UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL - UFRGS

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Tese de Doutorado:

DISTRIBUIÇÃO, NICHO POTENCIAL E ECOLOGIA MORFOLÓGICA DO GÊNERO *ENYALIUS* (SQUAMATA, LEIOSAURIDAE): TESTES DE HIPÓTESES PARA LAGARTOS DE FLORESTAS CONTINENTAIS BRASILEIRAS

ANDRÉ FELIPE BARRETO-LIMA

Porto Alegre - RS

Janeiro de 2012

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL - UFRGS

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

DISTRIBUTION, POTENTIAL NICHE AND MORPHOLOGICAL ECOLOGY OF *ENYALIUS* GENUS (SQUAMATA, LEIOSAURIDAE): HYPOTHESIS TESTS FOR LIZARDS FROM THE BRAZILIAN CONTINENTAL FORESTS

ANDRÉ FELIPE BARRETO-LIMA

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências, da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ciências, com ênfase em Ecologia.

Orientadora: Dra. Sandra Maria Hartz - UFRGS
Co-Orientador: Dr. Guarino Rinaldi Colli - UNB

Comissão Examinadora:
Profa. Dra. Sônia Zanini Cechin - UFSM
Prof. Dr. Alexandro Tozetti - UNISINOS
Prof. Dr. Thales Renato O. de Freitas - UFRGS

Porto Alegre - RS

Janeiro de 2012

CIP - Catalogação na Publicação

Barreto-Lima, André Felipe
Distribuição, nicho potencial e ecologia morfológica do gênero Enyalius (Squamata, Leiosauridae): testes de hipóteses para lagartos de florestas continentais brasileiras / André Felipe Barreto-Lima. -- 2012.
160 f.

Orientadora: Sandra Maria Hartz.
Coorientador: Guarino Rinaldi Colli.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Porto Alegre, BR-RS, 2012.

1. Distribuição geográfica. 2. Ecomorfologia. 3. Enyalius. 4. Lagartos. 5. Nicho potencial. I. Hartz, Sandra Maria, orient. II. Colli, Guarino Rinaldi, coorient. III. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

“Os meus dias começam quando os meus sonhos terminam.

Porque creio que só merece uma chance aquele que sabe aproveitá-la.

Então, você muda, adapta-se, readapta-se, supera-se e consegue chegar lá!

Pois sem sonhos a ‘realidade’ deixaria de fazer sentido.

E quem disse que o sonho não é uma realidade, uma realidade para um sentido …?”

André Felipe Barreto-Lima (2012)

"My day begins when my dreams end.

Because I believe that only deserves a chance that who knows how to seize it.

Then, you change, adapt, readapt, overcome and you can get there!

Without dreams the 'reality' would not make sense.

And who said that the dream is not a reality, a reality for a sense …?"

André Felipe Barreto-Lima (2012)

Dedico aos meus pais,

Carmen Barreto e Nilzo Lima Júnior,

aos meus irmãos: Adriana, Giovanna e Bruno.

E a avó Carmen da Luz Barreto, *in memoriam*.

I dedicate to my parents,

Carmen Barreto and Nilzo Lima Junior,

my sisters and brother: Adriana, Giovanna and Bruno.

And my grandmother Carmen da Luz Barreto, *in memoriam.*

AGRADECIMENTOS

Chegar aqui não foi nada fácil, rápido, tão pouco tranqüilo e se não fosse a colaboração de muitos provavelmente eu não conseguiria. Agradeço a força criadora que tive ‘em presença’ para realizar este trabalho como uma das metas de vida. Aos meus pais e irmãos que mesmo à distância estiveram comigo, apoiando-me. A Sandra Hartz pela orientação, atenção, apoio de recursos e leal amizade durante todo meu processo de amadurecimento acadêmico. A Guarino Colli pela co-orientação e apoio de recursos. A Paula, a “Oma” Ilda, Sheyla, Letícia, família Borowsky, Nadja e Michel, pela ajuda, carinho e incentivo ao longo desses anos de convivência, o meu agradecimento por serem a minha “família do sul”. Aos meus prestativos amigos Leandro, Vagner e a D. Helga que por muitas vezes acolheram-me em Poa. A Isadora pelo encontro, apoio, carinho e importante presença no final do doutorado. Aos tios Ronaldo e Márcia e primos que me apoiaram em Brasília, na fase de levantamento de dados. Aos colegas do CHUNB, a Fabrícius e Ísis pelos comentários estatísticos, a Cristiano Nogueira, Renata e Reuber Brandão pelo auxílio nos modelos potenciais do Capítulo 1. A Bruna Mensese e Karina Amaral pela elaboração dos mapas. A amiga Grazi Yobi e ao colega Jorge que através de conversas e questões veio-me a inspiração para criar o Capítulo 2. Aos colegas Leandro Duarte e Marlon Vasco pela colaboração no Capítulo 3. Aos colegas do LEPC: Jan, André Mendonça, André Lusa, Grasi, Camila, Fernanda, Fernandinha, Ronei, Marcos, Vinícius, Cissa, Denis, e da Pós-Graduação: Álan (*in memorian*), Cecília Nin, Tati, Verônica Sydow, Luciana, Taís, entre outros, pelo apoio, convivência e diálogos construtivos durante esta jornada. Aos professores do PPG-Ecologia, Fernando, Gilberto, Valério, Renato, Paulo, Terezinha, Andréas, Gilson e Adriano pelo aprendizado, vivência, apoio logístico, financeiro e aos funcionários, em especial, a Silvana e a Sônia pelas informações e auxílios do PPG até a minha defesa. Esta pesquisa teve o apoio da CAPES (bolsa de doutoramento). Pessoal, VALEU por esta feliz jornada!!!

RESUMO

No **Capítulo 1,** os principais fatores envolvidos com a distribuição geográfica do gênero *Enyalius* foram a temperatura média anual, a latitude e a amplitude média da temperatura diurna, indicando uma possível adaptação climática do gênero. A variação geográfica na morfologia de *Enyalius* foi observada em sua distribuição, como demonstrado pelas diferenças no tamanho do corpo e nas estruturas morfológicas, que foram explicadas por variáveis climáticas, espaciais e estruturais do ambiente. A regra de Allen foi corroborada com os padrões da variação na morfologia de *Enyalius*, que foram correlacionados com as condições climáticas e geográficas. Os padrões de variação morfológica também foram associados com cobertura vegetal (e provavelmente, à disponibilidade de água nas diferentes regiões), que pode exercer influência sobre a adaptação morfológica de *Enyalius* e explicar parte do crescimento diferencial alométrico sobre a vasta área geográfica. A hipótese de adaptação climática deve ser a base para explicar a distribuição de *Enyalius* em ambientes florestais do Brasil.

No **Capítulo 2,** nós estudamos as áreas de distribuição potencial de cada espécie do grupo e encontramos, para a maioria delas, características ambientais em comum, que foram importantes para a ocorrência do gênero em seus ambientes. A latitude e a amplitude média da temperatura diurna sobrepuseram-se na maioria dos modelos de nicho potencial, ao longo da costa leste brasileira, caracterizando a distribuição principal das espécies de *Enyalius* no domínio Florestal Atlântico. Isso nos indicou um padrão geral de fatores básicos importantes para a ocorrência do grupo neste bioma que, provavelmente, parte dos nichos ecológicos similares entre algumas espécies, em geral, ocorreram por influências ambientais de ampla magnitude, em associação à plasticidade fenotípica das espécies como resposta ecológica adaptativa.

E, no **Capítulo 3,** nós encontramos algumas respostas ecomorfológicas para as espécies de *Enyalius*, havendo padrões morfológicos e ambientais específicos associados, independentemente da relação filogenética ou da proximidade geográfica em que estas se encontram. Acreditamos que as características ambientais e o uso destas, como recursos, devem influenciar mais sobre a ocorrência das espécies em seus hábitats (pressão de seleção natural) do que por uma inércia filogenética herdada ao grupo. Este estudo também indicou que determinadas mudanças evolutivas nas proporções e no tamanho do corpo das espécies de *Enyalius* devem estar associadas à divergência de hábitats e suas características, bem como, ao uso diferente de substratos entre as espécies de lagartos, e que, consequentemente, necessitam de maiores investigações para o melhor conhecimento das causas dessas relações ecológicas verificadas. Por fim, os padrões observados sobre a variação morfológica de *Enyalius* devem ser uma conseqüência direta de respostas adaptativas à ação das condições ambientais locais (e.g. seleção natural), o que por sua vez, nos revelou importantes plasticidade adaptativa e fenotípica das espécies, baseado em suas ecologias diversificadas em variados ambientes florestais do continente.

Palavras-chaves: distribuição geográfica, ecomorfologia, *Enyalius*, lagartos, nicho potencial.

ABSTRACT

In the **First Chapter,** the main factors affecting the *Enyalius*' geographical distribution were the annual mean temperature, latitude and mean diurnal temperature range, which indicated a possible climatic adaptation as a base to explain the group distribution. The morphological geographical variation of *Enyalius* was observed in its distribution, as demonstrated by the differences in the body size and morphological structures, which were explained by climatic, spatial and structural variables. The Allen rule was corroborated, since the patterns in the morphological variation in *Enyalius* were correlated with climatic and geographical conditions. The climatic adaptation hypothesis may be the basis to explain the *Enyalius'* distribution in different Brazilian forests. In the **Second Chapter,** we studied the potential distribution areas for each species of the group, identifying the general environmental characteristics that affected in occurrence of the most species in their habitats. We suggest that latitude and the mean amplitude of daily temperature, along the Brazilian coast east, overlapped in most of models, characterizing the main distribution of the species of *Enyalius* in the Atlantic Forest biome. In the **Third Chapter,** we found that there were morphological and environmental patterns associated with the species, independent of their phylogenetic or geographical relationship. We observed that environmental features seem to be more critical to determine the species occurrence than their evolutionary heritage (phylogenetic inertia). Finally, this study indicated that some evolutionary changes in body size and proportions might be associated to the divergence in habitat requirements, as well as, the differences in substrate use, needing further investigation. We conclude that the morphological variation in *Enyalius* must be a direct consequence of adaptive responses to local environmental conditions, demonstrating important phenotypic plasticity of the species on their ecologies in different forests environment of the mainland.

Keywords: ecomorphology, *Enyalius*, geographic distribution, lizard, potential niche.

LISTA DE FIGURAS / FIGURE CAPTIONS

Capítulo 1 / Chapter 1

Capítulo 2 / Chapter 2

Capítulo 3 / Chapter 3

LISTA DE TABELAS / TABLE CAPTIONS

Capítulo 1 / Chapter 1

Capítulo 2 / Chapter 2

Capítulo 3 / Chapter 3

SUMÁRIO / SUMMARY

INTRODUÇÃO GERAL

Distribuição potencial e nicho ecológico

Estudos macroecológicos têm levado a importantes avanços na compreensão de padrões ecológicos em grande escala, embora as suas causas ainda necessitem de melhores explicações (Hawkins 2004). Algumas das características ecológicas mais importantes observadas na macroecologia são os gradientes climáticos e latitudinais de espécies. Desta forma, os modelos ecológicos desenvolvidos pressupõem que os padrões observados são conseqüências da influência do clima sobre as distribuições geográficas das espécies (Terribili 2009). De fato, os fatores que afetam a distribuição geográfica dos organismos incluem como estes estão relacionados com seus ambientes e às suas interações interespecíficas (Costa *et al.* 2008).

No que se refere aos modelos de nichos ambientais ou ecológicos, estes constituem métodos que usam dados de ocorrências e ambientais, para estabelecer um modelo de correlação das condições ambientais que encontra os requerimentos ecológicos adequados de uma espécie em um dado hábitat. Nas décadas recentes houve um interesse maior em estudos de distribuições de espécies através da modelagem de nicho potencial (Elith *et al.* 2006), o que pode ser explicado pela urgência de se conhecer a distribuição atual da biodiversidade no planeta. Assim, a modelagem tem sido uma ferramenta eficiente e útil para extrapolação de dados sobre a distribuição potencial das espécies no espaço e tempo, baseada em modelos estatísticos que usam diferentes tipos de algoritmos, tornando-se importante quando aplicada à Biologia da Conservação (Flanklin 2009).

Dada a importância do conhecimento da distribuição das espécies para a conservação, o monitoramento das mudanças climáticas e a avaliação contínua de modelos estatísticos, prevendo a distribuição de espécies, tornam-se necessários (Austin 2007). Uma forma direta e rápida para se acessar dados é através do refinamento de informações relevantes presentes em coleções científicas, que são utilizadas em estudos para se mapear as distribuições de espécies ou determinar áreas importantes à conservação destas (Ponder *et al.* 2001, Graham 2004, Elith & Leathwick 2007). Dependendo dos objetivos do trabalho, a aquisição de dados das espécies na literatura também pode ser um rápido método de acesso e uma fonte de melhor qualidade do que os dados de museus ou eletrônicos, que ocasionalmente contém erros taxonômicos.

Na ecologia, de forma geral, os répteis são considerados modelos em estudos ecológicos, inclusive, no que diz respeito às características dos efeitos climáticos e ambientais sobre a distribuição das espécies (Costa *et al.* 2008). Entre os Squamata, a influência de fatores ambientais bióticos e abióticos sobre os parâmetros da história de vida tem sido relatada através de estudos sobre variação e distribuição geográfica de espécies de lagartos (Mesquita & Colli 2003).

Variação geográfica e climática na morfologia

A predição de que a variação morfológica é relacionada com as características ambientais tem sido de interesse de ecólogos e biólogos evolutivos (Luxbacher & Knouft 2009). Dentro da distribuição geográfica de um táxon, as forças potenciais que explicam a variabilidade morfológica incluem diferentes tipos de presas, pressão de predação (Schneider *et al.* 1999), efeitos do clima, além de outros fatores ambientais sobre as razões de crescimento das espécies (Schäuble 2004).

Em geral, um componente da variação morfológica de uma espécie está mais relacionado à variabilidade climática, que é um importante fator para se entender a adaptação, distribuição, os mecanismos de diversificação e as respostas às mudanças globais (Millien *et al.* 2006). Porém, poucos trabalhos têm considerado a extensão de quais características morfológicas podem estar associadas a quais características ambientais, em amplas áreas geográficas (Luxbacher & Knouft 2009), onde poderiam explicar as causas da variação geográfica na morfologia das espécies, seja por fatores ecológicos adaptativos "atuais" ou históricos, no contexto evolutivo (i.e., filogenético).

A observação de que a forma do corpo dos organismos (morfologia) varia com a latitude é tão antiga quanto a percepção de um gradiente geográfico de diversidade de espécies (Blackburn *et al.* 1999). Assim, entende-se que o fator geográfico da latitude também pode estar associado à variação morfológica das espécies, pois este está relacionado ao clima de uma área e pode influenciar geograficamente o clima de uma região. O tamanho do corpo é uma das características mais importantes dos organismos (Rodríguez *et al.* 2006), onde muitos aspectos da vida destes sofrem influencia do tamanho do corpo na interação com o ambiente abiótico, nas taxas dos processos fisiológicos ou nas suas interações com outros organismos (Cushman *et al.* 1993, Terribile 2009). Ademais, o tamanho do corpo e das suas extremidades tende a seguir alguns padrões ecogeográficos como as regras clássicas de Bergmann (1847) e de Allen (1877) (Bidau & Marti 2008).

Inicialmente, Carl Bergmann observou que nos vertebrados endotérmicos, as espécies de regiões temperadas possuíam tamanho do corpo maior do que os seus parentes de regiões tropicais (ver James 1970). A explicação dele para tal padrão foi que as espécies maiores possuíam uma menor razão de superfície/volume corporal.

E tais espécies conseguiam armazenar mais calor com maior eficiência em regiões frias do que as espécies pequenas, enquanto que estas últimas apresentavam uma maior razão de superfície/volume, sendo mais eficiente em regiões quentes para dissipar calor corpóreo ao ambiente, evitando o 'estresse térmico' interno. Assim, a regra de Bergmann (1847) foi pioneiramente validada aos organismos endotérmicos, predizendo que o tamanho do corpo estaria correlacionado positivamente a latitude e a altitude, e negativamente a temperatura ambiente, como confirmado depois (e.g. James 1970, Blackburn & Gaston 1996, Blackburn *et al.* 1999, Blackburn & Hawkins 2004, Rodriguéz *et al.* 2006, Pincheira-Donoso *et al.* 2007, Luxbacher & Knouft 2009). Contudo, aparente suporte para esta teoria tem sido observado em ectotérmicos, tanto vertebrados como invertebrados (Ray 1960, Lindsey 1966, Cushman *et al.* 1993, Ashton 2002, Ashton & Feldman 2003, Morrison & Hero 2003, Angilletta *et al.* 2004, Cruz *et al.* 2005).

Porém, há divergências entre grupos de ectotérmicos, que podem ou não responder a regra, e também quanto ao nível taxonômico adotado no estudo deste padrão, ou seja, inter ou intra-específico. Bergmann originalmente sugeriu um padrão latitudinal no tamanho de espécies aparentadas, mas alguns autores discordaram, pois o padrão deveria ser um fenômeno apenas intra-específico (Mayr 1956). Provavelmente ele pensou que sua hipótese seria aplicada principalmente para espécies congêneres do que para grupos taxonômicos maiores (Meiri & Thomas 2007), como há gêneros que as espécies diferem no tamanho, onde as espécies menores requerem um clima mais quente (Bergmann 1847). O autor percebeu que a sua regra seria mais forte no nível de espécies, mas obviamente pensou que esta poderia ser também aplicada em outros níveis taxonômicos - para homeotérmicos em alto nível taxonômico (espécies dentro da mesma família ou ordem), para espécies dentro do mesmo gênero e para populações dentro da mesma espécie, embora ele provavelmente salientou o segundo padrão acima

(Meiri & Thomas 2007). Blackburn *et al.* (1999) afirmaram que haveria uma associação positiva entre o tamanho das espécies em um grupo monofilético e a latitude ocupada por este.

Para os vertebrados ectotérmicos, estudos sobre variações latitudinais no tamanho do corpo são controversos, como a regra de Bergmann que se aplica a certos grupos; anuros (Olalla-Tárraga & Rodríguez 2007), lagartos (Cruz *et al.* 2005, Olalla-Tárraga *et al.* 2006) e quelônios (Ashton & Feldman 2003). O inverso da regra de Bergmann é mais frequente entre os organismos ectotérmicos do que os endotérmicos, especialmente entre os insetos (Bidau & Martí 2008) e serpentes (Ashton & Feldman 2003, Olalla-Tárraga *et al.* 2006), com espécies maiores vivendo em regiões tropicais e e espécies menores em regiões temperadas. Sabe-se que o clima pode influenciar nas variações no tamanho do corpo dos organismos.

Outra crítica, está na validade da regra geral e na tendência latitudinal no tamanho do corpo ser entendida como uma resposta da temperatura ambiente (Blackburn *et al.* 1999), pois muitos fatores climáticos variam concomitantemente com a latitude e o real fator afetando as variações no tamanho do corpo é difícil de ser determinado (Yom-Tov *et al.* 2002).

No caso da regra de Allen, esta prediz que nos animais endotérmicos, o comprimento relativo das extremidades (e.g., asas, bicos, membros, caudas, orelhas, etc), é menor em regiões frias e maior em regiões quentes (Yom-Tov *et al.* 2002, Aho *et al.* 2011). Esta regra tem sido frequentemente ofuscada pela regra de Bergmann (Yom-Tov *et al.* 2002), pois no que diz respeito a padrões do tamanho do corpo, a maior parte dos trabalhos tem sido dedicada a padrões "Bergmannianos" intra e interespecífica, enquanto que a regra de Allen, embora diretamente relacionada à forma, tradicionalmente recebeu menos atenção (Bidau & Marti 2008). A regra de Allen foi também sugerida para ectotérmicos (Ray 1960), mas raramente testada na natureza (Bidau & Marti 2008).

A temperatura do corpo de um ectotérmico é principalmente aumentada pela exposição às fontes externas de calor (e.g., substratos) e a conservação da energia termal é obtida por uma menor área de superfície corpórea, que também é limitada para a absorção de calor (Aho *et al.* 2011). Isto pode ser uma vantagem em ambientes termicamente heterogêneos, como também pode ser uma necessidade para se evitar o superaquecimento em microhábitats quentes e se conservar a energia termal em microhábitats frios (Aho *et al.* 2011).

O gradiente das proporções corpóreas resulta do crescimento alométrico das extremidades do corpo em diferentes partes de distribuição, e, em geral, há tendências latitudinal e altitudinal nas proporções de partes do corpo, de modo que produz partes menores em maiores latitudes e altitudes (Bidau & Marti 2008). Esse gradiente pode coincidir com a tendência geográfica na massa ou no tamanho total do animal, de acordo com a regra de Bergmann; ou seja, os organismos de regiões de clima frio tendem a ser maiores do que os que vivem em áreas de clima quente (Bidau & Marti 2008). Contudo, embora a regra de Allen tenha sido demonstrada para um número limitado de táxons endotérmicos, esta foi melhor estudada em ectotérmicos (Ray 1960, Lindsey 1966, Cushman *et al.* 1993, Ashton 2002, Ashton & Feldman 2003, Morrison & Hero 2003, Angilletta *et al.* 2004, Knouft 2004, Cruz *et al.* 2005, Bidau & Marti 2008).

Embora estudos têm demonstrado variações tanto no tamanho do corpo, geográfica e temporalmente, quanto nos padrões alométricos de ectotérmicos invertebrados e vertebrados (Ashton 2002, Ashton & Feldman 2003), os fatores de entendimento dessas tendências podem não ser as mesmas no caso dos organismos endotérmicos (Bidau & Marti 2008). Algumas hipóteses da variação do tamanho do corpo têm sido propostas para os ectotérmicos invertebrados e vertebrados, com evidencias em grupos seguindo as regras de Bergmann e Allen, apresentando padrões em acordo, inversos ou outros sem qualquer padrão (Bidau & Marti 2008).

Por fim, dentre os répteis, os lagartos são considerados organismos modelos em estudos ecológicos e algumas pesquisas com lagartos neotropicais documentaram a variação na adaptação, reprodução, alimentação e padrões morfológicos nos gêneros *Cnemidophorus* e *Ameiva*, em associação com fatores físicos e/ou climáticos do ambiente, sendo esses organismos considerados espécies "ecotípicas" de dada área ou região (Pianka 1970, Mesquita & Colli 2003, Vitt & Colli 1994).

Ecologia e variação morfológica

Um tema fundamental na biologia evolutiva está nos fatores que influenciam a forma das radiações adaptativas, e um meio de endereçar este assunto é comparando as características morfológicas e ecológicas de grupos relativamente próximos de espécies, em diferentes ambientes (Macrini *et al.* 2003). A forte ligação evolucionária de uma dessas variáveis, entre as espécies, promove a evidência indireta da ação da seleção natural na formação de padrões macro-evolucionários (Elstrott & Irschick 2004). Na ecomorfologia, a maioria dos estudos tem utilizado com sucesso esse comparativo para entender a co-evolução da morfologia e do uso de hábitat (Miles & Ricklefs 1984, Pounds 1988, Irschick *et al.* 1997), enquanto que poucos estudos têm incluído capacidades funcionais e comportamentais do desempenho, como uma ligação intermediária entre estas (Losos 1990, Elstrott & Irschick 2004).

O termo ecomorfologia, cunhado por Karr & James (1975), é definido como uma abordagem teórica que estuda a relação entre a forma funcional dos organismos e o seu meio (Moermond 1986, Losos 1990, Ricklefs & Miles 1994). Este conceito utiliza dados de variação individual morfológica para estudar adaptação dentro de populações. Deste modo, o paradigma direciona a pergunta se a seleção natural está atuando na morfologia ou no desempenho dentro de uma simples população. Assim, múltiplas características morfológicas e de desempenho foram consideradas, bem como as correlações dentro desses dois níveis. Tais relações fomentam a ecomorfologia que se baseia no complexo "forma-função", traduzindo as adaptações das espécies às condições prevalentes do ambiente (Miles 1994). A ecologia morfológica caracteriza-se por tentar: 1) estimar as relações ecológicas entre espécies através de suas posições no espaço morfológico, possibilitando assim, inferências ecológicas a partir dos padrões morfológicos; 2) correlacionar a ecologia e a morfologia como uma forma de comprovar o objetivo anterior; 3) e elucidar da relação funcional entre morfologia e ecologia e como é interposta pelo comportamento e performance do organismo (Ricklefs & Miles 1994).

Vários grupos de vertebrados foram investigados nas relações entre a forma do corpo e suas funções em hábitats específicos, revelando traços ecológicos importantes sobre a biologia das espécies (Pianka 1969, Willians 1972, Moermond 1986). De certo, avaliações de desempenhos são importantes e os répteis podem ser fáceis objetos de estudo para isso. Uma importante diferença ecológica está certamente nas asas ou nos membros locomotores dos animais; entre os lagartos, por exemplo, a variação no comprimento dos membros, nos aspectos comportamentais e da ecologia são comumente correlacionados (Losos & Sinervo 1989). A evidência mais convincente da relação entre a morfologia de lagartos e uso de hábitats vem de estudos com *Anolis* nas Grandes Antilhas (Kohlsdorf *et al.* 2001).

Todavia, espécies com ampla distribuição normalmente experimentam variações ambientais em diferentes localidades, que podem envolver adaptações em resposta a pressões seletivas ambientais locais (Johnson *et al.* 2006). *Anolis* é o único caso de diversificação entre os lagartos com comprovada radiação ao longo das ilhas caribenhas (Kohlsdorf *et al.* 2001). Esses estudos clássicos descreveram seis tipos de "ecomorfos" que apresentam traços morfológicos similares de diferentes espécies entre as ilhas (Williams 1972, 1983). Desta forma, sugere-se que cada "ecomorfo" estaria presente entre as ilhas associado a um específico microhábitat por convergência evolutiva (Losos 1992, Beuttell & Losos 1999).

Se limites ambientais impõem sobre a adaptação dos organismos e são expressos simultaneamente em suas comparações morfológicas e ecológicas, assim, comparações morfológicas de conjunto de espécies coexistentes também devem ter propriedades ecológicas previsíveis (Karr & James 1975). De fato, convergências entre comunidades parecem ser mais restritas a biomas de ilhas (e.g., para *Anolis*) e ausentes em continentes (Melville *et al.* 2006). Porém, foi observada uma forte evidência de convergência entre as comunidades de lagartos de desertos da América do Norte e da Austrália, com referência à morfologia locomotora e ao uso de hábitat desses animais (Melville *et al.* 2006).

Problemática e os objetivos da tese:

Enyalius Wagler, 1830 é composto por espécies diurnas, umbrófilas de florestas brasileiras, ocorrendo em ampla distribuição territorial, comumente em áreas do domínio da Floresta Atlântica (Jackson 1978), além de florestas da Amazônia, Caatinga e do Cerrado. No momento estão descritas nove espécies de *Enyalius* (SBH 2011) e há, pelo menos, mais três em presente descrição; uma para o Cerrado central e duas para regiões de Mata Atlântica, sendo uma delas para o Estado de Minas Gerais (Morato, *com. pess.*) e a outra para o litoral do Estado do Rio Grande do Norte (Guedes, *com. pess.*). Ainda não está clara a distribuição real de *Enyalius*, bem como os parâmetros responsáveis por isso, uma vez que ainda há dados desatualizados e carência de informações ecológicas das espécies. Em uma visão macroecológica, devido a ampla distribuição geográfica deste gênero, de proporções continentais, em diferentes ambientes florestais do Brasil e em um amplo gradiente de temperatura, faz de *Enyalius* um modelo de estudo interessante sob as perspectivas das regras de Allen e de Bergmann, na variação geográfica e climática da morfologia, bem como, em uma abordagem sob a teoria da ecologia morfológica das diferentes espécies do grupo.

No **Capítulo 1,** nós investigamos a distribuição potencial e a variação climática e latitudinal na morfologia de *Enyalius*, listando os fatores ambientais envolvidos na distribuição e variação morfológica em nível de gênero (enviado ao *Biological Journal of the Linnean Society*).

No **Capítulo 2,** nós analisamos a distribuição potencial (nicho ecológico) das espécies de *Enyalius*, identificando as características ambientais, climáticas e geográficas, envolvidas na determinação da presença das espécies nas diferentes formações florestais do Brasil (direcionado à revista *Herpetologica*).

E no **Capítulo 3,** nós aplicamos uma abordagem multivariada integrando dados morfológicos, climáticos e espaciais para analisar a relação adaptativa entre as variáveis, a fim de se determinar padrões da ecologia morfológica das espécies de *Enyalius* (direcionado à *Journal of Animal Ecology*).

A morfologia ecológica de *Enyalius* não foi explorada e este trabalho traz resultados surpreendentes com informações inéditas sobre os aspectos ecomorfológicos particulares das espécies deste gênero. Nós consideramos este estudo um esforço preliminar para se preencher esta lacuna importante do conhecimento, representando um grande avanço para a compreensão da ecologia e história de vida deste grupo de lagartos.

REFERÊNCIAS BIBLIOGRÁFICAS

Aho, J. S., Herczeg, G., Laugen, A. T., Räsänen, K., Laurila, A. and Merila, J. 2011. Allen's rule revisited: quantitative genetics of extremity length in the common frog along a latitudinal gradient. J. Evol. Bio. 24: 59-70.

Allen J. A. 1877. The influence of physical conditions in the genesis of species. Radic. Rev. 1: 108-140.

Angilletta, M. J., Niewiarowski, P. H. Jr., Dunham, A. E., Leaché, A. D. and Porter, W. P. 2004. Bergmann's Clines in Ectotherms: Illustrating a Life–History Perspective with Sceloporine Lizards. Am. Nat. 164 (6): E168-E183.

Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecol. Biogeogr. 11:505-523.

Ashton, K. G. and C. R. Feldman. 2003. Bergmann's rule in non avian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57 (5): 1151-1163.

Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecol. Model. 200: 1-19.

Bergmann C. 1847. Uber die verhaltnisse der warmeokonomie der thiere zu ihrer grosse. Göttinger Studien 1: 595-708.

Beuttell, K. and Losos, J. B. 1999. Ecological morphology of Caribbean Anoles. Herpertol. Monog. 13: 1-28.

Bidau, C. J. and Marti, D. A. 2008. A test of Allen's rule in ectotherms: the case of two south American melanopline grasshoppers (Orthoptera: Acrididae) with partially overlapping geographic ranges. Neotrop. Entomol. 37: 370-380.

Blackburn, T. M. and Gaston, K. J. 1996. Spatial patterns in the body sizes of bird species in the New World. Oikos 77: 436-446.

Blackburn, T. M., Gaston, K. J. and Loder, N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Divers. Distrib. 5: 165-174.

Blackburn T. M. and Hawkins, B. A. 2004. Bergmann's rule and the mammal fauna of northern North America. Ecography 27: 715-724.

Costa G. C., Wolfe C., Shepard D. B., Caldwell, J. P. and Vitt, L. J. 2008. Detecting the influence of climatic variables on species distributions: a test using GIS niche–based models along a steep longitudinal environmental gradient. J. Biogeogr. 35: 637-646.

Cruz, F. B., Fitzgerald, L. A., Espinoza, R. E. and Schulte, J. A. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. J. Evol. Biol. 18: 1559-1574.

Cushman, J. H., Lawton, J. H. and Manly, B. F. J. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. Oecologia 95: 30-37.

Elith, J. et. al. 2006. Novel methods improve prediction of species distributions from occurrence data. Ecography 29:129-151.

Elith, J. and Leathwick, J. 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. Divers. Distrib. 13: 265-275.

Elstrott, J. and Irschick, D. J.2004. Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean *Anolis* lizards. Biol. J. Linn. Soc. 83: 389-398.

Flanklin, J. 2009. Mapping species distributions – special inference and prediction. University Press, Cambridge. 320 pp.

Graham, C. H., Ferrier, S., Huettman, F., Moritz, C. and Peterson, A. T. 2004. New developments in museum–based informatics and applications in biodiversity analysis. Trends Ecol.

Evol. 19 (9): 497-503.

Hawkins, B. A. 2004. Are we making progress toward understanding the global diversity gradiente? Basic and Appl Ecol 5:13.

Hawkins, B. A., Porter, E. E. and Diniz-Filho, J. A. F. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84: 1608-1623.

Irschick, D. J., L. J. Vitt, P. A. Zani and Losos, J. B. 1997. A comparation of evolutionary radiations in mainland and Caribbean *Anolis* lizards. Ecology 78 (7): 2191-2203.

Jackson, J. F. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. Arq. Zool. 30(1): 1-79.

James, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365-390.

Johnson, M. A., Kirby, Wang, S. and Losos, J. B. 2006. What drives variation in habitat use by *Anolis* lizards: habitat availability or selectivity? Can. J. Zool. 84: 877-866.

Karr, J. R. and James, F. C. 1975. Ecomorphological Configuration and Convergent Evolution in Species and Communities, p. 258-291. *In*: Cody, M. L. & Diamond, J. M. (eds). Ecology and evolution of communities. Massachusetts, Belknap Press, XII+545 pp.

Knouft, J. H. 2004. Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. Oecologia 139: 408-417.

Kohlsdorf, T., T. Garland Jr. and C. A. Navais. 2001. Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. J. Morphology, 248:151-164.

Lindsey, C. C. 1966. Body size in poikilotherm vertebrates at different latitudes. Evol. 20: 456-465.

Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecol. Monogr. 60: 369-388.

Losos, J. B. 1992. The evolution of convergent structure in caribbean *Anolis* communities. Syst. Biol. 41: 403-420.

Losos, J.B. and Sinervo, B. 1989. The effect of morphology and perch size on sprint performance in *Anolis* lizards. J. Exp. Biol. 145:23-30.

Luxbacher, A. M. and Knouft, J. H. 2009. Assessing concurrent patterns of environmental niche and morphological evolution among species of horned lizards (*Phrynosoma*). J. Evol. Biol. 22: 1669-1678.

Macrini, T. E., Irschick, D. J. and Losos, J. B. 2003. Ecomorphological Differences in Toepad Characteristics between Mainland and Island Anoles. J. Herpetol. 37 (1): 52-58.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10: 105-108.

Melville, J., Harmon, L. J. and Losos, J.B. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. Proc. Roy. Soc. Lond. B 273, 557-563.

Mesquita, R. and Colli, G. R. 2003. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia (2): 285-298.

Milles, D. B. 1994. Covariation between morphology and locomotory performance in sceloporine lizards. *In*: L. J.Vitt & E. R. Pianka. Lizard Ecology. Historical and experimental perspectives. Princeton University Press, New Jersey. pp. 207- 235.

Miles, D. B. and Ricklefs, R. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. Ecology 65:1629-1640.

Millien, V., Lyons, S. K., Olson, L., Smith, F. A., Wilson, A. B. and Yom–Tov, Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. Ecol. Lett. 9:853-869.

Moermond, T. C. 1986. A mechanistic approach to the structure of animals communities:

Anolis lizards and birds. Am. Zool. 26:23-37.

Morrison, C. and Hero, J. M. 2003. Geographic variation in life history characteristics of amphibians: a review. J. Anim. Ecol. 72:270-279.

Olalla–Tárraga, M. and Rodríguez, M. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. Global Ecol. Biogeogr. 16: 606-617.

Olalla–Tárraga, M., Rodríguez and M., Hawkins, B. A. 2006. Broad–scale patterns of body size in squamate reptiles of Europe and North America. J. Biogeogr. 33:781-793.

Pianka, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50: 1012-1030.

Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51: 703-720.

Pincheira–Donoso, D., Tregenza, T. and Hodgson, D. J. 2007. Body size evolution in South American *Liolaemus* lizards of the boulengeri clade: a contrasting reassessment. J. Evol. Biol. 20: 2067-2071.

Ponder, W. F., Carter, G. A., Flemons, P. and Chapman, R. R. 2001. Evaluation of museum collection data for use in biodiversity assessment. Conserv. Biol. 15 (3): 648-657.

Pounds, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. Ecol. Monogr. 58: 299-320.

Ray, C. 1960. The application of Bergmann's and Allen's rules to poikilotherms. J. Morphol. 106: 85-108.

Ricklefs, R. E., and Miles, D. B. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. 13-41 pp. *In:* P. C. Wainwright and S. M. Reilly (eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press.

Ricklefs, R. E. and Travis, J. 1980. A morphological approach to the study of avian community organization. Auk 97: 321-338.

Rodríguez, M. Á., López-Sañudo, I. L. and Hawkins, B. A. 2006. The geographic distribution of mammal body size in Europe. Global Ecol. Biogeogr. 15: 173-181.

SBH. 2011. Brazilian reptiles - List of species. Bérnils, R. S. & H. C. Costa. (Orgs.). Accessible at http://www.sbherpetologia.org.br/. Sociedade Brasileira de Herpetologia.

Schäuble, C. S. 2004. Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. Biol. J. Linn. Soc. 82: 39-56.

Schneider, C. J., Smith, T. B., Larison, B. and Moritz, C. 1999. A test of alternative models of diversification in tropical rainforests: Ecological gradients vs. rainforest refugia. Proc. Natl. Acad. Sci. 96: 13869-13873.

Terribili, L. V. 2009. Padrões ecológicos globais de dois clados de serpentes, Viperidae e Elapidae (Squamata, Serpentes). Tese de Doutorado, Universidade de São Paulo, Brazil, 212 p.

Vitt, L. J. and Colli, G. R. 1994. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Can. J. Zool. 72: 1986-2008.

Yom–Tov, Y., BenjaminI, Y. and Kark, S. 2002. Global warming, Bergmann's rule and body mass – are they related? The chukar partridge (*Alectoris chukar*) case. J. Zool. Lond. 257: 449-455.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in the complex island fauna: a trial analysis. Evol. Biol. 6:47-89.

Williams, E. E. 1983. Ecomorfhs, faunas, island size, and points in island radiations of *Anolis*, 326-370p. *In*: R. B. Huey; E. R Pianka & T. W. Schoener (eds.). Lizards ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.

CAPÍTULO 1 /Chapter 1

Potential distribution and geographic variation in *Enyalius* morphology (Iguanidae; Leiosaurinae), Brazil

ANDRÉ F. BARRETO-LIMA[1], CRISTIANO C. NOGUEIRA[2], SANDRA M. HARTZ[1] & GUARINO R. COLLI[2]

[1] *Laboratório de Ecologia de Populações e Comunidades, Programa de Pós-Graduação em Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves, 9.500, Setor 4, Prédio 43.422, Bairro Agronomia, Caixa Postal 15.007, Porto Alegre, RS, Brazil. CEP: 91.540–000.*

[2] *Laboratório de Herpetologia, Departamento de Zoologia, Universidade de Brasília, Brasília, DF, Brazil. CEP: 70.910–900.*

(Short running title)

Potential distribution and geographic variation in *Enyalius* morphology

Corresponding author: afblima@hotmail.com

ABSTRACT

This study aim investigates the potential distribution and geographic variation in the morphology of *Enyalius* lizards. Environmental information from each collection site was used to estimate the potential distribution of genus and determine possible associations with morphology. The potential distribution of the genus is mainly concentrated in the Atlantic Forest formations, suggesting that an important part of the evolutive history of *Enyalius* is linked to this biome. The most important variables in the distribution model were the mean annual temperature, latitude and diurnal temperature range. Precipitation of the coldest trimester was positively related to *Enyalius* body size. Precipitation in the coldest trimester, altitude and vegetal cover best explained the variation in body shape for the group as a whole. Latitudinal and altitudinal patterns were found for the extremities of the body as predicted by Allen's rule. However, patterns contrary to Allen's rule occurred for parts of body. Longitude had direct and inverse relationships with the extremities of the body. No pattern corresponding to Bergmann's rule was found for body size, in relation the latitude or ambient temperature. Climatic patterns were associated with the shape, as demonstrated by association between the precipitation and the fourth finger length, and associations between the vegetal cover with the hand, and with the body length. It is plausible that climatic and geographic requirements exert a greater influence over the morphological adaptation of *Enyalius* genus, explaining the differential allometric growth observed in an extensive geographic area.

