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**Estrutura de comunidades em transições ambientais: lagartos no ecótono Cerrado-
Amazônia**

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**Estrutura de comunidades em transições ambientais: lagartos no ecótono Cerrado-
Amazônia**

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1 **Resumo**

2 Os limites ecológicos desempenham um papel crucial no fluxo de espécies, de genes e
3 nutrientes entre áreas adjacentes. Os limites não apenas separam, mas também conectam
4 estas áreas, agindo como filtros de permeabilidade variável. A estrutura das comunidades
5 varia com a proximidade do ecótono e a riqueza de espécies no ecótono pode ser maior que,
6 menor que, ou intermediária entre as áreas adjacentes. Aqui, eu investigo como o ecótono
7 isola a Amazônia e o Cerrado, atuando como um filtro sobre as trocas faunísticas entre
8 comunidades de lagartos dos dois biomas neotropicais. Com base em dados de campo e da
9 literatura, foram realizadas análises de correlação entre índices de diversidade e a distância de
10 cada ponto amostral ao ecótono e ao centróide dos biomas. Para investigar os processos
11 responsáveis pelos padrões observados, foi realizada uma análise de correspondência
12 canônica (CCA) relacionando a ocorrência das espécies nas comunidades amostras à
13 variáveis ambientais. Os resultados demonstram que a proximidade ao ecótono Cerrado-
14 Amazônia afeta negativamente a diversidade das comunidades de lagartos, o que é
15 determinado por um processo de filtragem ambiental e possivelmente influenciado por
16 fatores históricos. A ordenação da CCA foi capaz de distinguir claramente dois grupos de
17 espécies (de habitats abertos e habitats florestais), e associá-los à variação na vegetação,
18 umidade do solo e variação diária da temperatura.

19

20 **Introdução Geral**

21 Os limites ecológicos e seus gradientes estão entre os assuntos mais abordados na
22 ecologia (Erdős *et al.*, 2011). Em despeito à pequena área que costumam ocupar, quando
23 comparados com o resto da paisagem, estes limites parecem desempenhar um papel crucial
24 no fluxo de espécies (Urbina-Cardona *et al.*, 2006), de genes (Smith *et al.*, 1997) e de matéria
25 (Kolasa & Zalewski, 1995) entre áreas adjacentes. A estrutura das comunidades varia com a

26 proximidade do ecótono (e.g., Hofer *et al.*, 2000; Menke, 2003b; Lloyd *et al.*, 2012) e a
27 riqueza de espécies no ecótono pode ser maior que, menor que, ou intermediária entre as áreas
28 adjacentes (van der Maarel, 1990). A compreensão dos padrões de riqueza nos ecótonos
29 requer ainda o entendimento de fatores ligados à história e biogeografia das áreas, já que, em
30 uma escala regional, os ecótonos resultam do contato de diferentes regiões biogeográficas
31 (Nogués-Bravo & Martinez-Rica, 2004).

32 Uma noção amplamente difundida sobre ecótonos é a de que possuem maior
33 diversidade biológica do que áreas adjacentes e, portanto, maior valor para a conservação
34 (Risser, 1995; Kirkman *et al.*, 1998; Kernaghan & Harper, 2001). Para tanto, os ecótonos
35 deveriam mostrar uma propriedade aditiva, sendo capazes de suportar espécies das áreas
36 adjacentes (Senft, 2009). De forma oposta, a diversidade em ecótonos pode ser menor
37 (Backeus, 1993a; Dangerfield *et al.*, 2003) caso suas condições ambientais sejam sub-ótimas
38 em relação ao centro das áreas adjacentes, prejudicando o estabelecimento e a permanência
39 das espécies (Temple, 1998).

40 A transição entre a Amazônia e o Cerrado é uma extensa zona de tensão ecológica na
41 América do Sul, formada por um mosaico de savanas e florestas (Ratter *et al.*, 1973; Ackerly
42 *et al.*, 1989a; Ratter, 1992). Este mosaico é irregular, apresentando características singulares
43 e recortes de diferentes tamanhos ao longo de sua extensão (Marimon *et al.*, 2006). A zona de
44 transição coincide espacialmente com o “arco do desmatamento”, que se inicia no Maranhão
45 e margeia os limites sudeste, sul e sudoeste da Bacia Amazônica (Ferreira *et al.*, 2005;
46 Fearnside & Graça, 2006; Aldrich *et al.*, 2012). Existe pouca informação sobre como as
47 espécies de vertebrados se distribuem através desta paisagem (Lacher & Alho, 2001) e a falta
48 de conservação desta área pouco estudada parece limitar a detecção de processos ecológicos
49 que estariam ocorrendo no ecótono (Marimon *et al.*, 2006).

50 Lagartos são considerados “organismos modelo” para estudos ecológicos,
51 apresentando características desejáveis como fácil captura, alta abundância e baixa dispersão
52 (Huey *et al.*, 1983; Carothers *et al.*, 1996; Pianka & Vitt, 2003; Camargo *et al.*, 2010), sendo
53 empregados com sucesso em estudos de áreas ecotonais (e.g., Hofer *et al.*, 1999, 2000;
54 Menke, 2003b; Nogués-Bravo & Martinez-Rica, 2004; Urbina-Cardona *et al.*, 2006). Aqui,
55 eu investigo como o ecótono isola a Amazônia e o Cerrado, atuando como um filtro sobre as
56 trocas faunísticas entre dois biomas neotropicais. Eu caracterizo os padrões e investigo os
57 processos responsáveis pelas mudanças na estrutura das comunidades de lagartos, em um
58 gradiente do centro para a periferia dos dois biomas. Caso o ecótono Amazônia-Cerrado
59 funcione como um filtro ambiental, isolando os dois biomas, é esperada uma redução nos
60 índices de diversidade (riqueza, endemismo, diversidade funcional e diversidade filogenética)
61 à medida que avançamos do centro para a periferia dos dois biomas, rumo ao ecótono, uma
62 vez que a maior instabilidade e heterogeneidade ambiental da transição devem dificultar o
63 estabelecimento e a permanência de espécies.

64

65 **Métodos**

66 Os dados relativos às comunidades de lagartos utilizados neste trabalho são
67 provenientes da literatura e de coletas sistemáticas realizadas pelo grupo de pesquisa
68 "Herpetologia do Cerrado". Eu considerei pontos amostrais localizados no Cerrado e na
69 Amazônia, onde coletas foram realizadas utilizando-se de métodos e esforços semelhantes
70 (busca ativa e armadilhas de interceptação-e-queda com cercas-guia por no mínimo três
71 semanas em cada local). As variáveis ambientais que utilizei são aquelas disponibilizadas
72 pelos projetos Worldclim (Hijmans *et al.*, 2005) e Atlas of the Biosphere (utilizado com
73 permissão do Center for Sustainability and the Global Environment, Nelson Institute for
74 Environmental Studies, Universidade de Wisconsin-Madison), correspondendo a dados de

75 temperatura, precipitação, altitude, evapotranspiração, produtividade primária líquida,
76 umidade do solo e vegetação potencial (variável categórica que discrimina o tipo de
77 cobertura que existiria em um grid caso não houvesse interferência humana). Eu obtive as
78 distâncias das comunidades amostradas ao ecótono e ao centróide dos biomas através do
79 programa ArcGIS 9.3 (ESRI, 2009).

80 Como índices de diversidade, além da riqueza e do endemismo, também utilizei a
81 diversidade filogenética e a diversidade funcional. Neste trabalho, empreguei o índice de
82 *phylogenetic diversity* (PD), calculado pela soma dos comprimentos dos ramos da árvore
83 filogenética das espécies de uma comunidade (Faith, 1992). Com o programa Mesquite 2.75
84 (Maddison & Maddison, 2011) e baseado em hipóteses filogenéticas recentes (D'Angiolella
85 *et al.*, 2011; Harvey *et al.*, 2012; Giugliano *et al.*, 2013b; Pyron *et al.*, 2013), construí uma
86 árvore filogenética que engloba todas as espécies registradas no presente trabalho. Calculei os
87 valores de PD para cada comunidade com o pacote *picante* (Kembel *et al.*, 2010) no
88 programa R (RCoreTeam, 2013). Para a medida da diversidade funcional, caracterizei as
89 espécies com relação à morfologia e utilização de recursos, obtidos através de consulta à
90 literatura especializada. Calculei a diversidade funcional de cada comunidade com base no
91 índice de riqueza funcional (*functional richness*- FRic) (Villéger *et al.*, 2008), obtido através
92 do volume ocupado por determinada comunidade em um espaço T-dimensional, relativo aos
93 traços funcionais utilizados na análise (Cornwell *et al.*, 2006; Villéger *et al.*, 2008). Para esta
94 análise, utilizei o pacote *FD* (Laliberté & Shipley, 2011b) do programa R (RCoreTeam,
95 2013).

96 Investiguei a relação entre os índices de diversidade e o ecótono Amazônia-Cerrado
97 através de análises de correlação entre cada índice e a distância da comunidade em questão
98 ao limite entre os dois biomas e ao centróide de cada bioma. Finalmente, eu investiguei os
99 processos responsáveis pelos padrões observados ao longo do gradiente através de uma

100 Análise de Correspondência Canônica (CCA) (Ter Braak, 1986) entre a composição das
101 comunidades e as variáveis ambientais dos respectivos locais.

102

103 **Resultados e Discussão**

104 O levantamento de dados proporcionou a obtenção de 46 comunidades, distribuídas
105 entre a Amazônia e o Cerrado. Nessas comunidades foram encontrados 11.519 espécimes de
106 lagartos, divididos em 123 espécies e 13 famílias.

107 Das 16 análises de correlação realizadas, nove apresentaram um resultado
108 estatisticamente significativo ($P < 0.05$). Para a Amazônia, as correlações significativas foram
109 aquelas que relacionaram a distância ao ecótono com a riqueza ($\rho = 0.436$ e $P = 0.013$),
110 endemismos do bioma ($\rho = 0.677$ e $P < 0.001$), diversidade filogenética ($\rho = 0.596$ e $P < 0.001$)
111 e diversidade funcional ($\rho = 0.403$ e $P = 0.023$), além daquelas que envolveram a distância ao
112 centróide com os endemismos do bioma ($\rho = -0.563$ e $P < 0.001$) e com a diversidade
113 filogenética ($\rho = -0.375$ e $P = 0.034$).

114 Para o Cerrado, as correlações significativas foram aquelas que relacionaram a
115 distância ao ecótono com os endemismos do bioma ($\rho = 0.468$ e $P = 0.018$), diversidade
116 filogenética ($\rho = 0.407$ e $P = 0.045$) e diversidade funcional ($\rho = 0.535$ e $P = 0.007$). Nenhuma
117 correlação que envolveu a distância ao centróide deste bioma com os índices de diversidade
118 foi estatisticamente significativa, porém podemos observar o mesmo padrão amazônico onde
119 os índices de diversidade tendem a ser mais altos conforme nos afastamos do ecótono.

