Synergistic effects of climate and landscape change on the conservation of Amazonian lizards

Cássia de Carvalho Teixeira [Corresp., 1] , **Leonardo Carreira Trevelin** [2] , **Maria Cristina dos Santos-Costa** [3] , **Ana Lúcia da Costa Prudente** [1] , **Daniel de Paiva Silva** [4]

[1] Departamento de Zoologia, Herpetologia, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

[2] Instituto Tecnológico Vale, Belém, Pará, Brazil

[3] Laboratório de Ecologia e Zoologia de Vertebrados, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Pará, Brazil

[4] COBIMA Lab, Departamento de Biologia, Instituto Federal Goiano - Campus Urutaí, Urutaí, Goiânia, Brazil

Corresponding Author: Cássia de Carvalho Teixeira
Email address: cassiacteixeira@gmail.com

The leading causes of the worldwide decline in biodiversity are global warming, allied with natural habitat loss and fragmentation. Here, we propose an analysis of the synergistic effects of these two factors in 63 species of Amazonian lizards. We predicted that the high-climatic suitability areas of species would be significantly impacted by different deforestation scenarios and the resultant landscape structure and considered that forest-dwelling species would be especially susceptible to deforestation scenarios. We also pointed out species threatened by both drivers and suggest critical areas for their future conservation. According to our results, most species will face future reductions in suitable areas for their occurrence according to five different patterns, two of which represent significant risks for 15 species. Some of these species already deal with severe habitat loss and fragmentation of their current distribution ranges, whereas others will suffer a considerable area reduction related to future range shifts. We emphasize the importance of protected areas (PAs), especially indigenous lands, and the need for planning combined strategies involving the maintenance of PAs and possible implementation of ecological corridors. Finally, we highlight eight species of thermoconformer lizards that constitute present and future conservation concerns related to the combined effects of climate change and habitat loss and that should be carefully evaluated in extinction risk assessments.

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2 Amazonian lizards

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4 Ana Lúcia da Costa Prudente[4] & Daniel de Paiva Silva[5]
5
6 [1] Programa de Pós-Graduação em Biodiversidade e Evolução, Museu Paraense Emílio Goeldi,
7 Belém, Pará, Brazil
8 [2] Instituto Tecnológico Vale, Belém, Pará, Brazil
9 [3] Laboratório de Ecologia e Zoologia de Vertebrados, Universidade Federal do Pará, Belém,
10 Pará, Brazil
11 [4] Departamento de Zoologia, Herpetologia, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil
12 [5] COBIMA Lab, Departamento de Biologia, Instituto Federal Goiano-Campus Urutaí, Urutaí,
13 Goiás, Brazil
14
15
16 Corresponding author:
17 Cássia Teixeira[1]
18 Av. Perimetral, 1901, Belém, Pará, 66077-530. Brazil
19 E-mail address: cassiacteixeira@gmail.com

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Abstract

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41 The leading causes of the worldwide decline in biodiversity are global warming, allied with the
42 loss and fragmentation of natural habitats. Here, we propose an analysis of the synergistic effects
43 of these two factors in 63 species of Amazonian lizards. We predicted that the high-climatic
44 suitability areas of species would be significantly impacted by different deforestation scenarios
45 and the resultant landscape structure and considered that forest-dwelling species would be
46 especially susceptible to deforestation scenarios. We also pointed out species threatened by both
47 drivers, suggesting critical areas for future conservation. According to our results, most species
48 will face future reductions in suitable areas for their occurrence according to five different
49 patterns, two of which represent significant risks for 15 species. Some of these species already
50 deal with severe habitat loss and fragmentation of their current distribution ranges, whereas
51 others will suffer a considerable area reduction related to future range shifts driven by climate
52 change. We emphasize the importance of protected areas (PAs), especially indigenous lands, and
53 the need for planning combined strategies involving the maintenance of PAs and the possible
54 implementation of ecological corridors. Finally, we highlight eight species of thermoconformer
55 lizards that constitute present and future conservation concerns related to the combined effects of
56 climate change and habitat loss and that should be carefully evaluated in extinction risk
57 assessments.

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59 Keywords: Climate change, Deforestation, Extinction threshold, Fragmented landscape, Species
60 distribution models, Protected areas.

61

Introduction

63   Anthropogenic global warming and climate changes, allied with the loss and
64 fragmentation of natural habitats, are the main processes responsible for the worldwide decline in
65 biodiversity (*Parmesan, 2006; Gallant et al., 2007*). Although often approached independently,
66 their combined effects may produce synergistic outcomes that need to be accounted for to
67 accurately evaluate the anthropogenic footprint on biodiversity (*Mantyka-Pringle, Martin &*
68 *Rhodes, 2012; Frishkoff et al., 2016*). For instance, cumulative evidence suggests a climatic
69 resilience threshold for the Amazon Forest, where deforestation may hinder most tree species
70 from geographically tracking the future climate and driving them to extinction, where climatic
71 conditions turn unsuitable (*Cowling et al., 2004; Feeley & Silman, 2016; Gomes et al., 2019*).
72 Climate-driven latitudinal range shifts (*Wilson et al., 2005; Hickling et al., 2006*) and potential
73 extinction due to the failure to track suitable climate conditions (*Sekercioglu et al., 2002; Pounds*
74 *et al., 2006*) may also be expected for animal taxa.
75   The historical concomitant increase in atmospheric concentrations of CO_2 and global
76 surface temperature is projected to continue rising throughout the 21st century, irrespective of
77 the greenhouse gas emission scenario considered (IPCC, 2014). The resulting changes in
78 regional precipitation patterns have been observed in the continental-scale Amazon, showing an