KEYWORDS: Biogeography - ecogeography - ecological niche - *Enyalius* - morphology - potential distribution.

INTRODUCTION

Information on the distribution of species is essential to knowledge on the areas of occupation and ecological relationships between populations and their environments. Biogeographic and speciation processes among regional flora and fauna are influenced by environmental variations in the time and space (Kozak, Graham & Wiens, 2008). Then, factors that affect the geographic distribution of species include how organisms are related to their environment and interspecific interactions (Costa *et al.,* 2008). Furthermore, potential niche models constitute methods that use occurrence data together with environmental data to establish a correlate model of environmental conditions, that meet the ecological requirements of species and predict the relative suitability of a given habitat.

Recently, greater attention has been paid to the use of potential niche modelling in studies on the distribution of species, due to the need to gain knowledge on the current distribution of biodiversity on the planet and contribute to its conservation. Such analytical advances are favored by the establishment of novel techniques and statistical methods, as well as, the availability of datasets on the climatic and ecological variations (Flanklin, 2009). These models are used to estimate niche potential and are employed for the multivariate niche model of species (Rottenberry, Preston & Knick, 2006) or other taxonomic levels of organisms. The refinement of relevant information in scientific collections is a fast, direct way to access data and it has been employed in a number of studies with the aim of mapping the distribution of species or determining important areas for the conservation them (Graham *et al.,* 2004). In addition to the distribution of species, the structure of habitats and respective climatic conditions can exert a direct influence over differences in the morphological and ecological parameters of species and populations, in function of geographic distribution (Pianka, 1970; Taylor, Walker & Cordes, 2000; Kiefer, Van Sluys & Rocha, 2005).

Within the geographic distribution of a taxon, the potential forces that explain morphological variability include differences in the type of prey, predation pressure (Schneider *et al.,* 1999) and the effects of climate and other environmental factors on the growth rates (Schäuble, 2004). A component of morphological variation in a species is generally more related to climatic variability, which is an important factor to understanding adaptation, distribution, diversification mechanisms and responses to global climate changes (Millien *et al.,* 2006). To identify such ecological patterns, ecographic rules have been proposed, which describe predictions associating climate and morphology in a variety of taxonomic groups (Luxbacher & Knouft, 2009). The geographic factor of latitude may also be associated to morphological variations in species, due this factor is related to the climate of a given region. Furthermore, the observation that the body shape of organisms varies with latitude is nearly as old as the perception of a geographic gradient of species diversity (Blackburn, Gaston & Loder, 1999).

Body size is one of the most important traits of an organism and many aspects of life are affected by interactions between body size and the abiotic environment, rates of physiological processes and interactions with other organisms (Cushman, Lawton & Manly, 1993). The size of the body and extremities tends to follow ecogeographic patterns; e.g.: Bergmann's rule (1847) and Allen's rule (1877). Bergmann's rule is probably the most well known rule in zoogeography and it has been interpreted as an adaptation to the ambient temperature (Yom-Tov, Benjamini & Kark, 2002). These rules were originally postulated for endothermic organisms (i.e., birds and mammals) and demonstrate the possibility of zoogeographic patterns in the body size, predicting that this variable may be positively correlated with the latitude and altitude, as well as, negatively correlated with the ambient temperature (Blackburn & Gaston, 1996; Blackburn *et al.,* 1999; Luxbacher & Knouft, 2009).

Apparent support to this theory has also been observed in ectothermic vertebrates and invertebrates (Ray, 1960; Cushman *et al.,* 1993; Ashton & Feldman, 2003; Angilletta *et al.,* 2004; Cruz *et al.,* 2005).

From a macroecological standpoint, it would be possible to study the evolutional and biogeographic mechanisms involved in the origin of such patterns, such as selection on the higher levels of the biological hierarchy (Diniz-Filho *et al.,* 2007). For ectothermic vertebrates, studies on the latitudinal variations in the body size are controversial, as Bergmann's rule applies to certain groups, such as anurans (Olalla-Tárraga & Rodríguez, 2007), lizards (Cruz *et al.,* 2005; Olalla-Tárraga, Rodríguez & Hawkins, 2006) and chelonians (Ashton & Feldman, 2003). The inverse of Bergmann's rule is more frequent among ectothermic than endothermic organisms, especially among insects (Bidau & Martí, 2008) and snakes (Ashton & Feldman, 2003; Olalla-Tárraga *et al.,* 2006), with larger species living in tropical regions and smaller species living in temperate regions.

Concerning Allen's rule, it predicts that the relative length of the extremities of endothermic animals (e.g., wings, beaks, limbs, tails and ears) is smaller in cold regions and larger in warm regions (Yom-Tov *et al.,* 2002; Aho *et al.,* 2010). Although directly related to shape, this rule has traditionally received less attention in the literature (Bidau & Marti, 2008). Its validity has also been suggested for ectothermic animals by Ray (1960), but it has rarely been tested in the wild (Bidau & Marti, 2008; Aho *et al.,* 2010).

Reptiles are considered good models for studying the effects of climatic and environmental characteristics on the species distribution (Costa *et al.,* 2008). Among Squamata, the influence of biotic and abiotic environmental factors over the life history parameters has been reported through studies on the variation and geographic distribution (Mesquita & Colli, 2003).

Studies with lizards (*Cnemidophorus* and *Ameiva*) have documented variations in the adaptive, reproductive, feeding and/or morphological patterns, in association with the physical and/or climatic characteristics of a given environment, being these organisms considered "ecotypic" species (Pianka, 1970; Mesquita & Colli, 2003; Vitt & Colli, 1994). *Enyalius* Wagler, 1830 is made up of diurnal, ombrophilous, and endemic species from Brazilian forests, with broad territorial distribution, commonly in areas Atlantic Forest (Jackson, 1978). Currently nine species are recognized; *E. bibronii, E. bilineatus, E. brasiliensis, E. catenaus, E. erythroceneus, E. leechii, E. iheringii, E. perditus* and *E. pictus* (SBH, 2011).

In present study, a multivariate approach was employed integrating morphological, climatic and spatial data, in order to analyze the relationship between the morphological and environmental characteristics of *Enyalius* genus. The aim was to determine whether there is an ecological niche with few environmental variables that may be expressed as common characteristics associated to this genus, even in different forest formations and over a broad area of distribution. The complete distribution of the *Enyalius* and the factors that account for this distribution have not yet been fully clarified, as the literature offers outdated information and there is lack of data on the species.

From the macroecological standpoint, the broad distribution of this genus in different Brazilian forest environments, along a temperature gradient, it makes *Enyalius* an interesting study model in terms of the Allen's rule and Bergmann's rule to be tested. The basic hypothesis is that climatic variables together with the influence of latitude are the main factors explaining the distribution and variations in the morphological pattern of *Enyalius* genus and these morphological variations would be a consequence of the geographically differentiated allometric growth pattern.

Based on Allen's rule, in higher latitude/altitude (or lower temperature) it is expected to be accompanied by smaller extremities on the body of *Enyalius* lizards. Regarding Bergmann's rule, in higher latitude (or lower temperature) it is expected to be accompanied by a larger body size. Thereby, we investigated the potential distribution and climatic and latitudinal variation on the *Enyalius* morphology. We aimed: 1) to analyze the geographic distribution of *Enyalius*, identifying important areas and the most correlate environmental variables that could explain the presence of the genus; 2) to test the validity of Allen and Bergmann's rules in a latitudinal and temperature cline, through the body size and the relative length of bodily extremities of the genus, determining whether there is differential allometric growth in an extensive geographic area; and 3) to list if there are environmental, climatic and geographic factors and environment structure involved in the morphological variations of the genus.

MATERIAL AND METHODS

DATA ACQUISITION

Information on *Enyalius* was obtained from nine scientific collections (specimens borrowed and list from collection) from Brazil (Appendix 1) and the literature with the respective collection sites (i.e., records of occurrence) of the specimens analyzed. The consideration only of genus made the complementary data more reliable by discarding the possibility of errors on the identification in species level. A total of 1,300 records of individuals from 363 sites were considered to analyses of potential distribution of the genus. Among these, 603 specimens of collections (Appendix 1) were used to measurement the morphology (by the first author) and for analyses regarding the geographic variation in morphology of *Enyalius*.

Body size is a common measure in studies on the life histories of different organisms.

However, the body mass of an animal undergoes significant intraspecific variations in different seasons of the year based on the breeding period (Gaston & Blackburn, 2000), on the seasonality of the available resources, and on the specimens which undergo alterations in the body mass and shape after be collected for conservation, which hinders the use of body mass as a reliable measure. Linear length measurements are commonly considered more appropriate for organisms with an elongated body shape, such as lizards. Thus, nine length measurements were taken from each specimen with a digital caliper (scale: 0.01 mm): snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (4f), posterior leg length (l), foot length (ft), and fourth toe length (4t).

Mapping of data

The data on the collection sites of the specimens from the collections and the literature were transformed in geographic coordinates (local or municipal) for the construction of the distribution map. The software Google Earth - v. 2010 (maps service) was used to confirm the sites through satellite images. Google was used for the search for geographic coordinates in the literature and/or official documents on the location of the Brazilian conservation units, where the lizards were mostly collected. All sites were considered in forest areas, even those close to or within cities. Sites recorded within metropolises with no vegetal cover, imprecise or dubious sites, those with no record of the place of origin and those located in forest fragments with a radius less than 2.5 Km were excluded from the analysis. The Maxent v.3.3.3 (Phillips, Anderson & Schapire, 2006) was used for the construction of the potential distribution map, using the principle of maximum entropy on the presence-only data to estimate a set of functions that relate environmental variables and habitat suitability, in order to approximate the niche and potential geographic distribution of the taxon studied (Phillips *et al.,* 2006).

Ten potential distribution models were generated with the mean used for the final map and a random selection of 30% of the sites recorded to test the models. The environmental variables were obtained from each location using the geographic coordinates on a resolution scale of 2.5 arc minutes and the Worldclim databank (Hijmans *et al.,* 2005) for the last 50 years. A total of 24 environmental variables were extracted: latitude and longitude (decimal degrees), altitude (m), aspect (direction of relief in %), vegetal cover or normalized difference vegetation index (intensity scale: 0 to 255), annual mean temperature (Bio1), mean diurnal temperature range (Bio2 – mean of monthly (maximum temperature – minimum temperature)), isothermality (Bio3 – mean diurnal temperature range/annual temperature range *100), temperature seasonality (Bio4 – standard deviation *100), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), temperature annual range (Bio7 = Bio5 - Bio6), mean temperature of the wettest quarter (Bio8), mean temperature of the driest quarter (Bio9), mean temperature of the warmest quarter (Bio10), mean temperature of the coldest quarter (Bio11), annual mean precipitation (Bio12), precipitation in the wettest month (Bio13), precipitation in the driest month (Bio14), precipitation seasonality (Bio15 – coefficient of variation), precipitation in the wettest quarter (Bio16), precipitation in the driest quarter (Bio17), precipitation in the warmest month (Bio18) and precipitation in the coldest quarter (Bio19). The maps of potential distribution of species were generated in the software ArcGIS v.9.3. The probability distribution of each species were grouped into three intervals (0 - 0.1, 0.2 - 0.5, 0.6 -1), using the *Reclassify* tool. Finally, the records of occurrences of *Enyalius* were plotted on the map of the potential distribution.

DATA ANALYSIS

The analyses were performed with R 2.10.1 statistical software (2009) with level of significance of 5% ($p \leq 0.05$) for all tests. For missing data on the morphological measurements of the lizards, the multiple imputation method was performed to complete the matrix of morphological data, which it is based on the prediction of mean values, using the "mice" package (Zhang, 2003) that it estimates missing values through a model based on the observed values. The morphometric data of the new complete matrix were log transformed. To separate the morphometric variation in body size and shape components, the body size was defined as the scores of an isometric vector, with p-values$^{0.5}$, in which p is the number of variables (Jolicoeur, 1963). The scores were calculated by post-multiplication of the n x p matrix of the log-transformed data, in which n is the number of observations by the isometric vector p x 1 (Somers, 1986). The effect of body size on the morphometric variables (represented by body shape) was removed using the formula proposed by Burnaby (1966):

$$L = Ip - V(V^T V)\text{-}1\ V^T$$

which Ip is the identity matrix p x p, V is the above-defined isometric vector and V^T is the transposed matrix of V. Thus, the morphometric variables become variables that explain the body shape. Correlation tests were performed among the environmental variables to avoid the collinearity of variables in the models. Variables with correlations above 75% were discarded ($p < 0.005$) to avoid redundancies in the model. Multiple regressions were then performed relating body size adjusted to environmental variables and using the coordinates (latitude and longitude) of each location and their respective polynomial extensions, considering the possibility of spatial autocorrelation among the data (Bocard, Legendre & Drapeau, 1992). This analysis was complemented by the selection of environmental variables based on the Akaike information criterion (AIC) and "model averaging" method (Burnham & Anderson, 2002).

Then, ten of the 24 environmental variables were considered independent and employed in the potential distribution analyses: altitude, aspect, latitude, vegetal cover (ndvi), annual mean temperature, mean diurnal temperature range, annual mean precipitation, precipitation in the driest quarter and precipitation in the coldest quarter. Latitude, longitude and the respective polynomial extensions were used in the morphological analysis due to possibility of spatial autocorrelation among the data. In the search for patterns of associations, the morphological data were used with other environmental variables selected. Based on the selection of the most important variable, a correlation analysis was performed between this variable and the adjusted body size, in order to determine the level and type of association between them.

Three canonical correspondence analyses (CCA) were performed using the mean values of the morphological characteristics and the mode of the environmental characteristics in three consecutive steps, using the “vegan” statistical package. The first step was a search for spatial autocorrelation through a CCA carried out with the latitudes and longitudes of the locations and the respective polynomial extensions, in order to investigate the components that may serve as co-variables (Borcard *et al.,* 1992). The second step was a search for a set of environmental variables that best explain the variation in morphology (using the variables selected as co-variables in the multiple regressions analysis), performing a partial CCA of the morphological variables with all available environmental variables, and subsequent selection of models using the AIC. A final CCA was carried out with the results of the previous steps (body variables x most important environmental variables), in order to explain the influence of the main environmental variables over the morphological variation in the *Enyalius* genus.

RESULTS

POTENTIAL DISTRIBUTION

The total area covering all sampling sites was a polygon of approximately 5,501,505.5 Km^2. There was a greater concentration of sites of occurrence of *Enyalius* in the Brazilian southeastern from the coast to the interior of the mainland, with the smallest portion of records dispersed along the coast of the northeastern region, and in the central-western and northern regions of the country (Fig. 1). In the potential distribution model, the mean of the tests for the replicas was AUC = 0.94 (sd = 0.008), representing optimal indices for the model proposed for the genus. The greatest probabilities of occurrence of *Enyalius* (77% to 100%) in the model were in the regions of the Atlantic Forest, which they are concentrated along the east coast from the north to the south of the country, with their distributions more concentrated from the southern portion of Bahia state to Rio de Janeiro state, through the interior of Minas Gerais state and the coast of Espírito Santo state. Five of these sub-regions are known as centers of endemism, such as the *Brejos Nordestinos*, *Chapada Diamantina* and *Serra do Mar* (sensu Da Silva & Casteleti, 2003).

The model also indicated continuous areas with a lesser likelihood of occurrence from inland of the São Paulo state toward the central-western region, through the western of Minas Gerais state. Beyond Brazil, the model also indicated a greater probability of occurrence of the genus (77%) in the northwest region of the Bolivia. Among the nine environmental variables used in the distribution model, those that most contributed to explaining the potential distribution model were: the mean annual temperature, latitude and mean diurnal temperature range (Table 1). When each variable was permuted in the model, considering either its absence or use separate from the others, the most important variables continued being those featured in the model, although changes occurred in the classification of importance for the first two variables (Table 1).

GEOGRAPHIC VARIATION IN MORPHOLOGY

When analyzed separately, the precipitation in the coldest trimester was the most important variable to explaining the variation in body size of *Enyalius,* in function of geographic distribution, with a significant positive correlation (Fig. 2: $r^2 = 0.221$, $t = 5.552$, $df = 600$, $p < 0.001$). The results of both CCAs were significant ($p = 0.005$). Considering the Fig. 3, the model explained 5.8% of the variation in body shape through the spatial factor (geographic coordinates). In this CCA, Axis 1 (latitude: longitude) accounted for 75% of the explained proportion, demonstrating geographic variation in the morphology of *Enyalius* (Table 2). Latitude and longitude together were positively associated with the fourth finger length and negatively associated with the foot length; latitude was positively associated with the foot length and negatively associated with the fourth finger length; and the longitude was positively associated with the hand length and negatively associated with the tail length. Interestingly, when analyzing latitude alone, a positive association was found with the foot length and a negative association was found with the fourth toe length, but when analyzing latitude and longitude together, the inverse of these patterns was observed. In the last CCA (Fig. 4), independent on the spatial autocorrelation, the model explained 15.3% of the variation in shape of the genus, with 5.8% explained by the spatial factor (geographic coordinates) and 9.5% explained by environmental variables; the axis 1 (altitude) accounted for 95% of the explained proportion (Table 3). In this model, altitude, vegetal cover (ndvi) and precipitation in the coldest quarter (bio19) were the variables that best explained the variation in the body shape according to geographic distribution. Altitude was positively associated with the tail length and negatively associated with the head length; vegetal cover was positively associated with the hand length and negatively associated with body length; and the precipitation in the coldest quarter was positively associated with the fourth finger length and negatively associated with body length.

DISCUSSION

The greater concentration of sites of occurrence of *Enyalius* in the southeastern Brazil may be explained by the greater sampling effort on the part of researchers in this region, as well as, the difficult access to particular areas, such as the Amazon Forest or *Cerrado*. Nonetheless, the data from the present study evidence a greater number of species in the southeastern region of the country (nine of 12 spp.; including the not described), especially in the Atlantic Forest biome which likely it had the greater latitudinal influence on the distribution model for the genus.

Currently, the Atlantic Forest is a fragment that harbors one of the largest percentages of endemic species in the world, with many species and genera of vertebrates still being described (Carnaval *et al.,* 2009 and references). Recent study (Carnaval & Moritz 2008) showed evidence for a large central refuge throughout the Late Quartenary, named 'Bahia refugium', which it was predicted based on a climatic modelling with palynological validation and contrasted with the current distribution of several vertebrate species; such as sloths, lizards, marsupials, sender mice, atlantic rats and frogs (Resende *et al.,* 2010).

On the other hand, the Atlantic Forest is one of the most threatened biomes in the world, and this loss of biodiversity brings harmful consequences to ecosystems, populations, genetic variability, species and the evolutionary processes that maintain it (Galindo-Leal & Câmara, 2005; Batalha-Filho & Miyaki, 2011).

There were small areas on the potential distribution map in the central-western Brazil (corresponding to the Federal District and surrounding areas) that had a considerable likelihood of occurrence, which it was associated with the presence of *Enyalius sp* n. 1 (in description) in the savanna region known as the *Cerrado* biome.

The probability of the occurrence of *Enyalius* in Bolivia may be explained by the influence of the Amazon forest in this region, suggesting that *E. leechii* (or perhaps a new species) may be found in this country. The most important factors in the *Enyalius* distribution model were the mean annual temperature, latitude and the mean diurnal temperature range. It is plausible that an adaptive climatic hypothesis be the basis to explaining the distribution of the genus in the areas found. It is known that habitats and their climatic conditions can influence the life history of organisms and the ecological processes of species in function of the geographic distribution (Pianka, 1970; Taylor *et al.,* 2000; Kiefer *et al.,* 2005).

According to Angilletta *et al.* (2004), the characteristics of the life history of the lizard *Sceloporus undulatus* were strongly associated with environmental factors, but the latitude exerted more influence than temperature. This suggests that the mean annual temperature and latitude along the coast of Brazil may be overlapped in the model of the present study, characterizing the extensive domain of the Atlantic Forest, which in turn it was associated with the predominant distribution of *Enyalius*. It is plausible that the life history of the group is closely linked to the evolution of the Atlantic Forest, along the eastern coast of Brazil, and its biology be predominantly dependent on geographic and climatic characteristics of this forest formation with broad latitudinal distribution. For the Atlantic Forest, studies point to the existence of phylogeographic discontinuities for different organisms (e.g., bees, amphibians, reptiles, birds, bats and plants), and the principal hypothesis used to explain the diversifying these discontinuities it was the theory refugia (Fig. 5 - A) (see Batalha-Filho & Miyaki, 2011 and references). Regarding the Refugia Theory (Vanzolini & Williams, 1970), these areas were dense humid forest “islands” isolated by open vegetation; which they were retracted during periods of glacial maximum (forming refugia) and would expand during warmer periods (interglacials), while areas of open vegetation behaved otherwise (Batalha-Filho & Miyaki, 2011).

Thereby, species dependent on forest environments would have accompanied these cycles of forests (contraction and expansion) in the Pleistocene, causing diversification on the populations of different refugium by allopatry, if the insulation had enough time to accumulate differences (Batalha-Filho & Miyaki, 2011). Authors suggest that populations of a given species, which remained in stable areas during the Pleistocene (refuges) should present higher DNA variability than those currently found in unstable areas, which should present genetic signature of population expansion, reflecting colonization from the adjacent refugial centres (Carnaval & Moritz 2008; Carnaval *et al.* 2009; Resende *et al.,* 2010). Moreover, Carnaval *et al.* (2009) showed that the southern Atlantic forest was climatically unstable relative to the central region, which served as a large climatic refugium for neotropical species in the late Pleistocene (Fig. 5 - B). Therefore, our data also showed importante occurrences on the potential distribution of *Enyalius* in these known refugia (e.g., Pernambuco, Bahia/Espírito Santo and São Paulo states). Furthermore, forest lizards also show high diversity in the central portion of the biome relative to southern areas, and provide evidence for population expansion in southern regions (Carnaval *et al.,* 2009 and references).

The geographically structured variation in morphology, especially body size, is common among a large number of species (Avise, 2000). The morphological variation in *Enyalius* was partially reflected on its geographic distribution. However, the hypothesis of the Bergmann's rule for the body size and the ambient temperature was not corroborated for the genus studied herein, such as in previous studies with lizards (Pincheira-Donoso, Tregenza & Hodgson, 2007; Pincheira-Donoso, Hodgson & Tregenza, 2008). In the broad clade *L. boulengeri*, Pincheira-Donoso *et al.* (2008) also observed that the species did not support the Bergmann's rule, stating that a large body mass would be a disadvantage for lizards in cold climates, and the heat conservation hypothesis could not be accepted for these organisms with an increase in body size in climates with low temperatures. Such statements are supported by a series of previous studies carried out on lizards, which reported dramatic consequences for the ecological performance and reproductive success (by sexual selection), and physiological functions (and consequently behavioral responses) occurring at suboptimal rates in temperatures below that of the metabolic ideal (Pincheira-Donoso *et al.,* 2008 and references). Possibly the scale (geographical distance) it was small to find associations between the body size and latitude. However, with few exceptions the Bergmann's rule applies to lizards on the species level carried out in Europe (Olalla-Tárraga *et al.,* 2006) and South America (Cruz *et al.,* 2005).

In study with *Liolaemus* lizards was found that species had a larger body size at higher latitudes and altitudes, concluding that the strong positive size-latitude relationship apparently represented a pattern observed for the entire dataset of congener species, resulting in a strong negative relationship between the latitudinal variation in body size and thermal variables (Cruz *et al.,* 2005). Climate is known to influence variations in the body size of organisms. These results demonstrated strong relationships of the latitude and body with thermal variables, together with the fact that the thermal inertia is profoundly affected by the body size in lizards (Huey, 1982), and that the hypothesis of heat conservation (Gaston & Blackburn, 2000) may be a mechanism underlying Bergmann's rule in *Liolaemus* lizards (Cruz *et al.,* 2005). However, a criticism concerning the general validity of the rule and latitudinal trend in body size is understood as a response to ambient temperature (Blackburn *et al.,* 1999), as many climate factors vary concomitantly with the latitude and the real factor affecting variations in body size is difficult to determine (Yom-Tov *et al.,* 2002). Though the variation in the strength of this pattern depended greatly on the phylogenetic scale of analysis considered (Cruz *et al.,* 2005).

Indeed, the lack of repeated support for the Bergmann’s rule in ectothermic organisms suggests that this rule should be recognized as a macroecological prediction model valid mainly for studying the evolution of body size in endothermic animals, as originally proposed (Pincheira-Donoso *et al.,* 2008).

On the other hand, the present study identified climatic (precipitation in the coldest trimester), geographic (altitude, latitude and longitude) and environment structure (vegetal cover) patterns associated to body shape in the *Enyalius* genus. Latitude is considered an influential agent in the evolution of the body shape (Hurd & Anders, 2007). It may suggests the importance of the fact that a large portion of lizards were collected from a narrow latitudinal range in the coastal region of Brazil, where considerable variation of altitude occurs.

Precipitation in the coldest trimester had the greatest negative impact on the both body size and positive impact on the fourth finger length. Regarding the body size, greater rainfall was generally associated with less variation in the size of the lizards. However, the mean size values for *Enyalius* are larger. It should be stressed that the greatest frequencies and variations in the size of lizards occurred within a rainfall range of 40 to 120ml. In the seasonal tropical forests, rainfall is typical and exerts an influence over the vegetation of the region – in the present case, predominantly within the broad coastal area, which the Atlantic Forest is found and the greatest number of records of *Enyalius* occurs.

It is considered that climatic conditions exert an influence on the morphology of many ectothermic and endothermic animals (Gvoždík, Moravec & Kratochvíl, 2008 and references). The body temperature of ectothermic organisms is mainly increased by exposure to external sources of heat (e.g. substrates) and the conservation of thermal energy is achieved by a relatively smaller body surface area, which it also limits the absorption of heat (Aho *et al.,* 2010).

This may be an advantage in thermally heterogeneous environments, as well as it may be a necessity to avoid overheating in hot microhabitats and conserve thermal energy in cold microhabitats (Aho *et al.,* 2010). The morphology of species can be regulated by physiological processes related to temperature and precipitation (Luxbacher & Knouft 2009 and references).

Regarding the geographic variation in the morphology of two species of parapatric frogs, Gvoždík *et al.* (2008) suggest that climatic conditions (e.g., temperature and precipitation) are important factors on the determination of morphological variations, and appear to have led to differences in the morphotypes of populations living in areas with ultra-peripheral climatic conditions, but with similar body shape in the populations of both species that occupy areas with comparable climates. Similar relationships in the environmental niche pattern and morphological evolution have been reported for *Phrynosoma* lizards, suggesting the influence of climatic variables over morphological variations among species, with implications regarding the understanding of how the distribution of species is limited by environmental variation (Luxbacher & Knouft, 2009). In the present study, since environmental conditions were found in association with morphological structures, the occurrence of the specimens analyzed must be limited by the evolutional history of the genus and the environmental variables may have influenced the geographic distribution of *Enyalius* through a mechanism of climatic adaptive response.

Data indicated that the environment structure (vegetal cover) was another factor associated with the morphological variation of the genus, due to reflect in the larger hand length and smaller body size. Since species of *Enyalius* live in forest environments and are considered semi-arboreal, the size of the hand and fourth finger are important morphological structures for climbing and moving over the substrate of the forest. Species of *Anolis* with 'trunk-ground' habits have the long back legs and long tails, whereas those with arboreal habitats (use of branches) are more elongated, with smaller back legs and shorter tails (Losos, 1990). In opposing relationships between the latitude and the size of the limbs, where the subtropical forests occur in higher latitudes and these are smaller than the tropical forests, a larger foot and a smaller hand may lead to greater use of the forest floor than trees by part of the *Enyalius* species. Biomechanical models state that species with relatively larger back limbs are capable of running faster and jumping farther (Losos, 1990). Likewise, larger hands in tropical (warm) regions may indicate a greater capacity for scaling the arboreal substrate.

Altitude was positively associated with the tail length and negatively associated with the head length. High forests have colder temperatures and the head was smaller in these areas, corroborating the Allen’s rule, whereas the tail was largest (i.e., opposite to rule). Unexpectedly, longitude also showed patterns either directly or inversely proportional to the extremities of the body, with larger hands and smaller tails found further inland, where the environment is hotter and drier [e.g. *Cerrado* (savanna)] and the forests undergo greater water stress, which are smaller and less dense than those wet forests along the coast; where, *a priori*, the use of the arboreal substrate by the lizards is expected be greater than the use of the forest ground in these driest regions. Another hypothesis to explaining the variation in the shape is that variations in the body proportions at different altitudes, latitudes and longitudes obey the variation in general body size dependent on the water availability more than an adaptation to mean temperature, as the Allen’s rule requires (Bidau & Martí, 2008). This may explains the negative correlations between the longitude x tail size and the latitude:longitude x foot size, since the water balance normally is negatively associated with the longitude in some areas sampled. Correlations between the body proportions and seasonality parameters (e.g. precipitation of the coldest trimester) lend support to this hypothesis (see Bidau & Martí, 2008). Therefore, the influence of environmental conditions over life history parameters in Squamata is usually accessed through studies on the geographic variation (Mesquita & Colli, 2003).

The geographic distribution of *Enyalius* genus is mainly concentrated in the ecological conditions of the Atlantic Forest, explained by the mean annual temperature, latitude and mean diurnal temperature range, and suggesting that the evolution of the taxon is closely related to this biome. The geographic variation in morphology of *Enyalius* was observed in the distribution of the group, as demonstrated by the differences in body size and morphological structures, which were explained by spatial, environmental structure (vegetal) and climatic variables. These environmental factores influenced the morphological adaptation of *Enyalius* that can be explained by the differential allometric growth over huge geographic area. Only Allen's rule corroborated as patterns in the variation in the morphology of *Enyalius,* being correlated to climatic and geographic conditions. It is plausible that an adaptive climatic hypothesis be the basis to explain the distribution of the *Enyalius* genus in the Brazilian forests.

ACKNOWLEDGMENTS

We are grateful to the heads of the collections for lending the material and data of specimens: Ana L. C. Prudente and Teresa C. S. de Ávila-Pires (MPEG), Hussam El D. Zaher and Carolina C. Mello (MZUSP), Luciana Nascimento (MCNR), Paulo Manzanni (ZUEC), Ísis Arantes (CHUNB), Rejane M. Lira-da-Silva (MZUFBA) and Paulo Passos (MNRJ). Thanks to Renata Françoso (UnB) for environmental data on the distribution models; Fabrício Maia and Ísis Arantes for support in the laboratory (CHUNB). To Alexandro Tozetti (UNISINOS), Leandro S. Duarte (UFRGS), Sônia Cechin (UFSM) and Thales Freitas (UFRGS) for suggestions on the manuscript. To Bruna Meneses (UFRGS) for the final map. We received logistical and financial support from PPG-Ecologia/UFRGS and the Department of Zoology/UNB, CAPES (Ph.D. scholarship to André F. Barreto-Lima). Sandra M. Hartz (processes 306816/2010-5) and Guarino R. Colli (563320/2010-9) are CNPq researchers.

REFERENCES

Aho JS, Herczeg G, Laugen AT, Räsänen K, Laurila A, Merila J. 2010. Allen's rule revisited: quantitative genetics of extremity length in the common frog along a latitudinal gradient. Journal of Evolutionary Biology **24**: 59–70.

Allen JA. 1877. The influence of physical conditions in the genesis of species. Radical Review **1**: 108–140.

Angilletta MJ, Niewiarowski PHJr, Dunham AE, Leaché AD, Porter WP. 2004. Bergmann's Clines in Ectotherms: Illustrating a Life–History Perspective with Sceloporine Lizards. American Naturalist **164** (6): E168–E183.

Ashton KG, Feldman CR. 2003. Bergmann's rule in non avian reptiles: turtles follow it, lizards and snakes reverse it. Evolution **57** (5): 1151–1163.

Avise JC. 2000. Phylogeography: the history and formation of species. Harvard Univ. Press, Cambridge, MA. 447 pp.

Batalha-Filho H, Miyaki CY. 2011. Phylogeography of the Atlantic Forest. Revista da Biologia, Vol. Esp. Biogeografia: 31–34.

Bergmann C. 1847. Uber die verhaltnisse der warmeokonomie der thiere zu ihrer grosse. Göttinger Studien **1**: 595–708.

Bidau CJ, Marti DA. 2008. A test of Allen's rule in ectotherms: the case of two south American melanopline grasshoppers (Orthoptera: Acrididae) with partially overlapping geographic ranges. Neotropical Entomology **37**: 370–380.

Blackburn TM, Gaston KJ. 1996. Spatial patterns in the body sizes of bird species in the New World. Oikos **77**: 436–446.

Blackburn TM, Gaston KJ, Loder N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distribution **5**: 165–174.

Bocard DP, Legendre P, Drapeau P. 1992. Partialing out the spatial component of ecological variation. Ecology **73** (3): 1045–1055.

Burnaby TP. 1966. Growth–invariant discriminant functions and generalized distances. Biometrics **22**: 96–110.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer–Verlag. New York.

Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C. 2009. Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot. Science **323**: 785-789.

Carnaval AC, Moritz C. 2008. Historical climate modeling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography **35**: 1187–1201.

Costa GC, Wolfe C, Shepard DB, Caldwell JP, Vitt LJ. 2008. Detecting the influence of climatic variables on species distributions: a test using GIS niche–based models along a steep longitudinal environmental gradient. Journal of Biogeography **35**: 637–646.

Cruz FB, Fitzgerald LA, Espinoza RE, Schulte JA. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. Journal of Evolutionary Biology **18**: 1559–1574.

Cushman JH, Lawton JH, Manly BFJ. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. Oecologia **95**: 30–37.

Da Silva JMC, Casteleti CHM. 2003. Status of biodiversity f Atlantic Forest of Brazil. In: Galindo–Leal C, Camera IG, eds. The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook. CABS and Island Press, 43–59.

Diniz–Filho JAF, Bini LM, Rodríguez M, Rangel TFLVB, Hawkins BA. 2007. Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnívora. Ecography **30:** 598–608.

Flanklin J. 2009. Mapping species distributions – special inference and prediction. University Press, Cambridge. 320 pp.

Galindo-Leal C and Câmara IG. 2005. Status do hotspot Mata Atlântica: uma síntese. Capítulo 1. In: Galindo-Leal C and Câmara IG. (Eds). Mata Atlântica: Biodiversidade, Ameaças e Perspectivas. Belo Horizonte: Conservação Internacional 3–11.

Gaston KJ, Blackburn TM. 2000. Pattern and process in macroecology. Blackwell Scientific, Oxford: 377 pp.

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT. 2004. New developments in museum–based informatics and applications in biodiversity analysis. Trends in Ecology & Evolution **19** (9): 497– 503.

Gvoždík V, Moravec J, Kratochvíl L. 2008. Geographic morphological variation in parapatric Western Palearctic tree frogs, *Hyla arborea* and *Hyla savignyi*: are related species similarly affected by climatic conditions? Biology Journal of Linnean Society **95**: 539–556.

Hijmans RJ, Cameron S, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**: 1965–1978.

Huey RB. 1982. Temperature, physiology, and the ecology of reptiles. In: Biology of the Reptilia, ed. Gans C, Pough FH. Academic Press London, 25–91.

Hurd PL, Anders SM Van. 2007. Latitude, Digit Ratios, and Allen's and Bergmann's Rules: A Comment on Loehlin, McFadden, Medland, and Martin (2006). Arch. Sex. Behav. **36**:139–141.

Jackson JF. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. Arquivos de Zoologia **30** (1): 1–79.

Jolicoeur P. 1963. The multivariate generalization of the allometry equation. Biometrics **19**: 497–499.

Kiefer MC, Van Sluys M, Rocha CFD. 2005. Body temperatures of *Tropidurus torquatus* (Squamata, Tropiduridae) from coastal populations: Do body temperatures vary along their geographic range? Journal of Thermal Biology **30**: 449–456.

Kozak KH, Graham CH, Wiens JJ. 2008. Integrating GIS–based environmental data into evolutionary biology. Trends in Ecology & Evolution **23**: 1–8.

Losos JB. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecological Monographs **60**: 369–388.

Luxbacher AM, Knouft JH. 2009. Assessing concurrent patterns of environmental niche and morphological evolution among species of horned lizards (*Phrynosoma*). Journal of Evolutionary Biology **22**: 1669–1678.

Mayr E. 1956. Geographical character gradients and climatic adaptation. Evolution **10**: 105–108.

Meiri S, Thomas GH. 2007. The geography of body size – challenges of the interspecific approach. Global Ecology and Biogeography **16**: 689–693.

Mesquita R, Colli GR. 2003. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia **2**: 285–298.

Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom–Tov Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. Ecological Letters. **9**: 853–869.

Olalla–Tárraga M, Rodríguez M. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. Global Ecology and Biogeography. **16**: 606–617.

Olalla–Tárraga M, Rodríguez M, Hawkins BA. 2006. Broad–scale patterns of body size in squamate reptiles of Europe and North America. Journal of Biogeography. **33**: 781–793.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**: 231–259.

Pianka ER. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology **51**: 703–720.

Pincheira–Donoso D, Hodgson DJ, Tregenza T. 2008. The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? Evolution Biology **68**:1–13.

Pincheira–Donoso D, Tregenza T, Hodgson DJ. 2007. Body size evolution in South American *Liolaemus* lizards of the boulengeri clade: a contrasting reassessment. Journal of Evolutionary Biology **20**: 2067–2071.

R Development Core Team. 2009. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.

Ray C. 1960. The application of Bergmann's and Allen's rules to poikilotherms. Journal of Morphology **106**: 85–108.

Resende HC, Yotoko KSC, Delabie JHC, Costa MA, Campiolo S, Tavares MG, Campos LAO, Fernandes-Salomão TM. 2010. Pliocene and pleistocene events shaping the genetic diversity within the central corridor of the Brazilian Atlantic Forest. Biological Journal of Linnean Society **101**: 949–960.

Rottenberry JT, Preston KL, Knick ST. 2006. GIS–based niche modeling for mapping species habitat. Ecology **87**: 1458–1464.

Schäuble CS. 2004. Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. Biological Journal of Linnean Society **82**: 39–56.

Schneider CJ, Smith TB, Larison B, Moritz C. 1999. A test of alternative models of diversification in tropical rainforests: Ecological gradients vs. rainforest refugia. Proceedings of the National Academy Science **96**: 13869–13873.

SBH. 2011. Brazilian reptiles - List of species. Bérnils, R. S. & H. C. Costa. (Orgs.). Accessible at http://www.sbherpetologia.org.br/. Sociedade Brasileira de Herpetologia.

Somers KM. 1986. Multivariate allometry and removal of size with principal component analysis. Systematic Zoology **35**: 359–368.

Taylor HL, Walker JM, Cordes JE. 2000. Ecological patterns of body size and clutch size variation in the parthenogenetic teiid lizard *Cnemidophorus tesselatus*. Herpetologica **56**: 45–54.

Vanzolini PE, Williams EE. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria: Iguanidae). Arquivos de Zoologia (S. Paulo) **19**: 1–298.

Vitt LJ, Colli GR. 1994. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Can. J. Zool. **72**: 1986–2008.

Yom–Tov Y, BenjaminI Y, Kark S. 2002. Global warming, Bergmann's rule and body mass – are they related? The chukar partridge (*Alectoris chukar*) case. Journal Zoology (London) **257**: 449–455.

Zhang, P. 2003. Multiple Imputation: Theory and Method. *International Statistical Review*, **71** (3): 581–592, Printed in The Netherlands, International Statistical Institute.

Table 1. Environmental variables, percentage contributions and their importance on the permutation in the potential distribution model of *Enyalius* genus.