120 A seleção de modelos mostrou que as variáveis ambientais que mais influenciam a
121 variação na composição das comunidades de lagartos são a vegetação potencial, a umidade
122 no solo e a variação média na temperatura diária, além de valores extremos como as
123 temperatura médias dos trimestres mais seco e mais frio, e a precipitação do trimestre mais
124 quente. Os resultados da CCA mostram que as espécies endêmicas da Amazônia tendem a se

125 agrupar com valores mais altos de umidade no solo, bem como de temperatura nos trimestres
126 mais secos e frios. As espécies endêmicas do Cerrado se associaram a solos mais secos,
127 maior variação na temperatura diária e a temperaturas e umidade no solo mais baixas. As
128 espécies com ampla distribuição estão espalhadas por toda a área do gráfico, demonstrando a
129 sua capacidade de ocupar os dois ambientes. Em escalas continentais, variáveis relacionadas
130 ao fluxo de energia são preponderantes para explicar os padrões de diversidade (Wright,
131 1983; Currie, 1991). Apesar de estarem presentes no pool de variáveis ambientais, estas
132 variáveis (produtividade primária líquida, evapotranspiração, evapotranspiração potencial)
133 não foram incluídas no modelo final como aquelas que mais contribuíram para a variação na
134 estrutura das comunidades estudadas. As variáveis que melhor explicam essa variação estão
135 intimamente ligadas com diferenças ambientais entre os biomas e com a história natural dos
136 lagartos.

137 Os resultados apresentados demonstram que o ecótono entre a Amazônia e o Cerrado
138 exerce uma influência negativa sobre os índices de diversidade de comunidades de lagartos.
139 A zona de transição estudada atua como um filtro ambiental, limitando a presença de
140 espécies endêmicas ou características de ambientes abertos/fechados. Em escalas amplas de
141 tempo e espaço, o ecótono Amazônia/Cerrado é uma zona altamente instável (Haffer, 1969;
142 Werneck *et al.*, 2012), o que a torna menos favorável para a colonização e permanência das
143 espécies (van der Maarel, 1990). No entanto, o ecótono Amazônia/Cerrado ainda é um
144 ambiente pouco estudado e a sua localização no arco do desmatamento torna ainda mais
145 difícil a compreensão de seus padrões e processos. Estudos com dinâmica e genética de
146 populações ao longo do gradiente seriam interessantes de ser conduzidos para um melhor
147 entendimento da dinâmica do ecótono.

148

149

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Community structure in biome transitions: lizards in the Cerrado-Amazon ecotone

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1 **Abstract**

2 Ecological gradients have a crucial role in the flow of species, genes and nutrients between
3 adjacent areas. Limits do not simply separate, but also connect areas, acting as filters of
4 varying permeability. Community structure varies with proximity to the ecotone, and species
5 richness in the ecotone can be higher than, lower than, or similar to adjacent areas. Here, we
6 investigate how the ecotone isolates two Neotropical biomes, the Amazon and the Cerrado,
7 acting as a filter on the lizard fauna exchange between them. Based on field and literature
8 data, we performed correlation analyses between diversity indices and the distance of each
9 sampling point to the ecotone and to the biomes centroids. To investigate the processes
10 responsible for the observed patterns along the gradient, we conducted a canonical
11 correspondence analysis (CCA) relating species incidences in sampled communities and
12 environmental variables. Our results demonstrate that proximity to the Amazon-Cerrado
13 ecotone negatively affects the diversity of lizard communities, which is determined by a
14 process of environmental filtering and possibly influenced by historical factors. The
15 ordination by the CCA was able to clearly distinguish two groups of species (from open and
16 from forest habitats), and associate them to potential vegetation, soil moisture and mean
17 diurnal range of temperature.

18

19 **Introduction**

20 Ecological limits and gradients are among the most studied subjects in ecology (Erdős
21 *et al.*, 2011). In spite of their small geographical ranges, when compared to the rest of the
22 regional landscape, these limits seem to have a crucial role in the flow of species (Urbina-
23 Cardona *et al.*, 2006), genes (Smith *et al.*, 1997) and nutrients (Kolasa & Zalewski, 1995)
24 between adjacent areas. Limits do not simply separate, but also connect areas, acting as filters
25 of varying permeability (Wiens *et al.*, 1985). The concept of ecotones originated with the

26 recognition of “tension zones” between plant communities (Livingston, 1903) and the term
27 "ecotone" was first used in the beginning of the 20th century, referring to the “stress line that
28 connects the points of accumulated or abrupt change” (Clements, 1904). In this study, we
29 refer to ecotone as a “zone of transition between adjacent ecological systems having a set of
30 characteristics uniquely defined by space and time scales, and by the strength of the
31 interactions between adjacent ecological systems” (di Castri *et al.*, 1988).

32 The structure of biological communities varies with the proximity to the ecotone (e.g.,
33 Hofer *et al.*, 2000; Menke, 2003a; Lloyd *et al.*, 2012), and species richness in the ecotone can
34 be higher than, lower than, or similar to the adjacent areas (van der Maarel, 1990).
35 Understanding richness patterns in the ecotones also requires knowledge about the
36 biogeographic history of the areas, since on a regional scale the ecotones result from the
37 contact of regions with different histories (Nogués-Bravo & Martínez-Rica, 2004). One
38 widespread idea is that ecotones present higher diversity levels than adjacent areas, and are
39 thus of great value to conservation (Risser, 1995; Kirkman *et al.*, 1998; Kernaghan & Harper,
40 2001). This would happen due to an additive process, in which the ecotone would be able to
41 support species from both areas (Senft, 2009). Contrary to this notion, some argue that the
42 diversity in ecotones can be lower, if local environmental conditions are suboptimal when
43 compared to the adjacent areas (Backeus, 1993b; Dangerfield *et al.*, 2003). In this case, the
44 establishment and survival of species would be jeopardized (Temple, 1998). Besides species
45 richness, other diversity measures should vary spatially with proximity to an ecotone. For
46 instance, functional diversity (Tilman, 2001) and phylogenetic diversity (Faith, 1992) should
47 also be affected by this gradient.

48 The core-periphery hypothesis postulates that selective pressures will vary from the
49 core to the periphery of a biome (Safriel *et al.*, 1994). This way, populations and
50 communities in the central regions would be structurally different from those in peripheral

51 regions (Garner *et al.*, 2004; Blevins *et al.*, 2011; Pandey & Rajora, 2012). In contrast to
52 ecotones, where the main pattern seems to be heterogeneity and instability (Kark & van
53 Rensburg, 2006), the central areas of a biome are stable (Safriel *et al.*, 1994; Carnaval *et al.*,
54 2009; Werneck *et al.*, 2012). Stable areas allow for a more constant flow of resources, which
55 may result in higher niche specialization (Pianka, 1966; Futuyma & Moreno, 1988), while
56 unstable areas require the evolution of a wider tolerance to environmental variability
57 (Becking, 1968; Oindo, 2002). Besides being related to local diversity, stability can also
58 explain higher rates of endemism (Fjeldså *et al.*, 1999) and lower rates of extinction
59 (Ricklefs, 2004).

60 The transition area between the Amazon and the Cerrado biomes is an extensive zone
61 of ecological tension in South America, formed by a mosaic of tropical savannas and forests
62 (Ratter *et al.*, 1973; Ackerly *et al.*, 1989b; Ratter, 1992). This mosaic is irregular in shape,
63 and presents unique features and different sizes along its length (Marimon *et al.*, 2006). Also,
64 the transition zone coincides with a region known in Brazil as the ‘arc of deforestation’,
65 which originates in the state of Maranhão and runs down along the south-eastern and
66 southern limits of the Amazon (Ferreira *et al.*, 2005; Fearnside & Graça, 2006; Aldrich *et al.*,
67 2012). This region is under great pressure due to the expansion of the agricultural frontier for
68 the establishment of soy plantations and cattle farms, specially in the states of Pará, Mato
69 Grosso and Rondônia (Fearnside, 2001; Laurance *et al.*, 2004; Fearnside, 2006). The
70 conversion of native vegetation in the region has caused large scale environmental changes,
71 such as alterations in the flow of carbon and biomass (Nogueira *et al.*, 2007), higher
72 emissions of greenhouse gases (Fearnside *et al.*, 2009), and the extension of the dry season
73 (Costa & Pires, 2010). There is still little information about how vertebrate species are
74 distributed throughout the landscape in the region (Lacher & Alho, 2001), and the loss of
75 these areas will prevent us from detecting natural ecological processes that take place in the

76 ecotone (Marimon *et al.*, 2006). Studies with plant communities in the Amazon-Cerrado
77 ecotone corroborate the hypotheses that (1) the ecotone presents higher diversity, through an
78 additive process (Ackerly *et al.*, 1989b), and that (2) central and peripheral communities are
79 structurally different (Marimon *et al.*, 2006).

80 Lizards are considered “model organisms” for ecological studies, since they present
81 desirable attributes such as high capturability, high abundance levels and low dispersal
82 capacity (Huey *et al.*, 1983; Carothers *et al.*, 1996; Pianka & Vitt, 2003; Camargo *et al.*,
83 2010). They have been successfully studied in ecotonal areas (e.g., Hofer *et al.*, 1999, 2000;
84 Menke, 2003a; Nogués-Bravo & Martinez-Rica, 2004; Urbina-Cardona *et al.*, 2006) but
85 without a definite pattern: lizard diversity in transition zones can be higher than (Urbina-
86 Cardona *et al.*, 2006), lower than (Menke, 2003a) or similar to (Conroy, 1999; Nogués-Bravo
87 & Martinez-Rica, 2004) that in adjacent areas. Here, we assess how the ecotone isolates the
88 Amazon and the Cerrado, acting as a filter on the faunal exchange between these two
89 Neotropical biomes. We describe the observed patterns and investigate the processes
90 responsible for changes in lizard communities along a gradient from the core towards the
91 periphery of the two biomes. If the Amazon-Cerrado ecotone functions as an environmental
92 filter, isolating the biomes, we expect a reduction in diversity indices (richness, endemism,
93 functional diversity and phylogenetic diversity) as we get closer to the ecotone, from the core
94 to the periphery of both biomes. We hypothesize that the higher instability and environmental
95 heterogeneity of the ecotone should limit the establishment and survival of species typical of
96 each biome.