79   intensification of its hydrological cycle in the last decades, with more frequent seasonal extremes
80   like floods and droughts (*Gloor et al., 2013, Chaudhari et al., 2019*). The Amazon forests
81   naturally exerts control over rainfall and temperature through evapotranspiration, especially
82   attenuating drier climatic extremes (*Sampaio et al., 2018*). Still, the synergic interactions of the
83   consequences of these climate projections with landscape change events, such as deforestation
84   and fire events, may limit this mechanism and result in adverse effects on biodiversity (*Marengo
85   et al., 2018*). Local-scale deforestation is predicted to change local climatic conditions, such as
86   mean temperature or rainfall frequency (*D'Almeida et al., 2007*). Regionally, a threshold in
87   deforestation, beyond which forests would no longer sustain their climate and collapse into drier
88   savanna-like physiognomies, is discussed (*Marengo et al., 2018*; *Lovejoy & Nobre, 2018*).
89   When considering deforestation, it is important to acknowledge that habitat loss and
90   fragmentation have long been understood as two different landscape processes with varying
91   effects on biodiversity (*Fahrig, 2003*). While less habitat area increases the likelihood of
92   stochastic extinction and declines in population sizes, fragmentation refers to dividing the
93   remaining habitat and isolating populations with limited dispersal capacity (*Fahrig, 1997;
94   Fischer & Lindenmayer, 2007*). Despite this marked difference, both processes usually co-occur
95   and interact non-linearly in landscapes (*Swift & Hannon, 2010*).
96   When habitat areas are abundantly available (i.e., large forested areas), connectivity is
97   still robust, and fragmented effects are negligible. The importance of such areas only increases
98   when the remaining habitat patches are so few and dispersed that isolation effects increases
99   (*Fahrig, 2002*). This situation was formalized as the extinction threshold hypothesis, which
100   states that species require a minimum habitat area to persist in a landscape (*Andrén, 1994;
101   Fahrig, 2013*). True fragmentation effects occur below this threshold, leading to abrupt declines
102   in species populations and an increased chance of extinction (*Fahrig, 2002; Swift & Hannon,
103   2010*). Based on simulation studies, less than 30% of the original habitat area in the landscape
104   was considered a critical threshold (*Andrén, 1994*). While it is demonstrated in empirical results
105   that this value can vary among species, landscape, and spatial scale, this theoretical value is an
106   important general reference point for studies with scant empirical data (*Pardini et al., 2010;
107   Swift & Hannon, 2010*).
108   Globally, reptiles have been proposed to be the primary animal taxa negatively affected
109   by habitat loss and fragmentation as temperatures rise (*Mantyka-Pringle, Martin & Rhodes,
110   2012*). Lizards have an ectothermic metabolism and control body temperature through intricate
111   behavioural and physiological processes that directly impact locomotory activities, such as
112   foraging and dispersal (*Camacho & Rusch, 2017*). These features make them particularly
113   vulnerable to the synergic consequences of climate and landscape change in tropical regions
114   (*Sinervo et al., 2010*). Some species need direct sunlight to thermoregulate and are usually
115   associated with open areas (thermoregulators). In contrast, other species related to closed-canopy
116   formations do not have this requirement (thermoconformers), some of which are commonly
117   found in the evergreen forest of the Brazilian Amazon (*Vitt et al., 2008*). Even in these more
118   climatically stable tropical regions, thermoconformers are active at low body temperatures, not

119 tolerating severe warming and thus more vulnerable to climate and landscape change (*Huey et*
120 *al., 2009*).

121   In recent studies, the effects of climate change on the distribution and thermal physiology
122 of some tropical species have been explored (*Diele-Viegas et al., 2018; Pontes-da-Silva et al.,*
123 *2018*). Likewise, landscape-change effects on tropical lizard species have been approached in
124 several studies, suggesting strong species-area relationships regulating these systems (*Silva,*
125 *Santos-Filho & Canale, 2014; Palmeirim, Vieira & Peres, 2017a*). Still, no studies have
126 correlated climate and landscape change and evaluated their effects on the distribution of lizard
127 species. A common approach to assessing the impact of climate on biodiversity is to use species
128 distribution models (SDMs). In SDMs, individual occurrences of the species are correlated with
129 local climatic characteristics to predict other high-suitability areas and project different climatic
130 scenarios for their occurrence (*Guisan & Zimmermann, 2000; Peterson, 2003*). Also, to these
131 SDMs, additional layers of information can be added later to refine the results and better inform
132 scenarios, including deforestation models (*De Marco Jr et al., 2018*; *Santos et al., 2020*;
133 *Miranda et al., 2021*).