Environmental variables	Percentage contribution (%)	Importance in the permutation (%)
Annual mean temperature	**32.4**	**26.0**
Latitude	**28.6**	**29.9**
Mean diurnal temperature range	**20.4**	**24.9**
Annual mean precipitation	10.7	7.7
Vegetal cover (ndvi)	2.1	1.4
Precipitation of the driest quarter	1.9	6.3
Altitude	1.8	1.3
Precipitation of the coldest quarter	1.2	1.9
Aspect (direction of relief)	0.8	0.6

Table 2. Eigenvalues, scores and their contribution of components in the CCA, on the variation of *Enyalius* morphology, in relation to spacial variables. Details: latitude (lat) and longitude (long); snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (4f), posterior leg length (l), foot length (f), and fourth toe length (4t).

Importance of components	CCA1 **lat:long**	CCA2 **lat**	CCA3 **long**	CA1	CA2	CA3	CA4	CA5	CA6	CA7	CA8
Eigenvalue	0.0001	2.62e-05	9.16e-06	0.001	0.0004	0.0003	0.0002	0.0001	7.66e-05	6.26e-05	5.27e-05
Proportion explained	0.0434	1.10e-02	3.84e-03	0.4455	0.1990	0.1094	0.0625	0.0443	3.21e-02	2.63e-02	2.21e-02
Cumulative proportion	0.0434	5.44e-02	5.83e-02	0.5037	0.7028	0.8122	0.8752	0.9195	9.52e-01	9.78e-01	1.00e+00

Accumulated constrained eigenvalues	CCA1 **lat : long**	CCA2 **lat**	CCA3 **long**
Eigenvalue	0.000104	2.62e-05	9.16e-06
Proportion explained	0.74567	1.88e-01	6.59e-02
Cumulative proportion	0.74567	9.34e-01	1.00e+00

Species scores

	CCA1	CCA2	CCA3	CA1	CA2	CA3
svl	0.0009297	0.0011985	0.0005825	0.002398	0.001764	-0.005451
t	0.0008480	0.0063991	-0.0014621	0.045122	0.023659	0.011834
h	0.0004901	-0.0002272	-0.0060737	-0.014173	-0.007122	-0.007042
a	0.0031305	-0.0050994	-0.0003525	-0.011796	-0.006336	-0.014192
ha	-0.0027270	-0.0116565	-0.0072162	-0.128056	0.056276	0.034398
4f	0.0283588	-0.0015433	0.0040826	-0.003069	-0.056544	0.038529
l	-0.0089514	-0.0062632	0.0027569	-0.010783	-0.003183	-0.016411
f	-0.0205706	0.0033720	0.0031789	-0.006000	-0.004809	-0.014902
4t	0.0032019	0.0017494	0.0018678	-0.001983	-0.010635	0.002897

Biplot scores for constraining variables

	CCA1	CCA2	CCA3	CA1	CA2	CA3
lat	-0.9026	0.4140	0.118216	0	0	0
long	-0.2842	-0.6047	-0.744032	0	0	0
lat:long	0.9835	-0.1809	0.007381	0	0	0

Table 3. Eigenvalues, scores and their contribution of components in the CCA, on the variation of *Enyalius* morphology in relation to ambiental variables (after removing the spacial variables). Details: precipitation of the coldest quarter (bio19), atitude (alt), and vegetal cover (ndvi); snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (4f), posterior leg length (l), foot length (f), and fourth toe length (4t).

Importance of components	CCA1 **alt**	CCA2 **ndvi**	CCA3 **bio19**	CA1	CA2	CA3	CA4	CA5	CA6	CA7	CA8
Eigenvalue	0.00022	1.04e-05	1.26e-06	0.0009	0.0005	0.0003	0.0002	0.0001	6.77e-05	5.89e-05	5.06e-05
Proportion explained	0.0958	4.61e-03	5.60e-04	0.3968	0.2023	0.1095	0.0665	0.0449	3.02e-02	2.62e-02	2.26e-02
Cumulative proportion	0.0958	1.00e-01	1.01e-01	0.4978	0.7001	0.8096	0.8761	0.9210	9.51e-01	9.77e-01	1.00e+00

Accumulated constrained eigenvalues	CCA1 **alt**	CCA2 **ndvi**	CCA3 **bio19**
Eigenvalue	0.0002	1.04e-05	1.26e-06
Proportion explained	0.9488	4.57e-02	5.57e-03
Cumulative proportion	0.9488	9.94e-01	1.00e+00

Species scores

	CCA1	CCA2	CCA3	CA1	CA2	CA3
svl	0.002503	0.0018588	0.0003241	-0.001413	0.001421	-0.0059965
t	0.023673	0.0006222	0.0002215	-0.036740	0.025858	0.0131651
h	-0.007871	0.0031052	0.0008287	0.011428	-0.007848	-0.0071288
a	-0.008342	-0.0012170	0.0002168	0.008582	-0.006270	-0.0142957
ha	-0.037503	0.0018581	0.0034766	0.127621	0.045052	0.0308044
4f	-0.004533	-0.0100974	0.0005894	-0.002543	-0.055915	0.0371890
l	-0.015524	0.0010827	-0.0022261	0.004163	-0.001278	-0.0134465
f	-0.000910	0.0021515	-0.0001414	0.005858	-0.006071	-0.0165163
4f	0.002605	-0.0030135	-0.0006030	0.002458	-0.011886	0.0007759

Biplot scores for constraining variables

	CCA1	CCA2	CCA3	CA1	CA2	CA3
bio19	-0.6969	-0.6021	-0.2266	0	0	0
ndvi	-0.7627	-0.1591	0.4885	0	0	0
alt	0.8648	-0.1918	0.4019	0	0	0

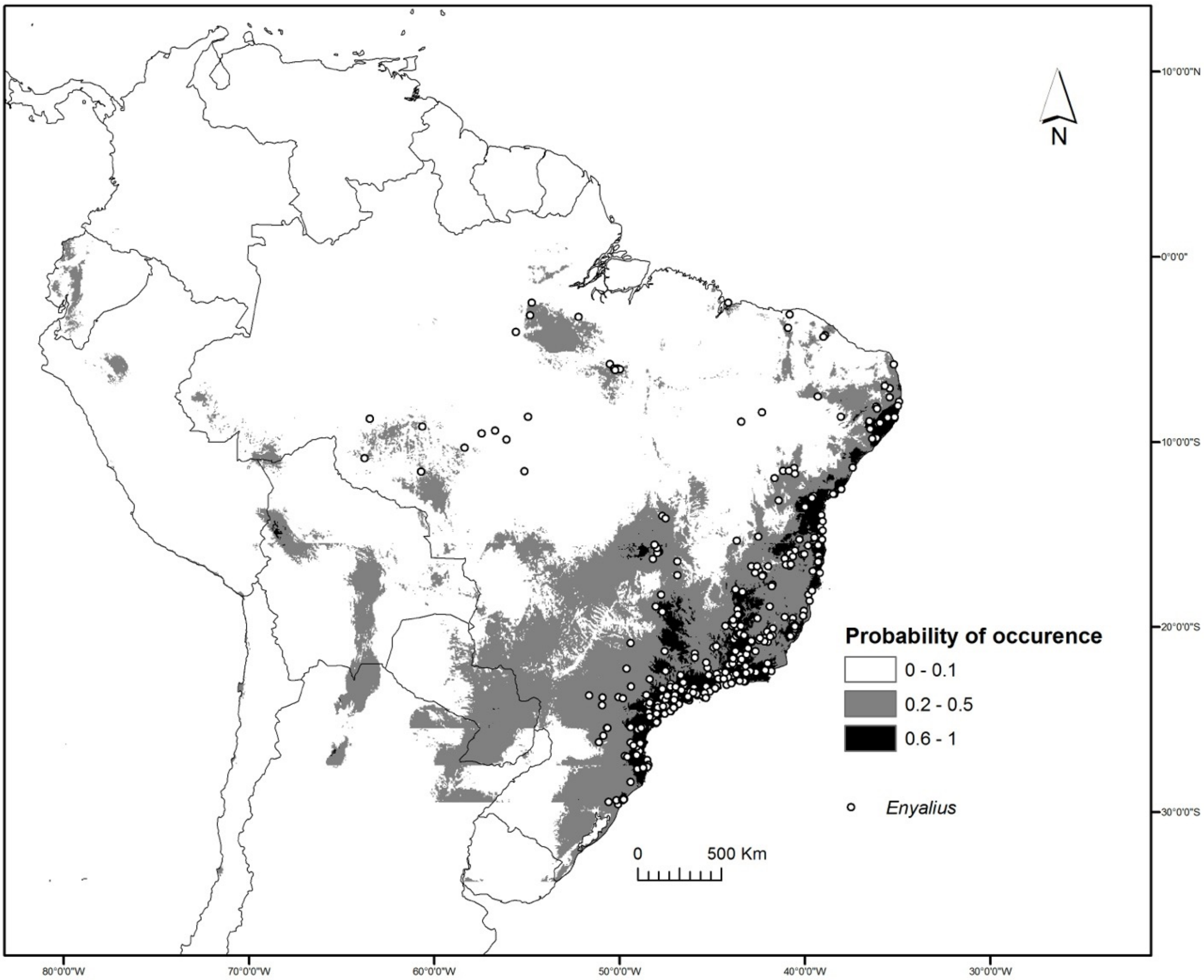


Figure 1. Map of potential distribution model of *Enyalius* genus with the probability of occurrence. The mean of tests for the replicas was AUC = 0.94 (sd = 0.008).

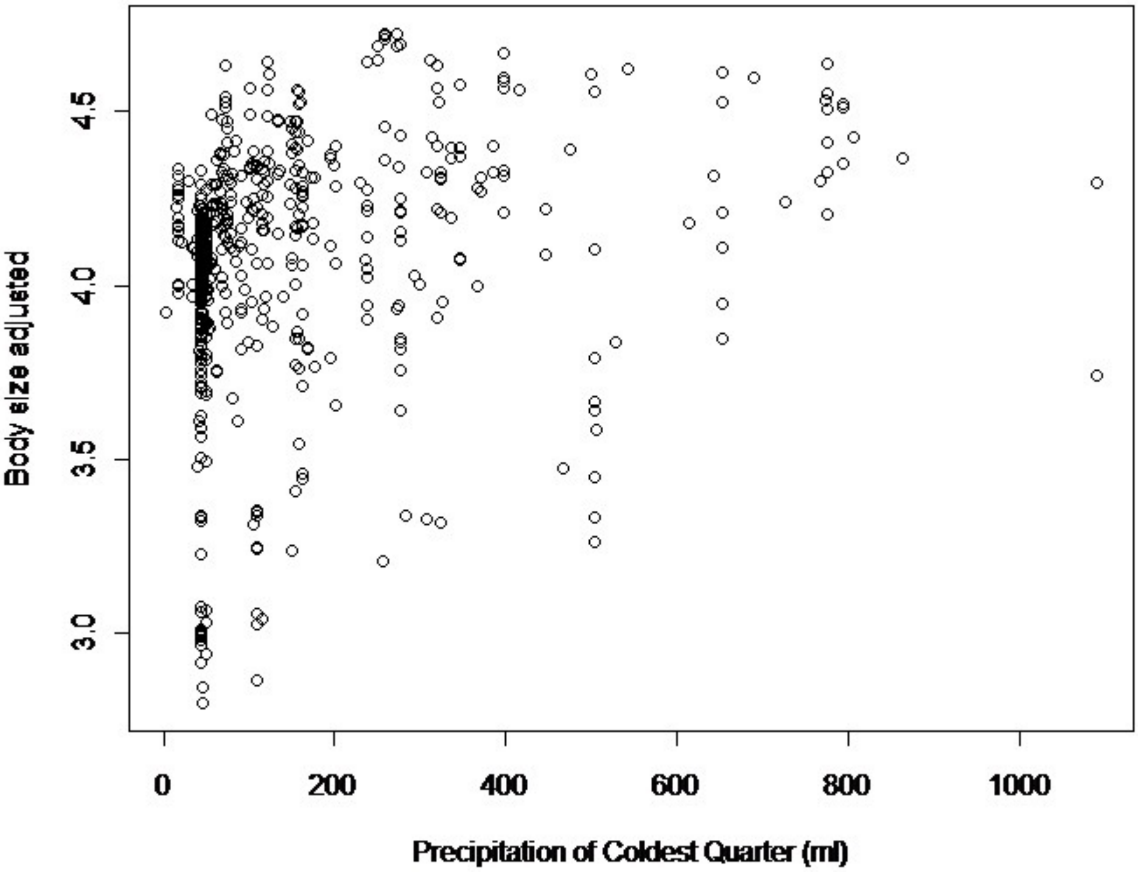


Figure 2. Graph of the correlation between *Enyalius* body size adjusted and the mean precipitation of the coldest quarter (ml).

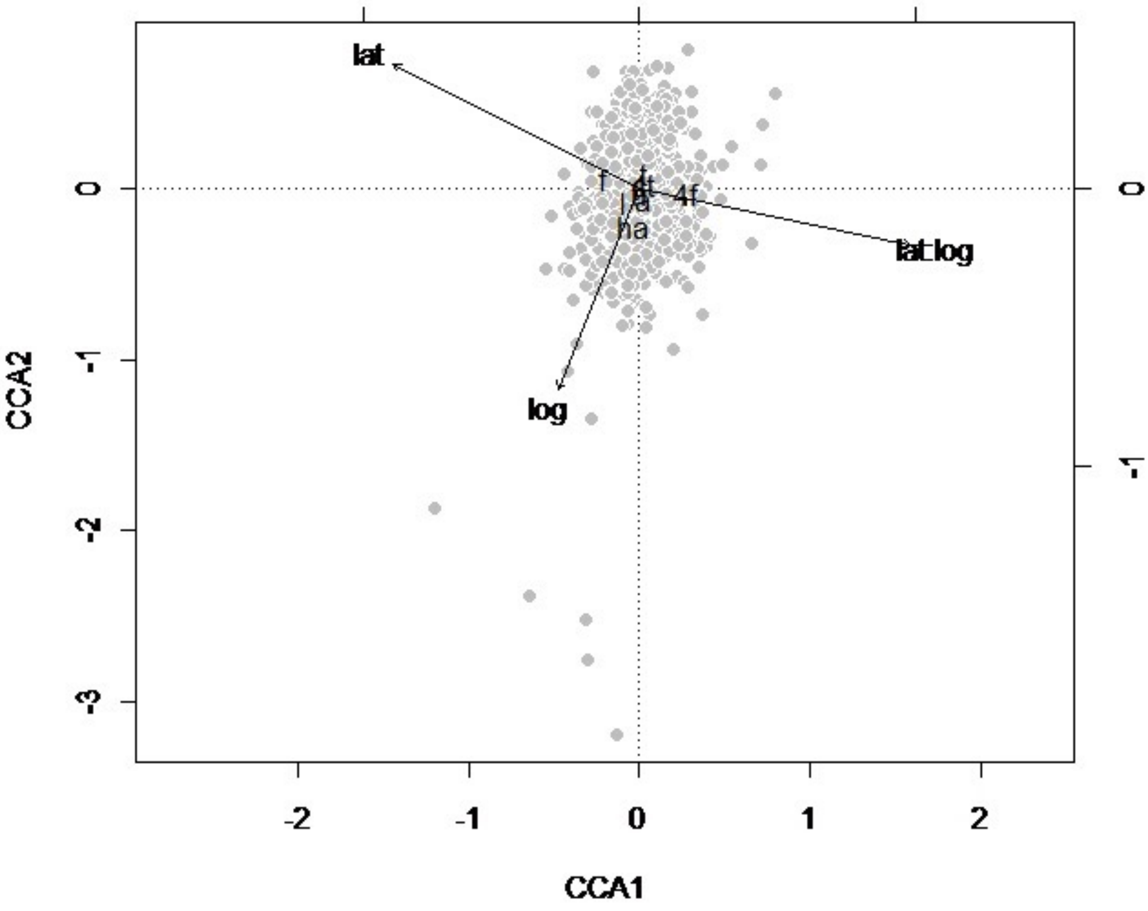


Figure 3. CCA graph: *Enyalius* morphology in relation to latitude and longitude (lat = latitude, log = longitude). Details: snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (4f), posterior leg length (l), foot length (f), and fourth toe length (4t).

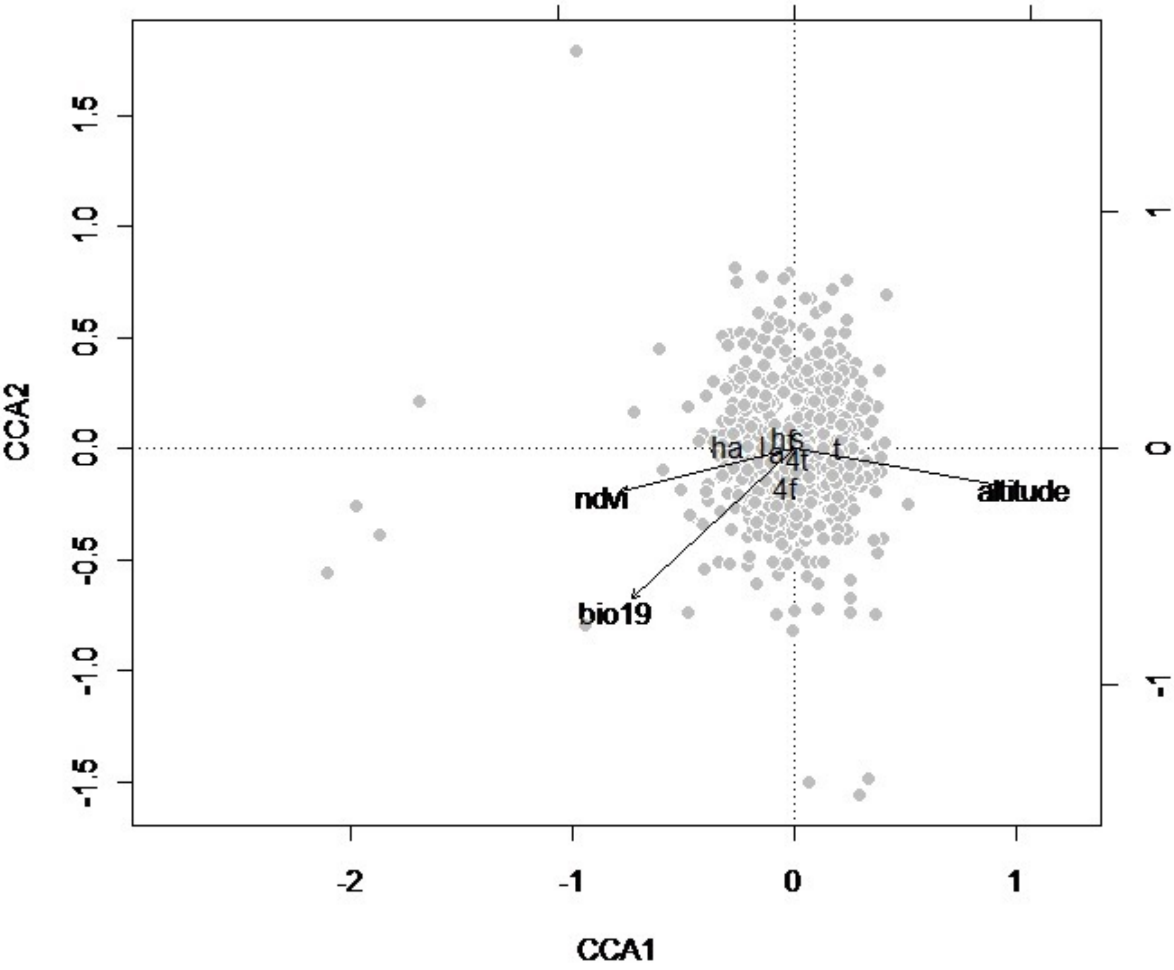


Figure 4. CCA graph: *Enyalius* morphology and the most important variables, avoiding spatial autocorrelation among the data. Details: precipitation of the coldest quarter (bio 19), vegetal cover (ndvi), snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (4f), posterior leg length (l), foot length (f), and fourth toe length (4t).

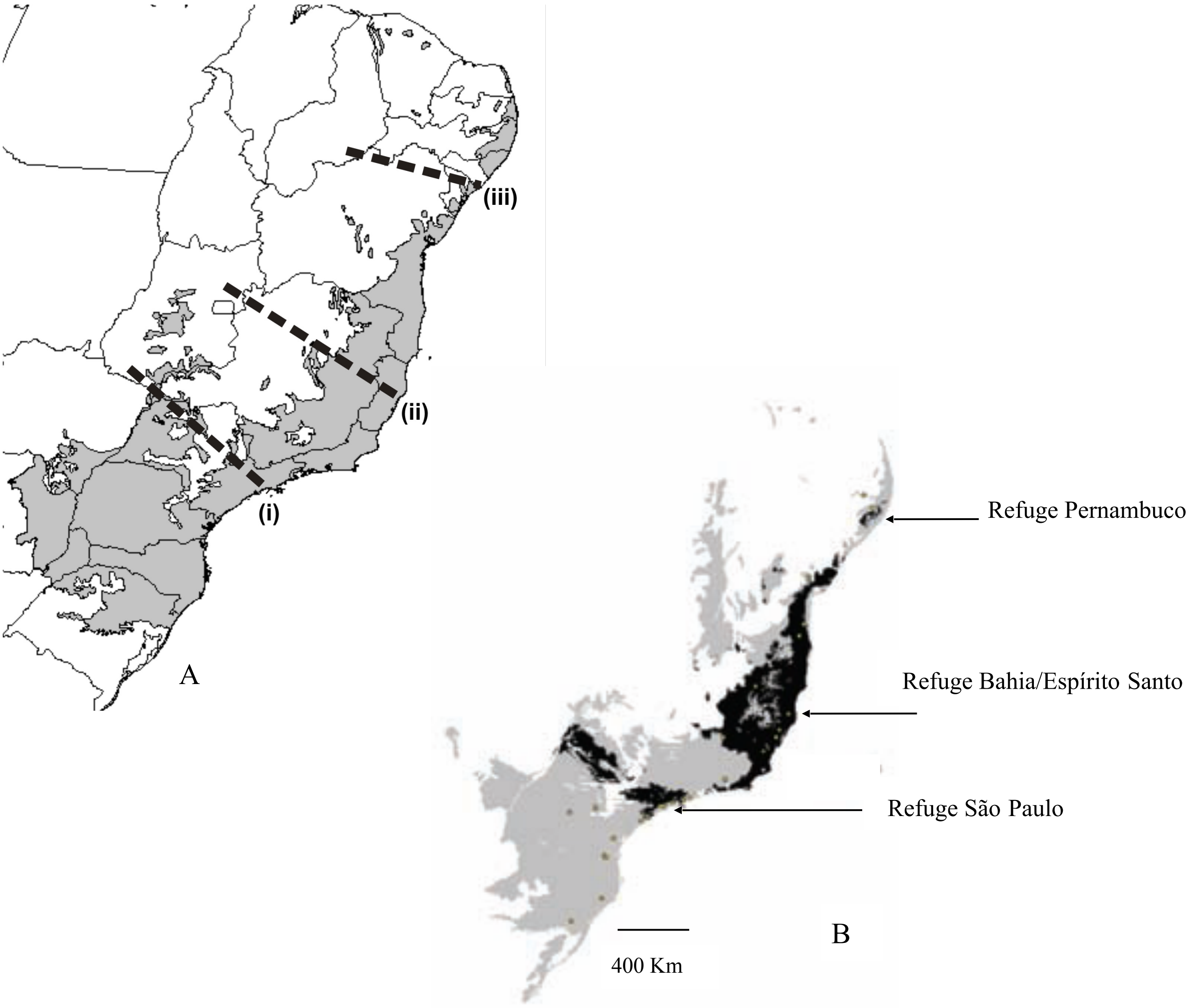


Figure 5. A - Approximate geographical location of the major phylogeographic discontinuities (dotted lines) in the Atlantic Forest (i, ii, iii). Gray area is the original Atlantic Forest (Source: Batalha-Filho & Miyaki 2011). B - Genetic diversity in putative *refugial* (stable) versus unstable areas in the Brazilian Atlantic Forest. Modeled refugia in black (Pernambuco, Bahia/Espírito Santo and São Paulo). Note the absence of large stable regions in the southern portion of the forest (south of the Bahia and São Paulo refugia) relative to the central and northern areas (Source: Carnaval *et al.* 2009).

APPENDIX 1

Brazilian scientific collections (species data from collections list or borrowed):

Museu de Zoologia de São Paulo, SP (MZUSP), Museu Nacional do Rio de Janeiro, RJ (MNRJ), Museu Paraense Emílio Goeldi, Belém, PA (MPEG), Coleção Herpetológica da Universidade de Brasília, DF (CHUNB), Museu de Zoologia da Universidade Estadual de Campinas, SP (ZUEC), Museu de Ciências Naturais da Pontifícia Universidade de Belo Horizonte, MG (MCNR), Coleção Herpetológica do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP), Museu de Zoologia da Universidade Federal de Viçosa, MG (MZUFV), and Museu de Zoologia da Universidade Federal da Bahia, Salvador (UFBA).

Additional literature for the collection sites of species:

Ávila-Pires TCS. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Verhandel, Leiden **299**, 1-706 pp.

Barreto-Lima AF. 2009. Gastric suction as an alternative method in studies of lizard diets: tests in two species of *Enyalius* (Squamata). Studies on Neotropical Fauna and Environment **44** (1): 23-29.

Barreto-Lima AF, Sousa BM. 2011. Feeding ecology and sexual dimorphism of *Enyalius perditus* in an Atlantic forest, Brazil. Herpetological Bulletin **118**: 1-9.

Bertolotto CEV. 2006. *Enyalius* (Leisauridae, Squamata): o que os dados moleculares e cromossômicos revelam sobre esse gênero de lagartos endêmicos do Brasil. PhD Thesis, Universidade de São Paulo, Brazil. 129 pp.

Etheridge R. 1969. A review of the iguanid lizard genus *Enyalius*. Bulletin of the British Museum (Natural History) Zoology **18** (8): 231-260.

Jackson JF. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. Arquivos de Zoologia **30** (1): 1-79.

Rodrigues MT, Freitas MA de, Silva TFS, Bertolloto CEV. 2006. A new species of lizard of genus *Enyalius* (Squamata, Leiosauridae) from the highlands, Chapada Diamantina, state of Bahia, Brazil, with a key to species. Phyllomedusa **5** (1):11-24.

Sousa BM, Cruz CAG. 2008. Hábitos alimentares de *Enyalius perditus* (Squamata, Leiosauridae) no Parque Estadual do Ibitipoca, Minas Gerais, Brasil. Iheringia **98** (2): 260-265.

Teixeira R, Roldi K, Vrcibradic D. 2005. Ecological Comparisons between the Sympatric Lizards *Enyalius bilineatus* and *Enyalius brasiliensis* (Iguanidae, Leiosaurinae) from an Atlantic Rain-Forest Area in Southeastern Brazil. Journal of Herpetology **39** (3): 504-509.

Vrcibradic D, Anjos LA, Vicente JJ, Bursey CR. 2008. Helminth parasites of two sympatric lizards, *Enyalius iheringii* and *E. perditus* (Leiosauridae), from an Atlantic Rainforest area of southeastern Brazil. Acta Parasitology **53**, 222-225.

Borrowed specimens (n = 603): ***E. bibronii*** (17): CHUNB - 6555/56918/57375-79, MZUFV 249/251/287/307/528/, MZUSP-62792/65628/66105/78721/87592. ***E. bilineatus*** (59): CHUNB - 36170-74, MCNR-115/277-78/445/5223/735/1342/1409/1411/1747/3156/3277/3557, MNRJ-6356-57/10136/10861-63/10868-1/1087374/1087980/10882/10890/10892/10919/14413/15575, MZUFV-213-14/241/278/286/314/337/473-74/498, MZUSP- 594/8216/10410/29698/39522/42778, MZUSP-71954/95184/95424-25. ***E. brasiliensis*** (27): MNRJ - 1611/3446/12091/12354-58/17614, MZUFV-109/179/320/472/499/500/508/619, MZUSP-3233-34/427677/10247/39533/39535/39537/95426, PUCRS-5355. ***E. catenatus*** (61): CHUNB - 08183/28984/36175-81, MCNR-542-45/1341/1343/1898, MNRJ-3464/3878/6341-42/6346/10397/10402/10899/12518-20/13238-42/15122, MPEG-1846, MZUFV - 398-99/425/451/454, MZUSP-23086/66174/66422-23/95403-09, PUCRS-9020, UFBA -908/

1085-86/1088-94. ***E. erythroceneus*** (6): MZUSP - 95416-21. ***E. iheringii*** (58): CHUNB - 08184/13460/28882-83, MZUSP - 95390/98131/6864/10136/10271/42713-15/ 76286/ 78954/ 79707/79709-10/95388-89/95391-95/98123-24/98128-30/98132, PUCRS - 1049/5341/6661/ 6673/6675/6703/7775/9525/9539/9726-27/10978/11374/12216/12765/12774/17796-97, ZUEC - 971/1185/1372/1834/2034/2167/2214/2644/3077/3079. ***E. leechii*** (25): CHUNB - 44808-09, MCNR-3558, MNRJ - 4434/18058, MPEG - 13999/14218/17518-19/17543/21926-27, MZUSP - 42728/81526-28/81621-23/81719-22/82412/89943. ***E. perditus*** (67): MCNR - 529/3550-55, MNRJ -1614/3447/6354-55/10141-45/10160/15044/17027, MZUFV - 288/529/ 631/674/728, MZUSP - 584/590/11464/74903/78120/79711/89188-91/91438-45/ 92270/ 94044/94835/95025-32/95427-30/95763-67/96922/97390/98143, ZUEC-1888/1894. ***E. pictus*** (6): MZUFV - 250/427/430/438, MZUSP - 39539-40. ***Enyalius sp*** (40): MCNR -993-94/1043 - 44/1489/1708/1907-08/2156/2217/2567-68/2569-72/2975-2976/3105/ 3392-93/ 3460-63/ 3533/3571, ZUEC-2924-29/2931-32/2940/2943/761-62, MCNR-2221. ***Enyalius sp*** **n.** (234): CHUNB - 3546/8167-68/8170-82/8906-09/8922-23/9588/16942/21808-09/21812-15/21856 /21859-60/21863-64/21873-92/21895-96/21898-99/22001/22022/22048/22741-45/23813/ 23847-53/23951/24056/24058/24212-13/24508/24511/24574/24590/24759/24771-73/24775-80/25021/25025-26/25050-51/25057/25062-63/25067-71/25079/25213-14/25216-17/25313/25315/25362-63/25569/25587-88/25591/25594/25596/25690/26074-79/26081-84/26086/26098/26993/27618-19/27624-25/27627/27631/27638/27682/27724/28884-85/28890/28909-10/29290-95/29311-16/29452-54/2965759/30342/30523/30953/32709/33630/33636-38/33640/33790-91/33797/33905/34000/34004/34013-15/34845-46/35714-15/36555/37462-67/38190-91/38503/38648-49/38651/3877278/38783/3895963/40284/40294/43264/43268/43294 44116/ 48357/52394/ 52396/52407-08, MZUSP-78812/87707/88857/93142-45. ***Enyalius sp*** **n. 2** (3): MCNR - 12222-4. * *All the collection sites of species were considered.*

CAPÍTULO 2/ Chapter 2

Potential niche of *Enyalius* species (Iguanidae, Leiosaurinae): environmental requirements for forest lizards from Brazil

André Felipe Barreto-Lima[a], Guarino Rinaldi Colli[b] and Sandra Maria Hartz[a]

[a] *Laboratório de Ecologia de Populações e Comunidades, Programa de Pós-Graduação em Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil;*

[b] *Laboratório de Herpetologia, Departamento de Zoologia, Instituto de Biociências, Universidade de Brasília, DF, Brazil.*

Corresponding author: E-mail: afblima@hotmail.com

Abstract

This study addressed the potential distribution of *Enyalius* species in the Brazilian biomes to determine the ecological requirements of them. There was a predominance of species in the Atlantic Forest biome. Altitude, latitude, mean diurnal temperature range, annual rainfall, rainfall in the coldest trimester and rainfall in the driest trimester were important for the species. Latitude and the mean diurnal temperature range were predominant variables in the species' distribution models, which expressed a niche of broad spectrum for the majority of species. It is suggested that climatic and geographic requirements exert considerable influence over the adaptation and distribution of *Enyalius*. It is plausible that the life history of the group is linked to the Atlantic Forest, due the biology of the most species dependent upon geographic and climatic characteristics of this biome. The similar potential niches may be explained by abundance of available resources in association with the important phenotypic plasticity of the *Enyalius* species and probably by a phylogenetic inertia presents in the group.

Keywords: biogeography; ecological niche; *Enyalius;* modeling; potential distribution.

Introduction

Macroecological studies have made important advances in the understanding of large-scale ecological patterns, although the causes of these patterns require better explanations (Hawkins 2004). Ecological models presuppose that the patterns observed are the consequence of the influence of climate on the geographic distribution of species, regardless of long-standing processes, such as speciation and extinction on the regional level, with the accumulation of species in more propitious climates (Terribili 2009). Among the different hypothesis put forth, the concept of environmental energy (see Hawkins et al. 2003) suggests that water and energy furnish a compelling explanation for the variation in the diversity of plants and animals from the macroecological standpoint.

Information on the distribution of species is essential to knowledge on areas of occupation and the ecological relationships of populations in their ecosystems or biomes. Potential or ecological niche models constitute a class of methods that employ occurrence data in conjunction with environmental data, in order to establish a correlate model of the environmental conditions that meet the ecological requirements of a given species, predicting the relative suitability to habitat. In recent years there has been increasing interest in studies on species distribution through potential niche modelling (Elith et al. 2006). The modelling technique may be referred to as a model of “species distribution”, “ecological, potential or climatic niche”, among others (Flanklin 2009), which estimates the fundamental niche or realized niche – the multivariate species niche (Rottenberry et al. 2006). Modeling has been a useful tool for the extrapolation of data on the potential distribution of species in time and space, based on statistical models that employ different types of algorithms, and being important to practices applied to Conservation Biology (Flanklin 2009).

Given the importance of knowledge on the distribution of species for conservation, it is necessary to monitor the climate changes and perform the continuous and progressive evaluation of statistical models for the prediction of species distribution (Austin 2007). Data from scientific collections has been used in a number of studies to map the distribution of species and determine conservation areas (Ponder et al. 2001; Elith and Leathwick 2007).

Amphibians and reptiles can serve as models for studying the effects of climatic and environmental characteristics on the distribution of species (Costa et al. 2008). The influence of biotic and abiotic environmental conditions over the life history parameters has been documented in geographic distribution studies (Tinkle and Dunhan 1986; Vitt 1992; Vitt et al. 1998). *Enyalius* genus Wagler, 1830 is made up of diurnal and ombrophilous lizard species endemic to forests from Brazilian biomes (Jackson 1978; Barreto-Lima and Sousa 2011), with broad distribution and commonly found in forests along the eastern coast of the country, in areas under the domain of the Atlantic Forest (Etheridge 1969; Vanzolini 1972). There are nine species recognized: *E. bibronii, E. bilineatus, E. brasiliensis, E. catenaus, E. erythroceneus, E. leechii, E. iheringii, E. perditus* and *E. pictus* (SBH 2011). Distribution ranges from the southeastern of Rio Grande do Norte state (northeastern Brazil) to the northeastern of the Rio Grande do Sul state (southern Brazil) (Jackson 1978), as well as, the southern of the Amazon Forest (where *E. leechii* occurs; Vanzolini 1973; Ávila-Pires 1995), beyond other areas difficult to finding the species, as the gallery forest in southern of the savanna region (e.g. *Cerrado*) and in isolated forests in the semi-arid region (e.g. *Caatinga*). *Enyalius bilineatus* is an exception to the exclusively arboreal habitat (Jackson 1978), also occurring near open formations (*Cerrado*) and in shrub land of *Caatinga* (Bertolotto et al. 2002). *Enyalius erythroceneus* is found only in woodlands in north of the *Serra do Espinhaço,* in central highlands of Chapada Diamantina, northeastern Brazil (Rodrigues et al. 2006).

Moreover, there are still not described species, as *Enyalius sp* n. which occurs in small forest areas in the *Cerrado,* especially in Federal District of Brazil and surrounding areas. Thereby, the broad geographic distribution in different forest formations and environments makes *Enyalius* an interesting study model for the potential niche modelling.

In a previous study, we investigated the potential distribution of the genus as a whole, in order to analyze its geographic distribution, identifying areas of importance and determining the main environmental variables that may explain its presence in Brazilian forests and biomes (Barreto-Lima et al., unpublished data). Because of the need to clarify the real distribution of the genus and the parameters associated with this, we believe that this study may assist in decision making and management of species, preventing the rapid destruction of their forests and the risk of accelerated extinction of species.

The present study models the potential distribution of *Enyalius* species in different biomes (*Cerrado*, *Caatinga*, Atlantic Forest and Amazon Forest). A multivariate approach was applied, integrating climatic and spatial data to analyze the potential distribution and to determine the most important environmental characteristics for each *Enyalius* species. We expect to find different ecological requirements among the species in accordance with the forest formation of each phytogeographic region.

Thus, the following questions were addressed in this study: 1) what environmental variables could express the ecological potential niches of *Enyalius* species in different forest formations?, 2) Are there common predominant environmental characteristics that stand out in the niche potential for the majority of species of the genus?, 3) Are there species with ecological niches with any degree of overlap within a single area and which those overlap more? At last, knowledge of the ecological and geographical limits of *Enyalius* species is important for both, the conservation of tropical forests and reptiles species.

Material and Methods

Data collection

Information on the *Enyalius* species was obtained from scientific collections of Brazil (borrowed and list from collection) and the literature, considering the collection sites and the numbers for each specimen studied (Appendix 1) - the species identification was performed by first author. We used data of 1,256 specimen records of nine species from 363 sites, in order to use in the potential distribution analysis (see Appendix 1). Only *E. erythroceneus* was not analyzed due there is one collect locality, being impossible to perform a modeling based in a single point. Data on the sites recorded were transformed in geographic coordinates (local or municipal) for the mapping of the distribution model of species. For the confirmation of the geographic coordinates, Google Earth (2010) was used for visualization by satellite images of the registered sites - data were used from the literature and official documents available on the web about the location of Brazilian conservation units, where the lizards were collected. All sites in forest areas, even those near or within cities, were considered. However, sites recorded in metropolises without current vegetal cover were not considered, nor the imprecise sites, dubious or those located in forest fragments and islands with a radius of less than 2.5 km.

Modeling

The Maxent v.3.3.3 (Phillips et al. 2006) was used to establish the distribution map of each species; this software uses the principle of maximum entropy on presence-only data to estimate a set of functions that relate environmental variables and habitat suitability, approximating the niche and potential geographic distribution of species. These approaches assume correlative associations between the sites where a species occurs and the local environmental conditions, providing useful information regarding the ecological requirements of the modeled species (Puschendorf et al. 2009).

Ten potential distribution models were generated considering the mean in the final map and using the random selection of 30% of the sites registered to test the models. The environmental variables were obtained from each location by geographic coordinates on a resolution scale of 2.5 arc minutes, using the Worldclim databank (Hjimans et al. 2005) for the last 50 years.