97

98

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100

101 **Methods**

102 *Study area*

103 The Amazon and the Cerrado are, respectively, the two largest Brazilian biomes
104 (IBGE, 2004). Both are extremely heterogeneous, presenting different geological,
105 pedological and vegetational features within their geographic ranges (Eiten, 1972; Prance &
106 Lovejoy, 1985). The Cerrado originally covered 2 million km² or approximately 25% of the
107 Brazilian territory (IBGE, 2004). The climate is markedly seasonal, with a rainy season
108 between October and March, and a dry season between April and September. The mean
109 temperature varies between 22°C and 27°C, and the mean annual precipitation is 1500 mm.
110 The climate in Cerrado allows the establishment of forest vegetation in a large part of its
111 range (Oliveira-Filho & Ratter, 2002), but latosols poor in nutrients, with high aluminum
112 levels (Haridasan, 1982) and frequent fires (Miranda *et al.*, 2002) determine the formation of
113 a savanic vegetation, characterized by abundant grasslands and fire-tolerant species
114 (Pennington *et al.*, 2000). The Amazon covers 8 million km², with about 4.2 million km² in
115 the Brazilian territory (IBGE, 2004). With a wet tropical climate, the mean temperature
116 ranges between 24°C and 26°C, and the mean annual precipitation is 2300 mm (Fisch *et al.*,
117 1998). Overall, the Amazon presents an acidic and poor soil, which is a limiting factor to
118 forest productivity (Cunha *et al.*, 2007). However, the lack of nutrients in the soil is
119 counterbalanced by a rich leaf litter, which, together with high temperatures and pluviosity, is
120 able to maintain a productive and diverse system (Schuur, 2003; Moreira & Costa, 2004).

121

122 *Data gathering and processing*

123 The data relative to the characterization of lizard communities used in this study
124 derived from field work and the literature (Appendix 1, Table A1). We selected sampling
125 points located in the Amazon and in the Cerrado, where sampling was performed using

126 similar methods and efforts (active search and pitfall traps with drift fences, for at least three
127 weeks in each location). The expressions used in the boolean search of the literature were
128 "lizard AND Amazon", "lizard AND Cerrado", "reptile AND Amazon", "reptile AND
129 Cerrado", herpetofauna AND Amazon" and "herpetofauna AND Cerrado, both in english and
130 in portuguese. To evaluate variations in richness, endemism rates, and functional and
131 phylogenetic diversities, we considered differences in community composition. The list of
132 endemic species in both biomes followed recent syntheses (Nogueira *et al.*, 2011; Ribeiro
133 Júnior, 2013). The environmental variables we used are available from the WorldClim
134 (Hijmans *et al.*, 2005) and the Atlas of the Biosphere (used by permission of The Center for
135 Sustainability and the Global Environment, Nelson Institute for Environmental Studies,
136 University of Wisconsin-Madison) projects, and correspond to temperature, precipitation,
137 altitude, evapotranspiration, primary productivity, soil moisture and potential vegetation (a
138 categorical variable which corresponds to the land cover type that would exist in a gridcell
139 had humans not interfered). The limits of the Cerrado and brazilian Amazon are those
140 proposed by IBGE, 2004. The limits of the Amazon outside Brazil follows (Olson *et al.*,
141 2001). The distance of each sampling point to the ecotone line and to biome centroids were
142 calculated with ArcGIS version 9.3 (ESRI, 2009). The centroid corresponds to the
143 geographical centre of each biome.

144

145 *Analyses*

146 The relationship between the diversity indices and Amazon-Cerrado ecotone were
147 determined by correlation analyses conducted between each index and the distance of each
148 sampling point to the ecotone and to the centroid of each biome. Since most variable pairs
149 did not present a normal distribution (verified by a Shapiro-Wilk test), we used the non-

150 parametric Spearman's correlation index (ρ). For those pairs which did present a normal
151 distribution, we used the Pearson correlation index (r).

152 To generate measures of functional diversity, we characterized each species according
153 to its morphology and resource use, using on the following traits: size (maximum snout-vent
154 length), presence of sexual dimorphism, habitat (open or closed vegetation), microhabitat
155 (arboreal, leaf litter, fossorial, terrestrial, saxicolous, semi-arboreal and semi-aquatic), diet
156 (carnivore or herbivore), foraging behavior (active search, sit-and-wait, or both), activity
157 pattern (diurnal or nocturnal), reproduction strategy (oviparous or viviparous), maximum
158 clutch size, temperature regulation strategy (thermoconformer or thermoregulator) and mean
159 activity temperature. These traits represent the species' functional aspects in relation to the
160 ecosystem. This information was obtained from the literature (Supplementary material
161 Appendix 2, Table A2). We calculated the functional diversity of each community based on
162 the index of functional richness (FRic) (Villéger *et al.*, 2008), because it is more sensible to
163 the structuring of communities than richness itself (Mouchet *et al.*, 2010). It is obtained by
164 calculating the volume occupied by a specific community in a n -dimensional space, relative
165 to the functional traits used in the analysis (Cornwell *et al.*, 2006; Villéger *et al.*, 2008). For
166 this step in the analysis, we used the package *FD* (Laliberté & Legendre, 2010; Laliberté &
167 Shipley, 2011a) in program R (R Core Team, 2014).

168 The phylogenetic diversity index of a community represents the relationship between
169 the number of species and the phylogenetic distance between them (Faith, 1992). This index
170 can be obtained by estimating the topological distance separating species in a phylogenetic
171 tree (Webb, 2000), and can be used to analyze the ecological processes that structure a
172 community (Webb *et al.*, 2002). In this study, we used a measure of phylogenetic diversity
173 (PD) calculated by the sum of the branch lengths of the phylogenetic tree separating species
174 in a given community (Faith, 1992). Long branch lengths correspond to longer evolutionary

175 time, and consequently, more distinct taxonomic groups (Cianciaruso *et al.*, 2009). Using
176 program Mesquite 2.75 (Maddison & Maddison, 2011), and based on recent phylogenies
177 (D'Angiolella *et al.*, 2011; Harvey *et al.*, 2012; Giugliano *et al.*, 2013a; Pyron *et al.*, 2013),
178 we built a phylogenetic tree that encompasses all species included in this study. We obtained
179 branch lengths from Pyron *et al.* (2013), which covers 96 of the 123 species used here. The
180 branch lengths uniting the remaining taxa to the tree were estimated by ultrametric distances.
181 We used package *picante* (Kembel *et al.*, 2010) in program R (R Core Team, 2014) to
182 calculate PD values for each community.

183 To investigate the processes responsible for the observed patterns along the gradient,
184 we conducted a canonical correspondence analysis (CCA) (Ter Braak, 1986) relating the
185 species composition in the sampled communities and the environmental variables for each
186 location. The CCA is an ordination exploratory analysis that is being successfully used for
187 investigating species variation across environmental gradients (Hofer *et al.*, 2000; Kernaghan
188 & Harper, 2001; Vitt *et al.*, 2007). The CCA associates the variation in the lizard community
189 composition matrix (dependent variable) to the environmental variables matrix (independent
190 variable). Beforehand, we performed a selection of environmental variables that most
191 influenced community composition, by comparing CCA models based on the Akaike
192 Information Criterion (AIC). The matrix for the dependent variables was structured with each
193 lizard species as columns and each sampling location as lines, and the presence/absence of a
194 species in a location was coded as 1/0, respectively. The matrix for the independent variables
195 was structured with the environmental variables as columns and locations as lines, and filled
196 out by the values of each variable in the sampling locations. To test the significance of the
197 CCA results, we performed a Monte Carlo permutation test, with 1,000 iterations, using
198 package *vegan* (Oksanen *et al.*, 2013) in program R (R Core Team, 2014).

199

200 **Results**

201 We had access to data from 118 communities, but to work with only high quality data
202 (larger sampling efforts and reliability in species identification), the total number was
203 reduced to 46 communities, from both the Amazon and the Cerrado (Fig. 1, Table 1). Overall
204 in these communities, 11,519 lizard specimens were collected, from 123 species and 13
205 families (Fig. 2). The obtained values of richness, endemism, functional diversity and
206 phylogenetic diversity are presented in Table 1. It is noteworthy that endemic species from
207 both biomes were found in those communities close to the ecotone.

208 For the Amazon, significant correlations were obtained which related distance to the
209 ecotone with richness ($\rho = 0.436$ and $P = 0.013$), with biome endemism ($\rho = 0.677$ and $P <$
210 0.001), with phylogenetic diversity ($\rho = 0.596$ and $P < 0.001$), with functional diversity ($\rho =$
211 0.403 and $P = 0.023$), and also those which related distance to the centroid with biome
212 endemism ($\rho = -0.563$ and $P < 0.001$) and with phylogenetic diversity ($r = -0.375$ and $P =$
213 0.034) (Fig. 3). Overall, the diversity indices presented a positive relationship with distance
214 to the ecotone and a negative relationship with distance to the biome centroid, which means
215 that as the distance from the ecotone increases, lizard diversity increases.

216 For the Cerrado, the significant correlations observed related distance to the ecotone
217 with biome endemism ($\rho = 0.468$ and $P = 0.018$), phylogenetic diversity ($\rho = 0.407$ and $P =$
218 0.045) and functional diversity ($\rho = 0.535$ and $P = 0.007$) (Fig. 4). No statistically significant
219 correlation between distance to the centroid and the measures of diversity was obtained.
220 However, in those significant relationships, we observed the same general pattern as for the
221 Amazon, in which diversity indices tended to be higher with increased distance to the
222 ecotone.

223 Model selection indicated that the most influential variables on lizard distributions are
224 potential vegetation, soil moisture, mean daily temperature range, as well as extreme

225 temperature values, such as mean temperature from the hottest and coldest quarters, and
226 mean precipitation of the hottest quarter. The Monte Carlo permutations revealed a
227 significant relationship between the environmental variables selected and the structure of
228 lizard communities ($F = 2.440$ and $P < 0.001$). The CCA (Fig. 5) indicated that Amazonian
229 endemic species, typically from forest habitats, tended to group together towards the right
230 end of the first CCA axis, characterized by higher values of soil moisture and temperatures
231 from the hottest and coldest quarters. Cerrado endemic species grouped together towards the
232 left end of the first CCA axis, being associated with drier soils, higher daily temperature
233 range, and lower values of temperature and precipitation. Widespread species were scattered
234 across the graphic area, demonstrating their ability to occupy both biomes.

235

236 **Discussion**

237 Our results demonstrate that the Amazon-Cerrado ecotone influences negatively the
238 diversity of lizard communities. Even though the idea of a greater diversity in ecotones is
239 more broadly accepted and corroborated in the literature (Risser, 1995; Kirkman *et al.*, 1998;
240 Kernaghan & Harper, 2001), this work, along with a few other studies, refutes this hypothesis
241 (Backeus, 1993b; Dangerfield *et al.*, 2003). Despite the low diversity indices for lizards,
242 ecotonal areas can harbor genetically diverse populations (Garner *et al.*, 2004; Blevins *et al.*,
243 2011; Pandey & Rajora, 2012), resistant to environmental changes (Parsons, 1990) and are
244 able to survive in unstable environments. In the face of the predicted global climate changes,
245 transition zones could prove to be an important genetic repository (Killeen & Solórzano,
246 2008).

247 The transition zone seems to act as an environmental filter, and does not allow species
248 that are endemic or typical from closed/open habitats to advance into the other biome.