134   We aimed to quantify the combined effects of climate and landscape change on the
135 species in Amazonian tropical rainforests (*Avila-Pires, 1995; Ribeiro-Júnior & Amaral, 2016a*)
136 to fill this knowledge gap and guide the effective conservation of Amazonian lizard species in
137 Brazil. Our approach involved understanding future scenarios of climate suitability for Brazilian
138 Amazonian lizards and how these may be influenced by deforestation and extinction thresholds.
139 We hypothesize that, given evidence of temperature-reduced locomotory performance (*Diele-*
140 *Viegas et al., 2018*) and area effect-related local extinctions (*Palmeirim, Vieira & Peres, 2017a*),
141 severe landscape changes may hinder Amazonian lizard species' dispersal and limit their abilities
142 to track suitable conditions, leading to greater extinction risk (*Urban, 2015*; *Frishkoff et al.,*
143 *2016*).

144   We predict that the potential climatic niche of the species will be significantly impacted
145 by different deforestation scenarios and the resultant landscape structure. We further discuss how
146 forest-dwelling species will be especially susceptible to such deforestation scenarios. Ultimately,
147 we pointed out species threatened by the synergy between climate and landscape change,
148 drawing geographic and temporal patterns of species responses and prioritising conservation
149 measures specifically driven by these patterns.

150

Materials & Methods

Species occurrence dataset

153   We initially defined the Amazon basin as the extent of our study region (*Soares-Filho et*
154 *al., 2006*; Fig. 1). Next, we created a list of lizard species endemic to this region and those whose
155 distributions are predominantly Amazonian within Brazilian borders (> 50% of the distribution).
156 Species distributions and the compilation of their occurrence records were based on the

157 comprehensive works of *Ribeiro-Júnior & Amaral (2016a)* and *Ribeiro-Júnior (2015)*, which
158 represent extensive taxonomical efforts of specimens deposited in scientific collections. When
159 not directly available, geographical coordinates within these works were accessed with the aid of
160 gazetteers and geolocation software based on historical information and collector's field notes,
161 some of which correspond to municipality centroids. Finally, we assumed a minimum of 10 valid
162 occurrences from this initial set as our primary criterion for modelling. The resulting species
163 pool contained 63 Amazonian lizards, 50 of which were endemic to the Amazon (Table S1). The
164 majority of species (53) had up to 35% of occurrences corresponding to municipality centroids,
165 whereas for the remaining 10 species, up to 59% were municipality centroids. Despite the lower
166 resolution of these specific occurrence data, we opted to keep them, as exclusion would cause a
167 considerable loss of historical distributional knowledge of these species. An essential caveat
168 within our approach is that occurrence data compiled from scientific collections contain a time
169 lag between the time lizards were collected and present-day land-cover conditions. Still, we feel
170 this is precisely a good reason to justify using additional present landcover data as a means to
171 refine the suitability outputs from the initial SDMs we analyzed.

172

Modeling Climate scenarios

173

174   We performed species distribution modelling using the species occurrence dataset and
175 environmental variables representing two climatic scenarios to estimate the impact of climate
176 change on the geographic distribution of Amazonian lizard species: current and future (Table 1).
177   Considering the current scenario within our predefined extent for analysis, we used 19
178 bioclimatic variables from WorldClim (*Hijmans et al., 2005*; http:\\ www.worldclim.org) under a
179 20.25 km^2 (~4 km side = 2.5 arc-min) grid resolution. Highly correlated variables were
180 arbitrarily removed before modelling, using Person's correlation ($r > 0.8$) to avoid collinearity in
181 our models (*Guisan & Thuiller, 2005*) (Table S2). The selected variables were: Annual Mean
182 Temperature (BIO1), Mean Diurnal Range (BIO2), Isothermality (BIO3), Temperature
183 Seasonality (BIO4), Annual Precipitation (BIO12), Precipitation of Driest Month (BIO14),
184 Precipitation of Warmest Quarter (BIO18) and Precipitation of Coldest Quarter (BIO19).
185   When considering the future scenario, we used the same bioclimatic variables
186 corresponding to the year 2050, this time derived from 17 Atmosphere-Ocean coupled General
187 Circulation Models (AOGCMs) also available from WorldClim: ACCESS1-0, BCC-CSM1-1,
188 CCSM4, CNRM-CM5, GFDL-CM3, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-
189 ES, INMCM4, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC5, MPI-ESM-LR, MRI-
190 CGCM3 e NorESM1-M. For all, we chose the most pessimistic carbon dioxide emission
191 perspective (Representative Carbon Pathway—RCP 8.5 - *IPCC, 2014*). The pessimistic
192 perspective was used, as it has recently been assumed to strongly agree with the historical
193 cumulative CO2 emissions (*Schwalm, Glendon & Duffy, 2020*). Lastly, we used an arithmetic

194 mean of the resulting predictions as the consensual future model for each species, a robust
195 approach to this end (*Marmion et al., 2009*).

196   The original occurrence datasets contained presence-only data. Therefore, we generated
197 pseudo-absence data randomly distributed for each species (*Lobo Jiménez-Valverde & Hortal,*
198 *2010*). Then, we used the "checkerboard" methodology to partition data approximately in half
199 between two spatially structured subsets, divided into cells resembling a checkerboard table.
200 Each subset was used to both fit the model and validate the model fitted onto the other subset, a
201 common approach in evaluating species distribution models (*Muscarella et al., 2014; Velazco et*
202 *al., 2017*).