Then, we extracted a total of 24 environmental variables for a pre-selection of these in analysis: latitude and longitude (decimal degrees), altitude (m), aspect (direction of relief in %), vegetal cover or normalized difference vegetation index (intensity scale: 0 to 255), annual mean temperature (Bio1), mean diurnal temperature range (Bio2 – mean of monthly (maximum temperature – minimum temperature)), isothermality (Bio3 – mean diurnal temperature range/annual temperature range), temperature seasonality (Bio4 – standard deviation * 100), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), temperature annual range (Bio7 = Bio5 – Bio6), mean temperature of the wettest quarter (Bio8), mean temperature of the driest quarter (Bio9), mean temperature of the warmest quarter (Bio10), mean temperature of the coldest quarter (Bio11), annual mean precipitation (Bio12), precipitation in the wettest month (Bio13), precipitation in the driest month (Bio14), precipitation seasonality (Bio15 – coefficient of variation), precipitation in the wettest quarter (Bio16), precipitation in the driest quarter (Bio17), precipitation in the warmest month (Bio18) and precipitation in the coldest quarter (Bio19).

Distribution maps

The potential distribution maps of the species were generated on the ArcGIS v.9.3 program. The distribution probabilities of each species were grouped into three intervals (0 to 0.1, 0.2 to 0.5 and 0.6 to 1) using the *Reclassify* tool. The records of occurrences of species were plotted on the potential distribution maps.

Calculation of areas of overlap

To calculate the area of overlap between species, the distribution area (DA) was defined as that which the probability of occurrence of species was greater than 50%. The maximal limits of the DA were the contours of Brazil to the east, south and north, as well as, the 54^{o} meridian to the west for the majority species (except for *E. leechii* and *Enyalius sp* n.). Thus, DAs were generated for each species using the *Reclassify* tool from ArcGIS v.9.3. Next, the *Intersect* tool was then used to determine the overlap area (OA) between pairs of species that visibly exhibit some degree of overlap throughout their distributions. The *X Tools* was used to calculate the DAs of each species and OAs (in Km^2). The percentage of overlap between two species (*x, y*) was calculated using the following formula:

$$\% \text{ of OA between } x \text{ and } y = (\text{OA}/\text{DA}x + \text{DA}y)*100$$

Data analysis

The pre-selection analyses of the environmental variables were performed using the R 2.10.1(2009) with the level of significance in all tests of 5% ($p < 0.05$). Multivariate correlation tests were first performed among the environmental variables to avoid collinearity in the models. Variables with correlations above 75% were discarded ($p < 0.005$) in order to avoid redundancies in the models of species.

After the pre-selection analysis, nine environmental variables were considered in the final analyses of potential distribution of the species: altitude, aspect, latitude, vegetal cover (ndvi), annual mean temperature, mean diurnal temperature range, annual precipitation, precipitation of the driest quarter and precipitation of the coldest quarter.

Results

Potential distribution and niche of species

All potential models generated had areas under the curve values above 0.90, indicating a high degree of coherence in relation to the distribution of actual records (Figure 1.a-i). In general, *E. bibronii*, *E. catenatus* and *E. leechii* were the most widely distributed in Brazil. The majority of species had greater probabilities of occurrence in the coastal areas of the Atlantic Forest; *E. bilineatus, E. bibronii, E. brasiliensis, E. catenatus, E. iheringii, E. perditus* and *E. pictus*.

However, some species had greater probabilities of occurrence in areas more inland within of Atlantic Forest domain; *E. bibronii, E. bilineatus, E. brasiliensis* and *E. pictus.* Beyond the domain of the Atlantic Forest, *E. leechii* had greater occurrence in the Amazon Forest and *Enyalius sp* n. had greater occurrence in forest areas of the *Cerrado*. In addition, *E. bibronii* had greater occurrence in areas of the *Caatinga.*

In general, among the environmental variables used in the distribution models (Table 1), altitude, latitude, mean diurnal temperature range, annual precipitation, precipitation in the coldest quarter and precipitation in the driest quarter were important to the *Enyalius* species. However, latitude and mean diurnal temperature range were the environmental variables that most stood out in the potential distribution models for most species of *Enyalius* (Table 1).

When permuting each variable, considering its absence or its use separately from others, the most important variables in the potential distribution models were the precipitation in the coldest quarter (for *E. bibronii, E. perditus* and *Enyalius sp* n.), precipitation in the driest quarter (for *E. bilineatus* and *E. brasiliensis*), mean diurnal temperature range (for *E. catenatus*) and latitude (for *E. iheringii, E. leechii* and *E. pictus*).

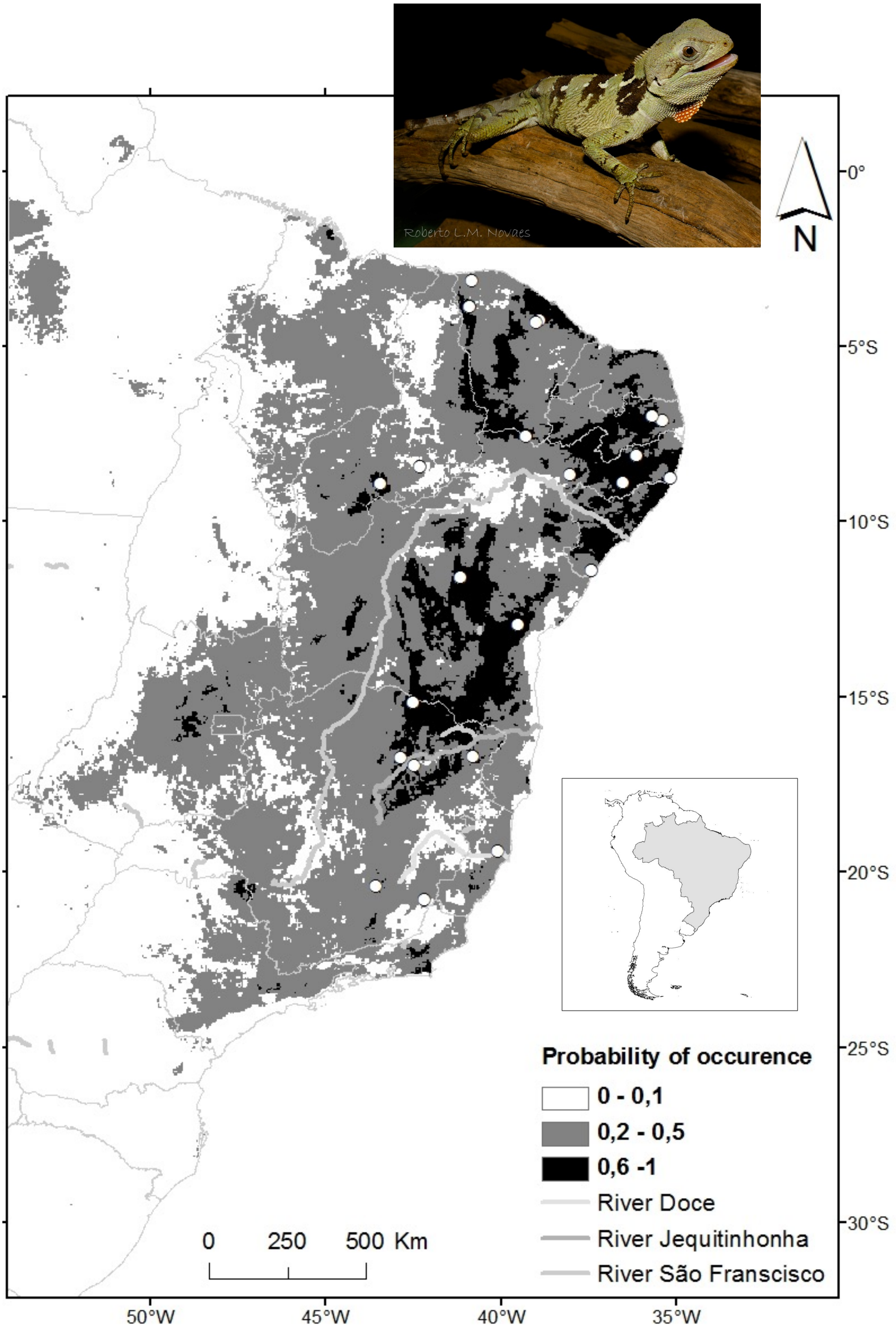


Figure 1.a) Potential distribution model for *Enyalius bibronii* (AUC = 0.91, dp = 0.047).

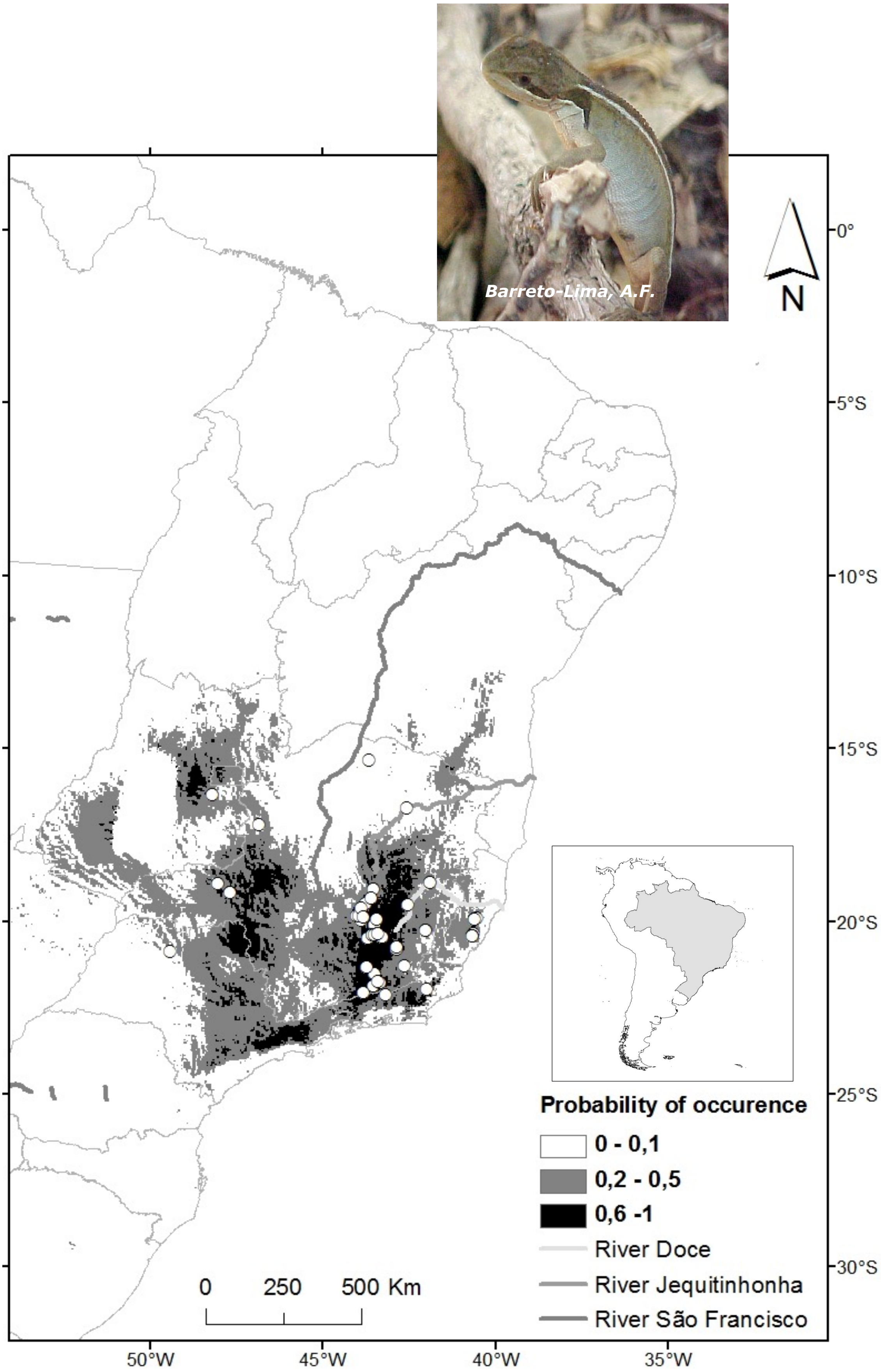


Figure 1.b) Potential distribution model for *Enyalius bilineatus* (AUC = 0.98, dp = 0.025).

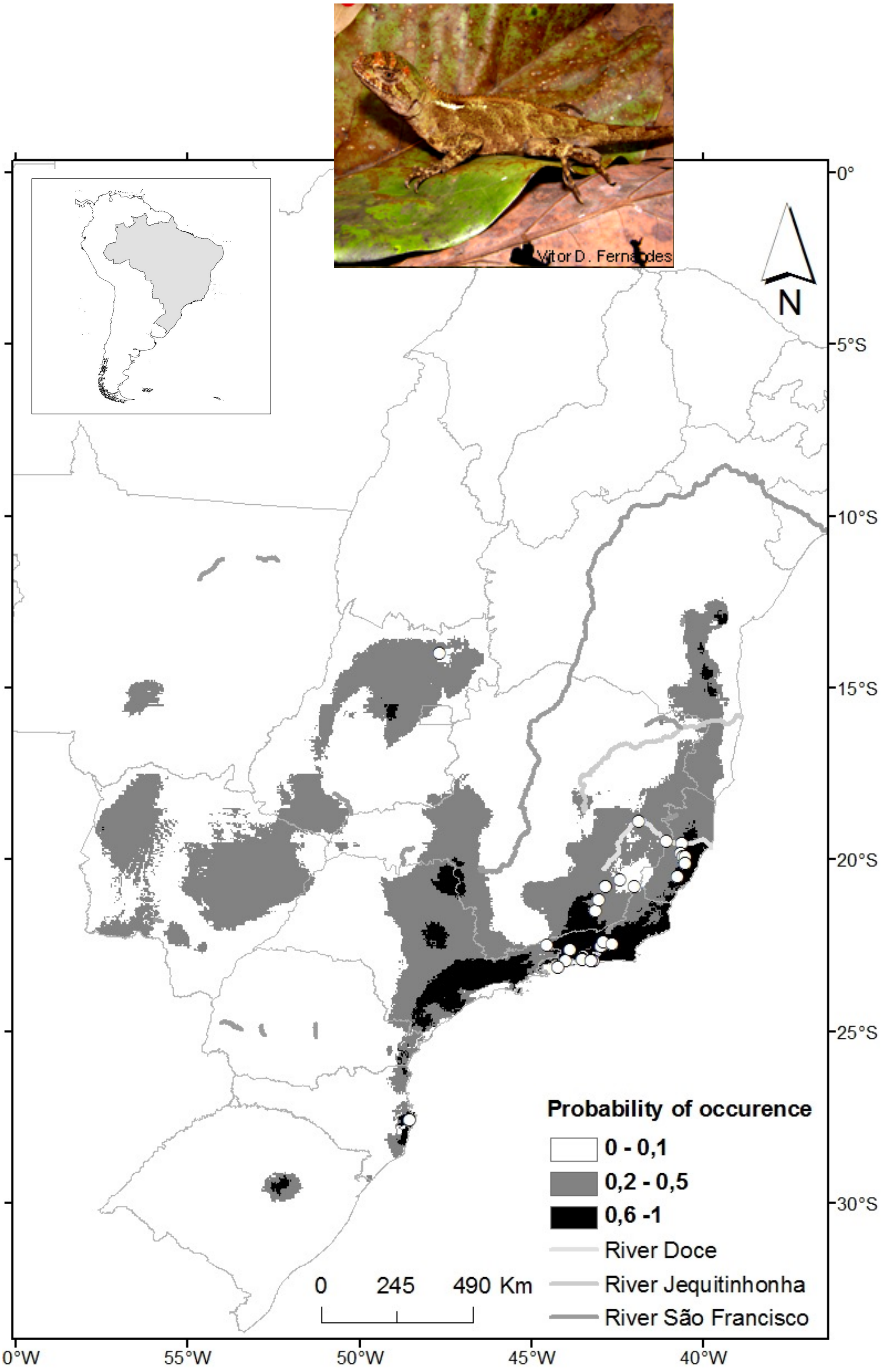


Figure 1.c) Potential distribution model for *Enyalius brasiliensis* (AUC = 0.98, dp = 0.016).

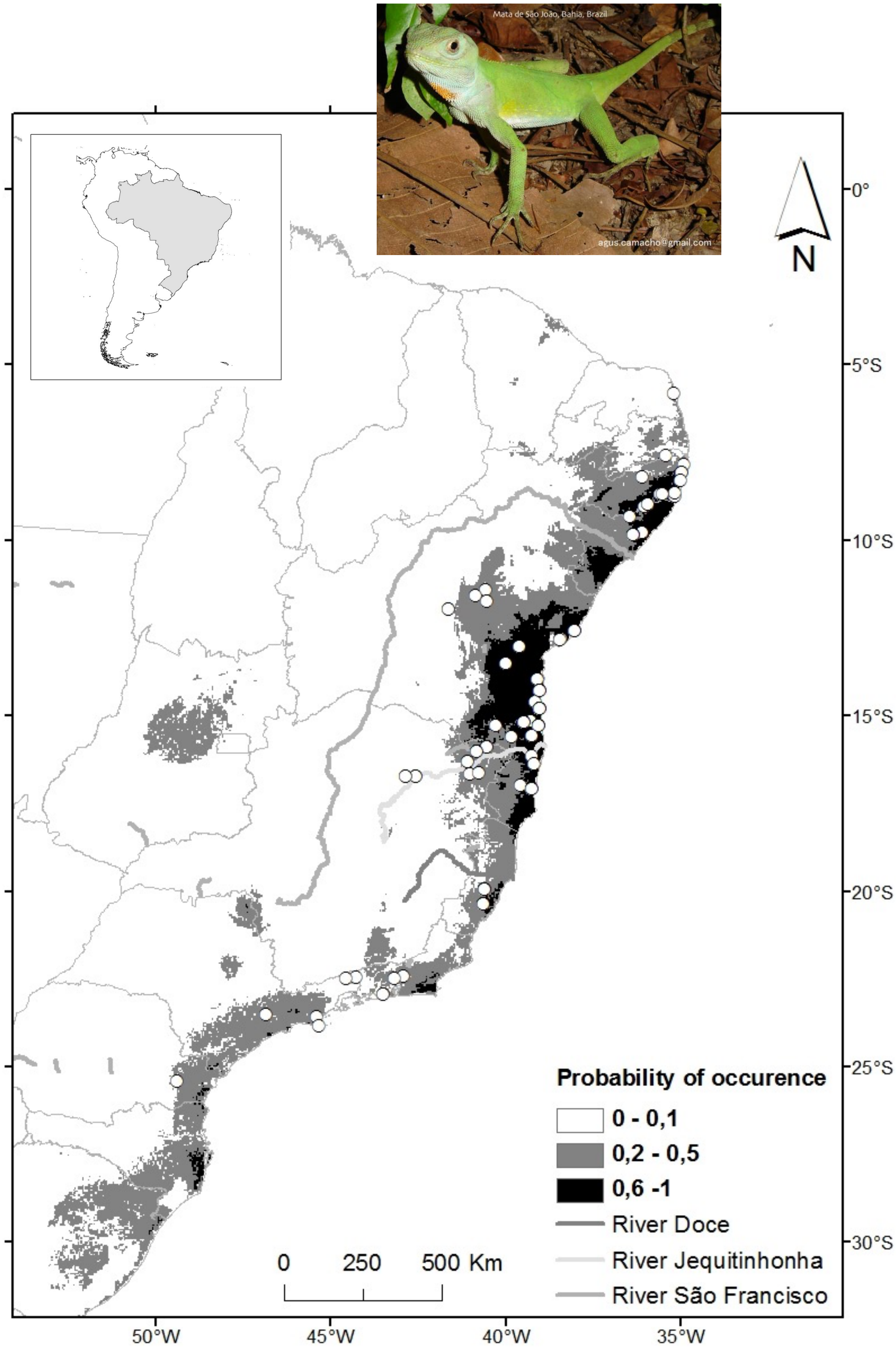


Figure 1.d) Potential distribution model for *Enyalius catenatus* (AUC = 0.97, dp = 0.013).

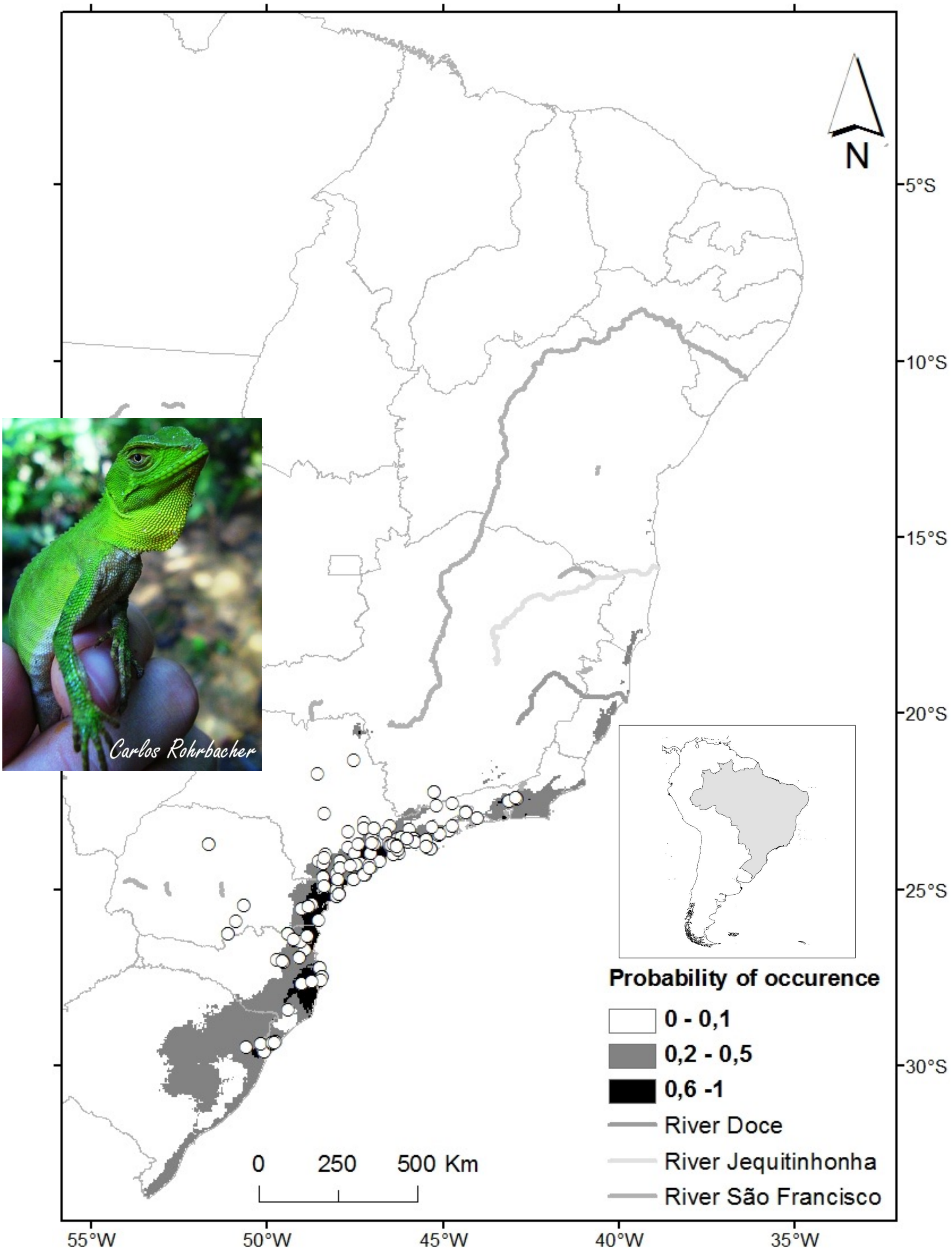


Figure 1.e) Potential distribution model for *Enyalius iheringii* (AUC = 0.99, dp = 0.003).

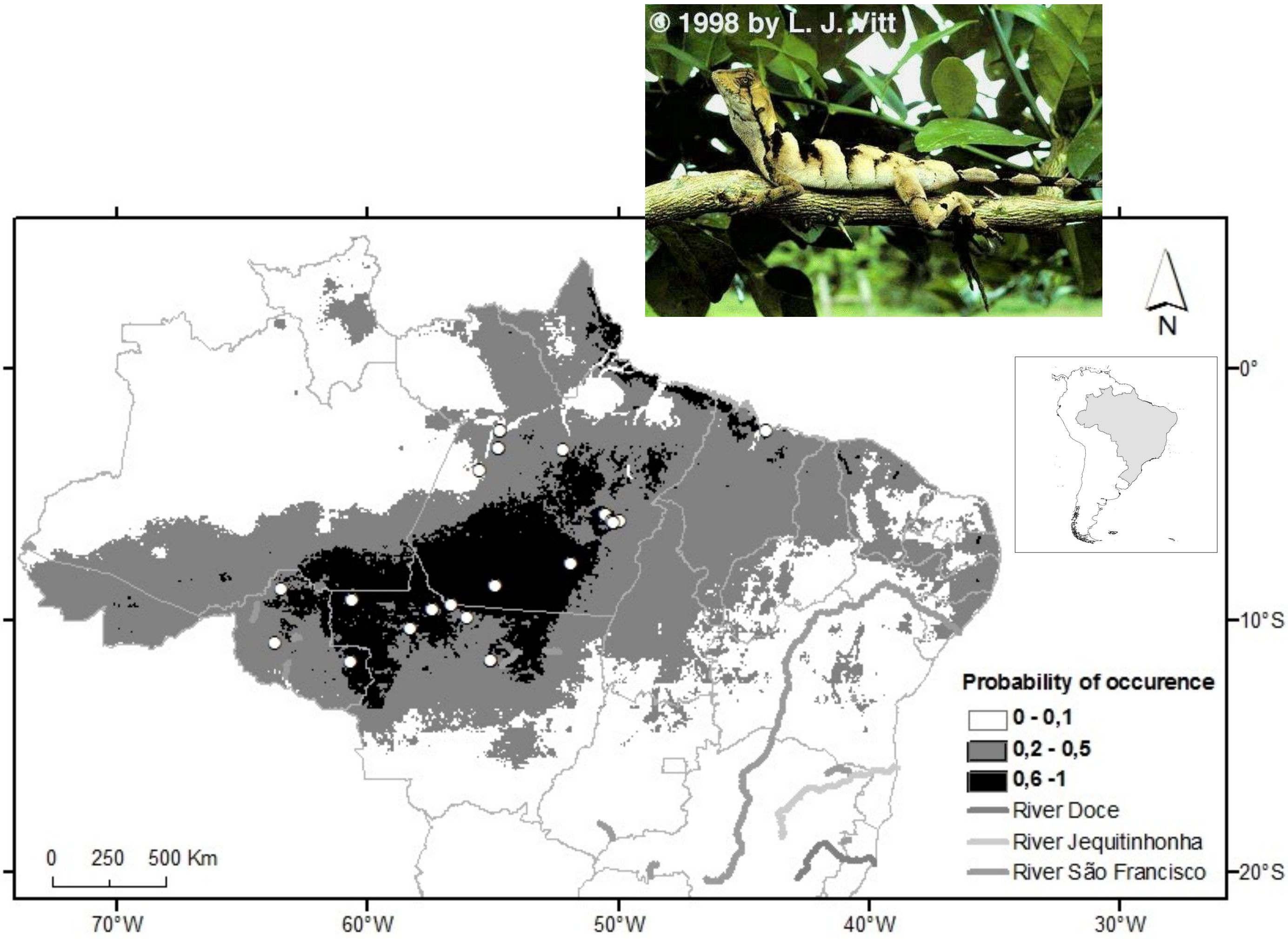


Figure 1.f) Potential distribution model for *Enyalius leechii* (AUC = 0.92, dp = 0.027).

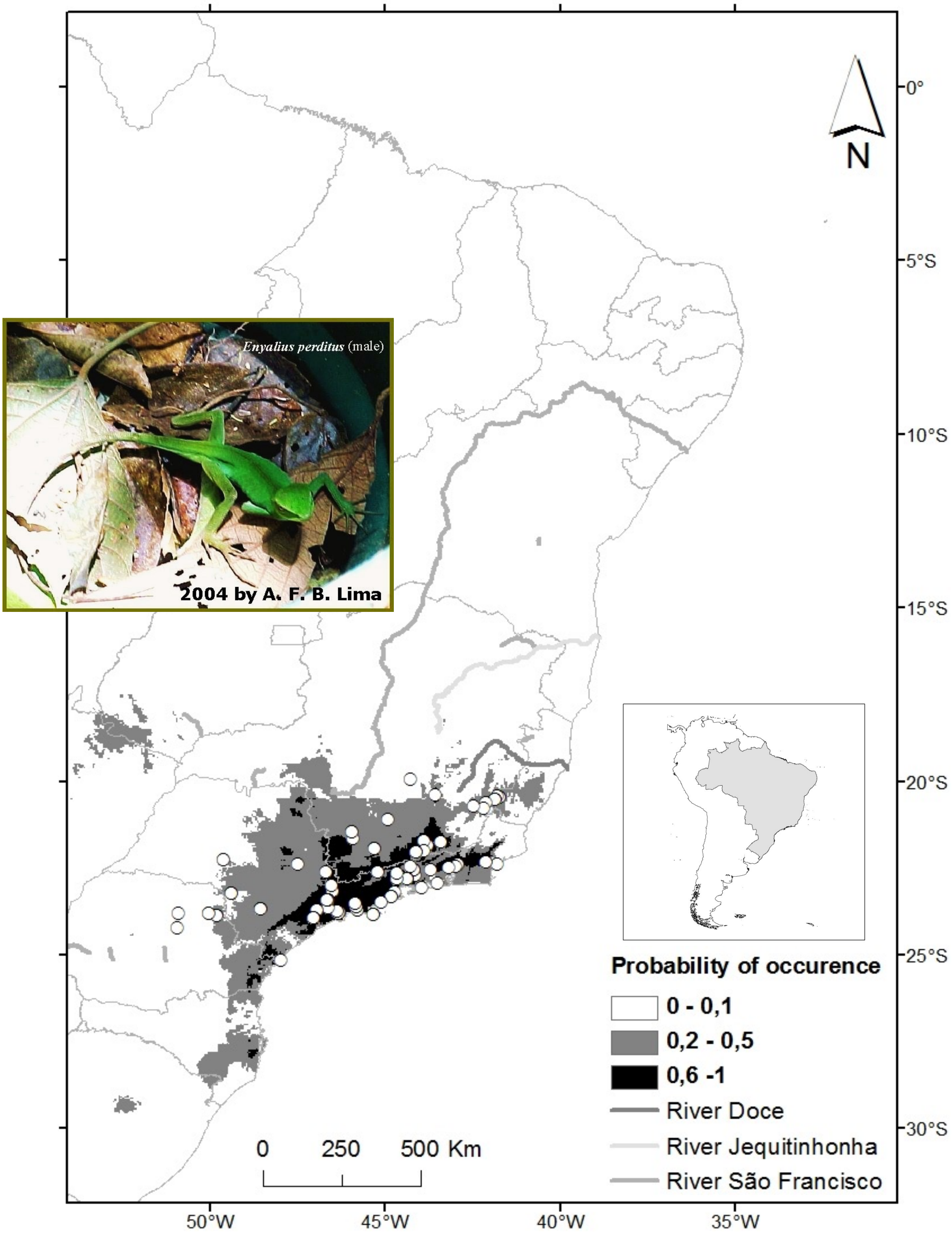


Figure 1.g) Potential distribution model for *Enyalius perditus* (AUC = 0.98, dp = 0.006).

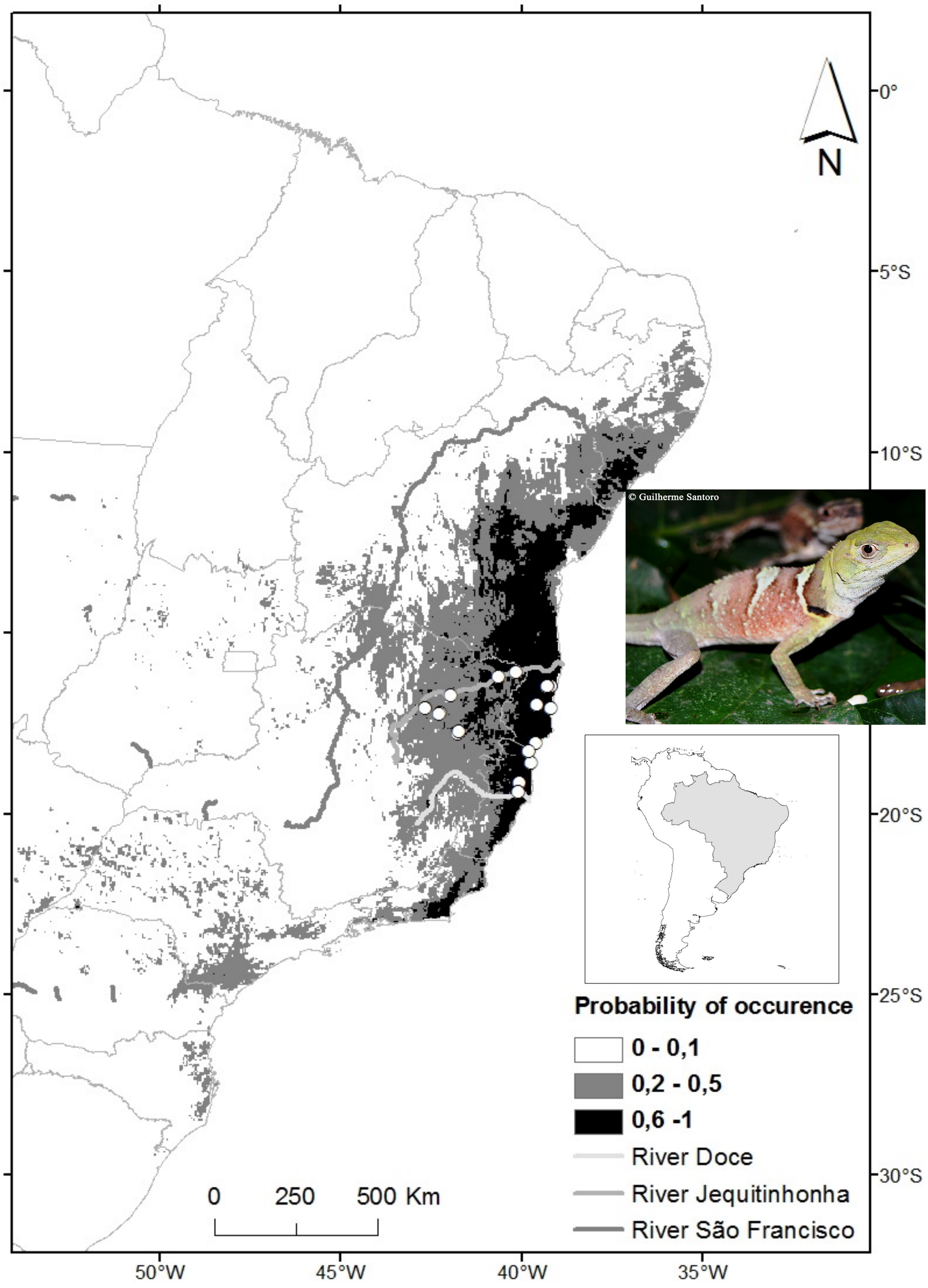


Figure 1.h) Potential distribution model for *Enyalius pictus* (AUC = 0.98, dp = 0.012).

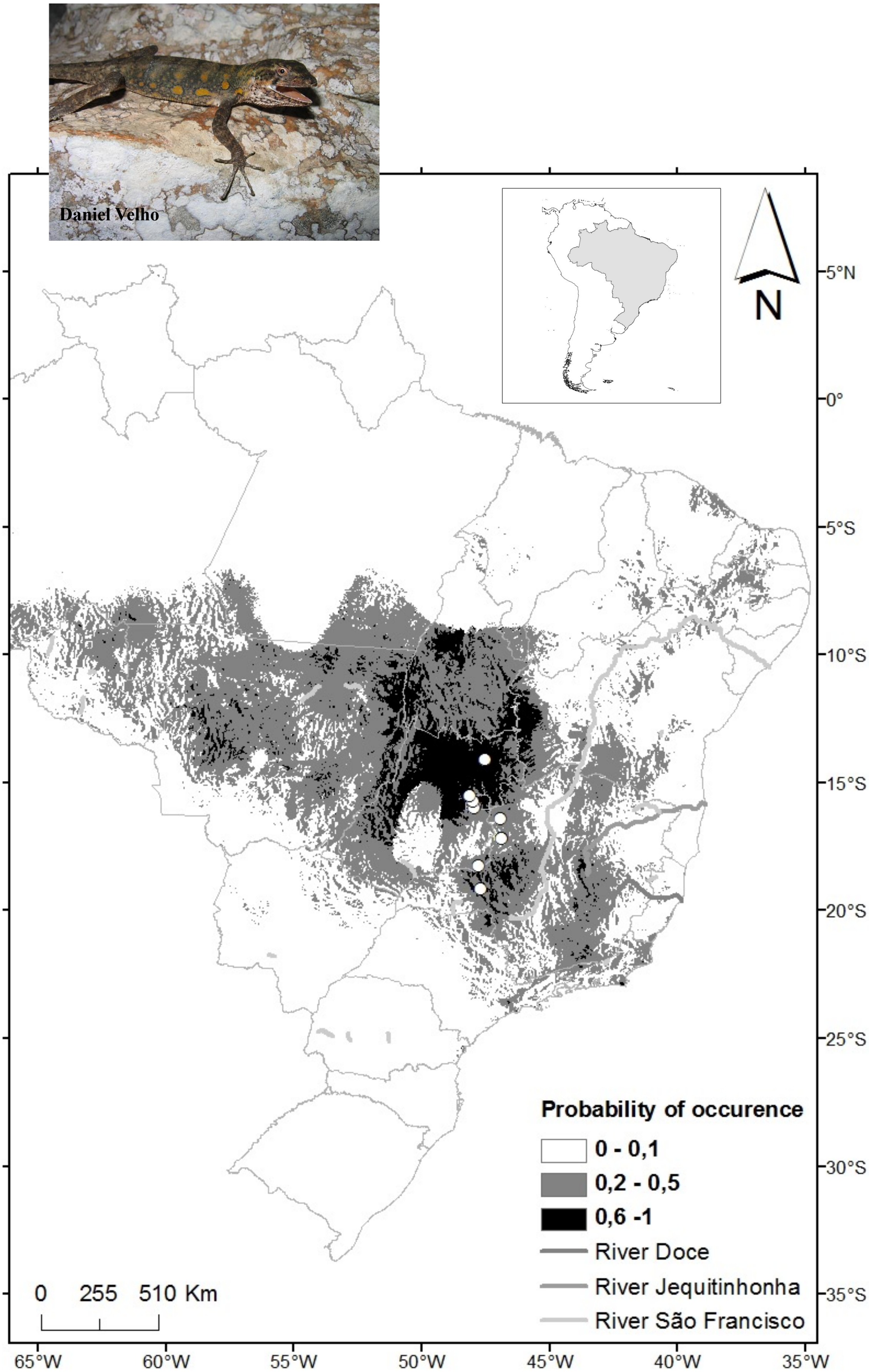


Figure 1.i) Potential distribution model for *Enyalius sp* n. (AUC = 0.94, dp = 0.055).