249 However, the presence of endemic species of both biomes in ecotonal communities is

250 evidence that this zone can support species from either closed or open environments,
251 although it does not sustain comparably high lizard diversity levels. This lower diversity can
252 be explained by the fact that, in large scales of space and time, the ecotone seems to be an
253 unstable zone (Haffer, 1969; Werneck *et al.*, 2012). This instability can turn the ecotone into
254 an unfavorable area to species colonization and permanence (van der Maarel, 1990). In large
255 biogeographic scales, ecotones can act as population sinks (Woodroffe & Ginsberg, 1998),
256 where some species are at the edge of their distributions. The fitness of marginal populations
257 is expected to be lower than that of central populations (Haak *et al.*, 2010; Zhigalskii, 2011),
258 and this would affect the establishment and survival rates of the species, and the community
259 structure as a whole (Temple, 1998). One way in which ecotones would present higher
260 diversity levels is by harboring ecotonal species (Jose *et al.*, 1996), which would be adapted
261 to the intermediate conditions found in the transition zone and would present an abundance
262 peak or even be endemic to the ecotone (Walker *et al.*, 2003). However, in this study, no
263 species with these characteristics were identified in the Amazon-Cerrado transition zone.

264 The results obtained for the Amazon indicate that all diversity indices analyzed were
265 positively correlated with distance to the ecotone, and two indices (biome endemism and
266 phylogenetic diversity) were negatively correlated with distance to the biome's centroid.
267 Correlation indices varied between 0.37 and 0.67, suggesting that there must be factors other
268 than distance that may also be influencing lizard community structure. This is perfectly
269 intuitive, since distances to the ecotone and to the centroid simply summarize a shift in
270 environmental conditions along the gradient. What remains clear is that the diversity indices
271 tend to decrease with proximity to the ecotone. These results corroborate our predictions,
272 despite some works that suggest higher diversity at disturbed areas due to a higher
273 environmental heterogeneity, which would promote the establishment and occupation of
274 more ecological niches (Biswas & Mallik, 2010; Carreño-Rocabado *et al.*, 2012). By

275 observing the opposite, we can suppose that this heterogeneity hinders the establishment of
276 species typical from either biomes, and only those species that are generalists or resistant to
277 environmental variations would be able to occupy the transition zone (Devictor *et al.*, 2008).
278 Another explanation, which would contribute to the understanding of the distribution of
279 species along the ecotonal gradient, is the Pleistocene Refugia hypothesis. Firstly proposed
280 by Haffer (1969) and Vanzolini & Williams (1970), this hypothesis suggests that climatic
281 oscillations in the Quaternary would have led to expansions and contractions of forest areas.
282 These events would isolate and concentrate species in forest islands with stable climatic
283 conditions (refugia), in times when conditions outside them were unsuitable for the survival
284 of the species (Simpson & Haffer, 1978). Refugia would have been concentrated in the core
285 of the biome, while peripheral areas would have been subject to a greater instability in
286 geological time scales. Despite being strongly discussed and criticized (Colinvaux *et al.*,
287 2000; Bush & Oliveira, 2006; Haffer, 2008), this hypothesis has gained support in recent
288 studies involving biogeography and phylogeography (Peterson & Nyari, 2008; Carnaval *et*
289 *al.*, 2009). Also, palynological and isotopic studies show that the peripheral areas have
290 undergone vegetation changes (Servant *et al.*, 1993; Desjardins *et al.*, 1996), suggesting that
291 the extent of forest and savanna have varied during the geological time and supporting the
292 notion of instability in the ecotone.

293 For the Cerrado, results obtained were similar, although less significant. Only three
294 correlations were statistically significant, and in all of them a positive relationship between
295 the diversity indices and distance to the ecotone were observed. The same way as for the
296 Amazon, correlation indices were not very high, varying between 0.40 and 0.53, indicating
297 that other factors apart from the distance should also be responsible for variations in diversity
298 levels. There were no significant correlations between the diversity indices and distance to
299 the centroid. This can be due to the central position of the biome in South America, which

300 brings the Cerrado in contact with other Brazilian biomes (Amazon, Caatinga, Atlantic Forest
301 and Pantanal) and create other ecotonal zones not considered in this study. Stable zones can
302 also explain a higher diversity in central areas of the Cerrado. Recently, stable climatic areas
303 have been proposed for the Cerrado and for other open habitat areas in South America
304 (Werneck *et al.*, 2011; Werneck *et al.*, 2012). These areas correspond to regions in the
305 Cerrado that have maintained stable environmental conditions for at least 120,000 years. The
306 area where the Amazon-Cerrado ecotone is located today seems to be an unstable area
307 (Werneck *et al.*, 2012), and must have undergone expansion and contraction events in both
308 savanna and forest areas. Studies on the biogeography of Cerrado squamates corroborate our
309 results, indicating that the area of contact with the Amazon tends to be less species-rich than
310 the core of the biome (Costa *et al.*, 2007), and that endemic species are more associated with
311 open habitats, while forest areas (in the ecotone and in gallery forests) play a role in faunal
312 exchange with other biomes (Nogueira *et al.*, 2011).

313 In this study, the ordination by the CCA was able to clearly distinguish two groups of
314 species (from open and from forest habitats), and associate them to variables that influenced
315 this clustering the most. In continental scales, energy-related variables are usually thought of
316 as predominant factors in explaining diversity patterns (Wright, 1983; Currie, 1991). Despite
317 being present in our initial pool of environmental variables, these energy-related variables
318 (net primary productivity, evapotranspiration, and potential evapotranspiration) were not
319 selected to compose the final model. The variables which better explained the variation in
320 community structure are intimately linked to the environmental differences between the two
321 biomes and to the lizards' natural history. Potential vegetation is the most apparent difference
322 between forest and savanna physiognomies, exerting a direct influence on the faunal
323 composition of these regions (Cavalcanti, 1992; Conroy, 1999). The mean daily temperature
324 range also differs clearly between both biomes. While in the Amazon the mean daily

325 temperature variation is 5 °C, ranging between 25 °C at night and 30 °C during the day
326 (Jacob & Wofsy, 1988), the Cerrado presents a far greater daily temperature range, with a
327 mean of 12 °C (Hijmans *et al.*, 2005). Soil moisture directly influences the microhabitat
328 occupied by many lizard species and is important in the selection of sites for oviposition and
329 egg incubation (Christian *et al.*, 1991; Warner & Andrews, 2002; Marco *et al.*, 2004).
330 Besides, soil moisture is an important limiting factor for vegetation growth (Li *et al.*, 2013)
331 and will vary greatly in an ecotonal gradient (Pockman & Small, 2010). The selection of
332 temperature in the driest and coldest quarters and precipitation in the hottest quarter by the
333 analysis highlights the lizard species' need to adapt to seasonality in these environments.
334 While the Cerrado presents a highly seasonal climate, the seasonality in the Amazon is
335 lessened, and this distinction can be perceived along the ecotonal gradient (da Rocha *et al.*,
336 2009). These differences put a selective pressure on the communities, which will
337 consequently influence species composition.

338 Overall, this study demonstrates that lizard communities in the Amazon and in the
339 Cerrado follow a pattern of diversity loss with proximity to the ecotone, which is determined
340 by a process of environmental filtering and possibly influenced by historical factors.
341 However, the Amazon-Cerrado ecotone is still poorly studied and its location in the Brazilian
342 'arc of deforestation' renders our knowledge of its natural patterns and processes even more
343 difficult. We thus highlight that future studies concerning the dynamics and genetics of the
344 populations along the gradient would be interesting for further understanding the ecotonal
345 dynamics.

346

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- 736

Table 1. Lizard communities in the Cerrado and in the Amazon. *A*: Amazon, *C*: Cerrado, *CN*: community number (according to Figure 1), *DC*: distance to the centroid (km), *DE*: distance to the ecotone (km), *E*: Ecotone, *EA*: Amazon endemisms, *EC*: Cerrado endemisms, *FRic*: functional diversity index, *Lat*: latitude, *Long*: longitude, *PD*: phylogenetic diversity index, *Ric*: richness. CHUNB: Coleção Herpetológica da Universidade de Brasília.

Locality	Biome	CN	Lat	Long	Ric	EA	EC	PD	FRic	DE	DC	Source
Almas	C	33	-11.205	-47.194	20	0	6	6.68	0.00384	274	418	Recoder et al. (2011)
Almeirim	A	1	-0.975	-52.500	12	7	0	4.98	0.00007	678	1138	Gardner et al. (2007)
Alta Floresta	A	2	-9.574	-55.918	15	5	1	5.53	0.00220	278	907	CHUNB
Amapá	A	3	2.053	-50.793	24	13	0	7.25	0.00439	849	1453	CHUNB
Aporé	C	34	-18.674	-51.881	18	0	6	6.09	0.00172	588	569	Vaz-Silva et al. (2007)
Barcarena	A	4	-1.592	-48.738	17	5	0	6.79	0.00197	408	1530	Silva et al. (2011)
Berbice	A	8	5.085	-58.237	17	9	0	6.72	0.00260	1603	1088	Cole et al. (2013)
Brasília 1	C	35	-15.776	-47.798	15	0	4	4.40	0.00329	500	202	CHUNB
Brasília 2	C	36	-16.000	-47.950	17	0	5	5.18	0.00395	500	214	Nogueira et al. (2005)
Cacoal	A	5	-11.467	-61.331	15	5	0	6.08	0.00157	143	820	Turci and Bernarde (2008)
Carolina	E	20	-7.333	-47.469	14	0	2	5.12	0.00069	72	823	CHUNB

Locality	Biome	CN	Lat	Long	Ric	EA	EC	PD	FRic	DE	DC	Source
Caseara	E	21	-9.372	-49.843	17	0	1	5.83	0.00163	23	582	CHUNB
Caxiuanã	A	6	-1.960	-51.615	17	8	0	6.28	0.00161	532	1204	Ribeiro Jr. et al. (2011)
Cerejeiras	E	22	-13.189	-60.812	13	4	1	4.63	0.00029	86	1022	CHUNB
Cocos	C	37	-14.545	-45.242	12	0	4	5.41	0.00129	698	396	CHUNB
Cruzeiro do Sul	A	7	-7.956	-72.077	29	17	0	8.51	0.00427	1362	1174	Bernarde et al. (2011)
Dubulay	A	9	5.682	-57.859	21	6	0	7.42	0.00192	1618	1163	Cole et al. (2013)
Emas	C	38	-18.333	-53.000	26	0	12	7.28	0.00536	532	605	Valdujo et al. (2009)
Espigão do Oeste	E	23	-11.608	-60.717	29	14	1	9.21	0.00382	77	846	Macedo et al. (2008)
Guajará-Mirim	E	24	-10.800	-65.367	25	14	0	7.65	0.00399	579	820	CHUNB
Humaitá	A	11	-7.200	-62.900	17	11	0	6.17	0.00131	590	345	CHUNB
Juara	E	25	-10.428	-57.634	12	5	2	5.09	0.00069	154	852	Ávila and Ribeiro (2011)
Juruti	A	12	-2.520	-56.158	24	14	0	8.26	0.00324	944	693	Prudente et al. (2013)
Konawaruk	A	9	5.219	-59.045	16	6	0	6.07	0.00204	1680	1067	Cole et al. (2013)
Marabá	A	13	-5.504	-50.279	14	6	0	5.71	0.00234	233	1322	Bernardo et al. (2012)
Mateiros 1	C	39	-10.263	-46.566	14	0	3	5.27	0.00138	251	543	CHUNB

