. 2011. Australia's first fossil marsupial mole (Notoryctemorphia) resolves controversies about their evolution and palaeoenvironmental origins. *Proceedings of the Royal Society B-Biological Sciences*. 278:1498-1506.
- BROOKS, D. R., e D. A. MCLENNAN. 1993. Historical ecology: examining phylogenetic components of community evolution, p. 267-280. *In: Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. R. E. Ricklefs e D. Schluter (eds.). The University of Chicago Press, Chicago.
- BROWN, K. S., e A. N. AB'SÁBER. 1979. Ice-age forest refuges and evolution in Neotropics: correlation of paleoclimatological, geomorphological and pedological data with biological endemism. *Paleoclimas*. 5:1-30.

- BROWN, K. S., e G. T. PRANCE. 1987. Soils and vegetation, p. 19-45. *In*: Biogeography and Quaternary History in Tropical America. T. C. Whitmore e G. T. Prance (eds.). Oxford University Press, New York.
- BUFFETAUT, E., e J. C. RAGE. 1993. Fossil amphibians and reptiles and the Africa-South America connection, p. 87-99. *In*: The Africa-South America Connection. W. George e R. Lavocat (eds.). Oxford University Press, New York.
- BUSH, M. B., e P. E. OLIVEIRA. 2006. The rise and fall of the refugial hypothesis of Amazonian speciation. *In*: Biota Neotropica. Vol. 6. <http://www.biotaneotropica.org.br>.
- BYRNE, M., D. K. YEATES, L. JOSEPH, M. KEARNEY, J. BOWLER, M. A. J. WILLIAMS, S. COOPER, S. C. DONNELLAN, J. S. KEOGH, R. LEYS, J. MELVILLE, D. J. MURPHY, N. PORCH, e K. H. WYRWOLL. 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*. 17:4398-4417.
- CADLE, J. E. 1985. The Neotropical colubrid snake fauna (Serpentes: Colubridae): lineage components and biogeography. *Systematic Zoology*. 34:1-20.
- CADLE, J. E. 1987. Geographic distribution: problems in phylogeny and zoogeography, p. 77-105. *In*: Snakes: Ecology and Evolutionary Biology. R. A. Seigel, J. T. Collins, e S. S. Novak (eds.). Macmillan Publishing Company, New York.
- CADLE, J. E., e H. W. GREENE. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages, p. 281-293. *In*: Species Diversity in Ecological Communities, Historical and Geographical Perspectives. R. E. Ricklefs e D. Schluter (eds.). University of Chicago Press, Chicago.
- CAMPOS, R. I., H. L. VASCONCELOS, A. N. ANDERSEN, T. L. M. FRIZZO, e K. C. SPENA. 2011. Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. *Austral Ecology*. 36:983-992.
- CARRASCO, P. A., G. C. LEYNAUD, e G. J. SCROCCHI. 2010. Redescription of the southernmost snake species, *Bothrops ammodytoides* (Serpentes: Viperidae: Crotalinae). *Amphibia-Reptilia*. 31:323-338.
- CAVENDER-BARES, J., D. D. ACKERLY, D. A. BAUM, e F. A. BAZZAZ. 2004. Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*. 163:823-843.
- CHIRAT, R., D. E. MOULTON, e A. GORIELY. 2013. Mechanical basis of morphogenesis and convergent evolution of spiny seashells. *Proceedings of the National Academy of Sciences of the United States of America*. 110:6015-20.
- COATES, A. G., e J. A. OBANDO. 1996. The geologic evolution of the Central American isthmus, p. 21-56. *In*: Evolution and Environment in Tropical America. J. B. C. Jackson, A. F. Budd, e A. G. Coates (eds.). University of Chicago Press, Chicago and London.
- COCHRANE, G. R. 1963. A physiognomic vegetation map of Australia. *Journal of Ecology*. 51:639-655.
- CODY, M. L. 1993. Bird diversity components within and between habitats in Australia, p. 147-158. *In*: Species Diversity in Ecological Communities, Historical and Geographical Perspectives. R. E. Ricklefs e D. Schluter (eds.). University of Chicago Press, Chicago.

- CODY, M. L., e H. A. MOONEY. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics*. 9:265-321.
- COGGER, H. G. 2000. *Reptiles and Amphibians of Australia*. Ralph Curtis Books.
- COLLI, G. R. 2005. As origens e a diversificação da herpetofauna do Cerrado, p. 447-264. *In: Cerrado: Ecologia, Biodiversidade e Conservação*. A. Scariot, J. C. Sousa-Silva, e J. M. Felfili (eds.). Ministério do Meio Ambiente, Brasília, DF.
- COLLI, G. R., R. CONSTANTINO, e G. C. COSTA. 2006. Lizards and termites revisited. *Austral Ecology*. 31:417-424.
- COLSTON, T. J., G. C. COSTA, e L. J. VITT. 2010. Snake diets and the deep history hypothesis. *Biological Journal of the Linnean Society*. 101:476-486.
- CONNELL, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*. 35:131-138.
- COSTA, B. M., D. L. PANTOJA, M. C. M. VIANNA, e G. R. COLLI. 2013. Direct and short-term effects of fire on lizard assemblages from a Neotropical Savanna hotspot. *Journal of Herpetology*. 47:502-510.
- COSTA, G. C., G. R. COLLI, e R. CONSTANTINO. 2008a. Can lizard richness be driven by termite diversity? Insights from the Brazilian Cerrado. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 86:1-9.
- COSTA, G. C., L. J. VITT, E. R. PIANKA, D. O. MESQUITA, e G. R. COLLI. 2008b. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography*. 17:670-677.
- COUPER, P. J., R. A. SADLER, G. M. SHEA, e J. W. WILMER. 2008. A reassessment of *Saltuarius swaini* (Lacertilia : Diplodactylidae) in southeastern Queensland and New South Wales; Two new taxa, phylogeny, biogeography and conservation. *Records of the Australian Museum*. 60:87-118.
- CRAWLEY, M. J. 2007. *The R Book*. 942.
- DARLINGTON, P. J., JR. 1965. *Biogeography of the Southern End of the World: Distribution and History of Far-Southern Life and Land, with an Assessment of Continental Drift*. Harvard University Press, Cambridge.
- DI MICELI, C. M., M. L. CARROLL, R. A. SOHLBERG, C. HUANG, M. C. HANSEN, e J. R. G. TOWNSHEND. 2011. Annual Global Automated MODIS Vegetation Continuous Fields (MOD44B) at 250 m Spatial Resolution for Data Years Beginning Day 65, 2000 - 2010, Collection 5 Percent Tree Cover. University of Maryland, College Park, MD, USA.
- DUELLMAN, W. E. 1979. The South American herpetofauna: a panoramic view, p. 1-28. *In: The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. W. E. Duellman (ed.). University of Kansas Printing Service, Lawrence.
- DUELLMAN, W. E., e E. R. PIANKA. 1990. Biogeography of nocturnal insectivores: historical events and ecological filters. *Annual Review of Ecology and Systematics*. 21:57-68.
- DUFRENE, M., e P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*. 67:345-366.
- ESTES, R., e A. BÁEZ. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange?, p. 139-197. *In: The Great American Biotic Interchange*. F. G. Stehli e S. D. Webb (eds.). Plenum Press, New York.

- FAITH, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation*. 61:1-10.
- FRANÇA, F. G. R., D. O. MESQUITA, C. C. NOGUEIRA, e A. F. B. ARAUJO. 2008. Phylogeny and ecology determine morphological structure in a snake assemblage in the central Brazilian Cerrado. *Copeia*:23-38.
- FREIRE, E. M. X., U. CARAMASCHI, e A. J. S. ARGÔLO. 2007. A new species of *Liotyphlops* (Serpentes: Anomalepididae) from the Atlantic Rain Forest of northeastern Brazil. *Zootaxa*. 1393:19-26.
- FUENTES, E. R. 1976. Ecological convergence of lizard communities in Chile and California. *Ecology*. 57:3-17.
- GOTELLI, N. J., e R. K. COLWELL. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*. 4:379-391.
- GREENE, H. W. 1997. *Snakes: the Evolution of Mystery in Nature*. University of California Press, California.
- GREER, A. E. 1997. *The Biology and Evolution of Australian Snakes*. Surrey Beatty & Sons, Chipping Norton, NSW.
- GUEDES, T. B., G. S. S. NUNES, A. L. C. PRUDENTE, e O. A. V. MARQUES. 2011. New records and geographical distribution of the tropical banded treesnake *Siphlophis compressus* (Dipsadidae) in Brazil. *Herpetology Notes*. 4:341-346.
- HAFFER, J. 1969. Speciation in Amazonian Forest birds. *Science*. 165:131-&.
- HAFFER, J. 1987. Quaternary history of tropical America, p. 1-18. *In: Biogeography and Quaternary History of Tropical America*. T. C. Whitmore e G. T. Prance (eds.). Oxford University Press, New York.
- HALL, R. 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea, p. 35-56. *In: Faunal and floral migrations and evolution in SE Asia-Australasia*. I. Metcalfe, J. M. B. Smith, M. Morwood, e I. Davidson (eds.). A.A. Balkema (Swets and Zeitlinger Publishers) Lisse.
- HARVEY, P. H., e M. D. PAGEL. 1998. *The Comparative Method in Evolutionary Biology*. 239.
- HEAD, J. J., A. F. RINCON, e C. SUAREZ. 2012. Fossil evidence for earliest Neogene American faunal interchange: *Boa* (Serpentes, Boinae) from the early Miocene of Panama. *Journal of Vertebrate Paleontology*. 32:1328-1334.
- HOOGMOED, M. S. 1982. Snakes of the Guianan region. *Memórias do Instituto Butantan (São Paulo)*. 46:219-254.
- HUTCHINSON, M. N., e S. C. DONNELLAN. 1993. Biogeography and phylogeny of the Squamata, p. 1-24. *In: Fauna of Australia Volume 2A*. C. G. Glasby, G. J. B. Ross, e P. L. Beesley (eds.). AGPS Canberra, Camberra.
- ITURRALDE-VINENT, M. A. 2006. Meso-Cenozoic Caribbean paleogeography: Implications for the historical biogeography of the region. *International Geology Review*. 48:791-827.
- KEAST, A. 1971. Continental drift and the evolution of the biota on southern continents. *The Quarterly Review of Biology*. 46:355-378.
- KEAST, A. 1972. Comparisons of contemporary mammal faunas of southern continents, p. 433-501. *In: Evolution, Mammals, and Southern Continents*. A. Keast, F. C. Erk, e B. Glass (eds.). State University of New York Press, Albany.
- KEAST, A., F. C. ERK, e B. GLASS. 1972. *Evolution, Mammals, and Southern Continents*, p. 543. State University of New York Press, Albany.

- KELLY, C. M. R., N. P. BARKER, M. H. VILLET, e D. G. BROADLEY. 2009. Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics-the International Journal of the Willi Hennig Society*. 25:38-63.
- KELT, D. A., K. ROGOVIN, G. SHENBROT, e J. H. BROWN. 1999. Patterns in the structure of Asian and North American desert small mammal communities. *Journal of Biogeography*. 26:825-841.
- KEMBEL, S. W., P. D. COWAN, M. R. HELMUS, W. K. CORNWELL, H. MORLON, D. D. ACKERLY, S. P. BLOMBERG, e C. O. WEBB. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*. 26:1463-1464.
- KEOGH, J. S. 1998. Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biological Journal of the Linnean Society*. 63:177-203.
- KEOGH, J. S., R. SHINE, e S. DONNELLAN. 1998. Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes (subfamily Hydrophiinae) based on cytochrome b and 16S rRNA sequences. *Molecular Phylogenetics and Evolution*. 10:67-81.
- KOK, P. J. R. 2010. A new species of *Chironius* Fitzinger, 1826 (Squamata: Colubridae) from the Pantepui region, northeastern South America. *Zootaxa*. 2611:31-44.
- KUCH, U., J. S. KEOGH, J. WEIGEL, L. A. SMITH, e D. MEBS. 2005. Phylogeography of Australia's king brown snake (*Pseudechis australis*) reveals Pliocene divergence and Pleistocene dispersal of a top predator. *Naturwissenschaften*. 92:121-127.
- LADUKE, T. C., D. W. KRAUSE, J. D. SCANLON, e N. J. KLEY. 2010. A late Cretaceous (Maastrichtian) snake assemblage from the Maevarano formation, Mahajanga basin, Madagascar. *Journal of Vertebrate Paleontology*. 30:109-138.
- LOMOLINO, M. 1993. Matching of granivorous mammals of the Great Basin and Sonoran Deserts on a species-for-species basis. *Journal of mammalogy*. 74:863-867.
- LOSOS, J. B. 1994. Historical contingency and lizard community ecology, p. 319-333. *In: Lizard Ecology: Historical and Experimental Perspectives*. L. J. Vitt e E. R. Pianka (eds.). Princeton University Press, Princeton, NJ.
- LOSOS, J. B. 1996. Phylogenetic perspectives on community ecology. *Ecology*. 77:1344-1354.
- LOSOS, J. B., T. R. JACKMAN, A. LARSON, K. DE QUEIROZ, e L. RODRIGUEZ-SCHETTINO. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science*. 279:2115-2118.
- MACARTHUR, R. H., J. W. MACARTHUR, e J. PREER. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *The American Naturalist*. 96:167-174.
- MARIN, J., S. C. DONNELLAN, S. B. HEDGES, N. PULLANDRE, K. P. APLIN, P. DOUGHTY, M. N. HUTCHINSON, A. COULOUX, e N. VIDAL. 2013. Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*). *Biological Journal of the Linnean Society*. 110:427-441.
- MCLOUGHLIN, S., e B. P. KEAR. 2010. The Australasian Cretaceous scene. *Alcheringa*. 34:197-203.
- MELVILLE, J., L. J. HARMON, e J. B. LOSOS. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society B-Biological Sciences*. 273:557-563.

- MIRANDA, H. S., M. M. C. BUSTAMANTE, e A. C. MIRANDA. 2002. The fire factor, p. 51-68. *In: The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. P. S. Oliveira e R. J. Marquis (eds.). Columbia University Press, New York.
- MOEN, D. S., S. A. SMITH, e J. J. WIENS. 2009. Community assembly through evolutionary diversification and dispersal in middle american treefrogs. *Evolution*. 63:3228-3247.
- MOONEY, H. A. 1977. *Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems*. 224.
- MORITZ, C., C. J. HOSKIN, J. B. MACKENZIE, B. L. PHILLIPS, M. TONIONE, N. SILVA, J. VANDERWAL, S. E. WILLIAMS, e C. H. GRAHAM. 2009. Identification and dynamics of a cryptic suture zone in tropical rainforest. *Proceedings of the Royal Society B-Biological Sciences*. 276:1235-1244.
- MORTON, S. R., D. M. S. SMITH, C. R. DICKMAN, D. L. DUNKERLEY, M. H. FRIEDEL, R. R. J. MCALLISTER, J. R. W. REID, D. A. ROSHIER, M. A. SMITH, F. J. WALSH, G. M. WARDLE, I. W. WATSON, e M. WESTOBY. 2011. A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*. 75:313-329.
- MULLIN, S. J., e R. A. SEIGEL. 2009. *Snakes: Ecology and Conservation*, p. 365. Comstock Pub. Associates/Cornell University Press.
- MURPHY, J. C. 2011. The nomenclature and systematics of some Australasian homalopsid snakes (Squamata: Serpentes: Homalopsidae). *The Raffles Bulletin of Zoology*. 59:229-236.
- NIPPERESS, D. A., e F. A. MATSEN. 2013. The mean and variance of phylogenetic diversity under rarefaction. *Methods in Ecology and Evolution*. 4:566-572.
- NIX, H. A. 1981. The environment of *Terra Australis*, p. 103-133. *In: Ecological Biogeography of Australia*. A. Keast (ed.). Dr. W. Junk, The Hague, Netherlands.
- NOGUEIRA, C., S. RIBEIRO, G. C. COSTA, e G. R. COLLI. 2011. Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography*. 38:1907-1922.
- NOONAN, B. P., e P. T. CHIPPINDALE. 2006. Dispersal and vicariance: the complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution*. 40:347-358.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, e H. WAGNER. 2013. Package 'vegan'. Community ecology package. R package version 2.0-9.
- OLIVEIRA, P. S., e R. J. MARQUIS. 2002. The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna, p. 398. Columbia University Press, New York.
- ORIAN, G. H., e R. T. PAINE. 1983. Convergent evolution at the community level, p. 431-458. *In: Coevolution*. D. J. Futuyma e M. Slatkin (eds.). Sinauer Associates, Inc., Sunderland, MA.
- ORIAN, G. H., e O. T. SOLBRIG. 1977. *Convergent Evolution in Warm Deserts: an examination of strategies and patterns in deserts of Argentina and the United States*. 333.
- ORME, A. R. 2007. Tectonism, climate, and landscape change, p. 23-44. *In: The Physical Geography of South America*. T. T. Veblen, K. R. Young, e A. R. Orme (eds.). Oxford University Press, New York, NY.

- PANTOJA, D. L. 2007. Efeitos do fogo sobre a taxocenose de lagartos em áreas de cerrado *sensu stricto* no Brasil Central, p. 113. *In*: Biologia Animal. Vol. Dissertação de Mestrado. Universidade de Brasília, Brasília, DF.
- . in prep. Biological comparisons between South America and Australia: the state of the art.
- . *in review*. On the South America and Australia connections: a framework for biological comparisons, p. 95.
- PANTOJA, D. L., B. M. COSTA, G. R. COLLI, e E. C. LIMA. in prep. Does fire drives lizard diversity in Cerrado?
- PASSOS, P., J. C. ARREDONDO, R. FERNANDES, e J. D. LYNCH. 2009a. Three new *Atractus* (Serpentes: Colubridae) from Andes of Colombia. *Copeia*. 2009:425-436.
- PASSOS, P., R. FERNANDES, R. S. BÉRNILS, e J. C. MOURA-LEITE. 2010. Taxonomic revision of the Brazilian Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae). *Zootaxa*. 2364:3-63.
- PASSOS, P., e J. D. LYNCH. 2010. Revision of *Atractus* (Serpentes: Dipsadidae) from middle and upper Magdalena drainage of Colombia. *Herpetological Monographs*. 24:149–173.
- PASSOS, P., J. J. MUESES-CISNEROS, J. D. LYNCH, e R. FERNANDES. 2009b. Pacific lowland snakes of the genus *Atractus* (Serpentes: Dipsadidae), with description of three new species. *Zootaxa*:1-34.
- PAVOINE, S., e M. B. BONSALE. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*. 86:792-812.
- PELEGRIN, N., e E. H. BUCHER. 2010. Long-term effects of a wildfire on a lizard assemblage in the Arid Chaco forest. *Journal of Arid Environments*. 74:368-372.
- PEPPER, M., M. K. FUJITA, C. MORITZ, e J. S. KEOGH. 2011. Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone. *Molecular Ecology*. 20:1529-1545.
- PIANKA, E. R. 1986. *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure* Princenton University Press, Princenton, NJ.
- . 1989. Desert lizard diversity: additional comments and some data. *American Naturalist*. 134:344-364.
- . 1996. Long-term changes in lizard assemblages in the Great Victoria Desert: dynamic habitat mosaics in response to wildfires, p. 191-215. *In*: Long-Term Studies of Vertebrate Communities. M. L. Cody e J. A. Smallwood (eds.). Academic Press, San Diego, California.
- PYRON, R. A., e F. T. BURBRINK. 2012. Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution*. 66:163-178.
- PYRON, R. A., F. T. BURBRINK, e J. A. WIENS. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*. 13:1-53.
- R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, <http://www.R-project.org>, Vienna, Austria.
- RAVEN, P. H., e D. I. AXELROD. 1972. Plate Tectonics and Australasian Paleobiogeography. *Science*. 176:1379-&.

- RAWLINGS, L. H., D. L. RABOSKY, S. C. DONNELLAN, e M. N. HUTCHINSON. 2008. *Python* phylogenetics: inference from morphology and mitochondrial DNA. *Biological Journal of the Linnean Society*. 93:603-619.
- RICKLEFS, R. E. 2008. Disintegration of the ecological community. *American Naturalist*. 172:741-750.
- ROBERTS, D. W. 2013. Package 'labdsv'. Ordination and multivariate analysis for ecology. R package version 1.6-1.
- ROZE, J. A. 1996. Coral Snakes of the Americas: Biology, Identification, and Venoms. Krieger.
- RULL, V. 2011. Neotropical biodiversity: timing and potential drivers. *Trends in Ecology & Evolution*. 26:508-513.
- SANDERS, K. L., M. S. Y. LEE, R. LEYS, R. FOSTER, e J. S. KEOGH. 2008. Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *Journal of Evolutionary Biology*. 21:682-695.
- SANDERS, K. L., M. S. Y. LEE, MUMPUNI, T. BERTOZZI, e A. R. RASMUSSEN. 2013. Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). *Molecular Phylogenetics and Evolution*. 66:575-591.
- SANDERS, K. L., MUMPUNI, A. HAMIDY, J. J. HEAD, e D. J. GOWER. 2010. Phylogeny and divergence times of filesnakes (*Acrochordus*): Inferences from morphology, fossils and three molecular loci. *Molecular Phylogenetics and Evolution*. 56:857-867.
- SANMARTÍN, I., e F. RONQUIST. 2004. Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology*. 53:216-243.
- SAWAYA, R. J., e I. SAZIMA. 2003. A new species of *Tantilla* (Serpentes: Colubridae) from southeastern Brazil. *Herpetologica*. 59:119-126.
- SCANLON, J. D. 2005a. Australia's oldest known snakes: *Patagoniophis*, *Alamitophis*, and cf. *Madtsoia* (Squamata: Madtsoiidae) from the Eocene of Queensland. *Memoirs of the Queensland Museum*. 51:215-235.
- . 2005b. Cranial morphology of the Plio-Pleistocene giant madtsoiid snake *Wonambi naracoortensis*. *Acta Palaeontologica Polonica*. 50:139-180.
- SCHLUTER, D., e R. E. RICKLEFS. 1993a. Convergence and the regional component of species diversity, p. 230-240. *In: Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. R. E. Ricklefs e D. Schluter (eds.). University of Chicago Press, Chicago.
- . 1993b. Species Diversity: an introduction to the problem, p. 1-10. *In: Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. R. E. Ricklefs e D. Schluter (eds.). University of Chicago Press, Chicago.
- SHINE, R. 1980. Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica*. 36:281-289.
- SHINE, R. 1991. *Australian Snakes: a Natural History*. Cornell University Press, Ithaca, NY.
- SHINE, R., e X. BONNET. 2000. Snakes: a new 'model organism' in ecological research? *Trends in Ecology and Evolution*. 15:221-222.
- SIMON, M. F., R. GREETHER, L. P. DE QUEIROZ, C. SKEMA, R. T. PENNINGTON, e C. E. HUGHES. 2009. Recent assembly of the Cerrado, a neotropical plant diversity

- hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America*. 106:20359-20364.
- SIMPSON, G. G. 1980. *Splendid Isolation: the Curious History of South American Mammals*. Yale University Press, New Haven and London.
- SITES, J. W., T. W. REEDER, e J. J. WIENS. 2011. Phylogenetic insights on evolutionary novelties in lizards and snakes: sex, birth, bodies, food, and venom. *Annual Review of Ecology, Evolution, and Systematics*. 42:227–244.
- SLINGSBY, J. A., e G. A. VERBOOM. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist*. 168:14-27.
- SPECHT, R. L. 1981. Major vegetation formations in Australia, p. 163-297. *In: Ecological Biogeography of Australia*. A. Keast (ed.). Dr. W. Junk, The Hague, Netherlands.
- STEHLI, F. G., e S. D. WEBB. 1985. The Great American Biotic Interchange, p. 532. *In: Topics in Geology*. Plenum Press, New York.
- STEPHENS, P. R., e J. J. WIENS. 2004. Convergence, divergence, and homogenization in the ecological structure of emydid turtle communities: The effects of phylogeny and dispersal. *American Naturalist*. 164:244-254.
- TWIDALE, C. R. 1972. Evolution of sand dunes in the simpson desert, central Australia. *Transactions of the Institute of British Geographers*:77-109.
- TYLER, M. J. 1979. Herpetofaunal relations of South America with Australia p. 73-106. *In: The South American Herpetofauna: Its Origen, Evolution, and Dispersal*. W. E. Duellman (ed.). University of Kansas Printing Service, Lawrence.
- VAN OOSTERZEE, P. 1997. *Where the Worlds Collide: the Wallace Line*. Reed Books Australia.
- VANZOLINI, P. E. 1963. Problemas faunísticos do Cerrado, p. 307-320. *In: Simpósio sobre o Cerrado*. M. G. Ferri (ed.). Editora da Universidade de São Paulo, São Paulo.
- VANZOLINI, P. E., e W. R. HEYER. 1985. The American herpetofauna and the interchange, p. 475-483. *In: The Great American Biotic Interchange*. F. G. Stehli e S. D. Webb (eds.). Plenum Press, New York.
- VANZOLINI, P. E., e E. E. WILLIAMS. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia*. 19:1-176.
- VANZOLINI, P. E., e E. E. WILLIAMS. 1981. The vanishing refuge: a mechanism for ecogeographic speciation. *Papéis Avulsos de Zoologia*. 34:251-255.
- VIDAL, N., J. C. RAGE, A. COULOUX, e S. B. HEDGES. 2009. Snakes (Serpentes), p. 390-397. *In: The Timetree of Life*. S. B. Hedges e S. Kumar (eds.). Oxford University Press, Oxford, UK.
- VITT, L. J. 1987. Communities, p. 335-365. *In: Snakes: Ecology and Evolutionary Biology*. R. A. Seigel, J. T. Collins, e S. S. Novak (eds.). Macmillan Publishing Company, New York.
- VITT, L. J., e J. P. CALDWELL. 2009. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. Academic Press.
- VITT, L. J., e E. R. PIANKA. 2005. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*. 102:7877-7881.

- WEBB, C. O., D. D. ACKERLY, M. A. MCPEEK, e M. J. DONOGHUE. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics*. 33:475-505.
- WEBB, S. D. 1995. Biological implications of the Middle Miocene Amazon Seaway. *Science*. 269:361-362.
- . 2006. The great American biotic interchange: patterns and processes. *Annals of the Missouri Botanical Garden*. 93:245-257.
- WERNECK, F. P. 2011. South American open/dry vegetation biomes biota diversification: historical biogeography patterns and perspectives. *Quaternary Science Reviews*. 30:1630 - 1648.
- WESTOBY, M. 1988. Comparing Australian ecosystems to those elsewhere: what is the significance of evolutionary history. *Bioscience*. 38:549-556.
- WESTOBY, M. 1993. Biodiversity in Australia compared with other continents, p. 170-177. *In: Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. R. E. Ricklefs e D. Schluter (eds.). University of Chicago Press, Chicago.
- WHITTAKER, R. H. 1977. Evolution of species diversity in land communities. *Evol. Biol.* 10:1-67.
- WIENS, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*. 58:193-197.
- WIENS, J. J., e M. J. DONOGHUE. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*. 19:639-644.
- WILSON, S., e G. SWAN. 2010. *A Complete Guide to Reptiles of Australia*. New Holland Publishers, Sydney.
- WINEMILLER, K. O., L. C. KELSO-WINEMILLER, e A. L. BRENKERF. 1995. Ecomorphological diversification and convergence in fluvial cichlid fishes. *Environmental Biology of Fishes*. 44:235-261.
- WÜSTER, W., L. PEPPIN, C. E. POOK, e D. E. WALKER. 2008. A nesting of vipers: Phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). *Molecular Phylogenetics and Evolution*. 49:445-459.

APÊNDICE 1 - Manuscrito submetido para publicação na revista *Biota Neotropica* em Dezembro de 2013.

**On the South America and Australia Connections:
A Framework for Biological Comparisons**

Davi Lima Pantoja*

*Programa de Pós-Graduação em Ecologia, Universidade de Brasília, 70910-900.

Brasília, DF. Brazil.

e-mail: pantoja.davi@gmail.com

Keywords: Gondwana, southern hemisphere, biogeography, biota, fauna, convergence.

Abstract

This paper evaluates in a comparative context the physical and ecological scenarios in which South America and Australia diversified and assembled their present biotas. It offers a framework for biological comparisons between these continents: (1) providing a list of basic bibliography; (2) describing the geographic and climatic history of both continents and their present environments; and (3) highlighting the supports for biological comparisons between South America and Australia. The biota assembly is consequence of historical-biogeographic events, past ecological relationships, and phylogenetic constraints, molded by present ecological interactions. The “natural” experiment offered by anciently disconnected continents is useful to interpret how community ecology and biogeography interact in developing the structure of present biotas. Both South America and Australia are similar in many ways, such as Gondwanan origin, present latitudes, general landscapes and ecosystems, among others. Most of both continents are covered by open structured habitats. For instance, South American Cerrado and Arid Australia are mostly covered by grassland and bush vegetation, very dry periods, poor, acidic, and aluminum-rich soils, frequent disturbance caused by fires, and abundant and diverse faunas of lizards and termites. Besides obvious particularities observed in the extant biota of each continent, shared lineages and convergences may account for similarities between biotas. The historical and contemporary scenarios of South American and Australia, including a set of similarities between present environments, support biological comparisons between these continents.

Resumo

Este trabalho avalia comparativamente os cenários físicos e ecológicos em que se formaram as comunidades biológicas da América do Sul e Austrália, e reúne os alicerces teóricos para comparações biológicas entre estes continentes: (1) fornecendo uma lista da bibliografia básica; (2) descrevendo a história geográfica e climática de ambos os continentes e seus ambientes atuais; e (3) destacando os elementos que dão suporte às comparações biológicas entre América do Sul e Austrália. A estrutura das biotas atuais é consequência de eventos histórico-biogeográficos, das relações ecológicas pretéritas, e das restrições filogenéticas de suas linhagens, que por fim, são moldadas pelas interações ecológicas atuais. Continentes com longo tempo de isolamento evoluem biotas sob significativa independência, funcionando como um experimento “natural” de longo prazo, útil para interpretar como ecologia de comunidades e biogeografia interagem no desenvolvimento das biotas atuais. América do Sul e Austrália se desmembraram de sua origem comum em Gondwana a mais de 30 milhões de anos atrás, e no presente são semelhantes em muitos aspectos, incluindo latitudes, e paisagens geral de seus ambientes. Ambos continentes são predominantemente cobertos por habitats estruturalmente abertos. Por exemplo, o Cerrado sulamericano e os desertos australianos são na sua maioria cobertos por pastagens e vegetação arbustiva, possuem períodos muito secos, solos ácidos, pobres em nutrientes, e ricos em alumínio, são frequentemente perturbados por incêndios, e possuem grande diversidade de lagartos e cupins. Além de particularidades óbvias observadas na biota atual de cada continente, similaridades entre biotas podem ser atribuídas a presença de linhagens compartilhadas e convergências. Os cenários históricos e contemporâneos da América do Sul e Austrália, incluindo um conjunto de semelhanças entre os ambientes atuais, dão suporte às comparações biológicas entre estes continentes.

1. Introduction

1.1. The history of the problem (preliminary surveys and approaches to the study of Biogeography)

Ever since Biogeography was an embryonic discipline, interest about the geographical distribution of species already stimulated researchers to use inter-continental comparisons, and the southern continents have been under major interest. Comte de Buffon (1707-1788) was one of the first scientists to postulate that disconnected parts of the world, including those with similar conditions, could be inhabited by distinct set of species. However, he also suggested that some southern continents (particularly South America and Africa) had potentially been connected by land, based on his observations on faunal similarities (Buffon 2004 [1761]). In the following century, Sir Joseph Dalton Hooker (1817-1911), Charles Darwin (1809-1882) and Alfred Russel Wallace (1823-1913) made amazing contributions to Biogeography, most of them based on long surveys in the southern hemisphere. For instance, Darwin took most of his samples and inspiration for the theory of evolution during the voyage of the Beagle throughout the southern world, from 1831-1836. Despite particularities in their own approaches, all these authors emphasized elementary differences between organisms from the southern hemisphere, even when organisms were found in the same latitudes under similar environment conditions. Hooker recognized affinities among southern hemisphere organisms in his classical “Lectures on Insular Flora” and “Flora Antarctica” published from 1840 to 1860 (see Turrill 1953; Williamson 1984). Darwin (1859) was mostly interested on the origin of species and their differentiation, and he based most of his conclusions from data collected in South America. Wallace (1860, 1876) practically established the framework for zoogeography, largely concentrated on the Australasian region.

About a century later, Philip J. Darlington Jr. (1904-1983) compiled the available information on the biogeography of the most southern continents (Darlington 1965). During this time period, theoretical discussion mainly focused on dispersal routes. General hypothesis pointed out species dispersal by land bridges (as hypothesized by Hooker and Buffon); by occasional means across water gaps (by Darwin); or by expansion and contraction ranges of immigrant species using northern routes, promoting some of the observed discontinuous distribution (Simpson 1940; Matthew 2004 [1915]). William D. Matthew (1871-1930) and George G. Simpson (1902-1984) notably defended the northern route hypothesis. Darlington recognized historical relationships among organisms living in the extreme south of the globe. He suggested that biodiversity in southern continents was formed by a complex process of invasions and colonizations, characterized by successive fluxes of northern immigrants with only occasional counter-fluxes from the southern parts (but see Sanmartín and Ronquist 2004). Despite Matthew, Simpson, and Darlington's vast works and relevant contributions to Biogeography, the confirmation that continents could move challenged their hypotheses (Dietz and Holden 1970).

During the sixties, evolution on the southern continents was enthusiastically investigated using the intercontinental parallelism approach, especially by paleontologists and mammalogists (see Simpson 1963, and the series of articles in the issues of *The Quarterly Review of Biology*, from September 1968 to June 1969). Allen Keast (1922-2009) gathered and updated the copious bibliography from this period (see Keast 1971; Keast *et al.* 1972). Keast organized a large set of examples on organisms with coincident southern distribution, arguing that circumpolar distribution patterns do not prove continental movements but represent inferential and corroborative evidences (also supported by geological data). In the early seventies,

paleontologists discovered the first assemblage of fossil tetrapods in Antarctica (Lower Triassic), which included the therapsid reptile *Lystrosaurus* (Elliot *et al.* 1970). *Lystrosaurus* was previously known from Gondwanic South Africa and India, but also from China, and its presence in Antarctica was taken as strong evidence of ancient contiguity throughout Africa, India and Antarctica, supporting the existence of a former Gondwana supercontinent, and continental drift (Keast 1972c). At this time, most biogeographers understood and agreed that distribution patterns of taxonomic groups were consequences of both dispersal mechanisms (based essentially on the ecological requirements of each group), and the geological history.

During the remaining years of the last century, remarkable works attempted to summarize the history of the southern continents and their biogeographic relationships (e.g. Simpson 1980; George and Lavocat 1993; Goldblatt 1993). The field was boosted by Wegener's theory of continental drift (Wegener 2004 [1924]), Croizat's innovative ideas of panbiogeography (Nelson 1978), and Humphries and Parenti's cladistic biogeography (Humphries and Parenti 1999). Furthermore, the field was strengthened with increasing amounts of stratigraphic, paleoclimatic and paleontological data. With the advent and acceptance of the plate tectonics and continental drift theories (Morgan 1968; Dietz and Holden 1970; Dickinson and Luth 1971; Gilluly 1971), the southern landmasses were deliberately treated under the assumption of a common origin in the Gondwanaland southern supercontinent, a term introduced by the geologist Eduard Suess in 1885 (see the concept history in Teichert 1959). Since then, the context of Gondwanaland (hereafter called only Gondwana) provides a starting point to study the distribution and evolution of southern organisms. Currently, several biogeographic discrepancies in both extant and fossil communities are explained by their shared Gondwanic origin (e.g. Waters *et al.*

2000b; Cisterna *et al.* 2006; Noonan and Chippindale 2006a; Barker *et al.* 2007; LaDuke *et al.* 2010; Rix and Harvey 2010), even though subsequent biogeographic events and assembly processes affected biotas differently in each continent. Overall, the southern distribution of continents and their relative isolation provide a “natural” long-term evolutionary experiment that has been largely used to develop basic approaches of historical biogeography such as dispersalism, phylogenetic biogeography, panbiogeography, cladistic biogeography, and parsimony analysis of endemism (PAE) (Myers and Giller 1988; Morrone and Crisci 1995).

At the beginning of the new millennium McLoughlin (2001) and Sanmartín and Ronquist (2004) supplied a collection of available data, comprehensive analyses, and the most recent understanding on historical biogeography in the southern hemisphere, highlighting the present discussion. Both plant and animal biogeography are characterized by hierarchical distribution in the southern hemisphere, although with different patterns. Extant animal distributions correspond significantly to the vicariant history of continents, whereas plant distributions are rather defined by more recent dispersal and extinction events obscuring old geologically induced vicariance. Moreover, South America and Australia were geologically connected via Antarctica for a long period of time, supporting the most common dispersal route for animals, whereas wind drift and resistant forms (e.g. seeds and pollens) are suggested to allow plant dispersal over unconnected landmasses. Reptile and amphibian fossils support the Antarctica terrestrial via of dispersal during the Early Triassic (Elliot *et al.* 1970; Colbert 1971), suggesting land connection and suitable climate. However, understanding the biological connections between South America and Australia is not trivial, requiring additional syntheses of comparative information.

1.2. *Why focus on South America and Australia?*

Comparative studies among continents have elucidated not only historical biogeography but also aspects of community ecology (e.g. Keast 1972a; Pianka 1986; Ricklefs and Schluter 1993; Luiselli 2006; Melville *et al.* 2006). South America and Australia are derived from the same supercontinent (Gondwana), experienced similar biogeographic events, and for a long time exchanged organisms with each other. They shared biological lineages in the past and still do it in the present, their extant biotas present notable particularities but also remarkable similarities between independent lineages (Keast 1969). South America and Australia are the largest extant pieces of land in the southern hemisphere, with the exception of the frozen Antarctic continent. Also, most of their areas are located between the latitude 30°S and the equator, and they frequently resemble each other in their typical landscapes and environments (including open and closed vegetation domains). This scenario provides opportunities to learn about the assembly of continental biotas by comparing their historical biogeography and the structure of present communities. However, intercontinental studies involving South America or Australia are typically contrasted to Africa and/or North America (see Goldblatt 1993; Schluter and Ricklefs 1993; Westoby 1993) rather than compared (but see Darlington 1965; Tyler 1979; Bayly 1993). Further, the few studies treating South America and Australia approached the above-mentioned disciplines independently. Researchers focused on effects of biogeographic events on species radiations (Lopretto and Morrone 1998), contemporary versus phylogenetic factors structuring current communities (Pianka 1969; Colli *et al.* 2006), or ecology of one species (Lampo and De Leo 1998). In addition, specific evolutionary-ecological hypotheses were tested using intercontinental comparisons including large amounts of data from South American and Australian faunas (e.g. the optimal foraging Costa *et*

al. 2008b, and the intermediate disturbance hypotheses). Nevertheless, a major challenge to explaining traits of extant species and communities is to find a bridge between community ecology and biogeography.

There are difficulties in including Africa and Antarctica in an inter-continental comparison with South America and Australia. Antarctica is partially or totally ice covered since the Oligocene (Lawver and Gahagan 2003), being very restrictive for life during the last 30 million years. Apart from fossil communities, a comparatively poor biota remained to be investigated, with scarce studies currently available. Africa was the first continent to split from Gondwana (during the Cretaceous), and presently the most widely connected with northern landmasses. Despite its largely austral portion, Africa has a trans-equatorial position including a vast northern hemisphere area, and duplicated temperate zones, which promoted a very distinct distribution of environments and dispersal dynamics (Keast 1972a). Furthermore, for several groups of organisms, Africa is poorly known compared to either South America or Australia (e.g. snakes (pers. comm.), and mammals Simpson 1963). For these reasons the inclusion of Africa and Antarctica in a conjoint inter-continental comparison is beyond the scope of this revision. Obviously, their inclusion in future studies will be fruitful to understand the biological connection between South America and Australia, as well as the whole southern hemisphere's biological history (which should also include Gondwanic India, Madagascar, Arabian Peninsula, and New Zealand). Hereafter, these additional landmasses will be mentioned only when providing indispensable data.

1.3. General biogeographic context

The last global continental coalescence (Pangaea) offered an amazing opportunity for terrestrial organisms to spread over the land, mixing biotas, especially under the scenario of relative climatic uniformity (e.g. Cisneros *et al.* 2012). During most of the Late Paleozoic and Mesozoic the Gondwanan terresenes posed in the southern high latitudes, resulting in the distribution of similar biotas across these united landmasses (McLoughlin 2001). However, the biological connection between continents changed drastically when they drifted apart from each other. Proto-oceans formed between the continents, making the exchange of organisms harder with time (Briggs 1987) and restarting the assembly of biological communities. For instance, many living and fossil lineages diverged and had their ranges widespread by the Late Paleozoic and Early Mesozoic (Sanmartín and Ronquist 2004). However, when continents experienced “splendid isolations” (Keast 1972b; Simpson 1980) they diversified independently, but also kept similarities. Both dispersal and vicariant evolutionary processes took place, playing significant roles in the diversification process (Croizat *et al.* 1974; Craw 1982; Noonan and Chippindale 2006b). There are several evidences of biotic exchanges (Sanmartín and Ronquist 2004), but how these events influenced the assembly of present biological communities remains poorly understood. The comparative history of species radiations and their assembly processes throughout the Late Mesozoic (beginning of Gondwana split), Tertiary, and into the Quaternary form the basis to understanding the extant biota in the southern continents.

1.4. Objectives

My main objective in this paper is to evaluate in a comparative context the physical and ecological scenarios in which South America and Australia diversified

and assembled their present communities in order to offer a framework for biological comparisons between these continents. More specifically to: (1) provide a list of basic bibliography; (2) describe the geographic and climatic history of both continents and their present environments; and (3) highlight the supports for biological comparisons between South America and Australia.

2. Palaeogeography and Palaeoclimates: a general history of continental motion and its climatic and biogeographic consequences.

2.1. Gondwana

Geography – Gondwana gave origin to most of the current southern hemisphere's landmasses, including South America, Africa, Madagascar, Antarctica, and Australia continents, but also the Arabian Peninsula and the Indian subcontinent. Similarities among presently isolated biotas of the southern hemisphere are at least partially due to their ancient history in Gondwana (e.g. Raven and Axelrod 1972; Rix and Harvey 2010). Some classic examples of southern hemisphere related organisms with present disjointed distribution are galaxioid-fishes and lungfishes (Waters *et al.* 2000a), clawed frogs (Cannatella and Trueb 1988), ratite flightless birds, southern beeches (Swenson *et al.* 2001; Heads 2006), acacia trees, and groups of ephemeropteran mayflies (Lomolino *et al.* 2010, p.396). Some mammals are also good examples of the preterit southern land connection. For instance, monotremes from the Cretaceous in South America and marsupials from the Eocene in Antarctica are commonly associated with Australia (Woodburne and Case 1996).

Although the precise timing is still controversial, evidences suggest that Gondwanan landmasses emerged during the Cambrian between 570-510 Mya (Million years ago), and the final assembly of Pangaea occurred during Permian-

Triassic period about 320-230 Mya (Meert 2003; Buchan 2004) (Table 1). Pangaea stretched from pole to pole but landmasses were in continuous movement. The Gondwana-Laurasia separation began in the Late Triassic-Early Jurassic about 200 Mya (Pitman *et al.* 1993). Gondwana began to breakup in the Middle-Early Jurassic around 180-150 Mya, drifting further south (Storey 1995; McLoughlin 2001). The geological area cladogram in Sanmartín *et al.* (2004) summarizes the available data and the sequence of vicariant events that followed the initial breakup of Gondwana (Figure 1). Veevers (2012) describes the most recent review on geological rifting between Antarctica and surrounding continents.

By the Middle-Late Jurassic about 160 Mya, the overland dispersal between western Laurasia (North America) and western Gondwana (South America) was interrupted (Iturralde-Vinent 2006). Some authors recognize two main land portions not completely isolated: West (Africa-South America) and East Gondwana [(India-Madagascar)+(Antarctica-Australia-New Zealand)] (Storey 1995). The India-Madagascar block firstly rifted from East Africa drifting southward and later rifted from Antarctica about 130 Mya. Finally, India drifted northward in the Late Cretaceous, about 84 Mya (Storey 1995; Briggs 2003). This block's drift involved several steps with the final step placing Madagascar-India as a sister group of Africa-northern South America in the area cladogram (Figure 1) (Sanmartín and Ronquist 2004). By the Late Cretaceous, the Atlantic Ocean opening increased the distance between South America and Africa, and the land block Australia-New Zealand started drift northwest disconnecting later from Antarctica at the pole (Storey 1995). However, the southern Gondwana connection throughout extreme southern parts of South America, Antarctica, and Australia lasted until Eocene-Oligocene (Veevers *et al.* 1991; Pitman *et al.* 1993; Sanmartín and Ronquist 2004). While the continents

were connected, climate differences were probably the most effective barriers to terrestrial dispersal of species, promoting distribution variations across latitudes.

Climate – Gondwana extended from the South Pole to the equator when it started to breakup. While the Late Paleozoic (especially during the Carboniferous to Permian period) witnessed glaciation events, with ice sheets in the southern portion of continents, the climate in most of this big continent was mild (Darlington 1965; Cisterna *et al.* 2006) (Table 1). During the Mesozoic the whole continent was considerably warmer than today (Parrish 1993a), although clearly, based on its broad latitudinal extension, the climate in Gondwana was not uniform. During the Triassic, Gondwana was tropical in its extreme northern portion and warm temperate southward, but with large arid intermediate portions (Axelrod 1972). The Polar region was also warm, even during the winter. Global climate change began during the Late Jurassic, particularly influenced by the new arrangement of land and water masses. During the Cretaceous, the general climate remained warm (Barron *et al.* 1993) and tropical areas flourished in West Gondwana, but the southern part of East Gondwana gradually developed a cool temperate climate (see the Climate History in the PALEOMAP Project, Scotese 2002). The Late Cretaceous was extremely warm (Parrish 1993a). The interior was drier than the coast, probably strongly seasonal, and temperature differences affected the distribution of terrestrial organisms such as Crocodyliformes (Carvalho *et al.* 2010).

During the Tertiary, the Paleocene was still warmer than today (Reguero *et al.* 2002) and the borders of Antarctica was warm temperate. Antarctic's interior remained cool temperate during the Eocene. Ice began to form only in the Late Eocene and covered the South Pole during the Oligocene (Lawver and Gahagan 2003). In general, from the Miocene onward, climate averages were similar to that in

the present (Scotese 2002). The Last Glacial Maximum and the maximum aridity (~18,000 years ago) added to oscillations during the Pleistocene were probably the most relevant large-scale climatic events after the Miocene (Bowler 1976; Colhoun 1993).

2.2. South America

Geography – Continental motion greatly influenced geographic distribution and radiation of organisms either by splitting or connecting populations. The South Atlantic began to open during the Early Cretaceous (Parrish 1993b). Crocodylian and chelonian data support the maintenance of terrestrial connections between South America and Africa during the Cretaceous (Buffetaut and Rage 1993), but the final separation probably occurred around the Middle-Late Cretaceous throughout the northern portion (Pitman *et al.* 1993). The Falklands Plateau was the last southern connection (Barron 1987), but when the exchange of terrestrial organisms using this southern route ended is still debated (see Table 2 for a comparative summary of palaeogeographic and palaeoclimatic events affecting South America and Australia since the Cretaceous and general effects upon their biotas).

During the breakup of Pangaea, South and North America disconnected during the Middle-Late Jurassic but may have reconnected several times in different ways as intermittent paths (Iturralde-Vinent 2006). By the Late Cretaceous the continent received the first Therian immigration, the foundation for the native South American land mammals (Pascual 2006). During the Tertiary (Middle Oligocene) the formation of the Drake Passage separated South America and Antarctica (Veevers 1991; Pitman *et al.* 1993; McLoughlin 2001; Lawver and Gahagan 2003). This was the last land connection uniting South America and any other southern continent. The

subsequent isolation and climate changes profoundly marked the evolution of their biological communities. The long isolation during the Tertiary (Whitmore and Stewart 1965) enabled the development of endemic biotas, and the subsequent connections provided enormous possibilities for biota's dispersals. The Mesozoic-Cenozoic transition (starting during the Tertiary period) enabled some exchanges and so did the Miocene (Parrish 1993b), but the Great American Biotic Interchange (GABI) took place later, during the Late Pliocene with the formation of the Panamanian land bridge (Simpson 1980; Stehli and Webb 1985; Coates *et al.* 1992; Iturralde-Vinent 2006; Webb 2006). Reptiles (Estes and Báez 1985; Vanzolini and Heyer 1985), birds (Vuilleumier 1984), and plants (Cody *et al.* 2010), which are better than terrestrial mammals at over-water colonization, probably started interchanging much earlier in the Cenozoic, prior to the completion of the Central American land bridge (but see Weir *et al.* 2009). Habitat generalist species probably dispersed first (Weir *et al.* 2009). The interchange was largest during the glacial Pleistocene, when sea levels were lower (more exposed land) and savanna habitats covered much of Central and northern South America (Webb 1991; Woodburne 2010). Most of the amphibian's exchanges took place after the isthmian link and predominantly from South America to North America, which contrast with the exchange pattern observed for mammals (Duellman 1979).

Climate – While belonging to vast Pangaea, most of South America's interior was arid. Only around the Middle-Late Cretaceous the northern border started slowly to become wetter, after separating from North America and Africa with the emergence of proto-oceans (Parrish 1993a; Scotese 2002) (Table 2). The southern cone was temperate when Pangaea assembled, getting warmer and wetter in the Triassic. During the Cretaceous the continent was latitudinally close to its present

position. Plant data provides evidence that the fundamental dichotomy between hot and wet versus cold and xeric regions was established during this time period (Romero 1993), presumably affecting the faunal diversification and potentially related to the present observed faunal ecological preferences for open (savannas) or closed (forests) habitats (Silva 1997; Colli 2005). The south polar front reached the southern cone after the separation between South America and Antarctica (Parrish 1993a). Around the Late Tertiary, warm and wet areas expanded in the north (Scotese 2002), but geological and biological evidences support the dominance of open landscapes and dry climates in the continent, mainly during the Neogene (Del'Arco and Bezerra 1989; Janis 1993). The Amazonian region was tropical to subtropical in the Late Miocene, resembling the present Neotropical flooded savannas: with dry seasons, covered by grasslands crossed by gallery forests, floating meadows in swamps, and shallow flood basin lakes (Latrubesse *et al.* 2010). The South American savanna biome as we currently know (a mixed grass-tree) appeared rapidly, about 8 Mya (Beerling and Osborne 2006).

Within-continent historical events – Glacial cycles and climatic fluctuations during the Pleistocene were the most recent within-continent historical event, promoting species isolation and speciation in habitat refuges (Haffer 1969; Vanzolini and Williams 1970; Brown and Ab'Sáber 1979; Vanzolini and Williams 1981). However, the importance given to the “refuge hypothesis” has been overestimated (Bush and Oliveira 2006). Several biological groups diversified before the Quaternary, and older vicariant events, especially during the Tertiary were probably more relevant for their evolutionary history (Colli 2005). Mesozoic-Tertiary tectonic interactions in the west border promoted the orogenic uplift of the Andes (Orme 2007b), which dramatically affected the entire climate and landscape in South

America (Simpson 1979; Garreaud and Aceituno 2007; Orme 2007a). The Andes reached its general shape during the Cretaceous (Taylor 1991) with an accelerated uplift since the Oligocene. Andes uplift affected drainage and sediment supplies, movement of air masses, biota's dispersal (imposing physical barriers), and promoted a sharp altitudinal gradient along the entire western portion of South America (Orme 2007a). These events created a diversity of habitats and altitudinal constraints for biota distribution, resulting in biotic specialization (Veblen 2007; Young *et al.* 2007b; Antonelli *et al.* 2009; Rull 2011). In addition, a rain shadow effect dried the Patagonian region. During the Early Tertiary (Paleocene-Eocene transition) a latitudinal gradient in temperature became more evident, leading to the continental compartmentalization of paleofloras (Romero 1993). The Central Brazilian Plateaus had its final uplift from the Late Tertiary to the Early Quaternary, providing a stark contrast to the subsidence of peripheral depressions such as the Chaco and the Pantanal (Cole 1986; Silva and Bates 2002; Porzecanski and Cracraft 2005). Divergent conditions between plateaus and depressions provided relevant conditions for vicariant events, and promoted fauna diversification in the savannas of Central South America (Nogueira *et al.* 2011).

Epicontinental seas disconnected northern and southern South America briefly during the Cretaceous (100-80 Mya) (Wilson and Arens 2001; Sanmartín and Ronquist 2004), dividing the territory along the proto-Andes into two terrestrial biogeographical provinces (Ortiz-Jaureguizar and Cladera 2006). Large portions were also covered by water during the Miocene, when the Central Brazilian Plateaus and the Guyana Shield were isolated, disconnected from each other and from the meridional continent. Several evidences support the marine transgressions hypothesis (Webb 1995; Nores 1999; Hovikoski *et al.* 2005; Hovikoski *et al.* 2007).

Nevertheless, the Andean drainage with permanent bodies of fresh water seems to have played significant roles, especially in the western Amazonia (Latrubesse *et al.* 2007; Latrubesse *et al.* 2010). During the Miocene-Pliocene transition, the Amazonas and Orinoco fluvial systems acquired their present appearance draining from the west (Andes) to the east and to the north respectively (Atlantic ocean), integrating the fluvial system in the northern South America (Hoorn *et al.* 1995; Latrubesse *et al.* 2010). However, characteristics of South American marine incursions and northern drainages from the Miocene to Quaternary are still controversial (see Irion *et al.* 2005; Rossetti *et al.* 2005b, 2005a). All these within-continent events affected faunal distribution and evolution by creating distinct environments and fragmenting species range; they were important to the South American biota's diversification, including the herpetofauna (Colli 2005; Werneck *et al.* 2009; Maciel *et al.* 2010; Nogueira *et al.* 2011), mammals (Pascual and Jaureguizar 1990), birds (Silva 1997) and other groups. However, the community level effects, specifically assembly processes remain poorly understood.

2.3. Australia

Geography – East Gondwana started its breakup (about 120 Mya – Early Cretaceous) when India and Madagascar started drifting northward (Parrish 1993b; Acharyya 2000) (Table 2). However, Antarctica and Australia remained connected for a long time, mainly through Tasmania, and did not split apart before the Late Eocene (Raven and Axelrod 1972; Veevers *et al.* 1991; Sanmartín and Ronquist 2004). Dispersal routes connecting South America were presumably feasible through a temperate Antarctica at this time period. Australia-New Guinea left the block gradually, eventually separating from Antarctica during the transition to Oligocene.

New Zealand probably separated from Antarctica much earlier, during the Cretaceous (Veevers 1991). During the Miocene, the Australian and Asian plates collided (Raven and Axelrod 1972; Hall 2001) establishing Wallace's line (Wallace 1860). This tectonic event enabled some Oriental and Australasian biota interchanges, especially through volcanic islands acting as “stepping stones” (Audley-Charles 1987; van Oosterzee 1997; Hall 2001). Earlier, during the Permian-Triassic period, potential connections between Australia and southeastern Asia also permitted some floral and faunal interchange, but this is poorly understood (Charlton 2001). Australia probably achieved its present latitude in the Late Tertiary (Scotese 2002).

Climate – During the Cretaceous, the Australasian continental fragments were at middle to high latitudes, with seasonally frigid conditions during the Early Cretaceous in high-latitudes and presumably warmed throughout the Late Cretaceous, with moderately high rainfall (McLoughlin and Kear 2010) (Table 2). Most of Australia was warm temperate during the Paleocene and Eocene and temperate forests covered the continent (Scotese 2002), even when it was connected to Antarctica. There were mangroves in the south and southeastern coasts and non-seasonal mesothermal rain forests with beech (*Nothofagus*) in the interior from the Middle to Late Eocene (Woodburne and Case 1996). A period of continued global cooling began from the Early Oligocene to Early Miocene, increasing rainfall seasonality and affecting the floras (Woodburne and Case 1996). Moreover, the entire continent got progressively warmer as it drifted northward to lower latitudes. Climatic cycles replaced the previous stable climate with wet environments, which contributed to aridification of large areas (Martin 2006; Byrne *et al.* 2008). When the Australian Plate collided onto the Pacific Plate during the Miocene, the uplift of the New Guinean highlands also changed climate patterns in Australia. The uplift created a

rain shadow effect, which increased aridity across the continent. Xeric shrublands and low woodlands, savannas, and tropical forests replaced the vast mixed gymnosperm-evergreen dicot forests (Raven and Axelrod 1972; Martin 2006). Furthermore, completely arid landforms were established from the Late Pliocene to Pleistocene (1-4 Mya) (Byrne *et al.* 2008). Therefore, similar to South America, contrasting climate belts replaced the relatively homogeneous climate during the Tertiary, which presumably affected the biota distribution and diversification. Similarities between South American and Australian climatic history (especially since the Early Tertiary) were previously suggested by Darlington (1965) when investigating the pattern of wind and rainfall in the southern hemisphere.