Table 1. Most important environmental variables in the distribution models for *Enyalius* species (52 *E. bibronii*, 111 *E. bilineatus*, 67 *E. brasiliensis*, 146 *E. catenatus*, 330 *E. iheringii*, 45 *E. leechii*, 221 *E. perditus*, 36 *E. pictus* and 248 *Enyalius sp* n.); PC - percentage of contribution to potential model; PI - permutation importance of potential model. Bio 1 - Annual mean temperature, Bio 2 - Mean diurnal temperature range, Alt - Altitude, Asp - Aspect, ndvi - vegetal cover, Lat - Latitude, Bio 12 - Annual mean precipitation, Bio 17 - Precipitation of the driest quarter, and Bio 19 - Precipitation of the coldest quarter. *Missing values in table indicate that variables were not representative in potential distribution modelling for the species.

	bibronii		*bilineatus*		*brasiliensis*		*catenatus*		*iheringii*		*leechii*		*perditus*		*pictus*		*sp* n.	
Variables	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
Bio1											1.8	12.8						
Bio2	**21.3**	11.6	7.2	11.1	**21.6**	16.4	**56.5**	49.5	**25.1**	16.4			7.8	4.0	9.1	4.3	9.9	5.6
Alt	**23.2**	11.8	**31.9**	3.0	4.1	11.9	7. 3	6.9	3.7	1.5	3.1	6.3	**19.8**	4.8	6.5	14.3	2.1	0.3
Aspect			3.3	0.6			1.2	1.3							6.0	0.9	2.7	0.3
ndvi	15.8	16.8					5.5	2.5			**31.0**	2.8			8.7	7.7	5.7	10.7
Lat	8.9	7.6	**24.2**	18.5	**40.9**	16.4	**22.5**	32.7	**43.2**	49.9	13.4	39.8	**38.7**	32.1	**30.4**	43.8		
Bio12	13.1	24.2	13.7	57.4	9.0	7.6	1.3	3.7	7.1	9.4	9.1	7.5	9.7	16.2	**20.5**	28.9	**22.5**	17.4
Bio17	17.7	28.0	6.1	4.8	8.1	1.6	5.8	3.3	17.1	3.8	**39.6**	30.7	17.3	7.7			3.5	2.8
Bio19					16.3	45.7			3.9	19.1	1.9	0.1	6.8	35.3	18.8		**53.5**	62.9

Niches overlap in species' areas

Partial niche overlap was found for *E. brasiliensis*, *E. iheringii*, *E. perditus* and *E. pictus*, being the latitude the most important variable with predominance in areas under the domain of the Atlantic Forest, in the southeastern region. Altitude was the most important with partial niche overlap for *E. bilineatus* and *E. bibronii*, in Atlantic Forest, although the OA was small (5.05%) (Table 2). The total area of potential distribution and combinations of overlap areas of each species pair (in %) were determined, as well as, the total polygon of sampling (Table 2). *Enyalius catenaus* and *E. pictus* had the highest overlapping areas (26.89%) in their distributions (Figure 2a.), although these showed a great variation of important environmental variables between them (Table 2). Among the most representative overlaps, *E. brasiliensis* and *E. perditus* overlapped the greatest number of times, including between themselves (Figure 2b.), being the second greatest overlap among the combinations (22.84%). In part, *E. bilineatus* overlaps with *E. brasiliensis* (18.2%) (Figure 2c.), whereas *E. perditus* shares specific environmental characteristics with *E. bilineatus* (15.01%) and *E. iheringii* (14.41%) (Figure 2d-e.). Moreover, *E. bibronii* shares part of its area with *E. catenatus* (15.29%) and *E. pictus* (16.04%) (Figure 2f-g.). A small area to *E. brasiliensis* in the central *Cerrado* is probably an extrapolation of model or a possible identification mistake in the literature or in data considered. The same can be told to *E. bilineatus*; it was quite confused with *Enyalius sp* n. until recently. According to the combinations among species and variables, the altitude was the most important indicating a partial overlap potential niche for *E. bilineatus* and *E. bibronii* in Atlantic Forest, although the first one is common in southeast and the second, in northeastern Brazil (*Caatinga*). There was a overlapping partially potential niche for *E. brasiliensis*, *E. iheringii*, *E. perditus* and *E. pictus*, where the latitude was the most important variable with predominance in southeastern Brazil, in the Atlantic forest, though *E. pictus* is commonly found in the northeast Brazil, in Bahia state.

Table 2. Total areas and overlap (%) among *Enyalius* species; areas in square kilometers (Km^2). Total area of Brazil = 8,718,892.6 Km^2; combinations of species; total area of species (TA); overlap areas (OA); percentage of overlap (OA/TA)*100. *Polygon of the total area of sampling points = 5,501,505.5 Km^2.

Species	Area	Combinations of species	Total area of species (TA)	Overlap areas (OA)	Percentage of overlap (OA/TA)*100
E. bibronii	553,426.60	*E. bibronii* + *E. bilineatus*	742,361.27	37,504.55	5.05
E. bilineatus	188,934.67	*E. bibronii* + *E. brasiliensis*	730,955.85	33,005.87	4.52
E. brasiliensis	177,529.25	***E. bibronii* + *E. catenatus***	749,026.52	114,500.60	**15.29**
E. catenatus	195,599.92	*E. bibronii* + *E. iheringii*	607,484.04	699.03	0.12
E. iheringii	54,057.44	*E. bibronii* + *E. perditus*	666,746.74	14,325.33	2.15
E. perditus	113,320.14	***E. bibronii* + *E. pictus***	825,340.59	132,414.91	**16.04**
E. pictus	271,913.99	***E. bilineatus* + *E. brasiliensis***	366,463.92	66,714.22	**18.20**
Enyalius sp n.	542,757.24	*E. bilineatus* + *E. catenatus*	384,534.59	4,538.85	1.18
E. leechii	1,473,044.21	*E. bilineatus* + *E. iheringii*	242,992.11	2,912.90	1.20
		E. bilineatus* + *E. perditus	302,254.81	45,355.70	**15.01**
		E. bilineatus + *E. pictus*	460,848.66	4,869.42	1.06
		E. brasiliensis + *E. catenatus*	373,129.16	25,733.06	6.90
		E. brasiliensis + *E. iheringii*	231,586.70	22,673.33	9.79
		E. brasiliensis* + *E. perditus	290,849.39	66,426.66	**22.84**
		E. brasiliensis + *E. pictus*	449,443.24	40,113.03	8.93
		E. catenatus + *E. iheringii*	249,657.35	12,355.58	4.95
		E. catenatus + *E. perditus*	308,920.06	9,450.88	3.06
		E. catenatus* + *E. pictus	467,513.91	123,693.64	**26.89**
		E. iheringii* + *E. perditus	167,277.58	24,113.95	**14.41**
		E. iheringii + *E. pictus*	325,971.43	823.31	0.25
		E. pictus + *E. perditus*	38.5234,13	1136,73	0,30
		E. leechii + *Enyalius sp* n.	2.015801,45	32.036,50	1,59

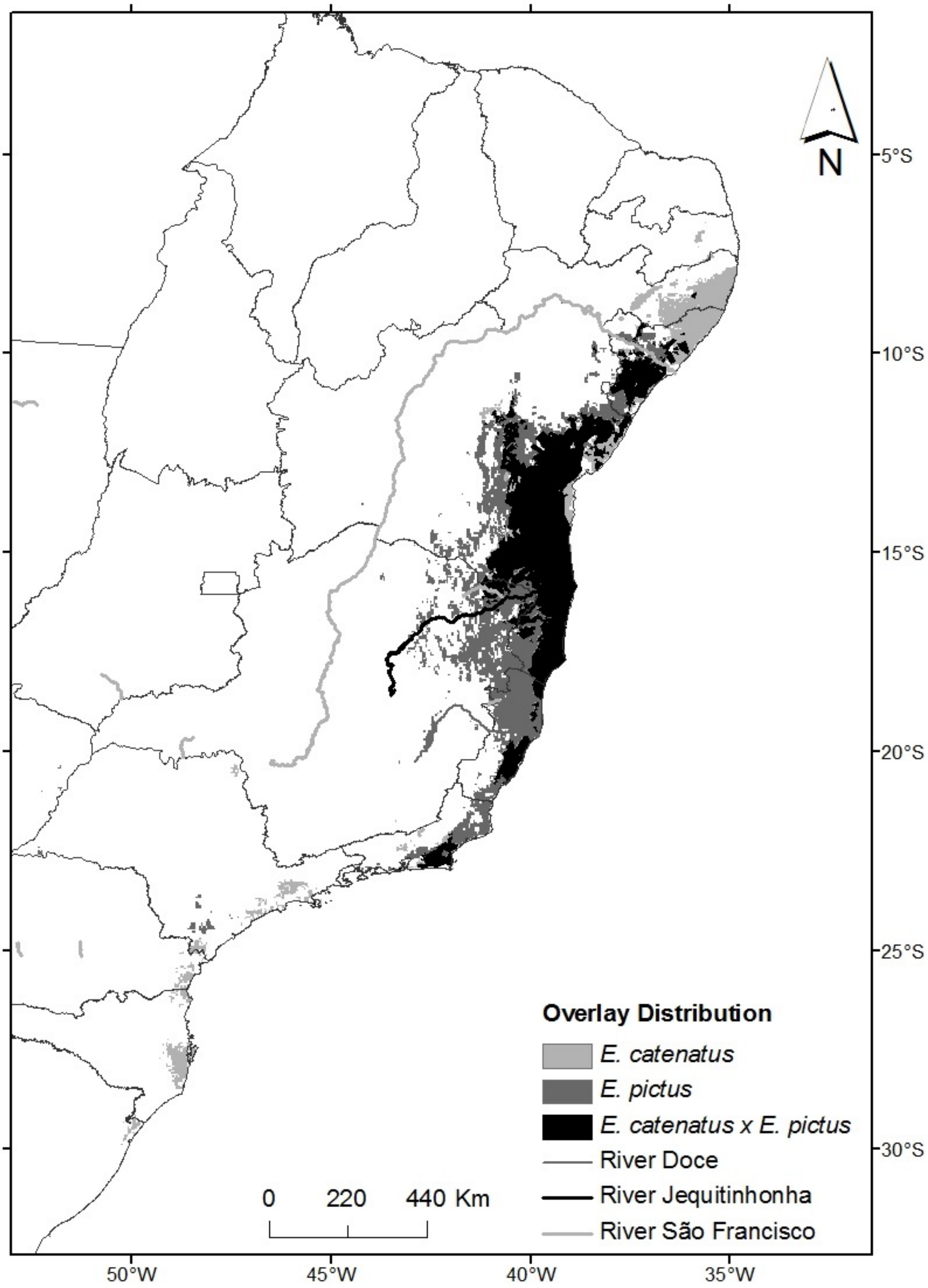


Figure 2.a) Overlapping areas between *Enyalius catenatus* and *Enyalius pictus*.

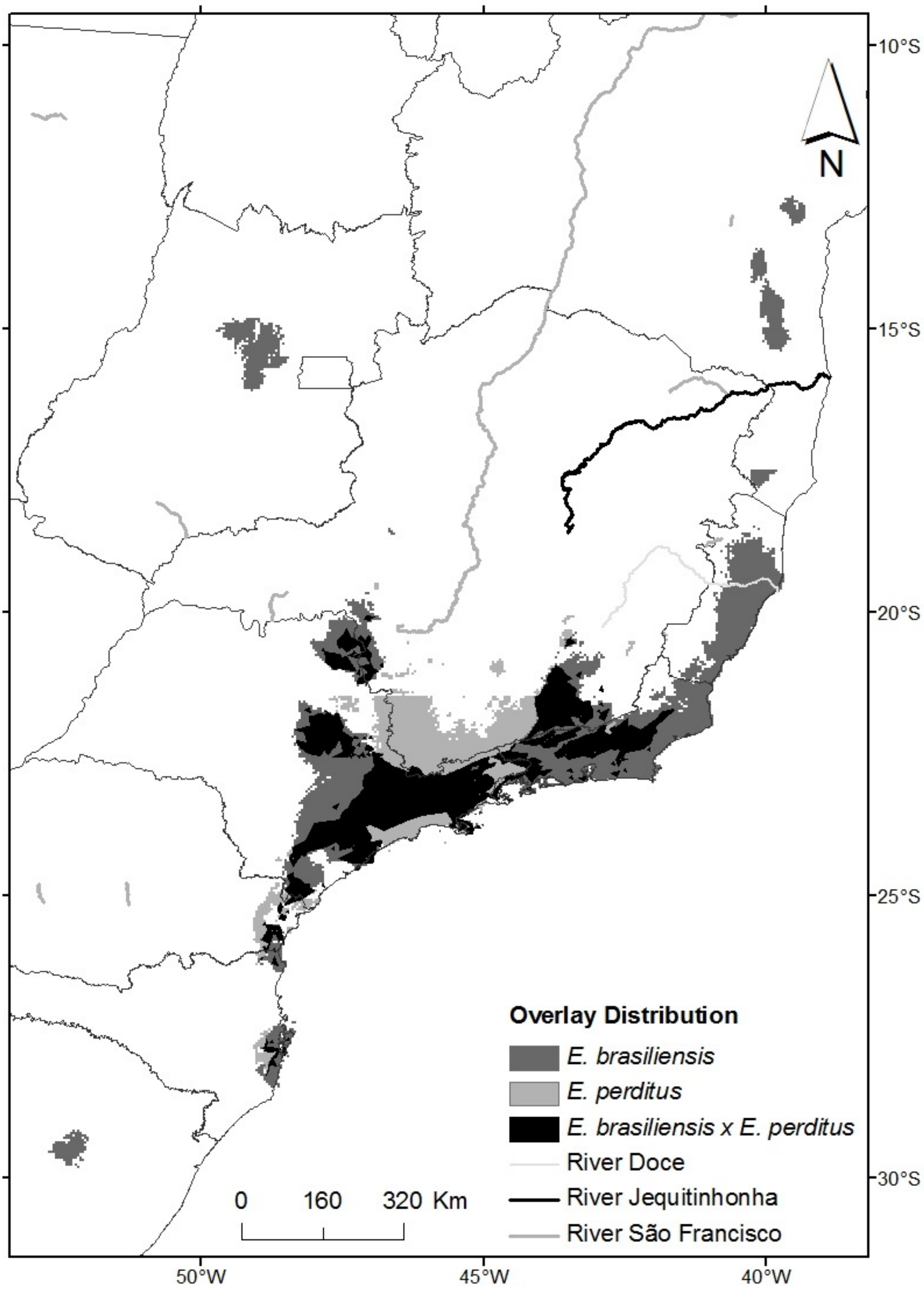


Figure 2.b) Overlapping areas between *Enyalius brasiliensis* and *Enyalius perditus*.

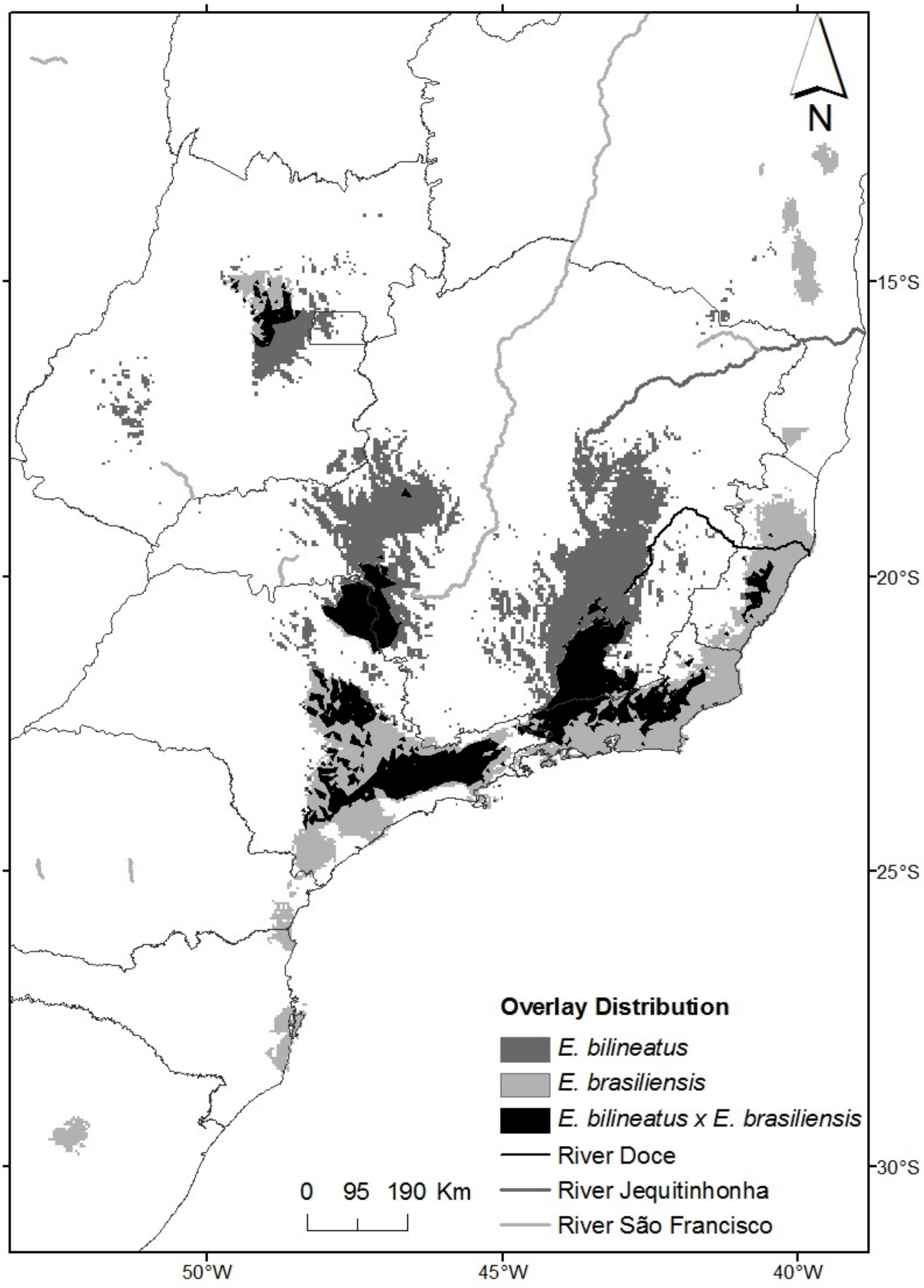


Figure 2.c) Overlapping areas between *Enyalius bilineatus* and *Enyalius brasiliensis*.

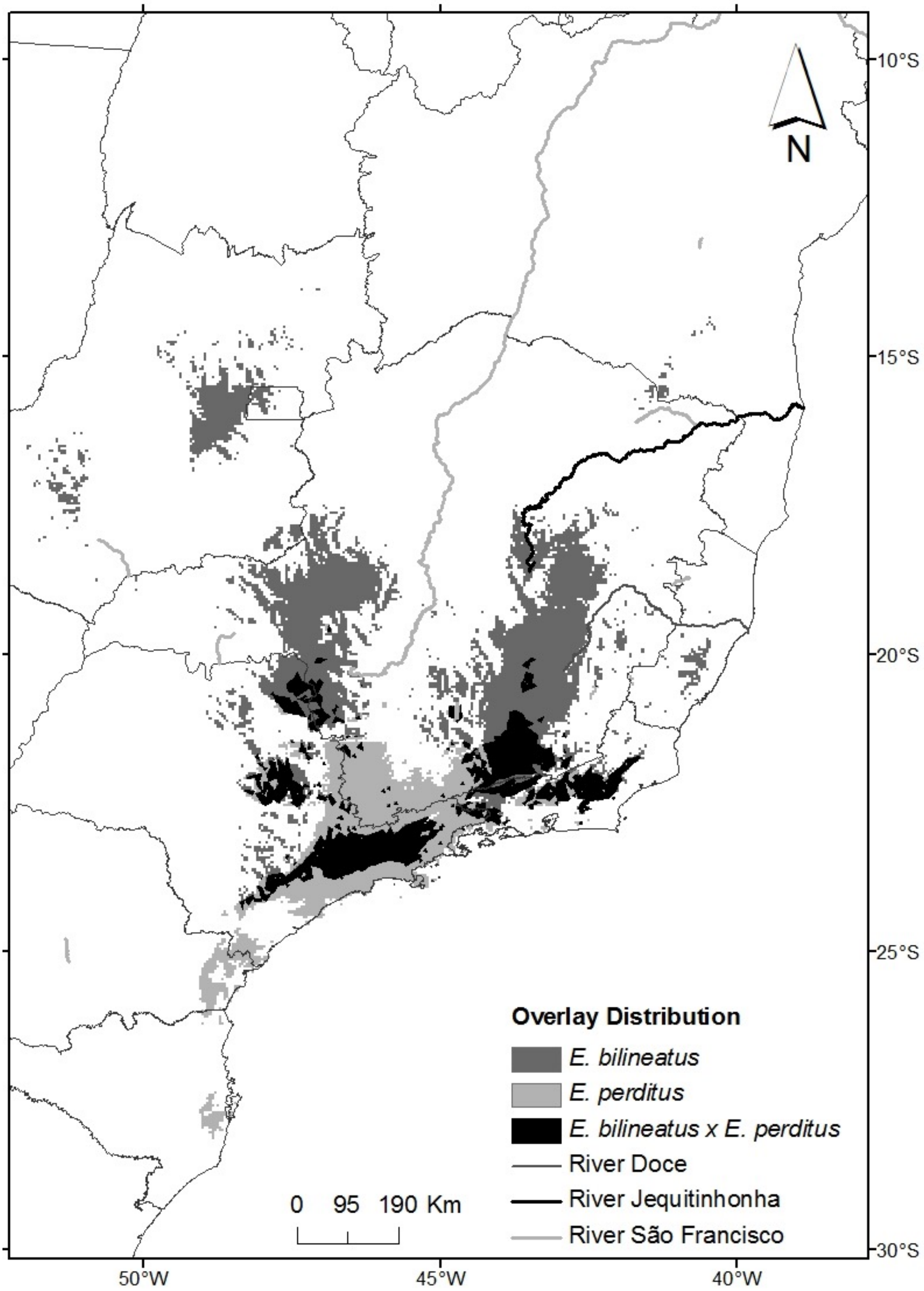


Figure 2.d) Overlapping areas between *Enyalius bilineatus* and *Enyalius perditus*.

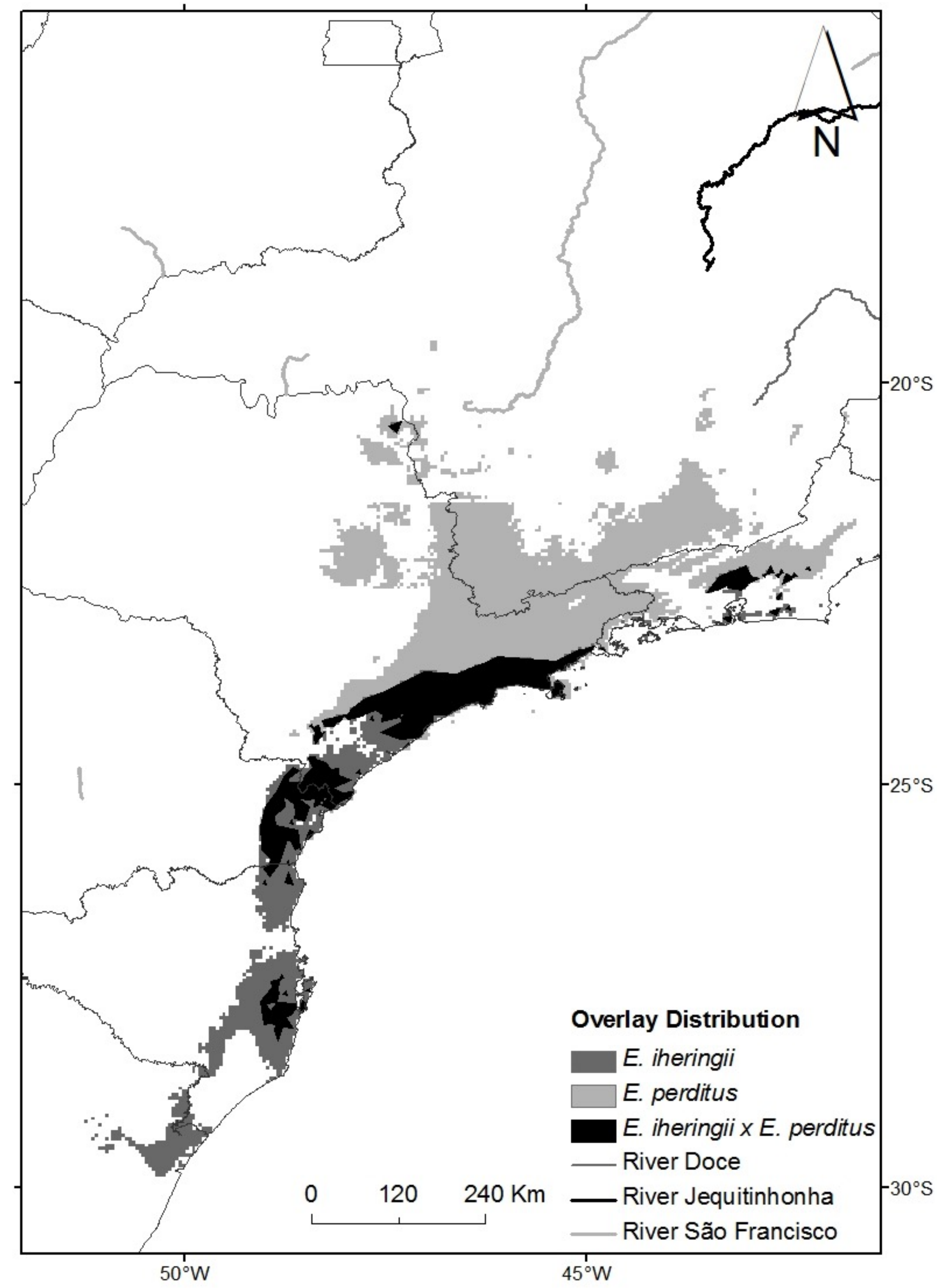


Figure 2.e) Overlapping areas between *Enyalius iheringii* and *Enyalius perditus*.

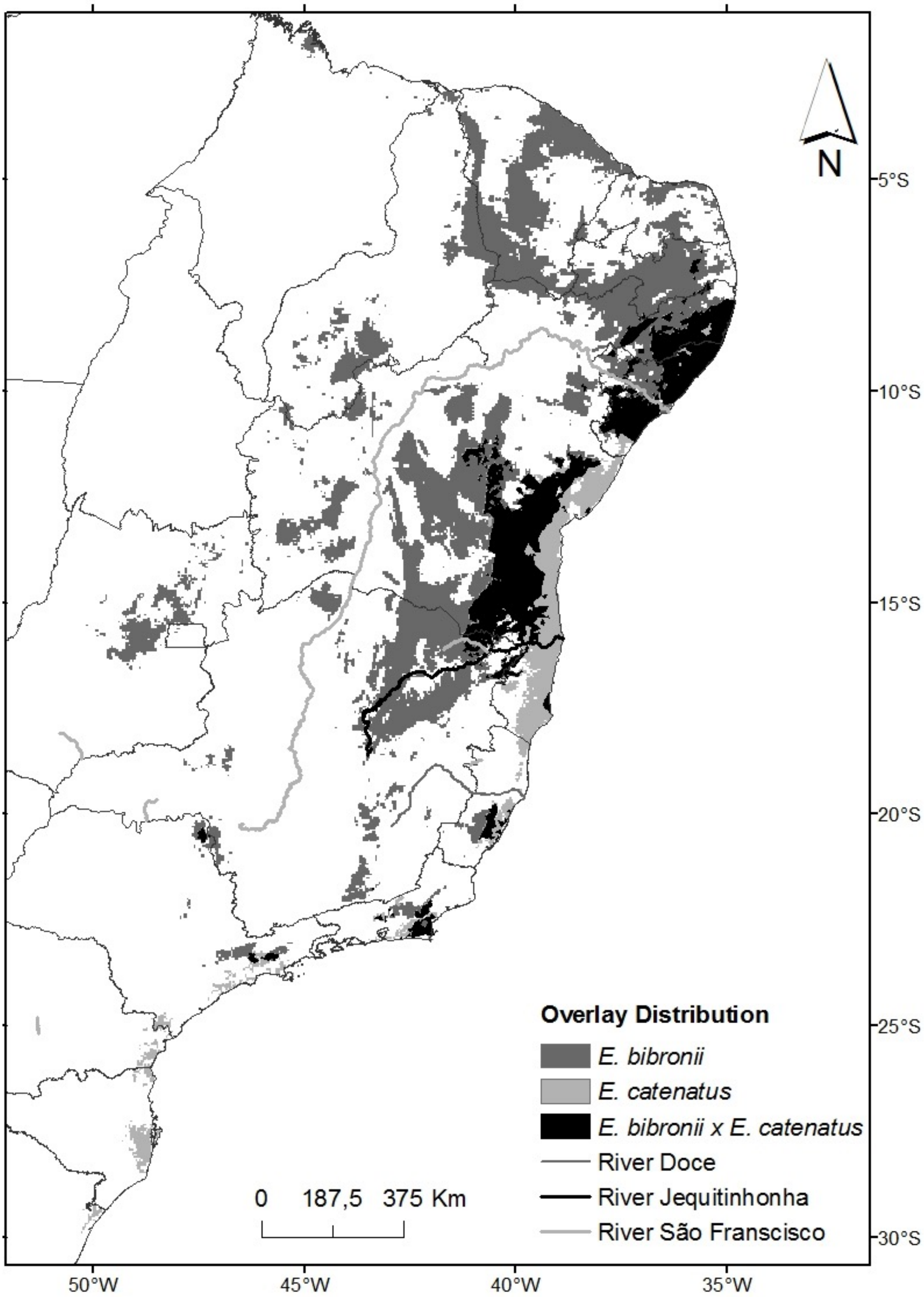


Figure 2.f) Overlapping areas between *Enyalius bibronii* and *Enyalius catenatus*.

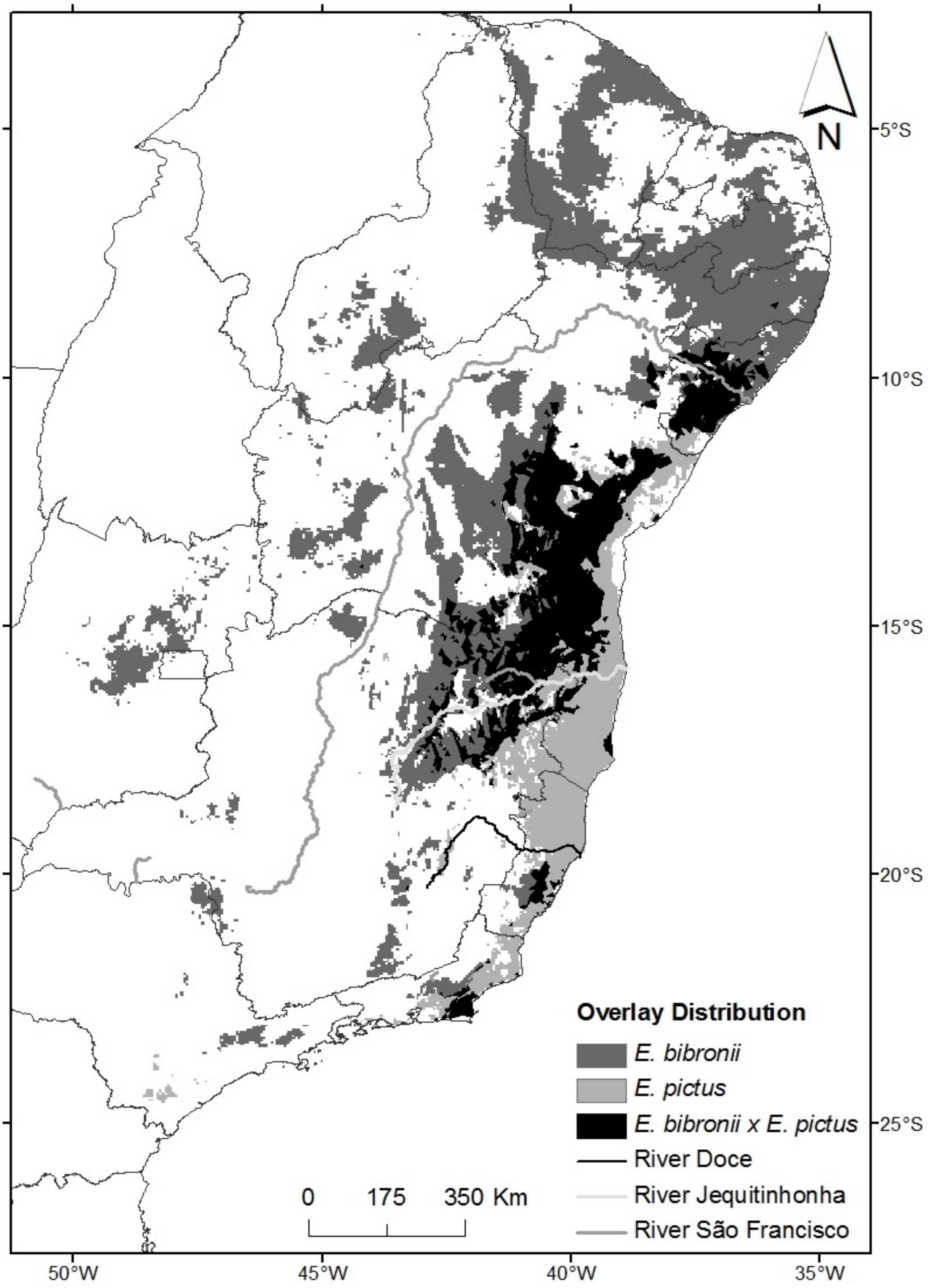


Figure 2.g) Overlapping areas between *Enyalius bibronii* and *Enyalius pictus*.

For *E. catenatus* the mean diurnal temperature range was the most important variable, whereas that for *E. leechii*, from Amazon Forest, the precipitation in the coldest quarter was the main variable in its potential distribution. Finally, for *Enyalius sp* n. from *Cerrado,* the precipitation of the coldest quarter was the most important variable in the model of distribution potential.

Discussion

In the present study, a greater number of species was found in areas under the domain of the Atlantic Forest, with greater latitudinal influence on approximately half of the distribution models generated, especially for *E. brasiliensis*, *E. iheringii*, *E. perditus* and *E. pictus*. The distribution was predominantly in the southeastern region of Brazil, which may be explained by the greater collection effort in this region. Indeed, the areas with the greatest odds of occurrence of the genus are linked to the recognized sub-regions of the Atlantic Forest (Ribeiro et al. 2009). Five of these sub-regions are recognized as centers of endemism, such as denominated: 'Brejos Nordestinos', 'Chapada Diamantina', in Bahia state and the 'Serra do Mar' hills (sensu Da Silva and Casteleti 2003).

Recent studies (Carnaval and Moritz 2008; Carnaval et al. 2009) presented evidence for a large central refuge throughout the Late Quartenary, named 'Bahia refugium', which it was predicted based on climatic modelling with palynological validation and contrasted with the current distribution of several vertebrate species, such as sloths, lizards, marsupials, sender mice, atlantic rats and frogs (Resende et al. 2010). The large portion of *Enyalius* species associated with the Atlantic Forest contributes to the fact that this biome is considered one of the 35 *hotspots* (see Williams et al. 2011) for the conservation of biodiversity worldwide.

In the potential distribution models, the most variables for the majority *Enyalius* species were the latitude and the mean diurnal temperature range, which could express a potential niche with a broad spectrum, meeting the basic requirements of these forest lizard species, and, in general, for the genus as whole. Habitats and their climatic conditions may affect the life history and ecological processes of species in accordance with their geographic distribution (Pianka 1970; Parker and Pianka 1975; Vitt 1991; Taylor et al. 2000; Kiefer et al. 2005). *A priori*, regarding the climatic variables as the main factors of influence in models, an adaptive climatic hypothesis may be the basis to explain the distribution of this genus, in areas found along of a broad latitudinal gradient (Barreto-Lima et al., unpublished data).

On the other hand, the life history characteristics of a lizard species were strongly associated with environmental parameters, but more with the latitude than temperature (Angilletta et al. 2004). The findings of the present study suggest that geographic (latitude) and climatic (mean diurnal temperature range) variables, along the coast of Brazil, may overlap in a large portion of the potential distribution models of the species, characterizing the extensive domain of the Atlantic Forest, and a striking distribution for the majority of *Enyalius* species. This indicated the importance of these variables for most species, suggesting a ‘conservation niche’ characteristic for the *Enyalius* group, and explaining the occurrence of the species in this *hotspot* biome.

For the Atlantic Forest the studies point to the existence of phylogeographic discontinuities in different taxon of organisms and the principal hypothesis to explain these diversifying is the Theory Refugia (Vanzolini and Williams 1970) - see Batalha-Filho and Miyaki (2011). Thereby, species dependent on forest environments would have accompanied these cycles of forests (i.e., contraction and expansion) in the Pleistocene, causing diversification on the populations of different refugium by allopatry, if the insulation had time enough to accumulate differences (Batalha-Filho and Miyaki 2011).

Carnaval and Moritz (2008) and Carnaval et al. (2009) suggest that populations of species which remained in stable areas (refuges) during the Pleistocene should present higher DNA variability than those currently found in unstable areas, which should present genetic signature of population expansion, reflecting the colonization from adjacent refugial centers (Resende et al. 2010). Carnaval et al. (2009) showed that the southern Atlantic Forest was climatically unstable relative to the central region, which served as a large climatic refugium for neotropical species in the late Pleistocene; the results identify the central region as a '*hotspot*' within the Atlantic rainforest *hotspot* and a special refuge for biodiversity. Furthermore, forest lizards also showed high diversity in the central portion of the biome relative to southern areas, and provide evidence for population expansion in southern regions (Carnaval et al. 2009 and references).

In specific cases, climatic variables typical of seasonality, such as rainfall, were more important in the models of species from different biomes, such as *E. leechii* from the Amazon Forest (e.g., precipitation in the driest quarter) and *Enyalius sp* n. from the *Cerrado* (e.g., precipitation in the coldest quarter). It is known that generally the balance of water is negatively associated with the longitude (Bidau and Martí 2008). This may be valid for the *Cerrado* that has low annual precipitation, especially in winter, as also happens in the western Amazon, in the third quarter of the year (severe drought). Despite its high annual precipitation, compared to other Brazilian regions, in the western Amazon the rainfall may be below 500 mm in the north-northeast and decrease to 50 mm in the southern part (Sousa 2003), which in turn, corresponded to basic regions of collection of *E. leechii*. In inland regions, altitude was the most important variable for *E. bibronii*, in the *Caatinga* biome, and for *E. bilineatus,* in the Atlantic Forest.

Curiously, vegetal cover, that is a striking characteristic for occurrence of *Enyalius* species, it did not constitute an important variable as expected, except for *E. leechii* from the Amazon Forest, being this the second most important variable for this species.

Regarding the phylogeny of the group, *E. leechii* was considered a basal species of the genus (Bertolotto 2006). This species is morphologically different (e.g. absence of paravertebral scales) and geographically far from the others, and since it has a longer evolution different than other species in the forest environment, in association with the dense vegetal cover of the Amazon Forest, this could explain the degree of importance of this variable for the species. Our data leads us to suggest that the route of dispersion of the *Enyalius* group must have been from the north to the central-west of Brazil, and thus, reaching the Brazilian east coast, from the northeast to the south of the Atlantic Forest.

Little is yet known about the ecology of *Enyalius* species (Lima and Sousa 2006), but in the last two decades, some studies showed similarities in aspects of diet, foraging mode. And in present study, a surprising overlapping areas (habitats) and potential niche among some species of *Enyalius* from the Atlantic Forest, reveling more than expected or supposed in literature. Studies with isolated species in localities, occurring in sympatry or not, provide valuable data on the environmental resources used and on the potential niche or habitat overlapping, which these may explain why the species occur and how they are distributed in a region. Regarding overlaps in the potential distribution, the data indicated that *E. catenatus* and *E. pictus* were the species that most exhibited areas overlapped. This may be explained by the closer relatedness of them, such as the phylogenetic trees of *Enyalius* (Bertolotto 2006), demonstrating these species share characteristics due to belonging to the same clade, which may have repercussions in the similarity of certain environmental requirements and the qualities that both species currently share.