203   We generated SDMs using three machine learning algorithms, regarded as highly
204 efficient for modelling species distribution (*Elith et al. 2006*; *Meynard & Quinn 2007*; *Oppel et*
205 *al. 2012*): the "Maximum Entropy (MaxEnt)", based on the maximum entropy principle
206 (*Phillips, Anderson & Schapire, 2006*); the "Random Forest", which separates data into
207 randomly defined decision trees and elect the most recurrent and likely distribution (*Schapire,*
208 *2001*); and the "Support Vector Machine (SVM)" method based on probability classes (*Guo,*
209 *Kelly & Graham, 2005*; *Phillips, Anderson & Schapire, 2006*). Adopted models' restrictions
210 resulted in few species with restricted distributions (< 25) within our species pool. Thus, we did
211 not feel the need to minimize the chance of omission error (in detriment to the commission
212 error). ROC generated slightly less inflated SDMs, allowing us to perceive the reported patterns
213 better. We used thresholds obtained with the "Receiver—Operator Curve" (ROC), which
214 balances both omission and commission errors while determining distributional ranges (*Phillips,*
215 *Anderson & Schapire, 2006*), to transform climatic suitability predictions into presence/absence
216 distribution maps. We used two approaches to evaluate the performance of the generated models:
217 the "Area Under the Receiver Operator Curve" (AUC) which varies from 0 to 1, with values $\leq$
218 0.5 representing models no better than random; and the "True Skilled Statistics" (TSS), which
219 varies from -1 to 1, with values close to or below 0 also representing models no better than
220 random. We considered models that scored above 0.7 in both statistics as acceptable (*Allouche,*
221 *Tsoar & Kadmon, 2006; Liu, White & Newell, 2011*). This modeling approach was implemented
222 in the R 3.6.0 environment (*R-Core Team, 2017*), using the ENMTML package (*Andrade,*
223 *Velazco & De Marco Júnior, 2020*). Ultimately, we identified priority conservation areas
224 coinciding with the highest amount of the analysed species.

225

Forest cover scenarios

227   We refined current and future climate change scenarios by overlapping forest cover
228 rasters generated with a deforestation model developed by the SimAmazonia project
229 (https://csr.ufmg.br/simamazonia - *Soares-Filho et al., 2006*) to further improve the SDMs of
230 each species and evaluate the synergic effects of climate and landscape change. Based on data
231 from the "Measurement of Deforestation by Remote Sensing in Amazonia Program -
232 (PRODES)"(www.terrabrasilis.dpi.inpe.br), cartographic algebra and celular automata

233 techniques are used by this model to simulate spatially-explicit deforestation models across the
234 Amazon basin within two contrasting management scenarios: the "business-as-usual" (BAU) and
235 the "governance" (GOV) scenarios (Table 1). BAU is a pessimistic scenario that assumes low
236 compliance with environmental laws and the paving of major highways, projecting rates of
237 deforestation based on historical figures that result in an expected 37% forest reduction up to
238 2050. On the other hand, GOV is an optimistic, environmental governance best-case scenario
239 that projects deforestation rates as an asymptotic logistic curve, imposing limits on the deforested
240 land that aims to reproduce public policies, resulting in estimates of approximately 17% of
241 deforestation for the same year 2050 (*Soares-Filho et al., 2006*).
242   We used both SimAmazonia projections to refine future climate scenarios and a single
243 SimAmazonia projection to refine the current present-day scenario (2019) instead of the actual
244 data. This is because the actual forest cover data are only partially available for some parts of the
245 study region. By doing this, we guaranteed the full extension of the analyzed area and
246 maintained standardisation for the temporal comparisons. We visually identified that the GOV
247 projections for 2019 were closely related to actual forest cover data and used them as our current
248 scenario (Table 1).
249

250 ## Habitat area in the landscape

251   We used nearest neighbour resampling to downscale all current and future forest cover
252 projections, initially available in a 1 km^2 resolution, to the same resolution matching the
253 bioclimatic SDMs. Then, we overlapped SDMs and forest cover projections and calculated the
254 total number of high-climatic suitability cells coinciding with predicted forested cells, assuming
255 them as potential habitat areas, which were estimated for each species in each scenario. Habitat
256 area is hypothesized as a critical predictor of biodiversity in landscapes (*Fahrig, 2013*) and here
257 we also evaluate habitat distribution in the landscapes. Thus, each resulting habitat area
258 prediction was gridded in a tessellation of hexagonal cells, with 1,200 km^2 each, representing a
259 sample of a landscape for the studied lizards for which we counted the number of available
260 habitat cells. Samples with these dimensions have been previously used to represent local
261 landscapes for amphibian species (*Becker et al., 2010*). Given the known spatial and energetic
262 requirements of lizards (*Pough, 1980*), we considered it a reasonable estimate of the habitat area
263 in the landscape for the studied lizards. According to the extinction threshold hypothesis
264 (Andrén, 1994), we considered those landscapes with at least 30% habitat as stable landscapes.
265 As a result, we generated estimates of total habitat areas and total stable habitat areas (only
266 considering those landscapes > 30% of forested habitats) for each species by each scenario.
267   Furthermore, we assessed the vulnerability of the studied species by evaluating the total
268 stable habitat areas within the Brazilian System of Protected Areas (PAs). For this, we adopted
269 the criteria proposed by *Rodrigues et al. (2004)*: species with < 1,000 km^2 are expected to be
270 100% within PAs; species with > 250,000 km^2 are expected to be at least 10% within PAs. In
271 between, the percentage is calculated based on logarithmic interpolation. Species that did not