Within-continent historical events – Faunal distribution and diversification presumably responded to variations in climate and vegetation patterns through space and time. Vast shallow seaways flooded the continent during the Early-Middle Cretaceous, fragmenting the landmasses and promoting allopatric speciation (Gurnis *et al.* 1998; McLoughlin and Kear 2010). The Australasian region experienced marine regressions in the Late Cretaceous, but epicontinental seas persisted along the western border of Australia (McLoughlin and Kear 2010). During the Cenozoic, the island chains connecting Australia and Southeast Asia created a propitious scenario for dispersal and vicariance (Hall 2001). Moreover, the uplift of cool-temperate mountains from Malaysia to New Guinea and Australia-New Zealand were used as dispersal routes by Holarctic herbs (Raven and Axelrod 1972). During the Miocene-Pliocene, the largest Australian mountain chain was formed, the Great Divide range, which literally divided the eastern Australian environments and biota in east and west elements (Keast 1972b). Finally, climatic fluctuations from the Middle Neogene, permitted diversification in refugia during the Tertiary (e.g. isolated mountains in the

arid zone Couper *et al.* 2008; Pepper *et al.* 2011) and Quaternary (Byrne *et al.* 2008; Moritz *et al.* 2009). Evidences from paleontological and geomorphological data support the assumption that mesic animals probably found several suitable niches in central Australia up to the Late Pleistocene (Twidale 1972).

2.4. Historical overview

Not surprisingly, the amazing continental motion in the southern hemisphere had remarkable consequences to the global dynamics of life on Earth. When the last land connection to Antarctica dissolved (Drake's formation during the Oligocene), global climate became cooler because of a developing cold circumpolar current in the southern ocean, around Antarctica (Woodburne and Case 1996; Lawver and Gahagan 2003). This marine current practically froze the entire Antarctic continent. The following new climatic constraints impeded most of the previous dispersal routes and held much of the world's freshwater as ice. Subsequently, Australia turned progressively more seasonal and arid (Woodburne and Case 1996). Moreover, the northern hemisphere was affected with the appearance of the Panamanian land bridge (in the Late Pliocene) cutting off the warm water circulation, enabling northwestern Europe to grow warmer, while the Arctic cooled (Crame 2004; Lomolino *et al.* 2010).

While united through Gondwanan fragments, large portions of South America and Australia had similar latitudes (especially considering the southern portion of South America) and shared lots of climate characteristics (see the maps in Scotese 2002). For instance, during the Late Jurassic South America and Australia shared a wet belt (from southern South America to northeastern Australia) rimming southern Pangaea. This wet belt probably allowed dispersal between areas with similar climates, including the Gondwanan continents. Evidences include coal deposits, and

fossils of frogs and araucarias (Parrish 1993a). Fossil *Nothofagus* species shared between South America and Australia suggest similar climates in both continents, at least from the Late Cretaceous to Late Oligocene, including evidences for subtropical and cool temperate climates southward (Schlinger 1974). During the Tertiary, even though Australia initially occupied a more southern position, both continents experienced similar climatic phases and types of environments (the same range of vegetation types must have been available) (Keast 1972b). Darlington (1965) strongly defended the importance of climate as the main constraint to dispersal. However, geography would have inhibited biotic exchanges from and during the Late Cretaceous more than climate (Parrish 1993a). Terrestrial connections among southern Gondwanan landmasses were finally broken in Late Eocene (Veevers *et al.* 1991), but when biotic exchanges were definitely interrupted is still matter of disputes (Sanmartín and Ronquist 2004) and could even have occurred earlier in the Tertiary, especially for mammals (McGowran 1973; Woodburne and Case 1996). The appearance of the South Tasman Rise (~ 64 Mya), a major climatic cooling (~ 46 Mya), and marine transgression in the Australian southern edge (~ 42 Mya) made overland dispersal between Antarctica and Australia very improbable (Woodburne and Case 1996). Land vertebrates most likely dispersed prior to these events.

In summary, in spite of differences between organisms, similar biogeographic events deeply marked both continents, crucially affecting their biotas character's formation (Table 1 and 2). These include: (1) a common origin in Gondwana (Mesozoic), where the major lineages (e.g. families) diverged (Sanmartín and Ronquist 2004); (2) a long period of isolation during most of the Tertiary, promoting development of a large number of autochthonous and endemic lineages (Keast 1972b; Simpson 1980; Westoby 1988); (3) approximation and collision against northern

continents promoting extinction of native elements, also allowing invasion and settlement of new elements that brought “new rules” to communities (Stehli and Webb 1985; van Oosterzee 1997); and (4) repeated cycles of aridity and humidity, associated with glacial and interglacial periods, respectively, promoting speciation during repeated isolations in appropriate shelters (at lower altitudes in cold and dry periods, and higher altitudes in warm and humid periods)(Brown and Ab’Sáber 1979; Moritz *et al.* 2009). Moreover, the Southern hemisphere continents did not experience glaciations and subfreezing temperatures in the same intensity than northern hemisphere, with lighter impacts on extinction rates in South America and Australia (Keast 1972b). Although different communities could react distinctly under the same sort of historical event, because responses are often taxon-specific, in theory, both continental biotas experienced similar potential influences. There are stark differences between present biotas of South America and Australia, but they also have some interesting similarities that can be explained by convergences between different lineages occupying similar environments or by presence of shared lineages. These historical shared events affecting organism’s radiations and community assembly justify comparative studies between these two continents, especially to understand how extant biological communities have attained their present characteristics.

3. Current features: present landscapes, environments, and biogeographic provinces

3.1. South America

The South American mainland covers an area of approximately 17,700,000 km², predominantly tropical and subtropical, extending around 68° of latitude from 12°N to 56°S (Orme 2007b). Three-quarters of the continent lies within tropical

latitudes, but the southern cone is mostly temperate. In the far south, the polar influence can support glaciers near sea level (Orme 2007a).

Five main geomorphic provinces are recognized in South America (see my Figure 2, and Figure 2.6 in Orme 2007a): 1) the Guiana Highlands at the extreme north; 2) the Brazilian Highlands covering the central-eastern continent; 3) the Andes, a long mountain range extending over 8,500 km throughout the entire occidental continent and rising to 4,000 m of altitude on average (Orme 2007b); 4) the Patagonia Plateaus covering the southeastern cone; and 5) the Lowlands, which carves the continent from north to south between the eastern (Guiana and Brazilian) and western (Andes) highlands, with three subdivisions: the northern lowlands – Orinoco and Amazonas basins and the Paraguay-Parana lowlands, which runs southward until it touches the Argentinean coast. This classification is also useful to understand how topography influences the continental climate. Marked seasonality (humid summers and dry winters) is characteristic for most of the continent. There are two conspicuous dry regions over the tropical-sub-tropical band (refer to biomes in Figure 3), a portion in northeastern Brazil (Caatinga region) and western Andes (including the Atacama desert). Actually, most of the western Andes are drier than the eastern face, but this pattern is reversed in mid-latitudes (Garreaud and Aceituno 2007) causing the Patagonian Plateaus (southward) to be semi-arid (Orme 2007a). The Andes and the continental southern extremity constitute the only regions with cold climate in South America. In addition to the physiographic influences, vegetation also responds to climate conditions, mainly to annual precipitation and seasonality (Figure 4 and 5).

Global analyses have tried to provide a framework for comparisons among biological units, identifying correspondences between habitats and species assemblages (e.g. Olson *et al.* 2001; Bailey 2009). Ecoregions potentially reflect the

distribution of species and communities more accurately (combining shared evolutionary history and ecological similarities), nesting them within biomes and realms. Olson *et al.* (2001) recognized ten biomes in South America (here presented in a decreasing order by size): 1) Tropical and Subtropical Moist Broadleaf Forest; 2) Tropical and Subtropical Grasslands, Savannas, and Shrublands; 3) Temperate Grasslands, Savannas, and Shrublands; 4) Deserts and Xeric Shrublands; 5) Tropical and Subtropical Dry Broadleaf Forest; 6) Montane Grassland and Shrublands; 7) Temperate Broadleaf and Mixed Forest; 8) Flooded Grasslands and Savannas; 9) Mediterranean Forest, Woodlands, and Scrub; and 10) Mangroves (Figure 3). The distribution of the main floristic regions and vegetation types in South America were summarized by Young *et al.* (2007a). The most extensive lowland region is the great Amazon basin, in the equatorial zone of the continent, covered by humid tropical forest (Haffer 1987; Clapperton 1993b). The Central Brazilian Plateau and the Cerrado ecoregion overlap at the center of the continent, where tropical savanna formations predominate (Eiten 1972; Oliveira and Marquis 2002). There is a diagonal of open/dry vegetation from the Caatinga (northeast) to the Chaco in Bolivia-Paraguay-Argentina, traversing the Cerrado (central) (Vanzolini 1963; Werneck 2011). This diagonal is a “corridor” between the two main tropical humid forests of South America, the Amazon Forest to the northwest and the Atlantic Forest to the southeast (Oliveira-Filho and Ratter 2002). Savannas also occur in northern South America (the vast plains of the Venezuelan Llanos across the Orinoco Lowlands, as well as in isolated Amazonian enclaves). Yet, warm temperate grasslands (Pampas) occur at the east of Argentina. The physical geography and history of South American environments are discussed by Whitmore and Prance (1987), Clapperton (1993a), and most recently by Josse *et al.* (2003) and Veblen *et al.* (2007).

South American biogeographic provinces are numerous and traditionally based primarily on the distribution of extant land plants; therefore, they reflect the geological and climatic features, and consequently biome distributions (Lomolino *et al.* 2010). Morrone (2001) defined provinces with particular characteristics of soil, temperature, and rainfall, and nested them in the following subregions: Amazónica (including the Napo, Imerí, Madeira, Tapajós-Xingú, Pantanal, and most of the northern provinces); Chaqueña (Caatinga, Cerrado, Chaco, Pampa, etc.); Paranaense (largely overlapped with the Atlantic Forest); and the Andean subregions, Páramo Puneña (Puna being the largest), Chilena Central, Subantártica, and Patagónica. Both animal and plant data support the notion that South American biota has a hybrid origin. Northern South America is formed by tropical elements, mostly related to Central and North America or tropical Africa, whereas southern South America is more closely related to temperate elements from Gondwanic austral landmass (e.g. Australia, Tasmania, and New Zealand), with low exchange between the tropical and temperate regions (Crisci *et al.* 1991; Lopretto and Morrone 1998; Humphries and Parenti 1999; Sanmartín and Ronquist 2004). Contrary to expectation (see Darlington 1965), within-continent fauna dispersal occurred more frequently than flora, from southern to northern continental portions rather than vice versa (Sanmartín and Ronquist 2004).

Around half of the South American modern-fauna has North American origin (Orme 2007a). However, the proportional contribution of North American elements differs among lineages. Among vertebrates, mammals' exchanges between North and South America are probably the best documented, with northern immigrants much better invaders than southern (Webb 2006). Bird exchanges were more balanced, whereas freshwater fishes, amphibians, and reptiles demonstrated the opposite pattern

(Lomolino *et al.* 2010). The present herpetofauna is formed by ancient rather than recent invader lineages (Duellman 1979; Colli 2005). Another fundamental pattern regarding distribution of organisms in southern South America is that biodiversity decreases southward, also supported by tree, mammal, bird, amphibian, reptile, and fish data. This distribution pattern was stressed as a fundamental consequence of climate (p. 19-21 Darlington 1965). Darlington (p. 25 Darlington 1965) suggests that climate can work as a selective barrier in South America's southern cone, where severe climate conditions can eliminate or reduce the population of predators and competitors. This selective barrier allows species with lower competitive ability and/or highly susceptible to predation to persist southward. Species inhabiting the southern cone are "weaker" in inter-specific interactions but "stronger" to cold tolerance (Darlington 1965).

3.2. *Australia*

The Australian mainland covers an area of approximately 7,600,000 km², with around 70% of the continent classified as arid or semi-arid and virtually more than one-third as desert. It extends around 30° of latitudes, from 10°S to 39°S, with one-third of its mainland area north of the Tropic of Capricorn (Department of Foreign Affairs and Trade 2008). The northern part of the continent has a tropical climate (Figure 5). The only well-watered regions, other than the tropical region, are the eastern coast and the southeastern and southwestern extremities (which possess a temperate climate and moderately fertile soils) (Keast 1959). In general, the south has a wet winter and a dry summer, whereas the north has a wet summer and a dry winter, but rainfall is very unpredictable through most of the drier Australian interior (Keast 1959; Leeper 1970).

There are three main physiographical sub-divisions in Australia with most of the continent's altitude below 300 m (Figure 2): the Great Plateau of Archaean Shield covers the western half of the continent and is generally less than 600 m high (a vast desert-like plain broken by some small isolated hills); the Central Basin, a lowland of drainages characterized by shallow sandy river beds; and the Eastern Highlands which includes the Great Dividing Range, a region of undulating country (mostly between 600 and 2000 m high) with broad plains and a line of lakes and swamps along the divide (Keast 1959; Mabbutt 1970; Ollier 1979). The contrasts along the landscape affect other environmental features (such as vegetation), which presumably has a major influence on species distribution and their biological communities. According to Olson *et al.* (2001), the Australian continent consists of six biomes: 1) Deserts and Xeric Shrublands; 2) Tropical and Subtropical Grasslands, Savannas, and Shrublands; 3) Temperate Grasslands, Savannas, and Shrublands; 4) Mediterranean Forest, Woodlands, and Scrub; 5) Temperate Broadleaf and Mixed Forest; and 6) Tropical and Subtropical Moist Broadleaf Forest (Figure 3). All of them are closely connected to climatic and topographic characteristics. In addition, Mangroves appear primarily on the northern and eastern coasts of the continent (Eslami-Andargoli *et al.* 2010). Australian deserts are very unique when contrasted to deserts in other continents. In geographical terminology, the Australian deserts include semi-arid and arid but not hyper-arid elements, mostly covered by shrublands, spinifex and tussock grasslands and is highly prone to fire (Morton *et al.* 2011). Furthermore, even where woodlands are established, foliage and canopy is very sparse. Therefore, most of the Australia mainland is fairly dominated by open stands of vegetation structure (Specht 1970; Beadle 1981). In addition to the physiographic influences, vegetation also responds to climate conditions, mainly to annual precipitation and seasonality (Figure 4 and 5).

Traditionally, the Australian environment has been classified into four main biogeographic provinces (Keast 1981), although more detailed classifications have recently been made available (Mackey *et al.* 2008). 1) Eyrean Province – a vast arid or semiarid region occupying the entire central to western continent, is mostly coincident with the Great Plateau position and lacks major internal barriers. 2) Torresian Province – a warm and tropical belt in northern Australia, connected to New Guinea by land bridges during glacial episodes (Pleistocene). Torresian has the closest biological affinities with Southeast Asia (isolation occurred 10,000 years ago). 3) Bassian Province – encompassing most of the east coast and southeastern continent includes Tasmania (which was also land-connected during the Pleistocene glacial maxima). Bassian contains the highest latitudes and altitudes, with biotic elements adapted to cool and mesic climates, including *Nothofagus* and other relicts from Gondwana. 4) Westralia – a mediterranean climatic region placed at the southwestern corner, sharing taxa with South Africa (groups of Proteaceae). The latter three provinces comprise the wetter fringe of Australia. It is still hard to draw a general conclusion on the origins of the entire Australian biota. However, there are strong evidences that, similar to South America, recent and old groups have different origins, the former with northern origins (Tyler 1979). The old stocks seem to be derived by ancestral lineages once widely distributed, or have southern origin in Antarctica or Gondwana (Bodenheimer 1959).

3.3. *What is interesting contrasting South America and Australia?*

Besides historical biogeography described above, South America and Australia share many similarities in general structure of present climate and environments. Both have wet north-tropical and wet south-temperate areas separated

by drier environments that can act as barriers. Furthermore, the east coast of both continents is wetter than the interior and presumably works as a corridor (North-South) to some arid-intolerant species. Corresponding to these climate characteristics, both developed dense forests at lower latitudes, mangroves in tropical coastal regions and large open physiognomies in central and southern regions. However, the proportion of forested areas in South America is larger than in Australia.

Interestingly, both South America and Australia are mostly covered by open landscapes (savannas, shrublands, and desert-like environments) sharing some characteristics between continents. The South American Cerrado (the largest tropical savanna) and the Arid Australia have acid, nutrient- poor, and aluminum-rich soils; frequent disturbance caused by natural fires; and abundant and diverse termite faunas (Pianka 1989; Oliveira and Marquis 2002; Colli *et al.* 2006; Morton *et al.* 2011).

Comparing the Cerrado with the typical Australian savanna only, they have similar sizes ($\sim 2,000,000 \text{ km}^2$), lie on similar latitudes, and deal with comparable rainfall and temperature regimes with marked seasonality (Campos *et al.* 2011). The aforementioned common features encourage comparisons between continents (e.g. Costa *et al.* 2008a; Campos *et al.* 2011).

4. Conclusion

The biota assembly is consequence of historical-biogeographic events, past ecological relationships, and phylogenetic constraints, molded by present ecological interactions (Connell 1980; Cadle and Greene 1993; Losos 1996). The “natural” experiment offered by anciently disconnected continents is useful to interpret how community ecology and biogeography interact in developing the structure of present biotas. The historical and contemporary scenarios of South American and Australia,

including a set of similarities between present environments, support biological comparisons between these continents.

5. Acknowledgements

DLP was supported by doctoral fellowships from the Brazilian agencies CAPES and CNPq. I thank G. R. Colli, C. C. Nogueira, E. R. Pianka, D. C. Cannatella, and J. Marinho-Filho for suggestions and helpful bibliography exchange; and A. M. Gainsbury and F. P. Werneck for reviewing previous versions of the manuscript. I wrote this manuscript during a sandwich-doctorate study mission at The University of Texas at Austin (USA), part of CAPES-UT collaborative project (029/2008 'Evolução, Ecologia e Conservação da Herpetofauna do Cerrado'), sponsored by G. R. Colli (UnB), E. R. Pianka, and D. C. Cannatella (UT), whom I especially thank.

6. References

- Acharyya, S.K. 2000. Break up of Australia-India-Madagascar block, opening of the Indian Ocean and continental accretion in Southeast Asia with special reference to the characteristics of the peri-Indian collision zones. *Gondwana Research* 3(4): 425-443.
- Antonelli, A., J.A.A. Nylander, C. Persson and I. Sanmartin. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences of the United States of America* 106(24): 9749-9754.
- Audley-Charles, M.G. 1987. Dispersal of Gondwanaland: relevance to the dispersal of the angiosperms; p. 2–25 In T.C. Whitmore (ed.). *Biogeographical Evolution of the Malay Archipelago*. Oxford: Clarendon Press.
- Axelrod, D.I. 1972. Edaphic aridity as a factor in angiosperm evolution. *American Naturalist* 106(949): 311-320.
- Bailey, R.G. 2009. *Ecosystem Geography: From Ecoregions to Sites*: Springer. 251 pp.
- Barker, N.P., P.H. Weston, F. Rutschmann and H. Sauquet. 2007. Molecular dating of the 'Gondwanan' plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. *Journal of Biogeography* 34(12): 2012-2027.

- Barron, E.J. 1987. Cretaceous Plate Tectonic Reconstructions. *Palaeogeography Palaeoclimatology Palaeoecology* 59(1-3): 3-29.
- Barron, E.J., P.J. Fawcett, D. Pollard, S. Thompson, A. Berger and P. Valdes. 1993. Model simulations of Cretaceous climates: the role of geography and carbon-dioxide [and discussion]. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 341(1297): 307-315.
- Bayly, I.A.E. 1993. The fauna of athalassic saline waters in Australia and the Altiplano of South America: comparisons and historical perspectives. *Hydrobiologia* 267(1-3): 225-231.
- Beadle, N.C.W. 1981. *The Vegetation of Australia*. New York: Gustav Fisher Verlag. 690 pp.
- Beerling, D.J. and C.P. Osborne. 2006. The origin of the savanna biome. *Global Change Biology* 12(11): 2023-2031.
- Bodenheimer, F.S. 1959. The uniqueness of Australia in biology; p. 9-14 In A. Keast, R.L. Crocker and C.S. Christian (ed.). *Biogeography and Ecology in Australia*, Uitgeverij Dr. W. Junk, Den Haag.
- Bowler, J.M. 1976. Aridity in Australia: age, origins and expression in aeolian landforms and sediments. *Earth-Science Reviews* 12(2, 3): 279-310.
- Briggs, J.C. 1987. *Biogeography and Plate Tectonics*. Amsterdam: Elsevier. 204 pp.
- Briggs, J.C. 2003. The biogeographic and tectonic history of India. *Journal of Biogeography* 30(3): 381-388.
- Brown, K.S. and A.N. Ab'Sáber. 1979. Ice-age forest refuges and evolution in Neotropics: correlation of paleoclimatological, geomorphological and pedological data with biological endemism. *Paleoclimas* 5: 1-30.
- Buchan, C. 2004. Linking subduction initiation, accretionary orogenesis and supercontinent assembly Denver:
- Buffetaut, E. and J.C. Rage. 1993. Fossil amphibians and reptiles and the Africa-South America connection; p. 87-99 In W. George and R. Lavocat (ed.). *The Africa-South America Connection*. New York: Oxford University Press.
- Buffon, G.L.L., Compte de. 2004 [1761]. Excerpts from "Natural History, General and Particular" p. 16-18 In M.V. Lomolino, D.F. Sax and J.H. Brown (ed.). *Foundations of Biogeography: Classic Papers with Commentaries*. Chicago and London: The University of Chicago Press.
- Bush, M.B. and P.E. Oliveira. 2006. *The rise and fall of the refugial hypothesis of Amazonian speciation*. In *Biota Neotropica*. Accessible at <http://www.biotaneotropica.org.br/v6n1/pt/abstract?point-of-view+bn00106012006>. Captured on
- Byrne, M., D.K. Yeates, L. Joseph, M. Kearney, J. Bowler, M.A.J. Williams, S. Cooper, S.C. Donnellan, J.S. Keogh, R. Leys, J. Melville, D.J. Murphy, N. Porch and K.H. Wyrwoll. 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology* 17(20): 4398-4417.
- Cadle, J.E. and H.W. Greene. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages; p. 281-293 In R.E. Ricklefs and D. Schluter (ed.). *Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Campos, R.I., H.L. Vasconcelos, A.N. Andersen, T.L.M. Frizzo and K.C. Spena. 2011. Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. *Austral Ecology* 36(8): 983-992.

- Cannatella, D.C. and L. Trueb. 1988. Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zoological Journal of the Linnean Society* 94(1): 1-38.
- Carvalho, I.D., Z.B. de Gasparini, L. Salgado, F.M. de Vasconcellos and T.D. Marinho. 2010. Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeography Palaeoclimatology Palaeoecology* 297(2): 252-262.
- Charlton, T.R. 2001. Permo-triassic evolution of Gondwanan eastern Indonesia, and the final Mesozoic separation of SE Asia from Australia. *Journal of Asian Earth Sciences* 19(5): 595-617.
- Cisneros, J.C., F. Abdala, S. Atayman-Gueven, B.S. Rubidge, A.M.C. Sengor and C.L. Schultz. 2012. Carnivorous dinocephalian from the Middle Permian of Brazil and tetrapod dispersal in Pangaea. *Proceedings of the National Academy of Sciences of the United States of America* 109(5): 1584-1588.
- Cisterna, G.A., N.W. Archbold and T. Simanaukas. 2006. Palaeobiogeographical affinities of the Argentine Precordilleran Late Palaeozoic brachiopod faunas. *Alcheringa* 30(2): 251-262.
- Clapperton, C. (ed.) 1993a. *Quaternary Geology and Geomorphology of South America*. London: Elsevier Science Publishers B. V.
- Clapperton, C. 1993b. The physical geography of South America; p. 1-30 In C. Clapperton (ed.). *Quaternary Geology and Geomorphology of South America*. London: Elsevier Science Publishers B. V.
- Coates, A.G., J.B.C. Jackson, L.S. Collins, T.M. Cronin, H.J. Dowsett, L.M. Bybell, P. Jung and J.A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. *Geological Society of America Bulletin* 104(7): 814-828.
- Coates, A.G. and J.A. Obando. 1996. The geologic evolution of the Central American isthmus; p. 21-56 In J.B.C. Jackson, A.F. Budd and A.G. Coates (ed.). *Evolution and Environment in Tropical America*. Chicago and London: University of Chicago Press.
- Cody, S., J.E. Richardson, V. Rull, C. Ellis and R.T. Pennington. 2010. The Great American Biotic Interchange revisited. *Ecography* 33(2): 326-332.
- Colbert, E.H. 1971. Tetrapods and continents. *The Quarterly Review of Biology* 46(3): 250-269.
- Cole, M.M. 1986. *The Savannas: Biogeography and Geobotany*. London: Academic Press pp.
- Colhoun, E.A. 1993. Global comparisons of southern-hemisphere climates during the last glacial maximum: elements concerning Australia according to biogeographic and geomorphological data. *Anthropologie* 97(2-3): 155-188.
- Colli, G.R. 2005. As origens e a diversificação da herpetofauna do Cerrado; p. 447-264 In A. Scariot, J.C. Sousa-Silva and J.M. Felfili (ed.). *Cerrado: Ecologia, Biodiversidade e Conservação*. Brasília, DF: Ministério do Meio Ambiente.
- Colli, G.R., R. Constantino and G.C. Costa. 2006. Lizards and termites revisited. *Austral Ecology* 31: 417-424.
- Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35(2): 131-138.
- Costa, G.C., G.R. Colli and R. Constantino. 2008a. Can lizard richness be driven by termite diversity? Insights from the Brazilian Cerrado. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 86(1): 1-9.

- Costa, G.C., L.J. Vitt, E.R. Pianka, D.O. Mesquita and G.R. Colli. 2008b. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17(5): 670-677.
- Couper, P.J., R.A. Sadler, G.M. Shea and J.W. Wilmer. 2008. A reassessment of *Saltuarius swaini* (Lacertilia : Diplodactylidae) in southeastern Queensland and New South Wales; Two new taxa, phylogeny, biogeography and conservation. *Records of the Australian Museum* 60(1): 87-118.
- Crame, J.A. 2004. Pattern and process in marine biogeography: A view from the poles; p. 272-292 In M.V. Lomolino and L.R. Heaney (ed.). *Frontiers of Biogeography I: New Directions in the Geography of Nature*. Sunderland, MA: Sinauer Associates.
- Craw, R.C. 1982. Phylogenetics, areas, geology and the biogeography of Croizat: a radical view. *Systematic Zoology* 31(3): 304-316.
- Crisci, J.V., M.M. Cigliano, J.J. Morrone and S. Roigjuntent. 1991. Historical biogeography of southern South America. *Systematic Zoology* 40(2): 152-171.
- Croizat, L., G. Nelson and D.E. Rosen. 1974. Centers of origin and related concepts. *Systematic Zoology* 23(2): 265-287.
- Darlington, P.J., Jr. 1965. *Biogeography of the Southern End of the World: Distribution and History of Far-Southern Life and Land, with an Assessment of Continental Drift*. Cambridge: Harvard University Press. 236 pp.
- Darwin, C. 1859. *The Origin of Species by Means of Natural Selection*. London: Murray. 502 pp.
- Del'Arco, J.O. and P.E.L. Bezerra. 1989. Geologia In Fundação Instituto Brasileiro de Geografia e Estatística (ed.). *Geografia do Brasil. Região Centro-Oeste*. Rio de Janeiro: IBGE.
- Department of Foreign Affairs and Trade. 2008. *Australia in brief*. Captured on captured in September 13, 2011; www.dfat.gov.au.
- Dickinson, W.R. and W.C. Luth. 1971. A model for plate tectonic evolution of mantle layers. *Science* 174(4007): 400-404.
- Dietz, R.S. and J.C. Holden. 1970. Reconstruction of Pangaea: breakup and dispersion of continents, Permian to present. *Journal of Geophysical Research* 75(26): 4939-4956.
- Duellman, W.E. 1979. The South American herpetofauna: a panoramic view; p. 1-28 In W.E. Duellman (ed.). *The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- Eiten, G. 1972. The Cerrado vegetation of Brazil. *The Botanical Review* 38(2): 201-341.
- Elliot, D.H., E.H. Colbert, W.J. Breed, J.A. Jensen and J.S. Powell. 1970. Triassic tetrapods from Antarctica: evidence for continental drift. *Science* 169(3951): 1197-1201.
- Eslami-Andargoli, L., P. Dale, N. Sipe and J. Chaseling. 2010. Local and landscape effects on spatial patterns of mangrove forest during wetter and drier periods: Moreton Bay, Southeast Queensland, Australia. *Estuarine Coastal and Shelf Science* 89(1): 53-61.
- Estes, R. and A. Báez. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange?; p. 139-197 In F.G. Stehli and S.D. Webb (ed.). *The Great American Biotic Interchange*. New York: Plenum Press.
- Garreaud, R.D. and P. Aceituno. 2007. Atmospheric circulation and climatic variability; p. 45-59 In T.T. Veblen, K.R. Young and A.R. Orme (ed.). *The*

- Physical Geography of South America*. New York, NY: Oxford University Press.
- George, W. and R. Lavocat (ed.) 1993. *The Africa-South America Connection*. New York: Oxford University Press.
- Gilluly, J. 1971. Plate tectonics and magmatic evolution. *Geological Society of America Bulletin* 82: 2383-2396.
- Goldblatt, P. (ed.) 1993. *Biological Relationships between Africa and South America*. New Haven and London: Yale University Press.
- Gurnis, M., R.D. Muller and L. Moresi. 1998. Cretaceous vertical motion of Australia and the Australian-Antarctic discordance. *Science* 279(5356): 1499-1504.
- Haffer, J. 1969. Speciation in Amazonian Forest birds. *Science* 165(3889): 131-&.
- Haffer, J. 1987. Quaternary history of tropical America; p. 1-18 In T.C. Whitmore and G.T. Prance (ed.). *Biogeography and Quaternary History of Tropical America*. New York: Oxford University Press.
- Hall, R. 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea; p. 35-56 In I. Metcalfe, J.M.B. Smith, M. Morwood and I. Davidson (ed.). *Faunal and floral migrations and evolution in SE Asia-Australasia*, A.A. Balkema (Swets and Zeitlinger Publishers) Lisse.
- Heads, M. 2006. Panbiogeography of *Nothofagus* (Nothofagaceae): analysis of the main species massings. *Journal of Biogeography* 33(6): 1066-1075.
- Hoorn, C., J. Guerrero, G.A. Sarmiento and M.A. Lorente. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* 23(3): 237-240.
- Hovikoski, J., M. Räsänen, M. Gingras, M. Roddaz, S. Brusset, W. Hermoza and L.R. Pittman. 2005. Miocene semidiurnal tidal rhythmites in Madre de dios, Peru. *Geology* 33(3): 177-180.
- Hovikoski, J., M. Gingras, M. Rasanen, L.A. Rebata, J. Guerrero, A. Ranzi, J. Melo, L. Romero, H.N. del Prado, F. Jaimes and S. Lopez. 2007. The nature of Miocene Amazonian epicontinental embayment: High-frequency shifts of the low-gradient coastline. *Geological Society of America Bulletin* 119(11-12): 1506-1520.
- Humphries, C.J. and L.R. Parenti. 1999. *Cladistic Biogeography: Interpreting Patterns of Plant and Animal Distributions*: Oxford University Press. 187 pp.
- Irion, G., M. Rasanen, N. de Mello, C. Hoorn, W. Junk and F. Wesselingh. 2005. D. Rossetti, P. Mann de Toledo, A.-M. Goes, New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution, quaternary research 63 (2005) 78-89. *Quaternary Research* 64(2): 279-280.
- Iturralde-Vinent, M.A. 2006. Meso-Cenozoic Caribbean paleogeography: Implications for the historical biogeography of the region. *International Geology Review* 48(9): 791-827.
- Janis, C.M. 1993. Tertiary Mammal Evolution in the Context of Changing Climates, Vegetation, and Tectonic Events. *Annual Review of Ecology and Systematics* 24: 467-500.
- Josse, C., G. Navarro, P. Comer, R. Evans, D. Faber-Langendoen, M. Fellows, G. Kittel, S. Menard, M. Pyne, M. Reid, K. Schulz, K. Snow and J. Teague. 2003. *Ecological systems of Latin America and the Caribbean: a working classification of terrestrial systems*. Arlington, VA: NatureServe. 47 pp.
- Keast, A. 1959. The Australian environment; p. 15-35 In A. Keast, R.L. Crocker and C.S. Christian (ed.). *Biogeography and Ecology in Australia*. Den Haag: Uitgeverij Dr. W. Junk.

- Keast, A. 1969. Comparisons of the contemporary mammalian faunas of the southern continents. *The Quarterly Review of Biology* 44(2): 121-167.
- Keast, A. 1971. Continental drift and the evolution of the biota on southern continents. *The Quarterly Review of Biology* 46(4): 355-378.
- Keast, A. 1972a. Comparisons of contemporary mammal faunas of southern continents; p. 433-501 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A. 1972b. Introduction: the southern continents as backgrounds for mammalian evolution; p. 19-22 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A. 1972c. Continental drift and the evolution of the biota on southern continents; p. 23-87 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A., F.C. Erk and B. Glass (ed.) 1972. *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A. 1981. Distributional patterns, regional biotas, and adaptations in the Australian biota: a synthesis; p. 1895-1997 In A. Keast (ed.). *Ecological Biogeography of Australia*. The Hague - Boston - London: Dr. W. Junk.
- Kershaw, P. 1981. Climate and Australian flora. *Australian Natural History* 20: 231-234.
- LaDuke, T.C., D.W. Krause, J.D. Scanlon and N.J. Kley. 2010. A late Cretaceous (Maastrichtian) snake assemblage from the Maevarano formation, Mahajanga basin, Madagascar. *Journal of Vertebrate Paleontology* 30(1): 109-138.
- Lampo, M. and G.A. De Leo. 1998. The invasion ecology of the toad *Bufo marinus*: From South America to Australia. *Ecological Applications* 8(2): 388-396.
- Latrubesse, E.M., S.A.F. da Silva, M. Cozzuol and M.L. Absy. 2007. Late Miocene continental sedimentation in southwestern Amazonia and its regional significance: Biotic and geological evidence. *Journal of South American Earth Sciences* 23(1): 61-80.
- Latrubesse, E.M., M. Cozzuol, S.A.F. da Silva-Caminha, C.A. Rigsby, M.L. Absy and C. Jaramillo. 2010. The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth-Science Reviews* 99(3-4): 99-124.
- Lawver, L.A. and L.M. Gahagan. 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography Palaeoclimatology Palaeoecology* 198(1-2): 11-37.
- Leeper, G.W. 1970. Climates; p. 12-20 In G.W. Leeper (ed.). *The Australian Environment*. Carlton: Commonwealth Scientific and Industrial Research Organization, Australia, in association with Melbourne University Press.
- Lomolino, M.V., B.R. Riddle, R.J. Whittaker and J.H. Brown. 2010. *Biogeography*. Sunderland, MA: Sinauer Associates. 878 pp.
- Lopretto, E.C. and J.J. Morrone. 1998. Anaspidacea, Bathynellacea (Crustacea, Syncarida), generalised tracks, and the biogeographical relationships of South America. *Zoologica Scripta* 27(4): 311-318.
- Losos, J.B. 1996. Phylogenetic perspectives on community ecology. *Ecology* 77(5): 1344-1354.

- Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. *Oikos* 114(2): 193-211.
- Mabbutt, J.A. 1970. Landforms; p. 1-11 In G.W. Leeper (ed.). *The Australian Environment*. Carlton: Commonwealth Scientific and Industrial Research Organization, Australia, in association with Melbourne University Press.
- Maciel, N.M., R.G. Collevatti, G.R. Colli and E.F. Schwartz. 2010. Late Miocene diversification and phylogenetic relationships of the huge toads in the *Rhinella marina* (Linnaeus, 1758) species group (Anura: Bufonidae). *Molecular Phylogenetics and Evolution* 57(2): 787-797.
- Mackey, B.G., S.L. Berry and T. Brown. 2008. Reconciling approaches to biogeographical regionalization: a systematic and generic framework examined with a case study of the Australian continent. *Journal of Biogeography* 35(2): 213-229.
- Martin, H.A. 2006. Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of Arid Environments* 66(3): 533-563.
- Matthew, W.D. 2004 [1915]. Excerpt from "Climate and Evolution"; p. 234-244 In M.V. Lomolino, D.F. Sax and J.H. Brown (ed.). *Foundations of Biogeography: Classic Papers with Commentaries*. Chicago and London: The University of Chicago Press.
- McGowran, B. 1973. Rifting and drift of Australia and migration of mammals. *Science* 180(4087): 759-761.
- McLoughlin, S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* 49(3): 271-300.
- McLoughlin, S. and B.P. Kear. 2010. The Australasian Cretaceous scene. *Alcheringa* 34(3): 197-203.
- Meert, J.G. 2003. A synopsis of events related to the assembly of eastern Gondwana. *Tectonophysics* 362(1-4): 1-40.
- Melville, J., L.J. Harmon and J.B. Losos. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society B-Biological Sciences* 273(1586): 557-563.
- Morgan, W.J. 1968. Rises trenches great faults and crustal blocks. *Journal of Geophysical Research* 73(6): 1959-1982.
- Moritz, C., C.J. Hoskin, J.B. MacKenzie, B.L. Phillips, M. Tonione, N. Silva, J. VanDerWal, S.E. Williams and C.H. Graham. 2009. Identification and dynamics of a cryptic suture zone in tropical rainforest. *Proceedings of the Royal Society B-Biological Sciences* 276(1660): 1235-1244.
- Morrone, J.J. and J.V. Crisci. 1995. Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics* 26: 373-401.
- Morrone, J.J. 2001. *Biogeografía de América Latina y el Caribe*. Zaragoza: CYTED, ORCYT-UNESCO & SEA. 148 pp.
- Morton, S.R., D.M.S. Smith, C.R. Dickman, D.L. Dunkerley, M.H. Friedel, R.R.J. McAllister, J.R.W. Reid, D.A. Roshier, M.A. Smith, F.J. Walsh, G.M. Wardle, I.W. Watson and M. Westoby. 2011. A fresh framework for the ecology of arid Australia. *Journal of Arid Environments* 75(4): 313-329.
- Myers, A.A. and P.S. Giller (ed.) 1988. *Analytical Biogeography: an Integrated Approach to the Study of Animal and Plant Distributions*. London: Chapman and Hall.
- Nelson, G. 1978. From Candolle to Croizat: comments on the history of biogeography. *Journal of the History of Biology* 11(2): 269-305.

- Nogueira, C., S. Ribeiro, G.C. Costa and G.R. Colli. 2011. Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography* 38(10): 1907–1922.
- Noonan, B.P. and P.T. Chippindale. 2006a. Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic land bridge. *American Naturalist* 168(6): 730-741.
- Noonan, B.P. and P.T. Chippindale. 2006b. Dispersal and vicariance: the complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution* 40(2): 347-358.
- Nores, M. 1999. An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography* 26(3): 475-485.
- Oliveira, P.S. and R.J. Marquis (ed.) 2002. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York: Columbia University Press.
- Oliveira-Filho, A.T. and J.A. Ratter. 2002. Vegetation physiognomies and woody flora of the Cerrado biome; p. 91-120 In P.S. Oliveira and R.J. Marquis (ed.). *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York: Columbia University Press.
- Ollier, C.D. 1979. Evolutionary geomorphology of Australia and Papua-New Guinea. *Transactions of the Institute of British Geographers, New Series* 4: 516-539.
- Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'Amico, I. Itoua, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, T.H. Ricketts, Y. Kura, J.F. Lamoreux, W.W. Wettengel, P. Hedao and K.R. Kassem. 2001. Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience* 51(11): 933-938.
- Orme, A.R. 2007a. Tectonism, climate, and landscape change; p. 23-44 In T.T. Veblen, K.R. Young and A.R. Orme (ed.). *The Physical Geography of South America*. New York, NY: Oxford University Press.
- Orme, A.R. 2007b. The tectonic framework of South America; p. 3-22 In T.T. Veblen, K.R. Young and A.R. Orme (ed.). *The Physical Geography of South America*. New York, NY: Oxford University Press.
- Ortiz-Jaureguizar, E. and G.A. Cladera. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments* 66(3): 498-532.
- Parrish, J.T. 1993a. The palaeoclimatic history of the opening South Atlantic; p. 28-43 In W. George and R. Lavocat (ed.). *The Africa-South America Connection*. New York: Oxford University Press.
- Parrish, J.T. 1993b. The palaeogeography of the opening South Atlantic; p. 8-27 In W. George and R. Lavocat (ed.). *The Africa-South America Connection*. New York: Oxford University Press.
- Pascual, R. and E.O. Jaureguizar. 1990. Evolving climates and mammal faunas in Cenozoic South America. *Journal of Human Evolution* 19(1-2): 23-60.
- Pascual, R. 2006. Evolution and geography: The biogeographic history of South American land mammals. *Annals of the Missouri Botanical Garden* 93(2): 209-230.
- Pepper, M., M.K. Fujita, C. Moritz and J.S. Keogh. 2011. Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone. *Molecular Ecology* 20(7): 1529-1545.
- Pianka, E.R. 1969. Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50(3): 498-502.

- Pianka, E.R. 1986. *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure* Princeton, NJ: Princeton University Press. 208 pp.
- Pianka, E.R. 1989. Desert lizard diversity: additional comments and some data. *American Naturalist* 134(3): 344-364.
- Pitman, W.C., S. Cande, J. LaBrecque and J. Pindel. 1993. Fragmentation of Gondwana: the separation of Africa from South America; p. 15-34 In P. Goldblatt (ed.). *Biological Relationships Between Africa and South America*. New Haven, CT: Yale University Press.
- Porzecanski, A.L. and J. Cracraft. 2005. Cladistic analysis of distributions and endemism (CADE): using raw distributions of birds to unravel the biogeography of the South American aridlands. *Journal of Biogeography* 32(2): 261-275.
- Raven, P.H. and D.I. Axelrod. 1972. Plate Tectonics and Australasian Paleobiogeography. *Science* 176(4042): 1379-&.
- Reguero, M.A., S.A. Marensi and S.N. Santillana. 2002. Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology* 179(3-4): 189-210.
- Reyment, R.A. and R.V. Dingle. 1987. Palaeogeography of Africa during the Cretaceous Period. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59: 93-116.
- Ricklefs, R.E. and D. Schluter (ed.) 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Rix, M.G. and M.S. Harvey. 2010. The spider family Micropholcommatidae (Arachnida, Araneae, Araneoidea): a relimitation and revision at the generic level. *Zookeys* (36): 1-321.
- Romero, E.J. 1993. South American paleofloras; p. 62-85 In P. Goldblatt (ed.). *Biological Relationships Between Africa and South America*. New Haven, CT: Yale University Press.
- Rossetti, D.D., P.M. de Toledo and A.M. Goes. 2005a. New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quaternary Research* 63(1): 78-89.
- Rossetti, D.D., P.M. de Toledo and A.M. Goes. 2005b. New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. Reply. *Quaternary Research* 64(2): 280-282.
- Rull, V. 2011. Neotropical biodiversity: timing and potential drivers. *Trends in Ecology & Evolution* 26(10): 508-513.
- Sanmartín, I. and F. Ronquist. 2004. Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology* 53(2): 216-243.
- Schlinger, E.I. 1974. Continental drift, *Nothofagus*, and some ecologically associated insects. *Annual Review of Entomology* 19: 323-343.
- Schluter, D. and R.E. Ricklefs. 1993. Convergence and the regional component of species diversity; p. 230-240 In R.E. Ricklefs and D. Schluter (ed.). *Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Scotese, C.R. 2002. *PALEOMAP website*. Captured on June 1st, 2011; <http://www.scotese.com>.

- Silva, J.M.C. 1997. Endemic bird species and conservation in the Cerrado Region, South America. *Biodiversity and Conservation* 6(3): 435-450.
- Silva, J.M.C. and J.M. Bates. 2002. Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. *Bioscience* 52(3): 225-233.
- Simpson, B.B. 1979. Quaternary biogeography of the high montane regions of South America; p. 157-188 In W.E. Duellman (ed.). *The South American Herpetofauna: Its Origen, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- Simpson, G.G. 1940. Mammals and land bridges. *Journal of the Washington Academy of Sciences* 30: 137-163.
- Simpson, G.G. 1963. Mammalian evolution on the southern continents: synthesis and summing-up. Washington D. C.: XVI International Congress of Zoology.
- Simpson, G.G. 1980. *Splendid Isolation: the Curious History of South American Mammals*. New Haven and London: Yale University Press. 266 pp.
- Specht, R.L. 1970. Vegetation; p. 44-67 In G.W. Leeper (ed.). *The Australian Environment*. Carlton: Commonwealth Scientific and Industrial Research Organization, Australia, in association with Melbourne University Press.
- Stehli, F.G. and S.D. Webb (ed.) 1985. *The Great American Biotic Interchange*. New York: Plenum Press.
- Storey, B.C. 1995. The role of mantle plumes in continental breakup: case histories from Gondwanaland. *Nature* 377(6547): 301-308.
- Swenson, U., R.S. Hill and S. McLoughlin. 2001. Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. *Taxon* 50(4): 1025-1041.
- Taylor, D.W. 1991. Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Pliocene age. *Palaeogeography Palaeoclimatology Palaeoecology* 88(1-2): 69-84.
- Teichert, C. 1959. Australia and Gondwanaland. *Geologische Rundschau* 47(2): 562-590.
- Turrill, W.B. 1953. *Pioneer Plant Geography: The Phytogeographical Researches of Sir Joseph Dalton Hooker*: The Hague, Martinus Nijhoff. 267 pp.
- Twidale, C.R. 1972. Evolution of sand dunes in the Simpson desert, central Australia. *Transactions of the Institute of British Geographers* (56): 77-109.
- Tyler, M.J. 1979. Herpetofaunal relations of South America with Australia p. 73-106 In W.E. Duellman (ed.). *The South American Herpetofauna: Its Origen, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- van Oosterzee, P. 1997. *Where the Worlds Collide: the Wallace Line*: Reed Books Australia. 234 pp.
- Vanzolini, P.E. 1963. Problemas faunísticos do Cerrado; p. 307-320 In M.G. Ferri (ed.). *Simpósio sobre o Cerrado*. São Paulo: Editora da Universidade de São Paulo.
- Vanzolini, P.E. and E.E. Williams. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia* 19: 1-176.
- Vanzolini, P.E. and E.E. Williams. 1981. The vanishing refuge: a mechanism for ecogeographic speciation. *Papeis Avulsos De Zoologia* 34(23): 251-255.
- Vanzolini, P.E. and W.R. Heyer. 1985. The American herpetofauna and the interchange; p. 475-483 In F.G. Stehli and S.D. Webb (ed.). *The Great American Biotic Interchange*. New York: Plenum Press.

- Veblen, T.T. 2007. Temperate forests of the southern Andean region; p. 217-231 *In* T.T. Veblen, K.R. Young and A.R. Orme (ed.). *The Physical Geography of South America*. New York, NY: Oxford University Press.
- Veblen, T.T., K.R. Young and A.R. Orme (ed.) 2007. *The Physical Geography of South America*. New York, NY: Oxford University Press.
- Veevers, J.J. 1991. Phanerozoic Australia in the changing configuration of Proto-Pangea through Gondwanaland and Pangea to the present dispersed continents. *Australian Systematic Botany* 4(1): 1-11.
- Veevers, J.J., C.M. Powell and S.R. Roots. 1991. Review of seafloor spreading around Australia. I. Synthesis of the patterns of spreading. *Australian Journal of Earth Sciences* 38(4): 373-389.
- Veevers, J.J. 2012. Reconstructions before rifting and drifting reveal the geological connections between Antarctica and its conjugates in Gondwanaland. *Earth-Science Reviews* 111(3-4): 249-318.
- Vuilleumier, F. 1984. Faunal turnover and development of fossil avifaunas in South America. *Evolution* 38(6): 1384-1396.
- Wallace, A.R. 1860. On the zoological geography of the Malay Archipelago. *Journal of the Linnaean Society of London* 4: 172-184.
- Wallace, A.R. 1876. *The Geographical Distribution of Animals*. New York: Harper and Brothers. 607 pp.
- Waters, J.M., L.H. Dijkstra and G.P. Wallis. 2000a. Biogeography of a southern hemisphere freshwater fish: how important is marine dispersal? *Molecular Ecology* 9(11): 1815-1821.
- Waters, J.M., J.A. Lopez and G.P. Wallis. 2000b. Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthyes : Galaxiidae): Dispersal, vicariance, and the position of Lepidogalaxias salamandroides. *Systematic Biology* 49(4): 777-795.
- Webb, S.D. 1991. Ecography and the great American interchange. *Paleobiology* 17(3): 266-280.
- Webb, S.D. 1995. Biological implications of the Middle Miocene Amazon Seaway. *Science* 269(5222): 361-362.
- Webb, S.D. 2006. The great American biotic interchange: patterns and processes. *Annals of the Missouri Botanical Garden* 93(2): 245-257.
- Wegener, A. 2004 [1924]. Excerpt from "The Origin of Continents and Oceans"; p. 277-294 *In* M.V. Lomolino, D.F. Sax and J.H. Brown (ed.). *Foundations of Biogeography: Classic Papers with Commentaries*. Chicago and London: The University of Chicago Press.
- Weir, J.T., E. Bermingham and D. Schluter. 2009. The Great American Biotic Interchange in birds. *Proceedings of the National Academy of Sciences of the United States of America* 106(51): 21737-21742.
- Werneck, F.P., L.G. Giugliano, R.G. Collevatti and G.R. Colli. 2009. Phylogeny, biogeography and evolution of clutch size in South American lizards of the genus *Kentropyx* (Squamata: Teiidae). *Molecular Ecology* 18(2): 262-278.
- Werneck, F.P. 2011. South American open/dry vegetation biomes biota diversification: historical biogeography patterns and perspectives. *Quaternary Science Reviews* 30: 1630 - 1648.
- Westoby, M. 1988. Comparing Australian ecosystems to those elsewhere: what is the significance of evolutionary history. *Bioscience* 38(8): 549-556.
- Westoby, M. 1993. Biodiversity in Australia compared with other continents; p. 170-177 *In* R.E. Ricklefs and D. Schluter (ed.). *Species Diversity in Ecological*

- Communities, Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Whitmore, F.C. and R.H. Stewart. 1965. Miocene mammals and central american seaways. *Science* 148(3667): 180-185.
- Whitmore, T.C. and G.T. Prance (ed.) 1987. *Biogeography and Quaternary History in Tropical America*. New York: Oxford University Press.
- Williamson, M. 1984. Sir Joseph Hooker's Lecture on Insular Floras. *Biological Journal of the Linnean Society* 22(1): 55-77.
- Wilson, G.P. and N.C. Arens. 2001. The evolutionary impact of an epeiric seaway on Late Cretaceous and Paleocene palynofloras of South America. *In VII International Symposium of Mesozoic Terrestrial Ecosystems*. Buenos Aires: Assoc. Paleontol. Argent.
- Woodburne, M.O. and J.A. Case. 1996. Dispersal, vicariance, and the Late Cretaceous to Early Tertiary land mammal biogeography from South America to Australia. *Journal of Mammalian Evolution* 3(2): 121-161.
- Woodburne, M.O. 2010. The Great American Biotic Interchange: Dispersals, Tectonics, Climate, Sea Level and Holding Pens. *Journal of Mammalian Evolution* 17(4): 245-264.
- Young, K.R., P.E. Berry and T.T. Veblen. 2007a. Flora and vegetation; p. 91-100 *In* T.T. Veblen, K.R. Young and A.R. Orme (ed.). *The Physical Geography of South America*. New York, NY: Oxford University Press.
- Young, K.R., B. León, P.M. Jørgensen and C.U. Ulloa. 2007b. Tropical and subtropical landscapes of the Andes; p. 200-216 *In* T.T. Veblen, K.R. Young and A.R. Orme (ed.). *The Physical Geography of South America*. New York, NY: Oxford University Press.

Table 1. Summary of palaeogeographic and palaeoclimatic events affecting the connection between the Gondwanic landmasses and their biological development. The table should be read from the bottom to the top. *Italic* = climate events; *Mya* = starting Epoch age in million years ago, dates follow the International Commission on Stratigraphy 2012 time scale.