Enyalius brasiliensis and *E. perditus* were the species that overlapped the most number of times in comparison to other species, including between themselves. Like a possible explanation, we observed that latitude and the precipitation of the coldest quarter were important variables in the potential niches of both species. Probably due to dry weather or to competition, the ancestral populations of *E. brasiliensis* were isolated in the Atlantic Forest, while *E. perditus* originated in refuges of São Paulo, 'Serra Bocaína' or 'Serra dos Órgãos' and *E. iheringii* in shelters of Santa Catarina (Jackson 1978), where its presence is typical in south of country. *Enyalius iheringii* followed the Atlantic Forest moving from north of Santa Catarina state to the east of São Paulo state, becoming sympatric with *E. perditus* and settling in a the new region.

Such as seen in present study, the distribution of these species overlapping in the 'Serra do Mar', with the *E. perditus* populations more centered in the inland and northeast of São Paulo state, while *E. iheringii* is more directed to southeast of this state. Such niche overlap - mainly along the cost of the São Paulo state - may also be explained phylogenetically by proximity within clades and groups that related *Enyalius* species share with each other (see Bertolotto 2006). This statement is valid for the overlap shared among *E. brasiliensis*, *E. iheringii* and *E. perditus*, which they are of the same clade. However, this concept is not valid for the partial overlap found for *E. bilineatus* with *E. brasiliensis* and *E. perditus,* due these species are from different clades (see Bertolotto 2006).

It was reported sympatry with *E. bilineatus* and *E. brasiliensis* in native Atlantic Forest, occurring in mountain near coffee plantations, in Espírito Santo state (Teixeira et al. 2005). It was also observed sympatry with *E. perditus* and *E. bilineatus* in regenerating secondary Atlantic Forest, in a farm coffee plantation, in Minas Gerais state, with *E. perditus* being more representative to area (Barreto-Lima 2009). Habitat disorders may affect degrees differently *Enyalius* species; e.g., *E. brasiliensis* seems more restricted to natural forests and more sensitive to disturbances (Teixeira et al. 2005), while *E. perditus* is reasonably resistant and *E. bilineatus* is more resistant to disturbances and can occur in semi-open areas with seedlings of *Coffea arabica* (Barreto-Lima 2009) or also it occurs in open areas of coffee plantations in direct contact with native forest (Teixeira et al. 2005).

Thus, we do not believe that *E. perditus* and *E. iheringii* are so sensitive to habitat fragmentation or not occurring near agricultural areas as supposed (see Dixo 2001, 2005; Liou 2008). Since recent studies shown the opposite with populations of *E. perditus*, *E. bilineatus* (Barreto-Lima 2009, Barreto-Lima and Sousa 2011) and *E. iheriingi* (Rautenberg and Laps 2010) in disturbed areas; the last species also was observed in banana plantations on hillsides north of Rio Grande do Sul (Torres), surrounded by Atlantic Forest (Lema 2002). We believe that other *Enyalius* species may have some level of resistance to forest fragmentation in contact also with agricultural activities, not only to the Atlantic Forest biome. However, we believe that maybe *E. brasiliensis* be sensitive to fragmentation in agricultural areas. In addition, we stressed that even with a tolerance to human disturbance in the forests of southeast, *E. perditus* is in list of species "probably endangered" in São Paulo state (Liou 2008).

Nevertheless, it has been already given attention to the areas of occurrences of *E. perditus* and *E. iheringii*, being suggested that these would not have a clear differentiation of niches (Jackson 1978), and due be close phylogenetically (Bertolotto 2008). Interestingly, these were the seventh overlap between *Enyalius* species, with overlapping of their areas lower than expected to the model. We observed that *E. catenatus* and *E. pictus* were the species most overlapped their distribution areas. Moreover, *E. brasiliensis* and *E. perditus* had more overlapping by number of times relative to the other species, with relative importance values among the overlapping areas, in general. Thus, if there is an important and partial sympatry and overlapping distributions of niches between *E. perditus* and *E. iheringii*, in the southern portion of southeastern Brazil, on the other hand, there are also major differences among allopatric populations, such as in the distributions of areas and in the resources used by both species observed in this study. Therefore, it is plausible that *Enyalius* species are still in a long process of separation of niches, though not fully complete among most of species.

In conclusion, although some species can occur in the *Cerrado* (*Enyalius sp* n.), *Caatinga* (*E. bibronii*, *E. pictus* and *E. catenatus*) and Amazon Forest (*E. leechii*) biomes, the life history of the group is specially linked to the Atlantic Forest, along of the Brazilian eastern coast, being the biology of majority of the species dependent upon the geographic and climatic characteristics of this forest formation, which it has a broad latitudinal range. It is plausible that part of the similar ecological niches observed among the species, in general, occurred due to environmental influence of large magnitude in association with the phenotypic plasticity of species and due to phylogenetic inertia regarding the environmental characteristics used as basic requirements for the species, though we can not yet fully state which these explanations is the precisely valid.

Acknowledgments

We are grateful to the heads of collections for lending the material and data about the specimens collections: Ana Lucia Costa Prudente and Teresa Cristina Sauer de Ávila-Pires (MPEG), Hussam El Dine Zaher and Carolina Castro Mello (MZUSP), Luciana Nascimento (MCNR), Paulo Manzanni (ZUEC), Ísis Arantes (CHUNB), Rejane Maria Lira-da-Silva (MZUFBA) and Paulo Passos (MNRJ). Thanks to Alexandro Tozetti (Unisinos), Sônia Cechin (UFSM) and Thales Freitas (UFRGS) for suggestions in the final manuscript. Thanks to Cristiano Nogueira and Renata Françoso (UnB) for information and environmental data on the distribution models, and Fabrícius Maia and Ísis Arantes for support in laboratory (CHUNB). Thanks to Bruna Meneses and Karina Amaral (UFRGS) for preparation of maps, and to Isadora Pagel (UFRGS) for the final review in the species numbers and literature. This study received logistical and financial support from the Programa de Pós-Graduação em Ecologia - UFRGS, Departamento de Zoologia/UNB, and CAPES (Ph.D. scholarship to André F. Barreto-Lima). Sandra M. Hartz (processes 306816/2010-5) and Guarino R. Colli (563320/2010-9) are CNPq researchers.

References

Angilletta MJ, Niewiarowski PH Jr, Dunham AE, Leaché AD, Porter WP. 2004. Bergmann's Clines in Ectotherms: Illustrating a Life-History Perspective with Sceloporine Lizards. Am Nat 164(6): E168-E183.

Austin M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecol Model 200: 1-19.

Ávila-Pires TCS. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool Verh 1995:3-706.

Barreto-Lima AF. 2009. Gastric suction as an alternative method in studies of lizard diets: tests in two species of *Enyalius* (Squamata). Stud. Neotrop. Fauna Environ. 44(1): 23-29.

Barreto-Lima AF, Sousa BM. 2011. Feeding ecology and sexual dimorphism of *Enyalius perditus* in an Atlantic forest, Brazil. Herpetol Bull 118: 1-9.

Batalha-Filho H, Miyaki CY. 2011. Phylogeography of the Atlantic Forest. Rev Biol Vol Especial Biogeografia: 31-34.

Bertolotto CEV. 2006. *Enyalius* (Leiosauridae, Squamta): o que os dados moleculares e cromossômicos revelam sobre esse gênero de lagartos endêmicos do Brasil. Ph.D. Thesis – Universidade de São Paulo. São Paulo, Brazil. 139 p.

Bertolotto CEV, Pellegrino KC, Rodrigues MT, Yonenaga-Yassuda Y. 2002. Comparative cytogenetics and supernumerary chromosomes in the Brazilian lizards genus *Enyalius* (Squamata, Polichrotidae). Hereditas 136: 51-57.

Bidau CJ, Marti DA. 2008. A test of Allen's rule in ectotherms: the case of two south American melanopline grasshoppers (Orthoptera: Acrididae) with partially overlapping geographic ranges. Neotrop Entomol 37: 370-380.

Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C. 2009. Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot. Science 323: 785-789.

Carnaval AC, Moritz C. 2008. Historical climate modeling predicts patterns of current biodiversity in the Brazilian Atlantic forest. J of Biogeogr 35: 1187-1201.

Costa GC, Wolfe C, Shepard DB, Caldwell JP, Vitt LJ. 2008. Detecting the influence of climatic variables on species distributions: a test using GIS niche-based models along a steep longitudinal environmental gradient. J of Biogeogr 35, 637-646.

Da Silva JMC, Casteleti CHM. 2003. Status of biodiversity of Atlantic Forest of Brazil. In: Galindo-Leal, C, Camera IG. (Eds.). The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook. CABS and Island Press, Washington, 43-59.

Dixo MBO. 2001. Efeito da fragmentação da floresta sobre a comunidade de sapos e lagartos da serrapilheira no sul da Bahia. Master dissertation, Universidade de São Paulo. São Paulo, Brazil. 77 p.

Dixo MBO. 2005. Diversidade de sapos e lagartos da serrapilheira numa paisagem fragmentada do Planalto Atlântico de São Paulo. PhD thesis, Universidade de São Paulo. São Paulo, Brazil. 180 p.

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species distributions from occurrence data. Ecography 29:129-151.

Elith J, Leathwick J. 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. Diversity and Distributions 13: 265-275.

Etheridge R. 1969. A review of the iguanid lizard genus *Enyalius*. Bull Brit Mus (Natural history) Zoology, London 18 (8):233-260.

Flanklin J. 2009. Mapping species distributions – special inference and prediction. Cambridge University Press, 320 pp.

Hawkins BA. 2004. Are we making progress toward understanding the global diversity gradient? Basic and Appl Ecol 5:13.

Hawkins BA, Porter EE, Diniz-Filho JAF. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84: 1608-1623.

Hijmans RJ, Cameron S, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25: 1965-1978.

Jackson JF. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. Arq Zool 30 (1):1-79.

Kiefer MC, Van Sluys M, Rocha CFD. 2005. Body temperatures of *Tropidurus torquatus* (Squamata, Tropiduridae) from coastal populations: Do body temperatures vary along their geographic range? J Thermal Biol 30:449-456.

Lema T. 2002. Os Répteis do Rio Grande do Sul. Atuais e Fósseis – Biogeografia – Ofidismo. Ed. EDIPUCRS – Pontifícia Universidade Católica do Rio Grande do Sul, Brazil. 264 pp.

Lima AFB, Sousa BM. 2006. Court and copulation behaviors of *Enyalius perditus* Jackson, 1978 (Sauria: Leiosauridae) in captivity conditions. Rev Bras Zoociên 8 (2):189-194.

Liou, NS. 2008. Historia natural de duas species simpátricas de *Enyalius* (Squamata, Leiosauridae) na Mata Atlântica do sudeste brasileiro. Master dissertation, Universidade de São Paulo. São Paulo, Brazil. 107 p.

Parker WS, Pianka ER. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. Copeia 615-632.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecol Model 190: 231-259.

Pianka ER. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703-720.

Ponder WF, Carter GA, Flemons P, Chapman RR. 2001. Evaluation of museum collection data for use in biodiversity assessment. Conserv Biol 15 (3):648-657.

Puschendorf R, Carnaval AC, VanDerWal J, Zumbado-Ulate H, Chaves G, Bolaños F, Alford RA. 2009. Distribution models for the amphibian chytrid *Batrachochytrium dendrobatidis* in Costa Rica: proposing climatic refuges as a conservation tool. Diversity Distrib 15:401-408.

R Development Core Team. 2009. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.

Rautenberg R, Laps RR. 2010. Natural history of the lizard *Enyalius iheringii* (Squamata, Leiosauridae) in southern Brazilian Atlantic forest. Iheringia (Zool), 100 (4): 287-290.

Resende HC, Yotoko KSC, Delabie JHC, Costa MA, Campiolo S, Tavares MG, Campos LAO, Fernandes-Salomão TM. 2010. Pliocene and pleistocene events shaping the genetic diversity within the central corridor of the Brazilian Atlantic Forest. Biol J Linn Soc 101: 949-960.

Ribeiro MC, Metzger JP, Martesen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142: 1141-1153.

Rodrigues, MT, Freitas, MA, Silva, TFS, Bertolotto, CEV. 2006. A new species of lizard genus *Enyalius* (Squamata, Leiosauridae) from the highlands of Chapada Diamantina, state of Bahia, Brazil, with a key to species. Phyllomedusa (5): 11-24.

Rotenberry JT, Preston KL, Knick ST. 2006. GIS-based niche modeling for mapping species' habitat. Ecology 87 (6): 1458-1464.

SBH. 2011. Brazilian reptiles - List of species. Bérnils, R. S. & H. C. Costa. (Orgs.). Accessible at http://www.sbherpetologia.org.br/. Sociedade Brasileira de Herpetologia.

Sousa EPP. 2003. Relações entre as anomalias de TSM do Atlântico e Pacífico e as precipitações na Amazônia oriental. Master Dissertation, Instituto Nacional de Pesquisas Espaciais. São José dos Campos, SP, Brazil. 78 p.

Taylor HL, Walker JM, Cordes JE. 2000. Ecological patterns of body size and clutch size variation in the parthenogenetic teiid lizard *Cnemidophorus tesselatus*. Herpetologica 56: 45-54.

Teixeira R, Roldi K, Vrcibradic D. 2005. Ecological Comparisons between the Sympatric Lizards *Enyalius bilineatus* and *Enyalius brasiliensis* (Iguanidae, Leiosaurinae) from an Atlantic Rain-Forest Area in Southeastern Brazil. J Herpetology 39 (3): 504-509.

Terribile LC. 2009. Padrões ecológicos globais de dois clados de serpents, Viperidae e Elapidae (Serpentes, Squamata). Ph.D. Thesis, Universidade de Brasília. Brazil. 212 p.

Tinkle DW, Dunhan AE. 1986. Comparative life histories of two syntopic Sceloporine lizards. Copeia 1986:1-18.

Vanzolini PE. 1972. Miscellaneous notes on the ecology for some Brazilian lizards (Sauria). Pap Avul Zool 26 (80): 83-115.

Vanzolini PE. 1973. Distribution and differentiation of animals along the coast and in continental islands of the state of S. Paulo, Brazil - 1. Introduction to the area and problems. Pap Avul Zool 26 (24):281-294.

Vanzolini PE, Williams EE. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria: Iguanidae). Arq Zool S Paulo 19:1-298.

Vitt LJ. 1991. An introduction to the ecology of Cerrado lizards. J Herpetol 25:79-90.

Vitt LJ. 1992. Diversity of reproductive strategies among Brazilian lizards and snakes: the significance of lineage and adaptation, 135–149. In: Reproductive Biology of South American Vertebrates. W. C. Hamlett (ed.). Springer-Verlag, New York.

Vitt LJ, Zani PA, Caldwell JP, Ávila-Pires TCS, Esposito MC. 1998. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecpleopus* in the Amazon rainforest. Can J Zool 76: 1671-1680.

Williams KJ, Ford A, Rosauer DF, De Silva N, Mittermeier R, Bruce C, Larsen FW, Margules C, 2011. Forests of east Australia: the 35th biodiversity hotspot, pp. 295–310. In: Zachos, F.E., Habel, J.C. (eds.). Biodiversity Hotspots. Springer Publishers, London.

APPENDIX 1

Brazilian scientific collections (species data from collection lists or borrowed):

Museu de Zoologia de São Paulo, SP (MZUSP), Museu Nacional do Rio de Janeiro, RJ (MNRJ), Museu Paraense Emílio Goeldi, Belém, PA (MPEG), Coleção Herpetológica da Universidade de Brasília, DF (CHUNB), Museu de Zoologia da Universidade Estadual de Campinas, São Paulo (ZUEC), Museu de Ciências Naturais da Pontifícia Universidade de Belo Horizonte, MG (MCNR), Coleção Herpetológica do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS (MCP), Museu de Zoologia da Universidade Federal de Viçosa, MG (MZUFV) and Museu de Zoologia da Universidade Federal da Bahia, Salvador, BA (UFBA).

Borrowed specimens (n = 564):

E. bibronii (17): CHUNB - 56555, CHUNB - 56918, CHUNB - 57375-79, MZUFV - 249, MZUFV - 251, MZUFV-287, MZUFV-307, MZUFV-528, MZUSP - 62792, MZUSP - 65628, MZUSP - 66105, MZUSP-78721, MZUSP-87592. *E. bilineatus* (59): CHUNB - 36170-74, MCNR -115, MCNR-277-78, MCNR-445, MCNR-522-23, MCNR-735, MCNR - 1342, MCNR-1409, MCNR-1411, MCNR-1747, MCNR-3156, MCNR-3277, MCNR - 3557, MNRJ-6356-57, MNRJ-10136, MNRJ-10861-63, MNRJ-10868-71, MNRJ-10873 - 74, MNRJ - 10879-80, MNRJ-10882, MNRJ-10890, MNRJ-10892, MNRJ-10919, MNRJ - 14413, MNRJ - 15575, MZUFV-213-14, MZUFV-241, MZUFV-278, MZUFV-286, MZUFV - 314, MZUFV - 337, MZUFV-473-74, MZUFV-498, MZUSP-594, MZUSP-8216, MZUSP-10410, MZUSP - 29698, MZUSP-39522, MZUSP-42778, MZUSP-71954, MZUSP-95184, MZUSP - 9 5424-25.

E. brasiliensis (27): MNRJ-1611, MNRJ-3446,MNRJ-12091, MNRJ-12354-58, MNRJ - 17614, MZUFV-109, MZUFV-179, MZUFV-320, MZUFV-472, MZUFV-499, MZUFV - 500, MZUFV

- 508, MZUFV-619, MZUSP-3233-34, MZUSP-4276-77, MZUSP-10247, MZUSP - 39533, MZUSP-39535, MZUSP-39537, MZUSP-95426, PUCRS-5355. *E. catenatus* (61): CHUNB - 08183, CHUNB-28984, CHUNB-36175-81, MCNR-542-45, MCNR - 1341, MCNR-1343, MCNR-1898, MNRJ-3464, MNRJ-3878, MNRJ-6341-42, MNRJ-6346,MNRJ-10397, MNRJ -10402, MNRJ-10899, MNRJ-12518-20, MNRJ-13238-42, MNRJ-15122, MPEG-1846, MZUFV - 398-99, MZUFV-425, MZUFV-451, MZUFV-454, MZUSP-23086, MZUSP-66174, MZUSP - 66422-23, MZUSP-95403-09, PUCRS-9020, UFBA-908, UFBA-1085-86, UFBA - 1088-94. *E. iheringii* (64): CHUNB-08184, CHUNB-13460, CHUNB-28882-83, MZUSP - 95390, MZUSP-98131, MZUSP-6864, MZUSP-10136, MZUSP-10271, MZUSP-42713-15, MZUSP - 76286, MZUSP-78954, MZUSP-79707, MZUSP-79709-10, MZUSP - 95388-89, MZUSP - 95391-95, MZUSP-98123-24, MZUSP-98128-30, MZUSP-98132, PUCRS -1049, PUCRS - 5341, PUCRS-6661, PUCRS-6673, PUCRS-6675, PUCRS - 6703, PUCRS - 7775, PUCRS - 9525, PUCRS-9539, PUCRS-9726-27, PUCRS-10978, PUCRS-11374, PUCRS - 12216, PUCRS-12765, PUCRS-12774, PUCRS-17796-97, ZUEC-971, ZUEC-1185, ZUEC - 1372, ZUEC-1834, ZUEC-2034, ZUEC-2167, ZUEC-2214, ZUEC-2644, ZUEC-2924, ZUEC - 2926-29, ZUEC-2931, ZUEC-3077, ZUEC-3079. *E. leechii* (25): CHUNB - 44808-09, MCNR - 3558, MNRJ-4434, MNRJ-18058, MPEG-13999, MPEG-14218, MPEG-17518-19, MPEG - 17543, MPEG-21926-27, MZUSP-42728, MZUSP-81526-28, MZUSP-81621-23, MZUSP - 81719-22, MZUSP-82412, MZUSP-89943. *E. perditus* (71): MCNR-529, MCNR-3550-55, MNRJ -1614, MNRJ-3447, MNRJ-6354-55, MNRJ-10141-45, MNRJ-10160, MNRJ-15044, MNRJ-17027, MZUFV-288, MZUFV-529, MZUFV-631, MZUFV-674, MZUFV-728, MZUSP - 584, MZUSP-590, MZUSP-11464, MZUSP-74903, MZUSP-78120, MZUSP-79711, MZUSP - 89188-91, MZUSP-91438-45, MZUSP-92270, MZUSP-94044, MZUSP-94835, MZUSP-95025-32, MZUSP-95427-30, MZUSP-95763-67, MZUSP-96922, MZUSP-97390, MZUSP-98143,

ZUEC -1888, ZUEC-1894, ZUEC-2925, ZUEC-2932, ZUEC-2940, ZUEC-2943. *E. pictus* (6): MZUFV-250, MZUFV-427, MZUFV-430, MZUFV-438, MZUSP-39539-40. *Enyalius sp* n. (234): CHUNB-3546, CHUNB-8167-68, CHUNB-8170-82, CHUNB-8906-09, CHUNB - 8922-23, CHUNB-9588, CHUNB-16942, CHUNB-21808-09, CHUNB-21812-15, CHUNB-21856, CHUNB-21859-60, CHUNB-21863-64, CHUNB-21873-92, CHUNB-21895-96, CHUNB - 21898-99, CHUNB - 22001, CHUNB-22022, CHUNB-22048, CHUNB-22741-45, CHUNB - 23813, CHUNB-23847-53, CHUNB-23951, CHUNB-24056, CHUNB-24058, CHUNB - 24212-13, CHUNB - 24508, CHUNB-24511, CHUNB-24574, CHUNB-24590, CHUNB - 24759, CHUNB - 24771-73, CHUNB-24775-80, CHUNB-25021, CHUNB-25025-26, CHUNB - 25050 -51, CHUNB-25057, CHUNB-25062-63, CHUNB-25067-71, CHUNB-25079, CHUNB - 25213 -14, CHUNB-25216-17, CHUNB-25313, CHUNB-25315, CHUNB-25362-63, CHUNB -25569, CHUNB - 25587-88, CHUNB-25591, CHUNB-25594, CHUNB-25596, CHUNB - 25690, CHUNB - 26074-79, CHUNB-26081-84, CHUNB-26086, CHUNB-26098, CHUNB-26993, CHUNB - 27618-19, CHUNB-27624-25, CHUNB-27627, CHUNB-27631, CHUNB- 27638, CHUNB - 27682, CHUNB-27724, CHUNB-28884-85, CHUNB-28890, CHUNB- 28909-10, CHUNB - 29290-95, CHUNB-29311-16, CHUNB-29452-54, CHUNB-29657-59, CHUNB - 30342, CHUNB-30523, CHUNB-30953, CHUNB-32709, CHUNB-33630, CHUNB-33636-38, CHUNB - 33640, CHUNB-33790-91, CHUNB-33797, CHUNB-33905, CHUNB - 34000, CHUNB - 34004, CHUNB-34013-15, CHUNB-34845-46, CHUNB-35714-15, CHUNB-36555, CHUNB - 37462-67, CHUNB-38190-91, CHUNB-38503, CHUNB-38648-49, CHUNB-38651, CHUNB - 38772-78, CHUNB-38783, CHUNB-38959-63, CHUNB-40284, CHUNB - 40294, CHUNB -43264, CHUNB-43268, CHUNB-43294, CHUNB-44116, CHUNB-48357, CHUNB - 52394, CHUNB-52396, CHUNB-52407-08, MZUSP-78812, MZUSP-87707, MZUSP - 88857, MZUSP - 93142-45. **All collection sites of species were considered.*

Additional literature considered for the species data:

Ávila-Pires TCS. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Verhandel, Leiden 299, 1-706 pp.

Barreto-Lima AF. 2009. Gastric suction as an alternative method in studies of lizard diets: tests in two species of *Enyalius* (Squamata). Stud. Neotrop. Fauna Environ. 44(1): 23-29.

Barreto-Lima AF, Sousa BM. 2011. Feeding ecology and sexual dimorphism of *Enyalius perditus* in an Atlantic forest, Brazil. Herpetological Bulletin 118: 1-9.

Bertolotto CEV. 2006. *Enyalius* (Leisauridae, Squamata): o que os dados moleculares e cromossômicos revelam sobre esse gênero de lagartos endêmicos do Brasil. PhD thesis, Universidade de São Paulo. 129p.

Etheridge R. 1969. A review of the iguanid lizard genus *Enyalius*. Bulletin of the British Museum (Natural History) Zoology 18 (8): 231-260.

Jackson JF. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. Arquivos de Zoologia 30 (1): 1-79.

Sousa BM, Cruz CAG. 2008. Hábitos alimentares de *Enyalius perditus* (Squamata, Leiosauridae) no Parque Estadual do Ibitipoca, Minas Gerais, Brasil. Iheringia S. Zool. 98(2): 260-265.

Teixeira R, Roldi K, Vrcibradic D. 2005. Ecological Comparisons between the Sympatric Lizards *Enyalius bilineatus* and *Enyalius brasiliensis* (Iguanidae, Leiosaurinae) from an Atlantic Rain-Forest Area in Southeastern Brazilian Journal of Herpetology 39 (3): 504-509.

Vrcibradic D, Anjos LA, Vicente JJ, Bursey CR. 2008. Helminth parasites of two sympatric lizards, *Enyalius iheringii* and *E. perditus* (Leiosauridae), from an Atlantic Rainforest area of southeastern Brazil. Acta Parasitologica 53, 222-225.

Specimens total (n = 1,256) considered:

E. bibronii (52): CHUNB-56555, CHUNB-56918, CHUNB-57375-79, LG-1377, MCNR-4728, MCV-82873, MZUFV-249, MZUFV-251, MZUFV-287, MZUFV-307, MZUFV-528, MZUSP - 10115, MZUSP-55945-47, MZUSP-62792, MZUSP-65628, MZUSP-65667-68, MZUSP-65766, MZUSP - 65908, MZUSP-66105, MZUSP-66130, MZUSP-78721, MZUSP-81002-03, MZUSP - 87589, MZUSP-87592, MZUSP-89463, MZUSP-92436-54. ***E. bilineatus*** (111): CHUNB - 36170 - 74, MCNR-115, MCNR-277-78, MCNR-445, MCNR-522-23, MCNR-735, MCNR - 1342, MCNR -1409, MCNR-1411, MCNR-1747, MCNR-3156, MCNR-3277, MCNR-3557, MCZ - 84034, MNRJ-1601, MNRJ-6356-57, MNRJ-10136, MNRJ-10861-63, MNRJ-10868-71, MNRJ - 10873-74, MNRJ-10879-80, MNRJ-10882, MNRJ-10890, MNRJ-10892, MNRJ-10919, MNRJ - 14413, MNRJ-15575, MVZ-14941, MZUFV-213-14, MZUFV-241, MZUFV-278, MZUFV - 286, MZUFV-314, MZUFV-337, MZUFV-473-74, MZUFV-498, MZUSP-546, MZUSP - 594, MZUSP -719, MZUSP-3729, MZUSP-5631, MZUSP-7069, MZUSP-8216, MZUSP - 10410, MZUSP -12302, MZUSP-17455-56, MZUSP-29698, MZUSP-39520-27, MZUSP - 42778, MZUSP-43019, MZUSP-43021-22, MZUSP-45748, MZUSP-57472, MZUSP - 71954, MZUSP-78809-11, MZUSP-79704, MZUSP-81399-400, MZUSP-95178-80, MZUSP - 95184, MZUSP-95424-25, MZUSP-95868, MZUSP-96565-67, MZUSP-96569-75, SMF-24890, ZMK-25, ZMK-26-29, ZUEC-2791, two without identification. ***E. brasiliensis*** (67): AMNH - 62143, MCZ-79025, MHNP-02.368, MHNP-6816 (A), MHNP-6816 (B), MNRJ-1611, MNRJ - 3446, MNRJ-3456, MNRJ-3458, MNRJ-12091, MNRJ-12354-58, MNRJ-17614, MZUFV-109, MZUFV -179, MZUFV-320, MZUFV-472, MZUFV-499, MZUFV-500, MZUFV-508, MZUFV - 619, MZUSP-2662, MZUSP-3232-34, MZUSP-4257-58, MZUSP-4276-77, MZUSP - 7756, MZUSP - 8825, MZUSP-10247, MZUSP-10251, MZUSP-10259, MZUSP-17452-54, MZUSP -

39528-38, MZUSP-39541-42, MZUSP-42687, MZUSP-43020, MZUSP-43023, MZUSP-75160, MZUSP - 95426, MZUSP-98041, PUCRS-5355, ZMH-2546-(A), ZMH-2546-(B), ICBUFV - without number, two without identification, UFRRJ- two without number. ***E. catenatus*** (146): AMNH - 108, BM-1888.4.18.5, BMNH-88.4.18.5, BMNH-93.9.30.I, CHUNB-08183 - 84, CHUNB - 28984, CHUNB-36175-81, DEUFP 659, LG 2182, MCNR-542-45, MCNR - 1341, MCNR - 1343, MCNR-1898, MCNR-4725-27, MCZ-7320, MNRJ-1610, MNRJ-1934, MNRJ - 3464, MNRJ-3878, MNRJ-6341-42, MNRJ-6346,MNRJ-10397, MNRJ-10402, MNRJ - 10899, MNRJ - 12518-20, MNRJ-13238-42, MNRJ-15122, MNRJ-17027, MPEG-1846, MRT - 5815, MRT - 5817, MRT-5844, MRT-5886, MRT-5889, MZUFV-398-99, MZUFV-425, MZUFV - 451, MZUFV - 454, MZUSP-421, MZUSP-443, MZUSP-724, MZUSP-8826, MZUSP - 23086, MZUSP - 30748, MZUSP-43014-16, MZUSP-49210, MZUSP-55936, MZUSP-59183 - 87, MZUSP-66174, MZUSP-66422-23, MZUSP-78382, MZUSP-79649, MZUSP-95400 - 15, MZUSP - 96074-76, MZUSP-96537-42, MZUSP-96827-32, MZUSP-96838-39, MZUSP - 96854, MZUSP-96920, PUCRS-9020, SMF-36217, SMF-60337, SMF-64697, UFBA - 908, UFBA - 1085-86, UFBA-1088-94, USG-37-38, USG-47, USG-52, USG-54, USG-70, BM - 1861.2.2.3.3, IBUEC-without number, MZUSP-without number, one without origin data-4017, eight without identification. ***E. iheringii*** (330): BMNH-88.9.21.2-3, CHUNB-13460, CHUNB - 28882-83, FMNH-11388-9, FMNH-11622-3, LG 1383, LG 2327, MTR 10873, MZUSP - 376, MZUSP - 417, MZUSP-427-28, MZUSP-431, MZUSP-586, MZUSP-588-89, MZUSP-595-96, MZUSP - 702, MZUSP-760, MZUSP-769, MZUSP-1056, MZUSP-2315-18, MZUSP-2322, MZUSP - 2533, MZUSP-3121, MZUSP-3142-43, MZUSP-3146, MZUSP-3148-50, MZUSP - 3728, MZUSP-4243-53, MZUSP-4256, MZUSP-4261-64, MZUSP-4268-74, MZUSP-6862 - 64, MZUSP - 10136, MZUSP - 10270 - 71, MZUSP - 10273 - 74, MZUSP -13593, MZUSP - 14429,

MZUSP - 19549, MZUSP-21466, MZUSP-23575, MZUSP-38380, MZUSP-39513-18, MZUSP - 39549, MZUSP-40608, MZUSP-42693, MZUSP-42695, MZUSP-42701, MZUSP - 42706, MZUSP - 42713-15, MZUSP-42718, MZUSP-42743, MZUSP-42760, MZUSP-4278-81, MZUSP - 42916, MZUSP-43024-25, MZUSP-55843, MZUSP-55930, MZUSP-56767, MZUSP-60602, MZUSP-62386-91, MZUSP-67026-29, MZUSP-67053, MZUSP - 67211 - 20, MZUSP - 67703, MZUSP-69282, MZUSP-71955-57, MZUSP-72535-36, MZUSP-73009, MZUSP-74901-02, MZUSP-74904-05, MZUSP-76283, MZUSP-76286-87, MZUSP-77001-03, MZUSP-78392, MZUSP-78439-43, MZUSP-78954-55, MZUSP-79347, MZUSP-79650-51, MZUSP-79705-10, MZUSP - 80630-32, MZUSP-89141, MZUSP-89801-02, MZUSP-92094, MZUSP - 94834, MZUSP - 95090, MZUSP-95129-30, MZUSP-95388-89, MZUSP-95391-95, MZUSP-95422-23, MZUSP - 95432, MZUSP-95438-41, MZUSP-95606-08, MZUSP-95614-17, MZUSP - 95663, MZUSP - 95665-78, MZUSP-95683-85, MZUSP-95735, MZUSP-95745-59, MZUSP-95779, MZUSP - 98024-25, MZUSP-98028, MZUSP-98032, MZUSP-98121-30, MZUSP-98132-42, NMW - 12957-58, NMW-12959 (A), NMW-12959 (B), NMW-12960-61, NMW - 12963 - 64, NMW - 12966-67, NMW-14947, PUCRS-1049, PUCRS-5341, PUCRS-6661, PUCRS - 6673, PUCRS - 6675, PUCRS-6703, PUCRS-7775, PUCRS-9525, PUCRS-9539, PUCRS - 9726-27, PUCRS - 10978, PUCRS-11374, PUCRS-12216, PUCRS-12765, PUCRS-12774, PUCRS - 17796-97, SMF-11050, SMF-11052, SMF-24833, SMF-30303, UNIBAN 2019/2097, ZMH - 2683, ZMH-2862, ZMH-3566, ZMH-4536, ZSBS-933/1920, ZUEC-681, ZUEC - 724, ZUEC - 883, ZUEC - 971, ZUEC - 1185, ZUEC-1372, ZUEC-1543, ZUEC-1834, ZUEC - 2034, ZUEC-2167, ZUEC - 2214, ZUEC-2644, ZUEC-2924, ZUEC-2926-29, ZUEC-2931, ZUEC - 3075, ZUEC - 3077, ZUEC-3079, ZUEC-882, ZUEC-2129, without origin data-39513, eight without identification. ***E. leechii*** (45): CHUNB-44808-09, MCNR-3558, MNRJ-4434, MNRJ - 18058,

MPEG - 13999, MPEG-14218, MPEG-14365, MPEG-14831, MPEG-16759, MPEG-17518-19, MPEG - 17543, MPEG-21926-27, MZUSP-705, MZUSP-42728, MZUSP - 55524, MZUSP - 67399, MZUSP-79659, MZUSP-81526-28, MZUSP-81621-23, MZUSP - 81677 - 80, MZUSP - 81719 - 22, MZUSP-81779-83, MZUSP-82412, MZUSP-82522, MZUSP-89943, ZUEC - 3368. ***E. perditus*** (221): MCNR-529, MCNR-3550-55, MNRJ-1614, MNRJ-3447, MNRJ-6354 - 55, MNRJ - 10141-45, MNRJ-10160, MNRJ-15044, MRT-10797-78, MZUFV-288, MZUFV - 529, MZUFV - 631, MZUFV-674, MZUFV-728, MZUSP-285, MZUSP-578, MZUSP - 584 - 85, MZUSP - 587, MZUSP-590, MZUSP-592-93, MZUSP-697, MZUSP-709, MZUSP - 756, MZUSP - 2319, MZUSP-2323, MZUSP-2532, MZUSP-3122-23, MZUSP - 3136 - 39, MZUSP - 3147, MZUSP - 4255, MZUSP-4259, MZUSP-4265-67, MZUSP-7692, MZUSP-8252, MZUSP - 8380, MZUSP-10272, MZUSP-10296, MZUSP-10375-76, MZUSP-11463-64, MZUSP - 12281, MZUSP - 36926, MZUSP-38381-82, MZUSP-39550, MZUSP-42685, MZUSP - 42918, MZUSP - 43017-18, MZUSP-45695-96, MZUSP-70268-69, MZUSP - 72537-38, MZUSP - 74903, MZUSP -78120, MZUSP-79711, MZUSP-80942-44, MZUSP-87720, MZUSP - 89188 - 91, MZUSP-89799, MZUSP-89942, MZUSP-91438-45, MZUSP-91449, MZUSP - 91451, MZUSP - 91648-54, MZUSP-92176, MZUSP-93089-113, MZUSP-94040-43, MZUSP - 94044, MZUSP - 94835, MZUSP-95000-06, MZUSP-95009-22, MZUSP-95025-32, MZUSP - 95427 - 30, MZUSP-95442-46, MZUSP-95452-60, MZUSP-95623-27, MZUSP - 95763 - 67, MZUSP - 96922, MZUSP-96993, MZUSP-97390, MZUSP-98143, ZUEC-1887-88, ZUEC - 1894, ZUEC - 2925, ZUEC-2930, ZUEC-2932, ZUEC-2933-43, UFJF- eight without number. ***E. pictus*** (36): JC - 1079-81, LG-2196, MRT 12080, MZUFV-250, MZUFV-427, MZUFV - 430, MZUFV - 436 -38, MZUSP-39539-40, MZUSP-42917, MZUSP-66151-62, MZUSP-91486-90, NMV - 13894, one without identification, CHUNB-three without number. ***Enyalius sp* n.** (248): CHUNB -3546, CHUNB - 8167-82, CHUNB-8906-09, CHUNB-8922-23, CHUNB-9588, CHUNB - 16942,

CHUNB - 21808-15, CHUNB-21856, CHUNB-21859-60, CHUNB-21863-64, CHUNB - 21873 - 92, CHUNB-21895-96, CHUNB-21898-99, CHUNB-22001, CHUNB-22022, CHUNB -22048, CHUNB - 22741-45, CHUNB-23813, CHUNB-23847-53, CHUNB - 23951, CHUNB - 24056, CHUNB - 24058, CHUNB-24212-13, CHUNB-24508, CHUNB-24511, CHUNB - 24574, CHUNB - 24590, CHUNB-24759, CHUNB-24771-73, CHUNB-24775-80, CHUNB - 25021, CHUNB - 25025-26, CHUNB-25050-51, CHUNB-25057, CHUNB-25061-63, CHUNB - 25067 -72, CHUNB-25079, CHUNB-25213-14, CHUNB-25215-17, CHUNB-25313, CHUNB - 25315, CHUNB - 25362-63, CHUNB-25569, CHUNB-25587-88, CHUNB-25591, CHUNB - 25594, CHUNB - 25596, CHUNB-25690, CHUNB-26074-79, CHUNB-26081-84, CHUNB - 26086, CHUNB - 26098, CHUNB-26993, CHUNB-27618-19, CHUNB-27624-27, CHUNB - 27631, CHUNB - 27638, CHUNB-27682, CHUNB-27724, CHUNB-28884-85, CHUNB - 28890, CHUNB - 28909-10, CHUNB-29209-10, CHUNB-29290-95, CHUNB-29311-16, CHUNB - 29452 - 54, CHUNB-29657-59, CHUNB-30342, CHUNB-30523, CHUNB-30953, CHUNB - 32709, CHUNB-33630, CHUNB-33636-38, CHUNB-33640, CHUNB-33790-91, CHUNB - 33797, CHUNB-33905, CHUNB-34000, CHUNB-34004, CHUNB-34013-15, CHUNB - 34845 - 46, CHUNB-35714-15, CHUNB-36555, CHUNB-37462-67, CHUNB-38190-91, CHUNB - 38503, CHUNB-38648-49, CHUNB-38651, CHUNB-38772-78, CHUNB-38783, CHUNB - 38959-63, CHUNB-40284, CHUNB-40294, CHUNB-43264, CHUNB-43268, CHUNB - 43294, CHUNB - 44116, CHUNB-48357, CHUNB-50251, CHUNB-52394, CHUNB-52396, CHUNB - 52407, CHUNB-53308, MZUSP-78812, MZUSP-87707, MZUSP-88856-57, MZUSP-93142-45, CHUNB - two without number and one without identification.