272 meet these criteria were considered vulnerable. It is important to remember that 11 out of the 63
273 studied species are not endemic to the Amazonia biome, so our approach assessed the
274 Amazonian status of these species.
275   We considered all three categories of PAs in our analysis: (a) full protection areas, whose
276 sole objective is to preserve biodiversity without any exploitation of natural resources, (b)
277 sustainable use areas, destined to conservation and sustainable use of natural resources and (c)
278 indigenous lands destined to the protection of indigenous populations, but with a relevant role in
279 biodiversity protection complementing the other PAs (*Begotti & Peres, 2020*). We used the
280 Protected Planet database as our source for this data (www.protectedplanet.net; *UNEP-WCMC,*
281 *2020*). Lastly, we summed the stable habitat areas for each species by scenario, aiming to
282 identify the richest and climatically stable locations as priority areas for conserving Amazonian
283 lizards.
284

Data analysis

286   We added the SDMs (high-climatic suitability cells refined by total stable habitat areas)
287 of all species to visualise priority areas for the conservation of lizard species across the Amazon
288 basin. This procedure resulted in species richness predictions for each climate + forest cover
289 scenario (Figs. 2 A–B, S1 A–B). We also used the same approach and produced richness
290 predictions only for the most vulnerable species identified in our study (paragraphs below).
291 Therefore, we indicate priority areas for conserving the most vulnerable species to the synergic
292 effects of future climate and landscape changes (Fig. 2 C–D, Fig. S1 C–D).
293   Next, we used species as replicates in each studied scenario to evaluate the overall effect
294 of deforestation and extinction thresholds on the predicted distribution of lizard species. To this
295 end, we compared the mean difference between the total habitat area and the total stable habitat
296 area (landscapes > 30% habitat threshold), using a non-parametric paired Wilcoxon signed-rank
297 test.
298   For each species, we created density plots to evaluate changes in the frequency
299 distribution of habitat area in landscapes within the predicted distribution for each climatic +
300 forest cover scenario. These plots aid in visualising the shape of data distributions over
301 continuous intervals (i.e., landscape habitat cover), using kernel smoothers to plot values and
302 minimize noises. Thus, we produced three data distribution curves for each species: one for the
303 present day (2019) and two for the future (2050), considering pessimistic and optimistic
304 scenarios. The peaks in these distributions aid us in visually identifying where landscape samples
305 concentrate, along with the habitat cover interval. In this way, landscapes with more than 75% of
306 habitat area suggest larger, continuos habitats, whereas landscapes with less than 30% of habitat
307 area suggest smaller, more fragmented habitats beyond the theoretical extinction thresholds
308 adopted in this study (*Andrén, 1994, Fahrig, 2013*). We visually compared the shape of these
309 distributions in all scenarios for each species individually, evaluating whether habitat availability
310 in current present-day landscapes changes according to the proposed future scenarios (Table 1).

311 By evaluating distribution curves simultaneously, we aimed to identify patterns of change that
312 were repeated among species. Finally, we assessed the significance of changes in frequency
313 distributions using the Anderson–Darling test, a statistic to compare two independent sample´s
314 distributions, sensitive towards differences in the tails of distributions (Engmann & Cosineau,
315 2011). The statistical significance was assessed by permutation tests (Quinn and Keough, 2002),
316 building null models containing 1000 sub-samples randomly drawn from the original dataset. All
317 analytical steps were implemented in the R 3.6.0 environment (*R-Core Team, 2017*), using the
318 *Ksamples* package (Scholz and Zhu, 2019). The complete methodological approach is
319 summarized in a flowchart depicted in Fig. 1, complemented by descriptions in Table 1.
320
321

Results

323 Among the 63 species evaluated in this study, *Stenocercus fimbriatus* Avila-Pires, 1995
324 showed the least number of records (N = 10) and *Ameiva ameiva* (Linnaeus, 1758) showed the
325 largest number of occurrences (N = 493) (Table S1). All species are considered to be *Least*
326 *Concern* in IUCN's Red List of threatened species (2018), while the species *Colobosaura*
327 *modesta* (Reinhardt & Luetken, 1862) and *Norops brasiliensis* (Vanzolini & Williams, 1970) are
328 considered to be threatened species in the state of Pará (Brazil) (*Albernaz & Avila-Pires, 2009*).
329 All models adjusted reached excellent predictive capacity when evaluating their AUC (range
330 0.99–1.0) and TSS (range 0.72–0.92) (Table S1).
331 When evaluating our species richness predictions, the current highest concentration of
332 predicted habitat areas was centralized in our study region. The highest and largest species
333 richness concentration is found in the Amazon river's lowlands, in the transition between the
334 northern portions of the Brazilian states of Amazonas and Pará, whereas smaller concentrations
335 of high species richness can be found northeast, towards the Guyana region (Fig. 2-A). In the
336 pessimistic future scenario, these high-concentration areas move north-eastward, encompassing a
337 wide stripe following the Atlantic coast with hotspots in the Guyanas region and mouth of the
338 Amazonas River (Fig. 2-B). Around half of all habitat areas were within PAs in all scenarios for
339 all species (Table S3). These concentrations represent areas of climatic stability for most
340 Amazonian lizard species and provide a general overview of their conservation status.
341 When comparing the mean difference between the total habitat area and the total stable
342 habitat area (Table S3), habitat area availability was significantly reduced in all tested scenarios,
343 with large effect sizes (Current: v = 2016, p < 0.001; r = 0.87 ; Pessimistic-Future: v = 2016, p <
344 0.001; r = 0.87; Optimistic-Future: v = 2016, p < 0.001; r = 0.87). For current present-day
345 projections, total habitat area reduced on average 2% (counted forest cells) when considering
346 habitat only on landscapes above the theoretical extinction habitat cover threshold. We found an
347 average decline of 9% for the pessimistic and 8% for the optimistic scenarios for future
348 projections.