Eras	Periods	Epoch	Mya	Palaeogeography and Palaeoclimate	Effects upon biotas	References
Cenozoic	Tertiary / Paleogene	Oligocene	33.9	<i>Oligocene: ice covered the South Pole</i> Eocene-Oligocene: dissolve the last South America-Australia land connection through Antarctica	Most of Antarctic biota was extinct; enhanced isolation between southern landmasses; vicariance Vicariance	(Lawver and Gahagan 2003) (Sanmartin and Ronquist 2004)
		Eocene	55.8	<i>Eocene: Antarctic interior stayed cool temperate</i>		(Reguero <i>et al.</i> 2002)
		Paleocene	65.5	<i>Late Paleocene: Seymour Island/Antarctica had much warmer climate than today, probably temperate till the end of the Eocene</i>	Potential dispersal route	(Reguero <i>et al.</i> 2002)
Mesozoic	Cretaceous	Late	99.6	<i>Late Cretaceous: it was an extremely warm time. Gondwana interior was drier than the coast, probably strongly seasonal</i> Early Cretaceous (~120 Mya): East Gondwana started its breakup Early Cretaceous (~130 Mya): India-Madagascar block firstly rifted from East Africa, and later rifted from Antarctica	Temperature differences affected distribution of terrestrial Crocodyliformes Vicariance Vicariance	(Parrish 1993a; Carvalho <i>et al.</i> 2010) (Parrish 1993b; Acharyya 2000) (Storey 1995; Briggs 2003)

Eras	Periods	Epoch	Mya	Palaeogeography and Palaeoclimate	Effects upon biotas	References
Cretaceous				Early Cretaceous (~140-120 Mya): the last landbridge between Laurasia and Gondwana was broken	Vicariance	(Pitman <i>et al.</i> 1993; Lomolino <i>et al.</i> 2010)
			145.5	<i>Cretaceous: climate was lightly cooler than earlier, but still warmer than today. East Gondwana gradually developed a cool temperate climate</i>		(Parrish 1993a; Scotese 2002)
Mesozoic	Jurassic	Late	161.2	<i>Late Jurassic: South America and Australia share a tropical wet belt on the southern Pangaea, still connected</i>	Similar environments (vegetation and habitat structure)	(Parrish 1993a)
		Middle	175.6	Middle-Late Jurassic (~160 Mya): South America-North America separation; division in East and West Gondwana	Vicariance	(Storey 1995; Iturralde-Vinent 2006)
	Early	199.6	Early-Middle Jurassic (~180-150 Mya): Gondwana began to break up	Vicariance	(Storey 1995; McLoughlin 2001)	
	Late	228.0	Late Triassic-Early Jurassic (~200 Mya): Gondwana-Laurasia separation began	Vicariance	(Pitman <i>et al.</i> 1993)	
	Middle	245.0				
Triassic				<i>Triassic: Gondwana was tropical in the northern extreme, warm temperate southward, and arid in intermediate portions; polar region was warm</i>		(Axelrod 1972)
				<i>Throughout Mesozoic: the whole Pangaea was considerably warmer than today</i>		(Parrish 1993a)

Eras	Periods	Epoch	Mya	Palaeogeography and Palaeoclimate	Effects upon biotas	References
Mesozoic	Triassic	Early	251.0	Permian-Triassic (320-230 Mya): assembly of Pangaea	Biota interchange	(Meert 2003)
Paleozoic	Permian		299.0	<i>Early Permian (~300 Mya): the last glaciation until the Pleistocene</i>		(Darlington 1965)

Epoch	Mya	South America Palaeogeography and Palaeoclimate	Effects upon biotas	Australia Palaeogeography and Palaeoclimate	Effects upon biotas
Cenozoic Tertiary / Neogene			Amazonian landscape covered by flooded savannas and grasslands, and gallery forests		Divided the eastern Australian environments and biota in east and west elements
		<i>Late Miocene: Amazonia was a seasonal tropical to subtropical region with dry seasons (Latrubesse et al. 2010)</i>		Miocene-Pliocene: elevated the Great Divide range (Keast 1972b) Middle Miocene (~10 Mya): collision of Australian and Asian plates, forming the Wallacea (Raven and Axelrod 1972; Hall 2001) <i>Middle Neogene: Climatic oscillation (Couper et al. 2008; Pepper et al. 2011)</i> Middle Miocene (~15 Mya): Australia connects to Asia throughout islands working as "stepping stones" (Hall 2001)	Biota interchanges - Oriental and Australasian taxa
		<i>Miocene: since then average climate has been roughly similar to the present (Scotese 2002)</i>			Diversification on refugia
		Miocene: Marine transgressions - Central Brazilian Plateaus and the Guyana Shield were isolated, disconnected from each other and from the meridional continent (Webb 1995; Nores 1999; Hovikoski et al. 2005; Hovikoski et al. 2007)	Vicariance; allopatric speciation	<i>Miocene: progressive warming and aridification (Raven and Axelrod 1972; Martin 2006; Byrne et al. 2008)</i>	Dispersal and vicariance Xeric shrublands, low woodlands, savannas, and tropical forests replaced most of the forests

Epoch	Mya	South America Palaeogeography and Palaeoclimate	Effects upon biotas	Australia Palaeogeography and Palaeoclimate	Effects upon biotas
Cenozoic Tertiary / Paleogene	Mioc.	23.0	<p><i>Neogene: open landscapes and dry climates probably prevailed in the continent (Del'Arco and Bezerra 1989; Janis 1993)</i></p> <p><i>Middle-Oligocene: Global climate became much colder due to the developing of a cold circumpolar (Antarctic) marine current (Woodburne and Case 1996; Lawver and Gahagan 2003)</i></p> <p>Middle-Oligocene: final separation between the southern South America and the West Antarctica, opening the Drake Passage (Pitman <i>et al.</i> 1993; McLoughlin 2001)</p>	<p><i>Miocene: since then average climate has been roughly similar to the present (Scotese 2002)</i></p>	
	Oligoc.	33.9	<p>Oligocene: Andes uplift was accelerated (Orme 2007a)</p>	<p><i>Early Oligocene - Early Miocene: global cooling increased seasonality, affecting the vegetation structure (Woodburne and Case 1996)</i></p>	<p>Progressive increment of open landscapes</p>

Epoch	Mya	South America Palaeogeography and Palaeoclimate	Effects upon biotas	Australia Palaeogeography and Palaeoclimate	Effects upon biotas
Cenozoic Tertiary / Paleogene	Eoc.	55.8		Eocene-Oligocene (~35 Mya): Australia and East Antarctica were separated by an intervening mid-ocean ridge (Veevers <i>et al.</i> 1991) <i>Eocene: temperate forests covered the continent (Scotese 2002)</i>	Vicariance in Isolation
	Paleoc.	65.5		<i>Paleocene: most of Australia was warm temperate (Scotese 2002)</i>	
Mesozoic Cretaceous	Late	99.6	Mesozoic-Cenozoic: orogenic uplift of the Andes (Orme 2007b) <i>Middle-Late Cretaceous: the northern border started slowly to be wetter (Parrish 1993a; Scotese 2002)</i>		Vicariance, and diversification throughout the new environments at the altitudinal gradient
			Middle-Late Cretaceous (~100-80 Mya): Marine transgression (Wilson and Arens 2001; Sanmartín and Ronquist 2004) Middle-Late Cretaceous (~105 Mya): final separation between South America and Africa (through the northern portion) (Reyment and Dingle 1987; Pitman <i>et al.</i> 1993)		Vicariance; allopatric speciation
					Vicariance

Epoch	Mya	South America Palaeogeography and Palaeoclimate	Effects upon biotas	Australia Palaeogeography and Palaeoclimate	Effects upon biotas
Mesozoic		Early Cretaceous: south Atlantic began to open; South America and Africa drift from each other but remain northern land-connections; overall climate was relatively warm (Buffetaut and Rage 1993; Parrish 1993b, 1993a; Storey 1995)	Vicariance	Early-Middle Cretaceous: seaways flooded the continent, fragmenting the landmasses (Gurnis <i>et al.</i> 1998; McLoughlin and Kear 2010)	Vicariance; allopatric speciation
				Early Cretaceous: <i>seasonally cold in high-latitudes, but warming throughout the Cretaceous (McLoughlin and Kear 2010)</i>	
			Dichotomy between hot and wet versus cold and xeric vegetation, affecting the fauna's evolution (Romero 1993; Colli 2005)	Early Cretaceous: Antarctica-Australia began their separation from other Gondwanic continents (Parrish 1993b)	
	145.5	Cretaceous: latitudinally close to its present position			
Early					

7. Legend of figures

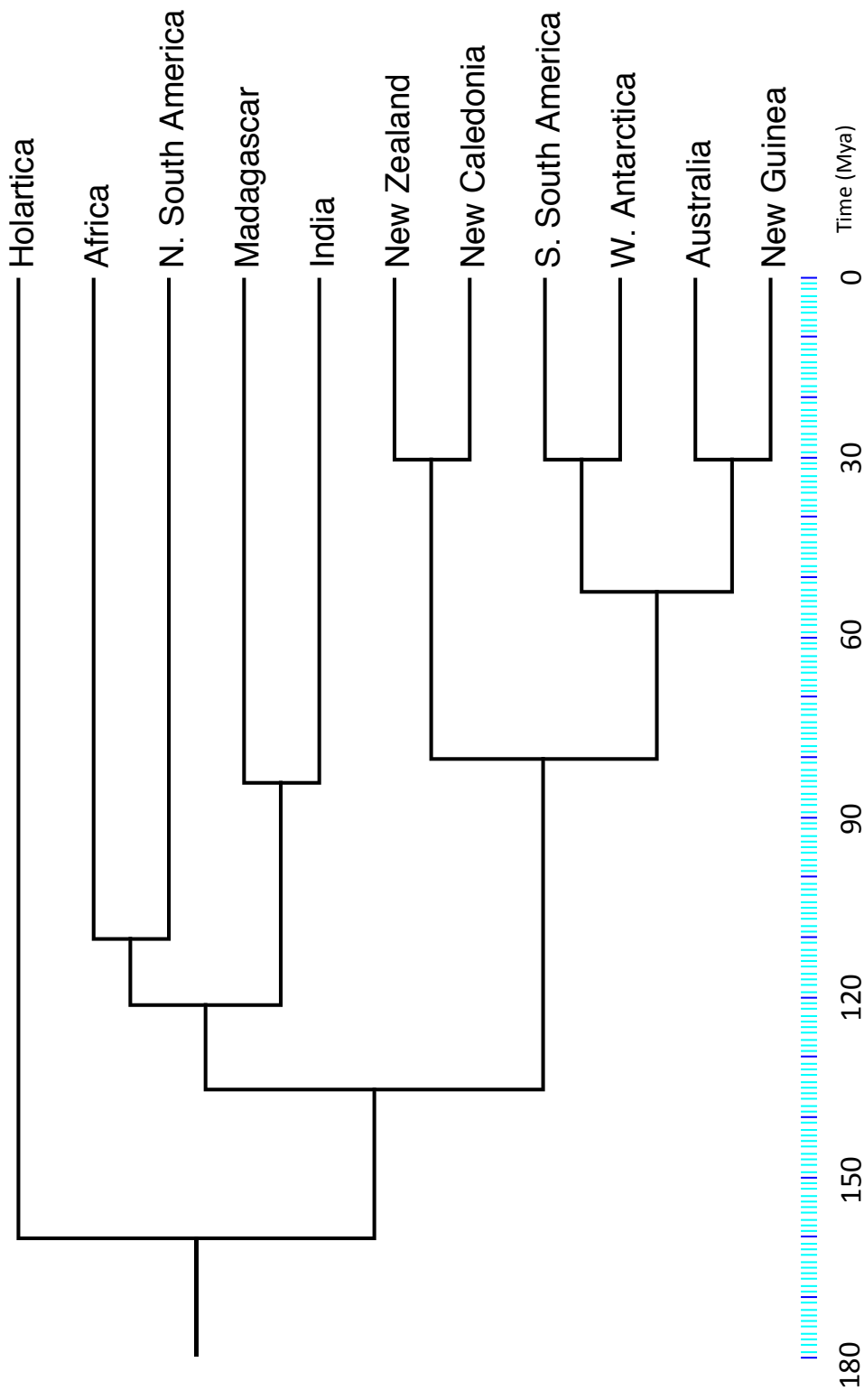
Figure 1. General history of continental motion and the relationships between landmasses once connected in Gondwana. This area cladogram is based on paleogeographic evidences and focused on the southern hemisphere. The time of vicariance is the assumed primary fragmentation (after Sanmartín and Ronquist, 2004).

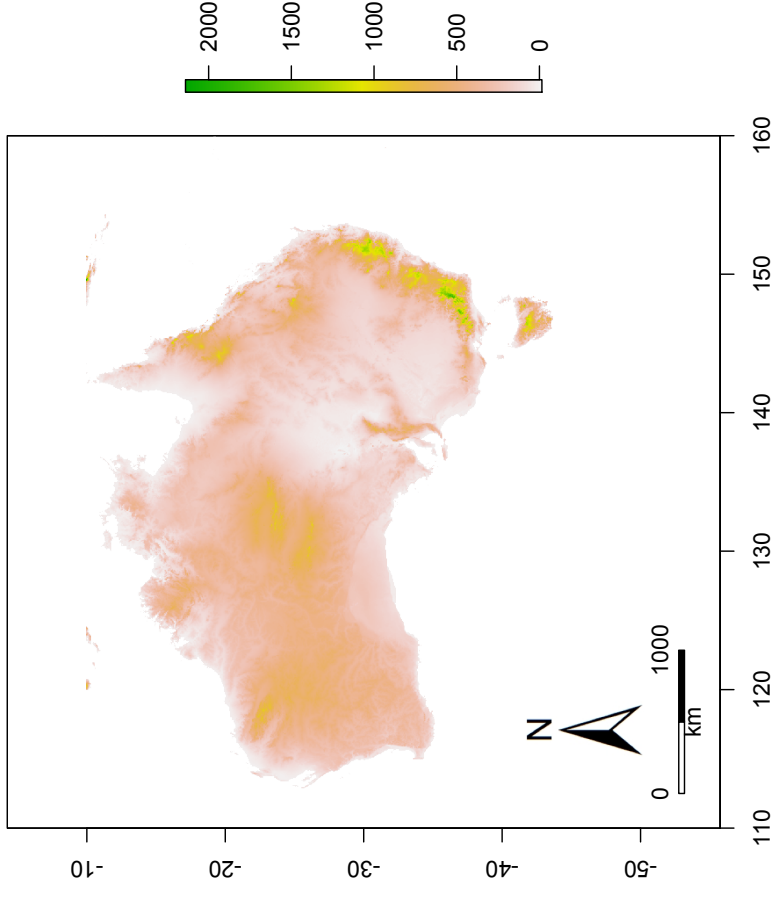
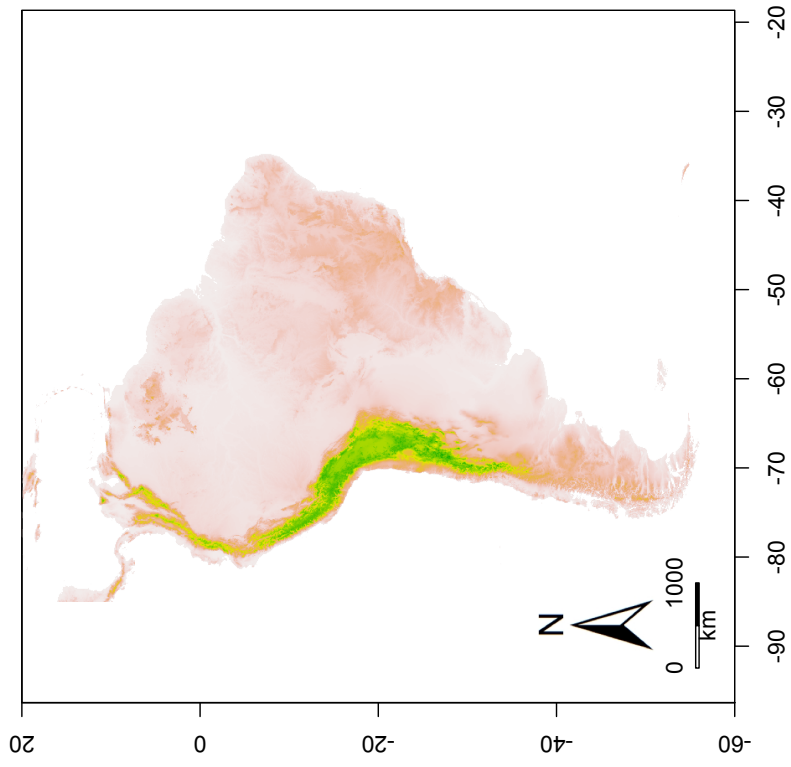
Figure 2. Present South America (left) and Australia (right) altitude. Data source: alt, WorldClim.

Figure 3. South American and Australian biomes, including the Malaysian islands. Continental relative sizes and latitudinal positions are fairly approximated, whereas longitudinal positions are arbitrary. Modified from The Nature Conservancy (TNC) Terrestrial Ecoregional Boundaries, 2009.

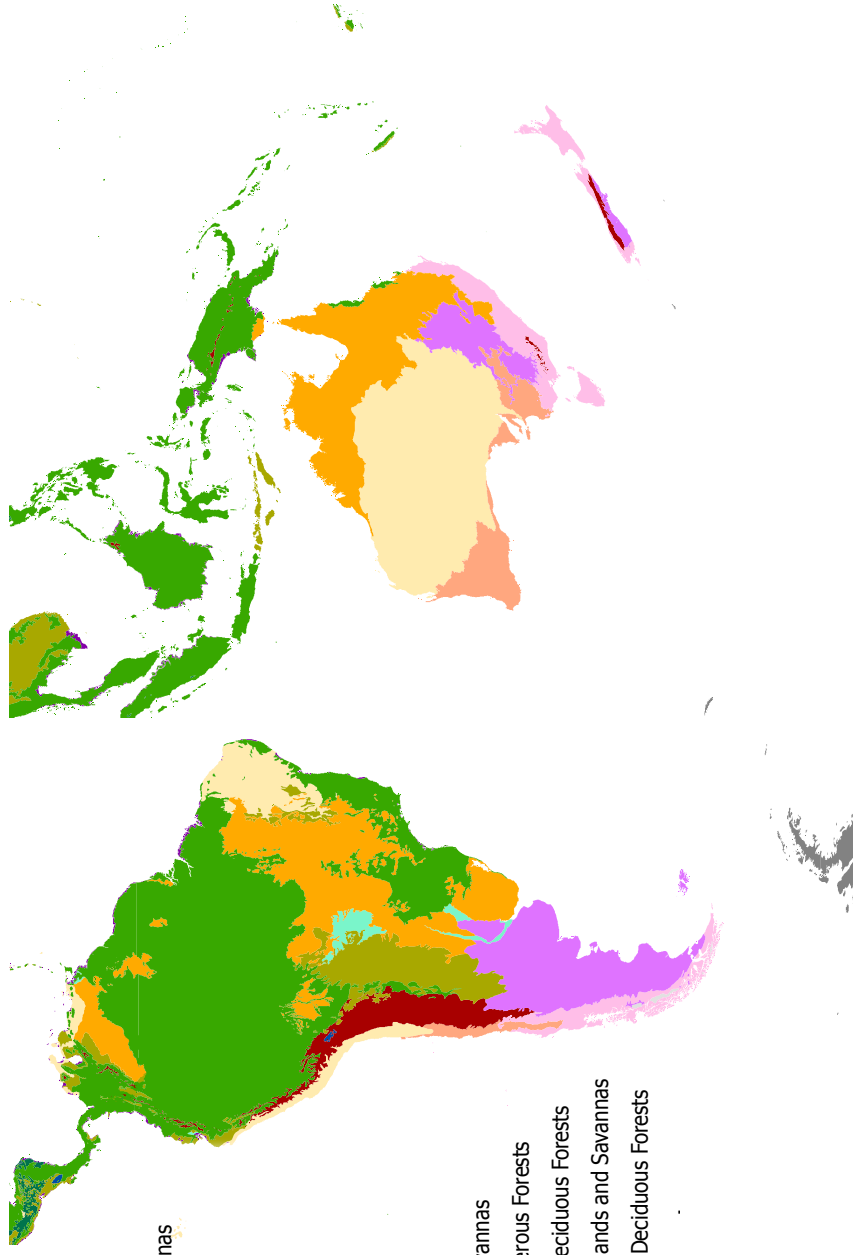
Figure 4. Present South America (left) and Australia (right) annual precipitation. Data source: bio12, WorldClim.

Figure 5. Present South America (left) and Australia (right) precipitation seasonality (coefficient of variation). Data source: bio 15, WorldClim.

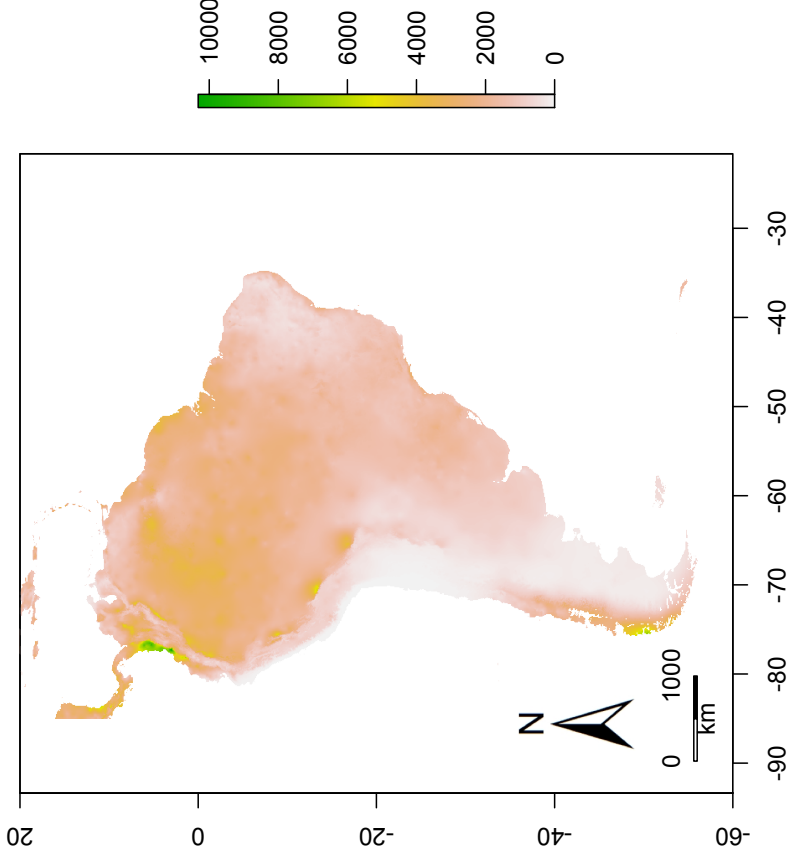
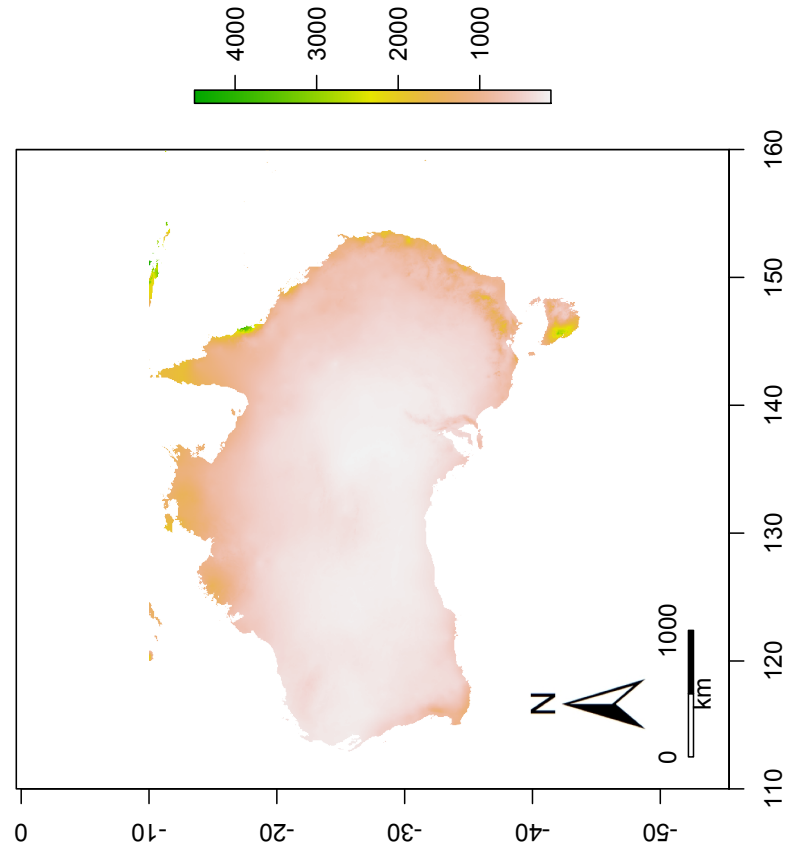


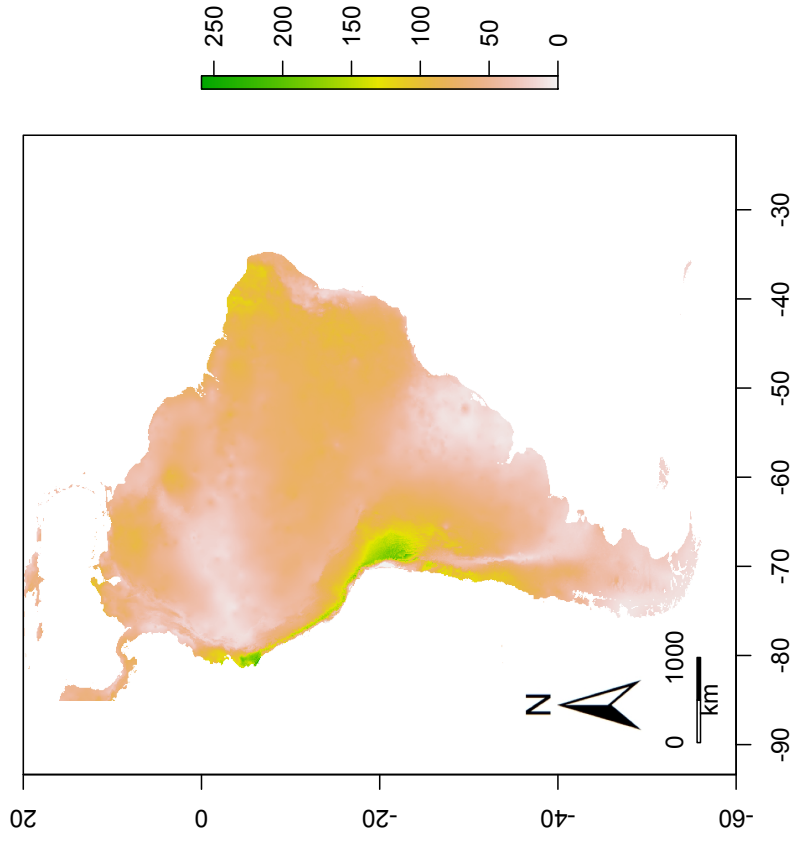
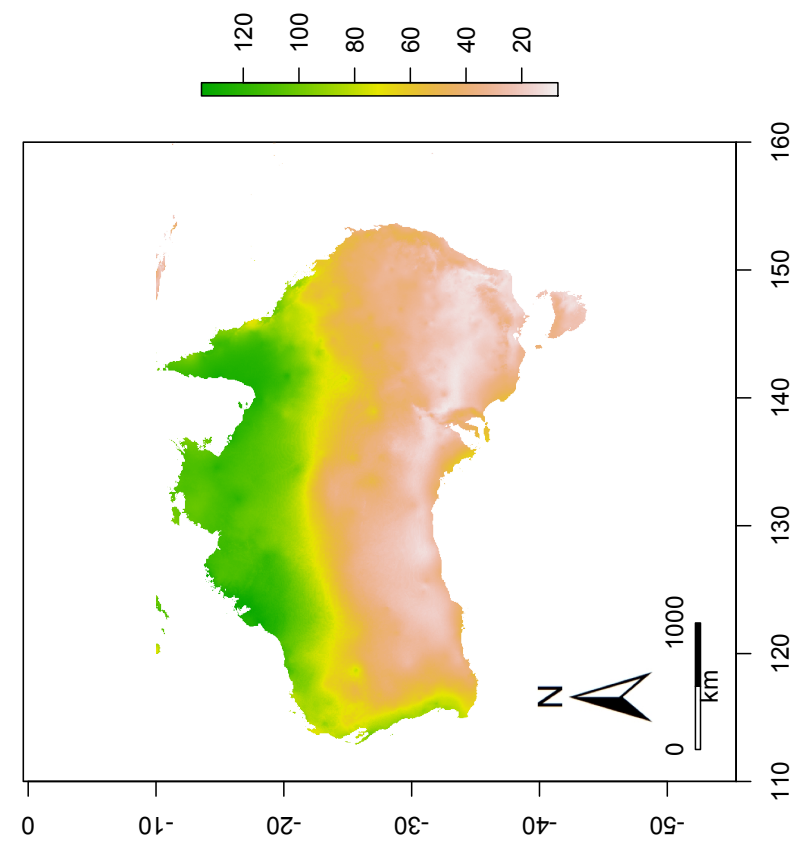


BIOMES



- Deserts
- Flooded Grasslands and Savannas
- Inland Water
- Mangroves
- Mediterranean Forests
- Montane Grasslands
- Rock and Ice
- Temperate Conifer Forests
- Temperate Deciduous Forests
- Temperate Grasslands and Savannas
- Tropical and Subtropical Coniferous Forests
- Tropical and Subtropical Dry Deciduous Forests
- Tropical and Subtropical Grasslands and Savannas
- Tropical and Subtropical Moist Deciduous Forests
- Tundra





APÊNDICE 2

Biological Comparisons between South America and Australia:

The State of the Art

Davi Lima Pantoja*

*Programa de Pós-Graduação em Ecologia, Universidade de Brasília, 70910-900.

Brasília, DF. Brazil.

e-mail: pantoja.davi@gmail.com

Keywords: Gondwana, southern hemisphere, biogeography, biota, fauna, convergence.

Introduction

Biological comparisons between South America and Australia started more than two centuries ago as indirect results from global comparisons, especially concerning the southern hemisphere landmasses (Pantoja *in review*). Early researchers noticed similar environments distributed in similar latitudes and discussed similarities and differences between their habitants (Darlington 1965). Later, the establishment of theories on evolution and continental drift lead scientists to interpret similarities between continental biotas as adaptive convergence or kinship (phylogenetic proximity) (Keast *et al.* 1972). There are several lineages of fossil and living organisms with southern hemisphere distribution, reflecting a historical combination of vicariant and dispersal events (Sanmartín and Ronquist 2004). Therefore, a good place to start understanding the South American and Australian connection is by listing the shared lineages.

The objective in this paper is to compile and organize the available knowledge on biological comparisons between South America and Australia. I also evaluate traditional and innovative approaches, review methods for analyses, list hypotheses on the biota's assembly in these continents, and raise questions to guide future research in the field.

Shared biota

Table 1 presents a set of examples of non-marine monophyletic taxa shared by South America and Australia. I did not include continentally endemic clades because they represent an independent history, whereas cosmopolitan clades were included only when predominantly distributed in the southern hemisphere. Microorganisms were not included either, although there are lineages common to South America and

Australia. Examples include several genera of fungi (Crisci *et al.* 1988) and ciliates (Foissner 1997). While this is not an exhaustive neither complete list, it is a result of an extensive effort to compile available data and offers an overview of southern shared groups occurring in South America and Australia, fairly reflecting proportions between shared taxa.

My sample contains 70 lineages: 55 animal (87% invertebrates) and 15 plant groups. Despite the present long distance between South America and Australia, the total number of taxa and the variety of clades included (from microorganisms to vertebrates) suggest that shared distribution is not an exception. It is a frequent pattern, although there is no evidence that this is the prevailing pattern. Furthermore, shared distribution implies two alternative explanations: 1) the focal clades had an ancient origin (usually since Gondwana), spreading through the southern hemisphere essentially due to continental drift and later followed by vicariant diversification within clades; or 2) focal clades reached landmasses more recently by dispersal events (usually over land bridges, by stepping stones over short water bodies, or carried by wind and ocean currents). The taxa list is dominated by invertebrates and plants, which are older lineages and better dispersers than vertebrates, especially insects. The relatively balanced numbers of insects between genus level and higher taxa suggest both old and recent biogeographic events. When recognizing an impressive number of lineages with common distribution, central questions remain to be answered. How does each common lineage shape the structure of present biotas in each continent? How did the interaction with unshared lineages and independent histories of each continent produce the differences in their present biota's structure? However, comparative studies including organisms from South America and Australia are fewer than the number of shared lineages.

Comparative studies

I listed 35 studies directly comparing South American and Australian organisms (Table 2). Studies primarily focused on taxonomy and/or systematic were not included. In contrast to the numbers of shared lineages, most comparative studies used strictly vertebrates as model organisms, representing almost half (16 studies). Among the remaining studies, most of them includes invertebrates (see Invertebrates, Vert. + Invert., and General fields at the Table 2). Publications comparing ecosystems, plants, or microorganisms are less frequent. Most of the available studies approach biological relationships between continents based on ecology (15), mainly comparing community parameters (9). Eight publications are primarily focused on biogeographical discussions, predominately using animals (5). Studies comparing entire faunas (10) or floras (2) are particularly relevant for intercontinental comparisons. Although using a relatively coarse scale, these studies usually discuss interactions between ecology and biogeography, and compare larger sets of organisms, in larger geographic scale.

Despite the larger number of comparisons considering entire faunas, I only found two studies on the ecology of specific taxa, both with frogs. Martin (1970) compared the embryonic development between South American and Australian amphibians, finding remarkably similar adaptive radiations. He recognized a parallel tendency in the embryonic development of the Neotropical Leptodactylidae and the Australian Limnodynastidae families (interpreted by Martin as part of the same family, the former), suggesting an “adaptive shift from a primarily riparian to a primarily terrestrial mode of life”. The acquisition of terrestriality was associated with characteristics of the foamy egg mass, such as large egg diameters and small clutch

sizes. However, the typical mucous foam nests are apparently produced by different methods in South America and Australia, suggesting independent selection and refinement in each continent. At least one South American amphibian species, the toad *Rhinella marina* (formerly *Bufo marinus* in the old taxonomy), is known to be introduced to Australia. A mark-recapture study reveals that *R. marina* live in denser populations in Australia than in their South American original habitat, attributing the difference to increased adult individuals survivorship in Australia (based on age-structured population models) (Lampo and De Leo 1998). The most intuitive hypothesis explaining the increased survivorship is the absence of natural predators in Australia (Phillips *et al.* 2003; Hayes *et al.* 2009).

Many researchers have compared communities. Medel (1995) contrasted harvester ant assemblages from arid and semi-arid South America and Australia using ANOVA procedures (Schluter 1986) and pairwise-continent comparisons with community attributes (abundance at bait, body size, and foraging distance/mode). He found overall absence of convergences and argued that the observed ecology was reflecting historic-regional constraints of each continent rather than responding to local selection pressures promoted by present-day environments. However, Campos *et al.* (2011) compared ant diversity in savanna woodlands of Brazil and Australia using a multi-scale approach (traps associated with a tree, trees within a transect, and transects within the savanna). Although both savannas have similar climate and environments, their ant faunas have different biogeographic origins, which is reflected in community structure. Species richness in the Brazilian savanna is higher at the tree, transect, and overall scales. Differences at the trap scale were imperceptible. On the other hand, total ant abundance was larger in Australia than in Brazil. Moreover, taxonomic compositions are similar considering higher taxa (*e.g.* subfamily), but they

share few genera and species. The scale-dependent difference between continents was attributed to the biogeographic history of each ant's fauna (regional processes). Most of the ants in the Brazilian savannas are derived from arboreal forms originally living in tropical rainforest habitats, whereas Australian savannas consist of arid-adapted lineages radiated from the vast arid zones of Australia. This hypothesis is supported by the fact that arboreal and ground ant faunas are significantly different in both Brazilian and Australian savannas, with larger divergences in the former presumably reflecting the larger proportion of forested areas in South America. The observed pattern should be tested with other organisms.

Duellman and Pianka (1990) used frogs and lizards to discuss biogeography and community structure of arboreal and nocturnal insectivores. Comparisons included total and local diversity of species from Neotropical, Australopapuan, Ethiopian, and Oriental regions. They found that the numbers of nocturnal species of frogs are inversely related to those of nocturnal lizards. The higher richness of frogs in Neotropica and nocturnal lizards in the Old World were attributed to their ecological requirements and recent-historical availability of suitable habitats, rather than to differences in geographical history of lineages or to competition between frogs and geckos. The greater climatic seasonality in the Old World tropics favored the diversification of nocturnal lizard lineages (i.e. geckos), rather than frog radiations that apparently benefit from the less seasonal climates and the presence of bromeliads (largely used as humid shelters by frogs) in Neotropica. This study supplies an illustration of how ecology filters the historical elements shaping the structure of biological communities through time.

The diet niche-dimension has been mostly used comparing lizard communities (Pianka 1986). Using lizard data from several continents, including South America

and Australia, Costa *et al.* (2008b) found a negative association between body size and niche breadth with larger lizards consuming larger prey (more profitable) instead of a range of small prey. Authors used the optimal foraging theory to explain this macroecological pattern. Termites are one of the main food items in lizard diets. Moreover, Brazilian savannas (Cerrado) and arid Australia have high richness and abundance of both lizards and termites. The diversity of lizards in the Cerrado is not driven by termite diversity as suggested for arid Australia (Morton and James 1988), but it is important in maintaining lizard richness (Colli *et al.* 2006; Costa *et al.* 2008a). However, local lizard assemblages are relatively impoverished in the former, and prey heavier on termites in the latter. Amazonian lizards also feed on a smaller proportion of termites than the Australian lizards. The pattern is explained by overall prey availability, the richer arthropod fauna in the Cerrado and Amazonia offers more options than the Australian deserts (Costa *et al.* 2008a). Yet, Colli *et al.* (2006) suggest that area and latitudinal effects moderated by present-day ecological factors account for the observed differences between lizard richness. Indeed, a set of specific environmental and ecological factors has been suggested to affect lizard communities in arid Australia (Pianka 1989) and Cerrado (Colli *et al.* 2002; Nogueira *et al.* 2009). Some of these factors, such as frequent fires, are largely shared between both regions (Pantoja 2007; Pianka and Goodyear 2012; Costa *et al.* 2013; Pantoja *et al.* in prep.).

Schluter and Ricklefs (1993) tested convergences in species diversity comparing assemblages from different continents using three scales: between climate zones, habitats, or microhabitats. Community convergence is expected when the number and types of co-existing species are locally determined. The absence of convergence is suggested as a consequence of predominantly historical and regional effects on species diversity. Therefore, convergence could quantify the habitat

capacity to predict species diversity across relatively independent regions. Of their intercontinental comparative list of species diversity from similar habitat around the world, only one example compared South America and Australia directly, demonstrating a strong main effect of region on local species diversity. The evidence comes from bird diversity decreases with increasing vegetation diversity (foliage height) in the temperate South America, with the opposite tendency in Australia and North America. However, different groups of organisms were globally compared (including plants, vertebrates, and invertebrates), with the overall result indicating that convergence in species diversity is highly expected in nature. Therefore, similar habitats (as an ecological attribute) are expected to cause similar effects on the number of coexisting species (it does not mean that species assembly and evolution promotes identical diversities on a regular basis).

The only study I found directly comparing South America and Australia considering microorganisms is very descriptive and marginally relies on community ecology. The Foissner's paper (1997) calculated alpha diversity of soil ciliates (Protozoa: Ciliophora) in evergreen rain forests from Neotropical and Australian regions. Besides recognizing 34 new species and describing four of them, the study provides a list of several shared species between South America and Australia. This paper presents an area cluster based on similarities in species diversity, calculated by Jaccard's coefficient. Amazonian localities in Brazil were clustered together, with the highest species diversity. However, because its overall data was strongly biased (see Foissner's discussion), the study poorly approached the community structure, and did not discuss the historic biogeography.

Morton (1985) conducted comparisons on the ecosystem level combining vertebrate and invertebrate (birds, mammals, and ants) granivory in arid Australia

versus South and North American deserts. North America has the highest rates of seed predation and mammals are non-significant seed consumers in Australia. Furthermore, removal rates of seeds by ants and birds are significantly greater in Australia than South America. Finally, Morton concluded that the intensity of seed predation in these similar ecosystems from different continents is not convergent. Ecosystem comparison was also conducted by Solbrig (1996), who studied the savanna ecosystem all over the tropical world. There are differences in vegetation structure and species composition between continents, but the range of soil types and climate regimes are quite similar, with marked seasonality. In the tropical savannas soils are usually dystrophic and the determinant climate characteristics are annual rainfall, length of the dry season, and temperature differences between the warmest and coldest month. Generally, the South American savannas are widespread with large and small patches south and north of the equator, whereas in Australia they occur in sub-humid regions from southeastern Queensland through the north of Australia. Within continents, the regional differences in soils and climate determine the main types of savannas, whereas the main effect of topography and geomorphology appears locally on the vegetation structure and floristic composition. Usually, grassland vegetation stands prevail where annual rainfall is low and the reverse for woodland vegetation, always molded by temperature, seasonality, and soil character. The South American savannas are by far richer than the Australian savannas, although sharing some lineages. At least five grass genera, among the principal species, occur in both continents. Two graminoid families that dominate the herbaceous stratum (Gramineae and Cyperaceae) and at least ten families among the principal trees are shared. The presences of Gondwanic elements (e.g. Bombacaceae,

Combretaceae, Proteaceae and others) suggest the existence of a proto-savanna before the Gondwana breakup.

Darlington (1965) investigated historical biogeography in the south hemisphere, emphasizing comparisons between its three extant cold-temperate lands: southern South America (including Tierra del Fuego), southeastern corner of Australia (with Tasmania), and New Zealand. Similarities include general position and dimensions, lying south of the tropics and extending into colder latitudes, and climatically affected by the sea if they are either islands or narrow peninsulas. They have been isolated since the Early Tertiary, experienced similar climatic histories (warmer than present during the Mesozoic and most of the Tertiary and glaciated in the Pleistocene), and reached similar present-day climates (cool-temperate, oceanic climates, and localized heavy rainfall). The observed climates in these small lands are apparently more similar to certain altitudes in the tropics than in corresponding north-temperate latitudes, affecting plant and animal distribution. Despite of the geographic origin of southern living organisms, the remarkable similarities between their biotas were attributed, at least partially, to those mentioned historical and environmental similarities. In addition, the Antarctic climates before the Pleistocene probably were very similar to those in southernmost South America, Tasmania, and New Zealand, at least along to the continental edges. This enabled them to share their biotas.

Darlington's classic book (1965) discussed the general distribution pattern of southern biota, focusing on southern beeches (*Nothofagus*), phytophagous peloridiid bugs, and some lineages of predaceous carabid beetles, all with southern distribution that generally resemble each other. Darlington (1965/ chapter 3 and 4) hypothesized that these groups evolved through dispersal events (what he called immigrant pattern) rather than by vicariance (relict pattern). Yet, Darlington considered the continental

drift theory to have little support (chapter 19), doubted the former existence of Pangaea and Gondwanaland, and argued that organism dispersions (although strongly constrained by climate) were more feasible than continental movement. Climate after the Permo-Carboniferous glaciation up to the freezing of Antarctica was assumed to be temperate and probably seasonal, although cooler than tropical. Thus, Darlington's explanations for southern plant and animal distributions do not require land connections. He suggests that dispersal took place between water gaps, probably narrower than nowadays, at least while Antarctic edges were habitable. Dispersal routes around the southern end of the world were suggested to prevail from the west to east, following the predominant direction of currents and winds. Finally, he concludes that southern biodiversity was formed by successive invasions from or across the tropics, with minor counter invasions from the southern tips.

Several independent lineages of crustaceans are recognized to occur in both South American and Australian continents, e.g., the Syncarida: Anaspidacea and Bathynellacea (Lopretto and Morrone 1998); Decapoda: Parastacidae (Williams 1981); Copepoda (Bayly 1993); and Cladocera (Hann 1986; Colbourne *et al.* 2006). Bayly (1993) studied the athalassic inland saline waters, looking for similarities and differences between South American and Australian faunas. Two genera of planktonic crustaceans are shared between saline lakes on both continents, *Boeckella* (Copepoda) and *Daphniopsis* (Cladocera), representing a large proportion of their faunas. Faunal similarities were attributed to ancient Gondwanic origin and similarities between the lake's environments. On the other hand, significant differences were attributed to the relatively recent extinction of predaceous birds in Australia. The Australian saline lakes developed an additional crustacean fauna (mainly ostracods and diatoms) apparently following the demise of carnivorous and

diatom-grazing birds (e.g. flamingos). Interestingly, the inland saline waters in Australia developed their own diatom-grazing, the macro-invertebrate *Haloniscus* (Isopoda).

Lopretto and Morrone (1998) used the panbiogeographic approach to investigate distributional patterns of South America syncarid crustaceans. The South American Syncarida occurs from north to south of the continent with clearly disjunct distributions, divided into four groups: Argentina and Chile, southern Brazil and Paraguay, northern Brazil, and Venezuela. Seventeen genera currently occur in South America, of which five also occur in Australia, corresponding to three families: Bathynellacea *Bathynella* (Bathynellidae), *Atopobathynella*, *Chilibathynella*, and *Hexabathynella* (Parabathynellidae), and Anaspidae *Stygocaris* (Stygocarididae). Analyses combining the distribution of shared genera recognized two generalized tracks forming the South American syncarid microfauna: the northern tropical track connecting tropical South America and tropical Africa with an Atlantic Ocean basin baseline, and a southern temperate track connecting southern South America and Australia-Tasmania-New Zealand with a Pacific basin baseline. This result corroborates previous studies (Crisci *et al.* 1991; Amorim and Tozoni 1994; Sanmartín and Ronquist 2004) suggesting two main biotic components with different biogeographic affinities forming the continental biota of South America. However, considering a wider range of taxa, there is no unique biological connection pattern among the southern landmasses, suggesting that South America has been closely linked to other southern areas at different times.

Tyler (1979) and Duellman (1979) probably provided the first data compilation accounting for affinities between South American and Australian herpetofauna. Tyler (1979) depicted the palaeoenvironmental context where the

modern non-marine Australian herpetofauna originated, including the nature of the Australopapuan-Oriental collision. Using fossil records, morphological divergences, geographic distribution (past and present), and phylogenetic relationships he distinguished the Australian herpetofauna origins and composition in Oriental, Gondwanan, and Autochthonous elements. Oriental elements include: Microhylidae, and Ranidae; Agamidae, Scincidae, and Varanidae; Acrochordidae, Boidae, Colubridae, Elapidae, Typhlopidae, and Uropeltidae (the latter referring to the present *Cylindrophiiidae* clade that historically reached the Aru Islands, but not the Australian mainland); Carettochelyidae, and Trionychidae. Gondwanan elements include: Hylidae, Leptodactylidae (the present Myobatrachidae + Limnodynastidae), and the frog genera *Australobatrachus*, *Geocrinia*, *Limnodynastes*, *Litoria*, and *Ranidella* (with fossils presumably Gondwanic, although they do not predate the Australopapuan-Oriental collision); Gekkonidae; Chelidae; and crocodiles (probably with mixed origins, both gondwanic and oriental). Autochthonous elements include the lizards Pygopodidae, and although with controversial origins, the faunas in the western pacific island (which include the rhynchocephalian *Sphenodon*; endemic Gekkonidae, Iguanidae, and Scincidae, and amphibian genera *Leiopelma* and *Ascaphus*). Interestingly, data from Tyler's review suggest there is no living family of snake in Australia with direct Gondwanan origin, i.e., all living lineages of Australian snakes are relatively recent elements, derived from Oriental ancestry. Compared to the North American invasion in South America, the Oriental influence upon Australian herpetofauna was probably heavier, because South American herpetofauna was more diverse and better established when received colonizers (Tyler 1979).

Likewise, Duellman (1979) discussed present-day families of South American herpetofauna based on their origin, temporal and geographical distribution, dispersal,

and differentiation. South American families have Pangaea (the oldest elements), Gondwanaland, or Laurasia (northern immigrants) origins. For taxonomic decisions in the late seventies, Family resemblances between South America and Australia include the alligators Crocodylidae, the lizards Gekkonidae and Scincidae, and the snakes Boidae, Colubridae, and Typhlopidae. Considering snakes, Duellman suggested that Boidae had a Pangaea origin; Anomalepididae, Tropidophiidae, and Micruridae (present Elapidae, also shared with Australia) had Gondwanaland origin; Aniliidae and Viperidae had Laurasia origin; and Colubridae, Leptotyphlopidae, and Typhlopidae with uncertain origin (but see Colli 2005/ for recent data and present interpretations). Until 1979, South America had 9 described families, 96 genera, and 556 recognized species of snakes, whereas Australia had 4 families, 36 genera, and 104 species of non-marine snakes. South America had higher snake diversity and species density, with 31.2 species/million km² compared to 13.5 for Australia. Lizards in Australia and frogs in South America had species density higher than expected, attributed to the larger proportion of xeric areas in Australia and humid tropical forest in South America. Contrary to Australia, tropical rainforest in South America is divided into distinct units (e.g. Amazonian, trans-Andean, and Atlantic coastal) enabling differentiation and endemism (Lynch 1979). Overall, the higher taxonomic diversity in South America was attributed to its higher habitat diversity, a consequence of a much more diverse landscape, climate and vegetation. Moreover, habitat diversity can be reflecting area effects, because South America is more than twice as large as Australia, given that larger areas can potentially house larger number of habitats. Using fossil data and climatic history, Duellman suggested that species composition of South American herpetofauna is, in general, a combination of recent speciation events in lowland tropics, Andes, and in some temperate groups adapted to

xeric conditions, plus old taxa that remained in habitat refugia provided by ancient highlands (Brazilian and the Guianan) and austral forests. Quaternary forest refugia were suggested to explain differentiation of amphibian (Duellman and Crump 1974), lizard (Vanzolini and Williams 1970; Vanzolini and Williams 1981), and snake (Dixon 1979) populations.

Dorst (1973) compared bird faunas using distributions of dominant families in South America, Australia, and Africa. The avifauna in the latter continent is more balanced, with a relatively greater number of representative families. Structurally, South American and Australian avifauna present similar patterns, an evident dominance of few families very rich in species. The observed pattern was explained by the greater isolation in South America and Australia, allowing greater diversification within the original faunas, rather than evolutionarily accommodating different lineages of frequent immigrants, which likely took place in Africa. Keast (1981a) briefly compared general patterns of Neotropical and Australian avifaunas and their relationships. Current avifaunas are very distinct, despite sharing a Gondwanic origin. Several endemic groups dominate the Neotropical avifauna, but morphological and ecological counterparts were recognized between the prominent sub-oscines (South American passerines) and the oscines in Australia and New Zealand. Although some older insect and plant lineages present 'southern cold temperate' affinities (Table 1), birds do not repeat this pattern.

The mammal fauna is probably the best-studied group of the South American and Australian biological relationships. Keast and collaborators (1972) edited a remarkable book about the evolution of mammals on the southern continents and adjoining areas. Chapters contrasted Africa, South America, and Australia based on their geological history, ancient and present environments, fossil and living

mammalian faunas, and the evolutionary history connecting these elements. For zoogeographic comparisons, authors excluded the northern Sahara African region, but considered South American fauna to include mammals living in Central America and tropical Mexico (the Neotropica), and Australian fauna included mammals in New Guinea. Emphasizing the southern historical particularities and the potential for comparing the southern continents, Keast (1972c) argued that differently than in the northern hemisphere, severe cold was not a major agent of extinction in the southern continents (except for Antarctica); even the Pleistocene glaciations was restricted to the highest mountains or latitudes (in the southern extremities); tropical and subtropical zones consistently persisted due to the continental proximity to the equator. Likewise, the diversity of habitats was continuously maintained due to broad latitudinal extensions and mountain building activities. Additionally, the continents benefited from a considerable geological stability because they are built on large Precambrian shields; consequently, only the margins were subjected to significant tectonic shifts.

Besides geological data, cosmopolitan fossil biota (fauna and flora) supports the junction and proximity of landmasses during the Mesozoic. In addition, there are many examples of contemporary biological affinities when considering taxa with exclusive southern hemisphere distribution (p.51-52). Focusing on groups of species exclusive to South America and Australia, Keast's (1971) studies reveal that most of vertebrate evidences supporting former connection between these two continents are controversial, but older groups such invertebrates and plants supply strong support. Several works were quoted exemplifying shared lineages of insects (e.g. Evans 1959; Illies 1965; Brundin 1966; Illies 1969), earthworms (Omodeo 1963), spiders and Opiliones (Besch 1969), and a variety of plant species including Proteaceae and

podocarp floras (Hooker 1860; du Rietz 1940; Florin 1963; van Steenis and van Balgooy 1966). In general, all these studies conclude that the South America-Australia connection is stronger (and existed for a longer time) than either one with Africa. For instance, using the Migidae spiders (Mygalomorphae) as a model, disjunctions occur at the subfamily level between South America and Africa-Madagascar, but at the genus level between South America and Australia-New Zealand (Besch 1969). Although informative, this range of common and exclusive groups does not cover the striking biotic differences between continents.

Keast (1972b) explained that the Australian mammal fauna was originally formed by marsupials and monotremes (presently endemic to the continent), later receiving the placental immigrants (only bats and rodents) presumably after the Middle Tertiary. The placentals have undergone marked radiation within the continent, especially rodents. Except for bats, all Australian groups present high levels of endemism, suggesting their diversification over long-term isolation. The marsupials diversified in morphology and ecology, occupying a variety of niches. They progressively developed life-forms convergent with placentals living in other continents. Contrasting Australian and South American faunas, some notable examples of “ecological equivalents” or “pairs of ecological counterparts” occupying similar niches are: the Australian Phalangeroidea and the Neotropical primates and squirrels; *Trichosurus* and *Sciurus*; the arboreal *Phascogale tapoatafa* and the small weasel *Mustela frenata*; the small to medium-sized wallabies (Macropodidae) and the lagomorphs; the koala (*Phascolarctus*) and the South American sloths (Bradyrodidae). During the Cenozoic, South America was more isolated than Africa but less isolated than Australia. Contrary to Australia, the early mammal fauna colonizing South America was a mix of marsupials and herbivorous placentals (Keast

1972b; Patterson and Pascual 1972). This historical particularity distinctly affected the mammal fauna assembly in South America, where most extant marsupials are small omnivorous species, terrestrial or arboreal, and have nocturnal habits (Hershkovitz 1972). South American placentals are much more diversified (taxonomically and ecologically) than the Australian ones and the South American marsupials.

Hershkovitz (1958, 1972) defined three zoogeographical subregions for the Neotropical fauna of living mammals: the Brazilian (which includes the central/north South America and the tropical Central America), Patagonian (the west Andes through the whole southern cone, including most of Argentina and Uruguay), and West Indian (most of the Caribbean islands). He hypothesized that northern invaders followed the Andean upland bases to the Patagonia and the Brazilian uplands during the Early and Middle Tertiary, and then dispersed to the South American lowlands and lower latitudes. An alternative to the traditional view (largely defended by G. Simpson) suggests that the posterior final completion of the Panamanian land bridge (in the Plio-Pleistocene) had potentially little biogeographical significance for mammals, once most of the lowland species from South and Central America were able to cross over minor water gaps during the Tertiary. Developing his point of view, Hershkovitz (1972) argued that exchanges between continents are primarily consequences of ecological factors, such as population pressures in the interchange point, rather than an effect of land bridges or water gap appearances.

The zoogeography of Australian mammals was discussed by Keast (1972b), whom pointed out that: 1) oriental placentals were more effective at invading and colonizing the Wallacea region (i.e. the Malay Archipelago) than Australian marsupials (p.201); 2) from the Late Pleistocene to the present many large-sized

species were extinct, and many dominant elements had their range significantly reduced, probably due to striking climatic changes (p.228); 3) the four Australian continental corners work as important wet refuge areas; and 4) species distributions are usually linked to the main vegetation types in the continent, e.g., rain forest, sclerophyll (eucalypt) forest, woodland, grassland, or desert (p.231). This latter aspect applies to speciation that actively takes place within the Australian mainland, for example where “tongues of dry open country” isolate forest species (p.233).

Similarly, in South America: 1) several North American forms, not adapted to tropical forests, probably colonized the South American interior through the high flanks of the Andes, whereas range expansions were much harder for southern forms not adapted to the large-scale continental glaciations in North America (Patterson and Pascual 1972); 2) most of the large South American mammals were extinct during the Late Pleistocene, the arrival of humans (Patterson and Pascual 1972) and the postglacial decrease of humidity (Hershkovitz 1972) were probably the main factors; 3) the broad latitudinal range, vegetational and physiographic complexity provided a variety of possibilities for refuges; and 4) Hershkovitz (1972) recognized “regional faunal centers” (i.e., Brazilian highlands and Bolivian uplands, Amazon valley, Orinoco valley and Llanos, Guiana District, Paraná-Paraguay valley, Andes, Páramos, and the Altiplano), which are regions with specific combinations of vegetation and topography, corresponding to coincident distribution of species and eventually functioning as evolutionary centers.

In his last chapter, Keast (1972a) offers additional and valuable comparisons on the contemporary mammal faunas of the southern continents. Neotropical and Australian (including New Guinea) mammal faunas present very distinct compositions, and usually different groups occupy the “adaptive zones” (“ecological

roles” or guilds) in each continent (e.g. small terrestrial omnivores, small insect-eaters, medium to large herbivores, etc). However the faunas are “structurally” similar, since they present the same range of adaptive zones (Keast suggested 15 adaptive zones). Although within continent the proportion of taxa in each zone is very different, between regions at least five zones present roughly similar percentages of genera and species. Marsupials were one of the first mammals colonizing Australia. They diversified in isolation for a long time, enabling them to fill and dominate almost all the major adaptive zones. The higher endemism in Australia corresponds to its longer isolation: 29% of the orders and superfamilies are endemic in Neotropica, versus 36% in Australia; 37% of the genera and 34% of the species belong to Neotropical endemic families, versus 54% and 41% respectively in Australia. However, overall percentage of endemic species is very similar (about 95%), suggesting also significant but more-recent diversifications and colonization. The use of percentages makes comparisons more realistic, because total number of species and richness of higher taxa in each continent are very different (e.g. 50 families, 278 genera, and 810 species in Neotropica [mainly due to rodents and bats], versus 18, 117, and 364 respectively in Australia). Likewise, since the Neotropical region is more than twice as large as the Australian region, the density of taxa may be more informative than just the taxa richness. Despite the conspicuous difference between their taxa richness, Neotropica and Australia are very similar considering the number of taxa per area. The number of taxa per 100,000 square miles in Neotropica and Australia are respectively: families 0.70 and 0.55; genera 3.86 and 3.55; and species 11.30 and 11.03. The number of species per genus is respectively 2.91 and 3.11, and genera per family 5.56 and 6.50. Thus, different richness but similar densities suggest significant area effect on the total continental richness of taxa, whereas similar

proportions between taxonomic levels (species per genera) assure us a reasonable consistency for biological comparisons between these regions.

Keast (1972a) interpreted faunistic differences between the southern continents considering both historical and contemporaneous influences. The scenario supporting the fauna assembly in each continent combines effects of their latitudinal position and extension, consequently affecting the percentage of area within the tropic, the distribution of rainfall, and the proportional cover of forests (especially rain forest) versus grasslands (including savannas, deserts and steppes). For instance, tropical regions are richer in number of species than temperate regions and tropical rain forests are richer than tropical savannas in several groups (e.g. plants, insects, birds, bats, and arboreal mammals). Moreover, about 70% of Neotropica receives more than 40 inches of rainfall annually (~40% receiving >60 inches), whereas about 85% of the Australian region receives less than 40 inches annually (~55% receiving <20 inches). Its larger proportion of area covered by closed vegetation with high levels of rainfall explains why rain forest mammals are usually prominent in Neotropica. On the other hand, the similar proportion of savanna and forest mammals in the Australian region (including New Guinea) is, at least partially, due to a higher proportion of open vegetational stands (more than half of Australia is covered by savannas, desertic vegetation or other open vegetational stands). Most of non-desert vegetation types in the Australia mainland are basically woodlands and open forests (eucalypt). The rain forest is mostly restricted to tropical New Guinea. Besides rain forests and typical savanna formations, Keast found other structurally similar vegetation between continents. The Patagonian arid belt in South America is dry grassland, comparable to deserts and semi-deserts of Australia due to similar annual rainfall and vegetation cover (Australian deserts are vegetated). Both continents also

present *Notophagus* forests (very distinctive vegetation) with small proportional ranges. In addition, Neotropica presents more opportunities for developing new species by “duplicating faunas” isolated in similar environments within continent. Pairs of isolated blocks of Neotropical rain forests are: west versus east Andean rain forest; Amazonia in the north versus the coastal rain forest in the Atlantic southeastern Brazil; and southern temperate (*Notophagus*) rain forest versus the equatorial rain forest. In the Australian region, true duplication occurs only between the Queensland and New Guinea rain forests. Comparisons of endemism levels are useful to understand the potential of these isolated regions producing new species. Therefore, the richness and observed faunistic differences are influenced by their potential for speciation within the continent (including the availability of refuges and opportunities for “faunal duplications”), the degree of vegetational and physiographic diversity, the dominant vegetation type (affecting the proportion of taxa in each “adaptive zone”), the proximity to another continent (allowing colonization and connecting faunas), and the degree of extinctions in the recent past (usually corresponding to environmental changes). In this way, its larger equatorial areas, broader latitudinal extension, and broader mountain systems allowed South America to persist with its large tropical and subtropical zones through time, and continuously maintain its diversity of habitats, being more effective than Australia in supporting mammal richness.

Australian marsupials are most probably South American descendents (Woodburne and Case 1996; Archer *et al.* 1999). The South American Didelphimorphia is the ancestral group of all remaining marsupials, and the only living Microbiotheria (in the temperate Andes) is the sister group of all Australian marsupial orders, forming with them the monophyletic Australidelphia (Nilsson *et al.*

2010). This phylogenetic structure indicates that Australian marsupials originated due to a single migration from South America through Antarctica (Nilsson *et al.* 2010). The Australian *Djarthia* is currently considered the oldest (~30 Mya) known marsupial fossil (Beck *et al.* 2008), whereas the early divergences of Marsupialia occurred between 65 and 85 Mya (Nilsson *et al.* 2010). Therefore, marsupial colonization in Australia should have happened at some point from the Late Cretaceous to the Early Tertiary (Woodburne and Case 1996). The single migration hypothesis suggests a random dispersal (i.e. by sweepstakes dispersal), alternatively, if multiple colonization occurred (see Woodburne and Case 1996; Springer *et al.* 1998), the entrance could have been rather selective, via a filter route. This discussion is relevant to assessing how suitable was the South America-Antarctica-Australia connection for faunal exchanges from the Late Cretaceous. Woodburne and Case (1996) supply an extensive review of the marsupial phylogeny and biogeographical relationships between South America and Australia via Antarctica. Their study interprets palaeoenvironments based on fossils, morphological, molecular, and geological data, and up to date discussions on marsupial origin and diversification. In addition, the vast contribution of Woodburne and Case's paper also up to date the general discussion on the South American and Australian biological connection.