Locality	Biome	CN	Lat	Long	Ric	EA	EC	PD	FRic	DE	DC	Source
Mateiros 2	C	40	-10.702	-46.413	19	0	3	6.22	0.00302	294	509	CHUNB
Minaçu	C	41	-13.496	-48.397	13	0	4	5.00	0.00122	353	127	CHUNB
Monte Alegre	A	14	-1.200	-54.400	11	1	0	5.15	0.00031	831	928	CHUNB
Nova Xavantina	E	26	-14.673	-52.353	24	0	8	6.30	0.00351	129	343	CHUNB
Novo Progresso	A	15	-8.600	-55.500	22	7	2	7.26	0.00627	392	877	CHUNB
Palmas	C	42	-10.189	-48.109	17	0	5	5.33	0.00274	124	494	CHUNB
Paracatu	C	43	-17.109	-46.872	17	0	6	5.26	0.00278	664	382	CHUNB
Paranã	C	44	-12.753	-47.759	16	0	2	5.11	0.00142	385	235	CHUNB
Pimenta Bueno	E	27	-12.500	-60.817	12	3	2	3.85	0.00022	81	944	Gainsbury and Colli (2003)
Purus	A	16	-4.407	-62.255	29	29	0	8.30	0.00355	844	29	Waldez et al. (2013)
Querência	E	28	-12.470	-52.370	7	0	1	3.34	0.00000	67	1407	CHUNB
Ribeirão Cascalheira	E	29	-12.940	-51.820	16	1	3	5.11	0.00104	4	1486	CHUNB
Rio Preto da Eva	A	17	-2.342	-59.214	20	9	0	7.06	0.00176	1014	383	Ilha and Dixo (2010)
Santa Terezinha	E	30	-10.288	-50.798	9	0	3	3.50	0.00021	4	507	CHUNB
Santarém	A	18	-2.481	-54.770	14	2	0	5.64	0.00064	801	845	Mendes-Pinto and Tello (2010)

Locality	Biome	CN	Lat	Long	Ric	EA	EC	PD	FRic	DE	DC	Source
São Domingos	C	45	-13.398	-46.268	18	0	2	5.83	0.00242	538	314	Werneck et al. (2009)
Silvânia	C	46	-16.659	-48.608	14	0	4	4.93	0.00084	495	261	Morais et al. (2012)
Trairão	A	19	-4.576	-55.404	23	13	0	7.37	0.00164	768	749	Mendes-Pinto and Souza (2011)
Vila Bela da SS. Trindade	E	31	-14.944	-60.013	17	2	4	5.82	0.00245	76	1234	CHUNB
Vilhena	E	32	-12.717	-60.117	15	3	5	4.60	0.00120	11	982	Gainsbury and Colli (2003)

Figure Legends

Figure 1. Map presenting the sampled communities. 1: Almeirim; 2: Alta Floresta; 3: Amapá; 4: Barcarena; 5: Cacoal; 6: Caxiuanã; 7: Cruzeiro do Sul; 8: Berbice; 9: Dubulay; 10: Konawaruk; 11: Humaitá; 12: Juruti; 13: Marabá; 14: Monte Alegre; 15: Novo Progresso; 16: Purus; 17: Rio Preto da Eva; 18: Santarém; 19: Trairão; 20: Carolina; 21: Caseara; 22: Cerejeiras; 23: Espigão do Oeste; 24: Guajará-Mirim; 25: Juara; 26: Nova Xavantina; 27: Pimenta Bueno; 28: Querência; 29: Ribeirão Cascalheira; 30: Santa Terezinha; 31: Vila Bela da Santíssima Trindade; 32: Vilhena; 33: Almas; 34: Aporé; 35: Brasília 1; 36: Brasília 2; 37: Cocos; 38: Emas; 39: Mateiros 1; 40: Mateiros 2; 41: Minaçu; 42: Palmas; 43: Paracatu; 44: Paranã; 45: São Domingos; 46: Silvânia.

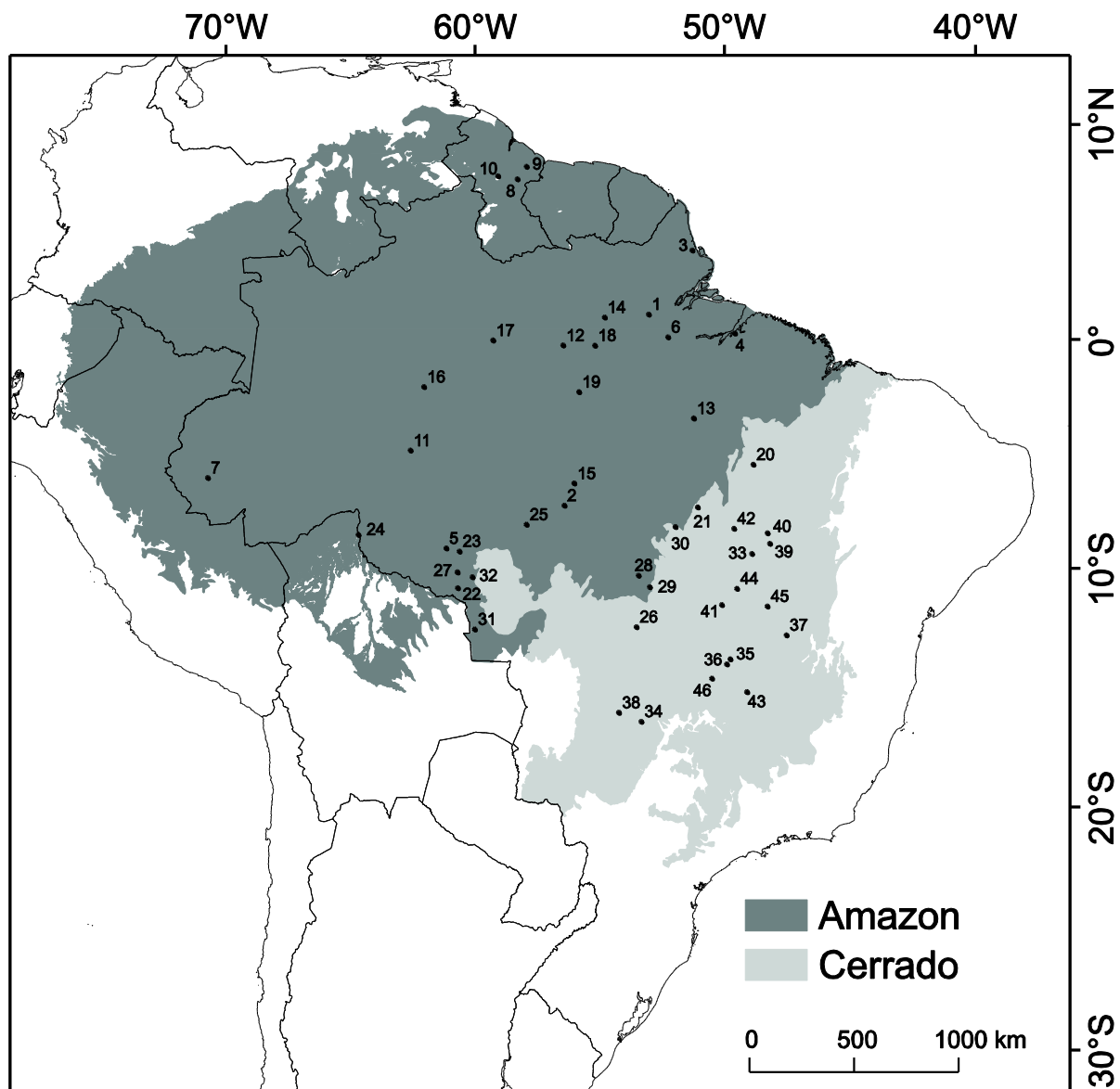
Figure 2. Phylogenetic tree representing the relationships among all the species used in this study. Branch lengths follow Pyron et al. (2013).

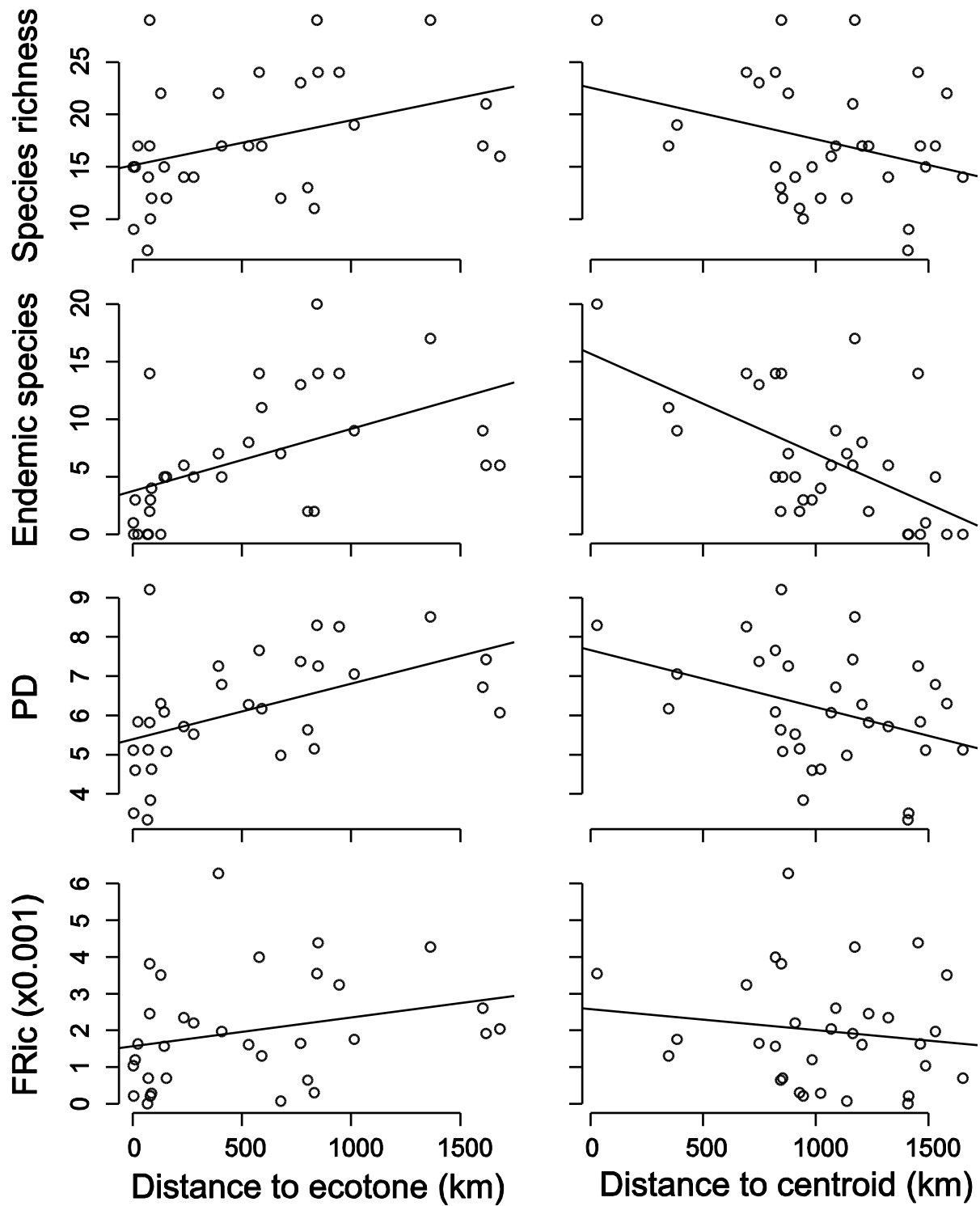
Figure 3. Correlations between species richness, endemisms, phylogenetic diversity (*PD*) and functional diversity (*FRic*) of communities located in the Amazon with distance to the ecotone and distance to the biome centroid. The correlation coefficients and significance values are: A: $\rho = 0.436$ and $P = 0.013$; B: $r = -0.314$ and $P = 0.08$; C: $\rho = 0.677$ and $P < 0.001$; D: $\rho = -0.563$ and $P < 0.001$; E: $\rho = 0.596$ and $P < 0.001$; F: $r = -0.375$ and $P = 0.034$; G: $\rho = 0.403$ and $P = 0.023$; H: $r = -0.118$ and $P = 0.520$.