349   When considering species independently, most species presented declines in the
350   availability of habitat areas in stable landscapes over time (Table S3). Out of the 63 species, 35
351   presented an average decrease of 32% in habitat area when considering the optimistic future
352   scenario, while this number rises to 51 species with an average reduction of 42% in habitat area
353   if we consider the pessimistic future scenario. Meanwhile, the remaining 28 species showed an
354   average increase of 73% in the optimistic future scenario, and the remaining 12 species in the
355   pessimistic scenario increased an average of 88% habitat area.

Response patterns to climate and landscape change

357   We observed five different patterns of change in the frequency distributions of the habitat
358   area in landscapes between scenarios. These patterns correspond to five different ways species
359   respond to the synergic effects of climate and landscape changes over time (Fig. 3 and Fig S2).
360   In the first three patterns, the relative stability between the present and future scenarios is
361   described. For example, pattern one (N = 34 species) corresponds to those species with a high
362   density of landscapes with > 75% of the habitat area in all scenarios, suggesting a low
363   vulnerability to the combined effects of climate and landcover changes over time. Pattern two (N
364   = 4) corresponds to species that display two similar peaks in the density of landscape habitat
365   coverage (around 30% and above 75% of habitat area) that remain relatively stable between the
366   present and future scenarios, also suggesting species with low vulnerability. On the other hand,
367   pattern three (N = 10) corresponds to species that currently show a high density of poorly
368   covered landscapes (below 30% habitat area), which tend to slightly increase in future scenarios,
369   depicting the most vulnerable species in this study.
370   Meanwhile, in the other two patterns, variable scenarios over time are described. For
371   example, in pattern four (N = 10) species with a higher density of landscapes with > 75% of
372   habitat area slightly shiftiting toward poorly covered landscapes in future scenarios are shown.
373   These species shift to a two-peak density pattern of landscape habitat coverage in both future
374   scenarios (similar to pattern 2), which still retain a similar amount of well-covered landscapes (>
375   75%) and thus were considered at low vulnerability. Finally, pattern five (N = 5) corresponded to
376   species that currently display a high density of landscapes with > 75% of habitat area cover but
377   are predicted to severely shift to poorly covered landscapes (> 30% of habitat area cover) in the
378   future scenarios. Such a condition suggests that these species do not currently display any
379   vulnerability but can do so in the future.
380   Among the 63 studied species, our approach points to 10 species considered as currently
381   vulnerable (pattern three) and to another five species that have the potential to become
382   vulnerable in future climate and deforestation scenarios (pattern five). Together, it is suggested
383   in our approach that 23% of the studied species need special attention to mitigate the adverse
384   synergic effects of climate and landscape changes.
385   The frequency distributions of landscape habitat covers in future scenarios were
386   significantly different from their present state for most species across all patterns (Table S4).
387   However, there was only one exception for the pessimistic scenario and five exceptions for the

388   optimistic scenario (8% of species) (Table S4). These noticeable differences among the
389   scenarios, variable among five patterns for all 63 species, highlight the relevance of designing
390   informed public policies that aim to reduce the specific effects of climate and landscape change
391   over biodiversity.
392
393