Summary of comparative hypotheses on the biota formations

- a. Biodiversity decreases southward. The latitudinal gradient in species richness is supported by tree, mammal, bird, amphibian, reptile, and fish data; probably a consequences of climate (Darlington 1965/ p.19-21).
- b. Northern South America is formed by tropical elements mostly related to Central and North America or tropical Africa, whereas southern South

America is more closely related to temperate elements from the Gondwanic austral landmass (e.g. Australia, Tasmania and New Zealand) with low exchange between the tropical and temperate regions (Crisci *et al.* 1991; Lopretto and Morrone 1998; Humphries and Parenti 1999; Sanmartín and Ronquist 2004). This hypothesis suggests two main biotic components with different biogeographic affinities forming the continental biota of South America.

- c. Within-continent fauna dispersal occurred more frequently than flora from southern to northern continental portions rather than vice versa (Sanmartín and Ronquist 2004).
- d. Northern faunal invaders in South America followed the Andean upland to Patagonia and Brazilian uplands and then dispersed to South American lowlands and lower latitudes. This hypothesis was suggested for mammals, especially those originally temperate-adapted (Hershkovitz 1972) and should be tested with other organisms.
- e. The higher taxonomic diversity in South America is a positive response to its higher habitat diversity, a consequence of a much more diverse landscape, climate, and vegetation. Moreover, habitat diversity can be reflecting area effects, once South America is more than twice as large as Australia and larger areas can potentially house larger number of habitats. (Duellman 1979).
- f. Considering continental faunas, the earlier colonizers correspond to the prevailing lineages, which first diversified during long-term isolation, filling and dominating major adaptive zones. Evidences come from Australian mammal data (Keast 1972a).

- g. The longer continental isolation the higher level of endemism. Evidences come from Australian mammal data (Keast 1972a).
- h. The higher richness of taxa in South America compared to Australia reflects its larger area, latitudinal extensions, area in the Tropics, proportion of forested areas, and higher rainfall. Evidences come from comparative plant data, invertebrates, mammals and other vertebrates (Keast 1972a). Data from several organisms support that tropical regions are richer in number of species than temperate regions, and tropical rain forests are richer than tropical savannas (Keast 1972a).
- i. South America presents more opportunities for developing new species by “duplicating faunas” isolated in similar environments within continent. The main example include the isolated blocks of rain forests disconnected by geographical and climatic barriers (Keast 1972a).
- j. More species of arboreal animals are expected in South America than in Australia. The hypothesis was suggested by comparative ant data (Campos *et al.* 2011). Explanation includes the present proportions of forested habitats and the historical association with specific lineages. Arboreal and ground ant faunas are significantly different in both Brazilian and Australian savannas, but with stronger contrast in the former. This happens because most of the largest South American savanna (the Brazilian Cerrado) faunal lineages are derived from arboreal forms originally living in the tropical rainforest, whereas Australian savannas lineages resulted from an original radiation in the vast arid zones of Australia.
- k. Similar habitats cause similar effects on the number of coexisting species. Evidences come from global comparisons between several groups of

organisms from different continents, which overall results indicate that convergence in species diversity is highly expected in nature (Orians and Paine 1983; Schluter and Ricklefs 1993).

1. How species attributes influence community and fauna structures? Assuming that contemporary, historical, local, and regional processes form community attributes (Ricklefs and Schluter 1993), it is interesting to investigate the existence of convergence in structure and organization of the South American and Australian faunas, and the relative importance of these processes. Despite similar evolutionary responses, such as adaptive convergences between South American and Australian species, if contemporarily and locally environmental conditions are the primary determinants of community parameters (e.g. species richness) we expect communities to converge in structure. Since South America and Australia are similar in the overall structure of their environments, it is possible to test this hypothesis by determining whether the average local species richness is similar in both continents, regardless of the total richness each continent (regional richness). One way to test this is to check whether the proportions of species living in open vegetation habitats vs. living in forest habitats mirrors the proportion of open and forested areas in the two continents (comparisons using both local and regional scales are useful). If local diversity reflects regional diversity, it provides evidence of a prevalent historical effect (Westoby 1993). If species densities (number of species per area unit) are equivalent between continents, it is evidence of community convergence. The use of species density as a community parameter for comparisons controls differences due to area effect.

m. Several evidences support the hypothesis that animal assemblages respond strongly to habitat structure (e.g. MacArthur *et al.* 1962; Nogueira *et al.* 2009) rather than its plant species composition (Orians and Paine 1983). The existence of emerging ecological and morphological species syndromes associated with close/forested or open areas, independently of their lineages or original continent, provides evidence of strong contemporary-ecological effects upon fauna assembly. In addition, if South American and Australian faunas converge, I expect similar distribution of richness, similar ecological guilds, and similar proportions of species in each correspondent guild between open habitats or between close habitats from opposite continents.

Acknowledgements

DLP was supported by doctoral fellowships from the Brazilian agencies CAPES and CNPq. I thank G. R. Colli, C. C. Nogueira, and J. Marinho-Filho for suggestions and helpful bibliography exchange; and A. M. Gainsbury for reviewing previous versions of the manuscript.

References

- Amorim, D.S. and S.H.S. Tozoni. 1994. Phylogenetic and biogeographic analysis of the Anisopodoidea (Diptera, Bibionomorpha), with an area cladogram for intercontinental relationships. *Revista Brasileira de Entomologia* 38(3/4): 517-543.
- Archer, M., R. Arena, M. Bassarova, K. Black, J. Brammall, B. Cooke, P. Creaser, K. Crosby, A. Gillespie, H. Godthelp, M. Gott, S.J. Hand, B. Kear, A. Krikmann, B. Mackness, J. Muirhead, A. Musser, T. Myers, N. Pledge, Y. Wang and S. Wroe. 1999. The evolutionary history and diversity of Australian mammals. *Australian Mammalogy* 21: 1-45.
- Arroyo, M.T.K., P.H. Zedler and M.D. Fox. 1995. *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia*: Springer-Verlag. 455 pp.

- Bayly, I.A.E. 1993. The fauna of athalassic saline waters in Australia and the Altiplano of South America: comparisons and historical perspectives. *Hydrobiologia* 267(1-3): 225-231.
- Beck, R.M.D., H. Godthelp, V. Weisbecker, M. Archer and S.J. Hand. 2008. Australia's oldest marsupial fossils and their biogeographical implications. *Plos One* 3(3).
- Besch, W. 1969. South America Arachnida; p. 723-740 In E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe and H. Sioli (ed.). *Biogeography and Ecology in South America*, vol. Vol. 2 W. Junk, The Hague.
- Brundin, L. 1966. Transantartic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagytiae. *Kongliga Svenska Vetenskaps-akademiens Handlingar* 11: 1-142.
- Campos, R.I., H.L. Vasconcelos, A.N. Andersen, T.L.M. Frizzo and K.C. Spena. 2011. Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. *Austral Ecology* 36(8): 983-992.
- Colbourne, J.K., C.C. Wilson and P.D.N. Hebert. 2006. The systematics of Australian *Daphnia* and *Daphniopsis* (Crustacea: Cladocera): a shared phylogenetic history transformed by habitat-specific rates of evolution. *Biological Journal of the Linnean Society* 89(3): 469-488.
- Colli, G.R., R.P. Bastos and A.F.B. Araújo. 2002. The character and dynamics of the Cerrado herpetofauna; p. 223-241 In P.S. Oliveira and R.J. Marquis (ed.). *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York, NY: Columbia University Press.
- Colli, G.R. 2005. As origens e a diversificação da herpetofauna do Cerrado; p. 447-264 In A. Scariot, J.C. Sousa-Silva and J.M. Felfili (ed.). *Cerrado: Ecologia, Biodiversidade e Conservação*. Brasília, DF: Ministério do Meio Ambiente.
- Colli, G.R., R. Constantino and G.C. Costa. 2006. Lizards and termites revisited. *Austral Ecology* 31: 417-424.
- Costa, B.M., D.L. Pantoja, M.C.M. Vianna and G.R. Colli. 2013. Direct and short-term effects of fire on lizard assemblages from a Neotropical Savanna hotspot. *Journal of Herpetology* 47: 502-510.
- Costa, G.C., G.R. Colli and R. Constantino. 2008a. Can lizard richness be driven by termite diversity? Insights from the Brazilian Cerrado. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 86(1): 1-9.
- Costa, G.C., L.J. Vitt, E.R. Pianka, D.O. Mesquita and G.R. Colli. 2008b. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17(5): 670-677.
- Crisci, J.V., I.J. Gamundi and M.N. Cabello. 1988. A cladistic analysis of the genus *Cyttaria* (Fungi, Ascomycotina). *Cladistics-the International Journal of the Willi Hennig Society* 4(3): 279-290.
- Crisci, J.V., M.M. Cigliano, J.J. Morrone and S. Roigjuntent. 1991. Historical biogeography of southern South America. *Systematic Zoology* 40(2): 152-171.
- Darlington, P.J., Jr. 1965. *Biogeography of the Southern End of the World: Distribution and History of Far-Southern Life and Land, with an Assessment of Continental Drift*. Cambridge: Harvard University Press. 236 pp.
- Dawson, J.W. 1958. Interrelationships of the Australasian and South American floras. *Tuatara* 7(1).
- Dixon, J.R. 1979. Origin and distribution of reptiles in lowland tropical rainforests of South America; p. 217-240 In W.E. Duellman (ed.). *The South American*

- Herpetofauna: Its Origen, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- Dorst, J. 1973. Distribution of dominant families in avifauna of South America, Africa and Australia and its relation to development in these continents. *Comptes Rendus Hebdomadaires Des Seances De L'Academie Des Sciences Serie D* 277(17): 1773-1777.
- du Rietz, G.E. 1940. Problems of bipolar plant distribution. *Acta Phytogeographica Suecica* 13: 215-282.
- Duellman, W.E. and M.L. Crump. 1974. Speciation in frogs of the *Hyla parviceps* group in the upper Amazon Basin. *University of Kansas Museum of Natural History Occasional Papers* 23: 1-40.
- Duellman, W.E. 1979. The South American herpetofauna: a panoramic view; p. 1-28 In W.E. Duellman (ed.). *The South American Herpetofauna: Its Origen, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- Duellman, W.E. and E.R. Pianka. 1990. Biogeography of nocturnal insectivores: historical events and ecological filters. *Annual Review of Ecology and Systematics* 21: 57-68.
- Evans, J.W. 1959. The zoogeography of some Australian insects; p. 150-163 In A. Keast, R.L. Crocker and C.S. Christian (ed.). *Biogeography and Ecology in Australia*. Den Haag: Uitgeverij Dr. W. Junk.
- Florin, R. 1963. The distribution of coniferand taxad genera in time and space. *Acta Horti Bergiani (Uppsala)* 20: 121-312.
- Foissner, W. 1997. Soil ciliates (Protozoa: Ciliophora) from evergreen rain forests of Australia, South America and Costa Rica: diversity and description of new species. *Biology and Fertility of Soils* 25(4): 317-339.
- Hann, B.J. 1986. Revision of the genus *Daphniopsis* Sars, 1903 (Cladocera: Daphniidae) and a description of *Daphniopsis chilensis*, new species, from South America. *Journal of Crustacean Biology* 6(2): 246-263.
- Hayes, R.A., M. Crossland, M. Hagman, R. Capon and R. Shine. 2009. Ontogenetic variation in the chemical defenses of cane toads (*Bufo marinus*): toxin profiles and effects on predators. *Journal of Chemical Ecology* 35(4): 391-399.
- Herskovitz, P. 1958. A geographical classification of neotropical mammals. *Fieldiana Zoology* 36(6): 581-620.
- Herskovitz, P. 1972. The recent mammals of the neotropical region: a zoogeographic and ecological review; p. 311-431 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Hooker, J.D. 1860. Botany of the Antarctic Voyage of H. M. Discovery Ships Erebus and Terror in the Years 1839-1843. Part III: Flora Tasmaniae, Vol. 1. Introductory Essay.
- Humphries, C.J. and L.R. Parenti. 1999. *Cladistic Biogeography: Interpreting Patterns of Plant and Animal Distributions*: Oxford University Press. 187 pp.
- Illies, J. 1965. Phylogeny and zoogeography of the Plecoptera. *Annual Review of Entomology* 10: 117-140.
- Illies, J. 1969. Biogeography and ecology of Neotropical freshwater insects, especially those from running water. Pages 685-708 in E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe and H. Sioli, eds. *Biogeography and Ecology in South America*. The Hague: W. Junk.
- Keast, A. 1968a. Introduction: the southern continents as backgrounds for mammalian evolution. *The Quarterly Review of Biology* 43(3): 225-233.

- Keast, A. 1968b. Australian mammals: zoogeography and evolution. *The Quarterly Review of Biology* 43(4): 373-408.
- Keast, A. 1969. Comparisons of the contemporary mammalian faunas of the southern continents. *The Quarterly Review of Biology* 44(2): 121-167.
- Keast, A. 1971. Continental drift and the evolution of the biota on southern continents. *The Quarterly Review of Biology* 46(4): 355-378.
- Keast, A. 1972a. Comparisons of contemporary mammal faunas of southern continents; p. 433-501 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A. 1972b. Australian mammals: zoogeography and evolution; p. 195-246 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A. 1972c. Introduction: the southern continents as backgrounds for mammalian evolution; p. 19-22 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A., F.C. Erk and B. Glass (ed.) 1972. *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Keast, A. (ed.) 1981a. *Ecological Biogeography of Australia*. The Hague - Boston - London: Dr. W. Junk.
- Keast, A. 1981b. The evolutionary biogeography of Australian birds; p. 1585-1635 In A. Keast (ed.). *Ecological Biogeography of Australia*. The Hague - Boston - London: Dr. W. Junk.
- Lampo, M. and G.A. De Leo. 1998. The invasion ecology of the toad *Bufo marinus*: From South America to Australia. *Ecological Applications* 8(2): 388-396.
- Lopretto, E.C. and J.J. Morrone. 1998. Anaspidacea, Bathynellacea (Crustacea, Syncarida), generalised tracks, and the biogeographical relationships of South America. *Zoologica Scripta* 27(4): 311-318.
- Lowman, M.D. 1985. Insect herbivory in Australian rain forests - is it higher than in the Neotropics? *Proceedings of the Ecological Society of Australia* 4: 109-119.
- Lynch, J.D. 1979. The amphibians of the lowland tropical forest; p. 189-216 In W.E. Duellman (ed.). *The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- MacArthur, R.H., J.W. MacArthur and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *The American Naturalist* 96: 167-174.
- Martin, A.A. 1970. Parallel evolution in adaptive ecology of leptodactylid frogs of South America and Australia. *Evolution* 24(3): 643-644.
- Medel, R.G. 1995. Convergence and historical effects in harvester ant assemblages of Australia, North America, and South America. *Biological Journal of the Linnean Society* 55(1): 29-44.
- Morton, S.R. 1985. Granivory in arid regions: comparison of Australia with North America and South America. *Ecology* 66(6): 1859-1866.
- Morton, S.R. and C.D. James. 1988. The diversity and abundance of lizards in arid Australia: a new hypothesis. *American Naturalist* 132(2): 237-256.
- Nilsson, M.A., G. Churakov, M. Sommer, N. Van Tran, A. Zemann, J. Brosius and J. Schmitz. 2010. Tracking Marsupial Evolution Using Archaic Genomic Retroposon Insertions. *PLoS Biology* 8(7): -.

- Nogueira, C., G.R. Colli and M. Martins. 2009. Local richness and distribution of the lizard fauna in natural habitat mosaics of the Brazilian Cerrado. *Austral Ecology* 34: 83-96.
- Omodeo, P. 1963. Distribution of the terricolous oligochaetes on the two shores of the Atlantic. Pages 127-151 in A. Löve and D. Löve, eds. *North Atlantic Biota and their History*. New York: Pergamon Press.
- Orians, G.H. and R.T. Paine. 1983. Convergent evolution at the community level; p. 431-458 In D.J. Futuyma and M. Slatkin (ed.). *Coevolution*. Sunderland, MA: Sinauer Associates, Inc.
- Pantoja, D.L. 2007. *Efeitos do fogo sobre a taxocenose de lagartos em áreas de cerrado sensu stricto no Brasil Central*. Dissertação de Mestrado. Brasília, DF: Universidade de Brasília. 113 pp.
- Pantoja, D.L. in prep. The assembly of continental snake faunas: a comparative study between South America and Australia.
- Pantoja, D.L., B.M. Costa, G.R. Colli and E.C. Lima. in prep. Does fire drives lizard diversity in Cerrado?
- Pantoja, D.L. in review. On the South America and Australia connections: a framework for biological comparisons. Pages 95.
- Paramonov, S.J. 1959. Zoogeographical aspects of the Australian dipterofauna; p. 164-191 In A. Keast, R.L. Crocker and C.S. Christian (ed.). *Biogeography and Ecology in Australia*. Den Haag: Uitgeverij Dr. W. Junk.
- Patterson, B. and R. Pascual. 1972. The fossil mammal fauna of South America; p. 247-309 In A. Keast, F.C. Erk and B. Glass (ed.). *Evolution, Mammals, and Southern Continents*. Albany: State University of New York Press.
- Phillips, B.L., G.P. Brown and R. Shine. 2003. Assessing the potential impact of cane toads on Australian snakes. *Conservation Biology* 17(6): 1738-1747.
- Pianka, E.R. 1986. *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure* Princenton, NJ: Princenton University Press. 208 pp.
- Pianka, E.R. 1989. Desert lizard diversity: additional comments and some data. *American Naturalist* 134(3): 344-364.
- Pianka, E.R. and S.E. Goodyear. 2012. Lizard responses to wildfire in arid interior Australia: long-term experimental data and commonalities with other studies. *Austral Ecology*: no-no.
- Ricklefs, R.E. and D. Schluter. 1993. Species diversity: regional and historical influences; p. 350-363 In R.E. Ricklefs and D. Schluter (ed.). *Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Sanmartín, I. and F. Ronquist. 2004. Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology* 53(2): 216-243.
- Schluter, D. 1986. Tests for similarity and convergence of finch communities. *Ecology* 67(4): 1073-1085.
- Schluter, D. and R.E. Ricklefs. 1993. Convergence and the regional component of species diversity; p. 230-240 In R.E. Ricklefs and D. Schluter (ed.). *Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Simpson, G.G. 1963. Mammalian evolution on the southern continents: synthesis and summing-up. Whashington D. C.: XVI International Congress of Zoology.

- Solbrig, O.T. 1996. The diversity of the savanna ecosystem; p. 1-27 *In* O.T. Solbrig, E. Medina and J.F. Silva (ed.). *Biodiversity and Savanna Ecosystem Process: a Global Perspective*. Berlin: Springer-Verlag.
- Springer, M.S., M. Westerman, J.R. Kavanagh, A. Burk, M.O. Woodburne, D.J. Kao and C. Krajewski. 1998. The origin of the Australasian marsupial fauna and the phylogenetic affinities of the enigmatic monito del monte and marsupial mole. *Proceedings of the Royal Society of London Series B-Biological Sciences* 265(1413): 2381-2386.
- Tyler, M.J. 1979. Herpetofaunal relations of South America with Australia p. 73-106 *In* W.E. Duellman (ed.). *The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. Lawrence: University of Kansas Printing Service.
- van Steenis, C.J. and M. van Balgooy. 1966. Pacific Plant Areas, Vol. 2. *Bloomea Supplement* 5.
- Vanzolini, P.E. and E.E. Williams. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia* 19: 1-176.
- Vanzolini, P.E. and E.E. Williams. 1981. The vanishing refuge: a mechanism for ecogeographic speciation. *Papeis Avulsos De Zoologia* 34(23): 251-255.
- Westoby, M. 1993. Biodiversity in Australia compared with other continents; p. 170-177 *In* R.E. Ricklefs and D. Schluter (ed.). *Species Diversity in Ecological Communities, Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Williams, W.D. 1981. The Crustacea of Australian inland waters; p. 1103-1133 *In* A. Keast (ed.). *Ecological Biogeography of Australia*. Junk: The Hague.
- Williamson, M. 1984. Sir Joseph Hooker's Lecture on Insular Floras. *Biological Journal of the Linnean Society* 22(1): 55-77.
- Woodburne, M.O. and J.A. Case. 1996. Dispersal, vicariance, and the Late Cretaceous to Early Tertiary land mammal biogeography from South America to Australia. *Journal of Mammalian Evolution* 3(2): 121-161.

Table 1. Examples of non-marine taxa shared by South America and Australia, and with predominant southern distribution. Occurrences in other main landmasses with particular histories are also indicated. NSA - North South America (northward from Brazil and Ecuador); SSA - South America; AUS - Australia (including Tasmania); NG - "New Guinea (including the Solomon and New; Hebrides islands)"; NZ - New Zealand; HOL - Holarctica (Palearctic + Nearctic); AFR - Africa (South of Sahara); MAD - Madagascar; NC - New Caledonia; SWP - Southwest Pacific (Melanesian archipelagos formed after the Oligocene collision of the Pacific and Australian plates (Fiji, Samoa, Tonga, and Vanuatu), and Hawaii); SEA - Southeast Asia (Malaysian Peninsula, Philippines, Sumatra, Borneo, and the Inner Banda Arc. Southeast Asia); IND - India (continent).

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
Vertebrates													
Galaxiidae (Teleostei,		X	X		X	X	X						Waters et al., 2000
Osteichthyes,													
Osmeriformes)													
Hylidae (Lissamphibia,	X	X	X	X								X	Vitt et al., 2009
Anura, Neobatrachia)													
Microhylidae	X	X	X	X			X	X	X	X		X	Vitt et al., 2009
(Lissamphibia, Anura,													
Neobatrachia)													
Chelidae (Reptilia,	X	X	X	X									Vitt et al., 2009
Testudines, Pleurodira)													
<i>Crocodylus</i> (Reptilia;	X		X	X			X	X	X	X			Vitt et al., 2009
Archosauria;													
Crocodylidae)													
Ratites + Tinamous (Aves,	X	X	X	X	X		X						Cooper et al., 2001; Haddrath
Paleognathae)													and Baker, 2001
													Springer et al., 1998; Palma
													and Spotorno, 1999;
												X	Krajewski et al., 2000 (for
													Dasyuromorphia); Nilsson
													2010
Marsupials (Mammalia,	X	X	X	X									
Metatheria)													

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
Invertebrates													
Podonominae (Insecta, Diptera, Chironomidae)	X	X	X	X	X	X	X					X	Brundin, 1966; Cranston and Edward, 1998; Cranston et al., 2002
Aphroteniinae (Insecta, Diptera, Chironomidae)	X	X	X			X	X						Brundin, 1966; Cranston and Edward, 1992
Heptagyae + allied tribes (Insecta, Diptera, Chironomidae, Diamesinae)	X	X	X	X	X	X	X					X	Brundin, 1966
<i>Botryocladus</i> (Insecta, Diptera, Chironomidae, Orthoclaadiinae)	X	X	X										Cranston and Edward, 1999
Apioceridae (Insecta, Diptera)	X	X	X				X					X	Yeates and Irwin, 1996
Megascelinae (Insecta, Diptera, Mydidae)	X	X	X				X						Yeates and Irwin, 1996
<i>Cerotelion - Mallochius</i> (Insecta, Diptera, Keroplatidae)	X	X	X	X	X					X		X	Matile, 1990
Macrocerini (Insecta, Diptera, Keroplatidae)	X	X	X	X	X		X	X	X	X			Matile, 1990
<i>Australosymmeris</i> (Insecta, Diptera, Mycetophilidae)	X	X	X	X	X							X	Munroe, 1974
Masarinae (Insecta, Hymenoptera, Vespidae)	X	X	X				X					X	Carpenter, 1993

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
Groteini (Insecta, Hymenoptera, Ichneumonidae)	X	X	X	X							X		Gauld and Wahl, 2000
Labenini + Xenothyriini (Insecta, Hymenoptera, Ichneumonidae)	X	X	X	X	X						X		Gauld and Wahl, 2000
Megalyridae (Insecta, Hymenoptera)	X	X	X	X	X	X	X	X	X				Shaw, 1990
Ceroplastinae (Insecta, Hemiptera, Coccidae, Coccoidea)	X						X	X	X				Qin et al., 1998 (based on Qin and Gullan, 1995)
Peloriidiidae (Insecta, Hemiptera)		X	X		X	X							Hoch et al., 2006; Larivière et al., 2011
Hydrobiosidae (Insecta, Trichoptera)	X	X	X	X	X	X					X		Henderson, 1991 (based on Schmidt, 1989)
Helicopsychidae (Insecta, Trichoptera)	X	X	X		X	X	X	X	X	X			Johanson, 1998
<i>Metacorneolabium</i> (Insecta, Coleoptera, Staphylinidae)		X	X		X								Thayer, 1985
Pilipalpinae (Insecta, Coleoptera, Pyrochroidae)		X	X		X			X					Pollock, 1995
Adeliini (Insecta, Coleoptera, Tenebrionidae)		X	X		X								Mathews, 1998
<i>Agalba</i> group (Insecta, Coleoptera, Elateroidea, Eucnemidae)	X		X	X	X						X		Muona, 1991

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
<i>Arrhipis</i> (Insecta, Coleoptera, Eucnemidae)	X		X	X			X		X	X	X		Muona, 1991
<i>Calptocerus</i> group (Insecta, Coleoptera, Eucnemidae)	X		X	X					X	X	X	X	Muona, 1991
<i>Cladidus</i> group (Insecta, Coleoptera, Eucnemidae)			X	X			X	X	X	X	X		Muona, 1991
<i>Dromaeoloides</i> (Insecta, Coleoptera, Eucnemidae)			X	X		X					X		Muona, 1991
<i>Dyscharachthis</i> (Insecta, Coleoptera, Eucnemidae)	X	X	X	X								X	Muona, 1991
<i>Entomosotapus</i> (Insecta, Coleoptera, Eucnemidae)	X		X				X						Muona, 1991
<i>Eudorus</i> group (Insecta, Coleoptera, Eucnemidae)	X		X	X			X	X		X			Muona, 1991
<i>Farsus</i> group (Insecta, Coleoptera, Eucnemidae)	X		X	X			X	X					Muona, 1991
<i>Feaia</i> group (Insecta, Coleoptera, Eucnemidae)	X		X	X				X		X		X	Muona, 1991
<i>Galbodema</i> group (Insecta, Coleoptera, Eucnemidae)	X		X	X						X			Muona, 1991
<i>Heterotaxis</i> group (Insecta, Coleoptera, Eucnemidae)	X		X	X			X	X		X	X	X	Muona, 1991
<i>Plesioformax</i> (Insecta, Coleoptera, Eucnemidae)	X		X	X			X	X		X			Muona, 1991
<i>Porraulacus</i> group (Insecta, Coleoptera, Eucnemidae)	X			X					X	X	X		Muona, 1991

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
<i>Prodirhagus</i> (Insecta, Coleoptera, Eucnemidae)	X		X	X			X						Muona, 1991
<i>Rhagomicrus</i> (Insecta, Coleoptera, Eucnemidae)	X		X	X			X	X		X	X	X	Muona, 1991
<i>Scython</i> (Insecta, Coleoptera, Eucnemidae)				X			X	X		X			Muona, 1991
<i>Serriformax</i> (Insecta, Coleoptera, Eucnemidae)	X			X			X	X		X	X		Muona, 1991
<i>Spiniformax</i> (Insecta, Coleoptera, Eucnemidae)	X			X					X	X			Muona, 1991
Migadopini (Insect, Coleoptera, Carabidae)		X	X	X	X								© Carabidae of the World, 2007-2012; Darlington, 1965
Trechina (Insect, Coleoptera, Carabidae, Trechini)	X	X	X	X	X			X	X	X		X	© Carabidae of the World, 2007-2012; Darlington, 1965
<i>Kenodachylus</i> (Insect, Coleoptera, Carabidae, Trechini)		X	X	X	X								© Carabidae of the World, 2007-2012; Darlington, 1965
<i>Plagiotelum</i> (Insect, Coleoptera, Carabidae, Ctenodactylinae)		X	X										© Carabidae of the World, 2007-2012; Darlington, 1965
Crebiina (Insect, Coleoptera, Carabidae, Broscini)		X	X		X								© Carabidae of the World, 2007-2012; Darlington, 1965
Nothobroschina (Insect, Coleoptera, Carabidae, Broscini)		X	X		X	X							© Carabidae of the World, 2007-2012; Darlington, 1965

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
<i>Plectostylus</i> group													
(Gastropoda,	X	X	X										Breure, 1979
Stylommatophora,													
Bulimulidae)													
Peripatopsidae													
(Onicophora)							X						Reid et al., 1995 (for <i>Cephalofovea</i>); Reid, 1996
Ballarriinae (Arachnida,													
Opiliones, Neopilionidae)							X						Hunt and Cokendolpher, 1991
Plants													
<i>Nothofagus</i> (Eudicots,													
Fagales, Nothofagaceae)	X	X	X	X	X	X							Swenson et al. 2001 (based on Manos, 1997); Linder and Crisp, 1995 (for <i>Brassospora</i>)
<i>Aristotelia</i> (Eudicots,													
Oxalidales,	X	X	X		X								Coode, 1985
Elaeocarpaceae)													
<i>Abrotanella</i> (Eudicots,													
Asterales, Asteraceae)	X	X	X	X	X								Swenson and Bremer, 1997
Alseuosmiaceae-													
Argophyllaceae-													
Phellinaceae (Eudicots,													
Asterales)	X	X	X	X	X	X							Karehed et al., 1999
Cunoniaceae (Eudicots,													
Oxalidales)	X	X	X	X	X	X	X	X	X	X	X		Bradford and Barnes, 2001
Cunoniaceae (Eudicots,													
Oxalidales, Cunoniaceae)	X	X	X	X	X	X	X	X	X	X	X		Bradford, 2002
Embothriaceae (Eudicots,													
Proteales, Proteaceae)	X	X	X	X									Weston and Crisp, 1994

Taxa	NSA	SSA	AUS	NG	NZ	NC	AFR	MAD	IND	SEA	SWP	HOL	References
Iridaceae (Monocots, Asparagales)	X	X	X				X	X				X	Reeves et al., 2001
<i>Oreobolus</i> (Monocots, Poales, Cyperaceae)		X	X	X	X				X	X			Linder and Crisp 1995 (based on Seberg, 1988)
Restionaceae (Monocots, Poales)		X	X	X	X		X	X					Linder, 2000
<i>Danthonia</i> clade (Monocots, Poales, Poaceae, Danthoniaceae)	X	X	X		X							X	Linder and Barker, 2000
<i>Rytidosperma</i> (Monocots, Poales, Poaceae, Danthoniaceae)		X	X	X	X								Linder, 1999
Haemodoraceae (Monocots, Commelinales)	X		X	X			X					X	Hopper et al., 1999
Winteraceae (Magnoliids, Canellales)		X	X	X	X	X		X					Karol et al., 2000
Atherospermataceae (Magnoliids, Laurales)		X	X	X	X	X							Renner et al., 2000

* Modified and amplified after Sanmartín and Ronquist (2004).

Table 2. List of studies comparing the South American and Australian organisms and their primary approach*.

Taxonomic groups	Primarily approach	Reference
Vertebrates		
amphibians	Comparative ecology - species	(Martin 1970)
amphibians	Comparative ecology - species	(Lampo and De Leo 1998)
birds	Comparative ecology - community	(Schluter and Ricklefs 1993)
birds	Faunas	(Dorst 1973)
birds	Faunas	(Keast 1981b)
herpetofauna	Faunas	(Duellman 1979)
herpetofauna	Faunas	(Tyler 1979)
lizards	Comparative ecology - community	(Pantoja 2007)
lizards	Comparative ecology - community	(Costa <i>et al.</i> 2008b)
lizards and amphibians	Comparative ecology - community	(Duellman and Pianka 1990)
mammals	Faunas	(Simpson 1963)
mammals	Faunas	(Keast 1968b)
mammals	Faunas	(Keast 1969)
mammals	Faunas	(Keast <i>et al.</i> 1972)
mammals: mainly marsupials	Zoogeography	(Woodburne and Case 1996)
snakes	Faunas	(Pantoja in prep.)
Invertebrates		
arachnida	Zoogeography	(Besch 1969)
crustaceous	Faunas	(Bayly 1993)
crustaceous: Anaspidacea, Bathynellacea (Syncarida)	Zoogeography	(Lopretto and Morrone 1998)
insects	Zoogeography	(Evans 1959)
insects: ants	Comparative ecology - community	(Medel 1995)
insects: ants	Comparative ecology - community	(Campos <i>et al.</i> 2011)
insects: Diptera	Zoogeography	(Paramonov 1959)
ants, birds, and mammals	Comparative ecology - ecosystems	(Morton 1985)
Vert. + Invert.		

Taxonomic groups	Primarily approach	Reference
lizards and termites	Comparative ecology - community	(Colli <i>et al.</i> 2006)
lizards and termites	Comparative ecology - community	(Costa <i>et al.</i> 2008a)
Ecosystems		
Rain forest and insects herbivory	Comparative ecology - ecosystems	(Lowman 1985)
Mediterranean	Comparative ecology - ecosystems	(Arroyo <i>et al.</i> 1995)
Savannas	Comparative ecology - ecosystems	(Solbrig 1996)
Microorganisms		
soil ciliates (Protozoa: Ciliophora)	Comparative ecology - community	(Foissner 1997)
Plants		
plants in general	Floras	(Dawson 1958)
plants in general	Floras	(Williamson 1984)
General		
general biota	Historical biogeography	(Keast 1968a)
general biota	Historical biogeography	(Keast 1971)
general biota (specially <i>Nothofagus</i> , and insects)	Historical biogeography	(Darlington 1965)

* Studies primarily focused on taxonomy and/or systematics were not included.

APÊNDICE 3

The Assembly of Continental Snake Faunas: A Comparative Study between South America and Australia

Davi Lima Pantoja*

*Programa de Pós-Graduação em Ecologia, Universidade de Brasília, 70910-900.

Brasília, DF. Brazil.

e-mail: pantoja.davi@gmail.com

Keywords: Serpentes, biogeography, natural history, community ecology, species diversity, phylogenetic diversity, habitat structure, and convergence.

ABSTRACT

I used species diversity, natural history, body size, and phylogeny to describe South American and Australian snake faunas. Then, I interpreted faunal assemblies based on historical, contemporary, regional, and local processes; and assessed faunal convergences by comparing taxonomic, biological, phylogenetic, and diversity structures at the continental scale. Faunal structures in each continent are coherent with its proportion of closed and open habitats, with South America presenting a higher proportion of species ecologically and phylogenetically associated to closed/forested habitats, and the reverse occurs in Australia with open habitats. I found convergences in several aspects, although marked differences also exist. Several biological attributes appear in similar proportion of species when comparing faunas. Terrestriality, nocturnality, oviparity, reptile-based diet, short and medium body length are the most common attributes in both faunas. For each main ecological guild in Australia there is a similar guild in South America. However, the proportion of species in each guild varies markedly. Habitat structure has a significant effect on snake natural history, with closed/forested habitats promoting diversity more than open habitat. Local diversities similarly reflect regional diversity in both continents, suggesting a strong historical effect upon faunal assembly, with convergent results at the continental scale. A higher “differentiation diversity rate” in Australian open habitats probably balances the strong effect of closed habitats in South America enabling species diversity to converge. Among differences, ecological traits consistently associated to the species-richest lineages largely define the main character of each fauna, which is also largely related to the proportion of closed and open habitats in each continent. The higher snake diversity in South America probably reflects a combination of: larger total area, latitudinal extensions, area within the tropics, proportion of forested areas, and altitudinal range; higher rainfall; more diverse landscape, climate, and vegetation; more opportunities for “duplicating faunas” in isolated similar environments; longer and older history; heavier stocks of autochthonous lineages; and stronger immigrant colonization than Australia. As expected, faunas are not completely convergent neither distinct.

INTRODUCTION

Besides kinship (phylogenetic proximity) similarities between organisms are consequences of convergent evolution. Convergent evolution between organisms from different geographical areas emerges as an evolutionary response to similar physical features of the environment (i.e., similar selective forces due to similar conditions and resource availability), and to biological interactions promoting similar patterns of coevolution (Orians & Paine, 1983). Examples of species convergence and parallelism are abundant and well known (e.g. Cody & Mooney, 1978; Archer *et al.*, 2011; Chirat *et al.*, 2013), but it is unclear whether this phenomenon occurs often enough to induce communities to converge (e.g. Lomolino, 1993; Kelt *et al.*, 1999). Indeed, independent of similarities between pairs of species, the coevolution within independent aggregates of species may lead them to develop similar organizations and functions (Orians & Paine, 1983).

For most available studies the traditional expectation that similar environments house similar communities is only weakly supported (Pianka, 1986; Schluter & Ricklefs, 1993a, b), especially when communities share little history. However, strong evidences suggest convergences in community structure, including species diversity, morphological, and behavioral traits, even when derived through different historical processes (e.g. MacArthur *et al.*, 1962; Fuentes, 1976; Mooney, 1977; Orians & Solbrig, 1977; Schluter & Ricklefs, 1993b; Winemiller *et al.*, 1995; Losos *et al.*, 1998; Stephens & Wiens, 2004; Melville *et al.*, 2006; Simon *et al.*, 2009). The lack of consensus between results supporting community-level convergence reveals our poor understanding on the macroecological patterns of community evolution, inappropriate approaches, or simply the lack of a natural pattern.

Present day characteristics of species and community structure are consequences of historical-biogeographic events, past ecological relationships, and phylogenetic constraints molded in response to present ecological interactions (Connell, 1980; Losos, 1996). Because related species are not truly independent evolutionary units, the present observed similarities in their attributes cannot be taken as pure evidences of recently selected responses (Harvey & Pagel, 1998). Likewise, the absence of similarities cannot be readily interpreted as a consequence of local or contemporary factors. For instance, different sets of trophic guilds in snake communities from similar habitats may be explained by phylogenetic and biogeographic constrains (Cadle & Greene, 1993). Studies with squamates demonstrated that morphological or behavioral features may enable some species to explore particular resources, but species attributes have deep phylogenetic roots that transcend present-day communities (Cadle & Greene, 1993; Losos, 1994; Vitt & Pianka, 2005; Colston *et al.*, 2010). Therefore, modern comparisons between communities must take into account the phylogenetic and biogeographic histories of species (Webb *et al.*, 2002; Ricklefs, 2008).

Intercontinental comparisons can be used as a “natural” experiment to interpret how community ecology and biogeography interact in developing the structure of present communities. Both South America and Australia are in the south hemisphere and present similarities in the general structure of existing climate and environments (Pantoja, *in review*). The Australian latitudinal limits overlap the core area of South America, and both have wet north-tropical and wet south-temperate areas separated by drier regions that acts as a barrier to some species (Nix, 1981; Haffer, 1987). The eastern coast of both continents is wetter than the interior, and presumably works as a corridor (North-South) to some arid-intolerant species

(Guedes *et al.*, 2011). They developed dense forests in lower latitudes, mangroves in tropical coastal regions, and large open physiognomies cover most of the continent through the central and southern regions (Specht, 1981; Brown & Prance, 1987; Werneck, 2011). However, the proportion of forested areas in South America is higher than in Australia (Figure 1). The open and dry landscapes that cover most of the Australian continent share some characteristics with the South American Patagonia, Caatinga, and Cerrado, which are the largest South American open-vegetation domains. Although not deserts, similarly to the Arid Australia they are savanna-like domains, mostly covered by grassland and bush vegetation, and have very dry periods. In particular, the Cerrado share a nutrient-poor, acidic, and aluminum-rich soils, frequent disturbance caused by natural fires, and abundant and diverse lizard and termite faunas (Pianka, 1989; Oliveira & Marquis, 2002; Colli *et al.*, 2006; Morton *et al.*, 2011). These shared features added to the long biological independence between continents encourage a comparative approach (Pantoja, in prep./ see Chapter 1 and 2; *in review*), and have supported studies on vertebrates and invertebrates (e.g. Keast *et al.*, 1972; Costa *et al.*, 2008a; Campos *et al.*, 2011; Costa *et al.*, 2013).

In spite of differences between South American and Australian biotas, similar biogeographical events deeply marked both continents (Keast, 1971; Pantoja, *in review/ see Chapter 1*), and were crucial in forming the character of their herpetofaunas (Duellman, 1979; Tyler, 1979; Colli, 2005). These include: (1) a common origin in Gondwana (Mesozoic) (Sanmartín & Ronquist, 2004); (2) a long period of isolation during most of the Tertiary promoting development of a large number of endemic lineages (Simpson, 1980; Westoby, 1988); (3) approach and collision against northern continents allowing invasion and settling of new elements

that started “new rules” on communities, also promoting extinction of native elements (Stehli & Webb, 1985; van Oosterzee, 1997); (4) marine transgressions that promote vicariant speciations (Webb, 1995; McLoughlin & Kear, 2010); and (5) repeated cycles of aridity and humidity, associated with glacial and interglacial periods, respectively, promoting speciation during repeated isolations and re-connections of populations in appropriate shelters (at lower areas in the cold and dry periods and altitude areas in the warm and humid periods) (Brown & Ab’Sáber, 1979; Moritz *et al.*, 2009). These historical shared events affected biological communities, influencing species distribution, diversification, and the community assembly. Because responses are often taxon-specific, independent communities should react distinctly under the same sort of historical event, however, in theory, they experienced similar potential influences, which is useful for understanding how extant communities have reached their present characteristics.

The plasticity of snake ecological traits (e.g., body size, habitats, habits, diet, etc.) makes them an excellent model for ecological studies (Shine & Bonnet, 2000; Mullin & Seigel, 2009; Sites *et al.*, 2011). As indicated above, phylogeny and biogeography are important components of studies on comparative ecology of communities (Brooks & McLennan, 1993; Wiens, 2004; Moen *et al.*, 2009), and have been broadly applied in research with Squamata (e.g. Cadle & Greene, 1993; Colli, 2005). The lizards have been used comparing South America and Australia (Colli *et al.*, 2006; Costa *et al.*, 2008a; Costa *et al.*, 2008b; Costa *et al.*, 2013; Pantoja *et al.*, in prep.). I propose to compare both continents using Serpentes (snakes), a clade of advanced Squamata. Despite of the classical examples of species convergence between snakes from South America and Australia (e.g. Shine, 1980; Shine, 1991; Greene, 1997), there are marked differences between snake faunas, whether combined

similarities and differences between their species components promote significantly different faunal structures and organization is poorly understood.

Herein, I will investigate the existence of convergences between South American and Australian snake faunas, given that historical, contemporary, regional, and local processes form community attributes, and that similar environments could offer similar selective forces. Community convergences have been traditionally assessed based on flow of energy and materials, physical structure, and species richness (Orians & Paine, 1983; Schluter & Ricklefs, 1993b). I utilize species richness and density, natural history, body size, and phylogeny to describe continental faunas, and hypothesize that habitats from different continents but with similar structures (closed/forested or open/non-forested habitats) should similarly affect snake ecology and evolution. In addition, if these faunas converge, their snake assemblages should present similar ecological guilds and similar proportions of species occupying these guilds. Globally, I expect the fauna structure in each continent to be coherent with its proportion of closed and open habitats, i.e., South America should present a higher proportion of species ecologically and phylogenetically associated to closed habitats, whereas the reverse occurs in Australia with open habitats.

METHODS

Data

The study encompasses the whole non-marine mainland of South America and Australia. Species endemic to any associated insular territory were not included, neither were marine or exotic species. The primary data set is a comprehensible compilation of published reliable (voucher based) records of snakes (clade Serpentes)

from inland South America and Australia, which offers an updated list of non-marine species occurring in each continent, supported by more than 200 references plus our own data (Appendix S1 in Supporting Information). Taxonomic choices and systematic classification through higher-clades are briefly described in the Appendix S2. The character of each species was defined by their natural history and body size, which account for six biological dimensions decomposed in 29 biological attributes. Data come from publications and my own experience in South America (data matrix and references in the Appendix S3). 1) *Habitat* – refers to the general stands of habitat structure where the species live: open habitat (Op) includes any savanna-like vegetation formation, shrublands, deserts, open forests/woodlands, etc; closed habitat (Cl) includes only the effectively closed forests, such as rainforests, gallery forests, wet temperate forests, and vine thickets; and both habitats (Bo) if species occurrence includes both open and closed habitats. 2) *Habit* – refers to the most common way that a given species use to spatially explore their environment, also referred elsewhere as microhabitat: aquatic (aq); semiaquatic (saq); strictly fossorial/burrowing (fo); cryptozoic+fossorial (cfo); strictly cryptozoic (cr); cryptozoic+terrestrial (cte); terrestrial (te); semiarboreal (sar); and arboreal (ar). 3) *Diel activity* – refers to the main period of activity: diurnal (D); nocturnal (N); and both periods (DN). 4) *Reproduction* – oviparous (O); viviparous (V); and both reproductive strategies (OV). 5) *Diet* – includes prey roughly corresponding to >30% of the species' diet. When available data were insufficient to determine the prevailing prey types, all items were included. Eggs were lumped with their parent taxon. When juveniles have a specialized diet, I assured the inclusion of their prey types in the species diet. This is the only adopted dimension in which biological attributes/categories are not mutually exclusive, i.e., one snake species may present more than one main prey type:

mammals (mam); birds (bir); reptiles (rep); amphibians (amp); fishes (fis); arthropods (art), but includes onychophorans; and goo (goo), a class containing soft-body invertebrates such as earthworms and mollusks (snails and slugs). 6) *Body length* – refers to the maximum total length, from the body fore-tip to the tail-tip. Body length was categorized in four classes: short length (S), up to 500 mm; medium (M), between 500 and 1000 mm; long (L), 1000 - 2000 mm; and very long (VL), more than 2000 mm. For a few species, when this measure was not available, the average total length was used.

The continental areas covered by open or closed habitats were estimated and localized using data from the Vegetation Continuous Fields, in Global Land Cover Facility (<http://www.landcover.org/data/vcf/>). Images were captured in 2000 by the MODIS sensor onboard NASA's Terra satellite, at 250 m spatial resolution (DiMiceli *et al.*, 2011), and combined using the Modis Reprojection Tools (http://gcmd.nasa.gov/records/MODIS_Reprojection_Tool.html). Pixels with vegetation cover indices lower than 60 identified areas of non-forested vegetation, assumed as open habitat; closed habitat (forests) follows indices from 60 to 100. Areas of interest were calculated after vectorialization in a world's cylindrical projection, using ArcGIS.

Besides continental species richness, I used species richness in open and closed habitats as measures of regional diversities. Species richness in five forested localities and six open-habitat localities in each continent were used to calculate an average local diversity for each type of habitat in each continent. Local assemblages in South America were localized from latitudes 03° to 24°S (closed forests), and 07° to 24°S (open habitats), whereas in Australia from 12° to 20°S, and 17° to 28°S,

respectively. The list of localities, coordinates, and references are described in the Appendix S4.

Analyses

Sample adequacy

To assess sample adequacy for continental species richness I plotted a curve of cumulative number of described species per year of description, for each continent, and visually compared tendency of the curves. To assess reliability of comparisons in richness of taxa due to differences in taxonomist's efforts in each continent I compared their average number of species per genus, subfamily, and family; the average number of genera per subfamily and family; and of subfamilies per family. Differences between taxonomic ratios from different continents suggest distinct level of taxonomic maturity, and were tested by Wilcoxon rank-sum test, a non-parametric method (Crawley, 2007, p.297).

Taxonomic structure

The taxonomic structure of each continental fauna was described based on the number of species and genera per family and higher clade, and by taxonomic dominance among clades, given by percentages. Differences between dominances in each continent were assessed by "binomial tests to compare two proportions", with 0.05 level of significance. This test answers whether the different percentage of species in a given clade in one continent differs from the percentage of species in the same clade in another continent, or yet, whether this sort of difference could arise through chance alone (Crawley, 2007, p.301). To partially control the area effect I also compared faunas based on densities (number of taxa per 1,000,000 km²).

Biological structure

The biological structures were described based on the number and proportion of species present in each biological attribute. The adequacy of samples for each biological dimension was assessed by the percentage of species with data. Between continents differences were tested through binomial tests to compare proportions of species (Crawley, 2007). Ecological guilds in each fauna were recognized through cluster methods (UPGMA) based on a matrix of Jaccard dissimilarity. Data input were presence/absence matrices with biological attributes as columns and species as rows; only including species for which all biological variables were available. Despite of restricting data set, these analyses were based on 337 species from South America and 156 from Australia, representing more than 84% and 97% of their respective genus richness. Dissimilarities were calculated with “vegdist” function, and the hierarchic clustering with “hclust”, both implemented by the package “vegan” (Oksanen *et al.*, 2013), in R statistical environment (R Core Team, 2013). The total cluster’s confidence was given by its cophenetic index value (= cophenetic correlation), which is the correlation between observed dissimilarities and cophenetic distances (i.e., distances among cluster’s centroids in average linkage, a method that maximizes such correlation).

Guilds of biologically similar species were suggested based on 0.70 threshold-level of maximum cophenetic distance within groups of species. Then, I calculated indicator values for each biological attribute in each guild (algorithm *indval*, implemented by the package “*labdsv*” Dufrene & Legendre, 1997; Roberts, 2013), which measures the relative contribution of each biological attribute. Significant indicator values were used to define the character of each guild. Prevalence of

ecological guilds in each snake fauna was assessed based on the percentage of species in each guild. Finally, I used the same method to check for qualitative similarities among ecological guilds from different continents, having the matrix of indicator values as data input, with guilds from both continents as rows. Faunal convergences were assessed based on the number of clustered pairs of guilds from different continents, and by testing differences between the proportions of species within pairs of guilds.

Phylogenetic structure

Phylogenetic analyses were based on the most complete current molecular phylogenetic hypothesis for Squamata (see Pyron *et al.*, 2013). From this huge squamate sample (4161 species), 1262 are snakes, 317 occurring in South America (235) or Australia (82) inland. This sample represents about 77% of the presently known inland genus richness of South America, and 90% of Australia. To obtain a measure of evolutionary history and differentiation I calculated the phylogenetic diversity (PD), by the sum of all branch lengths from the tree root to the terminal branches in each continent (Faith, 1992). The observed PD significances were determined by comparisons against the expected PD values estimated by null models based on 999 permutations using the 1262 snake species present in the Pyron *et al.*'s (2013) cladogram (algorithm `taxa.labels`, implemented by the package “`picante`” Kembel *et al.*, 2010). The mean PD-values were standardized to Z-values and the faunas were considered more or less diverse than randomly expected if values are higher or lower than 1.96 and -1.96 respectively (Cavender-Bares *et al.*, 2004). I also tested PD differences between faunas controlled by the same species richness (Nipperess & Matsen, 2013) rarefying the PD of the richest fauna and comparing its

mean PD for species richness equal to the poorest fauna using *Z* test (sensu Gotelli & Colwell, 2001). The null models were generated by 1,000 iterations without replacement, based on the algorithm *phylocurve.perm*, implemented by the package “ape” for the R statistical environment (R Core Team, 2013). The same procedures were used to compare the phylogenetic diversity and structure between open and closed habitats in both continents.

Species diversity

The continental local richness of species were compared by Wilcoxon rank-sum test. Local richness differences between closed and open habitats were tested through pairwise comparisons using *t* tests with pooled standard deviation, and *p*-values adjusted with the “holm” method (Crawley, 2007, p.482). The relationships between local and regional diversities were assessed by an adaptation of Westoby’s (1993) method. The behavior of this relationship is represented graphically by the projection of the average local and regional richness in a species-area plot (Figure 2), where the slope of the line connecting the local to regional richness is the “differentiation diversity” (Whittaker, 1977), which in turn is a measure of species replacement over the habitats (beta diversity) and geographical gradients (delta diversity) (Cody, 1993). Figure 1 depicts four possible arrangements: (H₁) local diversity in similar environments is limited by local processes acting similarly in both continents, regardless of their regional diversity; (H₂) local diversity reflects the regional diversity (historical effect), although it may be driven by similar processes operating on both continents; (H₃) the differentiation diversity rates can be distinct in each continent due to the particularities of each biogeographic region, and not due to potential constraints in the local universe, but keeping the regional effect on local

diversity (evidence of historical effect); and (H₄) represents the absence of differences. Once the regional diversity is a consequence of synthesis of evolutionary history and landscape history excluding and generating new species over evolutionary time, there is no reason to expect similar regional diversities in two continents with long independent histories. Therefore, scenario H₄ is considered an unlikely coincidence (Westoby, 1993). Similar local diversities or differentiation rates will be taken as evidences of fauna's convergence between continents. I used three filters to compare continents: between total faunas, between closed habitats, and between open habitats. Total species richness occurring in closed habitats and open habitats were considered regional diversities.

RESULTS

Taxonomic structure

Snake diversity in South America is evidently higher than in Australia (Table 1), housing 4.7 times more species, 2.7 more genera, 1.9 more subfamilies, 1.5 more families, and 1.2 more higher-clades. The only situations in which Australia overcomes South American numbers are the higher number of families in Caenophidia and Afrophidia (Table 2), of species in the family Typhlopidae, and of genera and species in Elapidae (Table 3). Six families occurring in South America do not occur in Australia, whereas three families are exclusive to Australia, three other families are shared (Typhlopidae, Elapidae, and Colubridae). The South American Amerophidia is the only higher clade not shared between continents. The South America continent is 2.3 times larger than Australia; its species and genera density is 2.0 and 1.2 times higher respectively (Table 1). However, densities of subfamilies, families, and higher clades are higher in Australia (1.3, 1.5, and 1.9 times

respectively). There is no significant differences between continents in average number of species per genus, subfamily, and family; genera per subfamily and family; neither in subfamilies per family (Table 4), suggesting that sample is not biased by eventually different efforts or approaches used by taxonomists in each continent. However, the very steep slope in the South American species accumulation curve suggests a significant number of undescribed species, whereas the gentle slope in the Australian curve indicates a better sample (Figure 3).

Appendix S1 presents the complete list of snakes occurring in the South America and Australia inlands, and the Appendix S5 describes the faunal taxonomic structures. Most of South American snake species (91.6%) are found within the Alethinophidia clade, and the remaining species are part of the basal clade Scolecophidia, which includes all blindsnakes and threadsnakes. There are three scolecophidian families occurring in South America: Leptotyphlopidae (the most diverse), Anomalepididae, and Typhlopidae (in South America represented by *Typhlops* only). Amerophidia is the most basal lineage within Alethinophidia, composed of Aniliidae (*Anilius scytale*) and Tropidophiidae, and represents a very low proportion of the continental fauna (1.1%). The largest Alethinophidia lineage, Afrophiidia, is divided in two major groups, the ancient Henophidia, and the advanced Caenophidia, representing 2.4% and 88.1% of the total fauna respectively. All South American henophidian species are part of the family Boidae (Boinae and Ungaliophiinae), whereas the advanced snakes are classified in three additional families: Colubridae, Viperidae, and Elapidae. Colubridae is the most species rich family in South America, including 73.7% of its snake fauna. Four main lineages occur among the South American colubrids: Xenodontinae, Dipsadinae, Colubrinae, and Sibynophiinae. Xenodontinae is the most diverse, and with Dipsadinae sums to

63.3% of all South American snakes. Sixteen tribes have been formally described to taxonomically organize these very rich clades (Appendices S2 and S5), also referred with family status (Dipsadidae) by several authors (see Zaher *et al.*, 2009; Vidal *et al.*, 2010a; Grazziotin *et al.*, 2012). The remaining South American subfamilies within Colubridae (Colubrinae and Sibynophiinae) encompass 9.9% and 0.3% respectively. The highly venomous snake families Viperidae and Elapidae appear in similar proportion of species, 7.0% and 7.4% respectively. In addition, one marine species occurs in the Pacific coast of Colombia, Ecuador, and Peru, northern South America (Elapidae: Hydrophiinae: *Hydrophis (Pelamis) platurus*).

Most of Australian snake species (75.8%) lie within the Atlethinophidia clade, and all remaining species in Scolecophidia, family Typhlopidae, genus *Ramphotyphlops* (Appendix S1, Appendix S5). All Australian Alethinophidia are Afrophidia, split in Henophidia (8.1%) and Caenophidia (67.7%). Australian henophidians are Pythonidae, whereas the advanced snakes are distributed in four additional families: Elapidae, Colubridae, Homalopsidae, and Acrochordidae. Elapidae is the most species rich family in Australia, encompassing 60.2% of its snake fauna. The remaining smaller families (Colubridae, Homalopsidae, and Acrochordidae) represent together 7.3%. The file snakes Acrochordidae form the most basal clade of advanced snakes (Appendix S2), and the least species rich family. In addition to this inland fauna, about 36 species (Elapidae: Hydrophiinae: Hydrophiini 34 species, and *Laticauda* spp. 2 species) live in the sea surrounding the Australia mainland (most species virtually never touch the land surface), and at least one exotic species has colonized Australia, the blind snake *Ramphotyphlops braminus*.

Percentages of species within shared clades differ significantly between continents (Table 3). Exclusive South American families that count for less than 2.5% of the total fauna (i.e., Anomalepididae, Aniliidae, Tropidophiidae, and Boidae) do not contribute significantly to between-continent differences in the dominance relationships among clades.