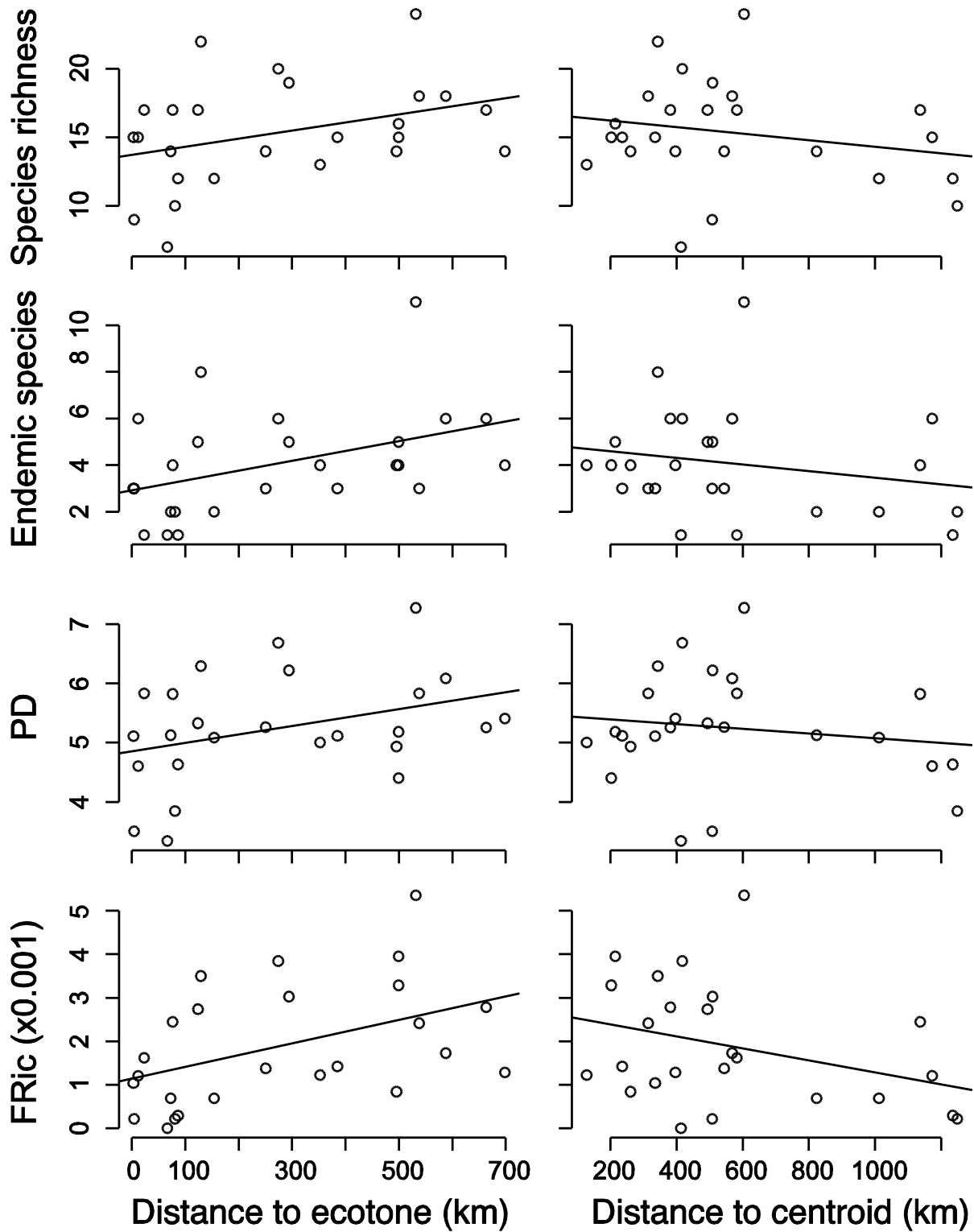
Figure 4. Correlations between species richness, endemisms, phylogenetic diversity (*PD*) and functional diversity (*FRic*) of communities located in the Cerrado with distance to the ecotone and distance to the biome centroid. The correlation coefficients and significance values are: A: $\rho = 0.369$ and $P = 0.070$; B: $\rho = -0.119$ and $P = 0.595$; C: $\rho = 0.468$ and $P =$

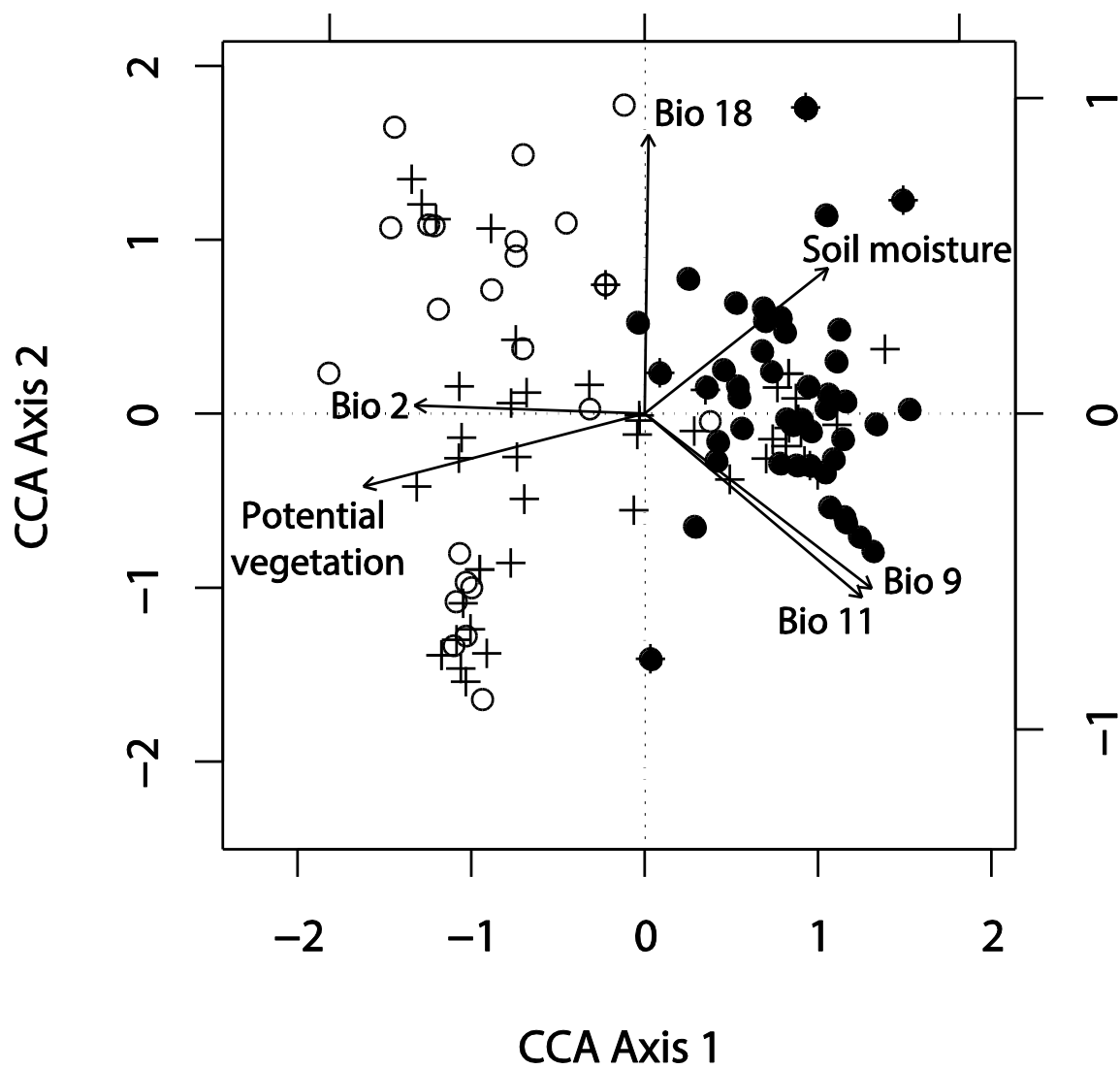
0.018; D: $\rho = -0.210$ and $P = 0.314$; E: $\rho = 0.407$ and $P = 0.045$; F: $\rho = 0.013$ and $P = 0.952$;
G: $\rho = 0.535$ and $P = 0.007$; H: $\rho = -0.311$ and $P = 0.131$.

Figure 5. Ordination diagram resulting from a canonical correspondence analysis (CCA), presenting relationships among lizard species and environmental variables. Species scores represented by circles and crosses, and environmental variables represented by arrows, jointly reflect species distributions along each environmental vector. White circles = Cerrado endemic species; black circles = Amazon endemic species; crosses = widespread species; Bio 2 = mean diurnal temperature range; Bio 9 = mean temperature of driest quarter; Bio 11 = mean temperature of coldest quarter; Bio 18 = precipitation of warmest quarter.