**All collection sites of species were considered.*

CAPÍTULO 3/ Chapter 3

Ecological patterns and morphological variation in *Enyalius* species (Iguanidae, Leiosaurinae): testing hypotheses for Brazilian forest lizards

ANDRÉ FELIPE BARRETO-LIMA[1,3], LEANDRO DUARTE DA SILVA[1],
GUARINO RINALDI COLLI[2] & SANDRA MARIA HARTZ[1]

[1] UFRGS – Universidade Federal do Rio Grande do Sul - Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Laboratório de Ecologia de Populações e Comunidades. Av. Bento Gonçalves, nº 9500, Setor 4, Prédio 43.422, Bairro Agronomia, Cx. Postal 15.007, Porto Alegre, RS, Brazil. CEP: 91.540-000.

[2] UNB - Universidade de Brasília, Instituto de Biociências, Departamento de Zoologia, Laboratório de Herpetologia, Brasília, DF, Brazil. CEP: 70.910–900.

[3] Corresponding author: afblima@hotmail.com

Summary

1. The morphological ecology is a theoretical approach that studies the relationship between the functional form of the organisms and their habitats, using data to study individual variation in morphological adaptation within populations or communities.

2. Information on the *Enyalius* species were obtained from scientific collections and literature, based on the sites of collections. We used 558 individuals from eight species of *Enyalius,* which we obtained morphological and environmental data, and their respective collection points transformed in geographic coordinates.

3. The forests, where the lizards were collected, were classified as open or closed habitats. The environmental variables were obtained from each location through the geographic coordinates, which 10 variables were considered independent for analysis. The morphological data were used with selected environmental variables in a canonical correlation analysis to explain the species identity and the source of the variation pattern.

4. We obtained 64% of explanation for the variation in the model species. Most it was explained by environmental variables and a smaller part by the species' morphology.

5. This study showed that some changes in body proportions and body size may be reported to the divergence of habitats and/or substrates use among the different *Enyalius* species. Finally, we suggest that the morphological variation of the species should be an adaptive response to local environmental conditions than a direct consequence of phylogeny inertia inherited from the *Enyalius* group.

Key-words: ecomorphology, *Enyalius*, forest lizards, morphological variation.

Introduction

The theory of biomechanics describes a clear relationship between the morphology and the habitat use, as different physical requirements in different habitats affect the locomotion system of organisms. Thus, understanding how the morphology, habitat use and locomotor performance co-evolve may help to clarify how species adapt to different environments (Losos 1990; Elstrott & Irschick 2004). The strong evolutionary link of one of these variables among species offers indirect evidence of the action of the natural selection in the formation of macro-evolutionary patterns (Larson & Losos 1996; Elstrott & Irschick 2004).

Morphological ecology is the study of the relationship between the morphology (phenotype) and ecology (variations in the use of resources) among communities, populations, guilds and/or individuals (Peres-Neto 1999). Concerning this approach is possible to detect morphological differences among species and to relate these differences to environmental pressure and important ecological factors (Irschik & Losos 1999). Thus, morphological measurements can be helpful in clarifying issues such as the niche concept, the sharing of resources and the structuring of communities (Wainwright & Reilly 1994).

Morphological ecology implicitly focuses on intra-population or inter-population fitness and adaptation, which high degrees of morphological variation may be related to variations in Darwinian fitness, indicating adaptation to different lifestyles (Garland & Losos 1994). If environmental limits exert pressure on the adaptation of organisms, being expressed in morphological and ecological comparisons, morphological comparisons among sets of coexisting species should also have predictable ecological properties (Karr & James 1975). Species with broad distribution often experience environmental variations in different locations and they may evolve different adaptations in response to local environmental selective pressure (Johnson *et al.* 2006).

Thereby, if the environment has the molded evolution in predictable directions, the structure of communities that occurs under the same environmental conditions is expected to be similar (Melville *et al.* 2006). Various groups of vertebrates have been investigated in relationship between the body shape and the function in specific habitats. Such investigations have revealed important ecological traits regarding the biology of species (Pianka 1969; Willians 1972; Ricklefts & Travis 1980; Moermond 1986). Indeed, reptiles may be an interesting choice of study in the evaluation of locomotor performance. In recent decades, a number of studies have examined ecological correlations regarding morphological diversity in a variety of lizards: *Anolis, Tropidurus, Ctenotus*, chameleons etc (Pianka 1986; Scheibe 1987; Losos 1992; Irschick *et al.* 1997; Kohlsdorf, Garland & Navas 2001). Such studies report a large variety of ecomorphological correlations; the adaptive nature of many of these lizards has been clarified by behavioral, functional and phylogenetic data.

Convergences among communities appear to be more restricted to island biomes (e.g., *Anolis*) and absent on the mainland (Melville *et al.* 2006). Nonetheless, there is strong evidence of convergence among lizard communities in the deserts of North America and Australia concerning locomotor morphology and habitat use (Melville *et al.* 2006). However, ecomorphometric of lizards has been concentrated on the essentially anatomic characteristics of body shape and habitat/microhabitat use (Moermond 1979, 1986; Pounds 1988; Ribas *et al*. 2004) in order to establish general rules for form and function (Rocha *et al.* 2000), as reported in pioneering studies (Pianka 1969; Pianka & Paker 1972; Pianka & Pianka 1976; Ricklefts *et al.* 1981). The ecological diversity of lizards is associated with variations in body size and shape, with special attention given to size and proportion of the limbs which can affect the different modes of locomotor performance in these organisms (Losos & Sinervo 1989; Losos 1990; Losos *et al.* 1991; Garland & Losos 1994; Macrini & Irschick 1998; Bonine & Garland 1999; Kohlsdorf *et al.* 2001).

In general, longer legs are generally associated to open areas whereas shorter legs are associated to closed areas of dense vegetation (Pianka 1969). However, among the lizards of North America, iguanids from open areas tend to be smaller and thinner, having shorter legs than species from habitats with dense vegetation (Scheibe 1987).

Studies on the *Enyalius* genus, which encompasses diurnal, ombrophylous and endemic lizards to Brazilian rainforests, have been limited regarding a number of aspects of the biology of species (Lima & Sousa 2006). Indeed, there are nine recognized species (SBH 2011) and other three are being described [one from the *Cerrado* (Brazilian savanna), which was considered in the present study]. Although small and under-investigated, this group shows a broad territorial distribution, especially in area of the Atlantic Forest biome, in the eastern coast of Brazil (Etheridge 1969; Vanzolini 1972); stretching from the Rio Grande do Sul state, in southern region, to Rio Grande do Norte state, in the northeastern region from Brazil (Jackson 1978). However, some species may occur in open areas and forests of the central *Cerrado*, forests of the *Caatinga* (semi-arid brush) (Bertolotto *et al.* 2002; Loebmann & Haddad 2010), and in the dense vegetation of the Amazon Forest (Ávila-Pires 1995). Thereby, this genus has species in open and closed forest areas in different Brazilian phytogeography regions.

The morphological ecology of *Enyalius* has not previously been investigated, from the macroecological standpoint, and the broad distribution of this genus in different forests from Brazil, along a temperature gradient, it makes *Enyalius* an interesting study model to test, for the first time, this new approach in a continental area. Ecomorphological hypothesis states that it is possible to predict the use of resources by a species through its morphological attributes.

Due to the broad distribution of species in differentiated areas of Brazil and the environmental variations throughout the distinct biomes, then, would be expected adaptive morphological diferences among the *Enyalius* spp. for habitat and resources use, being correlated with such environmental variables, that would explain the evolutionary history of the group. The aim of the present study was to investigate ecological patterns of associations between the morphology and the environment, based on the distribution of *Enyalius* spp.*,* using multivariate comparative methods that involve morphological, climatic and spatial data. How *Enyalius* is found in different forests and biomes from Brazil, it is expected that morphological patterns are based on the local adaptations, distinguish among genus' species. Among the environmental factors, the influence of the type of vegetation cover was investigated to explain the presence of the species in distinct forest environments.

This study also argues on the data encountered for the group within the ecological and phylogenetic contexts, in order to clarify the relationships observed. At last, the investigation resulted in surprising data on the basic aspects of the morphological ecology of *Enyalius* and it may be considered a preliminary effort to fill this gap in the knowledge.

Methods

DATA COLLECTION

Information on the *Enyalius* species was obtained from the literature on the respective collection sites and from the Brazilian scientific collections (borrowed and list of collections), including the number of specimens studied (Appendix 1). We used data of 558 specimens from eight *Enyalius* spp.: *E. bibronii* (17)*, E. bilineatus* (59), *E.brasiliensis* (27), *E. catenatus* (61)*, E. leechii* (25), *E. iheringii* (64), *E. perditus* (71) and *Enyalius sp* n. (234). Species identification was performed by the first author. Only *E. pictus* and *E. erythroceneus* were not considered due there are few samples (i.e., morphological and/or collection sites data) being impossible to perform in the models.

We obtained morphological and environmental records of their respective occurrence (geographic coordinates) to analyze of the morphological variation patterns in the ecological context. The length of an organism is a linear measurement pattern that can be used in studies on the history of life of organisms. The measures in length are used to animals elongated as snakes (Terribili 2009), lizards, among others, since parts of the body of animals (e.g., locomotor members) may represent a result adaptive to different factors and varied use of environmental resources. Thus, nine length measurements were taken from each specimen using a digital caliper (scale: 0.01 mm): snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (ff), posterior leg length (l), foot length (ft), and fourth toe length (fl). Google Earth - v. 2010 (maps service) was used to confirm the sites through satellite images, while Google was used for the search for geographic coordinates in the literature and/or official documents on the location of the Brazilian conservation units, where the most lizards were collected.

All sites were considered in forest areas, even those close or within cities. Sites recorded within metropolises with no vegetal cover, imprecise or dubious sites, those no record of the place of origin and those located in forest fragments with a radius less than 2.5 Km were excluded of the analysis. The habitats of lizards were classified into groups of areas open or closed (i.e., discrete data). Thereby, specimens from gallery forest fragments in the *Cerrado* and *Caatinga* forests were considered of "open forests" (0), while those from dense forests of the Atlantic or Amazon Forest were considered of "closed forests" (1).

The environmental variables were obtained from each location by geographic coordinates on a resolution scale of 2.5 arc minutes, using the Worldclim databank (Hijmans *et al.* 2005) for the last 50 years. A total of 24 environmental variables were extracted: the latitude and longitude (decimal degrees), altitude (m), aspect (direction of relief in %), vegetal cover or ndvi (scale: 0 to 255), annual mean temperature (Bio1), mean diurnal temperature range (Bio2 – mean of monthly (maximum temperature – minimum temperature)), isothermality (Bio3 – mean diurnal temperature range/annual temperature range *100), temperature seasonality (Bio4 – standard deviation *100), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), temperature annual range (Bio7 = Bio5 - Bio6), mean temperature of the wettest quarter (Bio8), mean temperature of the the driest quarter (Bio9), mean temperature of the warmest quarter (Bio10), mean temperature of the coldest quarter (Bio11), annual mean precipitation (Bio12), precipitation in the wettest month (Bio13), precipitation in the driest month (Bio14), precipitation seasonality (Bio15 - coefficient of variation), precipitation in the wettest quarter (Bio16), precipitation in the driest quarter (Bio17), precipitation in the warmest month (Bio18) and precipitation in the coldest quarter (Bio19).

DATA ANALYSIS

For missing data on the morphological measurements of the lizards, the multiple imputation method was performed to complete the matrix of morphological data, which is based on the prediction by mean values, using the “mice” package (Zhang 2003), which estimates missing values through a model based on the observed values. The morphometric data of the new complete matrix were log transformed. In order to separate the morphometric variation in body size and shape components, the body size was defined as the scores of an isometric vector, with p-values$^{0.5}$, which p is the number of variables (Jolicoeur 1963). The scores were calculated by post-multiplication of the n x p matrix of log-transformed data, which n is the number of observations by the isometric vector p x 1 (Somers 1986).

After, the effect of body size on the morphometric variables (represented by body shape) was removed using the formula proposed by Burnaby (1966):

$$L = Ip - V(V^T V)\text{-}1\ V^T$$

which: Ip is the identity matrix p x p, V is the above-defined isometric vector and V^T is the transposed matrix of V. Then, the morphometric variables become variables that explain body shape. Correlation tests were performed among the environmental variables to avoid the collinearity of variables in the models. Variables with correlations above 75% were discarded ($p < 0.005$) to avoid redundancies in the model. Multiple regressions were performed relating body size adjusted to environmental variables and using the coordinates (latitude and longitude) of each location, as well as, the respective polynomial extensions, considering the possibility of spatial autocorrelation among the data (Bocard, Legendre & Drapeau 1992).

This analysis was complemented by the selection of environmental variables based on the Akaike information criterion (AIC) and "model averaging" method (Burnham & Anderson 2002). Thereby, ten of 24 environmental variables were independent and employed in the potential distribution analyses: altitude, aspect, latitude, vegetal cover (ndvi), annual mean temperature, mean diurnal temperature range, annual mean precipitation, precipitation in the driest quarter and precipitation in the coldest quarter. We created a binary matrix of identity the species to correlate morphological and environmental data sets. In the search for patterns of associations, morphological data were used with the environmental variables selected.

Canonical correspondence analyses (CCA) were performed with the mean values of the morphological characteristics and the mode of the environmental characteristics in three consecutive steps, using the “vegan” statistic package: 1) searching for spatial autocorrelation through a CCA carried out with the latitudes and longitudes and respective polynomial extensions, in order to find co-variables (Borcard *et al.,* 1992); 2) searching for a set of environmental variables that best explain the variation in morphology (using the co-variables selected in the regressions), performing a partial CCA of the morphological variables with the environmental variables and selection of models by AIC; 3) final CCA was carried out with the results of the previous steps, in order to explain the influence of the environmental variables on the species' morphology. Significance tests of model from CCA were performed with analysis of variance (1,000 permutations). All analyses were performed with the R 2.10.1 (2009) and level of significance of 5% ($p \leq 0.05$).

Results

The CCA involved morphological and environmental variables for the species' identity matrix, with the partition of the model explaining approximately 64% of the variation in the species (Fig. 1A–B; Tables 1-2). The largest proportion was explained by the environmental variables (36.6%), whereas only 6.5% was explained by morphology. The effect of morphology and environment together explained 20.4% of variation of the model and the residual was 36.4%. In the ANOVA tests, significant results were found for the proportion of the effect of morphology on the species ($F = 10.4240$, $p = 0.001$) and the proportion of the effect of the environment ($F = 41.4035$, $p = 0.001$), indicating that both data sets were numerically satisfactory for the model. The Axis 1 of the CCA explained 52%, whereas the Axis 2 explained 27% of the model.

Concerning the morphological variables (Fig. 1A), *E. iheringii* and *E. bibronii* were the species most positively associated with body size (s), head length (h) and length of the fourth toe of the foot (ff), representing the largest species of the genus. Regarding tail length (t), *E. bilineatus* exhibited a positive association and it was the species with the largest size for this measure. *E. brasiliensis* and *E. catenatus* had the greatest positive associations with the arm length (a) and the hand length (ha). Tail length (l) was negatively associated for *E. brasiliensis* and *E. catenatus,* while the arm length (a) was negatively associated for *E. bilineatus*. *Enyalius leechii* exhibited the largest positive association with the posterior leg length (l) and foot length (f), while *E. perditus* was positively associated with the fourth finger of the hand (ft).

Regarding the environmental variables (Fig. 1B), the CCA revealed three distinct groups. First, *E. leechii* was the most atypical and the most positively associated with the annual precipitation (bio 12) and the mean diurnal temperature range (bio 2). The second group consisted of *Enyalius sp* n., which was positively correlated with the latitude and the mean annual temperature (bio 1), *E. iheringii* positively correlated with bio 12 and *E. bibronii* positively correlated with bio 1. The third group consisted of *E. perditus,* which was associated with the aspect and vegetal cover (ndvi), *E. bilineatus* and *E. brasiliensis* which were the most positively associated with bio 17 and *E. catenatus* which was the most positively associated to longitude.

In the CCA for the body shape x type of vegetation for the identity matrix (Fig. 1C), the partition of the model explained approximately 47% of the variation. The largest portion was explained by the type of vegetation (20%), whereas the environmental variables explained 12.5% of the variation and the unexplained portion was of 53% (residual). The effect of morphology and environment together explained 14.5% of the variation of the model. The test of models for both datasets were significant ($p < 0.001$; morphology, $F = 13.5180$; type of vegetation, $F = 93.0440$). Three groups were formed, considering *E. brasiliensis* a distinct group in relation to the second axis, separated from the larger group to the left of the graph (Fig. 1C). The species from drier areas, such as the *Cerrado* (*Enyalius sp* n.) and *Caatinga* (*E. bibronii*), were found on the right side of the graph (Fig. 1C). At last, species on the left side of the graph were found in wetter areas with dense forests, such as Amazon Forest (*E. leechii*) and Atlantic Forest (*E. bilineatus, E. brasiliensis, E. catenatus*, *E. iheringii* and *E. perditus*) (Fig. 1C).

Discussion

Given yet the scarcity of ecological and behavioral data, it is not possible a detailed analysis to investigate whether morphological variations in *Enyalius* species are correlated with the ecological differences. Otherwise, within a general standpoint, new information regarding patterns of ecomorphological differentiation may be examined for the group on a broad geographic scale. The model used in the present study explained a large portion of the variation among species, while also considered the effect of the morphology and environment together, with the last one explaining the model better than the morphology. To determine the existence of correlations between characters and variables, morphological measures have been used to clarify issues as the niche concept, the segregation of resources and the structuring of communities (Wainwright & Reilly 1994).

However, data on the *Enyalius'* morphology had a relatively low power of explanation in comparison to environmental factors. This, *a priori*, probably may indicate a low degree of phylogenetic inertia present, as a way of explanation of the evolutionary history for the group. Apparently some *Enyalius* species differ slightly from each other in morphological terms, basically more in sizes and colorations among species and genders (i.e., sexual dimorphism), which it has contributed to much identification errors of some species documented in the literature. Furthermore, Ricklefs *et al.* (1981) compared morphological patterns of lizards on three continents and found that the body size gradient was the main dimension of morphological space; moreover, analysis with null models demonstrated that species from different communities did not differ morphologically more than what would be expected by chance.

Such as seen, *Enyalius* is widely distributed in different biomes in Brazil. Our data also indicated an adaptive phenotypic plasticity presents among these species in the ecology context.

It is plausible that environmental characteristics exert a more influence on the presence and adaptation of the species than the phylogeny. This notion is supported by the positive associations among the *Enyalius* species analyzed and the environmental variables. Like different sets of morphological traits respond to different selective pressures (e.g., limbs for the selection of locomotion), it expected that variations among species within a set of variables could also be correlated geographically or phylogenetically among closer species. However, this inference was not supported by the grouping of species in the first CCA, according the *Enyalius'* phylogenetic tree (Bertolotto 2006), that it can be resumed in two clades (see Appendix 2); the first by *E. perditus*, *E. iheringii* and *E. brasiliensis*, predominantly found in the east coast (southeastern and southern regions), and the second made up by *E. leechii* (north region), *E. bilineatus* (middle-west/southeast)*, E. bibronii* and *E. pictus* (mainly in northeast of Brazil). Thus, the patterns were divergent regarding the phylogenetic organization of the group (i.e., there was no overlapping of morphological traits). Indeed, *E. bibronii* and *E. iheringii* are distinct clades geographically distant from each other (northeastern and southern regions, respectively) and live in quite different forest environments (*Caatinga* x Atlantic Forest mixed, respectively), but both were the most positively associated with the body size, head and fourth toe lengths. In other example, *E. brasiliensis* and *E. catenatus* are from phylogenetically different clades, but they were the most associated with arm and hand lengths, exhibiting similar morphological traits to live in Atlantic Forest.

Nevertheless, environmental variables that acted on species with similar morphological traits were different - e.g.: *E. iheringii* and *E. bibronii* were positively associated with body size and other parts, but *E. iheringii* was associated with the altitude and mean diurnal temperature range, whereas *E. bibronii* with the mean annual temperature. This was expected because the environments of these species are completely different and geographically distant from each other.

In case of *E. brasiliensis* and *E. catenatus,* which were positively associated with the same parts of body, the first was positively associated with the precipitation in the driest quarter, whereas the last one was associated with the longitude - such as it was expected also according to the first example above. Such evidence leads to infer that environmental pressures must be the main 'modeling action' on the morphology of the *Enyalius'* species*,* through the natural selection. Like mentioned, the hypothesis of ecomorphology states that it is possible to predict the use of resources through the morphological attributes of a given species. However, biomechanical considerations that offer a functional basis for correlations that led *Anolis* species to converge repeatedly in western India were not found in continental regions, but environmental factors may exert a strong influence over the form of evolutionary radiations (Irschick *et al.* 1997).

In relationship between the morphology and the habitat use in species of chameleons, a correlation has been found in morphological traits that represent a characteristic functional set (Bickel & Losos 2002). However, from a broader historical standpoint, the ascendency of a species is more important than recent morphological adaptations when it is analyzed a set of examples from different taxonomic orders (Douglas & Matthews 1992). Nevertheless, these authors reached to conclusion that from the viewpoint of ecomorphological analysis is more consistent when limited in specimens from the same family, as the phylogenetic effects are controlled to a certain extent and adaptations to environmental factors are more evident (Douglas & Matthews 1992). The importance of taking in account the phylogenetic ascendency of the group studied, it resides in the fact that many characteristics that may be considered adaptive are nothing more than a characteristic of a group of species with a common evolutionary history. However, conclusions from previous studies do not support one another because the adequate attention has not been given to the possibility of confusions, exerting an influence over the variations in the body size and/or in phylogenetic relations (Garland & Losos 1994).

Even a small group of species such as *Enyalius* exhibits a degree of morphological differentiation that it adapted and continues to adapt to different forest environments, being well distributed on a country with scale of continental dimensions (including islands of southeastern coast of Brazil), along of the last 23 million years (see Bertolotto 2006).

Animals need locomotion to perform their daily activities, such as searching for food sources, catching preys, fleeing from predators and seeking shelter and breeding partners (Moermond 1986; Delciellos 2005 and references). Their morphological features and functions associated to types of habitats or microhabitats used it may tell us much about how and what direction the species evolved in their environments. Regarding the type of vegetation and the species' morphology, adaptive aspects may be associated with the type of forest in which these lizards occur, as morphological specialization to habits (e.g., semi-arboreal), that it would be expected and likely molded by natural selection. Most of species lives in dense and wet forests (*E. leechii* in Amazon Forest, and *E. bilineatus, E. brasiliensis, E. catenatus*, *E. iheringii* and *E. perditus* in Atlantic Forest), exhibiting morphological differences in each environment, and suggesting different or similarities lifestyles and habits. For example, although *E. bibronii* and *E. iheringii* live in completely distinct environments (woodlands in the inland of the northeastern and coastal forests in the southeast/southern, respectively), and they do not sharing any common area, both species showed the same highlighted morphological issue; the largest fourth toe. This may be explained by the larger size of these lizards in comparison to other species, as a larger base structure is expected for locomotion, sustaining of body and climbing. Species that living in open areas are expected to have larger locomotor appendages than those in closed areas (Pianka 1969). This make sense for *E. bibronii* which is typically from the sparse *Caatinga* forests, but not for *E. iheringii* that lives in the wet Atlantic Forest, or even for *E. leechii* that had larger leg and feet it lives in the dense Amazon Forest, and maybe use more the forest floor than the arboreal strata.

Although *E. leechii* is not the largest species of the group, it exhibited the most developed structures of the leg and foot, living in a dense area, which it is in contrast to the biomechanical tendency; such as morphological structure would be more adequate for open areas (Pianka 1969). Among species of *Anolis* from the Caribbean, the arm length and body mass were positively associated with the perch diameter, whereas the tail and leg lengths were negatively associated with the perch diameter (Irschick *et al.* 1997). Thereby, *E. catenatus* and *E. brasiliensis* exhibit the arm and hand lengths more developed probably for a arboreal lifestyle (i.e., to climbing), suitable to the Atlantic Forest from the northeastern and southeastern of Brazil, respectively. Using the same argument regarding the habitat, *E. perditu*s had the most developed fourth toe, whereas *E. bilineatus* had the longest tail, which it can used better in the floor of the forest; both species live in the Atlantic Forest, in southeastern Brazil. Such as is known, *E. bilineatus* is the species of group tolerant to semi-open or open areas close to forests (Jackson 1978) and a longer tail makes total sense to a terrestrial adaptation (Irschick *et al.* 1997).

In long term, the locomotion capacity of a species may influence its geographic distribution, as expansion occurs through dispersion events (Pounds 1991). Moreover, differences in the locomotion capacity among species may give rise different degrees of strata or microhabitats used of a given habitat, contributing to sharing of resources (Delciellos 2005 and references). Related species are expected to have particular locomotor properties, but may also share some traits from a recent common ancestor (Losos 1990; Delciellos 2005).

The theory of biomechanic describes a clear relationship between the morphology and the habitat used, once different physical requirements in different habitats affect the locomotion system of organisms of different way. Thereby, the niche specializations of climber lizards should be accompanied by adaptive morphological evolution (Herrel *et al.* 2002 and references).

Biomechanical models suggest that climbers lizards should have a body and head flat to maintain the center of mass of the body as close to the substrate as possible (Vanhooydonchk & Van Damm 1999; Herrel *et al.* 2002). Hence, the anterior limbs take on particular importance for climbing, but the differences between anterior and posterior limbs should be minimal.

In addition, a study on the lizard from North America reports that iguanids from open areas tend to be smaller and thinner and have shorter legs than species from habitats with denser vegetation (Scheibe 1987). Such evidence was corroborated in *Enyalilus sp* n., which it lives in dry areas, in gallery forests from the Brazilian savanna (*Cerrado*; open area) and it is the smallest species observed of the group.

A number of recent studies have examined the evolutionary relationship between the morphology and the habitat use among lizards, such as *Liolaemus sp*., *Anolis sp*., Sceloporinos, Lacertidae, *Niveoscincus sp*., *Tropidurus sp*. and Gekkonidae (Herrel *et al.* 2001, 2002 and references). Surprisingly, for the majority of results on these studies, it was observed little association between the habitat use and the body shape, with the classic exception of *Anolis,* in the Caribbean (Losos 1990). Thereby, *a priori*, little or no relationship between the adaptive morphology and the ecology has been documented and supported for these organisms.

Nevertheless, problems linked to the analyses should be pointed out, such as low statistical power due to collection of a large number of ecological variables, poorly resolved phylogenies and a lack of precise information on habitat use, resulting in a simplistic characterization of the habitat (Herrel *et al.* 2002).

In summary, until this point, we may say that the morphological and environmental specific patterns are associated to *Enyalius* species, independently of the phylogenetic or geographic relationships in that these species are found.

The environmental characteristics exerted a stronger influence on the species in their habitats than the phylogeny for the group. Most of the species in the genus studied is found in wet forests on the eastern coast of Brazil (Atlantic Forest), although *E. leechii* lives isolated in the Amazon forest. The exceptions about the dense vegetation are *E. bibronii* and *Enyalius sp* n. which are found in forest of dry areas from the *Caatinga* and *Cerrado* biomes. The findings of the present study suggest that evolutionary changes in the proportions of body and the body size must be related to divergences in habitats and their different uses among *Enyalius* species, which it merits future investigations. We suggest that the pattern of morphological variations among *Enyalius* species must be a direct consequence of adaptive responses to modeling action of local environmental conditions, and that in turn, the species demonstrated a considerable phenotypic plasticity through their ecologies in different environments. For the first time, our findings corroborated to expected, since the specific morphological patterns distinguished among the *Enyalius* through local adaptive factors according to the environments variables from mainland forests.

Acknowledgments

We are grateful to the heads of the collections for lending the material and data of specimens: Ana L.C. Prudente and Teresa C. Sauer de Ávila-Pires (MPEG), Hussam El D. Zaher and Carolina C. Mello (MZUSP), Luciana Nascimento (MCNR), Paulo Manzanni (ZUEC), Ísis Arantes (CHUNB), Rejane M. Lira-da-Silva (MZUFBA) and Paulo Passos (MNRJ). Thanks to Alexandro Tozetti (Unisinos), Sônia Cechin (UFSM) and Thales Freitas (UFRGS) for suggestions on the final manuscript, and to Marlon (UFRGS) for statistical support. This study received logistical and financial support from PPG-Ecologia/UFRGS and the Departamento de Zoologia/UNB, CAPES (Ph.D. scholarship to André F. Barreto-Lima). Sandra M. Hartz (processes 306816/2010-5) and Guarino R. Colli (563320/2010-9) are CNPq researchers.

References

Ávila-Pires, T. C. S. (1995) Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen*, Leiden, **299**: 1-706.

Bertolotto, C. E. V. (2006) *Enyalius* (Leiosauridae, Squamta): o que os dados moleculares e cromossômicos revelam sobre esse gênero de lagartos endêmicos do Brasil. PhD Thesis – Universidade de São Paulo, SP, Brazil. 139 p.

Bertolotto C. E. V., Pellegrino K. C., Rodrigues M. T. & Yonenaga-Yassuda Y. (2002) Comparative cytogenetics and supernumerary chromosomes in the Brazilian lizards genus *Enyalius* (Squamata, Polychrotidae). *Hereditas*, 136: 51-57.

Bickel, R. & Losos, J. B. (2002) Patterns of morphological variation and correlates of habitat use in Chameleons. *Biology Journal of Linnean Society,* **76**: 91-103.

Bocard D. P., Legendre P. & Drapeau P. (1992) Partialing out the spatial component of ecological variation. *Ecololgy,* **73** (3): 1045-1055.

Bonine K. E. & Garland T. Jr. (1999) Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology, London* **248**: 255-265.

Burnaby T. P. (1966) Growth–invariant discriminant functions and generalized distances. *Biometrics,* **22**: 96-110.

Burnham K. P. &Anderson D. R. (2002) Model selection and multimodel inference: a practical information–theoretic approach. Springer–Verlag. New York.

Delciellos, A. C. (2005) Desempenho arborícola e nicho locomotor potencial de sete espécies de marsupiais (Didelphimorphia) da Mata Atlântica. Master Dissertation – Universidade Federal do Rio de Janeiro, RJ, Brazil, 120 p.

Douglas, M. E. & Matthews, W. J. (1992) Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos,* **65**: 213-224.

Elstrott, J. & Irschick, J. (2004) Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean *Anolis* lizards. *Biological Journal of the Linnean* Society, **83**: 389-398.

Etheridge, R. (1969) A review of the iguanid lizard genus *Enyalius*. *Bulletin of the British Museum (Natural History) Zoology,* **18** (8): 231-260.

Garland, T. Jr. & Losos, J. B. (1994) Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright, P.C.; Reilly, S.M. (eds.). Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago, 1994, 240-302p.

Herrel, A., Meyers, J. J. & Vanhooydonck, B. (2001) Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biological Journal of the Linnean Society,* **74**: 305-314.

Herrel, A., Meyers, J. J. & Vanhooydonck, B. (2002) Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biological Journal of the Linnean Society,* **77**, 149-163.

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

Irschick, D. J. & Losos, J. B. (1999) Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribben Anoles. *The American Naturalist,* **154** (3): 293-305.

Irschick, D. J., Vitt, L. J., Zani, P. A. & Losos, J. B. (1997) A comparison of evolutionary radiations in mainland and Caribbean Anolis lizards. *Ecology,* **78** (7): 2191-2203.

Jackson, J. F. (1978) Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. *Arquivos de Zoologia,* **30** (1): 1-79.

Johnson, M. A., Kirby, R.,Wang, S. &Losos, J. B. (2006) What drives variation in habitat use by *Anolis* lizards: habitat availability or selectivity? *Canadian Journal of Zoology,* **84**: 877-866.

Jolicoeur, P. (1963) The multivariate generalization of the allometry equation. *Biometrics,* **19**: 497-499.

Karr, J. R. & James, F. C. (1975) Ecomorphological Configuration and Convergent Evolution in Species and Communities, p. 258-291. In: Cody, M. L. & Diamond, J. M. (eds). Ecology and evolution of communities. Massachusetts, Belknap Press, XII+545 pp.

Kohlsdorf, T., T., Garland Jr. & Navais, C. A. (2001) Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology*, **248**: 151-164.

Larson, A. & Losos, J. B. (1996) Phylogenetic systematics of adaptation. In: M. R. Rose and G. V. Lauder (eds.) Adaptation. Academic Press, San Diego. 187-220 pp.

Lima, A. F. B. & Sousa, B. M. de. (2006) Court and copulation behaviors of *Enyalius perditus* Jackson, 1978 (Sauria: Leiosauridae) in captivity conditions. *Revista Brasileira de Zoociências,* **8** (2): 189-194.

Loebmann D. & Haddad C. F. B. (2010) Amphibians and reptiles from a highly diverse area of the Caatinga domain: composition and conservation implications. *Biota Neotropical,* **10**: 227-256.

Losos, J. B. (1990) Ecomorphology, performace capability, and scaling of west indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs,* **60**: 369-388.

Losos, J. B. (1992) The evolution of convergent structure in caribbean *Anolis* communities. *Systematic Biology,* **41**: 403-420.

Losos J. B., Andrews, R. M., Owen, J. S. & Schuler, A. L. (1991) Behaviour, ecology, and locomotor performance of the giant Anole, *Anolis frenatus*. *Caribbean Journal of Science,* **27** (3-4): 173-179.

Losos, J. B. & Sinervo, B. (1989) The effect of morphology and perch size on sprint performance in *Anolis* lizards. *Journal of Experimental Biology,* **145**:23-30.

Macrini, T. E. & Irschick, D. J. (1998) An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biological Journal of the Linnean Society,* **63**: 579-591.

Melville J., Harmon, L. J. & Losos, J. B. (2006) Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedins of the Royal Society London,* B **273**, 557-563.

Moermond, T. C. (1979) Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology,* **60**: 152-164.

Moermond, T. C. (1986) A mechanistic approach to the structure of animals communities: *Anolis* lizards and birds. *American Zoology,* **26**: 23-37.

Peres-Neto, P. R. (1999) Alguns métodos e estudos em ecomorfologia de peixes de riacho. Pp. 209-236. In: Caramaschi, E. P., R. Mazzoni & P. R. Peres-Neto (Eds.). Ecologia de peixes de riachos. Série *Oecologia Brasiliensis*, Vol. VI. PPGE- Universidade Federal do Rio de Janeiro, RJ, Brazil, 260 pp.

Pianka, E. R. (1969) Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology,* **50**:1012-1030.

Pianka, E. R. (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton University Press, Princeton, N. J.

Pianka, E. R. & Parker, W. S. (1972) Ecology of de iguanid lizard *Callisaurus draconoides*. *Copeia,* **1972**: 493-508.

Pianka, E. R & Pianka, H. D. (1976) Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australia desert. *Copeia,* **1976**: 125-142.

Pounds, J. A. (1988) Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecological Monographs,* **58**: 299-320.

Pounds, J. A. (1991) Habitat structure and morphological patterns in arboreal vertebrates. *In*: Bell, S. S., Mccoy, E. D. & Mushinsky, H. R. (Eds.). Habitat structure: the physical arrangement of objects in space. Chapter 6. London, New York: Chapman & Hall.

Ricklefts, R. E. & Travis, J. (1980) A morphological approach to the study of avian community organization. *Auk,* **97**: 321-338.

Ricklefs, R. E., Cochran, D. & Pianka, E. R. (1981) A morphological analysis of the structure of communities of lizards in desert habitats. *Ecology,* **62**: 1474-1483.

Ribas, S. C., Velloso, A. L. R., Teixeira-Filho, P., Rocha-Barbosa, O., Evangelista, H. & Santos, E. A. (2004) Structure of claws and toes of two tropidurid lizard species of Restinga from Southeastern Brazil: adaptations to the vertical use the habitat. *Revista Chilena de Historia Natural,* **77**: 599-606.

Rocha, C. F. D., Vrcibradic, D. & Araújo, A. F. B. (2000) Biogeografia de Répteis de Restingas: Distribuição, ocorrências e endemismos. 99-116p. *In*: F. A. Esteves & Lacerda (eds.). Ecologia de restingas e lagoas costeiras. NUPEM/Universidade Federal do Rio de Janeiro, Macaé, Brazil. 394 pp.

SBH. (2011) Brazilian reptiles - List of species. Bérnils, R. S. & H. C. Costa. (Orgs.). Accessible at http://www.sbherpetologia.org.br/. Sociedade Brasileira de Herpetologia.

Scheibe J. S. (1987) Climate, competition, and the structure of temperate zone lizard communities. *Ecology,* **68**:1424-1436.

Somers K. M. (1986) Multivariate allometry and removal of size with principal component analysis. *Systematic Zoology*, **35**: 359-368.

Terribili, L. V. (2009) Padrões ecológicos globais de dois clados de serpentes, Viperidae e Elapidae (Squamata, Serpentes). PhD Thesis, Universidade de São Paulo, SP, Brazil, 212 pp.

Vanhooydonck, B. & Van Damme R. (1999) Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evolutionary Ecology Research,* **1**: 785-805.

Vanzolini P. E. (1972) Miscellaneous notes on the ecology for some Brazilian lizards (Sauria). *Papéis Avulsos de Zoologia,* **26** (80): 83-115.

Wainwright, P. C. & Reilly, S. M. (1994) Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago. 367 pp.

Williams E. E. (1972) The origin of faunas. Evolution of lizard congeners in the complex island fauna: a trial analysis. *Evolutionary Biology,* **6**:47-89.

Zhang, P. (2003) Multiple Imputation: Theory and Method. *International Statistical Review*, **71** (3): 581-592, Printed in The Netherlands, International Statistical Institute.

Table 1. Eigenvalues, scores and importance of components in the CCA on the variation of *Enyalius* species in relation to morphological measurements. Details: snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (ff), posterior leg length (l), foot length (f), and fourth toe length (ft); Ebib – *Enyalius bibronii,* Ebil – *Enyalius bilineatus*, Ebra – *Enyalius brasiliensis*, Ecat – *Enyalius catenatus,* Elee – *Enyalius leechii,* Eihe – *Enyalius iheringii,* Eper – *Enyalius perditus*, and Esp – *Enyalius sp* n.