Discussion

395   In our results, we show the joint effects of climate and landscape change on 63
396   Amazonian lizard species, highlighting potential, previously overlooked, adverse effects on 15 of
397   these species. We found a large extent of suitable area for all species, and almost half of these
398   extents comprised PAs. This proportion inside PAs is similar to the results found by Ribeiro-
399   Júnior & Amaral (2016a), and we considered them to meet the conservation goals proposed by
400   (*Rodrigues et al., 2004*). However, when limited to landscapes above 30% of the habitat area, the
401   expected range of these species reduced significantly. The 15 abovementioned species display
402   present, future, or both scenarios that could represent conservation concerns.
403   We corroborated our initial prediction by showing that for most species (51), an average
404   reduction of 42% of the habitat area is expected by 2050. These results are consistent with the
405   overall deforestation expected for the region (*Soares-Filho et al., 2006*). Even in an eventual
406   optimistic future scenario, 35 species will still face an average 32% reduction in their expected
407   habitat area. This average reduction is sufficient for us to suggest a risk of extinction according
408   to the IUCN A4 criterion (*Gomes et al., 2019; IUCN, 2020*). There is considerable specific
409   variation around these average values (minimum of 2% to maximum of 97%), and some of the
410   remaining species will benefit from future increases in the suitable area. Nonetheless, resulting
411   from our 30% habitat area criterion, a group of 10 species already deals with habitat loss at the
412   landscape level, which will be further aggravated until 2050 (pattern three). The distribution
413   ranges of another five species will primarily shift to deforested landscapes in the future (pattern
414   five).
415   *Palmeirim, Vieira & Peres (2017a)* studied lizard assemblages in an insular Amazonian
416   landscape and found strong species-area effects. They observed functionally impoverished
417   assemblages within smaller isolated islands, favoring larger-bodied thermoregulator species
418   tolerant to forest edges and open areas. Similar results were also found for lizard assemblages in
419   fragmented continental landscapes (*Bell & Donnely, 2006; Almeida-Gomes & Rocha, 2014*), and
420   metabolism-related microhabitat use is discussed as the primary explanation for species turnover
421   along a forest degradation gradient in studies across the Neotropics (*Vitt, Zani & Esposito, 1999;*
422   *Palmeirim, Vieira & Peres, 2017b*). It is feasible to expect these same processes in landscapes
423   with a low habitat area in our analyses (below 30%; *Andrén, 1994; Fahrig, 2003*). From this
424   perspective, eight out of the 15 concerning species from our study are considered truly
425   thermoconformators and are directly implicated with local landscape or future range shift
426   extinction risks.

427   In pattern three, we recognized 10 species that already face habitat loss at the landscape
428   level, which will be aggravated in future scenarios. Six of them are thermoconformers: *Enyalius*
429   *leechii* (Boulenger, 1885), *Polychrus liogaster* Boulenger, 1908, *Stenocercus roseiventris*
430   Duméril & Bibron, 1837, *Uracentron a. azureum* (Linnaeus, 1758), *Cercosaura eigenmanni*
431   (Griffin, 1917) and *Neusticurus rudis* Boulenger, 1900. Relative smaller patches of habitat areas
432   are found northeastern to the Amazon River, while the majority is widely distributed south of the
433   river, overlapping to some extent with the region known as the "arch of deforestation," which
434   indeed accounts for their current threats (*Fearnside, 2005*). Future scenarios predicted for species
435   in this group do not represent major latitudinal or longitudinal shifts in the distribution of habitat
436   areas but rather a "rarefying effect" within the current distribution (Fig. 2-C). The exception is
437   the northeastern patch dislocating towards the Guiana shield region. Approximately half the PAs
438   within the potential distribution of these species are in indigenous lands, current strongholds of
439   biodiversity (*UNEP-WCMC, 2020*; *Begotti & Peres, 2020*), extremely relevant to the
440   conservation of these lizard species. Based on these patterns, we suggest that the strategy here
441   for PAs that currently harbor these species should receive significant attention in any
442   conservation planning towards these taxa.
443   As for pattern five, we recognized that five species would be threatened in future
444   scenarios by experiencing climate range shifts to predicted highly deforested landscapes. Two of
445   these species, *Dactyloa punctata* (Daudin, 1802) and *Bachia flavescens* (Bonnaterre, 1789), are
446   classified as thermoconformers. These species are predicted to have extensive habitat areas
447   across the biome that will suffer a severe reduction in future availability, promoting a range shift
448   toward the equator, especially in the Guiana shield (Fig. 2-D). Despite being considered a
449   knowledge gap in lizard distribution, 62% of the herpetofauna species found in this region are
450   expected to be exclusive to it (*Hoogmoed, 1979; Avila-Pires, Hoogmoed & Vitt, 2007*). With our
451   results, we show it as a stable climatic refuge, distant from deforestation frontiers and
452   exceptionally relevant for species and general lizard conservation in Amazonia. In a business-as-
453   usual scenario in Brazil, future conservation of these species will eventually depend on policies
454   of other countries (Guiana, Suriname, French Guiana). Therefore, present-day conservation
455   strategies should focus on allocating resources to promote connectivity between PAs (*Araújo et*
456   *al., 2004; Millar, Stephenson & Stephens, 2007*), primarily because of the temperature-reduced
457   locomotory performance expected for them (*Diele-Viegas et al., 2018*). Ecological corridors are
458   favored in a densely forested region such as the north of the Amazon River, and are the most
459   logical plan. Nonetheless, secondary forests and shaded plantations are effective ecological
460   corridors for leaf-litter species in anthropogenic landscapes (*Dixo & Metzger, 2009*), as they are
461   for other organisms (*Faria et al., 2007; Pardini et al., 2009*) and should be considered in future
462   scenarios.
463   Ecological niche models assume equilibrium between species and the environment, thus
464   not considering the ability of the species to adapt to new environmental circumstances (*Araújo et*
465   *al., 2004*). Given the metabolic needs and microhabitat use of the species, thermoregulators
466   could display different and even positive responses to these same climate-landscape processes.