Biological structure

The biological structure of both faunas are described in Table 5, and detailed in Appendix S3. Samples contain data for most of the known species in all of the studied biological dimensions. The least known biological dimensions are diet and diel activity in South America, with data from more than 54% and 57% of species, respectively. The remaining dimensions in South America are described based on data from more than 88% of species. The biological character of the Australian fauna was based on data from more than 98% of species, for all biological dimensions. The biological structure of the South American fauna is characterized by a high proportion of species using only closed habitats, with terrestrial or cryptozoic+fossorial habits, nocturnal activity, oviparous reproduction, feeding mainly on reptiles and/or amphibians, and with short to medium body length (Table 5). Also, by a low proportion of species using only open habitats, with semiaquatic or strictly cryptozoic habits, active in both periods, with both reproductive strategies, feeding on birds and/or fishes, and with long body length. The Australian fauna is characterized by a high proportion of species using only open habitats, with terrestrial or strictly fossorial habits, nocturnal activity, oviparous reproduction, feeding mainly on reptiles and/or arthropods, and with short to medium body length. Also, by a low proportion of species using only closed habitats, with semiaquatic or cryptozoic+fossorial habits,

active in both periods, viviparous reproduction, feeding on birds and/or fishes, and with very long body length. The remaining biological attributes are less explored. Comparisons between continents reveal that South American fauna have significantly higher proportion of species using only closed habitats, with cryptozoic+fossorial or arboreal habits, diurnal or both periods of activity, oviparous reproduction, and feeding mainly on amphibians or soft-body invertebrates (“goo eaters”) (Table 5). Conversely, Australian fauna have significantly higher proportion of species using only open habitats, with strictly fossorial or cryptozoic habits, nocturnal, viviparous, and feeding mainly on reptiles or arthropods. None of the Australian species have both reproductive strategies, oviparous and viviparous, and neither feeds on goo. The relative contribution of each snake family to the continental biological structure is summarized in Appendix S3.

Biological structures were also investigated by assessing the proportion of species through combinations of attributes from different biological dimensions. The cluster dendrogram of South American snakes (UPGMA, cophenetic index = 0.677) suggested 11 groups of biologically similar species, hereafter called ecological guilds (Appendix S6). Each South American ecological guild (from SG1 to SG11) was significantly described by 6 to 10 biological attributes (Appendix S6c) and their character are described in Table 6. The guilds SG3, SG7, SG8, and SG9 comprise the highest proportion of species, each with more than 12% of the fauna, summing to 72.70% of the fauna (Table 7). SG4 and SG10 have the lowest proportion of species, each with less than 1% of the fauna. The cluster dendrogram of Australian snakes (cophenetic index = 0.866) suggested 7 ecological guilds (AG1 – AG7) (Appendix S7), significantly described by 7 to 12 biological attributes (Appendix S7c), and described in Table 6. The guilds AG2, AG3, and AG5 comprise the highest

proportion of species, each with more than 16% of the fauna, summing to 86.54% (Table 7). AG4 has the lowest proportion of species (1.28%). The combined cluster dendrogram of ecological guilds from both continents paired each Australian guild with a South American guild (cophenetic index = 0.647), suggesting qualitative correspondences between guilds from opposite continents (Figure 4). The most similar pairs of guilds are formed predominantly by species combining:

- 1) SG5 with AG3 – fossorial habit, nocturnal activity, oviparous reproduction, arthropod based diet, and small body;
- 2) SG3 with AG6 – both closed and open habitat, arboreal habit, nocturnal activity, mammal and/or bird based diet, and large body;
- 3) SG9 with AG7 – both closed and open habitat, terrestrial habit, diurnal activity, and amphibian and/or reptile based diet;
- 4) SG4 with AG1 – aquatic habit, viviparous reproduction, and fish based diet (arthropod secondarily).

On the other hand, only one pair of similar guilds presented similar proportion of species (Table 7): SG2 with AG4, formed by few species sharing diurnal+nocturnal activity, viviparous reproduction, and amphibian and/or mammal based diet. Among South American guilds with the highest proportion of species, only SG7 did not pair with any Australian guild.

Phylogenetic structure and the effect of habitat

Both South American ($Z_{PD} = -11.94$) and Australian ($Z_{PD} = -8.34$) faunas are phylogenetically structured with lower phylogenetic diversity (PD) than expected by chance (negative values of z-standardized PD values). The calculated South American PD is 16.69 subst./site, significantly higher than Australian PD, 7.24 subst./site ($Z = -$

2.46, $p < 0.05$). In addition, all but closed habitats in Australia are phylogenetic structured with lower PD than expected by chance (Table 8). Phylogenetic diversity in South American closed habitats is significantly higher than in open habitats from either continents.

South America and Australia have smaller areas covered by structurally closed habitats (forests) than covered by open habitats, but in significantly different proportions (Table 8). Closed habitats in South America cover less than 35% of the continent, roughly corresponding to half of the continental open habitat area. However, closed habitats have 1.6 times more species and 1.3 more genera, reflecting in species and genera density 3.4 and 2.7 times higher, respectively. In Australia, closed habitats cover less than 2% of the continent; have lower species and genus richness than open habitats, but higher species and genus density. Open habitats in Australia have 3.1 and 1.3 more species and genera than closed habitats. Conversely, closed habitats present almost 20 times higher species density, and about 47 times higher genus density. Direct comparisons between continents reveal that total area of South American closed habitats are 46.4 times larger than Australian closed habitats, and open habitats are 1.6 times larger (Table 8). In addition, 11.2 more species and 3.5 more genera occur in South American closed habitat than in the same type of habitat in Australia. Likewise, South American open habitats have 2.3 and 2.1 more species and genera than Australian open habitats. On the other hand, the numbers of species per area indicates lower density of species and genera in South American closed habitats than in the same type of habitat in Australia (4.1 more species per area and 13.3 more genera per area in Australia). Species and genus densities in open habitat are higher in South America (1.4 more species and 1.3 more genera). Densities in closed habitats are higher than in open habitats in all comparisons. The proportions

of species in both closed and open South American habitats are significantly higher than the proportion of species in Australian closed habitats. The reverse occurs in comparisons with Australian open habitats.

Species diversity

Local richness of species in South America is higher than in Australia (mean 38.00 ± 13.48 vs. 8.28 ± 5.79 , $W = 0$, $p \ll 0.001$), and the projection of relationships between local and continental diversities reveal similar behaviors (Figure 5A), fitting the model H_2 (Figure 2). Pairwise comparisons between continents indicate that local richness in closed or open South American habitat is higher than either Australian habitats ($p \ll 0.001$). Considering only closed habitats, differences between local diversities roughly follows the same proportion of differences between regional diversities (total species richness in closed habitats, Figure 5B), repeating the continental pattern (Figure 5A). On the other hand, considering only open habitats, a higher differentiation diversity rate occurs through Australian open habitats, although local diversities still reflect regional diversities (Figure 5C), fitting model H_3 (Figure 2). All described scenarios support a significant area effect upon species diversity.

DISCUSSION

Snake richness in South America is one of the greatest in the world (Duellman, 1979), highly endemic (Passos *et al.*, 2010; Nogueira *et al.*, 2011). South America has higher richness than Australia in all taxonomic levels within Serpentes. Differences fade out from species level to high-level clades, suggesting that present differences in taxonomic richness are consequence of recent diversifications rather than ancient radiations. Comparing diversity between shared higher-clades, the higher

number of families in Australian Caenophidia and Afrophidia are explained by the presence of two exclusive caenophidian families, contrasting with just one in South America. However, the total South American fauna has twice number of exclusive families, mainly due to the contribution of five old lineages: one henophidian, two scolecophidians, and two amerophidians. This result suggests that South American snake fauna has an older history. The curve of cumulative number of described species reveals that observed species richness in Australia is close to its actual faunal diversity, but the contrast between curve's tendencies suggests that differences between total diversities should be greater than demonstrated here, with a much greater diversity in South America.

The higher richness of taxa in South America compared to Australia probably reflects a combined effect of several correlated features. South America has: (1) larger total area, (2) larger latitudinal extensions, (3) larger tropical area, (3) higher rainfall, and (4) larger proportion of forested areas (Keast, 1972). Higher taxonomic diversity is a positive response to higher habitat diversity, consequence of the much more diverse (5) landscape, (6) climate, and (7) vegetation, and (8) larger altitudinal extension (Duellman, 1979). For instance, South America presents more opportunities for developing new species by "duplicating faunas" isolated in similar environments within continent (Keast, 1972). In addition, South America snake fauna has (9) a longer and older history, (10) heavier stock of autochthonous lineages, and (11) received stronger immigrant colonization due to a shorter-term isolation (Duellman, 1979; Tyler, 1979).

The higher species richness in South America is primarily explained by the area effect, since South America is more than twice as larger as Australia. However, the area size *per se* does not completely explain differences. South America has

almost five times more species than Australia, but only twice the species density. This corroborates South American higher species diversity partially controlling the straight area effect. Moreover, the smaller difference between continental species densities compared to difference in species richness can be explained by large areas in South America without snakes or with very low number of species. Few species can survive the cold high latitudes and altitudes available in South America. For instance, *Micrurus pyrhocryptus* is the southernmost elapid in South America, reaching 35°S (Roze, 1996), and no snake occurs farther south than the viperid *Bothrops ammodytoides*, reaching 47°S (Greene, 1997; Carrasco *et al.*, 2010). South America mainland reaches its extremity circa 53°S (Cape Froward, Chile.), whereas Australian southernmost point is located at 39°S, almost 15° northward. Snake species richness decreases with latitude in both continents, although patterns vary between lineages (Darlington, 1965, p.20; Shine, 1991; Cadle & Greene, 1993), and there is no Australian mountain chain comparable to the Andes (uninhabited by snakes in its southwest portion and at the highest elevations).

Habitat diversity reflects the area effect and latitudinal extension and has a major influence upon species diversity. South America extends circa 68° of latitude reaching 12°N (within the tropical zone). Australia does not cross the equator, extending circa 30° of latitude and reaching 10°S. Latitudinal variation strongly affects climate and vegetation, which define snake habitat conditions. In addition, South America has a larger altitudinal extension and higher contrasts between main geomorphic provinces. The Andes promote wide altitudinal gradients along the entire western portion of South America (Orme, 2007), with no resemblance in Australia. The Brazilian Highlands covering central-eastern South America is comparable to the Australian Eastern Highlands (mostly between 600 and 2000 m in elevation), but

there is no Australian counterpart for the isolated Guiana Highlands at the extreme north. All these factors contribute to create a variety of habitats, relative isolations, and consequent fauna diversification (Sawaya & Sazima, 2003; Antonelli *et al.*, 2009; Passos *et al.*, 2009a; Kok, 2010; Passos & Lynch, 2010; Rull, 2011). Also, ranges of several snake species are associated with major rivers (Arzamendia & Giraud, 2009) and the extensive river system in South America (not in Australia) has a potential positive effect on its snake diversity.

Arrangement of the main physiographical elements in South America formed a relevant scenario for speciation by “duplicating faunas” isolated in similar environments (Keast, 1972). The main pairs of isolated blocks are: (1) the rain forest west vs. east of the Andes; (2) the Amazonia in the north vs. Atlantic Forest, cut by the diagonal of open/dry vegetation (Vanzolini, 1963; Werneck, 2011); and (3) the Brazilian Highlands vs. Guiana Highlands, especially contrasting the Cerrado and the isolated plains of the Venezuelan Llanos. The high level of endemism associated to these blocks provides evidence for the duplication effect (Hoogmoed, 1982; Passos *et al.*, 2009b; Passos *et al.*, 2010; Nogueira *et al.*, 2011). There is no true faunal duplication within the Australia mainland (Keast, 1972).

The snake fauna development in South America clearly started earlier than in Australia, reflecting its higher number of old lineages and autochthonous radiations. This distinct initial input of lineages had relevant consequences for current differences in continental richness of taxa. The clade Serpentes arose in Gondwana around the Jurassic-Cretaceous boundary and diversified primarily during the Cenozoic (Vidal *et al.*, 2009; Vitt & Caldwell, 2009; Pyron & Burbrink, 2012). The South American Aniliidae (Estes & Báez, 1985), Boidae (Estes & Báez, 1985; Albino, 1996), Tropidophiidae (Vitt & Caldwell, 2009), and the Scolecophidia

[Anomalepididae (Vitt & Caldwell, 2009), Leptotyphlopidae, and Typhlopidae (Vanzolini & Heyer, 1985)] form the autochthonous stocks, with Gondwanan origin (Table 9) (Duellman, 1979; Colli, 2005). Colubroidea (Elapidae, Viperidae, and Colubridae) contains the northern and relatively recent elements (Estes & Báez, 1985; Vanzolini & Heyer, 1985; Cadle, 1987; Kelly *et al.*, 2009). On the other hand, all living lineages of Australian snakes are relatively recent elements, derived from Oriental ancestry (Tyler, 1979; Hutchinson & Donnellan, 1993; Greer, 1997; Keogh, 1998; Scanlon *et al.*, 2003; Kelly *et al.*, 2009). Oriental invasions were presumably facilitated when the Australian plate collided with Southeast Asia about 10 Mya during the Middle Miocene (Raven & Axelrod, 1972; Hall, 2001). The last remnant of a Gondwanic snake fauna shared between South America and Australia was the family Madtsoiidae (Buffetaut & Rage, 1993; Greer, 1997; Scanlon, 2005a), widespread on Gondwana during the Late Cretaceous and Paleogene. The madtsoiids are related to the present henophidians (boas and pythons), became extinct in South America during the Eocene, but survived into the Australian Pleistocene (Scanlon, 2005b; LaDuke *et al.*, 2010). The oldest Australian living lineage is Acrochordidae, also the most basal Caenophidia, which diverged in the Late Cretaceous (Pyron & Burbrink, 2012). However, fossil distributions suggest west or south Asian origin, instead of Gondwana (Sanders *et al.*, 2010). The current northern/eastern tropical distribution in Australia and its phylogenetic proximity with oriental clades also support oriental origin (Tyler, 1979; Sanders *et al.*, 2010). Therefore, immigrant colonizers form the framework of the Australian snake fauna. Nonetheless, South America still received stronger immigrations. The formation of the Panamanian land bridge during the Late Pliocene-Early Pleistocene (Simpson, 1980; Stehli & Webb, 1985; Coates & Obando, 1996; Iturralde-Vinent, 2006; Webb, 2006) remarkably

intensified faunal interchanges started earlier in the Neogene (Estes & Báez, 1985; Vanzolini & Heyer, 1985) and played a significant role in shaping the South American snake fauna (Cadle, 1985; Head *et al.*, 2012). The Australian continent currently has no land bridge with other continents and has never experienced such intense faunal input, although a Quaternary land bridge connection to New Guinea enabled relevant exchanges of snake species (Shine, 1991, p.52).

Taxonomic structure

In both faunas Alethinophidia prevails over Scolecophidia, although in a lower proportion in Australia. Despite the higher number of scolecophidian families, genera, and species in South America, the larger proportion in Australia is supported by the highly diverse genus *Ramphotyphlops* (Typhlopidae), which still encompass significant cryptic diversity. A combination of biogeographical barriers and complex phytogeographical and geological patterns is documented for *Ramphotyphlops* diversification (Marin *et al.*, 2013). Although shared between continents, the cosmopolitan Typhlopidae represents lower proportion of the South American fauna.

The advanced snakes Caenophidia prevails over the remaining Afrophidia (i.e., Henophidia: South American boas, and Australian pythons), representing the greatest number of snake species in both South American and Australian faunas, although in a lower proportion in Australia. Despite the slightly higher number (subfamilies, genera and species) of boas compared to pythons, the former corresponds to a smaller fraction of the South American fauna than pythons in Australia. However, both represent low percentages of their respective faunas (less than 10%). The diversity of advanced snakes is distributed throughout three families in South America and four in Australia. Colubridae and Elapidae are shared between

continents, the former prevailing in South America and the latter in Australia, in higher proportion in the former. Besides Colubridae, the remaining caenophidian lineages in South America represent 14.4% of the entire fauna, whereas non-elapid caenophidians correspond to about half of this value (7.3%) in the Australian fauna. These differences are mainly due to a relatively higher proportion of South American pit vipers (Viperidae) and coral snakes (Elapidae) compared to the sum of Australian file snakes (Acrochordidae), colubrids (Colubridae), and mangrove snakes (Homalopsidae). Therefore, we have advanced snakes in a significantly higher proportion in South American compared to Australia. The species-rich South American Colubridae is taxonomically well structured in comparison to Australian families, with four subfamilies and several tribes, whereas the few Australian colubrids are divided in just two subfamilies. Australian elapids are in a unique subfamily, Hydrophiinae. Elapidae and Colubridae (including Colubrinae) have cosmopolitan distributions (Vitt & Caldwell, 2009).

One exclusive higher clade and six exclusive families occur in South America, contrasting with three exclusive families in Australia. The Amerophidia (red pipesnakes and dwarf “boas”) and Anomalepididae (blind snakes) do not occur out of the Neotropics (Freire *et al.*, 2007; Vidal *et al.*, 2009), and the thread snakes (Leptotyphlopidae) have a Western Gondwanan distribution, occurring primarily in the Neotropics and Africa (Adalsteinsson *et al.*, 2009). The family Boidae has a large distribution, occurring throughout the New World, from central Africa to South Asia, Madagascar, and Southwest Pacific islands, but not in Australia (Noonan & Chippindale, 2006; Vitt & Caldwell, 2009). The family Viperidae is distributed worldwide, except by the Papua-Australian region, the oceanic islands, and the poles (Greene, 1997; Wüster *et al.*, 2008). Acrochordidae and Homalopsidae have similar

distributions throughout southern Asian coast from India to China, and northern Australia (Sanders *et al.*, 2010; Murphy, 2011). The Family Pythonidae occurs throughout the sub-Saharan Africa, and from the South and Southeast Asia to Australia (Rawlings *et al.*, 2008). Quantitatively, the contributions of these exclusive families to the dominance relationships between clades in Australia are more relevant than in South America, with stronger effect on faunal taxonomic structure in Australia.

It is noteworthy to mention that one species presently occurs in both continents, the sea snake *Hydrophis platurus*, distributed throughout all tropical and subtropical seas, except in the Atlantic ocean (Campbell & Lamar, 2004). Its recent origin post-dates the final closure of the Isthmus of Panama (Sanders *et al.*, 2013). Furthermore, as far as I know, only Australia presents well established widespread populations of introduced species (*Ramphotyphlops braminus*) (Wilson & Swan, 2010), although records of exotic species in South America also occur (Eterovic & Duarte, 2002). Overall, the observed general pattern of species richness among clades is in agreement with the expectedly global snake diversity, i.e., numerous species-poor lineages and several species-rich young clades (Pyron & Burbrink, 2012). Despite the historical and present similarities, South America and Australia developed snake faunas with particular characteristics. The challenge lies in quantifying the relative contribution of phylogeny, biogeography and the present-day ecological process shaping the structure of the extant snake fauna.

Biological structure

Species can converge in some biological dimensions but not in others (Orians & Paine, 1983). My results suggest this phenomenon occurs with the South American

and Australian snake faunas. Biological similarities and discrepancies between faunas can be explained by both their historical-phylogenetic contingencies and the present proportions of close vs. open habitats available in each continent affecting present ecology. Both South American and Australian faunas predominantly consist of terrestrial, nocturnal, and oviparous species, with reptile-based diet, and short to medium body length. Moreover, faunas do not differ in the proportion of species that use both closed and open habitats; with aquatic, semiaquatic, cryptozoic+terrestrial, strictly terrestrial, or semiarboreal habits; diet based on fish, birds, and/or mammals; neither between any class of body length. These similarities suggest significant levels of convergence between faunas.

On the other hand, the higher proportion of species in South America using strictly closed habitats, with arboreal habits, diurnal or both periods of activity, and feeding mainly on amphibians or goo should be reflecting the higher proportion of closed/forested areas in South America. Besides the obviously larger availability of trees enabling arboreal habits, closed habitats offer more opportunities than open habitats to develop diurnality, because individuals enjoy less exposure to predation even during the day. South America also has much higher rainfall than Australia, enabling the continent to evolve an abundant and diverse fauna of soft-body invertebrates and amphibians. South America is the most frog-rich continent in the globe (Duellman, 1979). Frogs appear in excessive number, i.e., species density higher than expected, what is also attributed to the higher proportion of humid and less seasonal tropical forests in South America (Duellman, 1979; Duellman & Pianka, 1990). Yet, the most snake-rich South American lineages, the Xenodontinae and Dipsadinae, mostly feed on frogs and goo respectively, suggesting a strong phylogenetic effects on faunal-biologic structure in South America (Cadle & Greene,

1993). It is noteworthy to mention that total area of closed habitats in South America is around half the size of the open habitats and contain a larger number species, which strongly demonstrates the ability of forests in promoting snake diversity (see additional discussion below, at the Species diversity section). The higher proportion of oviparous species in South America is explained by having the most species-rich families (Colubridae and Elapidae) predominately oviparous, with the exception of a low percentage of viviparous colubrid species (see Appendix S3a).

Contrasting to South America, the higher proportion of species in Australia using strictly open habitats, with strictly fossorial habits, nocturnal activity, and feeding mainly on reptiles or arthropods should be reflecting the higher proportion of open areas in Australia. Fossoriality and nocturnality are probably very associated to open habitat use, especially considering an evident high level of exposure to predators and weather. Greater climatic seasonality favors nocturnality (Duellman & Pianka, 1990). Australia houses one of the most diverse reptile faunas in the world, with more than 920 currently described species (Cogger, 2000; Wilson & Swan, 2010), lizards present the highest known richness, density, and abundance of species (Pianka, 1989, 1996), which is attributed to the higher proportion of open and xeric areas in Australia (Duellman, 1979; Duellman & Pianka, 1990). Moreover, the phylogenetic effect on faunal-biologic structure is very evident. The most snake-rich Australian lineages, Elapidae and Typhlopidae, mostly feeds on reptiles and arthropods respectively, the latter being strictly fossorial and nocturnal (Appendix S3b). Also, fossoriality is widespread through the cosmopolitan elapids all over the world. Viviparity is commonly found associated to the aquatic habit. Australia has two entirely aquatic viviparous families, Acrochordidae and Homalopsidae, representing a small proportion of the total fauna. Also, Australian elapids developed a whole tribe of true

sea snakes (the viviparous Hydrophiini) (Sanders *et al.*, 2013), as diverse as their continental relatives (non-marine viviparous elapids); however, the latter never acquired aquatic habits. Therefore, aquatic habit do not seems to be related to the higher proportion of viviparous species in Australia. On the other hand, even though oviparity is the ancestral reproductive condition of Australian elapids (Keogh *et al.*, 1998), viviparity appears in almost half of the non-marine species. The marked radiation of viviparous elapids in Australia started soon after the north/oriental invasion and is strongly associated with cold weather and climatic oscillations (Shine, 1991; Keogh *et al.*, 1998). South America has four viviparous families Aniliidae, Tropidophiidae, Boidae, and Viperidae (except *Lachesis*), only the latter proportionally representing significant amount of species (Table 3, and Appendix S3b). The species-rich South American Colubridae are predominantly oviparous but also evolved viviparity, however representing low proportion of species.

South America and Australia present different numbers of ecological guilds. The higher number in South America apparently reflects its higher density of species and higher pressure to develop ecological combinations in structurally closed habitats. Ecological guilds can be examined as “macro adaptive zones” (Keast, 1972) that appear throughout evolutionary time probably relaxing inter-specific competition. Evidently, species in a guild are not ecologically uniform, but ecological differences between species within the same guild are lower than between species from different guilds, which implies higher competition within a guild than between guilds. Furthermore, ecological differences between guilds are higher within continents than between continents, suggesting that for each Australian guild an equivalent counterpart could occur in South America. These correspondences between guilds support a qualitative level of convergence between faunas.

Certain combinations of biological attributes probably increase species fitness better than others, which should be favoring similarities between guilds. For instance, pairs of similar guilds corroborate consistencies between habit and diet, specifically between fossorial habit and arthropod based diet; arboreal habit and endothermic based diet; terrestrial habit and ectothermic based diet; and between aquatic habit and fish based diet. Strong correspondences between snake biological attributes have been previously suggested, especially between habit and body form (Vitt, 1987; Cadle & Greene, 1993; França *et al.*, 2008). These potentially “optimal” combinations probably contribute to the observed pattern in which most species are in a small number of guilds. Nonetheless, there is no guild in Australia resembling the South American species-rich guild SG7, predominantly formed by species that combine a strictly closed habitat, arboreal habit, nocturnal activity, oviparous reproduction, diet based primarily on goo and/or reptiles, and with medium body length. These characteristics are largely present in the subfamily Dipsadinae (Cadle & Greene, 1993). The lack of correspondence between proportions of species in similar guilds seems to reflect the high proportion of South American species in guilds characterized by closed habitat use and a high proportion of Australian species in guilds characterized by open habitat use.

Phylogenetic structure and the effect of habitat

Phylogenetic relationships are not randomly distributed within South American or Australian faunas, signifying both faunas have phylogenetic structures. However negative z-standardized PD values in both faunas indicate lower PD than expected, i.e., species are phylogenetically closer than expected by chance. This result suggests that assembly of both faunas were significantly marked by recent events of

diversification and/or colonization (Webb *et al.*, 2002; Wiens & Donoghue, 2004). The combination between species diversity and metrics of phylogenetic diversity are useful to understand historical effects on faunal structure (Pavoine & Bonsall, 2011). Within South America, the higher species richness and higher PD in closed habitats suggest a long time of diversification (Wiens & Donoghue, 2004), whereas lower species richness and PD in open habitats suggest more recent colonization and shorter time for diversification. This pattern corroborates the hypothesis that most of the South American snake species are representatives of northern immigrant families (Cadle & Greene, 1993; Colli, 2005) that probably colonized tropical forested habitats before reaching the South American savannas. The opposite pattern is observed within Australia with lower species richness and PD in closed habitats, suggesting recent events of colonization and shorter time for diversification. However, the high species richness and low PD in Australian open habitats suggest recent events of adaptive radiation (Slingsby & Verboom, 2006). The recent and rapid radiations of Australian elapids (10 – 6 Mya) are associated with the increasing aridification in the continent (Kuch *et al.*, 2005; Byrne *et al.*, 2008; Sanders *et al.*, 2008). The higher South American PD compared to Australia reflects the higher number of species, older lineages, and ancient history in South America (see also discussions above).

Species diversity

The above discussion highlights a combination of convergent and divergent patterns comparing South American and Australian snake faunas. Community convergence is expected when the number and types of co-existing species are locally determined (Schluter & Ricklefs, 1993b). Despite the larger size of South America compared to Australia, both continents have larger areas covered by habitats that are

structurally open compared to closed/forested habitats. However most comparisons using closed vs. open habitats suggest that closed habitats are better than open habitats in promoting snake diversity, with higher species densities and higher local diversities in both continents. This shared pattern supports the importance of local and contemporary processes in shaping present communities.

On the other hand, independent histories may have similar consequences in different biogeographic regions, also driving biotas to converge (Orians & Paine, 1983; Schluter & Ricklefs, 1993b; Westoby, 1993). I found another shared pattern by comparing the relationships between local and continental diversities of snakes. South America and Australia are marked by distinct local diversities, but are similarly reflecting regional diversity, which implies a strong historical effect upon faunal diversity structure (Westoby, 1993). The consistent area effect with similar “differentiation diversity rates” suggests that species diversity was reached through similar processes operating on both continents. This shared pattern supports the hypothesis of convergence between faunas. Similar habitats are expected to cause similar effects on the number of coexisting species (Orians & Paine, 1983; Schluter & Ricklefs, 1993b). Both South America and Australia have larger areas covered by open habitats than by closed habitats and this could be shaping faunal diversity similarly in both continents. However, we have seen above that the higher proportion of closed habitats in South America compared to Australia has major impacts promoting species richness differences. Total species richness in South American closed habitats (regional diversity) is higher than in open habitats, despite covering a smaller area. How do faunas converge in species diversity considering the comparatively small area covered by closed habitats in Australia?

Potential explanations emerge by comparing the “differentiation diversity” within the same type of habitat but from opposite continents. Results suggest that a higher differentiation diversity rate occurs throughout Australian open habitats than throughout South American open habitats (Figure 5C), probably balancing the strong effect of closed habitats in South America, and leading species diversity to converge at the continental scale. The contrast between differentiation diversity rates in open habitats from opposite continents is probably due to particularities of each biogeographic region, and not due to constraints at the local scale, although keeping the regional effect on local diversity. This hypothesis strongly evokes the importance of historical processes shaping the continental faunal structure (Westoby, 1993).

Despite evident similarities between open landscapes from South America and Australia that support comparative studies (see Colli *et al.*, 2006; Campos *et al.*, 2011; Pantoja, in prep., *in review*), habitat features probably are not as similar as previously thought. I present three potential explanations for higher differentiation diversity rates throughout Australian open habitats compared to open habitats in South America: 1) open landscapes are probably more heterogeneous in Australia than in South America, with higher number of phyto-physiognomies, and consequent higher habitat complexity (Cochrane, 1963; Specht, 1981; Brown & Prance, 1987; Oliveira & Marquis, 2002; Werneck, 2011); 2) habitat complexity can be increased by natural fires, a phenomenon probably more effective in Australia (Pianka, 1996; Miranda *et al.*, 2002; Pantoja, 2007; Pelegrin & Bucher, 2010; Morton *et al.*, 2011; Costa *et al.*, 2013); and 3) climatic fluctuations from the Middle Neogene through the Quaternary promoted repeated cycles of aridity and humidity (associated with glacial periods), which permitted diversification in refugia (e.g. isolated mountains in the arid zone Twidale, 1972; Byrne *et al.*, 2008; Couper *et al.*, 2008; Moritz *et al.*, 2009;

Pepper *et al.*, 2011). These historical-climatic events played significant roles on snake diversification throughout Australian open landscapes (Shine, 1991) and also worked on South American biota's diversification (Haffer, 1969; Vanzolini & Williams, 1970; Brown & Ab'Sáber, 1979; Vanzolini & Williams, 1981); however, probably with a smaller effect on the South American snakes (Colli, 2005; Bush & Oliveira, 2006).

Conclusion

In summation, I found convergences in several aspects of the snake faunas from South America and Australia, although marked differences also exist. Both faunas are formed by higher proportions of terrestrial species, nocturnal species, oviparous species, reptile-eaters, and species with short or medium body length, although the combinations between these biological attributes vary between continents. Also, they present similar proportion of species for several biological attributes. Furthermore, I found groups of ecologically similar species (guilds) in each fauna, for each Australian guild there is another similar counterpart in South America, although the proportion of species in each guild varies markedly between continents. Habitat structure has a significant effect on species natural history and diversity, with closed/forested habitats more influential than open habitats in promoting snake diversity. Local species diversities similarly reflect regional diversity in both continents, which suggests a strong historical effect upon faunal assembly, with convergence at the continental scale. A higher differentiation diversity rate in Australian open habitats probably balance the strong effect of closed habitats in South America promoting species diversity to converge. Among differences, ecological traits consistently associated to the species-richest lineages largely define the main

character of each fauna, which is also largely related to the higher proportion of closed habitats in South America vs. higher proportion of open habitats in Australia. The massive higher richness in all taxonomic levels and higher phylogenetic diversity in South America probably reflect a combined effect of several correlated features: (1) larger total area; (2) larger latitudinal extensions; (3) larger tropical area; (3) higher rainfall; (4) larger proportion of forested areas; (5) more diverse landscape, including (6) climate, (7) vegetation, and (8) larger altitudinal extension; more opportunities for “duplicating faunas” isolated in similar environments within continent; (9) longer and older faunal history; (10) heavier stocks of autochthonous lineages; and (11) stronger immigrant colonization. As expected, faunas are not completely convergent neither distinct.

ACKNOWLEDGEMENTS

DLP was supported by doctoral fellowships from the Brazilian agencies CAPES and CNPq; and a sandwich-doctorate fellowship, part of the CAPES-UT collaborative project (029/2008 ‘Evolução, Ecologia e Conservação da Herpetofauna do Cerrado’) sponsored by G. R. Colli (UnB), E. R. Pianka, and D. C. Cannatella (UT). I thank A. C. M. R. Lima, J. A. L. Pantoja, and S. Rodrigues for assistance on data collection; G. R. Colli, F. R. G. França, C. C. Nogueira, E. R. Pianka, L. J. Harmon, D. O. Mesquita, G. C. Vieira, H. C. Costa, I. C. Arantes, F. P. Werneck; A. M. Gainsbury; S. Goodyear, R. Fernandes; R. B. Machado; and M. Almeida-Neto for suggestions and a helpful bibliographic exchange; P. P. U. Aquino, A. de Paula, and G. R. Colli for comments on analyses; R. B. Machado, Y. B. Salmona, and P. P. U. Aquino for assistance with GIS; P. R. L. Pantoja for assistance with figures; P. Passos, P. K. Sertzen, J. Marinho-Filho, L. J. Vitt, D. B. Provete, and the Wiki Herps community for a helpful bibliographic exchange. South American data was partially

collected during a technical visit to F. R. G. França's lab (Universidade Federal da Paraíba, Brazil). Australian data was partially collected during a technical visit to E. R. Pianka's lab (The University of Texas at Austin, USA).

REFERENCES

- Adalsteinsson, S.A., Branch, W.R., Trape, S., Vitt, L.J. & Hedges, S.B. (2009) Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). *Zootaxa*, 1-50.
- Albino, A.M. (1996) The South American fossil Squamata (Reptilia: Lepidosauria). *Münchner Geowiss Abh*, (A) 30, 185-202.
- Antonelli, A., Nylander, J.A.A., Persson, C. & Sanmartin, I. (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9749-9754.
- Archer, M., Beck, R., Gott, M., Hand, S., Godthelp, H. & Black, K. (2011) Australia's first fossil marsupial mole (Notoryctemorphia) resolves controversies about their evolution and palaeoenvironmental origins. *Proceedings of the Royal Society B-Biological Sciences*, 278, 1498-1506.
- Arzamendia, V. & Giraud, A.R. (2009) Influence of large South American rivers of the Plata basin on distributional patterns of tropical snakes: a panbiogeographical analysis. *Journal of Biogeography*, 36, 1739-1749.
- Brooks, D.R. & McLennan, D.A. (1993) Historical ecology: examining phylogenetic components of community evolution. *Species Diversity in Ecological Communities, Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 267-280. The University of Chicago Press, Chicago.
- Brown, K.S. & Ab'Sáber, A.N. (1979) Ice-age forest refuges and evolution in Neotropics: correlation of paleoclimatological, geomorphological and pedological data with biological endemism. *Paleoclimas*, 5, 1-30.
- Brown, K.S. & Prance, G.T. (1987) Soils and vegetation. *Biogeography and Quaternary History in Tropical America* (ed. by T.C. Whitmore and G.T. Prance), pp. 19-45. Oxford University Press, New York.
- Buffetaut, E. & Rage, J.C. (1993) Fossil amphibians and reptiles and the Africa-South America connection. *The Africa-South America Connection* (ed. by W. George and R. Lavocat), pp. 87-99. Oxford University Press, New York.
- Burbrink, F.T. & Lawson, R. (2007) How and when did Old World ratsnakes disperse into the New World? *Molecular Phylogenetics and Evolution*, 43, 173-189.
- Burbrink, F.T. & Pyron, R.A. (2008) The taming of the skew: estimating proper confidence intervals for divergence dates. *Systematic Biology*, 57, 317-328.
- Burbrink, F.T. & Crother, B.I. (2011) Evolution and taxonomy of snakes. *Reproductive Biology and Phylogeny of Snakes* (ed. by R.D. Aldridge and D.M. Sever), pp. 19-53. Science Publishers, and CRC Press, Enfield, NH.
- Bush, M.B. & Oliveira, P.E. (2006) The rise and fall of the refugial hypothesis of Amazonian speciation. In: *Biota Neotropica*. <http://www.biotaneotropica.org.br>

- Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. & Wyrwoll, K.H. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, 17, 4398-4417.
- Cadle, J.E. (1985) The Neotropical colubrid snake fauna (Serpentes: Colubridae): lineage components and biogeography. *Systematic Zoology*, 34, 1-20.
- Cadle, J.E. (1987) Geographic distribution: problems in phylogeny and zoogeography. *Snakes: Ecology and Evolutionary Biology* (ed. by R.A. Seigel, J.T. Collins and S.S. Novak), pp. 77-105. Macmillan Publishing Company, New York.
- Cadle, J.E. & Greene, H.W. (1993) Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. *Species Diversity in Ecological Communities, Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 281-293. University of Chicago Press, Chicago.
- Campbell, J.A. & Lamar, W.W. (2004) *The Venomous Reptiles of the Western Hemisphere*. Cornell University.
- Campos, R.I., Vasconcelos, H.L., Andersen, A.N., Frizzo, T.L.M. & Spena, K.C. (2011) Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. *Austral Ecology*, 36, 983-992.
- Carrasco, P.A., Leynaud, G.C. & Scrocchi, G.J. (2010) Redescription of the southernmost snake species, *Bothrops ammodytoides* (Serpentes: Viperidae: Crotalinae). *Amphibia-Reptilia*, 31, 323-338.
- Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. (2004) Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*, 163, 823-843.
- Chen, X., Huang, S., Guo, P., Colli, G.R., Montes de Oca, A.N., Vitt, L.J., Pyron, R.A. & Burbrink, F.T. (2013) Understanding the formation of ancient intertropical disjunct distributions using Asian and Neotropical hinged-teeth snakes (*Sibynophis* and *Scaphiodontophis*: Serpentes: Colubridae). *Molecular Phylogenetics and Evolution*, 66, 254-261.
- Chirat, R., Moulton, D.E. & Goriely, A. (2013) Mechanical basis of morphogenesis and convergent evolution of spiny seashells. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6015-20.
- Coates, A.G. & Obando, J.A. (1996) The geologic evolution of the Central American isthmus. *Evolution and Environment in Tropical America* (ed. by J.B.C. Jackson, A.F. Budd and A.G. Coates), pp. 21-56. University of Chicago Press, Chicago and London.
- Cochrane, G.R. (1963) A physiognomic vegetation map of Australia. *Journal of Ecology*, 51, 639-655.
- Cody, M.L. (1993) Bird diversity components within and between habitats in Australia. *Species Diversity in Ecological Communities, Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 147-158. University of Chicago Press, Chicago.
- Cody, M.L. & Mooney, H.A. (1978) Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics*, 9, 265-321.
- Cogger, H.G. (2000) *Reptiles and Amphibians of Australia*. Ralph Curtis Books.

- Colli, G.R. (2005) As origens e a diversificação da herpetofauna do Cerrado. *Cerrado: Ecologia, Biodiversidade e Conservação* (ed. by A. Scariot, J.C. Sousa-Silva and J.M. Felfili), pp. 447-264. Ministério do Meio Ambiente, Brasília, DF.
- Colli, G.R., Constantino, R. & Costa, G.C. (2006) Lizards and termites revisited. *Austral Ecology*, 31, 417-424.
- Colston, T.J., Costa, G.C. & Vitt, L.J. (2010) Snake diets and the deep history hypothesis. *Biological Journal of the Linnean Society*, 101, 476-486.
- Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35, 131-138.
- Costa, B.M., Pantoja, D.L., Vianna, M.C.M. & Colli, G.R. (2013) Direct and short-term effects of fire on lizard assemblages from a Neotropical Savanna hotspot. *Journal of Herpetology*, 47, 502-510.
- Costa, G.C., Colli, G.R. & Constantino, R. (2008a) Can lizard richness be driven by termite diversity? Insights from the Brazilian Cerrado. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 86, 1-9.
- Costa, G.C., Vitt, L.J., Pianka, E.R., Mesquita, D.O. & Colli, G.R. (2008b) Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography*, 17, 670-677.
- Couper, P.J., Sadler, R.A., Shea, G.M. & Wilmer, J.W. (2008) A reassessment of *Saltuarius swaini* (Lacertilia : Diplodactylidae) in southeastern Queensland and New South Wales; Two new taxa, phylogeny, biogeography and conservation. *Records of the Australian Museum*, 60, 87-118.
- Crawley, M.J. (2007) *The R Book*. 942.
- Darlington, P.J., Jr (1965) *Biogeography of the Southern End of the World: Distribution and History of Far-Southern Life and Land, with an Assessment of Continental Drift*. Harvard University Press, Cambridge.
- DiMiceli, C.M., Carroll, M.L., Sohlberg, R.A., Huang, C., Hansen, M.C. & Townshend, J.R.G. (2011) Annual Global Automated MODIS Vegetation Continuous Fields (MOD44B) at 250 m Spatial Resolution for Data Years Beginning Day 65, 2000 - 2010, Collection 5 Percent Tree Cover. In: University of Maryland, College Park, MD, USA
- Duellman, W.E. (1979) The South American herpetofauna: a panoramic view. *The South American Herpetofauna: Its Origen, Evolution, and Dispersal* (ed. by W.E. Duellman), pp. 1-28. University of Kansas Printing Service, Lawrence.
- Duellman, W.E. & Pianka, E.R. (1990) Biogeography of nocturnal insectivores: historical events and ecological filters. *Annual Review of Ecology and Systematics*, 21, 57-68.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345-366.
- Estes, R. & Báez, A. (1985) Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange? *The Great American Biotic Interchange* (ed. by F.G. Stehli and S.D. Webb), pp. 139-197. Plenum Press, New York.
- Eterovic, A. & Duarte, M.R. (2002) Exotic snakes in São Paulo city, southeastern Brazil: why xenophobia? *Biodiversity and Conservation*, 11, 327-339.
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1-10.

- França, F.G.R., Mesquita, D.O., Nogueira, C.C. & Araujo, A.F.B. (2008) Phylogeny and ecology determine morphological structure in a snake assemblage in the central Brazilian Cerrado. *Copeia*, 23-38.
- Freire, E.M.X., Caramaschi, U. & Argôlo, A.J.S. (2007) A new species of *Liotyphlops* (Serpentes: Anomalepididae) from the Atlantic Rain Forest of northeastern Brazil. *Zootaxa*, 1393, 19-26.
- Fuentes, E.R. (1976) Ecological convergence of lizard communities in Chile and California. *Ecology*, 57, 3-17.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391.
- Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y.-P. & Bonatto, S.L. (2012) Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 1, 1-23.
- Greene, H.W. (1997) *Snakes: the Evolution of Mystery in Nature*. University of California Press, California.
- Greer, A.E. (1997) *The Biology and Evolution of Australian Snakes*. Surrey Beatty & Sons, Chipping Norton, NSW.
- Guedes, T.B., Nunes, G.S.S., Prudente, A.L.C. & Marques, O.A.V. (2011) New records and geographical distribution of the tropical banded treesnake *Siphlophis compressus* (Dipsadidae) in Brazil. *Herpetology Notes*, 4, 341-346.
- Gutberlet, R.L. & Harvey, M.B. (2004) The evolution of New World venomous snakes. In: *The Venomous Reptiles of the Western Hemisphere* eds. L.A. Campbell and W.W. Lamar, pp. 634-682. Cornell University Press
- Haffer, J. (1969) Speciation in Amazonian Forest birds. *Science*, 165, 131-&.
- Haffer, J. (1987) Quaternary history of tropical America. *Biogeography and Quaternary History of Tropical America* (ed. by T.C. Whitmore and G.T. Prance), pp. 1-18. Oxford University Press, New York.
- Hall, R. (2001) Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. *Faunal and floral migrations and evolution in SE Asia-Australasia* (ed. by I. Metcalfe, J.M.B. Smith, M. Morwood and I. Davidson), pp. 35-56. A.A. Balkema (Swets and Zeitlinger Publishers) Lisse.
- Harvey, P.H. & Pagel, M.D. (1998) *The Comparative Method in Evolutionary Biology*. 239.
- Head, J.J., Rincon, A.F. & Suarez, C. (2012) Fossil evidence for earliest Neogene American faunal interchange: Boa (Serpentes, Boinae) from the early Miocene of Panama. *Journal of Vertebrate Paleontology*, 32, 1328-1334.
- Hoogmoed, M.S. (1982) Snakes of the Guianan region. *Memórias do Instituto Butantan (São Paulo)*, 46, 219-254.
- Hutchinson, M.N. & Donnellan, S.C. (1993) Biogeography and phylogeny of the Squamata. *Fauna of Australia Volume 2A* (ed. by C.G. Glasby, G.J.B. Ross and P.L. Beesley), pp. 1-24. AGPS Canberra, Canberra.
- Iturralde-Vinent, M.A. (2006) Meso-Cenozoic Caribbean paleogeography: Implications for the historical biogeography of the region. *International Geology Review*, 48, 791-827.
- Keast, A. (1971) Continental drift and the evolution of the biota on southern continents. *The Quarterly Review of Biology*, 46, 355-378.
- Keast, A. (1972) Comparisons of contemporary mammal faunas of southern continents. *Evolution, Mammals, and Southern Continents* (ed. by A. Keast,

- F.C. Erk and B. Glass), pp. 433-501. State University of New York Press, Albany.
- Keast, A., Erk, F.C. & Glass, B. (eds) (1972) *Evolution, Mammals, and Southern Continents*. State University of New York Press, Albany.
- Kelly, C.M.R., Barker, N.P., Villet, M.H. & Broadley, D.G. (2009) Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics-the International Journal of the Willi Hennig Society*, 25, 38-63.
- Kelt, D.A., Rogovin, K., Shenbrot, G. & Brown, J.H. (1999) Patterns in the structure of Asian and North American desert small mammal communities. *Journal of Biogeography*, 26, 825-841.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463-1464.
- Keogh, J.S. (1998) Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biological Journal of the Linnean Society*, 63, 177-203.
- Keogh, J.S., Shine, R. & Donnellan, S. (1998) Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes (subfamily Hydrophiinae) based on cytochrome b and 16S rRNA sequences. *Molecular Phylogenetics and Evolution*, 10, 67-81.
- Kok, P.J.R. (2010) A new species of *Chironius* Fitzinger, 1826 (Squamata: Colubridae) from the Pantepui region, northeastern South America. *Zootaxa*, 2611, 31-44.
- Kuch, U., Keogh, J.S., Weigel, J., Smith, L.A. & Mebs, D. (2005) Phylogeography of Australia's king brown snake (*Pseudechis australis*) reveals Pliocene divergence and Pleistocene dispersal of a top predator. *Naturwissenschaften*, 92, 121-127.
- LaDuke, T.C., Krause, D.W., Scanlon, J.D. & Kley, N.J. (2010) A late Cretaceous (Maastrichtian) snake assemblage from the Maevarano formation, Mahajanga basin, Madagascar. *Journal of Vertebrate Paleontology*, 30, 109-138.
- Lomolino, M. (1993) Matching of granivorous mammals of the Great Basin and Sonoran Deserts on a species-for-species basis. *Journal of mammalogy*, 74, 863-867.
- Losos, J.B. (1994) Historical contingency and lizard community ecology. *Lizard Ecology: Historical and Experimental Perspectives* (ed. by L.J. Vitt and E.R. Pianka), pp. 319-333. Princeton University Press, Princeton, NJ.
- Losos, J.B. (1996) Phylogenetic perspectives on community ecology. *Ecology*, 77, 1344-1354.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. & Rodriguez-Schettino, L. (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, 279, 2115-2118.
- MacArthur, R.H., MacArthur, J.W. & Preer, J. (1962) On bird species diversity. II. Prediction of bird census from habitat measurements. *The American Naturalist*, 96, 167-174.
- Marin, J., Donnellan, S.C., Hedges, S.B., Puillandre, N., Aplin, K.P., Doughty, P., Hutchinson, M.N., Couloux, A. & Vidal, N. (2013) Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*). *Biological Journal of the Linnean Society*, 110, 427-441.
- McLoughlin, S. & Kear, B.P. (2010) The Australasian Cretaceous scene. *Alcheringa*, 34, 197-203.

- Melville, J., Harmon, L.J. & Losos, J.B. (2006) Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society B-Biological Sciences*, 273, 557-563.
- Miranda, H.S., Bustamante, M.M.C. & Miranda, A.C. (2002) The fire factor. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (ed. by P.S. Oliveira and R.J. Marquis), pp. 51-68. Columbia University Press, New York.
- Moen, D.S., Smith, S.A. & Wiens, J.J. (2009) Community assembly through evolutionary diversification and dispersal in middle american treefrogs. *Evolution*, 63, 3228-3247.
- Mooney, H.A. (1977) Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems. 224.
- Moritz, C., Hoskin, C.J., MacKenzie, J.B., Phillips, B.L., Tonione, M., Silva, N., VanDerWal, J., Williams, S.E. & Graham, C.H. (2009) Identification and dynamics of a cryptic suture zone in tropical rainforest. *Proceedings of the Royal Society B-Biological Sciences*, 276, 1235-1244.
- Morton, S.R., Smith, D.M.S., Dickman, C.R., Dunkerley, D.L., Friedel, M.H., McAllister, R.R.J., Reid, J.R.W., Roshier, D.A., Smith, M.A., Walsh, F.J., Wardle, G.M., Watson, I.W. & Westoby, M. (2011) A fresh framework for the ecology of arid Australia. *Journal of Arid Environments*, 75, 313-329.
- Mullin, S.J. & Seigel, R.A. (ed.^eds) (2009) *Snakes: Ecology and Conservation*. Comstock Pub. Associates/Cornell University Press.
- Murphy, J.C. (2011) The nomenclature and systematics of some Australasian homalopsid snakes (Squamata: Serpentes: Homalopsidae). *The Raffles Bulletin of Zoology*, 59, 229-236.
- Nipperess, D.A. & Matsen, F.A. (2013) The mean and variance of phylogenetic diversity under rarefaction. *Methods in Ecology and Evolution*, 4, 566-572.
- Nix, H.A. (1981) The environment of *Terra Australis*. In: *Ecological Biogeography of Australia* (ed. A. Keast), pp. 103-133. Dr. W. Junk, The Hague, Netherlands.
- Nogueira, C., Ribeiro, S., Costa, G.C. & Colli, G.R. (2011) Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography*, 38, 1907-1922.
- Noonan, B.P. & Chippindale, P.T. (2006) Dispersal and vicariance: the complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution*, 40, 347-358.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) *Package 'vegan'. Community ecology package. R package version 2.0-9*.
- Oliveira, P.S. & Marquis, R.J. (ed.^eds) (2002) *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York.
- Orians, G.H. & Solbrig, O.T. (1977) Convergent Evolution in Warm Deserts: an examination of strategies and patterns in deserts of Argentina and the United States. 333.
- Orians, G.H. & Paine, R.T. (1983) Convergent evolution at the community level. *Coevolution* (ed. by D.J. Futuyma and M. Slatkin), pp. 431-458. Sinauer Associates, Inc., Sunderland, MA.

- Orme, A.R. (2007) Tectonism, climate, and landscape change. *The Physical Geography of South America* (ed. by T.T. Veblen, K.R. Young and A.R. Orme), pp. 23-44. Oxford University Press, New York, NY.
- Pantoja, D.L. (2007) *Efeitos do fogo sobre a taxocenose de lagartos em áreas de cerrado sensu stricto no Brasil Central*. Universidade de Brasília, Brasília, DF.
- Pantoja, D.L. (*in prep.*) Biological comparisons between South America and Australia: the state of the art.
- Pantoja, D.L. (*in review*) On the South America and Australia connections: a framework for biological comparisons.
- Pantoja, D.L., Costa, B.M., Colli, G.R. & Lima, E.C. (*in prep.*) Does fire drives lizard diversity in Cerrado?
- Passos, P. & Lynch, J.D. (2010) Revision of *Atractus* (Serpentes: Dipsadidae) from middle and upper Magdalena drainage of Colombia. *Herpetological Monographs*, 24, 149–173.
- Passos, P., Arredondo, J.C., Fernandes, R. & Lynch, J.D. (2009a) Three new *Atractus* (Serpentes: Colubridae) from Andes of Colombia. *Copeia*, 2009, 425-436.
- Passos, P., Mueses-Cisneros, J.J., Lynch, J.D. & Fernandes, R. (2009b) Pacific lowland snakes of the genus *Atractus* (Serpentes: Dipsadidae), with description of three new species. *Zootaxa*, 1-34.
- Passos, P., Fernandes, R., Bérnils, R.S. & Moura-Leite, J.C. (2010) Taxonomic revision of the Brazilian Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae). *Zootaxa*, 2364, 3-63.
- Pavoine, S. & Bonsall, M.B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, 86, 792-812.
- Pelegrin, N. & Bucher, E.H. (2010) Long-term effects of a wildfire on a lizard assemblage in the Arid Chaco forest. *Journal of Arid Environments*, 74, 368-372.
- Pepper, M., Fujita, M.K., Moritz, C. & Keogh, J.S. (2011) Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone. *Molecular Ecology*, 20, 1529-1545.
- Pianka, E.R. (1986) *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure* Princeton University Press, Princeton, NJ.
- Pianka, E.R. (1989) Desert lizard diversity: additional comments and some data. *American Naturalist*, 134, 344-364.
- Pianka, E.R. (1996) Long-term changes in lizard assemblages in the Great Victoria Desert: dynamic habitat mosaics in response to wildfires. *Long-Term Studies of Vertebrate Communities* (ed. by M.L. Cody and J.A. Smallwood), pp. 191-215. Academic Press, San Diego, California.
- Pyron, R.A. & Burbrink, F.T. (2012) Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution*, 66, 163-178.
- Pyron, R.A., Burbrink, F.T. & Wiens, J.A. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 1-53.
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, <http://www.R-project.org>.
- Rage, J. & Werner, C. (1999) Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: the earliest snake assemblage. *Palaeontologia africana*, 35, 85-110.

- Raven, P.H. & Axelrod, D.I. (1972) Plate Tectonics and Australasian Paleobiogeography. *Science*, 176, 1379-&.
- Rawlings, L.H., Rabosky, D.L., Donnellan, S.C. & Hutchinson, M.N. (2008) *Python* phylogenetics: inference from morphology and mitochondrial DNA. *Biological Journal of the Linnean Society*, 93, 603-619.
- Ricklefs, R.E. (2008) Disintegration of the ecological community. *American Naturalist*, 172, 741–750.
- Roberts, D.W. (2013) Package 'labdsv'. *Ordination and multivariate analysis for ecology. R package version 1.6-1*.
- Roze, J.A. (1996) *Coral Snakes of the Americas: Biology, Identification, and Venoms*. Krieger.
- Rull, V. (2011) Neotropical biodiversity: timing and potential drivers. *Trends in Ecology & Evolution*, 26, 508-513.
- Sanders, K.L., Lee, M.S.Y., Leys, R., Foster, R. & Keogh, J.S. (2008) Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *Journal of Evolutionary Biology*, 21, 682-695.
- Sanders, K.L., Mumpuni, Hamidy, A., Head, J.J. & Gower, D.J. (2010) Phylogeny and divergence times of filesnakes (*Acrochordus*): Inferences from morphology, fossils and three molecular loci. *Molecular Phylogenetics and Evolution*, 56, 857-867.
- Sanders, K.L., Lee, M.S.Y., Mumpuni, Bertozzi, T. & Rasmussen, A.R. (2013) Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). *Molecular Phylogenetics and Evolution*, 66, 575-591.
- Sanmartin, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology*, 53, 216-243.
- Sawaya, R.J. & Sazima, I. (2003) A new species of *Tantilla* (Serpentes: Colubridae) from southeastern Brazil. *Herpetologica*, 59, 119-126.
- Scanlon, J.D. (2005a) Australia's oldest known snakes: *Patagoniophis*, *Alamitophis*, and cf. *Madtsoia* (Squamata: Madtsoiidae) from the Eocene of Queensland. *Memoirs of the Queensland Museum*, 51, 215-235.
- Scanlon, J.D. (2005b) Cranial morphology of the Plio-Pleistocene giant madtsoiid snake *Wonambi naracoortensis*. *Acta Palaeontologica Polonica*, 50, 139-180.
- Scanlon, J.D. & Lee, M.S.Y. (2011) The major clades of living snakes: morphological evolution, molecular phylogeny, and divergence dates. *Reproductive Biology and Phylogeny of Snakes* (ed. by R.D. Aldridge and D.M. Sever), pp. 54-95. Science Publishers, and CRC Press, Enfield, NH.
- Scanlon, J.D., Lee, M.S.Y. & Archer, M. (2003) Mid-Tertiary elapid snakes (Squamata, Colubroidea) from Riversleigh, northern Australia: early steps in a continent-wide adaptive radiation. *Geobios*, 36, 573-600.
- Schluter, D. & Ricklefs, R.E. (1993a) Species Diversity: an introduction to the problem. *Species Diversity in Ecological Communities, Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 1-10. University of Chicago Press, Chicago.
- Schluter, D. & Ricklefs, R.E. (1993b) Convergence and the regional component of species diversity. *Species Diversity in Ecological Communities, Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 230-240. University of Chicago Press, Chicago.

- Shine, R. (1980) Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica*, 36, 281-289.
- Shine, R. (1991) *Australian Snakes: a Natural History*. Cornell University Press, Ithaca, NY.
- Shine, R. & Bonnet, X. (2000) Snakes: a new 'model organism' in ecological research? *Trends in Ecology and Evolution*, 15, 221-222.
- Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T. & Hughes, C.E. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 20359-20364.
- Simpson, G.G. (1980) *Splendid Isolation: the Curious History of South American Mammals*. Yale University Press, New Haven and London.
- Sites, J.W., Reeder, T.W. & Wiens, J.J. (2011) Phylogenetic insights on evolutionary novelties in lizards and snakes: sex, birth, bodies, food, and venom. *Annual Review of Ecology, Evolution, and Systematics*, 42, 227-244.
- Slingsby, J.A. & Verboom, G.A. (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist*, 168, 14-27.
- Specht, R.L. (1981) Major vegetation formations in Australia. In: *Ecological Biogeography of Australia* (ed. A. Keast), pp. 163-297. Dr. W. Junk, The Hague, Netherlands.
- Stehli, F.G. & Webb, S.D. (eds) (1985) *The Great American Biotic Interchange*. Plenum Press, New York.
- Stephens, P.R. & Wiens, J.J. (2004) Convergence, divergence, and homogenization in the ecological structure of emydid turtle communities: The effects of phylogeny and dispersal. *American Naturalist*, 164, 244-254.
- Twidale, C.R. (1972) Evolution of sand dunes in the Simpson desert, central Australia. *Transactions of the Institute of British Geographers*, 77-109.
- Tyler, M.J. (1979) Herpetofaunal relations of South America with Australia *The South American Herpetofauna: Its Origin, Evolution, and Dispersal* (ed. by W.E. Duellman), pp. 73-106. University of Kansas Printing Service, Lawrence.
- van Oosterzee, P. (1997) *Where the Worlds Collide: the Wallace Line*. Reed Books Australia.
- Vanzolini, P.E. (1963) Problemas faunísticos do Cerrado. *Simpósio sobre o Cerrado* (ed. by M.G. Ferri), pp. 307-320. Editora da Universidade de São Paulo, São Paulo.
- Vanzolini, P.E. & Williams, E.E. (1970) South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia*, 19, 1-176.
- Vanzolini, P.E. & Williams, E.E. (1981) The vanishing refuge: a mechanism for ecogeographic speciation. *Papéis Avulsos de Zoologia*, 34, 251-255.
- Vanzolini, P.E. & Heyer, W.R. (1985) The American herpetofauna and the interchange. *The Great American Biotic Interchange* (ed. by F.G. Stehli and S.D. Webb), pp. 475-483. Plenum Press, New York.
- Vidal, N., Dewynter, M. & Gower, D.J. (2010a) Dissecting the major American snake radiation: a molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies*, 333, 48-55.