Importance of components	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6	CCA7	CA1	CA2	CA3	CA4	CA5	CA6	CA7
Eigenvalue	0.284	0.1481	0.0697	0.0236	0.01686	0.00428	0.00103	0.899	0.720	0.651	0.474	0.1980	0.129	0.0697
Proportion explained	0.077	0.0401	0.0189	0.0064	0.00457	0.00116	0.00028	0.244	0.195	0.177	0.128	0.0537	0.035	0.0189
Cumulative proportion	0.077	0.1172	0.1361	0.1425	0.14705	0.14821	0.14849	0.392	0.588	0.764	0.892	0.9461	0.981	1.0000
Accumulated constrained eigenvalues	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6	CCA7							
Eingenvalue	0.284	0.148	0.0697	0.0236	0.0168	0.0043	0.0010							
Proportion explained	0.519	0.270	0.1273	0.0431	0.0308	0.0078	0.0019							
Cumulative proportion	0.519	0.789	0.9164	0.9595	0.9903	0.9981	1.0000							

Species scores

	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Elee	0.5828	-0.0938591	0.020430	-0.49224	0.18825	0.057879
Eper	0.9048	0.2645340	0.356214	-0.04677	-0.10938	-0.006586
Esp	-0.0801	-0.0001309	0.001812	0.12828	-0.02777	0.025166
Ebil	-0.4434	0.8852906	-0.227888	-0.05890	0.12909	-0.012462
Ebra	0.4575	-0.7148096	-0.274912	0.04847	0.24954	0.149261
Ebib	-1.2112	-0.4535622	1.047261	0.01881	0.34579	-0.097023
Ecat	0.3949	-0.3543699	-0.309822	0.01501	0.04025	-0.150104
Eihe	-0.7775	-0.3126559	-0.066597	-0.21033	-0.20515	0.010042

Biplot scores for constraining variables

	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
s	-0.28047	-0.326846	-0.21923	0.21750	0.171991	0.29802
t	-0.37146	0.703970	-0.03948	-0.02310	0.165536	-0.15371
h	-0.38595	-0.670070	-0.20884	0.19892	0.080423	0.10640
a	0.32231	-0.493278	0.13483	0.05156	-0.247180	-0.42161
ha	0.12744	-0.420536	-0.12763	-0.02148	-0.113717	-0.42004
ff	-0.08753	-0.146643	0.34361	-0.49775	-0.390854	0.50403
l	0.59380	-0.090691	-0.20861	-0.15082	0.386474	0.02679
f	0.53317	0.006994	0.20955	0.50666	0.003583	0.22081
ft	0.28776	0.186175	0.19390	0.05618	-0.340101	0.14923

Table 2. Eigenvalues, scores and importance of components in the CCA on the variation of *Enyalius* species in relation to environmental variables. Details: altitude (alt), aspect (asp), latitude (lat), longitude (log), vegetal cover (ndvi), annual mean temperature (bio 1), mean diurnal temperature range (bio 2), annual mean precipitation (bio 12), precipitation of the driest quarter (bio 17) and precipitation of the coldest quarter (bio 19); Ebib – *Enyalius bibronii,* Ebil – *Enyalius bilineatus*, Ebra – *Enyalius brasiliensis*, Ecat – *Enyalius catenatus,* Elee – *Enyalius leechii,* Eihe – *Enyalius iheringii,* Eper – *Enyalius perditus*, and Esp – *Enyalius sp* n.

Importance of components	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6	CA1	CA2	CA3	CA4	CA5	CA6
Eigenvalue	0.5027	0.294	0.1843	0.0617	0.04163	0.00744	0.993	0.958	0.938	0.816	0.706	0.4973
Proportion explained	0.0838	0.049	0.0307	0.0103	0.00694	0.00124	0.165	0.160	0.156	0.136	0.118	0.0829
Cumulative proportion	0.0838	0.133	0.1635	0.1738	0.18071	0.18195	0.347	0.507	0.663	0.799	0.917	1.0000

Accumulated constrained eigenvalues	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Eigenvalue	0.5027	0.294	0.1843	0.0617	0.04163	0.00744
Proportion explained	0.460	0.269	0.169	0.0565	0.0381	0.00682
Cumulative proportion	0.460	0.730	0.899	0.9550	0.9932	1.00000

Species scores

	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Elee	-3.3320	0.3521	1.20759	-0.4223	-0.38654	0.29824
Eper	0.6060	1.3564	-0.05903	0.2961	0.59261	0.14805
Esp	-0.4012	-0.3713	-0.43464	0.3434	0.06148	-0.03028
Ebil	0.7864	0.4381	0.70620	0.1120	-0.80032	0.12420
Ebra	0.9759	0.1415	-0.19194	0.2805	-1.27260	-0.28742
Ebib	0.1466	-0.4084	2.81923	0.4698	0.91281	-0.63127
Ecat	1.1144	-1.2102	0.34409	-0.5932	0.25047	0.24870
Eihe	-0.1417	0.5138	-0.46396	-1.2000	0.06225	-0.23262

Biplot scores for constraining variables

	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
lat	-0.42231	-0.46720	0.40176	0.22313	0.11183	-0.009855
long	0.88856	-0.16731	0.30146	0.02886	0.06263	-0.033823
alt	-0.08266	0.11299	-0.23760	0.61499	0.27154	0.105457
asp	0.06565	0.17286	-0.01940	-0.36055	0.20473	0.129688
bio1	-0.13734	-0.56052	0.15026	-0.26420	-0.25144	0.152935
bio2	-0.16264	0.06727	0.14593	0.25479	-0.15764	0.404829
bio12	-0.37439	0.34026	-0.30158	-0.29367	0.31227	0.252580
bio17	0.30141	0.05699	-0.13290	-0.68466	0.29151	0.131334
bio19	-0.04385	-0.03383	0.34458	-0.50081	0.32982	-0.291584
ndvi	0.10819	0.30225	0.29295	-0.41442	-0.05385	0.275180

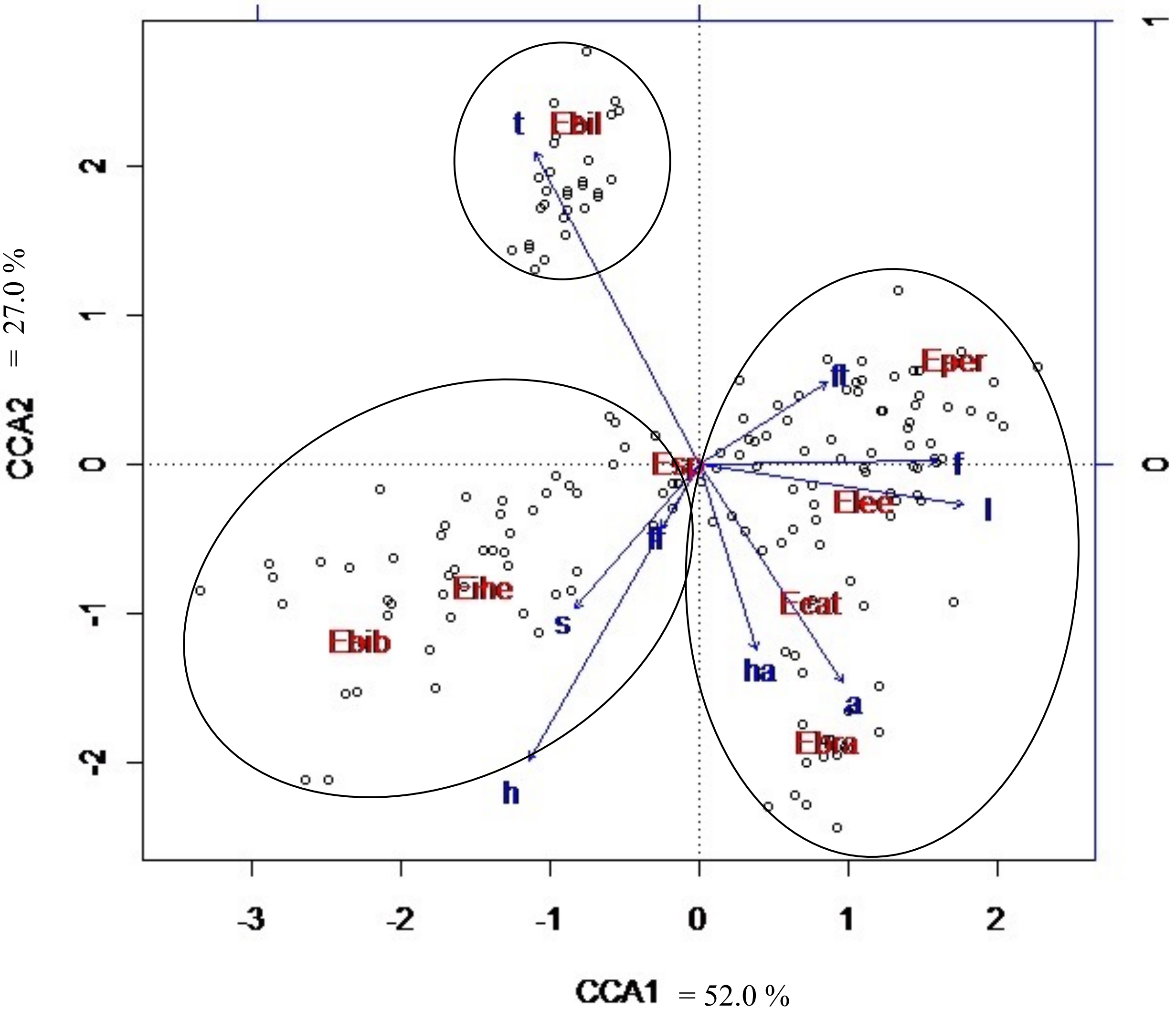


Fig. 1 a) CCA graph: *Enyalius* species in relation to morphological measurements. Details: snout-vent length (s), tail length (t), head length (h), anterior leg length (a), hand length (ha), fourth finger length (ff), posterior leg length (l), foot length (f), and fourth toe length (ft); Ebib - *Enyalius bibronii*, Ebil - *Enyalius bilineatus*, Ebra - *Enyalius brasiliensis*, Ecat - *Enyalius catenatus*, Elee - *Enyalius leechii*, Eihe - *Enyalius iheringii*, Esp - *Enyalius sp* n., and Eper - *Enyalius perditus*.

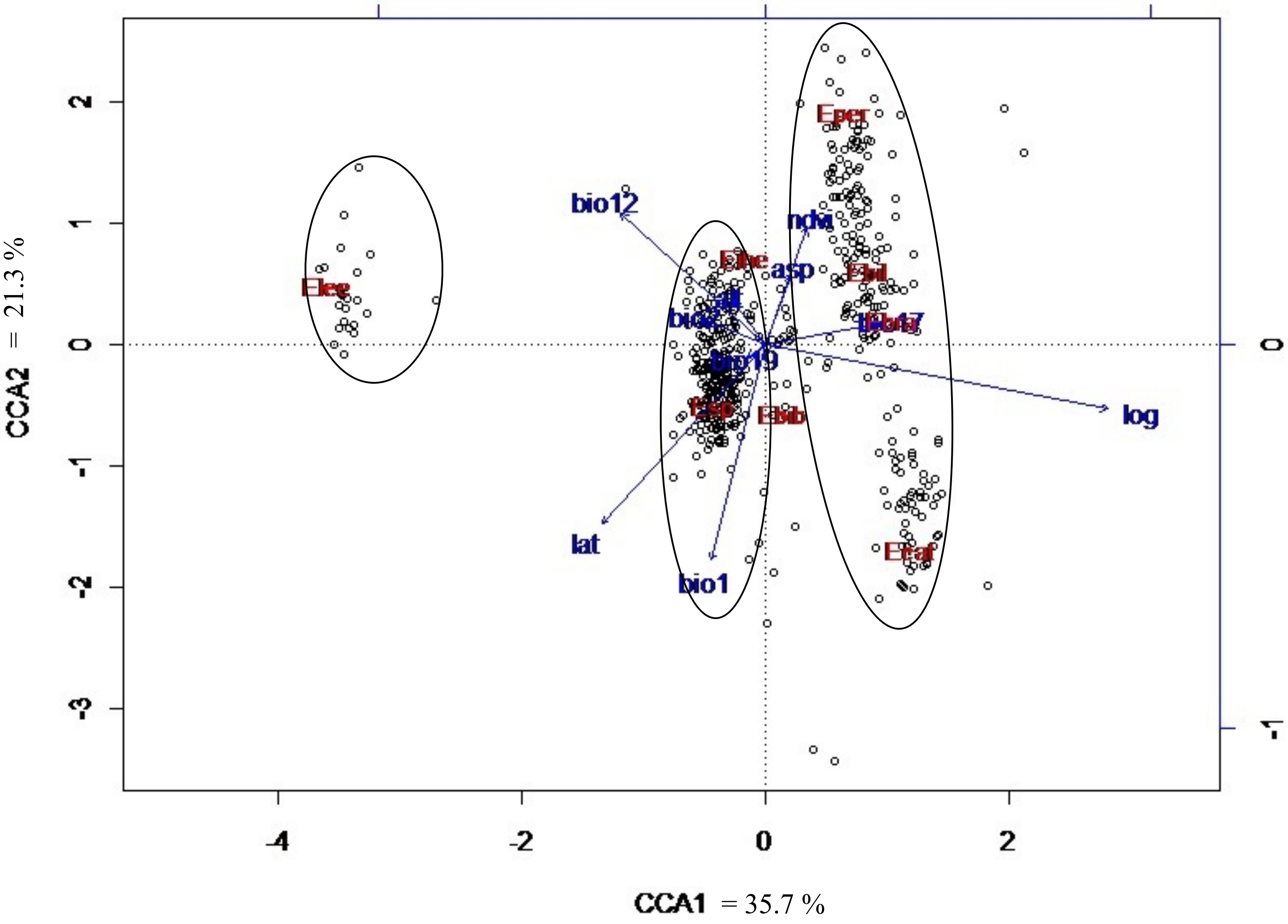


Fig. 1. b) CCA graph: *Enyalius* species in relation to environment variables. Details: altitude (alt), aspect (asp), latitude (lat), longitude (log), vegetal cover (ndvi), annual mean temperature (bio 1), mean diurnal temperature range (bio 2), annual mean precipitation (bio 12), precipitation of the driest quarter (bio 17) and precipitation of the coldest quarter (bio 19); Ebib – *Enyalius bibronii,* Ebil – *Enyalius bilineatus*, Ebra – *Enyalius brasiliensis*, Ecat – *Enyalius catenatus,* Elee – *Enyalius leechii,* Eihe – *Enyalius iheringii,* Esp – *Enyalius sp* n.*,* and Eper – *Enyalius perditus*.

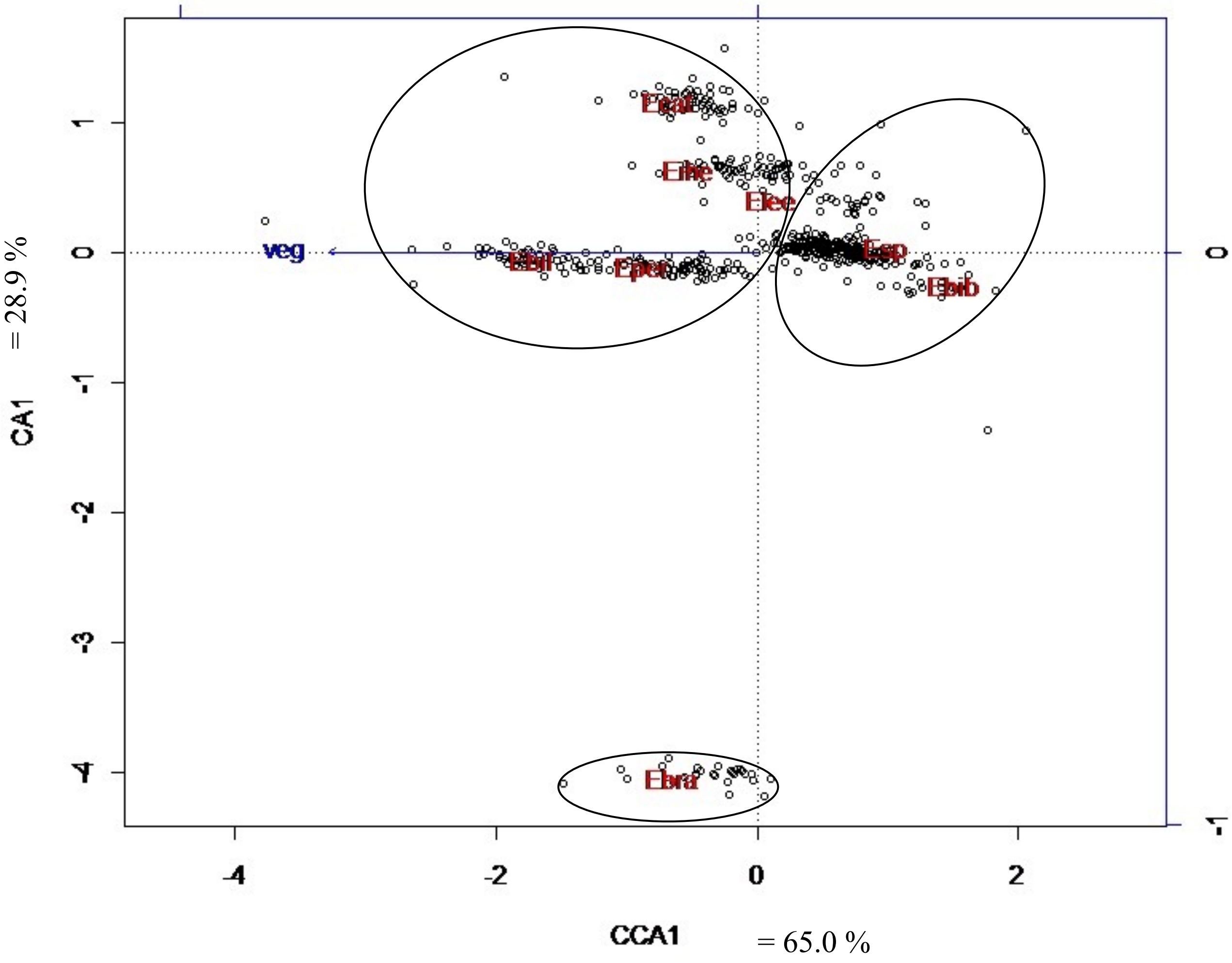


Fig. 1. c) CCA graph: *Enyalius* species in relation to type of vegetation (veg). Details: Ebib – *Enyalius bibronii,* Ebil – *Enyalius bilineatus*, Ebra – *Enyalius brasiliensis*, Ecat – *Enyalius catenatus,* Elee – *Enyalius leechii,* Eihe – *Enyalius iheringii,* Esp – *Enyalius sp* n.*,* Eper – *Enyalius perditus*. On the left, represents the species from closed forests (Amazon and Atlantic Forests). On the right, the species from open woodlands (*Cerrado* and *Caatinga*).

Appendix 1

Brazilian scientific collections (species data borrowed):

Museu de Zoologia de São Paulo (MZUSP), Museu Nacional do Rio de Janeiro (MNRJ), Museu Paraense Emílio Goeldi, Belém, PA (MPEG), Coleção Herpetológica da Universidade de Brasília, Distrito Federal (CHUNB), Museu de Zoologia da Universidade Estadual de Campinas, SP (ZUEC), Museu de Ciências Naturais da Pontifícia Universidade de Belo Horizonte, MG (MCNR), Coleção Herpetológica do Museu de Ciência e Tecnologia da Pontifícia Universidade Católica, Porto Alegre, RG (MCP), Museu de Zoologia da Universidade Federal de Viçosa, MG (MZUFV) and Museu de Zoologia da Universidade Federal da Bahia, Salvador, BA (UFBA).

Specimens examined from collections (n = 558):

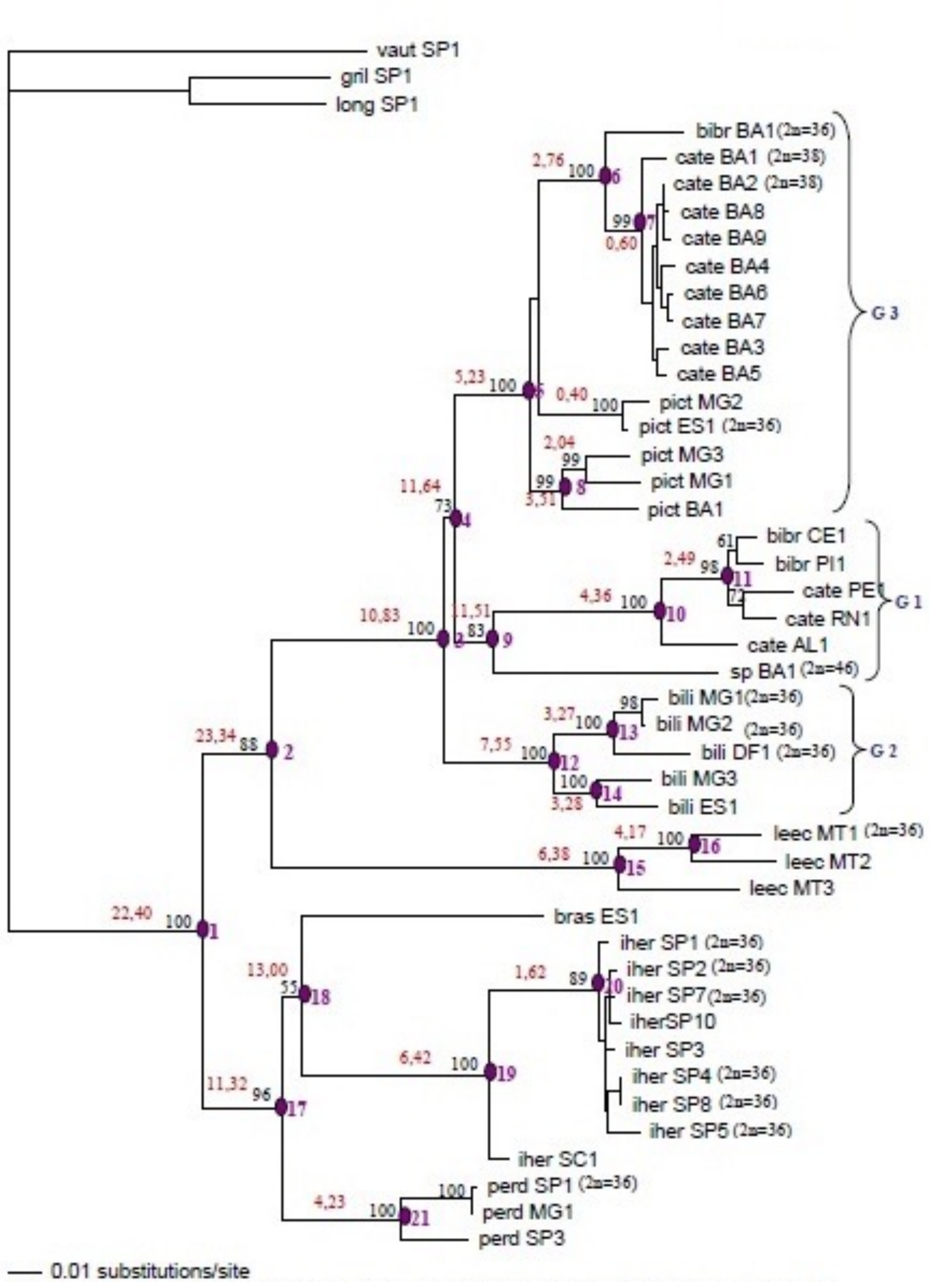
E. bibronii (17): CHUNB - 56555, CHUNB-56918, CHUNB-57375-79, MZUFV-249, MZUFV - 251, MZUFV - 287, MZUFV-307, MZUFV-528, MZUSP - 62792, MZUSP - 65628, MZUSP - 66105, MZUSP - 78721, MZUSP-87592. *E. bilineatus* (59): CHUNB - 36170-74, MCNR - 115, MCNR - 277-78, MCNR-445, MCNR-522-23, MCNR-735, MCNR-1342, MCNR-1409, MCNR - 1411, MCNR-1747, MCNR-3156, MCNR-3277, MCNR-3557, MNRJ-6356-57, MNRJ-10136, MNRJ - 10861-63, MNRJ-10868-71, MNRJ-10873-74, MNRJ-10879-80, MNRJ-10882, MNRJ - 10890, MNRJ-10892, MNRJ-10919, MNRJ-14413, MNRJ-15575, MZUFV - 213-14, MZUFV - 241, MZUFV-278, MZUFV-286, MZUFV-314, MZUFV-337, MZUFV-473-74, MZUFV - 498, MZUSP -594, MZUSP-8216, MZUSP-10410, MZUSP-29698, MZUSP-39522, MZUSP -42778, MZUSP - 71954, MZUSP-95184, MZUSP-95424-25. *E. brasiliensis* (27): MNRJ - 1611, MNRJ - 3446,MNRJ-12091, MNRJ-12354-58, MNRJ-17614, MZUFV-109, MZUFV - 179, MZUFV -

320, MZUFV-472, MZUFV-499, MZUFV-500, MZUFV-508, MZUFV-619, MZUSP -3233-34, MZUSP - 4276-77, MZUSP-10247, MZUSP-39533, MZUSP-39535, MZUSP-39537, MZUSP - 95426, PUCRS-5355. *E. catenatus* (61): CHUNB-08183, CHUNB-28984, CHUNB - 36175-81, MCNR - 542-45,MCNR-1341, MCNR-1343, MCNR-1898, MNRJ-3464, MNRJ-3878, MNRJ - 6341-42, MNRJ-6346,MNRJ-10397, MNRJ-10402, MNRJ-10899, MNRJ-12518-20, MNRJ - 13238-42, MNRJ-15122, MPEG-1846, MZUFV-398-99, MZUFV-425, MZUFV-451, MZUFV - 454, MZUSP-23086, MZUSP-66174, MZUSP-66422-23, MZUSP-95403-09, PUCRS - 9020, UFBA - 908, UFBA-1085-86, UFBA-1088-94. *E. iheringii* (64): CHUNB-08184, CHUNB - 13460, CHUNB-28882-83, MZUSP-95390, MZUSP-98131, MZUSP-6864, MZUSP - 10136, MZUSP - 10271, MZUSP-42713-15, MZUSP-76286, MZUSP-78954, MZUSP-79707, MZUSP - 79709-10, MZUSP - 95388-89, MZUSP - 95391-95, MZUSP - 98123-24, MZUSP - 98128-30, MZUSP - 98132, PUCRS-1049, PUCRS-5341, PUCRS-6661, PUCRS-6673, PUCRS-6675, PUCRS - 6703, PUCRS-7775, PUCRS-9525, PUCRS-9539, PUCRS-9726-27, PUCRS - 10978, PUCRS - 11374, PUCRS-12216, PUCRS-12765, PUCRS-12774, PUCRS-17796-97, ZUEC - 971, ZUEC-1185, ZUEC-1372, ZUEC-1834, ZUEC-2034, ZUEC-2167, ZUEC - 2214, ZUEC - 2644, ZUEC -2924, ZUEC -2926-29, ZUEC -2931, ZUEC -3077, ZUEC - 3079. *E. leechii* (25): CHUNB - 44808-09, MCNR-3558, MNRJ-4434, MNRJ-18058, MPEG-13999, MPEG - 14218, MPEG - 17518-19, MPEG - 17543, MPEG - 21926-27, MZUSP - 42728, MZUSP - 81526-28, MZUSP - 81621-23, MZUSP -81719-22, MZUSP -82412, MZUSP -89943. *E. perditus* (71): MCNR - 529, MCNR - 3550-55, MNRJ-1614, MNRJ-3447, MNRJ-6354-55, MNRJ -10141-45, MNRJ - 10160, MNRJ -15044, MNRJ -17027, MZUFV -288, MZUFV -529, MZUFV - 631, MZUFV - 674, MZUFV-728, MZUSP -584, MZUSP -590, MZUSP -11464, MZUSP -74903, MZUSP - 78120, MZUSP - 79711, MZUSP -89188-91, MZUSP -91438-45, MZUSP - 92270, MZUSP - 94044, MZUSP-94835, MZUSP-95025-32, MZUSP-95427-30, MZUSP - 95763-67,

MZUSP-96922, MZUSP-97390, MZUSP-98143, ZUEC-1888, ZUEC-1894, ZUEC-2925, ZUEC - 2932, ZUEC - 2940, ZUEC - 2943. *Enyalius sp* n. (234): CHUNB - 3546, CHUNB - 8167-68, CHUNB - 8170-82, CHUNB - 8906-09, CHUNB - 8922-23, CHUNB - 9588, CHUNB - 16942, CHUNB - 21808-09, CHUNB-21812-15, CHUNB-21856, CHUNB-21859-60, CHUNB -21863-64, CHUNB - 21873-92, CHUNB-21895-96, CHUNB-21898-99, CHUNB - 22001, CHUNB - 22022, CHUNB -22048, CHUNB - 22741-45, CHUNB - 23813, CHUNB - 23847-53, CHUNB - 23951, CHUNB-24056, CHUNB-24058, CHUNB-24212-13, CHUNB-24508, CHUNB - 24511, CHUNB - 24574, CHUNB - 24590, CHUNB - 24759, CHUNB -24771-73, CHUNB - 24775-80, CHUNB - 25021, CHUNB-25025-26, CHUNB-25050-51, CHUNB-25057, CHUNB - 25062-63, CHUNB - 25067-71, CHUNB-25079, CHUNB-25213-14, CHUNB-25216-17, CHUNB-25313, CHUNB - 25315, CHUNB - 25362-63, CHUNB - 25569, CHUNB - 25587-88, CHUNB -25591, CHUNB - 25594, CHUNB - 25596, CHUNB - 25690, CHUNB -26074-79, CHUNB - 26081-84, CHUNB - 26086, CHUNB-26098, CHUNB-26993, CHUNB-27618-19, CHUNB - 27624-25, CHUNB - 27627, CHUNB-27631, CHUNB-27638, CHUNB-27682, CHUNB-27724, CHUNB - 28884 - 85, CHUNB-28890, CHUNB-28909-10, CHUNB-29290-95, CHUNB - 29311-16, CHUNB - 29452-54, CHUNB-29657-59, CHUNB-30342, CHUNB-30523, CHUNB - 30953, CHUNB - 32709, CHUNB-33630, CHUNB-33636-38, CHUNB-33640, CHUNB - 33790-91, CHUNB - 33797, CHUNB-33905, CHUNB-34000, CHUNB-34004, CHUNB - 34013-15, CHUNB - 34845-46, CHUNB-35714-15, CHUNB-36555, CHUNB-37462-67, CHUNB - 38190-91, CHUNB-38503, CHUNB-38648-49, CHUNB-38651, CHUNB-38772-78, CHUNB - 38783, CHUNB-38959-63, CHUNB-40284, CHUNB-40294, CHUNB-43264, CHUNB - 43268, CHUNB - 43294, CHUNB-44116, CHUNB-48357, CHUNB-52394, CHUNB-52396, CHUNB - 52407 - 08, MZUSP - 78812, MZUSP - 87707, MZUSP - 88857, MZUSP - 93142 - 45.

** All collection sites of species were considered.*

Appendix 2



*Current phylogenetic tree for the group *Enyalius* (source: Bertolotto, 2006).

CONCLUSÕES GERAIS

No **Capítulo 1,** vimos que os principais fatores para a distribuição geográfica do gênero *Enyalius*, em geral, foram a temperatura média anual, a latitude e a amplitude média da temperatura diurna, indicando-nos uma possível adaptação climática como base para explicação da distribuição do grupo.

Como sabemos, os hábitats e suas condições climáticas podem influenciar a história de vida dos organismos e os processos ecológicos das espécies em suas distribuições geográficas. Assim, nós sugerimos que a temperatura média anual e a latitude na costa leste do Brasil tenha se sobreposto no modelo, caracterizando o domínio da Floresta Atlântica e repercutindo na distribuição e história de vida de *Enyalius*.

Como as espécies de *Enyalius* vivem em ambientes florestais e são semi-arborícolas, o tamanho das mãos e dos dedos destas são importantes estruturas morfológicas para a escalar e para se mover entre os estratos da floresta. Da mesma forma, membros anteriores e mãos maiores em regiões tropicais podem indicar uma maior capacidade de escalar no substrato arbóreo.

A variação geográfica na morfologia do grupo foi observada em sua distribuição, como demonstrado pelas diferenças no tamanho do corpo e estruturas morfológicas que foram explicadas por variáveis climáticas, espaciais e estruturais (i.e., cobertura vegetal) do ambiente.

A regra de Allen foi corroborada como padrões na variação na morfologia de *Enyalius,* que foram correlacionados com as condições climáticas e geográficas analisadas.

Estes padrões de variação morfológica também foram associados com a cobertura vegetal e provavelmente à disponibilidade de água (i.e., chuvas) nas diferentes regiões, que exerceu influência sobre a adaptação morfológica de *Enyalius.*

Isto pode explicar o crescimento diferencial alométrico observado sobre uma vasta área geográfica. Assim, nós sugerimos que uma hipótese de adaptação climática seja a base para explicar a distribuição de *Enyalius* em ambientes florestais do Brasil.

No **Capítulo 2,** estudamos detalhadamente as áreas de distribuição potencial de cada espécie do grupo e encontramos, para a maioria das espécies, características ambientais gerais que foram importantes para a ocorrência do gênero nos seus ambientes.

Nós sugerimos que as variáveis latitude e amplitude média da temperatura diurna, ao longo da costa brasileira, sobrepõem-se na maior parte dos modelos potenciais das espécies, caracterizando a distribuição principal das espécies de *Enyalius* pelo bioma da Floresta Atlântica, cuja é uma formação florestal de ampla variação latitudinal. Isso nos indicou a importância dessas variáveis para a maioria das espécies do grupo, revelando um padrão geral de fatores ambientais para a presença das espécies neste bioma.

Porém, em casos específicos as variáveis climáticas características de sazonalidade, como as precipitações do trimestre mais seco e mais frio, foram importantes nos modelos de duas espécies de biomas diferentes; *E. leechii,* na Floresta Amazônica e *Enyalius sp* n., no Cerrado.

No caso do Cerrado, o equilíbrio de água desta região está negativamente associado com a longitude, que por sua vez apresenta um dos menores índices de precipitação dos biomas brasileiros, sendo apenas superado pelo da Caatinga.

Sugerimos que os requerimentos específicos climáticos e geográficos influenciaram na adaptação e distribuição das espécies de *Enyalius,* explicando a sua presença na extensa área geográfica ao longo da costa leste brasileira e confirmando assim, a suspeita levantada com os resultados iniciais do Capítulo 1.

Em geral, parte dos nichos ecológicos similares entre espécies devem existir por influência ambiental de ampla magnitude em associação com a plasticidade fenotípica e adaptativa das espécies e, provavelmente, por uma importante inércia filogenética presente no grupo *Enyalius*, em relação às características ambientais utilizadas como requerimentos básicos das espécies.

A questão importante que permaneceu no final do Capítulo 2 é se tal evidência seria mais um resultado da filogenia como algo comum às espécies mais aparentadas ou seria uma conseqüência ecológica adaptativa por atuação da seleção natural sobre a distribuição e a morfologia das espécies.

Finalmente no **Capítulo 3,** nós encontramos respostas para esta questão levantada no final do Capítulo 2, pois evidenciamos que para *Enyalius* há padrões morfológicos e ambientais específicos associados às espécies, independente da relação filogenética e da distância geográfica entre as espécies do grupo.

Assim, observamos que as características ambientais locais atuaram mais sobre a ocorrência das espécies em seus hábitats do que simplesmente por uma questão de herança evolutiva do grupo (i.e., filogenia).

Este estudo seqüencial indicou que determinadas mudanças evolutivas nas proporções e no tamanho do corpo das espécies de *Enyalius* devem estar associadas à divergência de hábitats e suas características, bem como ao uso de substratos diferentes entre as espécies deste gênero de lagartos, que por sua vez, necessitam de maiores investigações em futuros trabalhos.

Concluímos que os padrões observados sobre a variação morfológica entre as espécies de *Enyalius* devem ser uma conseqüência direta de respostas adaptativas à 'ação modeladora' das condições ambientais locais, o que por sua vez indicou-nos uma alta plasticidade adaptativa através de diversas ecologias em diferentes ambientes florestais e biomas do continente.

Como perspectivas deste estudo, será necessária a inclusão de dados das espécies novas ao grupo (i.e., não descritas ainda), bem como a caracterização adequada do ambiente em que elas residem, a fim de complementar os dados aqui estudados.

Não obstante, somente uma filogenia mais completa e esclarecedora sobre as espécies de *Enyalius* poderá auxiliar-nos em novas questões ainda não completamente explicadas sobre as relações ecomorfológicas do grupo. Desta forma, nós pretendemos dar continuidade a este estudo integrando novos dados filogenéticos do grupo, como próximo passo às análises realizadas, visando atingir futuramente novas respostas sobre os padrões da ecologia evolutiva do gênero de lagartos *Enyalius*.

GENERAL CONCLUSIONS

In the **Chapter 1,** we saw that the main factors for the geographical distribution of the *Enyalius* genus, in general, were the annual mean temperature, latitude and mean diurnal temperature range, indicating a possible climate adaptation as a basis for explanation of the distribution of group.

Such as we know, the habitats and their climatic conditions may influence the life story of the organisms and the ecological processes of species in their geographical distributions. Thereby, we suggest that the annual mean temperature and latitude on the east coast of Brazil have been overlapping on the obtained model, featuring the Atlantic forest domain which reflected in the distribution and life history of *Enyalius*.

Since *Enyalius* species live in forest environments and they are semi-arboreal, the size of the hands and fingers are important morphological structures for climbing and to move between the strata of the forest. Similarly, larger anterior members and hands in tropical regions may indicate a greater ability to climb on the tree substrate.

The geographic variation in morphology of the group was observed in its distribution, as shown by differences in body size and morphological structures which were explained by climatic variables, spatial and structural (i.e., vegetal cover) of the environment.

The rule of Allen was corroborated as patterns in the variation in the morphology of *Enyalius,* which were correlated with the climatic and geographical conditions analyzed.

These patterns of morphological variation were also associated with the vegetation cover and, probably, with the availability of water (i.e., rains) in the different regions, which exerted influence on the morphological adaptation of *Enyalius*. Therefore, these environmental factors may explain the differential allometric growth observed over a wide geographical area.

Therefore, we suggest that a climate adaptation hypothesis be the basis to explain the distribution of *Enyalius* in the forest environments from Brazil.

In the **Chapter 2,** we studied in details the areas of potential distribution of each species in the group and we found, for most species, general environmental characteristics that were important for the development of the genus in their environments.

We suggest that the latitude and mean diurnal temperature range, along the Brazilian coast, overlapped in most of the potential models of the species, characterizing the main distribution of *Enyalius* species by the Atlantic forest biome, which it is a forestry formation of wide latitudinal variation. Thereby, this led us to the importance of these variables for most species, revealing a general pattern of factors for the presence of the group in this important *hotspot* biome.

However, in specific cases the weather variables of seasonal features, as the precipitations in the driest and the coldest quarter, were important in the models of two species from different biomes; for *Enyalius leechii,* in Amazonia Forest and for *Enyalius sp* n., in the *Cerrado*. In case of the *Cerrado*, the balance of water in this region is negatively associated with the longitude, which in turn it has one of the lowest rates of precipitation of the Brazilian biomes, only surpassed by the *Caatinga*.

We suggest that the specific climatic and geographic requirements influenced on the adaptation and the species' distribution of *Enyalius*, explaining their presence in the extensive geographical area along the Brazilian east coast, and thus confirming the suspicion raised in the initial results of Chapter 1.

In general, part of similar ecological niches among species should exists due an environmental influence of huge magnitude in association with the adaptive phenotypic plasticity of the species, and probably due a important phylogenetic inertia present in the *Enyalius* group, concerning the environmental characteristics used as basic requirements of the species.

The important point that remained at the end of Chapter 2 is whether such evidence would be a result of phylogeny as something common to the related species or it is an adaptive ecological consequence by natural selection on the distribution and morphology of species.

Finally in the **Chapter 3,** we find answers to this question raised at the end of Chapter 2, since it was observed that for *Enyalius* there are morphological and environmental specific patterns relating to species, independent of the phylogenetic relationship and geographical distance among the species of the group.

Thereby, we observed that local environmental features worked more on the occurrence of the species in their habitats than simply by an evolutionary inheritance (i.e., phylogeny).

This sequential study indicated that certain evolutionary changes in proportions and body size of *Enyalius* must be associated with the divergence of habitats and their characteristics, as well as the use of different substrates among the species this genus of lizards, which in turn needs to be further investigated in future works.

The patterns observed on the morphological variation among the species should be a direct consequence of adaptive responses to 'modelling action' from the local environmental conditions, which in turn, point to a great adaptive phenotypic plasticity through of diverse ecologies in different forestry environments of the continent.

Will be required to include data from the new species of the group (i.e., not described yet), as well as the adequate characterization of the environment where these species live, in order to complement the data here studied.

Only with an enlightening and complete phylogeny of the species of *Enyalius* will help us in new issues not fully explained on the ecomorphological relations of the group. Therefore, as next step we intend to continue the study integrating new phylogenetic data of the group, in order to achieve us new answers on the patterns of evolutive ecology of the *Enyalius* lizards.