Appendix 1

Table A1. Incidence matrix of lizard species recorded in 46 sites from the Amazon and Cerrado biomes. 1: *Alopoglossus angulatus*; 2: *Al. atriventris*; 3: *Al. buckleyi*; 4: *Ameiva ameiva*; 5: *Am. parecis*; 6: *Anolis auratus*; 7: *An. brasiliensis*; 8: *An. chrysolepis*; 9: *An. fuscoauratus*; 10: *An. meridionalis*; 11: *An. ortonii*; 12: *An. philopunctatus*; 13: *An. planiceps*; 14: *An. punctatus*; 15: *An. tandai*; 16: *An. trachyderma*; 17: *An. transversalis*; 18: *Arthrosaura kockii*; 19: *Ar. reticulata*; 20: *Bachia bresslaui*; 21: *B. cacerensis*; 22: *B. dorbignyi*; 23: *B. flavescens*; 24: *B. oxyrhina*; 25: *B. peruana*; 26: *B. psamophila*; 27: *B. scolecoides*; 28: *Cercosaura argulus*; 29: *Cercosaura eigenmanni*; 30: *Ce. ocellata*; 31: *Ce. schreibersii*; 32: *Cercosaura* sp.; 33: *Chatogekko amazonicus*; 34: *Cnemidophorus cryptus*; 35: *Cn. gramivagus*; 36: *Cn. jalapensis*; 37: *Cn. lemniscatus*; 38: *Cn. mumbuca*; 39: *Cn. ocellifer*; 40: *Coleodactylus brachystoma*; 41: *Coleodactylus meridionalis*; 42: *Colobosaura modesta*; 43: *Crocodylus amazonicus*; 44: *Dracaena guianensis*; 45: *Enyalioides laticeps*; 46: *E. palpebralis*; 47: *Enyalius leechii*; 48: *Enyalius* sp.; 49: *Gonatodes alexandermendesi*; 50: *Go. annularis*; 51: *Go. eladioi*; 52: *Go. hasemani*; 53: *Go. humeralis*; 54: *Gymnodactylus amarali*; 55: *Gd. geckoides*; 56: *Gymnophthalmus speciosus*; 57: *Gp. underwoodi*; 58: *Hemidactylus brasilianus*; 59: *He. mabouia*; 60: *He. palaichthus*; 61: *Hoplocercus spinosus*; 62: *Iguana iguana*; 63: *Iphisa elegans*; 64: *Kentropyx altamazonica*; 65: *K. calcarata*; 66: *K. paulensis*; 67: *K. pelviceps*; 68: *Kentropyx* sp n; 69: *K. striata*; 70: *K. vanzoi*; 71: *Lepidoblepharis heyerorum*; 72: *Leposoma guianense*; 73: *Lo. osvaldoi*; 74: *Lo. percarinatum*; 75: *Leposoma* sp n; 76: *Lygodactylus klugei*; 77: *Mabuya agilis*; 78: *Ma. bistrinata*; 79: *Ma. dorsivittata*; 80: *Ma. frenata*; 81: *Ma. guaporicola*; 82: *Ma. heathi*; 83: *Ma. nigropunctata*; 84: *Mabuya* sp.; 85: *Micrablepharus atticolus*; 86: *Mi. maximiliani*; 87: *Neusticurus bicarinatus*; 88: *N. rudis*; 89: *Ophiodes striatus*; 90: *Phyllopezus pollicaris*; 91: *Plica plica*; 92: *Pl. umbra*; 93: *Polychrus acutirostris*; 94: *Py.*

marmoratus; 95: *Potamites ecpleopus*; 96: *Pseudogonatodes guianensis*; 97: *Ptychoglossus brevifrontalis*; 98: *Stenocercus caducus*; 99: *S. fimbriatus*; 100: *S. quinarius*; 101: *S. roseiventris*; 102: *S. sinesaccus*; 103: *Thecadactylus rapicauda*; 104: *Th. solimoensis*; 105: *Tretioscincus agilis*; 106: *Te. oriximinensis*; 107: *Tropidurus callathelys*; 108: *Tr. chromatops*; 109: *Tr. guarani*; 110: *Tr. hispidus*; 111: *Tr. insulanus*; 112: *Tr. itambere*; 113: *Tr. oreadicus*; 114: *Tropidurus* sp.; 115: *Tr. torquatus*; 116: *Tupinambis duseni*; 117: *Tu merianae*; 118: *Tu quadrilineatus*; 119: *Tu teguixin*; 120: *Uracentron azureum*; 121: *Uc. flaviceps*; 122: *Uranoscodon superciliosus*; 123: *Vanzosaura rubricauda*.

Community	sp22	sp23	sp24	sp25	sp26	sp27	sp28	sp29	sp30	sp31	sp32	sp33	sp34	sp35	sp36	sp37	sp38	sp39	sp40	sp41
Almas	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0
Almeirim	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0
Alta Floresta	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Amapá	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Aporé	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
Barcarena	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Berbice	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brasília 1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
Brasília 2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Cacoal	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Carolina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Caseara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Caxiuanã	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Cerejeiras	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Cocos	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Cruzeiro do Sul	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Dubulay	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Emas	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0
Espigão do Oeste	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Guajará-Mirim	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Humaitá	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Juara	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Juruti	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Konawaruk	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marabá	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Mateiros 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mateiros 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0

Community	sp42	sp43	sp44	sp45	sp46	sp47	sp48	sp49	sp50	sp51	sp52	sp53	sp54	sp55	sp56	sp57	sp58	sp59	sp60	sp61
Almas	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1
Almeirim	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Alta Floresta	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1
Amapá	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Aporé	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Barcarena	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Berbice	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Brasília 1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Brasília 2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cacoal	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Carolina	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Caseara	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0
Caxiuanã	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cerejeiras	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cocos	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cruzeiro do Sul	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Dubulay	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0
Emas	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Espigão do Oeste	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Guajará-Mirim	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Humaitá	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Juara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Juruti	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Konawaruk	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Marabá	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Mateiros 1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Mateiros 2	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Minaçu	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Community	sp82	sp83	sp84	sp85	sp86	sp87	sp88	sp89	sp90	sp91	sp92	sp93	sp94	sp95	sp96	sp97	sp98	sp99	sp100
Almas	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Almeirim	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Alta Floresta	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Amapá	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
Aporé	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Barcarena	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Berbice	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Brasília 1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Brasília 2	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Cacoal	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Carolina	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caseara	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Caxiuanã	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Cerejeiras	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cocos	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Cruzeiro do Sul	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0
Dubulay	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
Emas	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Espigão do Oeste	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Guajará-Mirim	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
Humaitá	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Juara	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juruti	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0
Konawaruk	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0
Marabá	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Mateiros 1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mateiros 2	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Minaçu	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Community	sp82	sp83	sp84	sp85	sp86	sp87	sp88	sp89	sp90	sp91	sp92	sp93	sp94	sp95	sp96	sp97	sp98	sp99	sp100
Monte Alegre	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nova Xavantina	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Novo Progresso	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Palmas	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracatu	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Paranã	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pimenta Bueno	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Purus	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Querência	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribeirão Cascalheira	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Rio Preto da Eva	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0
Santa Terezinha	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Santarém	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
São Domingos	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Silvânia	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Trairão	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0
Vila Bela	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Vilhena	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Community	sp101	sp102	sp103	sp104	sp105	sp106	sp107	sp108	sp109	sp110	sp111	sp112	sp113	sp114	sp115	sp116
Almas	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Almeirim	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Alta Floresta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amapá	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Aporé	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Barcarena	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Berbice	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Brasília 1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Brasília 2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Cacoal	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carolina	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Caseara	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Caxiuanã	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cerejeiras	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cocos	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Cruzeiro do Sul	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Dubulay	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Emas	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Espigão do Oeste	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Guajará-Mirim	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Humaitá	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Juara	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Juruti	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Konawaruk	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Marabá	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mateiros 1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mateiros 2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Minaçu	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0

Community	sp117	sp118	sp119	sp120	sp121	sp122	sp123
Almas	0	0	0	0	0	0	0
Almeirim	0	0	0	0	0	0	0
Alta Floresta	0	0	1	0	0	1	0
Amapá	0	0	1	0	0	1	0
Aporé	1	0	0	0	0	0	0
Barcarena	0	0	0	0	0	1	0
Berbice	0	0	0	0	0	1	0
Brasília 1	0	0	0	0	0	0	0
Brasília 2	0	0	0	0	0	0	0
Cacoal	0	0	0	0	0	0	0
Carolina	1	0	1	0	0	0	0
Caseara	0	0	1	0	0	0	0
Caxiuanã	0	0	0	0	0	0	0
Cerejeiras	1	0	1	0	0	0	0
Cocos	0	0	0	0	0	0	1
Cruzeiro do Sul	0	0	1	0	0	0	0
Dubulay	0	0	1	0	0	1	0
Emas	1	0	0	0	0	0	1
Espigão do Oeste	0	0	1	0	0	1	0
Guajará-Mirim	0	0	0	0	1	0	0
Humaitá	1	0	0	0	0	1	0
Juara	0	0	0	0	0	1	0
Juruti	0	0	0	1	0	1	0
Konawaruk	0	0	1	0	0	1	0
Marabá	0	0	0	0	0	1	0
Mateiros 1	0	1	0	0	0	0	1
Mateiros 2	1	1	0	0	0	0	1
Minaçú	0	0	0	0	0	0	0

Community	sp117	sp118	sp119	sp120	sp121	sp122	sp123
Monte Alegre	0	0	1	0	0	0	0
Nova Xavantina	1	1	0	0	0	0	0
Novo Progresso	0	0	1	0	0	0	0
Palmas	1	1	0	0	0	0	0
Paracatu	0	0	0	0	0	0	0
Paranã	0	1	1	0	0	0	0
Pimenta Bueno	1	0	0	0	0	0	0
Purus	0	0	1	1	0	1	0
Querência	0	0	0	0	0	0	0
Ribeirão Cascalheira	1	0	1	0	0	0	0
Rio Preto da Eva	0	0	1	0	0	0	0
Santa Terezinha	0	0	1	0	0	0	0
Santarém	0	0	0	0	0	0	0
São Domingos	1	1	0	0	0	0	0
Silvânia	1	0	0	0	0	0	0
Trairão	0	0	1	0	0	1	0
Vila Bela	1	0	1	0	0	0	0
Vilhena	1	0	0	0	0	0	0

Appendix 2

Table A2. Functional attributes matrix for each species. The species numbers follow the coding in Table A1. Max_size: maximum size reached; Dimorp_fem: females larger than males (1 and 0); Dimorp_mal: males larger than females (1 and 0); Dimorp_no: no dimorphism (1 and 0); Habitat_for: forest habitat; Habita_open: open habitat; Microhab_arb: arboreal microhabitat use; Microhab_semiarb: semi-arboreal microhabitat use; Microhab_semiaqu: semi-aquatic microhabitat use; Microhab_fos: fossorial microhabitat use; Microhab_lit: leaf litter microhabitat use; Microhab_terr: terrestrial microhabitat use; Microhab_saxi: saxicolus microhabitat use; Diet_carn: carnivore diet; Diet_herb: herbivore diet; Forag_act: active foraging; Forag_sw: sit-and-wait foraging; Forag_mix: mixed foraging; Activ_diur: diurnal activity; Activ_noc: nocturnal activity; Repr_ovi: oviparous reproduction; Repr_vivi: viviparous reproduction; Max_clutch: maximum clutch size; Temp: mean activity temperature; Regtemp_helio: thermoregulator; Regtemp_conf: thermoconformer. NA: no data.