- Vidal, N., Rage, J.C., Couloux, A. & Hedges, S.B. (2009) Snakes (Serpentes). *The Timetree of Life* (ed. by S.B. Hedges and S. Kumar), pp. 390-397. Oxford University Press, Oxford, UK.
- Vidal, N., Marin, J., Morini, M., Donnellan, S., Branch, W.R., Thomas, R., Vences, M., Wynn, A., Cruaud, C. & Hedges, S.B. (2010b) Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters*, 6, 558-561.
- Vitt, L.J. (1987) Communities. *Snakes: Ecology and Evolutionary Biology* (ed. by R.A. Seigel, J.T. Collins and S.S. Novak), pp. 335-365. Macmillan Publishing Company, New York.
- Vitt, L.J. & Pianka, E.R. (2005) Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 7877-7881.
- Vitt, L.J. & Caldwell, J.P. (2009) *Herpetology: An Introductory Biology of Amphibians and Reptiles*, 3rd edn. Academic Press.
- Wallach, V. & Günther, R. (1998) Visceral anatomy of the Malaysian snake genus *Xenophidion*, including a cladistic analysis and allocation to a new family (Serpentes: Xenophidiidae). *Amphibia-Reptilia*, 19, 385-405.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475-505.
- Webb, S.D. (1995) Biological implications of the Middle Miocene Amazon Seaway. *Science*, 269, 361-362.
- Webb, S.D. (2006) The great American biotic interchange: patterns and processes. *Annals of the Missouri Botanical Garden*, 93, 245-257.
- Werneck, F.P. (2011) South American open/dry vegetation biomes biota diversification: historical biogeography patterns and perspectives. *Quaternary Science Reviews*, 30, 1630 - 1648.
- Westoby, M. (1988) Comparing Australian ecosystems to those elsewhere: what is the significance of evolutionary history. *Bioscience*, 38, 549-556.
- Westoby, M. (1993) Biodiversity in Australia compared with other continents. *Species Diversity in Ecological Communities, Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 170-177. University of Chicago Press, Chicago.
- White, M.E., Kelly-Smith, M. & Crother, B.I. (2005) Higher-level snake phylogeny as inferred from 28s ribosomal DNA and morphology. *Ecology and Evolution in the Tropics: A Herpetological Perspective* (ed. by M.A. Donnelly), pp. 156-173. University of Chicago Press, Chicago, IL.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evol. Biol.*, 10, 1-67.
- Wiens, J.J. (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, 58, 193-197.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, 19, 639-644.
- Wilson, S. & Swan, G. (2010) *A Complete Guide to Reptiles of Australia*, 3rd edn. New Holland Publishers, Sydney.
- Winemiller, K.O., Kelso-Winemiller, L.C. & Brenkerf, A.L. (1995) Ecomorphological diversification and convergence in fluvial cichlid fishes. *Environmental Biology of Fishes*, 44, 235-261.

- Wüster, W., Peppin, L., Pook, C.E. & Walker, D.E. (2008) A nesting of vipers: Phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). *Molecular Phylogenetics and Evolution*, 49, 445-459.
- Zaher, H., Graziotin, F.G., Cadle, J.E., Murphy, R.W., De Moura-Leite, J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia (São Paulo)*, 49, 115-153.

Table 1. Richness and density of non-marine snake clades from South America and Australia mainland.

	South America	Australia
Area (km ²)	17,706,610.97	7,618,865.13
Richness		
N° of higher-clades	6	5
N° of families	9	6
N° of subfamilies	13	7
N° of genera	107	40
N° of species	758	161
Density		
Higher-clades/ 1,000,000 km ²	0.339	0.656
Families/ 1,000,000 km ²	0.508	0.788
Subfamilies/ 1,000,000 km ²	0.734	0.919
Genera/ 1,000,000 km ²	6.043	5.250
Species/ 1,000,000 km ²	42.809	21.132

Table 2. Total number of families (F) and subfamilies (SF) in each higher clade of South American and Australian snake faunas*.

Higher clades	South America		Australia	
	F	SF	F	SF
SCOLECOPHIDIA	3	3	1	1
ALETHINOPHIDIA	6	10	5	6
Amerophidia	2	2		
Afrophidia	4	8	5	6
Henophidia	1	2	1	1
Caenophidia	3	6	4	5
Total Fauna	9	13	6	7

* Lineages without nominated subfamilies count as having one.

Table 3. Number of snake species per family and per higher clade (uppercase) in South America and Australia. Numbers in italic are the percentages of total faunas, reflecting taxonomic dominance among clades. Differences between dominances in each continent are given for each clade (p-values lower than 0.05, marked with *). Marine species, island endemic, or exotic species were not quantified here.

	South America	Australia	χ^2_{NA}	p-value
SCOLECOPHIDIA	64	39	31.66	<0.001*
Anomalepididae	15		2.12	0.145
Leptotyphlopidae	42		8.12	0.004*
Typhlopidae	7	39	146.76	<0.001*
ALETHINOPHIDIA	694	122	31.66	<0.001*
AMEROPHIDIA	8		0.71	0.400
Aniliidae	1		0.00	1.000
Tropidopfiidae	7		0.53	0.469
AFROPHIDIA	686	122	25.74	<0.001*
HENOPHIDIA	18	13	11.55	0.001*
Boidae	18		2.76	0.097
Pythonidae		13	56.43	<0.001*
CAENOPHIDIA	668	109	40.86	<0.001*
Acrochordidae		2	4.58	0.032*
Viperidae	53		10.69	0.001*
Elapidae	56	97	263.60	<0.001*
Homalopsidae		5	18.28	<0.001*
Colubridae	559	5	276.55	<0.001*
Total Fauna	758	161		

Table 4. Ratios among taxonomic levels (only lower clades, species to family); average, standard deviation (SD), maximum (Max) and minimum (Min) values. W and p values refer to the Wilcoxon rank statistics and the significance of differences between continents.

	South America			Australia			Significance	
	Average	SD (Min-Max)	Richest clade	Average	SD (Min-Max)	Richest clade	W	p
species/genus	7.08	14.88 (1-130)	<i>Atractus</i>	4.03	6.20 (1-39)	<i>Ramphotyphlops</i>	1955	0.4119
species/subfamily	58.15	85.14 (1-270)	Xenodontinae	23.00	35.22 (1-97)	Hydrophiinae	33	0.3208
species/family	84.22	179.23 (1-559)	Colubridae	26.83	36.97 (2-97)	Elapidae	19	0.3759
genera/subfamily	8.08	11.79 (1-41)	Xenodontinae	5.71	9.05 (1-26)	Hydrophiinae	39	0.6242
genera/family	11.89	26.35 (1-82)	Colubridae	6.67	9.58 (1-26)	Elapidae	25	0.8557
subfamilies/family	1.44	1.01 (1-4)	Colubridae	1.17	0.41 (1-2)	Colubridae	25	0.8001

Table 5. The South American and Australian inland fauna of snakes, their biological structure decomposed in six biological dimensions (in italic), and distributed through twenty nine biological attributes. The numbers of species in each biological dimension refer to the sample size and are followed by their respective adequacy (percentage of the total fauna, within parentheses). The prevalence of each biological attribute is presented as the number of species and its proportion within the respective biological dimension (percentage of the number of species sampled). Differences between proportion of species are given for each biological attribute, by p-values lower than 0.05. Diet percentages do not sum 100% because categories are not mutually exclusive. See the methods for abbreviations.

	South American	Australia	X^2_{NA}	p-value
<i>Habitat</i>	<i>672 (88.65)</i>	<i>160 (99.38)</i>		
Op	121 (18.01)	111 (69.38)	167.04	<<0.001*
Bo	221 (32.89)	41 (25.63)	2.83	0.092
Cl	330 (49.11)	8 (5.00)	102.41	<<0.001*
<i>Habit</i>	<i>680 (89.71)</i>	<i>160 (99.38)</i>		
aq	34 (5.00)	8 (5.00)	0.00	1.000
saq	13 (1.91)	1 (0.63)	0.64	0.423
fo	109 (16.03)	56 (35.00)	28.34	<<0.001*
cfo	151 (22.21)	2 (1.25)	36.79	<<0.001*
cr	21 (3.09)	13 (8.13)	7.21	0.007*
cte	52 (7.65)	11 (6.88)	0.03	0.868
te	197 (28.97)	56 (35.00)	1.96	0.162
sar	44 (6.47)	9 (5.63)	0.05	0.830
ar	59 (8.68)	4 (2.50)	6.26	0.012*
<i>Diel activity</i>	<i>437 (57.65)</i>	<i>160 (99.38)</i>		
D	165 (37.76)	31 (19.38)	17.12	<<0.001*
DN	82 (18.76)	15 (9.38)	6.91	0.009*
N	190 (43.48)	114 (71.25)	35.04	<<0.001*
<i>Reproduction</i>	<i>703 (92.74)</i>	<i>161 (100.00)</i>		
O	585 (83.21)	115 (71.43)	11.08	0.001*
OV	4 (0.57)	0 (0.00)	0.10	0.752
V	114 (16.22)	46 (28.57)	12.45	<<0.001*
<i>Diet</i>	<i>412 (54.35)</i>	<i>158 (98.14)</i>		
goo	55 (13.35)	0 (0.00)	21.84	<<0.001*
art	33 (8.01)	41 (25.95)	30.97	<<0.001*
fis	31 (7.52)	11 (6.96)	0.00	0.959
amp	160 (38.83)	22 (13.92)	31.47	<<0.001*
rep	172 (41.75)	94 (59.49)	13.75	<<0.001*
bir	21 (5.10)	12 (7.59)	0.89	0.346
mam	72 (17.48)	31 (19.62)	0.22	0.636
<i>Body length</i>	<i>668 (88.13)</i>	<i>161 (100.00)</i>		
S	238 (35.63)	68 (42.24)	2.16	0.142
M	249 (37.28)	56 (34.78)	0.25	0.619
L	147 (22.01)	27 (16.77)	1.84	0.175
VL	34 (5.09)	10 (6.21)	0.14	0.709

Table 6. The character of South American (SG) and Australian (AG) snake ecological guilds. The combination of biological attributes in each guild was defined by choosing those attributes with the highest significant indicator value in each biological dimension (see Appendix S6c and Appendix S7c). Attributes between parentheses have secondary contribution. See the text for abbreviations. Repr. = Reproduction.

	Habitat	Habit	Activity	Repr.	Diet	Length
<i>South America</i>						
SG1	Bo	aq	N	V	fis (amp)	M
SG2	Cl	sar (te)	DN	V	amp (mam)	VL
SG3	Bo	ar (cte)	N	V	mam (bir)	L
SG4	Bo	aq	DN	OV	fis (art)	L
SG5	Cl	fo (cte)	N	O	art (goo)	S
SG6	na	fo (saq)	DN	O	rep (amp)	M
SG7	Cl	ar	N	O	goo (rep)	M
SG8	Bo	cfo (te)	N	O	rep	L
SG9	Bo	te	D	O	amp (rep)	na
SG10	Op	te	D	V	goo	M
SG11	Op	te	D	V	amp (rep)	S
<i>Australia</i>						
AG1	Cl	aq	N	V	fis (art)	M
AG2	OP	cr (cte)	N	V	rep	M
AG3	Op	fo	N	O	art (rep)	S
AG4	Bo	aq (te)	DN	V	amp (mam)	M
AG5	Op	te	D	O	rep (mam)	VL
AG6	Bo	sar (ar)	N	O	bir (mam)	L
AG7	Bo	ar (te)	D	V	amp (rep)	L

Table 7. Ecological guilds, number of species (N), and proportion of species (%) in South American and Australian snake faunas (see Table 6 for guild's description). Pairs of similar guilds were clustered based on their cophenetic distances (Figure 4), and significant differences between proportions of species in similar guilds are given by p-values lower than 0.05 (*).

South America			Australia			X^2_{NA}	p-value
Guilds	N	%	Guilds	N	%		
SG1	19	5.64					
SG2	4	1.19	AG4	2	1.28	0.00	1.000
SG3	47	13.95	AG6	7	4.49	8.84	0.003 *
SG4	3	0.89	AG1	7	4.49	5.25	0.022 *
SG5	29	8.61	AG3	65	41.67	73.41	<<0.001 *
SG6	28	8.31					
SG7	43	12.76					
SG8	47	13.95	AG5	44	28.21	13.47	<<0.001 *
SG9	108	32.05	AG7	5	3.21	48.59	<<0.001 *
SG10	2	0.59	AG2	26	16.67	48.47	<<0.001 *
SG11	7	2.08					

Table 8. Faunal comparisons between closed/forested and open habitats in South America and Australia. Species and genus richness, density, phylogenetic diversity (PD), and phylogenetic structure (Z_{PD}). Differences between proportions of species were assessed by binomial tests. The phylogenetic structure significances and PD differences were Z tested. All tests considered 0.05 of significance (*).

	South America		Australia	
	Closed	Open	Closed	Open
Area (km ²)	5,615,793.90	11,871,999.94	120,932.50	7,461,926.54
Species richness	551 (82%)	342 (51%)	49 (31%)	152 (95%)
Genus richness	98	76	28	37
PD (subst./site)	15.23	10.75	4.06	6.87
Phylogenetic structure	-5.388*	-5.846*	-1.624	-5.043*
Densities of species and genera (richness / 1,000,000 km²)				
Species	98.116	28.807	405.185	20.370
Genera	17.451	6.402	231.534	4.959
Proportion of species (p-values \ X^2_{NA})				
South America				
Closed	-	-	167.036	15.708
Open	-	-	20.506	102.408
Australia				
Closed	<<0.001*	<<0.001*	-	-
Open	<<0.001*	<<0.001*	-	-
Phylogenetic diversity (p-values \ Z-values)				
South America				
Closed	-	-3.567	-0.165	-2.664
Open	<<0.001*	-	0.669	-1.308
Australia				
Closed	0.869	0.503	-	1.399
Open	0.008*	0.191	0.162	-

Table 9. South America and Australian snake faunas, period of origin, and estimated age.

	Period	Age (Mya)	Source
SERPENTES	Jurassic - Cretaceous	140.80	(Burbrink & Pyron, 2008; Pyron & Burbrink, 2012)
SCOLECOPHIDIA	Late Jurassic - Early Cretaceous	> 140.00	(Burbrink & Pyron, 2008; Vidal <i>et al.</i> , 2009; Burbrink & Crother, 2011)
Anomalepididae	Early Cretaceous	134.59	(Pyron & Burbrink, 2012)
Leptotyphlopidae	Early Cretaceous	131.27	(Pyron & Burbrink, 2012)
Typhlopidae	Paleocene	59.41	(Pyron & Burbrink, 2012)
South American Typhlopidae	Oligocene	> 23.00	(Vidal <i>et al.</i> , 2010)
Australian Typhlopidae	Oligocene	> 27.00	(Vidal <i>et al.</i> , 2010)
ALETHINOPHIDIA	Mid-Cretaceous	101.5	(Rage & Werner, 1999; Pyron & Burbrink, 2012)
AMEROPHIDIA	Late Cretaceous	~95.00	(Pyron & Burbrink, 2012)
Aniliidae	Late Cretaceous	91.80	(Burbrink & Pyron, 2008; Pyron & Burbrink, 2012)
Tropidophiidae	Late Cretaceous	91.80	(Wallach & Günther, 1998; Pyron & Burbrink, 2012)
AFROPHIDIA	Early Cretaceous	103.70	(Vidal <i>et al.</i> , 2009)
HENOPHIDIA	Late Cretaceous	~90.00	(Pyron & Burbrink, 2012)
Boidae	Late Cretaceous	> 70.00	(White <i>et al.</i> , 2005; Noonan & Chippindale, 2006; Burbrink & Pyron, 2008; Vidal <i>et al.</i> , 2009)
Boinae	Eocene	45.02	(Pyron & Burbrink, 2012)

	Age	Period	Source
	(Mya)		
Ungaliophiinae	60.27	Paleocene	(Scanlon & Lee, 2011)
Pythonidae	47.12	Eocene	(Pyron & Burbrink, 2012)
CAENOPHIDIA	~85.0	Late Cretaceous	(Pyron & Burbrink, 2012)
Acrochordidae	84.66	Late Cretaceous	(Burbrink & Pyron, 2008; Pyron & Burbrink, 2012)
Viperidae	54.30	Eocene	(Wüster <i>et al.</i> , 2008; Vidal <i>et al.</i> , 2009)
Crotalinae	35.66	Eocene	(Pyron & Burbrink, 2012)
Elapidae	34.86	Eocene	(Kelly <i>et al.</i> , 2009; Pyron & Burbrink, 2012)
Elapinae	~ 30.00	Oligocene - Miocene	(Gutberlet & Harvey, 2004)
Hydrophiinae		Mid-Tertiary	(Hutchinson & Donnellan, 1993)
Homalopsidae	53.38	Eocene	(Pyron & Burbrink, 2012)
Colubridae	~ 37.00	Eocene - Oligocene	(Vidal <i>et al.</i> , 2009; Pyron & Burbrink, 2012)
Sibynophiinae	39.71	Eocene	(Pyron & Burbrink, 2012; Chen <i>et al.</i> , 2013)
Colubrinae	35.63	Eocene	(Burbrink & Lawson, 2007; Pyron & Burbrink, 2012)
Natricinae	38.28	Eocene	(Pyron & Burbrink, 2012)
Dipsadinae + Xenodontinae	33.65	Oligocene	(Pyron & Burbrink, 2012)

Colubroidea (i.e., Caenophidia except Acrochordidae): Late Cretaceous, 84.70 Mya (White *et al.*, 2005; Burbrink & Pyron, 2008; Pyron & Burbrink, 2012)

Legend of Figures

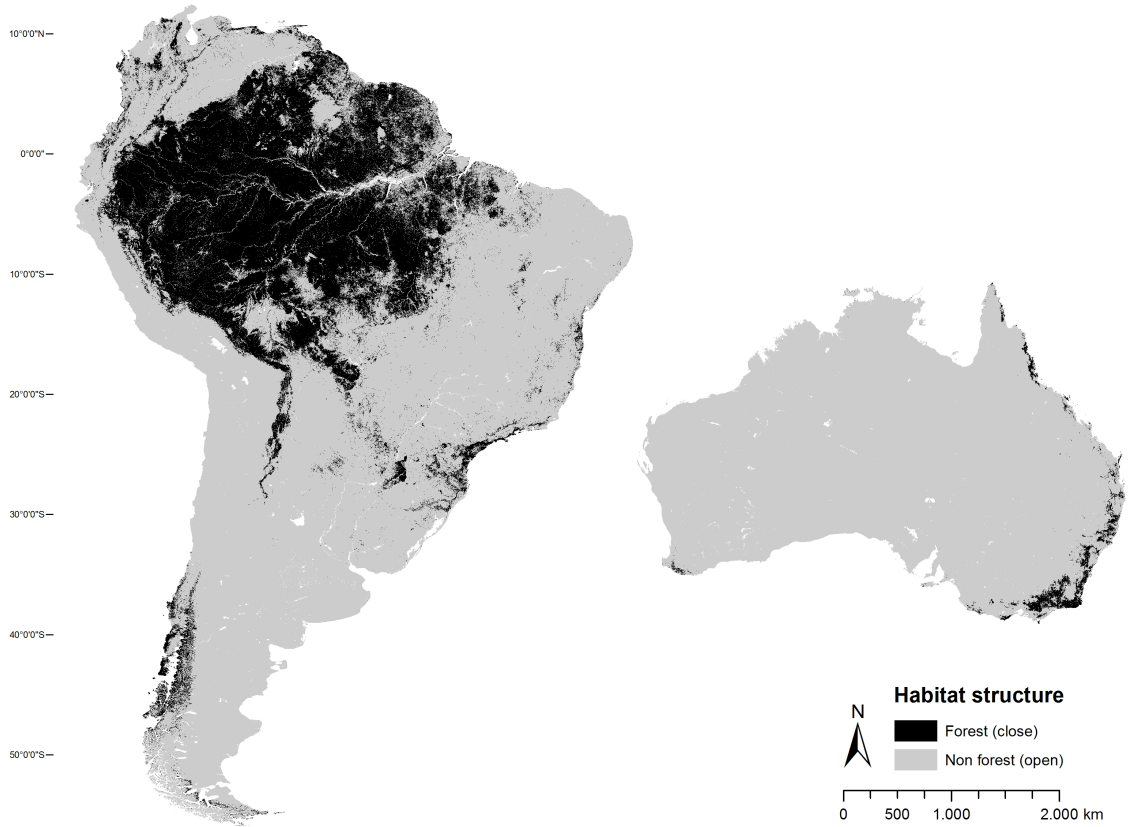
Figure 1. Relative latitudinal position and size of South American and Australian continents. Open habitats in both continents cover larger areas than forested/closed habitats. The area covered by close habitats in South America is very larger than in Australia, and in size, it is roughly equivalent to the area covered by open habitats in Australia.

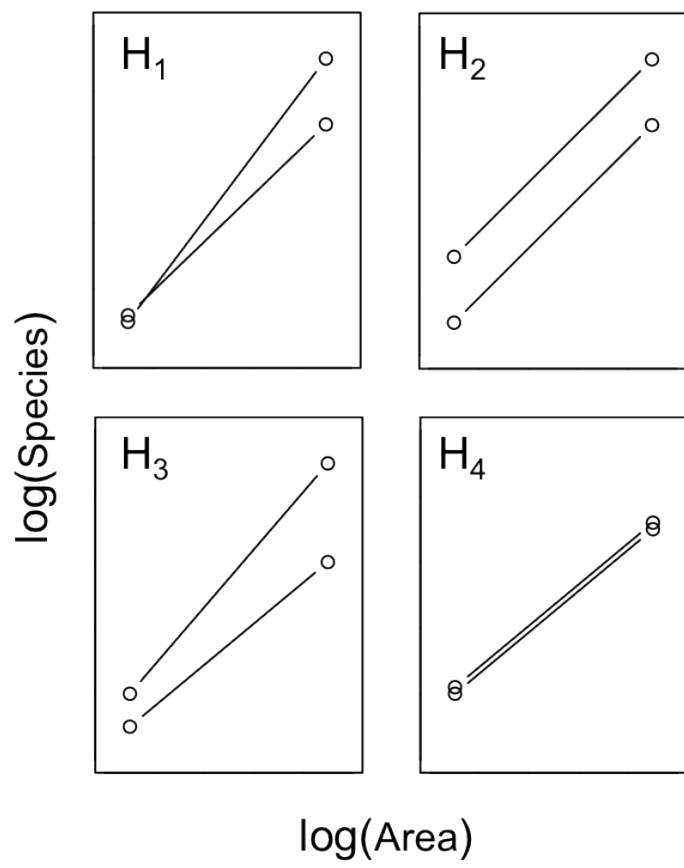
Figure 2. Schematic diagram of the four hypotheses (potential patterns) relating species richness and area; two biogeographic regions are compared in each case (from H₁ to H₄). Points below and to the left are local diversities, above and to the right are regional diversities. The slope of the lines is “differentiation diversity” and represents a measure of habitat effects, i.e., differences in diversity among habitats within a region. The regional effects are depicted by the differences between regional diversity, i.e., the difference between the two lines reflects the historical effect on each continent (after Westoby, 1993).

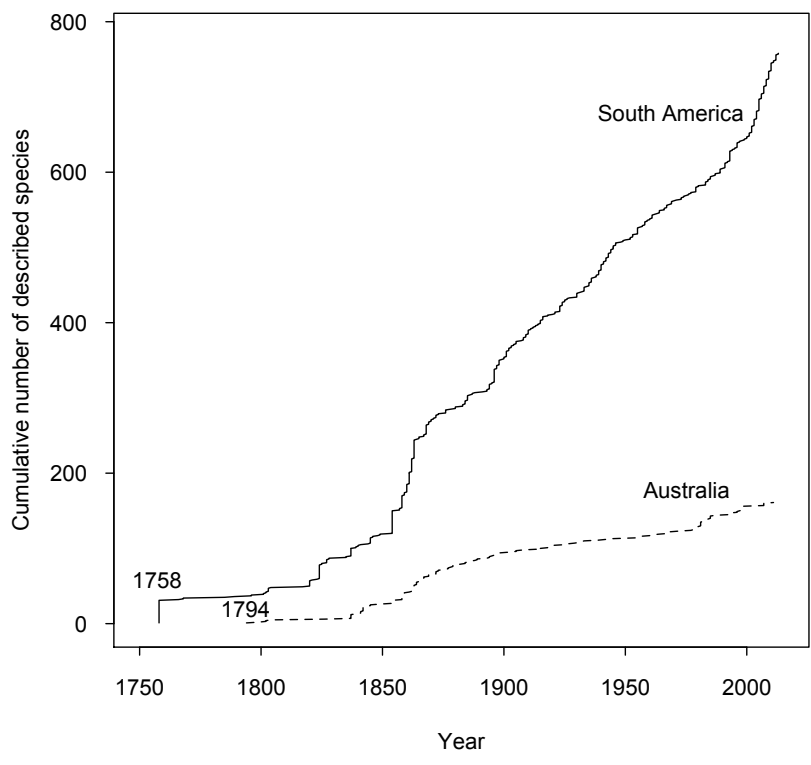
Figure 3. Curves of cumulative numbers of described snakes in South America and Australia (considering only non-marine species living at the continental mainland). Formal description of snake species in South America started in 1758, and 1794 in Australia.

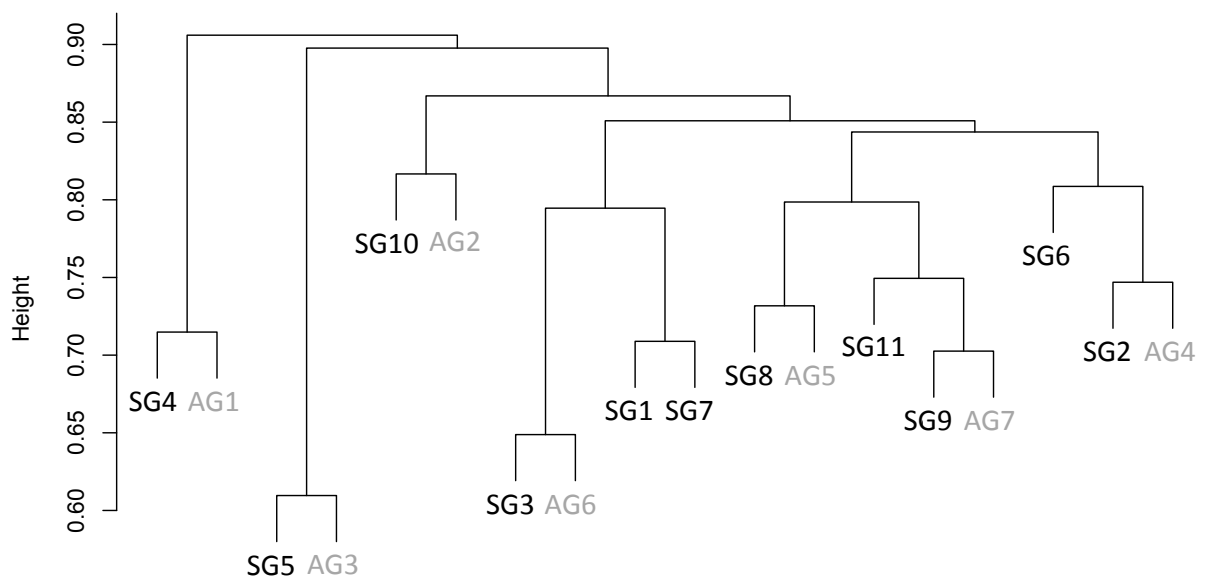
Figure 4. Cluster dendrogram (UPGMA, cophenetic index = 0.647) of ecological guilds from South American (SG1-SG11) and Australian (AG1-AG7) snake faunas. The vertical axis shows the distances among cluster centroids calculated by “average linkage” method upon a distance matrix of Jaccard dissimilarities. Similar guilds were clustered based on 29 qualitative biological attributes.

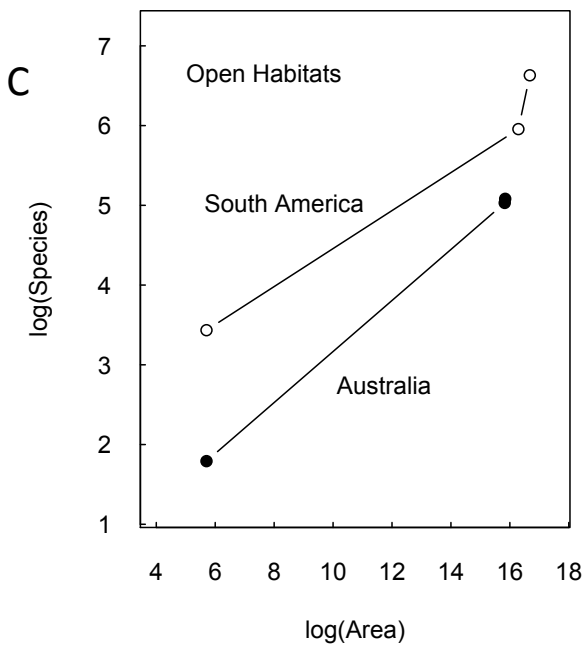
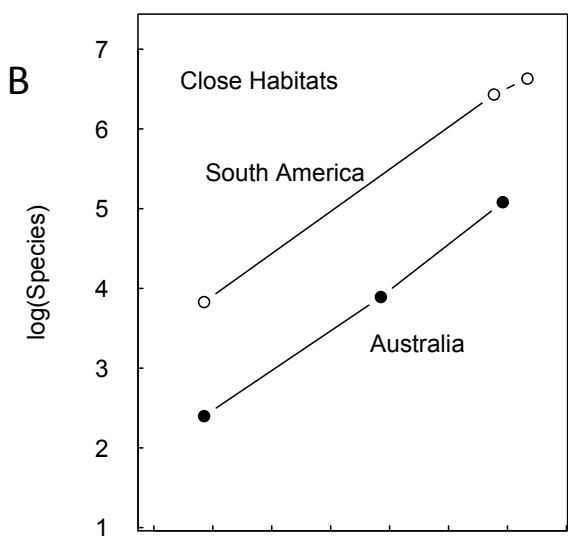
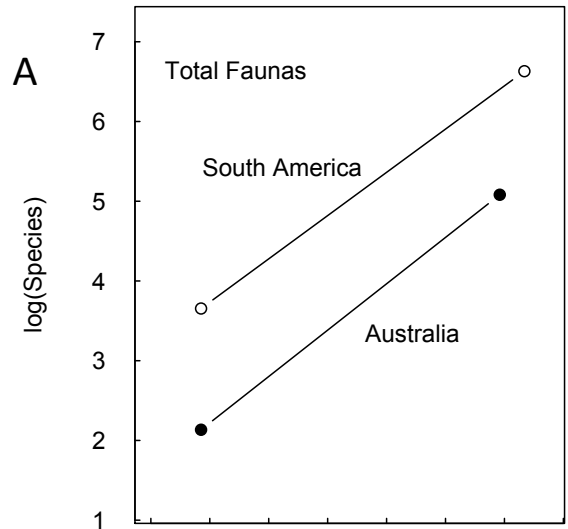
Figure 5. Species-area relations for snake faunas, comparing South America with Australia (A). Left points indicate average local richness of species (about 300 km²); right points indicate total richness (continent); and intermediate points indicate regional richness (close or open habitats). Graphics B and C decompose A in closed and open habitat, respectively. Area (km²) and species richness values were log transformed. Local species richness, latitudes and references are described in Appendix S4 (Supporting Information), regional and continental species richness were calculated in this study (see the text).











		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Bothrops diporus</i>	Cope 1862	X		X						X					3
<i>Bothrops erythromelas</i>	Amaral 1923			X											1
<i>Bothrops fonsecai</i>	Hoge & Belluomini 1959			X											1
<i>Bothrops itapetiningae</i>	(Boulenger 1907)			X											1
<i>Bothrops jararaca</i>	(Wied-Neuwied 1824)	X		X						X					3
<i>Bothrops jararacussu</i>	Lacerda 1884	X		X						X					3
<i>Bothrops jonathani</i>	Harvey 1994	X	X												2
<i>Bothrops leucurus</i>	Wagler 1824			X											1
<i>Bothrops lojanus</i>	Parker 1930						X								1
<i>Bothrops lutzi</i>	(Miranda-Ribeiro 1915)				X										1
<i>Bothrops marajoensis</i>	Hoge 1966			X											1
<i>Bothrops marmoratus</i>	Silva & Rodrigues 2008			X											1
<i>Bothrops mattogrossensis</i>	Amaral 1925	X	X	X						X	X				5
<i>Bothrops medusa</i>	(Sternfeld 1920)												X		1
<i>Bothrops moojeni</i>	Hoge 1966	X	X	X						X					4
<i>Bothrops muriciensis</i>	Ferrarezzi & Freire 2001			X											1
<i>Bothrops neuwiedi</i>	Wagler 1824			X											1
<i>Bothrops oligolepis</i>	(Werner 1901)		X								X				2
<i>Bothrops osbornei</i>	Freire-Lascano 1991						X				X				2
<i>Bothrops pauloensis</i>	Amaral 1925		X	X											2
<i>Bothrops pictus</i>	(Tschudi 1845)										X				1
<i>Bothrops pirajai</i>	Amaral 1923			X											1
<i>Bothrops pubescens</i>	(Cope 1870)			X									X		2
<i>Bothrops pulcher</i>	(Peters 1862)					X	X				X				3
<i>Bothrops punctatus</i>	(Garcia 1896)					X	X								2
<i>Bothrops rhombeatus</i>	(Garcia 1896)					X									1
<i>Bothrops roedingeri</i>	Mertens 1942										X				1
<i>Bothrops sanctaerucris</i>	Hoge 1966		X												1
<i>Bothrops taeniatus</i>	(Wagler 1824)		X	X		X	X	X	X		X	X		X	9
<i>Bothrops venezuelensis</i>	Sandner-Montilla 1952					X								X	2
<i>Crotalus durissus</i>	Linnaeus 1758	X	X	X		X		X	X	X	X	X	X	X	11
<i>Lachesis acrochorda</i>	(Garcia 1896)					X	X								2
<i>Lachesis muta</i>	(Linnaeus 1766)		X	X		X	X	X	X		X	X		X	9
<i>Porthidium arcosae</i>	Schätti & Kramer 1993						X								1
<i>Porthidium lansbergii</i>	(Schlegel 1841)					X								X	2
<i>Porthidium nasutum</i>	(Bocourt 1868)					X	X								2

Elapidae

Elapinae

Calliophini

<i>Leptomicrurus collaris</i>	(Schlegel 1837)			X				X	X			X		X	5
<i>Leptomicrurus narduccii</i>	(Jan 1863)		X	X		X	X				X				5
<i>Leptomicrurus renjifo</i>	Lamar 2003					X									1
<i>Leptomicrurus scutiventris</i>	(Cope 1870)			X		X	X				X				4
<i>Micrurus albicinctus</i>	Amaral 1925			X		X									2
<i>Micrurus altirostris</i>	(Cope 1860)	X		X						X			X		4
<i>Micrurus ancoralis</i>	Jan 1872					X	X								2
<i>Micrurus annellatus</i>	(Peters 1871)		X	X		X	X				X				5
<i>Micrurus averyi</i>	Schmidt 1939			X					X			X			3
<i>Micrurus baliocoryphus</i>	(Cope 1862)	X		X						X					3
<i>Micrurus bocourti</i>	Jan 1872					X					X				2
<i>Micrurus brasiliensis</i>	Roze 1967			X											1
<i>Micrurus camilae</i>	Renjifo & Lundberg 2003					X									1
<i>Micrurus catamayensis</i>	Roze 1989						X								1
<i>Micrurus circinalis</i>	(Duméril, Bibron & Duméril 1854)												X		1
<i>Micrurus clarki</i>	Schmidt 1936					X									1
<i>Micrurus corallinus</i>	(Merrem 1820)	X		X						X					3
<i>Micrurus decoratus</i>	(Jan 1858)			X											1
<i>Micrurus diana</i>	Roze 1983		X	X											2
<i>Micrurus dissoleucus</i>	(Cope 1860)					X								X	2
<i>Micrurus dumerilii</i>	Jan 1858					X	X							X	3
<i>Micrurus filiformis</i>	(Günther 1859)			X		X	X				X				4
<i>Micrurus frontalis</i>	(Duméril, Bibron & Duméril 1854)	X		X						X					3
<i>Micrurus hemprichii</i>	(Jan 1858)		X	X		X	X	X	X		X	X		X	9
<i>Micrurus ibiboboca</i>	(Merrem 1820)			X											1
<i>Micrurus isozonus</i>	(Cope 1860)			X		X			X					X	4
<i>Micrurus langsdorffi</i>	Wagler 1824			X		X	X				X				4
<i>Micrurus lemniscatus</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X		X	11
<i>Micrurus margaritiferus</i>	Roze 1967						X				X				2
<i>Micrurus medemi</i>	Roze 1967					X									1
<i>Micrurus meridensis</i>	Roze 1989													X	1
<i>Micrurus mertensi</i>	Schmidt 1936						X				X				2

		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Mastigodryas heathii</i>	(Cope 1876)						X				X				2
<i>Mastigodryas melanolomus</i>	(Cope 1868)					X									1
<i>Mastigodryas moratoi</i>	Montingelli & Zaher 2011			X					X						2
<i>Mastigodryas pleei</i>	(Duméril, Bibron & Duméril 1854)			X		X						X		X	4
<i>Mastigodryas pulchriceps</i>	(Cope 1868)					X	X				X				3
<i>Mastigodryas reticulatus</i>	(Peters 1863)						X								1
<i>Oxybelis aeneus</i>	(Wagler 1824)		X	X		X	X	X	X		X	X		X	9
<i>Oxybelis brevirostris</i>	(Cope 1861)					X	X								2
<i>Oxybelis fulgidus</i>	(Daudin 1803)		X	X		X	X	X	X		X	X		X	9
<i>Pseustes poecilonotus</i>	(Günther 1858)		X	X		X	X	X	X		X	X		X	9
<i>Pseustes sexcarinatus</i>	(Wagler 1824)			X											1
<i>Pseustes shropshirei</i>	(Barbour & Amaral 1924)					X	X							X	3
<i>Pseustes sulphureus</i>	(Wagler 1824)		X	X		X	X	X	X		X	X		X	9
<i>Rhinobothryum bovallii</i>	(Andersson 1916)					X	X							X	3
<i>Rhinobothryum lentiginosum</i>	(Scopoli 1785)		X	X		X		X	X		X	X		X	8
<i>Simophis rhinostoma</i>	(Schlegel 1837)			X						X					2
<i>Spilotes pullatus</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X		X	11
<i>Stenorrhina degenhardtii</i>	(Berthold 1846)					X	X							X	3
<i>Tantilla alticola</i>	(Boulenger 1903)					X									1
<i>Tantilla andinista</i>	Wilson & Mena 1980						X								1
<i>Tantilla boipiranga</i>	Sawaya & Sazima 2003			X											1
<i>Tantilla capistrata</i>	Cope 1876						X				X				2
<i>Tantilla fraseri</i>	(Günther 1895)						X				X				2
<i>Tantilla insulamontana</i>	Wilson & Mena 1980						X								1
<i>Tantilla marcovani</i>	Lema 2004			X											1
<i>Tantilla melanocephala</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X	X	X	12
<i>Tantilla miyatai</i>	Wilson & Knight 1987						X								1
<i>Tantilla nigra</i>	(Boulenger 1914)					X									1
<i>Tantilla petersi</i>	Wilson 1979						X								1
<i>Tantilla reticulata</i>	(Cope 1860)					X									1
<i>Tantilla semicincta</i>	(Duméril, Bibron & Duméril 1854)					X								X	2
<i>Tantilla supracincta</i>	(Peters 1863)						X								1
Dipsadinae															
Dipsadini															
<i>Dipsas albifrons</i>	(Sauvage 1884)			X											1
<i>Dipsas alternans</i>	(Fischer 1885)			X											1
<i>Dipsas andiana</i>	(Boulenger 1896)						X								1
<i>Dipsas baliomelas</i>	Harvey 2008					X									1
<i>Dipsas bucephala</i>	(Shaw 1802)	X	X	X						X					4
<i>Dipsas catesbyi</i>	(Sentzen 1796)		X	X		X	X	X	X		X	X		X	9
<i>Dipsas chaparensis</i>	Reynolds & Foster 1992		X												1
<i>Dipsas copei</i>	(Günther 1872)							X	X			X		X	4
<i>Dipsas elegans</i>	(Boulenger 1896)						X								1
<i>Dipsas ellipsifera</i>	(Boulenger 1898)						X								1
<i>Dipsas gracilis</i>	(Boulenger 1902)					X	X				X				3
<i>Dipsas incerta</i>	(Jan 1863)			X				X				X			3
<i>Dipsas indica</i>	Laurenti 1768		X	X		X	X	X	X		X	X		X	9
<i>Dipsas oreas</i>	(Cope 1868)						X				X				2
<i>Dipsas pakaraima</i>	Macculloch & Lathrop 2004								X						1
<i>Dipsas pavonina</i>	Schlegel 1837		X	X		X	X	X	X		X	X		X	9
<i>Dipsas peruana</i>	(Boettger 1898)		X			X	X				X			X	5
<i>Dipsas praeornata</i>	(Werner 1909)													X	1
<i>Dipsas pratti</i>	(Boulenger 1897)					X								X	2
<i>Dipsas sanctijoannis</i>	(Boulenger 1911)					X									1
<i>Dipsas sazimai</i>	Fernandes, Marques & Argólo 2010			X											1
<i>Dipsas schunkii</i>	(Boulenger 1908)										X				1
<i>Dipsas temporalis</i>	(Werner 1909)					X	X								2
<i>Dipsas variegata</i>	(Duméril, Bibron & Duméril 1854)		X	X				X	X		X	X		X	7
<i>Dipsas vermiculata</i>	Peters 1960						X				X				2
<i>Dipsas viguieri</i>	(Bocourt 1884)					X									1
<i>Ninia atrata</i>	(Hallowell 1845)					X	X							X	3
<i>Ninia hudsoni</i>	Parker 1940			X		X	X		X		X				4
<i>Ninia maculata</i>	(Peters 1861)					X									1
<i>Plesiodipsas perijanensis</i>	(Aleman 1953)					X								X	2
<i>Sibon dunni</i>	Peters 1957						X								1
<i>Sibon nebulatus</i>	(Linnaeus 1758)			X		X	X	X	X			X		X	7
<i>Sibynomorphus lavillai</i>	Scrocchi, Porto & Rey 1993	X	X	X						X					4
<i>Sibynomorphus mikanii</i>	(Schlegel 1837)	X		X						X					3
<i>Sibynomorphus newwiedi</i>	(Ihering 1911)			X											1
<i>Sibynomorphus oligozonatus</i>	Orces & Almendariz 1989						X				X				2
<i>Sibynomorphus oneilli</i>	Rossmann & Thomas 1979										X				1

		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Atractus francoi</i>	Passos, Fernandes, Bérnils & Moura-Leite 2010			X											1
<i>Atractus fuliginosus</i>	(Hallowell 1845)													X	1
<i>Atractus gaigeae</i>	Savage 1955						X				X				2
<i>Atractus gigas</i>	Myers & Schargel 2006						X								1
<i>Atractus guentheri</i>	(Wucherer 1861)			X											1
<i>Atractus guerreroi</i>	Myers & Donnelly 2008													X	1
<i>Atractus heliobelluomini</i>	Silva-Haad 2004					X									1
<i>Atractus hoogmoedi</i>	Prudente & Passos 2010			X											1
<i>Atractus indistinctus</i>	Prado 1940					X									1
<i>Atractus insipidus</i>	Roze 1961			X									X		2
<i>Atractus iridescens</i>	Peracca 1896					X									1
<i>Atractus lancinii</i>	Roze 1961												X		1
<i>Atractus lasallei</i>	Amaral 1931					X									1
<i>Atractus latifrons</i>	(Günther 1868)		X	X		X		X			X	X			6
<i>Atractus lehmanni</i>	Boettger 1898					X	X								2
<i>Atractus limitaneus</i>	(Amaral 1935)					X									1
<i>Atractus loveridgei</i>	Amaral 1930					X									1
<i>Atractus macondo</i>	Passos, Lynch & Fernandes 2009					X									1
<i>Atractus maculatus</i>	(Günther 1858)			X											1
<i>Atractus major</i>	Boulenger 1894		X	X		X	X				X			X	6
<i>Atractus manizalesensis</i>	Prado 1940					X									1
<i>Atractus marisela</i>	Lancini 1969													X	1
<i>Atractus matthewi</i>	Markezich & Barrio-Amorós 2004													X	1
<i>Atractus melanogaster</i>	Werner 1916					X									1
<i>Atractus melas</i>	Boulenger 1908					X									1
<i>Atractus meridensis</i>	Esqueda & La Marca 2005													X	1
<i>Atractus micheleae</i>	Esqueda & La Marca 2005													X	1
<i>Atractus microrhynchus</i>	(Cope 1868)						X				X				2
<i>Atractus mijaresi</i>	Esqueda & La Marca 2005													X	1
<i>Atractus modestus</i>	Boulenger 1894						X								1
<i>Atractus multinctus</i>	(Jan 1865)					X	X								2
<i>Atractus multidentatus</i>	Passos, Rivas & Barrio-Amorós 2009													X	1
<i>Atractus nasutus</i>	Passos, Fernandes & Lynch 2009					X									1
<i>Atractus natans</i>	Hoogmoed & Prudente 2003			X		X					X				3
<i>Atractus nicefori</i>	Amaral 1930					X									1
<i>Atractus nigricaudus</i>	Schmidt & Walker 1943										X				1
<i>Atractus nigriventris</i>	Amaral 1933					X									1
<i>Atractus obesus</i>	Marx 1960					X									1
<i>Atractus obtusirostris</i>	Werner 1916					X									1
<i>Atractus occidentalis</i>	Savage 1955						X								1
<i>Atractus occipitoalbus</i>	(Jan 1862)		X			X	X				X				4
<i>Atractus ochrosetrus</i>	Esqueda & La Marca 2005													X	1
<i>Atractus oculotemporalis</i>	Amaral 1932					X									1
<i>Atractus orcesi</i>	Savage 1955					X	X								2
<i>Atractus paisa</i>	Passos, Fernandes & Lynch 2009					X									1
<i>Atractus pamplonensis</i>	Amaral 1937					X								X	2
<i>Atractus pantostictus</i>	Fernandes & Puerto 1993			X											1
<i>Atractus paraguayensis</i>	Werner 1924	X		X						X					3
<i>Atractus paravertebralis</i>	Henle & Ehl 1991										X				1
<i>Atractus paucidens</i>	Despax 1910						X								1
<i>Atractus pauciscutatus</i>	Schmidt & Walker 1943										X				1
<i>Atractus peruvianus</i>	(Jan 1862)										X				1
<i>Atractus poeppigi</i>	(Jan 1862)			X		X					X				3
<i>Atractus potschi</i>	Fernandes 1995			X											1
<i>Atractus punctiventris</i>	Amaral 1933					X									1
<i>Atractus resplendens</i>	Werner 1901						X								1
<i>Atractus reticulatus</i>	(Boulenger 1885)	X		X						X			X		4
<i>Atractus riveroi</i>	Roze 1961													X	1
<i>Atractus ronnie</i>	Passos, Fernandes & Borges-Nojosa 2007			X											1
<i>Atractus roulei</i>	Despax 1910						X								1
<i>Atractus sanctaemartae</i>	Dunn 1946					X									1
<i>Atractus sanguineus</i>	Prado 1944					X									1
<i>Atractus schach</i>	(Boie 1827)			X				X	X		X	X			5
<i>Atractus serranus</i>	Amaral 1930			X											1
<i>Atractus snethlageae</i>	Cunha & Nascimento 1983	X	X	X		X	X				X				6

		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Echinanthera cephalostriata</i>	Di-Bernardo 1996			X											1
<i>Echinanthera cyanopleura</i>	(Cope 1885)	X		X											2
<i>Echinanthera melanostigma</i>	(Wagler 1824)			X											1
<i>Echinanthera undulata</i>	(Wied-Neuwied 1824)			X			X								2
<i>Sordellina punctata</i>	(Peters 1880)			X											1
<i>Taeniophallus affinis</i>	(Günther 1858)			X											1
<i>Taeniophallus bilineatus</i>	(Fischer 1885)			X											1
<i>Taeniophallus brevirostris</i>	(Peters 1863)		X	X		X	X				X	X			7
<i>Taeniophallus nebularis</i>	Schargel, Rivas & Myers 2005													X	1
<i>Taeniophallus nicagus</i>	(Cope 1868)			X				X				X			3
<i>Taeniophallus occipitalis</i>	(Jan 1863)	X	X	X		X				X	X		X		7
<i>Taeniophallus persimilis</i>	(Cope 1869)			X											1
<i>Taeniophallus poecilopogon</i>	(Cope 1863)	X		X										X	3
<i>Taeniophallus quadriocellatus</i>	Santos, Di-Bernardo & Lema 2008			X											1
Elapomorphini															
<i>Apostolepis albicollaris</i>	Lema 2002			X											1
<i>Apostolepis ambiniger</i>	(Peters 1869)		X	X						X					3
<i>Apostolepis ammodites</i>	Ferrarezzi, Barbo & Albuquerque 2005			X											1
<i>Apostolepis arenaria</i>	Rodrigues 1993			X											1
<i>Apostolepis assimilis</i>	(Reinhardt 1861)	X		X						X					3
<i>Apostolepis breviceps</i>	Harvey, Gonzales & Scrocchi 2001		X												1
<i>Apostolepis cearensis</i>	Gomes 1915			X											1
<i>Apostolepis cerradoensis</i>	Lema 2003			X											1
<i>Apostolepis christineae</i>	Lema 2002			X											1
<i>Apostolepis dimidiata</i>	(Jan 1862)	X		X						X					3
<i>Apostolepis dorbignyi</i>	(Schlegel 1837)			X											2
<i>Apostolepis flavotorquata</i>	(Duméril, Bibron & Duméril 1854)			X											1
<i>Apostolepis gaboi</i>	Rodrigues 1992			X											1
<i>Apostolepis goiasensis</i>	Prado 1942			X											1
<i>Apostolepis intermedia</i>	Koslowsky 1898			X											1
<i>Apostolepis lineata</i>	Cope 1887			X											1
<i>Apostolepis longicaudata</i>	Gomes 1921			X											1
<i>Apostolepis multicincta</i>	Harvey 1999		X												1
<i>Apostolepis nelsonjorgei</i>	Lema & Renner 2004			X											1
<i>Apostolepis niceforoi</i>	Amaral 1935					X									1
<i>Apostolepis nigrolineata</i>	(Peters 1896)			X											1
<i>Apostolepis nigroterminata</i>	Boulenger 1896		X	X							X				3
<i>Apostolepis parassimilis</i>	Lema & Renner 2012			X											1
<i>Apostolepis phillipsae</i>	Harvey 1999		X												1
<i>Apostolepis polylepsis</i>	Amaral 1921			X											1
<i>Apostolepis quinquelineata</i>	Boulenger 1896			X				X	X			X			4
<i>Apostolepis quirogai</i>	Giraud & Scrocchi 1998	X		X											2
<i>Apostolepis serrana</i>	Lema & Renner 2006			X											1
<i>Apostolepis striata</i>	Lema 2004			X											1
<i>Apostolepis tenuis</i>	Ruthven 1927		X												1
<i>Apostolepis tertulianoebui</i>	Lema 2004			X											1
<i>Apostolepis vittata</i>	(Cope 1887)		X	X											2
<i>Coronelaps lepidus</i>	(Reinhardt 1861)			X											1
<i>Elapomorphus quinquelineatus</i>	(Raddi 1820)			X					X						2
<i>Elapomorphus wuchereri</i>	Günther 1861			X											1
<i>Phalotris bilineatus</i>	(Duméril, Bibron & Duméril 1854)	X								X			X		3
<i>Phalotris concolor</i>	Ferrarezzi 1993			X											1
<i>Phalotris cuyanus</i>	(Cei 1984)	X													1
<i>Phalotris labiomaculatus</i>	Lema 2002			X											1
<i>Phalotris lativittatus</i>	Ferrarezzi 1993			X											1
<i>Phalotris lemniscatus</i>	(Duméril, Bibron & Duméril 1854)	X	X	X									X		4
<i>Phalotris matogrossensis</i>	Lema, D'Agostini & Cappelari 2005			X						X					2
<i>Phalotris mertensi</i>	(Hoge 1955)			X											1
<i>Phalotris multipunctatus</i>	Puerto & Ferrarezzi 1993			X											1
<i>Phalotris nasutus</i>	(Gomes 1915)			X											2
<i>Phalotris nigrilatus</i>	Ferrarezzi 1993									X					1
<i>Phalotris reticulatus</i>	(Peters 1860)	X		X											2
<i>Phalotris sansebastiani</i>	Jansen & Köhler 2008	X	X												2
<i>Phalotris tricolor</i>	(Duméril, Bibron & Duméril 1854)	X	X	X						X					4
Hydrodynastini															
<i>Hydrodynastes bicinctus</i>	(Herrmann 1804)			X		X		X	X			X		X	6

		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Hydrodynastes gigas</i>	(Duméril, Bibron & Duméril 1854)	X	X	X				X		X		X			6
<i>Hydrodynastes melanogigas</i>	Franco, Fernandes & Bentim 2007			X											1
Hydropsini															
<i>Helicops angulatus</i>	(Linnaeus 1758)		X	X		X	X	X	X		X	X		X	9
<i>Helicops apiaka</i>	Kawashita-Ribeiro, Ávila & Morais 2013			X											1
<i>Helicops carinicaudus</i>	(Wied-Neuwied 1825)			X		X							X		3
<i>Helicops danieli</i>	Amaral 1938					X									1
<i>Helicops gomesi</i>	Amaral 1921			X											1
<i>Helicops hagmanni</i>	Roux 1910			X										X	2
<i>Helicops hogei</i>	Lancini 1979													X	1
<i>Helicops infrataeniatus</i>	Jan 1865	X		X						X			X		4
<i>Helicops leopardinus</i>	(Schlegel 1837)	X	X	X		X	X	X		X	X	X			9
<i>Helicops modestus</i>	Günther 1861			X											1
<i>Helicops pastazae</i>	Shreve 1934					X	X				X			X	4
<i>Helicops petersi</i>	Rossman 1976						X								1
<i>Helicops polylepis</i>	Günther 1861		X	X		X					X				4
<i>Helicops scalaris</i>	Jan 1865					X								X	2
<i>Helicops tapajonicus</i>	Frota 2005			X											1
<i>Helicops trivittatus</i>	(Gray 1849)			X											1
<i>Hlicops yacu</i>	Amaral 1924										X				1
<i>Hydrops caesurus</i>	Scrocchi, Ferreira, Giraud, Avila & Motte 2005	X		X						X					3
<i>Hydrops martii</i>	(Wagler 1824)			X		X	X				X			X	5
<i>Hydrops triangularis</i>	(Wagler 1824)	X	X	X		X	X	X	X		X	X		X	10
<i>Pseudoeryx plicatilis</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X		X	11
<i>Pseudoeryx relictuialis</i>	Schargel, Rivas-Fuenmayor, Barros, Péfaur & Navarrete 2007													X	1
Philodryadini															
<i>Ditaxodon taeniatus</i>	(Peters 1868)			X											1
<i>Philodryas aestiva</i>	(Duméril, Bibron & Duméril 1854)	X	X	X						X			X		5
<i>Philodryas agassizii</i>	(Jan 1863)	X		X						X			X		4
<i>Philodryas argentea</i>	(Daudin 1803)		X	X		X	X	X	X		X	X		X	9
<i>Philodryas arnaldoi</i>	(Amaral 1933)			X											1
<i>Philodryas baroni</i>	Berg 1895	X	X							X					3
<i>Philodryas chamissonis</i>	(Wiegmann 1835)	X			X										2
<i>Philodryas cordata</i>	Donnelly & Myers 1991													X	1
<i>Philodryas georgeboulengeri</i>	Grazziotin, Zaher, Murphy, Scrocchi, Benavides, Zhang & Bonatto 2012		X	X							X				3
<i>Philodryas laticeps</i>	Werner 1900		X	X											2
<i>Philodryas livida</i>	(Amaral 1923)			X						X					2
<i>Philodryas mattogrossensis</i>	Koslowsky 1898	X	X	X						X					4
<i>Philodryas nattereri</i>	Steindachner 1870			X						X					2
<i>Philodryas olfersii</i>	(Lichtenstein 1823)	X	X	X		X		X	X	X	X	X	X	X	11
<i>Philodryas patagoniensis</i>	(Girard 1858)	X	X	X						X			X		5
<i>Philodryas psammophidea</i>	Günther 1872	X	X	X						X					4
<i>Philodryas simonsii</i>	Boulenger 1900				X		X				X				3
<i>Philodryas tachymenoides</i>	(Schmidt & Walker 1943)				X						X				2
<i>Philodryas trilineata</i>	(Burmeister 1861)	X													1
<i>Philodryas varia</i>	(Jan 1863)	X	X												2
<i>Philodryas viridissima</i>	(Linnaeus 1758)		X	X		X	X	X	X		X	X		X	9
Pseudoboini															
<i>Boiruna maculata</i>	(Boulenger 1896)	X	X	X						X			X		5
<i>Boiruna sertaneja</i>	Zaher 1996			X											1
<i>Clelia clelia</i>	(Daudin 1803)	X	X	X		X	X	X	X	X	X	X		X	11
<i>Clelia equatoriana</i>	(Amaral 1924)					X	X								2
<i>Clelia hussami</i>	Morato, Franco & Sanches 2003			X											1
<i>Clelia langeri</i>	Reichle & Embert 2005			X											1
<i>Clelia plumbea</i>	(Wied-Neuwied 1820)	X		X						X					3
<i>Clelia scytalina</i>	(Cope 1867)					X	X								2
<i>Drepanoides anomalus</i>	(Jan 1863)		X	X		X	X	X	X		X	X			8
<i>Mussurana bicolor</i>	(Peracca 1904)	X	X	X						X					4
<i>Mussurana montana</i>	(Franco, Marques & Puerto 1997)			X											1
<i>Mussurana quimi</i>	(Franco, Marques & Puerto 1997)	X		X						X					3
<i>Oxyrhopus clathratus</i>	Duméril, Bibron & Duméril 1854	X		X											2
<i>Oxyrhopus doliatus</i>	Duméril, Bibron & Duméril 1854													X	1
<i>Oxyrhopus erdisii</i>	(Barbour 1913)										X				1
<i>Oxyrhopus fitzingeri</i>	(Tschudi 1845)						X				X				2