Functional Trait	sp1	sp2	sp3	sp4	sp5	sp6	sp7	sp8	sp9	sp10	sp11	sp12	sp13	sp14	sp15	sp16	sp17	sp18	sp19	sp20
Max_size	64	53	62	180	90	57	69	74	52	59	57	75	76	90	74	61	88	54	71	106
Dimorp_fem	0	0	0	0	0	1	0	NA	1	0	0	NA	NA	0	0	1	0	0	0	NA
Dimorp_mal	0	0	1	1	0	0	0	NA	0	0	1	NA	NA	1	0	0	0	0	0	NA
Dimorp_no	1	1	0	0	1	0	1	NA	0	1	0	NA	NA	0	1	0	1	1	1	NA
Habitat_for	1	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Habita_open	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1
Microhab_arb	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0
Microhab_semiarb	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0
Microhab_semiaqu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_fos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Microhab_lit	1	1	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0
Microhab_terr	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0
Microhab_saxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diet_carn	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Diet_herb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forag_act	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Forag_sw	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Forag_mix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Activ_diur	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Activ_noc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Repr_ovi	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Repr_vivi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Max_clutch	NA	NA	NA	11	2	2	NA	2	2	2	2	NA	NA	2	NA	2	2	2	2	NA
Temp	26	26	NA	38	38	31	31	NA	29	NA	NA	NA	NA	29.2	27.7	27.8	29.8	NA	NA	NA
Regtemp_helio	0	0	0	1	1	0	0	NA	0	NA	0	0	NA	0	0	0	0	1	0	0
Regtemp_conf	1	1	1	0	0	1	1	NA	1	NA	1	1	NA	1	1	1	1	0	1	1

Functional Trait	sp21	sp22	sp23	sp24	sp25	sp26	sp27	sp28	sp29	sp30	sp31	sp32	sp33	sp34	sp35	sp36	sp37	sp38	sp39	sp40
Max_size	82	80	80	80	107	74	78	47	47	65	43	NA	25	72	76	56	78	59	117	25
Dimorp_fem	NA	NA	1	NA	NA	NA	NA	1	1	0	1	NA	NA	0	1	0	0	0	0	NA
Dimorp_mal	NA	NA	0	NA	NA	NA	NA	0	0	0	0	NA	NA	0	0	0	1	0	1	NA
Dimorp_no	NA	NA	0	NA	NA	NA	NA	0	0	1	0	NA	NA	1	0	1	0	1	0	NA
Habitat_for	1	1	1	0	1	0	1	1	1	1	0	NA	1	1	0	0	0	0	1	1
Habita_open	0	0	0	1	0	1	0	0	0	1	1	NA	0	1	1	1	1	1	1	1
Microhab_arb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_semiarb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_semiaqu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_fos	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_lit	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1
Microhab_terr	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1
Microhab_saxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diet_carn	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Diet_herb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forag_act	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0
Forag_sw	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Forag_mix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Activ_diur	NA	NA	0	NA	NA	NA	NA	1	1	1	1	1	1	1	1	1	1	1	1	1
Activ_noc	NA	NA	1	NA	NA	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0	1
Repr_ovi	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Repr_vivi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Max_clutch	NA	NA	1	NA	NA	NA	NA	2	NA	NA	2	NA	1	3	3	1	4	1	4	1
Temp	NA	NA	NA	NA	NA	NA	NA	NA	27.2	NA	NA	NA	NA	39.4	37.7	37	38	36.9	37.5	NA
Regtemp_helio	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	0
Regtemp_conf	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1

Functional Trait	sp41	sp42	sp43	sp44	sp45	sp46	sp47	sp48	sp49	sp50	sp51	sp52	sp53	sp54	sp55	sp56	sp57	sp58	sp59	sp60
Max_size	25	55	250	360	157	117	115	NA	50	55	34	46	42	54	48	39	40	64	68	71
Dimorp_fem	NA	0	0	NA	0	0	1	NA	NA	NA	NA	1	0	1	1	NA	NA	NA	0	NA
Dimorp_mal	NA	1	0	NA	1	0	0	NA	NA	NA	NA	0	1	0	0	NA	NA	NA	0	NA
Dimorp_no	NA	0	1	NA	0	1	0	NA	NA	NA	NA	0	0	0	0	NA	NA	NA	1	NA
Habitat_for	1	1	1	1	1	1	1	NA	1	1	1	1	1	0	0	NA	0	0	1	1
Habita_open	0	1	0	0	0	0	0	NA	0	0	0	0	0	1	1	NA	1	1	1	1
Microhab_arb	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Microhab_semiarb	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	1	1
Microhab_semiaqu	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_fos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_lit	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Microhab_terr	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0
Microhab_saxi	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Diet_carn	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Diet_herb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forag_act	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Forag_sw	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1
Forag_mix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Activ_diur	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	NA	NA	0	0	0
Activ_noc	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	NA	NA	1	1	1
Repr_ovi	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Repr_vivi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Max_clutch	1	NA	6	6	7	4	14	NA	2	NA	NA	1	1	2	2	NA	NA	NA	2	NA
Temp	NA	NA	31.2	32.2	NA	NA	NA	NA	NA	NA	NA	30.6	30.3	30.2	NA	NA	NA	NA	27.2	NA
Regtemp_helio	0	NA	1	1	NA	NA	NA	NA	NA	NA	0	0	0	0	NA	NA	NA	NA	0	0
Regtemp_conf	1	NA	0	0	NA	NA	NA	NA	NA	NA	1	1	1	1	NA	NA	NA	NA	1	1

Functional Trait	sp61	sp62	sp63	sp64	sp65	sp66	sp67	sp68	sp69	sp70	sp71	sp72	sp73	sp74	sp75	sp76	sp77	sp78	sp79	sp80
Max_size	105	445	62	114	119	73	130	NA	127	65	35	39	37	37	NA	34	96	109	84	91
Dimorp_fem	NA	0	NA	0	0	NA	0	NA	0	0	0	NA	NA	NA	NA	1	1	1	1	1
Dimorp_mal	NA	1	NA	1	1	NA	1	NA	1	1	0	NA	NA	NA	NA	0	0	0	0	0
Dimorp_no	NA	0	NA	0	0	NA	0	NA	0	0	1	NA	NA	NA	NA	0	0	0	0	0
Habitat_for	0	1	1	1	1	1	1	NA	0	0	1	1	1	1	NA	0	0	1	1	0
Habita_open	1	1	0	0	0	1	0	NA	1	1	0	0	0	0	NA	1	1	0	1	1
Microhab_arb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Microhab_semiarb	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Microhab_semiaqu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_fos	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microhab_lit	0	0	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	1	1	1
Microhab_terr	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0
Microhab_saxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diet_carn	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Diet_herb	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forag_act	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0
Forag_sw	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Forag_mix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Activ_diur	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Activ_noc	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Repr_ovi	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Repr_vivi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Max_clutch	NA	71	2	9	10	6	7	NA	12	6	1	2	NA	2	NA	2	9	9	9	8
Temp	NA	38	28.2	35.9	36.5	NA	34.1	NA	37	NA	NA	NA	NA	NA	NA	NA	33.1	32.9	29.1	33.4
Regtemp_helio	0	1	NA	1	1	1	1	1	1	1	NA	0	0	0	NA	NA	1	1	1	1
Regtemp_conf	1	0	NA	0	0	0	0	0	0	0	NA	1	1	1	NA	NA	0	0	0	0

Functional Trait	sp81	sp82	sp83	sp84	sp85	sp86	sp87	sp88	sp89	sp90	sp91	sp92	sp93	sp94	sp95	sp96	sp97	sp98	sp99	sp100
Max_size	98	88	109	NA	43	41	109	94	300	78	177	97	146	147	84	30	64	93	91	90
Dimorp_fem	1	1	1	NA	0	0	0	0	1	0	0	0	1	1	0	0	1	1	1	1
Dimorp_mal	0	0	0	NA	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0
Dimorp_no	0	0	0	NA	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0
Habitat_for	1	0	1	NA	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	0
Habita_open	1	1	1	NA	1	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1
Microhab_arb	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Microhab_semiarb	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Microhab_semiaqu	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Microhab_fos	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Microhab_lit	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Microhab_terr	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1
Microhab_saxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diet_carn	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Diet_herb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forag_act	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0
Forag_sw	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	1	1
Forag_mix	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Activ_diur	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Activ_noc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Repr_ovi	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Repr_vivi	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Max_clutch	NA	9	9	NA	2	2	2	2	13	3	5	2	31	12	2	1	2	4	NA	NA
Temp	35.1	NA	32.6	NA	34.6	29.1	NA	NA	NA	28.5	30.5	29.1	NA	NA	27	NA	NA	NA	NA	NA
Regtemp_helio	1	1	1	1	1	1	1	1	NA	NA	NA	NA	NA	NA	1	NA	NA	1	1	1
Regtemp_conf	0	0	0	0	0	0	0	0	NA	NA	NA	NA	NA	NA	0	NA	NA	0	0	0

Functional Trait	sp117	sp118	sp119	sp120	sp121	sp122	sp123
Max_size	488	254	345	87	130	166	38
Dimorp_fem	0	NA	0	0	0	0	1
Dimorp_mal	1	NA	1	0	1	0	0
Dimorp_no	0	NA	0	1	0	1	0
Habitat_for	1	1	1	1	1	1	0
Habita_open	1	0	1	0	0	0	1
Microhab_arb	0	0	0	1	1	1	0
Microhab_semiarb	0	0	0	0	0	0	0
Microhab_semiaqu	0	0	0	0	0	0	0
Microhab_fos	0	0	0	0	0	0	0
Microhab_lit	0	0	0	0	0	0	1
Microhab_terr	1	1	1	0	0	0	1
Microhab_saxi	0	0	0	0	0	0	0
Diet_carn	1	1	1	1	1	1	1
Diet_herb	0	0	0	0	0	0	0
Forag_act	1	1	1	0	0	0	1
Forag_sw	0	0	0	1	1	1	0
Forag_mix	0	0	0	0	0	0	0
Activ_diur	1	1	1	1	1	1	1
Activ_noc	0	0	0	0	0	0	0
Repr_ovi	1	1	1	1	1	1	1
Repr_vivi	0	0	0	0	0	0	0
Max_clutch	NA	NA	49	2	2	8	2
Temp	NA	37.2	35	NA	31.2	NA	NA
Regtemp_helio	1	1	1	NA	NA	NA	1
Regtemp_conf	0	0	0	NA	NA	NA	0