		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Thamnodynastes sertanejo</i>	Bailey, Thomas & Silva-Jr 2005			X											1
<i>Thamnodynastes strigatus</i>	(Günther 1858)	X		X						X			X		4
<i>Thamnodynastes yavi</i>	Myers & Donnelly 1996													X	1
<i>Tomodon dorsatus</i>	Duméril, Bibron & Duméril 1854	X		X						X			X		4
<i>Tomodon ocellatus</i>	Duméril, Bibron & Duméril 1854	X		X									X		3
<i>Tomodon orestes</i>	Harvey & Muñoz 2004	X	X												2
Tropidodryadini															
<i>Tropidodryas serra</i>	(Schlegel 1837)						X								1
<i>Tropidodryas striaticeps</i>	(Cope 1869)						X								1
Xenodontini															
<i>Erythrolamprus aesculapii</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X		X	11
<i>Erythrolamprus albertguentheri</i>	(Peracca 1897)	X	X							X					3
<i>Erythrolamprus almadensis</i>	(Wagler 1824)	X	X	X						X			X		5
<i>Erythrolamprus andinus</i>	(Dixon 1983)			X											1
<i>Erythrolamprus atraventer</i>	(Dixon & Thomas 1985)				X										1
<i>Erythrolamprus bizona</i>	(Jan 1863)					X								X	2
<i>Erythrolamprus breviceps</i>	(Cope 1860)		X	X		X	X	X	X		X	X		X	9
<i>Erythrolamprus carajasensis</i>	(Cunha, Nascimento & Ávila-Pires 1985)			X											1
<i>Erythrolamprus ceii</i>	(Dixon 1991)	X	X												2
<i>Erythrolamprus cobella</i>	(Linnaeus 1758)			X		X	X	X	X			X		X	7
<i>Erythrolamprus dorsocorallinus</i>	(Esqueda, Natera, La Marca & Ilija-Fistar 2007)			X										X	2
<i>Erythrolamprus epinephelus</i>	(Cope 1862)					X	X				X			X	4
<i>Erythrolamprus festae</i>	(Peracca 1897)						X				X				2
<i>Erythrolamprus frenatus</i>	(Werner 1909)	X		X						X					3
<i>Erythrolamprus guentheri</i>	Garman 1883					X					X				2
<i>Erythrolamprus ingeri</i>	(Roze 1958)													X	1
<i>Erythrolamprus jaegeri</i>	(Günther 1858)	X	X	X						X			X		5
<i>Erythrolamprus janaleeae</i>	(Dixon 2000)										X				1
<i>Erythrolamprus maryellenae</i>	(Dixon 1985)			X											1
<i>Erythrolamprus melanotus</i>	(Shaw 1802)					X								X	2
<i>Erythrolamprus mertensi</i>	(Roze 1964)													X	1
<i>Erythrolamprus miliaris</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X	X	X	12
<i>Erythrolamprus mimus</i>	(Cope 1868)			X		X	X								3
<i>Erythrolamprus mossoroensis</i>	(Hoge & Lima-Verde 1973)			X											1
<i>Erythrolamprus oligolepis</i>	(Boulenger 1905)			X											1
<i>Erythrolamprus poecilogyrus</i>	(Wied-Neuwied 1825)	X	X	X			X		X	X		X	X	X	9
<i>Erythrolamprus problematicus</i>	(Myers 1986)										X				1
<i>Erythrolamprus pseudocorallus</i>	Roze 1959					X								X	2
<i>Erythrolamprus pyburni</i>	(Markezich & Dixon 1979)					X									1
<i>Erythrolamprus pygmaeus</i>	(Cope 1868)			X		X	X	X			X				5
<i>Erythrolamprus reginae</i>	(Linnaeus 1758)	X	X	X		X	X	X	X	X	X	X		X	11
<i>Erythrolamprus sagittifer</i>	(Jan 1863)	X	X							X					3
<i>Erythrolamprus semiaureus</i>	(Cope 1862)	X		X						X			X		4
<i>Erythrolamprus steinbachi</i>	(Boulenger 1905)			X											1
<i>Erythrolamprus subocularis</i>	(Boulenger 1902)						X								1
<i>Erythrolamprus taeniogaster</i>	(Jan 1863)		X	X		X					X				4
<i>Erythrolamprus taeniurus</i>	(Tschudi 1845)			X		X					X				3
<i>Erythrolamprus torrenicola</i>	(Donnelly & Myers 1991)													X	1
<i>Erythrolamprus trebbaii</i>	(Roze 1958)													X	1
<i>Erythrolamprus typhlus</i>	(Linnaeus 1758)		X	X		X	X	X	X	X	X	X		X	10
<i>Erythrolamprus viridis</i>	(Günther 1862)			X											1
<i>Erythrolamprus vittii</i>	(Dixon 2000)						X								1
<i>Erythrolamprus williamsi</i>	(Roze 1958)													X	1
<i>Lygophis anomalus</i>	(Günther 1858)	X	X	X									X		4
<i>Lygophis dilepis</i>	Cope 1862	X	X	X						X					4
<i>Lygophis elegantissimus</i>	(Koslowsky 1896)	X													1
<i>Lygophis flavifrenatus</i>	Cope 1862	X	X	X						X			X		5
<i>Lygophis lineatus</i>	(Linnaeus 1758)		X	X		X	X	X	X	X		X		X	9
<i>Lygophis meridionalis</i>	(Schenkel 1901)	X	X	X						X					4
<i>Lygophis paucidens</i>	Hoge 1953			X						X					2
<i>Lygophis vanzolinii</i>	(Dixon 1985)	X													1
<i>Xenodon dorbignyi</i>	(Duméril, Bibron & Duméril 1854)	X		X						X			X		4
<i>Xenodon guentheri</i>	Boulenger 1894			X											1
<i>Xenodon histricus</i>	(Jan 1863)	X		X						X			X		4
<i>Xenodon matogrossensis</i>	(Scrocchi & Cruz 1993)			X											1
<i>Xenodon merremii</i>	(Wagler 1824)	X	X	X				X	X	X		X	X	X	9
<i>Xenodon nattereri</i>	(Steindachner 1867)			X											1
<i>Xenodon neuwiedii</i>	Günther 1863	X	X	X											3
<i>Xenodon pulcher</i>	(Jan 1863)	X	X	X						X					3
<i>Xenodon rabdocephalus</i>	(Wied-Neuwied 1824)		X	X		X	X	X	X		X	X		X	9

		Ar	Bo	Br	Ch	Co	Ec	FG	Gu	Pa	Pe	Su	Ur	Ve	occ.
<i>Xenodon semicinctus</i>	(Duméril, Bibron & Duméril 1854)	X	X												2
<i>Xenodon severus</i>	(Linnaeus 1758)		X	X		X	X	X	X		X	X		X	9
<i>Xenodon weneri</i>	Eiselt 1963			X				X				X			3
Xenodontinae <i>Incertae sedis</i>															
<i>Xenopholis scalaris</i>	(Wucherer 1861)		X	X		X	X	X	X		X	X			8
<i>Xenopholis undulatus</i>	(Jensen 1900)			X						X					2
<i>Xenopholis werdingorum</i>	Jansen, Álvarez & Köhler 2009		X	X											2
Colubridae <i>Incertae sedis</i>															
<i>Enuliophis sclateri</i>	(Boulenger 1894)						X								1
<i>Enulius flavitorques</i>	(Cope 1868)						X						X		2

* Species endemic to the Antilles and other insular territories such as Trinidad, Tobago, Gorgona, Queimada Grande, Alcatrazes, etc were not included.
One species of marine snake *Hydrophis (Pelamis) platyrus* (Elapidae: Hydrophiinae: Hydrophiini) also occurs in South America, through the Pacific coast of Colombia, Ecuador, and Peru (Campbell and Lamar 2004), it was not quantified in this table either.

Appendix S1b. Check list of inland Australian snakes and their respective states and territories of occurrence*. ACT - Australian Capital Territory; NSW - New South Wales; NT - Northern Territory, Qld - Queensland; SA - South Australia; Vic - Victoria; WA - Western Australia; occ. - “number of regional occurrences”. Snake lineages are alphabetically ordered, and quotation marks refer to unnamed clades.

		ACT	NSW	NT	Qld	SA	Vic	WA	occ.
Total Species Richness (161)		14	56	68	86	47	29	96	
SCOLECOPHIDIA									
Typhlopidae									
<i>Ramphotyphlops affinis</i>	(Boulenger 1889)		X	X	X				3
<i>Ramphotyphlops ammodytes</i>	(Montague 1914)							X	1
<i>Ramphotyphlops aspina</i>	Couper, Covacevich & Wilson 1998				X				1
<i>Ramphotyphlops australis</i>	(Gray 1845)		X			X	X	X	4
<i>Ramphotyphlops batillus</i>	(Waite 1894)		X						1
<i>Ramphotyphlops bicolor</i>	(Peters 1858)		X			X	X	X	4
<i>Ramphotyphlops bituberculatus</i>	(Peters 1863)		X	X	X	X	X	X	6
<i>Ramphotyphlops broomi</i>	(Boulenger 1898)		X	X	X	X	X		5
<i>Ramphotyphlops centralis</i>	Storr 1984			X					1
<i>Ramphotyphlops chamodracaena</i>	Ingram & Covacevich 1993				X				1
<i>Ramphotyphlops diversus</i>	(Waite 1894)			X	X			X	3
<i>Ramphotyphlops endoterus</i>	(Waite 1918)		X	X	X	X		X	5
<i>Ramphotyphlops ganei</i>	Aplin 1998							X	1
<i>Ramphotyphlops grypus</i>	(Waite 1918)			X	X			X	3
<i>Ramphotyphlops guentheri</i>	(Peters 1865)			X				X	2
<i>Ramphotyphlops hamatus</i>	Storr 1981							X	1
<i>Ramphotyphlops howi</i>	Storr 1983							X	1
<i>Ramphotyphlops kimberleyensis</i>	Storr 1981			X				X	2
<i>Ramphotyphlops leptosoma</i>	Robb 1972							X	1
<i>Ramphotyphlops leucoproctus</i>	(Boulenger 1889)				X				1
<i>Ramphotyphlops ligatus</i>	(Peters 1879)		X	X	X	X	X	X	6
<i>Ramphotyphlops margaretae</i>	Storr 1981							X	1
<i>Ramphotyphlops micromma</i>	Storr 1981							X	1
<i>Ramphotyphlops minimus</i>	(Kinghorn 1929)				X				1
<i>Ramphotyphlops nema</i>	Shea & Horner 1997			X					1
<i>Ramphotyphlops nigrescens</i>	(Gray 1845)	X	X		X		X		4
<i>Ramphotyphlops pilbarensis</i>	Aplin & Donnellan 1993							X	1
<i>Ramphotyphlops pinguis</i>	(Waite 1897)					X	X	X	3
<i>Ramphotyphlops polygrammicus</i>	(Schlegel 1839)				X				1
<i>Ramphotyphlops proximus</i>	(Waite 1893)		X		X	X	X		4
<i>Ramphotyphlops robertsi</i>	(Couper, Covacevich, Wilson 1998)				X				1
<i>Ramphotyphlops silvia</i>	Ingram & Covacevich 1993				X				1
<i>Ramphotyphlops splendidus</i>	Aplin 1998							X	1
<i>Ramphotyphlops toveli</i>	(Loveridge 1945)			X					1
<i>Ramphotyphlops troglodytes</i>	Storr 1981							X	1
<i>Ramphotyphlops unguirostris</i>	(Peters 1867)			X	X			X	3
<i>Ramphotyphlops waitii</i>	(Boulenger 1895)							X	1
<i>Ramphotyphlops wiedii</i>	(Peters 1867)		X	X	X	X	X		5
<i>Ramphotyphlops yirrikalae</i>	(Kinghorn 1942)			X					1
ALETHINOPHIDIA									
AFROPHIDIA									
HENOPHIDIA									
Pythonidae									
<i>Antaresia childreni</i>	(Gray 1842)			X	X			X	3
<i>Antaresia maculosa</i>	(Peters 1873)		X		X				2
<i>Antaresia perthensis</i>	(Stull 1932)							X	1
<i>Antaresia stimsoni</i>	(Smith 1985)		X	X	X	X		X	5
<i>Aspidites melanocephalus</i>	(Krefft 1864)			X	X			X	3
<i>Aspidites ramsayi</i>	(Macleay 1882)		X	X	X	X		X	5

		ACT	NSW	NT	Qld	SA	Vic	WA	Occ.
<i>Liasis mackloti</i>	Duméril & Bibron 1844			X	X			X	3
<i>Liasis olivaceus</i>	Gray 1842			X	X			X	3
<i>Morelia carinata</i>	(Smith 1981)							X	1
<i>Morelia kinghorni</i>	(Stull 1933)				X				1
<i>Morelia oenpelliensis</i>	(Gow 1977)			X					1
<i>Morelia spilota</i>	(Lacépède 1804)	X	X	X	X	X	X	X	7
<i>Morelia viridis</i>	(Schlegel 1872)				X				1
<i>Acrochordus arafuræ</i>	McDowell 1979			X	X			X	3
<i>Acrochordus granulatus</i>	(Schneider 1799)			X	X			X	3

CAENOPHIDIA

Elapidae

Hydrophiinae

<i>Acanthophis antarcticus</i>	(Shaw 1802)	X	X	X	X	X	X	X	7
<i>Acanthophis praelongus</i>	Ramsay 1877			X	X			X	3
<i>Acanthophis pyrrhus</i>	Boulenger 1898			X	X	X		X	4
<i>Acanthophis wellsi</i>	Hoser 1998							X	1
<i>Antaioserpens warro</i>	(De Vis 1884)				X				1
<i>Austrelaps labialis</i>	(Jan 1859)					X			1
<i>Austrelaps ramsayi</i>	(Krefft 1864)	X	X				X		3
<i>Austrelaps superbus</i>	(Günther 1858)		X			X	X		3
<i>Brachyuropis approximans</i>	(Glauert 1954)							X	1
<i>Brachyuropis australis</i>	(Krefft 1864)		X		X	X	X		4
<i>Brachyuropis fasciolatus</i>	(Günther 1872)		X	X	X	X		X	5
<i>Brachyuropis incinctus</i>	(Storr 1968)			X	X				2
<i>Brachyuropis morrisi</i>	Horner 1998			X					1
<i>Brachyuropis roperi</i>	(Kinghorn 1931)			X				X	2
<i>Brachyuropis semifasciatus</i>	(Günther 1863)			X	X	X		X	4
<i>Cacophis churchilli</i>	Wells & Wellington 1985				X				1
<i>Cacophis harriettae</i>	Krefft 1869		X		X				2
<i>Cacophis krefftii</i>	Günther 1863		X		X				2
<i>Cacophis squamulosus</i>	(Duméril, Bibron & Duméril 1854)		X		X				2
<i>Cryptophis boschmai</i>	(Brongersma & Knaap Van Meeuwen 1961)				X				1
<i>Cryptophis nigrescens</i>	(Günther 1862)	X	X		X		X		4
<i>Cryptophis nigrostriatus</i>	(Krefft 1864)				X				1
<i>Cryptophis pallidiceps</i>	(Günther 1858)			X				X	2
<i>Demansia angusticeps</i>	(Macleay 1888)			X				X	2
<i>Demansia calodera</i>	Storr 1978							X	1
<i>Demansia flagellatio</i>	Wells & Wellington 1985				X				1
<i>Demansia olivacea</i>	(Gray 1842)			X	X			X	3
<i>Demansia papuensis</i>	(Macleay 1877)			X	X			X	3
<i>Demansia psammophis</i>	(Schlegel 1837)	X	X	X	X	X	X	X	7
<i>Demansia quaesitor</i>	Shea 2007			X	X			X	3
<i>Demansia rimicola</i>	Scanlon 2007		X	X	X	X		X	5
<i>Demansia rufescens</i>	Storr 1978							X	1
<i>Demansia shinei</i>	Shea 2007			X				X	2
<i>Demansia simplex</i>	Storr 1978			X				X	2
<i>Demansia torquata</i>	(Günther 1862)				X				1
<i>Demansia vestigiata</i>	(De Vis 1884)			X	X			X	3
<i>Denisonia devisi</i>	(Wait & Longman 1920)		X		X				2
<i>Denisonia maculata</i>	(Steindachner 1867)				X				1
<i>Drysdalia coronoides</i>	(Günther 1858)	X	X			X			3
<i>Drysdalia mastersii</i>	(Krefft 1866)		X			X	X	X	4
<i>Drysdalia rhodogaster</i>	(Jan 1873)		X						1
<i>Echiopsis curta</i>	(Schlegel 1837)		X			X	X	X	4
<i>Elapognathus coronatus</i>	(Schlegel 1837)							X	1
<i>Elapognathus minor</i>	(Günther 1863)							X	1
<i>Furina barnardi</i>	(Kinghorn 1939)				X				1
<i>Furina diadema</i>	(Schlegel 1837)	X	X		X	X	X		5
<i>Furina dunmalli</i>	(Worrell 1955)				X				1

		ACT	NSW	NT	Qld	SA	Vic	WA	Occ.
<i>Furina ornata</i>	(Gray 1842)			X	X	X		X	4
<i>Furina tristis</i>	(Günther 1858)				X				1
<i>Hemiaspis damelii</i>	(Günther 1876)		X		X				2
<i>Hemiaspis signata</i>	(Jan 1859)		X		X				2
<i>Hoplocephalus bitorquatus</i>	(Jan 1859)		X		X				2
<i>Hoplocephalus bungaroides</i>	(Schlegel 1837)		X						1
<i>Hoplocephalus stephensii</i>	Kreffft 1869		X		X				2
<i>Neelaps bimaculatus</i>	(Duméril, Bibron & Duméril 1854)					X		X	2
<i>Neelaps calonotus</i>	(Duméril, Bibron & Duméril 1854)							X	1
<i>Notechis scutatus</i>	(Peters 1861)	X	X		X	X	X	X	6
<i>Oxyuranus microlepidotus</i>	(Mccoy 1879)		X	X	X	X			4
<i>Oxyuranus scutellatus</i>	(Peters 1867)		X	X	X			X	4
<i>Oxyuranus temporalis</i>	Doughty, Maryan, Donnellan & Hutchinson 2007							X	1
<i>Parasuta dwyeri</i>	(Worrell 1956)		X		X		X		3
<i>Parasuta flagellum</i>	(Mccoy 1878)	X	X			X	X		4
<i>Parasuta gouldii</i>	(Gray 1841)							X	1
<i>Parasuta monachus</i>	(Storr 1964)		X	X		X		X	4
<i>Parasuta nigriceps</i>	(Günther 1863)		X			X	X	X	4
<i>Parasuta spectabilis</i>	Kreffft 1869	X	X		X	X	X	X	6
<i>Paroplocephalus atriceps</i>	(Storr 1980)							X	1
<i>Pseudechis australis</i>	(Gray 1842)		X	X	X	X		X	5
<i>Pseudechis butleri</i>	Smith 1982							X	1
<i>Pseudechis colletti</i>	Boulenger 1902				X				1
<i>Pseudechis guttatus</i>	De Vis 1905		X		X				2
<i>Pseudechis porphyriacus</i>	(Shaw 1794)	X	X		X	X	X		5
<i>Pseudechis weigeli</i>	(Wells & Wellington 1987)			X	X			X	3
<i>Pseudonaja affinis</i>	Günther 1872					X		X	2
<i>Pseudonaja aspidorhyncha</i>	(Mccoy 1879)		X			X			2
<i>Pseudonaja guttata</i>	(Parker 1926)			X	X	X			3
<i>Pseudonaja infracacula</i>	(Waite 1925)					X		X	2
<i>Pseudonaja ingrami</i>	(Boulenger 1908)			X	X			X	3
<i>Pseudonaja mengdeni</i>	Wells & Wellington 1985		X	X		X		X	4
<i>Pseudonaja modesta</i>	(Günther 1872)		X	X	X	X		X	5
<i>Pseudonaja nuchalis</i>	Günther 1858		X	X	X	X	X	X	6
<i>Pseudonaja textilis</i>	(Duméril, Bibron & Duméril 1854)	X	X	X	X	X	X	X	7
<i>Rhinoplocephalus bicolor</i>	Müller 1885							X	1
<i>Simoselaps anomalus</i>	(Sternfeld 1919)			X		X		X	3
<i>Simoselaps bertholdi</i>	(Jan 1859)			X		X		X	3
<i>Simoselaps littoralis</i>	(Storr 1968)							X	1
<i>Simoselaps minimus</i>	(Worrell 1960)							X	1
<i>Suta fasciata</i>	(Rosen 1905)							X	1
<i>Suta ordensis</i>	(Storr 1984)			X				X	2
<i>Suta punctata</i>	(Boulenger 1896)			X	X			X	3
<i>Suta suta</i>	(Peters 1863)		X	X	X	X	X	X	6
<i>Tropidechis carinatus</i>	(Kreffft 1863)		X		X				2
<i>Vermicella annulata</i>	(Gray 1841)	X	X	X	X	X	X	X	7
<i>Vermicella intermedia</i>	Keogh & Smith 1996			X				X	2
<i>Vermicella multifasciata</i>	(Longman 1915)			X				X	2
<i>Vermicella snelli</i>	Storr 1968							X	1
<i>Vermicella vermiformis</i>	Keogh & Smith 1996							X	1
Homalopsidae									
<i>Cerberus australis</i>	Gray 1842			X	X			X	3
<i>Fordonia leucobalia</i>	(Schlegel 1837)			X	X			X	3
<i>Myron resetari</i>	Murphy 2011							X	1
<i>Myron richardsonii</i>	Gray 1849			X	X			X	3
<i>Pseudoferania polylepis</i>	(Fischer 1886)			X	X				2

		ACT	NSW	NT	Qld	SA	Vic	WA	Occ.
Colubridae									
Colubrinae									
<i>Boiga irregularis</i>	(Bechstein 1802)		X	X	X			X	4
<i>Dendrelaphis calligastra</i>	(Günther 1867)				X				1
<i>Dendrelaphis punctulatus</i>	(Gray 1826)		X	X	X			X	4
<i>Stegonotus cucullatus</i>	(Duméril, Bibron & Duméril 1854)				X	X		X	3
<i>Tropidonophis mairii</i>	(Gray 1841)		X	X	X			X	4

* Species records in Tasmania and other insular territories were not taken into account. Likewise, about 36 species of marine snakes (Elapidae: Hydrophiinae) live in the sea surrounding Australia mainland, they are not quantified in this table. South Australia is the only mainland state/territory without marine snakes in its coast. The recently introduced species *Ramphotyphlops braminus* was not included either.

Appendix S2 – Taxonomy and Systematic

I listed below (in bullets) the set of high-level clades adopted in this work (see also the list of species and the taxonomic structure tables at [Appendices S1 and S5](#)). Each clade-content was defined in agreement with the following references (quotation marks refer to unnamed clades). I'm mentioning below only the most up dated and embracing references; taxonomic disputes and history should be checked through these references and citations they used. Most of my taxonomic choices, mainly in the genus and species level, follow Bérnils and Costa (2012), and Campbell and Lamar (2004) to South America; and Wilson and Swan (2010), and Macdonald (2012) to Australia, plus up dated references for both. The phylogenetic relationships among higher-level clades of snakes occurring in South America and Australia follows Pyron *et al.* (2013) and are depicted at [Figures 1S2 and 2S2](#).

- Scolecophidia sensu Vidal *et al.* (2010b); Scanlon and Lee (2011); and following classification of Bérnils and Costa (2012). However, Scolecophiadia is potentially a paraphyletic group due to the Neotropical clade Anomalepididae, sensu Vidal *et al.* (2009); and Pyron *et al.* (2013).
- Leptotyphlopidae, Epictinae, and Epictini sensu Adalsteinsson *et al.* (2009); and Hedges (2011); and following Bérnils and Costa (2012).
- Typhlopidae and "South American Typhlopidae" clade sensu Vidal *et al.* (2010b).
- "Australian Typhlopidae" clade sensu Vidal *et al.* (2010b), and Marin *et al.* (2013).
- Anomalepididae sensu Greene (1997).
- Amerophidia sensu Vidal *et al.* (2009); Scanlon and Lee (2011); and following Bérnils and Costa (2012). Anilioidea sensu Pyron *et al.* (2013).
- Tropidophiidae sensu Wilcox (2002); Curcio *et al.* (2012); and Pyron *et al.* (2013).
- Afrophidia sensu Vidal *et al.* (2009); and following Bérnils and Costa (2012).
- Henophidia sensu Vidal *et al.* (2009); and following Bérnils and Costa (2012). Booidea sensu Pyron *et al.* (2013).
- Boidae, Boinae and Ungaliophiinae sensu Noonan and Chippindale (2006), and supported by Pyron *et al.* (2013).
- Pythonidae sensu Rawlings *et al.* (2008); Schleip and O'Shea (2010); Pyron *et al.* (2013); and following Wilson and Swan (2010).

- *Caenophidia* sensu Vidal *et al.* (2009); Scanlon and Lee (2011); Grazziotin *et al.* (2012); Pyron *et al.* (2013); and following Bérnils and Costa (2012).
- Acrochordidae sensu Sanders *et al.* (2010).
- "New World Crotalinae" clade sensu discussed by (Gutberlet & Harvey, 2004); defended by Castoe and Parkinson (2006) and Wüster *et al.* (2008); and supported by Pyron *et al.* (2013).
- Homalopsidae sensu Lawson *et al.* (2005); Murphy (2011); Pyron *et al.* (2013); and following Wilson and Swan (2010).
- Colubridae sensu Pyron *et al.* (2013).
- Colubrinae and Natricinae sensu Pyron *et al.* (2013); following classification of Wilson and Swan (2010), and Bérnils and Costa (2012).
- Dipsadinae and Xenodontinae sensu Zaher *et al.* (2009); Vidal *et al.* (2010a); Grazziotin *et al.* (2012); and following Bérnils and Costa (2012).
- Dipsadinae: "Atractus clade", Dipsadini, Imantodini sensu Zaher *et al.* (2009); Grazziotin *et al.* (2012); and following Bérnils and Costa (2012).
- Xenodontinae: Amnesteophiini, Caaeteboiini, Echinantherini, Elapomorphini, Hydrodynastini, Hydrophini, Philodryadini, Pseudoboini, Psomophiini, Saphenophiini, Tachymenini, Tropidodryadini, and Xenodontini sensu Zaher *et al.* (2009); Grazziotin *et al.* (2012); and following Bérnils and Costa (2012).
- Sibynophiinae sensu Chen *et al.* (Chen *et al.*, 2013); and Pyron *et al.* (2013).
- Elapidae sensu Kelly *et al.* (2009); and Pyron *et al.* (2013).
- Elapinae sensu Castoe *et al.* (2007) and following Bérnils and Costa (2012). The dichotomy Elapinae (housing the "American-Asian" and "African-Asian" elapids) *versus* Hydrophiinae (included within the "Australo-Melanesian clade") are supported by Castoe *et al.* (2007), however, only Hydrophiinae has been strongly supported in more recent studies (Kelly *et al.*, 2009; Pyron *et al.*, 2013). Avoiding to deal with this potential paraphyly, hereafter I'm using Elapinae referring to the "American-Asian clade" only, which has been a well-supported clade (see Kelly *et al.*, 2009; Pyron *et al.*, 2013).
- Calliophini sensu Castoe *et al.* (2007), although not supported by Pyron *et al.* (2013).
- Hydrophiinae sensu Scanlon and Lee (2004); and Sanders *et al.* (2008); in which non-marine snakes is an artificial-paraphyletic group, due to the viviparous sea snakes, tribe Hydrophiini (Sanders *et al.*, 2013).

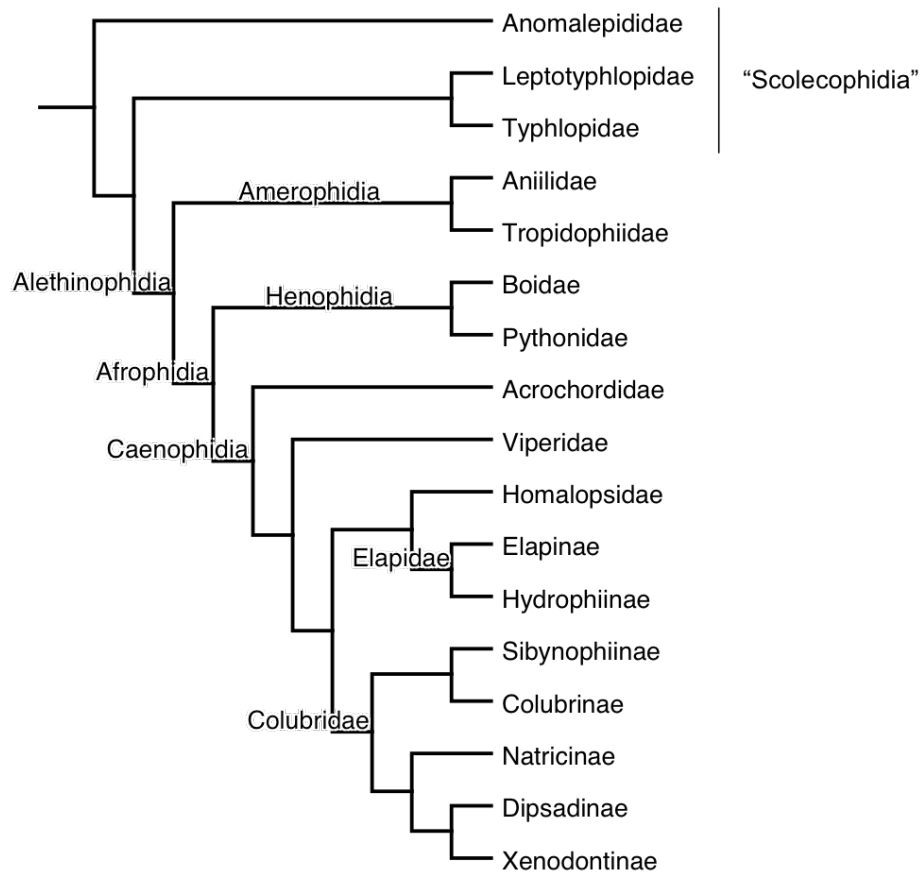


Figure 1S2. Ultrametric phylogenetic tree of higher clades within Serpentes occurring in South America and/or Australia (phylogenetic hypothesis based on Pyron *et al.*, 2013).

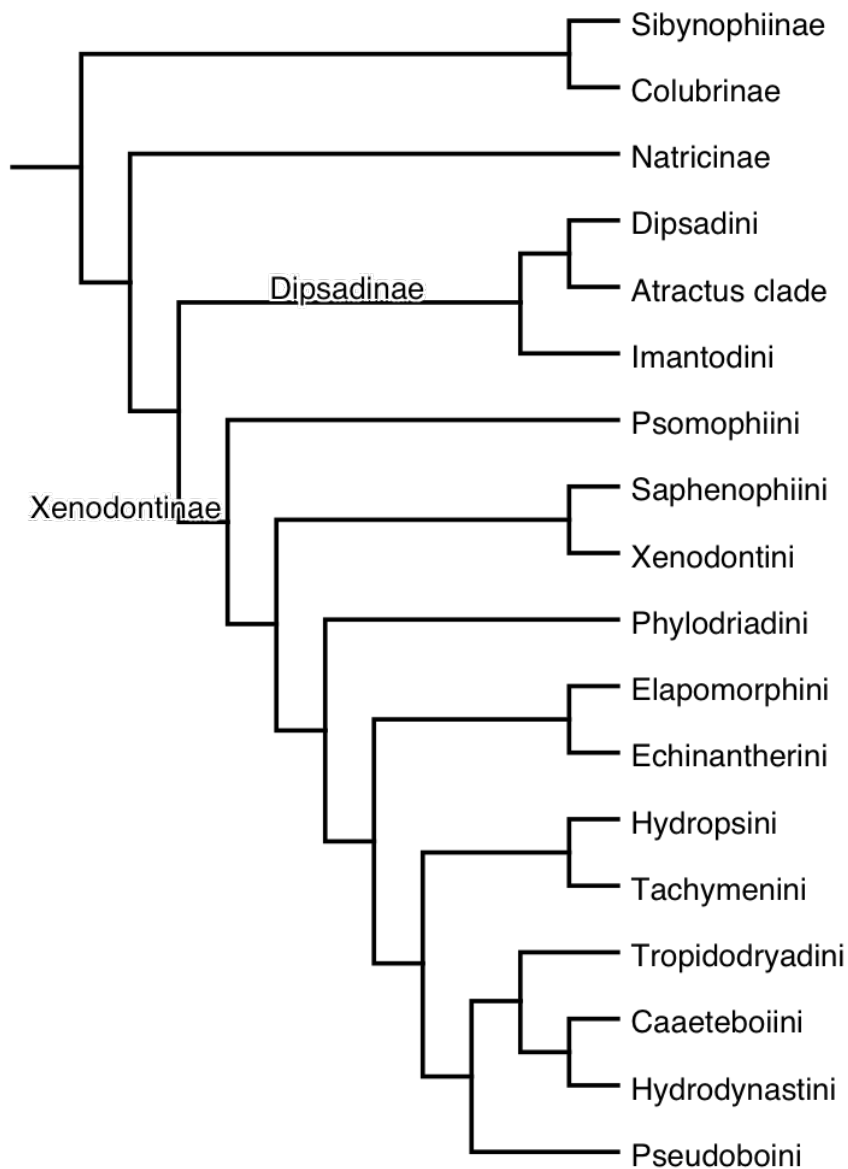


Figure 2S2. Molecular phylogenetic relationships among South American and Australian subfamilies and tribes within the family Colubridae. Phylogenetic hypothesis based on Pyron *et al.* (2013); tribe's names follows Grazziotin *et al.* (2012). The tribe Amnesteophiini Myers 2011 occurring in South America is currently considers part of the subfamily Xenodontinae, but it was never considered in any previously phylogenetic analysis, and its phylogenetic relationships are unknown (herein considered as *insertae sedis* it was not included in this figure).

REFERENCES

- Adalsteinsson, S.A., Branch, W.R., Trape, S., Vitt, L.J. & Hedges, S.B. (2009) Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). *Zootaxa*, 1-50.
- Bérnils, R.S. & Costa, H.C. (2012) Répteis brasileiros: Lista de espécies. Versão 2012.2. In. Sociedade Brasileira de Herpetologia

- Campbell, J.A. & Lamar, W.W. (2004) *The Venomous Reptiles of the Western Hemisphere*. Cornell University.
- Castoe, T.A. & Parkinson, C.L. (2006) Bayesian mixed models and the phylogeny of pitvipers (Viperidae: Serpentes). *Molecular Phylogenetics and Evolution*, **39**, 91-110.
- Castoe, T.A., Smith, E.N., Brown, R.M. & Parkinson, C.L. (2007) Higher-level phylogeny of Asian and American coralsnakes, their placement within the Elapidae (Squamata), and the systematic affinities of the enigmatic Asian coralsnake *Hemibungarus calligaster* Wiegmann, 1834. *Zoological Journal of the Linnean Society*, **151**, 809-831.
- Chen, X., Huang, S., Guo, P., Colli, G.R., Montes de Oca, A.N., Vitt, L.J., Pyron, R.A. & Burbrink, F.T. (2013) Understanding the formation of ancient intertropical disjunct distributions using Asian and Neotropical hinged-teeth snakes (*Sibynophis* and *Scaphiodontophis*: Serpentes: Colubridae). *Molecular Phylogenetics and Evolution*, **66**, 254-261.
- Curcio, F.F., Nunes, P.M.S., Argolo, A.J.S., Skuk, G. & Rodrigues, M.T. (2012) Taxonomy of the South American dwarf boas of the genus *Tropidophis* Bibron, 1840, with the description of two new species from the Atlantic Forest (Serpentes: Tropidophiidae). *Herpetological Monographs*, 80-121.
- Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y.-P. & Bonatto, S.L. (2012) Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, **1**, 1-23.
- Greene, H.W. (1997) *Snakes: the Evolution of Mystery in Nature*. University of California Press, California.
- Gutberlet, R.L. & Harvey, M.B. (2004) The evolution of New World venomous snakes. In: *The Venomous Reptiles of the Western Hemisphere* eds. L.A. Campbell and W.W. Lamar, pp. 634-682. Cornell University Press
- Hedges, S.B. (2011) The type species of the threadsnake genus *Tricheilostoma* Jan revisited (Squamata, Leptotyphlopidae). *Zootaxa*, 63-64.
- Kelly, C.M.R., Barker, N.P., Villet, M.H. & Broadley, D.G. (2009) Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics-the International Journal of the Willi Hennig Society*, **25**, 38-63.
- Lawson, R., Slowinski, J.B., Crother, B.I. & Burbrink, F.T. (2005) Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, **37**, 581-601.
- Macdonald, S. (2012) Australian Reptile Online Database. In:
- Marin, J., Donnellan, S.C., Hedges, S.B., Doughty, P., Hutchinson, M.N., Cruaud, C. & Vidal, N. (2013) Tracing the history and biogeography of the Australian blindsnake radiation. *Journal of Biogeography*, **40**, 928-937.
- Murphy, J.C. (2011) The nomenclature and systematics of some Australasian homalopsid snakes (Squamata: Serpentes: Homalopsidae). *The Raffles Bulletin of Zoology*, **59**, 229-236.
- Noonan, B.P. & Chippindale, P.T. (2006) Dispersal and vicariance: the complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution*, **40**, 347-358.
- Pyron, R.A., Burbrink, F.T. & Wiens, J.A. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, **13**, 1-53.

- Rawlings, L.H., Rabosky, D.L., Donnellan, S.C. & Hutchinson, M.N. (2008) *Python* phylogenetics: inference from morphology and mitochondrial DNA. *Biological Journal of the Linnean Society*, **93**, 603-619.
- Sanders, K.L., Lee, M.S.Y., Leys, R., Foster, R. & Keogh, J.S. (2008) Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *Journal of Evolutionary Biology*, **21**, 682-695.
- Sanders, K.L., Mumpuni, Hamidy, A., Head, J.J. & Gower, D.J. (2010) Phylogeny and divergence times of filesnakes (*Acrochordus*): Inferences from morphology, fossils and three molecular loci. *Molecular Phylogenetics and Evolution*, **56**, 857-867.
- Sanders, K.L., Lee, M.S.Y., Mumpuni, Bertozzi, T. & Rasmussen, A.R. (2013) Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). *Molecular Phylogenetics and Evolution*, **66**, 575-591.
- Scanlon, J.D. & Lee, M.S.Y. (2004) Phylogeny of Australasian venomous snakes (Colubroidea, Elapidae, Hydrophiinae) based on phenotypic and molecular evidence. *Zoologica Scripta*, **33**, 335-366.
- Scanlon, J.D. & Lee, M.S.Y. (2011) The major clades of living snakes: morphological evolution, molecular phylogeny, and divergence dates. *Reproductive Biology and Phylogeny of Snakes* (ed. by R.D. Aldridge and D.M. Sever), pp. 54-95. Science Publishers, and CRC Press, Enfield, NH.
- Schleip, W.D. & O'Shea, M. (2010) Annotated checklist of the recent and extinct pythons (Serpentes, Pythonidae), with notes on nomenclature, taxonomy, and distribution. *Zookeys*, 29-79.
- Vidal, N., Dewynter, M. & Gower, D.J. (2010a) Dissecting the major American snake radiation: a molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies*, **333**, 48-55.
- Vidal, N., Rage, J.C., Couloux, A. & Hedges, S.B. (2009) Snakes (Serpentes). *The Timetree of Life* (ed. by S.B. Hedges and S. Kumar), pp. 390-397. Oxford University Press, Oxford, UK.
- Vidal, N., Marin, J., Morini, M., Donnellan, S., Branch, W.R., Thomas, R., Vences, M., Wynn, A., Cruaud, C. & Hedges, S.B. (2010b) Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters*, **6**, 558-561.
- Wilcox, T.P., Zwickl, D.J., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, **25**, 361-371.
- Wilson, S. & Swan, G. (2010) *A Complete Guide to Reptiles of Australia*, 3rd edn. New Holland Publishers, Sydney.
- Wüster, W., Peppin, L., Pook, C.E. & Walker, D.E. (2008) A nesting of vipers: Phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). *Molecular Phylogenetics and Evolution*, **49**, 445-459.
- Zaher, H., Graziotin, F.G., Cadle, J.E., Murphy, R.W., De Moura-Leite, J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia (São Paulo)*, **49**, 115-153.

Appendix S3a (South America)

Biological structure of the South American snake fauna decomposed in nine families, six biological dimensions (in *italic*), and distributed through twenty nine biological attributes. The numbers of species in each biological dimension refer to the sample size and are followed by their respective adequacy (percentage of the total fauna, within parentheses). The prevalence of each biological attribute is presented as the number of species and its proportion within the respective biological dimension (percentage of the number of species sampled). Diet percentages do not sum 100% because categories are not mutually exclusive. See the text for abbreviations.

	Anomalepididae (15)	Leptotyphlopidae (42)	Typhlopidae (7)
<i>Habitat</i>	9 (60.00)	23 (54.76)	5 (71.43)
Op	0 (0.00)	8 (34.78)	2 (40.00)
Bo	3 (33.33)	7 (30.43)	1 (20.00)
Cl	6 (66.67)	8 (34.78)	2 (40.00)
<i>Habit</i>	15 (100.00)	42 (100.00)	7 (100.00)
aq	0 (0.00)	0 (0.00)	0 (0.00)
saq	0 (0.00)	0 (0.00)	0 (0.00)
fo	10 (66.67)	40 (95.24)	7 (100.00)
cfo	5 (33.33)	1 (2.38)	0 (0.00)
cr	0 (0.00)	0 (0.00)	0 (0.00)
cte	0 (0.00)	0 (0.00)	0 (0.00)
te	0 (0.00)	1 (2.38)	0 (0.00)
sar	0 (0.00)	0 (0.00)	0 (0.00)
ar	0 (0.00)	0 (0.00)	0 (0.00)
<i>Diel activity</i>	3 (20.00)	6 (14.29)	2 (28.57)
D	1 (33.33)	1 (16.67)	0 (0.00)
DN	0 (0.00)	2 (33.33)	1 (50.00)
N	2 (66.67)	3 (50.00)	1 (50.00)
<i>Reproduction</i>	15 (100.00)	42 (100.00)	7 (100.00)
O	15 (100.00)	42 (100.00)	7 (100.00)
OV	0 (0.00)	0 (0.00)	0 (0.00)
V	0 (0.00)	0 (0.00)	0 (0.00)
<i>Diet</i>	4 (26.67)	13 (30.95)	2 (28.57)
goo	0 (0.00)	0 (0.00)	0 (0.00)
art	4 (100.00)	13 (100.00)	2 (100.00)
fis	0 (0.00)	0 (0.00)	0 (0.00)
amp	0 (0.00)	0 (0.00)	0 (0.00)
rep	0 (0.00)	0 (0.00)	0 (0.00)
bir	0 (0.00)	0 (0.00)	0 (0.00)
mam	0 (0.00)	0 (0.00)	0 (0.00)
<i>Body length</i>	11 (73.33)	34 (80.95)	7 (100.00)
S	11 (100.00)	34 (100.00)	6 (85.71)
M	0 (0.00)	0 (0.00)	1 (14.29)
L	0 (0.00)	0 (0.00)	0 (0.00)
VL	0 (0.00)	0 (0.00)	0 (0.00)

Appendix S3a (South America). Cont ...

	Aniliidae (1)	Tropidophiidae (7)	Boidae (18)
<i>Habitat</i>	<i>1 (100.00)</i>	<i>6 (85.71)</i>	<i>18 (100.00)</i>
Op	0 (0.00)	1 (16.67)	3 (16.67)
Bo	0 (0.00)	1 (16.67)	8 (44.44)
Cl	1 (100.00)	4 (66.67)	7 (38.89)
<i>Habit</i>	<i>1 (100.00)</i>	<i>6 (85.71)</i>	<i>18 (100.00)</i>
aq	0 (0.00)	0 (0.00)	4 (22.22)
saq	0 (0.00)	0 (0.00)	0 (0.00)
fo	1 (100.00)	0 (0.00)	0 (0.00)
cfo	0 (0.00)	0 (0.00)	0 (0.00)
cr	0 (0.00)	0 (0.00)	0 (0.00)
cte	0 (0.00)	0 (0.00)	0 (0.00)
te	0 (0.00)	2 (33.33)	5 (27.78)
sar	0 (0.00)	1 (16.67)	2 (11.11)
ar	0 (0.00)	3 (50.00)	7 (38.89)
<i>Diel activity</i>	<i>1 (100.00)</i>	<i>6 (85.71)</i>	<i>17 (94.44)</i>
D	0 (0.00)	0 (0.00)	0 (0.00)
DN	0 (0.00)	0 (0.00)	2 (11.76)
N	1 (100.00)	6 (100.00)	15 (88.24)
<i>Reproduction</i>	<i>1 (100.00)</i>	<i>7 (100.00)</i>	<i>18 (100.00)</i>
O	0 (0.00)	0 (0.00)	0 (0.00)
OV	0 (0.00)	0 (0.00)	0 (0.00)
V	1 (100.00)	7 (100.00)	18 (100.00)
<i>Diet</i>	<i>1 (100.00)</i>	<i>4 (57.14)</i>	<i>17 (94.44)</i>
goo	0 (0.00)	0 (0.00)	0 (0.00)
art	0 (0.00)	0 (0.00)	0 (0.00)
fis	0 (0.00)	0 (0.00)	1 (5.88)
amp	0 (0.00)	2 (50.00)	0 (0.00)
rep	1 (100.00)	2 (50.00)	1 (5.88)
bir	0 (0.00)	2 (50.00)	7 (41.18)
mam	0 (0.00)	0 (0.00)	17 (100.00)
<i>Body length</i>	<i>1 (100.00)</i>	<i>6 (85.71)</i>	<i>18 (100.00)</i>
S	0 (0.00)	6 (100.00)	0 (0.00)
M	0 (0.00)	0 (0.00)	1 (5.56)
L	1 (100.00)	0 (0.00)	8 (44.44)
VL	0 (0.00)	0 (0.00)	9 (50.00)

Appendix S3a (South America). Cont ...

	Viperidae (53)	Elapidae (56)	Colubridae (559)
<i>Habitat</i>	53 (100.00)	55 (98.21)	502 (89.80)
Op	8 (15.09)	6 (10.91)	93 (18.53)
Bo	19 (35.85)	25 (45.45)	157 (31.27)
Cl	26 (49.06)	24 (43.64)	252 (50.20)
<i>Habit</i>	53 (100.00)	42 (75.00)	496 (88.73)
aq	0 (0.00)	2 (4.76)	28 (5.65)
saq	0 (0.00)	1 (2.38)	12 (2.42)
fo	0 (0.00)	3 (7.14)	48 (9.68)
cfo	0 (0.00)	12 (28.57)	133 (26.81)
cr	0 (0.00)	4 (9.52)	17 (3.43)
cte	0 (0.00)	19 (45.24)	33 (6.65)
te	43 (81.13)	1 (2.38)	145 (29.23)
sar	2 (3.77)	0 (0.00)	39 (7.86)
ar	8 (15.09)	0 (0.00)	41 (8.27)
<i>Diel activity</i>	34 (64.15)	39 (69.64)	329 (58.86)
D	1 (2.94)	5 (12.82)	157 (47.72)
DN	7 (20.59)	12 (30.77)	58 (17.63)
N	26 (76.47)	22 (56.41)	114 (34.65)
<i>Reproduction</i>	53 (100.00)	56 (100.00)	504 (90.16)
O	2 (3.77)	56 (100.00)	463 (91.87)
OV	0 (0.00)	0 (0.00)	4 (0.79)
V	51 (96.23)	0 (0.00)	37 (7.34)
<i>Diet</i>	32 (60.38)	35 (62.50)	304 (54.38)
goo	0 (0.00)	0 (0.00)	55 (18.09)
art	0 (0.00)	2 (5.71)	12 (3.95)
fis	0 (0.00)	4 (11.43)	26 (8.55)
amp	14 (43.75)	3 (8.57)	141 (46.38)
rep	15 (46.88)	31 (88.57)	122 (40.13)
bir	2 (6.25)	0 (0.00)	10 (3.29)
mam	29 (90.63)	0 (0.00)	26 (8.55)
<i>Body length</i>	53 (100.00)	55 (98.21)	483 (86.40)
S	1 (1.89)	6 (10.91)	174 (36.02)
M	21 (39.62)	31 (56.36)	195 (40.37)
L	26 (49.06)	18 (32.73)	94 (19.46)
VL	5 (9.43)	0 (0.00)	20 (4.14)

Appendix S3b (Australia)

Biological structure of the Australian snake fauna decomposed through six families, six biological dimensions (in italic), and distributed in twenty seven biological attributes. The numbers of species in each biological dimension refer to the sample size and are followed by their respective adequacy (percentage of the total fauna, within parentheses). The prevalence of each biological attribute is presented as the number of species and its proportion within the respective biological dimension (percentage of the number of species sampled). Diet percentages do not sum 100% because categories are not mutually exclusive. See the text for abbreviations.

	Typhlopidae (39)	Pythonidae (13)	Acrochordidae (2)
<i>Habitat</i>	38 (97.44)	13 (100.00)	2 (100.00)
Op	31 (81.58)	6 (46.15)	0 (0.00)
Bo	6 (15.79)	5 (38.46)	2 (100.00)
Cl	1 (2.63)	2 (15.38)	0 (0.00)
<i>Habit</i>	39 (100.00)	13 (100.00)	2 (100.00)
aq	0 (0.00)	0 (0.00)	2 (100.00)
saq	0 (0.00)	1 (7.69)	0 (0.00)
fo	39 (100.00)	0 (0.00)	0 (0.00)
cfo	0 (0.00)	0 (0.00)	0 (0.00)
cr	0 (0.00)	0 (0.00)	0 (0.00)
cte	0 (0.00)	0 (0.00)	0 (0.00)
te	0 (0.00)	8 (61.54)	0 (0.00)
sar	0 (0.00)	3 (23.08)	0 (0.00)
ar	0 (0.00)	1 (7.69)	0 (0.00)
<i>Diel activity</i>	39 (100.00)	13 (100.00)	2 (100.00)
D	0 (0.00)	0 (0.00)	0 (0.00)
DN	0 (0.00)	1 (7.69)	0 (0.00)
N	39 (100.00)	12 (92.31)	2 (100.00)
<i>Reproduction</i>	39 (100.00)	13 (100.00)	2 (100.00)
O	39 (100.00)	13 (100.00)	0 (0.00)
V	0 (0.00)	0 (0.00)	2 (100.00)
<i>Diet</i>	39 (100.00)	13 (100.00)	2 (100.00)
art	39 (100.00)	0 (0.00)	0 (0.00)
fis	0 (0.00)	0 (0.00)	2 (100.00)
amp	0 (0.00)	1 (7.69)	0 (0.00)
rep	0 (0.00)	7 (53.85)	0 (0.00)
bir	0 (0.00)	4 (30.77)	0 (0.00)
mam	0 (0.00)	9 (69.23)	0 (0.00)
<i>Body length</i>	39 (100.00)	13 (100.00)	2 (100.00)
S	35 (89.74)	0 (0.00)	0 (0.00)
M	4 (10.26)	2 (15.38)	0 (0.00)
L	0 (0.00)	4 (30.77)	1 (50.00)
VL	0 (0.00)	7 (53.85)	1 (50.00)

Appendix S3b (Australia). Cont ...

	Elapidae (97)	Homalopsidae (5)	Colubridae (5)
<i>Habitat</i>	<i>97 (100.00)</i>	<i>5 (100.00)</i>	<i>5 (100.00)</i>
Op	74 (76.29)	0 (0.00)	0 (0.00)
Bo	22 (22.68)	1 (20.00)	5 (100.00)
Cl	1 (1.03)	4 (80.00)	0 (0.00)
<i>Habit</i>	<i>96 (98.97)</i>	<i>5 (100.00)</i>	<i>5 (100.00)</i>
aq	0 (0.00)	5 (100.00)	1 (20.00)
saq	0 (0.00)	0 (0.00)	0 (0.00)
fo	17 (17.71)	0 (0.00)	0 (0.00)
cfo	2 (2.08)	0 (0.00)	0 (0.00)
cr	13 (13.54)	0 (0.00)	0 (0.00)
cte	11 (11.46)	0 (0.00)	0 (0.00)
te	47 (48.96)	0 (0.00)	1 (20.00)
sar	6 (6.25)	0 (0.00)	0 (0.00)
ar	0 (0.00)	0 (0.00)	3 (60.00)
<i>Diel activity</i>	<i>96 (98.97)</i>	<i>5 (100.00)</i>	<i>5 (100.00)</i>
D	29 (30.21)	0 (0.00)	2 (40.00)
DN	13 (13.54)	0 (0.00)	1 (20.00)
N	54 (56.25)	5 (100.00)	2 (40.00)
<i>Reproduction</i>	<i>97 (100.00)</i>	<i>5 (100.00)</i>	<i>5 (100.00)</i>
O	58 (59.79)	0 (0.00)	5 (100.00)
V	39 (40.21)	5 (100.00)	0 (0.00)
<i>Diet</i>	<i>94 (96.91)</i>	<i>5 (100.00)</i>	<i>5 (100.00)</i>
art	0 (0.00)	2 (40.00)	0 (0.00)
fis	5 (5.32)	4 (80.00)	0 (0.00)
amp	16 (17.02)	1 (20.00)	4 (80.00)
rep	85 (90.43)	0 (0.00)	2 (40.00)
bir	7 (7.45)	0 (0.00)	1 (20.00)
mam	21 (22.34)	0 (0.00)	1 (20.00)
<i>Body length</i>	<i>97 (100.00)</i>	<i>5 (100.00)</i>	<i>5 (100.00)</i>
S	31 (31.96)	2 (40.00)	0 (0.00)
M	45 (46.39)	3 (60.00)	2 (40.00)
L	19 (19.59)	0 (0.00)	3 (60.00)
VL	2 (2.06)	0 (0.00)	0 (0.00)

Appendix S4a

Local snake assemblages in close/forested and open habitats from South America, coordinates, and species richness (S).

	Coordinates	S	References
SOUTH AMERICA			
Close habitat			
Parque Nacional da Serra dos Órgãos, RJ. Brazil	22°29'S, 43°04'W	56	(Levandreira-Gonçalves <i>et al.</i> , 2007; Barros-Filho, 2008)
Viçosa, MG. Brazil	20°45'S, 42°52'W	34	(Costa <i>et al.</i> , 2010)
Estação Ecológica de Juréia-Itatins, SP. Brazil	24°20'S, 47°15'W	32	(Marques & Sazima, 2004)
Reserva Florestal Adolpho Ducke, AM. Brazil	03°08'S, 59°52'W	52	(Martins & Oliveira, 1998)
Espigão do Oeste, RO. Brazil	11°30'S, 60°40'W	56	(Bernarde & Abe, 2006)
Open habitat			
Los Colorados Biological Station and Campo Grande, Western Chaco. Argentina	24°41'S, 63°18'W	21	(Leynaud & Bucher, 2001)
APA Gama Cabeça de Veado, DF. Brazil	15°56'S, 47°53'W	37	(Colli <i>et al.</i> , 2011)
RPPN Acurizal, MS. Brazil	17°49'S, 57°33'W	41	(Kawashita-Ribeiro, 2007)
Exu, PE. Brazil	07°25'S, 40°10'W	19	(Vitt & Vangilder, 1983)
Santa Maria, RS. Brazil	29°44'S, 53°45'W	24	(Winck <i>et al.</i> , 2007)
Jalapão, TO. Brazil	10°32'S, 46°25'W	46	(Vitt <i>et al.</i> , 2005)

Appendix S4b

Local snake assemblages in close/forested and open habitats from Australia, coordinates, and species richness (S).

	Coordinates	S	References
AUSTRALIA			
Close habitat			
Conway National Park, Qld	20°15'S, 148°45'E	13	(Department of Environment and Heritage Protection, 2013)
Eungella National Park, Qld	20°51'S, 148°39'E	11	(Department of Environment and Heritage Protection, 2013)
Kutini-Payamu (Iron Range) National Park, Qld	12°39'S, 143°20'E	15	(Department of Environment and Heritage Protection, 2013)
Daintree National Park, Qld	15°57'S, 145°24'E	15	(Department of Environment and Heritage Protection, 2013)
Barron Gorge National Park, Qld	16°50'S, 145°39'E	3	(Department of Environment and Heritage Protection, 2013)
Open habitat			
Areas L, R and B (Pianka's sites in the Victoria Desert), WA	28°12'S, 123°35'E	15	This study, and E.R.Pianka unpub. data
Bulleringa National Park, Qld	17°34'S, 143°49'E	2	(Department of Environment and Heritage Protection, 2013)
Blackbraes National Park, Qld	19°28'S, 144°10'E	2	(Department of Environment and Heritage Protection, 2013)
Bladensburg National Park, Qld	22°30'S, 142°59'E	8	(Department of Environment and Heritage Protection, 2013)
White Mountains National Park, Qld	20°21'S, 144°42'E	5	(Department of Environment and Heritage Protection, 2013)
Camooweal Caves National Park, Qld	20°01'S, 138°10'E	1	(Department of Environment and Heritage Protection, 2013)

Appendix S4c. References used in Appendices S4a and S4b, local snake assemblages in close/forested and open habitats from South America and Australia, coordinates, and species richness (S).

- Barros-Filho, J.D. (2008) Répteis do Parque Nacional da Serra dos Órgãos: novos registros, comentários e perspectivas. *Revista Espaço Geográfico*, **11**, 73-86.
- Bernarde, P.S. & Abe, A.S. (2006) A snake community at Espigão do Oeste, Rondônia, southwestern Amazon, Brazil. *South American Journal of Herpetology*, **1**, 102-113.
- Colli, G.R., Nogueira, C.C., Pantoja, D.L., Costa, B.M., Ledo, R.M.D. & Brandão, R.A. (2011) Herpetofauna da Reserva Ecológica do IBGE e seu entorno. *Reserva Ecológica do IBGE: Biodiversidade Terrestre* (ed. by M.L. Ribeiro), pp. 133-145. IBGE, Rio de Janeiro.
- Costa, H.C., Pantoja, D.L., Pontes, J.L. & Feio, R.N. (2010) Snakes of the municipality of Viçosa, Atlantic Forest of southeastern Brazil. In: *Biota Neotropica*, pp. 353-377.
<http://www.biotaneotropica.org.br/v10n3/en/abstract?inventory+bn03610032010>.
- Department of Environment and Heritage Protection (2013) The State of Queensland. In: Available at <http://www.ehp.qld.gov.au/wildlife/wildlife-online>. Captured in 08 November 2013
- Kawashita-Ribeiro, R.A. (2007) História natural de uma taxocenose de serpentes da RPPN Acurizal e áreas adjacentes, Serra do Amolar, borda Oeste do Pantanal, Corumbá, Mato Grosso do Sul, Brasil. In, p. 137
- Levandeira-Gonçalves, M.A.P., Aguiar, F.V.O., Camargo, J.V.C., Barros-Filho, J.D. & Carvalho-e-Silva, S.P. (2007) Levantamento preliminar da fauna de répteis do Parque Nacional da Serra dos Órgãos. In: *Ciência e Conservação na Serra dos Órgãos* eds. C. Cronemberger and E.B. Viveiros-De-Castro), pp. 135-153. Instituto Chico Mendes de Conservação da Biodiversidade, Brasília.
- Leynaud, G.C. & Bucher, E.H. (2001) Composition, relative abundance and activity patterns of the snake fauna of Los Colorados biological station (Western Chaco of Argentina). *Boletín de la Academia Nacional de Ciencias*, **66**, 125-132.
- Marques, O.A.V. & Sazima, I. (2004) Historia Natural dos Répteis da Estação Ecológica Juréia-Itatins. *Estação Ecológica Juréia-Itatins, ambiente físico, flora e fauna* (ed. by O.a.V. Marques and W. Duleba), pp. 257-277. Holos.
- Martins, M. & Oliveira, M.E. (1998) Natural history of snakes in tropical forests of the Manaus region, Central Amazônia, Brazil. *Herpetological Natural History*, **6**, 78-150.
- Vitt, L.J. & Vangilder, L.D. (1983) Ecology of a snake community in northeastern Brazil. *Amphibia-Reptilia*, 273 - 296.
- Vitt, L.J., Caldwell, J.P., Colli, G.R., Garda, A.A., Mesquita, D.O., França, F.G.R., Shepard, D.B., Costa, G.C., Vasconcellos, M.M. & Silva, V.N. (2005) Uma atualização do guia fotográfico dos répteis e anfíbios da região do Jalapão no Cerrado brasileiro. *Special Publications in Herpetology, Sam Noble Oklahoma Museum of Natural History*, **2**, 1-24.
- Winck, G.R., dos Santos, T.G. & Cechin, S.Z. (2007) Snake assemblage in a disturbed grassland environment in Rio Grande do Sul State, southern Brazil: population fluctuations of *Liophis poecilogyrus* and *Pseudablables agassizii*. *Annales Zoologici Fennici*, **44**, 321-332.

Appendix S5a

Taxonomic structure of the South American inland snake fauna, number of species and genera, and the taxonomic dominance among clades (percentages in *italic*).

	Genera		Species	
SCOLECOPHIDIA	9	<i>8.4</i>	64	<i>8.4</i>
Anomalepididae	4	<i>3.7</i>	15	<i>2.0</i>
Leptotyphlopidae	4	<i>3.7</i>	42	<i>5.5</i>
Epictinae	4	<i>3.7</i>	42	<i>5.5</i>
Epictini	4	<i>3.7</i>	42	<i>5.5</i>
Typhlopidae	1	<i>0.9</i>	7	<i>0.9</i>
"South American Typhlopidae"	1	<i>0.9</i>	7	<i>0.9</i>
ALETHINOPHIDIA	98	<i>91.6</i>	694	<i>91.6</i>
AMEROPHIDIA / ANILIOIDEA	3	<i>2.8</i>	8	<i>1.1</i>
Aniliidae	1	<i>0.9</i>	1	<i>0.1</i>
Tropidophiidae	2	<i>1.9</i>	7	<i>0.9</i>
AFROPHIDIA	96	<i>89.7</i>	686	<i>90.5</i>
HENOPHIDIA / BOOIDEA	5	<i>4.7</i>	18	<i>2.4</i>
Boidae	5	<i>4.7</i>	18	<i>2.4</i>
Boinae	4	<i>3.7</i>	17	<i>2.2</i>
Ungaliophiinae	1	<i>0.9</i>	1	<i>0.1</i>
CAENOPHIDIA	90	<i>84.1</i>	668	<i>88.1</i>
Viperidae	6	<i>5.6</i>	53	<i>7.0</i>
Crotalinae	6	<i>5.6</i>	53	<i>7.0</i>
"New World Crotalinae"	6	<i>5.6</i>	53	<i>7.0</i>
Elapidae	2	<i>1.9</i>	56	<i>7.4</i>
Elapinae	2	<i>1.9</i>	56	<i>7.4</i>
Calliophini	2	<i>1.9</i>	56	<i>7.4</i>
Colubridae	82	<i>76.6</i>	559	<i>73.7</i>
Colubrinae	16	<i>15.0</i>	75	<i>9.9</i>
Dipsadinae	22	<i>20.6</i>	210	<i>27.7</i>
"Atractus clade"	2	<i>1.9</i>	133	<i>17.5</i>
Dipsadini	5	<i>4.7</i>	43	<i>5.7</i>
Imantodini	2	<i>1.9</i>	8	<i>1.1</i>

Dipsadinae <i>Incertae sedis</i>	13	12.1	26	3.4
Sibynophiinae	1	0.9	2	0.3
Scaphiodontophiini	1	0.9	2	0.3
Xenodontinae	41	38.3	270	35.6
Amnesteophiini	1	0.9	1	0.1
Caeteboiini	1	0.9	1	0.1
Echinantherini	3	2.8	16	2.1
Elapomorphini	4	3.7	49	6.5
Hydrodynastini	1	0.9	3	0.4
Hydropsini	3	2.8	22	2.9
Philodryadini	2	1.9	21	2.8
Pseudoboini	11	10.3	46	6.1
Psomophiini	1	0.9	3	0.4
Saphenophiini	2	1.9	6	0.8
Tachymenini	7	6.5	34	4.5
Tropidodryadini	1	0.9	2	0.3
Xenodontini	3	2.8	63	8.3
Xenodontinae <i>Incertae sedis</i>	1	0.9	3	0.4
Colubridae <i>Incertae sedis</i>	2	1.9	2	0.3

Total Fauna	107	758
--------------------	------------	------------

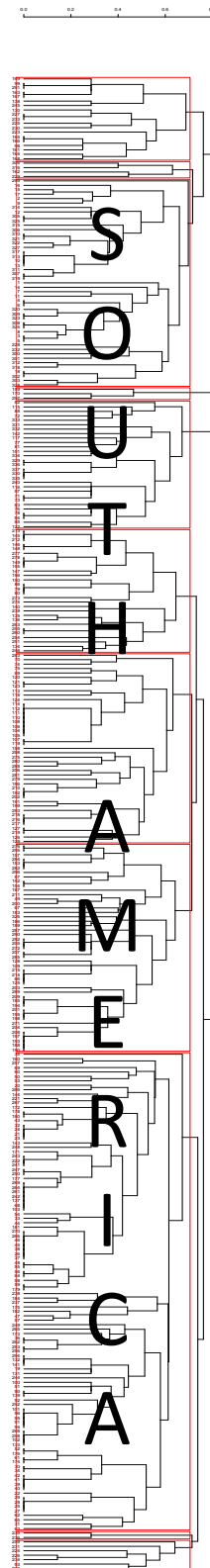
Quotation marks are informal names referring to unnamed clades.

Appendix S5b

Taxonomic structure of the Australian inland snake fauna, number of species and genera, and the taxonomic dominance among clades (percentages in italic).

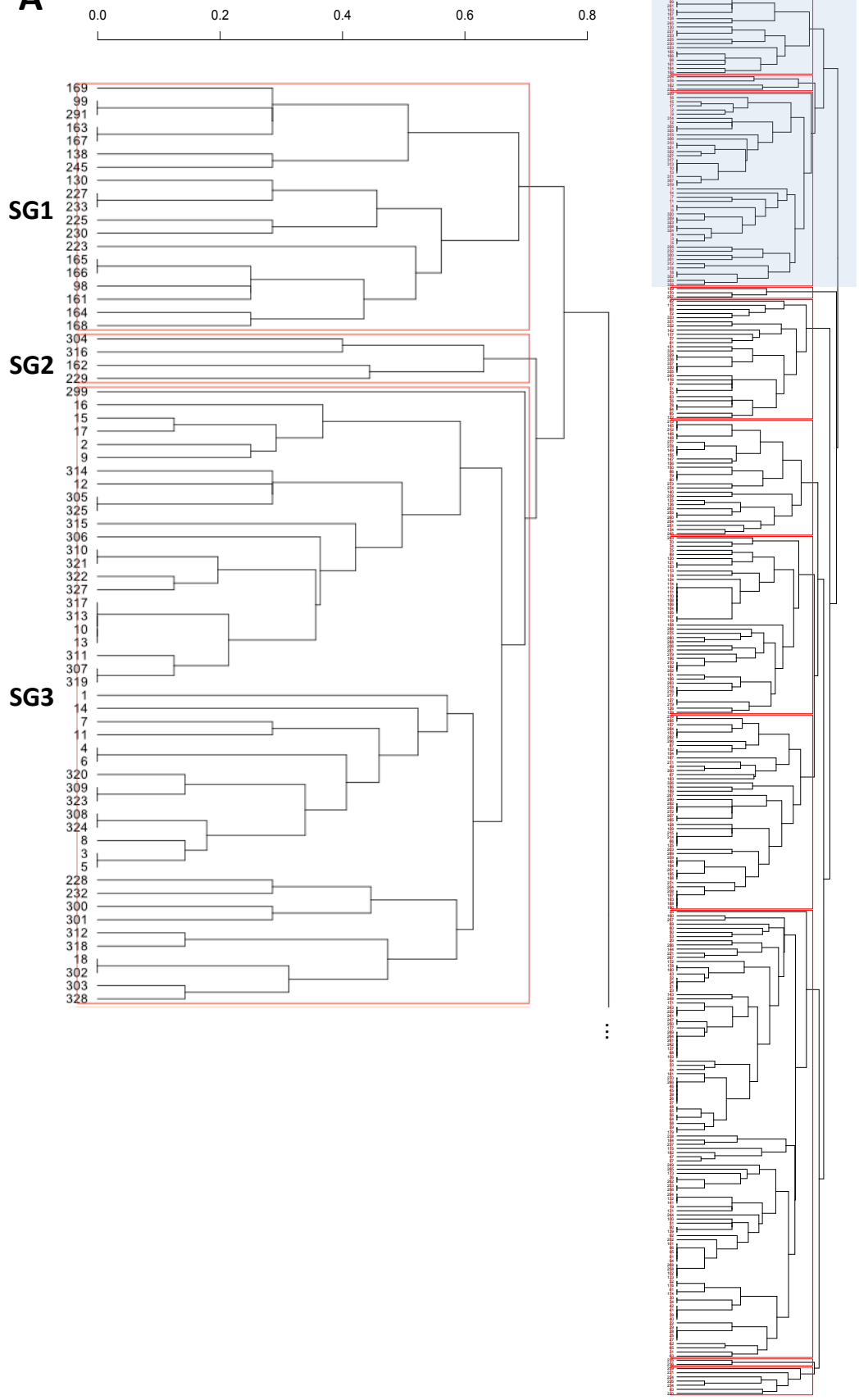
	Genera		Species	
SCOLECOPHIDIA	1	<i>2.5</i>	39	<i>24.2</i>
Typhlopidae	1	<i>2.5</i>	39	<i>24.2</i>
"Australian Typhlopidae"*	1	<i>2.5</i>	39	<i>24.2</i>
ALETHINOPHIDIA	39	<i>97.5</i>	122	<i>75.8</i>
AFROPHIDIA	39	<i>97.5</i>	122	<i>75.8</i>
HENOPHIDIA / BOOIDEA	4	<i>10.0</i>	13	<i>8.1</i>
Pythonidae	4	<i>10.0</i>	13	<i>8.1</i>
CAENOPHIDIA	35	<i>87.5</i>	109	<i>67.7</i>
Acrochordidae	1	<i>2.5</i>	2	<i>1.2</i>
Elapidae	26	<i>65.0</i>	97	<i>60.2</i>
Hydrophiinae (non-marine)	26	<i>65.0</i>	97	<i>60.2</i>
Homalopsidae	4	<i>10.0</i>	5	<i>3.1</i>
Colubridae	4	<i>10.0</i>	5	<i>3.1</i>
Colubrinae	3	<i>7.5</i>	4	<i>2.5</i>
Natricinae	1	<i>2.5</i>	1	<i>0.6</i>
Total Fauna	40		161	

* The introduced species *Ramphotyphlops braminus* is not quantified here. Quotation marks are informal names referring to unnamed clades.

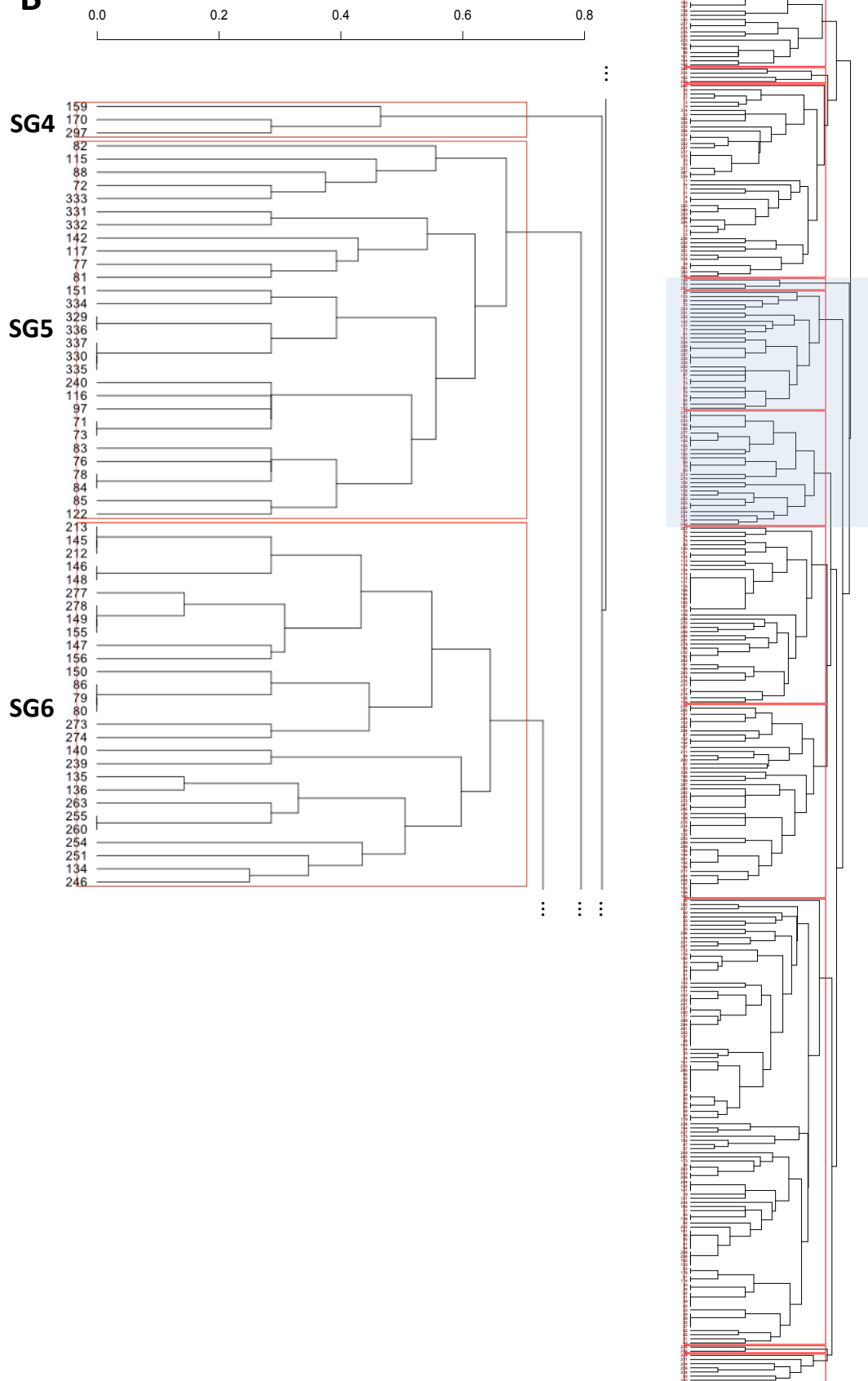


Appendix S6a. Dendrogram from clustering analysis (UPGMA, cophenetic index = 0.677) of South American snakes, based on qualitative biological attributes. The vertical axe shows the distances among cluster centroids calculated by the method “average linkage” upon a distance matrix of dissimilarities of Jaccard. Boxes refer to 11 suggested ecological guilds more cophenetic-distant than 0.70. Ecological similarities within guilds are higher than between guilds.

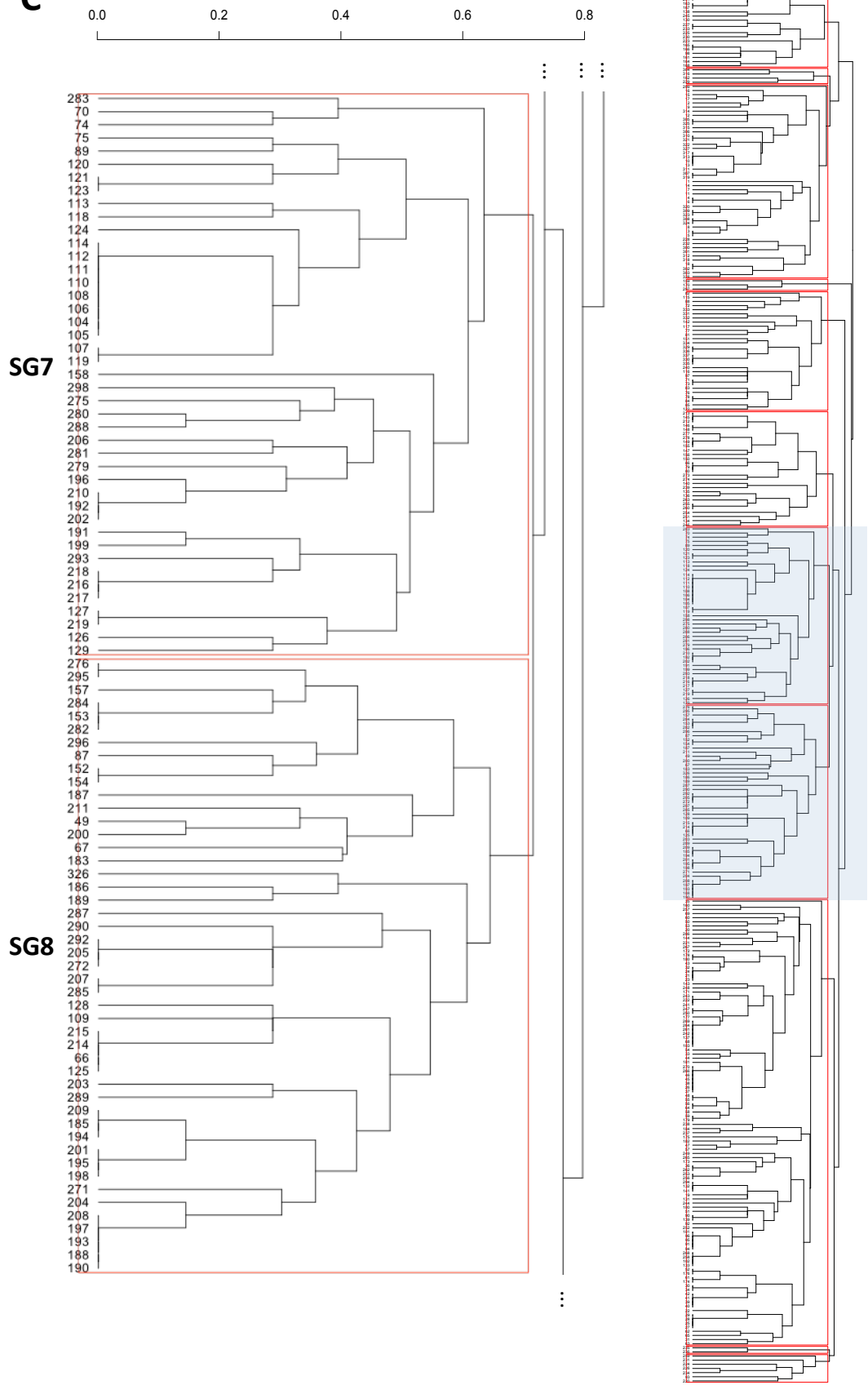
A



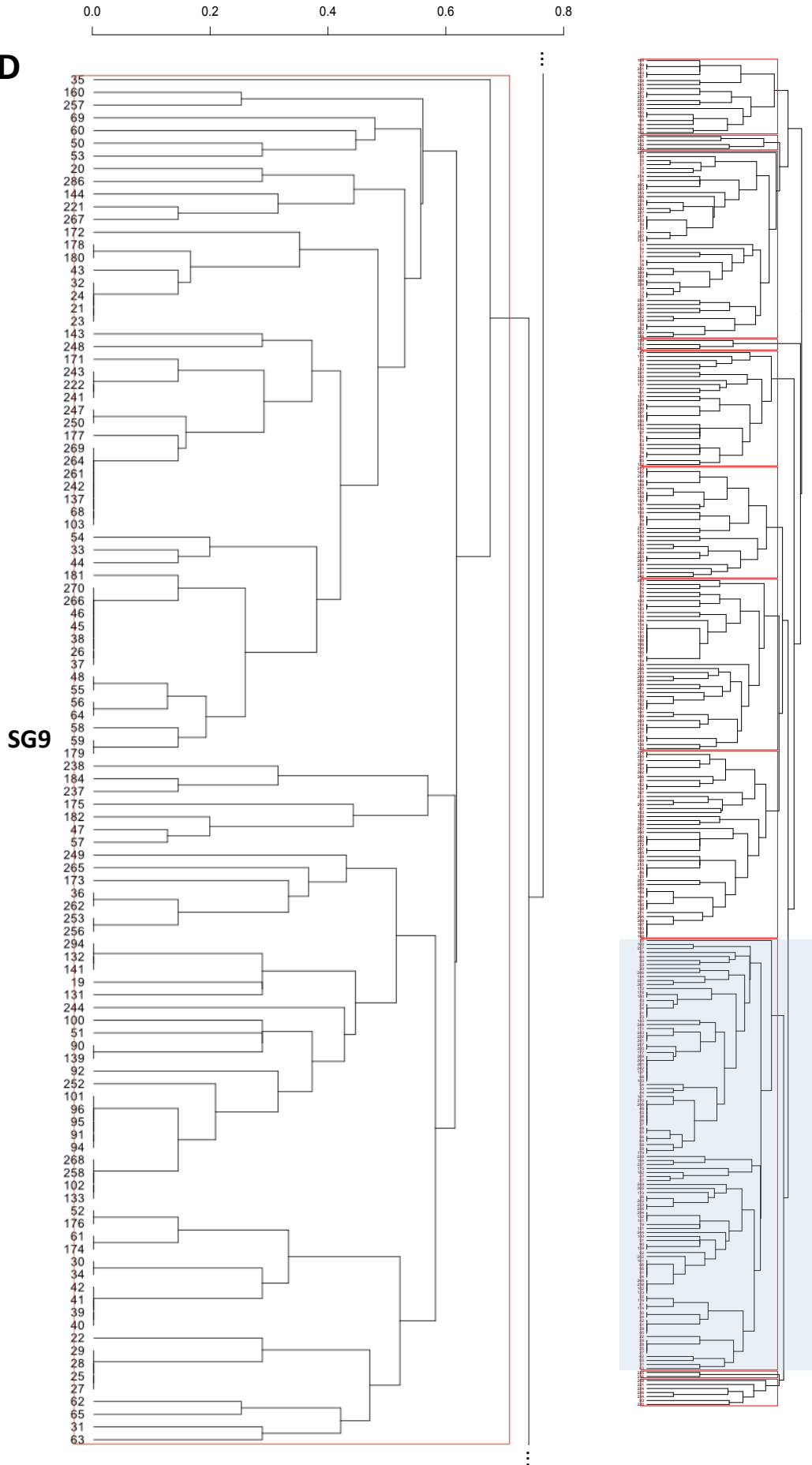
B



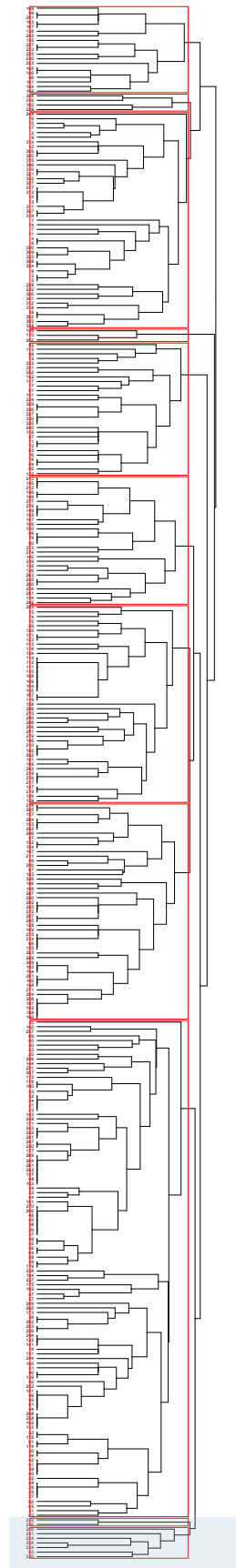
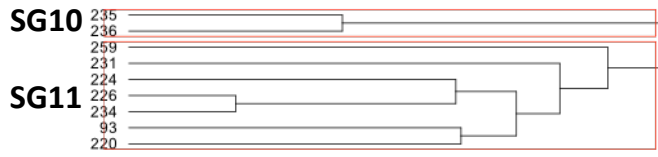
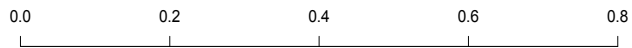
C



D



E



Appendix S6b

List of South American species of snakes used to estimate ecological guilds through cluster analyses (UPGMA).

1) *Anilius scytale*; 2) *Boa constrictor*; 3) *Corallus annulatus*; 4) *Corallus batesii*; 5) *Corallus blombergi*; 6) *Corallus caninus*; 7) *Corallus cropanii*; 8) *Corallus hortulanus*; 9) *Corallus ruschenbergerii*; 10) *Epicrates alvarezi*; 11) *Epicrates assisi*; 12) *Epicrates cenchria*; 13) *Epicrates crassus*; 14) *Epicrates maurus*; 15) *Eunectes deschauenseei*; 16) *Eunectes murinus*; 17) *Eunectes notaeus*; 18) *Ungaliophis panamensis*; 19) *Enuliophis sclateri*; 20) *Enulius flavitorques*; 21) *Chironius bicarinatus*; 22) *Chironius carinatus*; 23) *Chironius exoletus*; 24) *Chironius flavolineatus*; 25) *Chironius foveatus*; 26) *Chironius fuscus*; 27) *Chironius grandisquamis*; 28) *Chironius laeivcollis*; 29) *Chironius laurenti*; 30) *Chironius monticola*; 31) *Chironius multiventris*; 32) *Chironius quadricarinatus*; 33) *Chironius scurrulus*; 34) *Chironius septentrionalis*; 35) *Coluber mentovarius*; 36) *Dendrophidion bivittatum*; 37) *Dendrophidion brunneum*; 38) *Dendrophidion clarkii*; 39) *Dendrophidion dendrophis*; 40) *Dendrophidion graciliverpa*; 41) *Dendrophidion nuchale*; 42) *Dendrophidion percarinatum*; 43) *Drymarchon corais*; 44) *Drymarchon melanurus*; 45) *Drymobius margaritiferus*; 46) *Drymobius rhombifer*; 47) *Drymoluber brazili*; 48) *Drymoluber dichrous*; 49) *Lampropeltis triangulum*; 50) *Leptophis ahaetulla*; 51) *Leptophis cupreus*; 52) *Leptophis depressirostris*; 53) *Leptophis riveti*; 54) *Mastigodryas bifossatus*; 55) *Mastigodryas boddaerti*; 56) *Mastigodryas danieli*; 57) *Mastigodryas heathii*; 58) *Mastigodryas melanolomus*; 59) *Mastigodryas pleei*; 60) *Oxybelis aeneus*; 61) *Oxybelis brevirostris*; 62) *Oxybelis fulgidus*; 63) *Pseustes poecilonotus*; 64) *Pseustes shropshirei*; 65) *Pseustes sulphureus*; 66) *Rhinobothryum bovallii*; 67) *Rhinobothryum lentiginosum*; 68) *Simophis rhinostoma*; 69) *Spilotes pullatus*; 70) *Stenorrhina degenhardtii*; 71) *Tantilla alticola*; 72) *Tantilla melanocephala*; 73) *Tantilla reticulata*; 74) *Tantilla supracincta*; 75) *Atractus albuquerquei*; 76) *Atractus badius*; 77) *Atractus elaps*; 78) *Atractus flammigerus*; 79) *Atractus latifrons*; 80) *Atractus major*; 81) *Atractus occipitoalbus*; 82) *Atractus pantostictus*; 83) *Atractus schach*; 84) *Atractus sneathlageae*; 85) *Atractus tamessari*; 86) *Atractus torquatus*; 87) *Atractus trihedrurus*; 88) *Atractus univittatus*; 89) *Atractus zebrinus*; 90) *Amastridium veliferum*; 91) *Coniophanes fissidens*; 92) *Emmochliophis miops*; 93) *Rhadinaea decorata*; 94) *Synophis bicolor*; 95) *Synophis calamitus*; 96) *Synophis lasallei*; 97) *Synophis plectovertebralis*; 98) *Tretanorhinus nigroluteus*; 99) *Tretanorhinus taeniatus*; 100) *Uromacerina ricardinii*; 101) *Urotheca decipiens*; 102) *Urotheca fulviceps*; 103) *Urotheca lateristriga*; 104) *Dipsas albifrons*; 105) *Dipsas bucephala*; 106) *Dipsas catesbyi*; 107) *Dipsas elegans*; 108) *Dipsas gracilis*; 109) *Dipsas indica*; 110) *Dipsas pavonina*; 111) *Dipsas peruana*; 112) *Dipsas sanctiyoannis*; 113) *Dipsas sazimai*; 114) *Dipsas variegata*; 115) *Ninia atrata*; 116) *Ninia hudsoni*; 117) *Ninia maculata*; 118) *Plesiodipsas perijanensis*; 119) *Sibon dunni*; 120) *Sibon nebulatus*; 121) *Sibynomorphus mikanii*; 122) *Sibynomorphus neuwiedi*; 123) *Sibynomorphus turgidus*; 124) *Sibynomorphus ventrimaculatus*; 125) *Imantodes cenchoa*; 126) *Imantodes gemmistratus*; 127) *Imantodes inornatus*; 128) *Imantodes lentiferus*; 129) *Leptodeira annulata*; 130) *Leptodeira septentrionalis*; 131) *Scaphiodontophis annulatus*; 132) *Scaphiodontophis venustissimus*; 133) *Echianthera amoena*; 134) *Echianthera cephalostriata*; 135) *Echianthera cyanopleura*; 136) *Echianthera melanostigma*; 137) *Echianthera undulata*; 138) *Sordellina punctata*; 139)

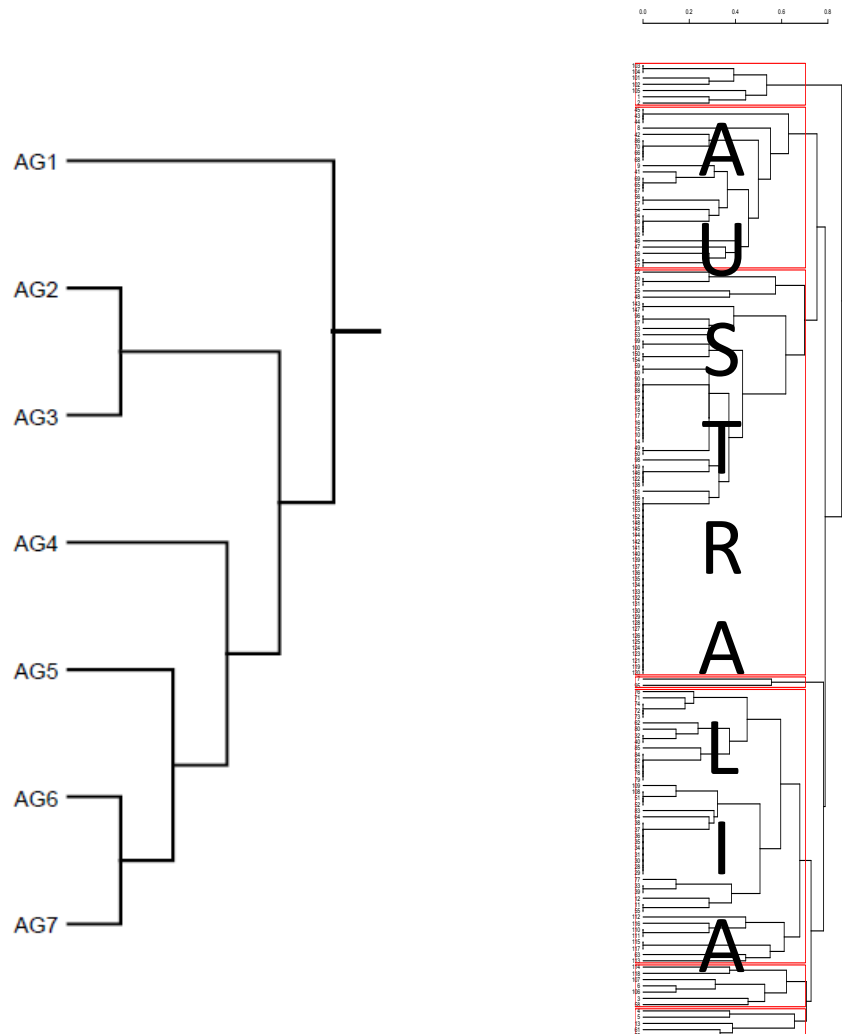
Taeniophallus affinis; 140) *Taeniophallus bilineatus*; 141) *Taeniophallus brevisrostris*; 142) *Taeniophallus nicagus*; 143) *Taeniophallus occipitalis*; 144) *Taeniophallus persimilis*; 145) *Apostolepis albicollaris*; 146) *Apostolepis ammodites*; 147) *Apostolepis assimilis*; 148) *Apostolepis cearensis*; 149) *Apostolepis dimidiata*; 150) *Apostolepis flavotorquata*; 151) *Apostolepis multicincta*; 152) *Coronelaps lepidus*; 153) *Elapomorphus quinquelineatus*; 154) *Elapomorphus wuchereri*; 155) *Phalotris lativittatus*; 156) *Phalotris mertensi*; 157) *Phalotris nasutus*; 158) *Phalotris tricolor*; 159) *Hydrodynastes bicinctus*; 160) *Hydrodynastes gigas*; 161) *Helicops angulatus*; 162) *Helicops carinicaudus*; 163) *Helicops hagmanni*; 164) *Helicops infrataeniatus*; 165) *Helicops leopardinus*; 166) *Helicops modestus*; 167) *Helicops petersi*; 168) *Helicops polylepis*; 169) *Helicops trivittatus*; 170) *Pseudoeryx plicatilis*; 171) *Ditaxodon taeniatus*; 172) *Philodryas aestiva*; 173) *Philodryas agassizii*; 174) *Philodryas argentea*; 175) *Philodryas baroni*; 176) *Philodryas georgeboulengeri*; 177) *Philodryas livida*; 178) *Philodryas mattogrossensis*; 179) *Philodryas nattereri*; 180) *Philodryas olfersii*; 181) *Philodryas patagoniensis*; 182) *Philodryas psammophidea*; 183) *Philodryas trilineata*; 184) *Philodryas viridissima*; 185) *Boiruna maculata*; 186) *Boiruna sertaneja*; 187) *Clelia clelia*; 188) *Clelia equatoriana*; 189) *Clelia plumbea*; 190) *Clelia scytalina*; 191) *Drepanoides anomalus*; 192) *Mussurana bicolor*; 193) *Mussurana montana*; 194) *Mussurana quimi*; 195) *Oxyrhopus clathratus*; 196) *Oxyrhopus fitzingeri*; 197) *Oxyrhopus formosus*; 198) *Oxyrhopus guibei*; 199) *Oxyrhopus leucomelas*; 200) *Oxyrhopus melanogenys*; 201) *Oxyrhopus petolarius*; 202) *Oxyrhopus rhombifer*; 203) *Oxyrhopus trigeminus*; 204) *Paraphimophis rustica*; 205) *Phimophis guerini*; 206) *Phimophis guianensis*; 207) *Pseudoboa coronata*; 208) *Pseudoboa haasi*; 209) *Pseudoboa neuwiedii*; 210) *Pseudoboa nigra*; 211) *Rhachidelus brazilii*; 212) *Rodriguesophis iglesiasii*; 213) *Rodriguesophis scriptorcibatus*; 214) *Siphlophis cervinus*; 215) *Siphlophis compressus*; 216) *Siphlophis leucocephalus*; 217) *Siphlophis longicaudatus*; 218) *Siphlophis pulcher*; 219) *Siphlophis worontzowi*; 220) *Psomophis genimaculatus*; 221) *Psomophis joberti*; 222) *Pseudalsophis elegans*; 223) *Gomesophis brasiliensis*; 224) *Tachymenis peruviana*; 225) *Thamnodynastes chaquensis*; 226) *Thamnodynastes chimanta*; 227) *Thamnodynastes hypoconia*; 228) *Thamnodynastes longicaudus*; 229) *Thamnodynastes nattereri*; 230) *Thamnodynastes pallidus*; 231) *Thamnodynastes ramonriveroi*; 232) *Thamnodynastes rutilus*; 233) *Thamnodynastes strigatus*; 234) *Thamnodynastes yavi*; 235) *Tomodon dorsatus*; 236) *Tomodon ocellatus*; 237) *Tropidodryas serra*; 238) *Tropidodryas striaticeps*; 239) *Xenopholis scalaris*; 240) *Xenopholis undulatus*; 241) *Erythrolamprus aesculapii*; 242) *Erythrolamprus almadensis*; 243) *Erythrolamprus bizona*; 244) *Erythrolamprus breviceps*; 245) *Erythrolamprus ceii*; 246) *Erythrolamprus cobella*; 247) *Erythrolamprus epinephelus*; 248) *Erythrolamprus jaegeri*; 249) *Erythrolamprus maryellenae*; 250) *Erythrolamprus melanotus*; 251) *Erythrolamprus miliaris*; 252) *Erythrolamprus mimus*; 253) *Erythrolamprus mossoroensis*; 254) *Erythrolamprus poecilogyrus*; 255) *Erythrolamprus reginae*; 256) *Erythrolamprus sagittifer*; 257) *Erythrolamprus semiaureus*; 258) *Erythrolamprus taeniogaster*; 259) *Erythrolamprus torrenicola*; 260) *Erythrolamprus typhlus*; 261) *Erythrolamprus viridis*; 262) *Lygophis dilepis*; 263) *Lygophis lineatus*; 264) *Lygophis meridionalis*; 265) *Xenodon dorbignyi*; 266) *Xenodon merremii*; 267) *Xenodon nattereri*; 268) *Xenodon neuwiedii*; 269) *Xenodon rabdocephalus*; 270) *Xenodon severus*; 271) *Leptomicrurus narduccii*; 272) *Micrurus ancoralis*; 273) *Micrurus annellatus*; 274) *Micrurus averyi*; 275) *Micrurus bocourti*; 276) *Micrurus brasiliensis*; 277) *Micrurus corallinus*; 278) *Micrurus decoratus*; 279) *Micrurus dissolucus*; 280) *Micrurus dumerilii*; 281)

Micrurus filiformis; 282) *Micrurus frontalis*; 283) *Micrurus hemprichii*; 284) *Micrurus ibiboboca*; 285) *Micrurus isozonus*; 286) *Micrurus langsdorffi*; 287) *Micrurus lemniscatus*; 288) *Micrurus medemi*; 289) *Micrurus mertensi*; 290) *Micrurus mipartitus*; 291) *Micrurus nattereri*; 292) *Micrurus nigrocinctus*; 293) *Micrurus psyches*; 294) *Micrurus putumayensis*; 295) *Micrurus pyrrhocryptus*; 296) *Micrurus spixii*; 297) *Micrurus surinamensis*; 298) *Micrurus tschudii*; 299) *Trachyboa gularis*; 300) *Tropidophis paucisquamis*; 301) *Tropidophis taczanowskyi*; 302) *Bothriechis schlegelii*; 303) *Bothrocophias hyoprora*; 304) *Bothrocophias microphthalmus*; 305) *Bothrops alternatus*; 306) *Bothrops asper*; 307) *Bothrops atrox*; 308) *Bothrops bilineatus*; 309) *Bothrops brazili*; 310) *Bothrops cotiara*; 311) *Bothrops diporus*; 312) *Bothrops erythromelas*; 313) *Bothrops fonsecai*; 314) *Bothrops itapetiningae*; 315) *Bothrops jararaca*; 316) *Bothrops jararacussu*; 317) *Bothrops leucurus*; 318) *Bothrops lutzi*; 319) *Bothrops mattogrossensis*; 320) *Bothrops moojeni*; 321) *Bothrops neuwiedi*; 322) *Bothrops pauloensis*; 323) *Bothrops pirajai*; 324) *Bothrops taeniatus*; 325) *Crotalus durissus*; 326) *Lachesis muta*; 327) *Porthidium lansbergii*; 328) *Porthidium nasutum*; 329) *Liotyphlops albirostris*; 330) *Liotyphlops ternetzii*; 331) *Typhlophis squamosus*; 332) *Epictia diaplocia*; 333) *Epictia tenella*; 334) *Trilepida fuliginosa*; 335) *Trilepida koppesi*; 336) *Trilepida macrolepis*; 337) *Typhlops brongersmianus*.

Appendix S6c

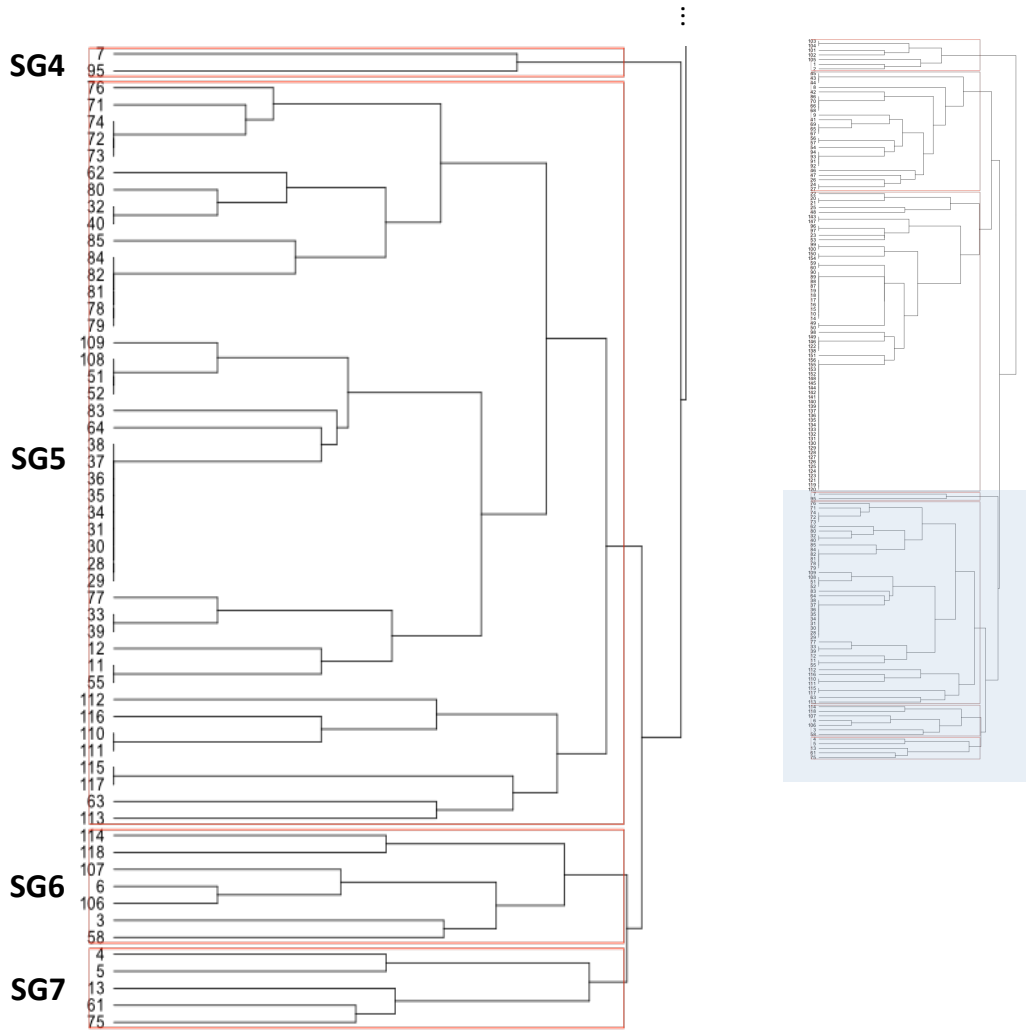
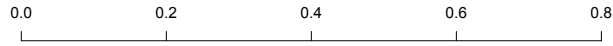
Biological structure of the South American snake fauna based on six biological dimension and eleven ecological guilds (SG1-SG11). The contribution of each biological attribute for each guild is described by its significant indicator values (probability of random distribution among guilds). See the text for biological attribute's abbreviations, and sample size.

	Ecological guilds										
	SG1	SG2	SG3	SG4	SG5	SG6	SG7	SG8	SG9	SG10	SG11
<i>Habitat</i>											
Op										0.12	0.36
Bo	0.07		0.06	0.23				0.05	0.06		
Cl		0.21			0.09		0.06			0.05	
<i>Habit</i>											
aq	0.25			0.46							
saq						0.06					
fo					0.19	0.28					
cfo								0.10			
cr											
cte					0.11						
te		0.06	0.07					0.05	0.07	0.24	0.08
sar		0.07									
ar			0.09				0.14				
<i>Diel activity</i>											
D									0.25	0.25	0.25
DN		0.18		0.14		0.32		0.05			
N	0.21		0.20		0.09		0.22	0.09			
<i>Reproduction</i>											
O				0.07	0.16	0.16	0.16	0.16	0.16		
OV	0.05			0.23							
V	0.07	0.24	0.24							0.24	0.08
<i>Diet</i>											
goo					0.09		0.08			0.44	
art				0.13	0.23						
fis	0.17			0.43							
amp	0.08	0.25				0.05			0.14		0.13
rep		0.14				0.09	0.06	0.19	0.05		0.05
bir			0.10								
mam		0.15	0.39								
<i>Body length</i>											
S					0.40						0.42
M	0.17	0.05				0.11	0.19			0.21	
L			0.07	0.32				0.25			
VL		0.09	0.05								



Appendix S7a. Dendrogram from clustering analysis (UPGMA, cophenetic index = 0.866) of Australian snakes, based on qualitative biological attributes. The vertical axis shows the distances among cluster centroids calculated by the method “average linkage” upon a distance matrix of dissimilarities of Jaccard. Boxes refer to seven suggested ecological guilds more cophenetic-distant than 0.70. Ecological similarities within guilds are higher than between guilds.

G



Appendix S7b

List of Australian species of snakes used to estimate ecological guilds through cluster analyses (UPGMA).

1) *Acrochordus arafurae*; 2) *Acrochordus granulatus*; 3) *Boiga irregularis*; 4) *Dendrelaphis calligastra*; 5) *Dendrelaphis punctulatus*; 6) *Stegonotus cucullatus*; 7) *Tropidonophis mairii*; 8) *Acanthophis antarcticus*; 9) *Acanthophis praelongus*; 10) *Antaioserpens warro*; 11) *Austrelaps labialis*; 12) *Austrelaps ramsayi*; 13) *Austrelaps superbus*; 14) *Brachyuropis approximans*; 15) *Brachyuropis australis*; 16) *Brachyuropis fasciolatus*; 17) *Brachyuropis incinctus*; 18) *Brachyuropis roperi*; 19) *Brachyuropis semifasciatus*; 20) *Cacophis churchilli*; 21) *Cacophis harriettae*; 22) *Cacophis krefftii*; 23) *Cacophis squamulosus*; 24) *Cryptophis boschmai*; 25) *Cryptophis nigrescens*; 26) *Cryptophis nigrostriatus*; 27) *Cryptophis pallidiceps*; 28) *Demansia angusticeps*; 29) *Demansia calodera*; 30) *Demansia flagellatio*; 31) *Demansia olivacea*; 32) *Demansia papuensis*; 33) *Demansia psammophis*; 34) *Demansia quaesitor*; 35) *Demansia rimicola*; 36) *Demansia rufescens*; 37) *Demansia shinei*; 38) *Demansia simplex*; 39) *Demansia torquata*; 40) *Demansia vestigiata*; 41) *Denisonia devisi*; 42) *Denisonia maculata*; 43) *Drysdalia coronoides*; 44) *Drysdalia mastersii*; 45) *Drysdalia rhodogaster*; 46) *Echiopsis curta*; 47) *Elapognathus coronatus*; 48) *Elapognathus minor*; 49) *Furina barnardi*; 50) *Furina diadema*; 51) *Furina dunmalli*; 52) *Furina ornata*; 53) *Furina tristis*; 54) *Hemiaspis damelii*; 55) *Hemiaspis signata*; 56) *Hoplocephalus bitorquatus*; 57) *Hoplocephalus bungaroides*; 58) *Hoplocephalus stephensii*; 59) *Neelaps bimaculatus*; 60) *Neelaps calonotus*; 61) *Notechis scutatus*; 62) *Oxyuranus microlepidotus*; 63) *Oxyuranus scutellatus*; 64) *Oxyuranus temporalis*; 65) *Parasuta dwyeri*; 66) *Parasuta flagellum*; 67) *Parasuta gouldii*; 68) *Parasuta monachus*; 69) *Parasuta nigriceps*; 70) *Parasuta spectabilis*; 71) *Pseudechis australis*; 72) *Pseudechis butleri*; 73) *Pseudechis colletti*; 74) *Pseudechis guttatus*; 75) *Pseudechis porphyriacus*; 76) *Pseudechis weigeli*; 77) *Pseudonaja affinis*; 78) *Pseudonaja aspidorhyncha*; 79) *Pseudonaja guttata*; 80) *Pseudonaja inframacula*; 81) *Pseudonaja ingrami*; 82) *Pseudonaja mengdeni*; 83) *Pseudonaja modesta*; 84) *Pseudonaja nuchalis*; 85) *Pseudonaja textilis*; 86) *Rhinoplocephalus bicolor*; 87) *Simoselaps anomalus*; 88) *Simoselaps bertholdi*; 89) *Simoselaps littoralis*; 90) *Simoselaps minimus*; 91) *Suta fasciata*; 92) *Suta ordensis*; 93) *Suta punctata*; 94) *Suta suta*; 95) *Tropidechis carinatus*; 96) *Vermicella annulata*; 97) *Vermicella intermedia*; 98) *Vermicella multifasciata*; 99) *Vermicella snelli*; 100) *Vermicella vermiformis*; 101) *Cerberus australis*; 102) *Fordonia leucobalia*; 103) *Myron resetari*; 104) *Myron richardsonii*; 105) *Pseudoferania polylepis*; 106) *Antaresia childreni*; 107) *Antaresia maculosa*; 108) *Antaresia perthensis*; 109) *Antaresia stimsoni*; 110) *Aspidites melanocephalus*; 111) *Aspidites ramsayi*; 112) *Liasis mackloti*; 113) *Liasis olivaceus*; 114) *Morelia carinata*; 115) *Morelia kinghorni*; 116) *Morelia oenpelliensis*; 117) *Morelia spilota*; 118) *Morelia viridis*; 119) *Ramphotyphlops affinis*; 120) *Ramphotyphlops ammodytes*; 121) *Ramphotyphlops aspina*; 122) *Ramphotyphlops australis*; 123) *Ramphotyphlops batillus*; 124) *Ramphotyphlops bicolor*; 125) *Ramphotyphlops bituberculatus*; 126) *Ramphotyphlops broomi*; 127) *Ramphotyphlops centralis*; 128) *Ramphotyphlops chamodracaena*; 129) *Ramphotyphlops diversus*; 130) *Ramphotyphlops endoterus*; 131) *Ramphotyphlops ganei*; 132) *Ramphotyphlops grypus*; 133) *Ramphotyphlops guentheri*; 134) *Ramphotyphlops hamatus*; 135) *Ramphotyphlops howi*; 136) *Ramphotyphlops kimberleyensis*; 137) *Ramphotyphlops leptosoma*; 138)

Ramphotyphlops leucoproctus; **139)** *Ramphotyphlops ligatus*; **140)** *Ramphotyphlops margaretae*; **141)** *Ramphotyphlops micromma*; **142)** *Ramphotyphlops minimus*; **143)** *Ramphotyphlops nigrescens*; **144)** *Ramphotyphlops pilbarensis*; **145)** *Ramphotyphlops pinguis*; **146)** *Ramphotyphlops polygrammicus*; **147)** *Ramphotyphlops proximus*; **148)** *Ramphotyphlops robertsi*; **149)** *Ramphotyphlops silvia*; **150)** *Ramphotyphlops splendidus*; **151)** *Ramphotyphlops tovelli*; **152)** *Ramphotyphlops troglodytes*; **153)** *Ramphotyphlops unguirostris*; **154)** *Ramphotyphlops waitii*; **155)** *Ramphotyphlops wiedii*; **156)** *Ramphotyphlops yirrikalae*.

Appendix S7c

Biological structure of the Australian snake fauna based on six biological dimension and seven ecological guilds (AG1-AG7). The contribution of each biological attribute for each guild is described by its significant indicator values (probability of random distribution among guilds). See the text for biological attribute's abbreviations, and sample size.

	Ecological guilds						
	AG1	AG2	AG3	AG4	AG5	AG6	AG7
<i>Habitat</i>							
Op		0.35	0.21		0.21		
Bo	0.05			0.29		0.15	0.18
Cl	0.37					0.09	
<i>Habit</i>							
aq	0.67			0.17			
saq							
fo			0.83				
cfo							
cr		0.42					
cte		0.13					
te				0.09	0.32	0.07	0.13
sar		0.07				0.16	
ar						0.12	0.23
<i>Diel activity</i>							
D					0.14		0.61
DN				0.76	0.06		
N	0.25	0.16	0.24			0.25	
<i>Reproduction</i>							
O			0.26	0.07	0.24	0.20	
OV							
V	0.30	0.30		0.07			0.11
<i>Diet</i>							
goo							
art	0.09		0.39				
fis	0.76						
amp				0.35		0.06	0.35
rep		0.25	0.05		0.23	0.06	0.11
bir						0.35	
mam				0.13	0.13	0.26	
<i>Body length</i>							
S	0.06	0.08	0.48				
M	0.06	0.15		0.35	0.07		
L					0.05	0.44	0.28
VL	0.06				0.12		