467 *Frishkoff et al. (2016)* demonstrated for bird species that affiliation to drier climates is associated
468 with an ability to persist in and colonize anthropogenic landscapes, arguing for the same
469 homogenizing potential described for lizard communities (*Palmeirim, Vieira & Peres, 2017a,*
470 *2017b*). Four thermoregulator species suggested as vulnerable in our analytical approach also
471 occur in the savanna vegetation of the adjacent Cerrado biome: *N. brasiliensis*, *Hoplocercus*
472 *spinosus* Fitzinger, 1843, *C. modesta* and *Tropidurus oreadicus* Rodrigues, 1987 (*Costa &*
473 *Bérnils, 2018; Silva & Bates, 2002*). Furthermore, the latter, as well as *Tupinambis teguixin*
474 (Linnaeus, 1758) *and Kentropyx calcarata* Spix, 1825 are discussed as tolerant to some level of
475 habitat disruption, and both *T. oreadicus* and *T. teguixin* as perianthropic (*Lima, Suárez &*
476 *Higuchi, 2001; Ribeiro-Júnior, 2015; Ribeiro-Júnior & Amaral, 2016b; Palmeirim, Vieira &*
477 *Peres, 2017b*). These species should also be monitored. We suggest further studies to clarify
478 whether they can be used as indicators of climate and landscape changes, considering their
479 peculiarities (e.g., the known association of *T. teguixin* to water bodies; *Avila-Pires, 1995*).
480   Our findings represent an original contribution towards understanding the expected
481 consequences to Amazonian reptile biodiversity (*Cordier et al., 2021*) that arise from the
482 expected negative feedback between changes in the landscape and regional climate of Amazonia
483 (*Marengo et al., 2018*). New studies that aim for the underlying ecological mechanisms resulting
484 in the pessimistic outcomes we described for some species would certainly further explore these
485 results and refine conservation actions (*Schulte to Bühne et al., 2020*). From the landscape
486 change perspective, new approaches breaking apart the processes involved in the extinction
487 threshold hypothesis and studying the independent effects of habitat area and connectivity at a
488 landscape scale would better inform management actions for specific taxa (*Miranda et al., 2021*).
489 From the climate change perspective, more recent climate predictions (Coupled Model
490 Intercomparison Project Phase 6, CMIP6, – https://www.wcrp-climate.org/wgcm-cmip/wgcm-
491 cmip6) would certainly refine and improve future scenarios (although only available for 2040
492 and 2060). Finally, improvements in lizard taxonomy may certainly reveal further obscured
493 patterns, as species like *Bachia flavencens* e *Neusticurus rudis* are already considered as
494 potential complexes of species (*Kizirian & McDiarmid, 1998*; *Kok et al., 2018*), which probably
495 results in the division of expected distributions and new, more endangered species (*Bickford et*
496 *al., 2007*).

Conclusions

498   Despite the significant knowledge gaps regarding the Amazonian lizard species we
499 analysed here, we demonstrated that using the current resolution in the knowledge on species
500 occurences and a simulation-based habitat threshold was an appropriate approximation to
501 elucidate the variable synergic effects through which climate and landscape change can
502 potentially affect them. Researchers should focus on specific species suggested here (*Enyalius*
503 *leechii*, *Polychrus liogaster*, *Stenocercus roseiventris*, *Uracentron a. azureum*, *Cercosaura*
504 *eigenmanni*, *Neusticurus rudis, Dactyloa punctata* and *Bachia flavescens*) as primary vulnerable
505 species, whose extinction thresholds may vary according to specific natural history. Nonetheless,

506 empirical data generally corroborated the simulations in their ability to identify vulnerable taxa
507 (*Swift & Hannon, 2010; Mendes & De Marco Júnior, 2018*). The eight thermoconformer lizards
508 highlighted here represent present and future conservation concerns that should be carefully
509 evaluated in extinction risk assessments. We propose mitigation strategies related to their
510 specific response patterns to climate and landscape combined effects, complementing species
511 representations in current PA networks and promoting connectivity between them (*Araújo et al.,*
512 *2004; Hannah et al., 2007; Millar, Stephenson & Stephens, 2007*). Early response is the best
513 cost-saving and cost-benefit strategy for anticipating climate change (*Hannah et al., 2007*).
514   Worldwide, water availability is changing significantly, and South America is expected
515 to experience significant hydric stress in the medium term (*Rodell et al., 2018*). Additionally, the
516 current greenhouse gas emissions levels indicate that the global system will follow an
517 irreversible pathway of global climate change ("Hothouse Earth"). In this sense, the Amazon
518 Forest has an essential role as a sink for carbon dioxide, whereas decreasing greenhouse gas
519 emissions are of utmost importance and priority (*Steffen et al., 2018*). Still, the current political
520 scene in Brazil—the country bearing the most significant portion of the Amazon Forest—
521 indicates a pathway going in the opposite direction from sustainability. Anthropic activities, such
522 as cattle raising, crop plantation, and mining activities, account for most of the deforestation
523 rates in the Amazon basin (*Soares-Filho & Rajão, 2018; Dobrovolski et al., 2018*). The current
524 rates observed this year (in the first quarter of 2021) were higher than those observed in the
525 previous year and the most extensive rates observed in the last years (*IMAZON, 2021*).
526 Therefore, the climatic and landscape changes expected to affect the Amazonian lizards we
527 evaluated here could be underestimated. Additionally, we also believe that other environmental
528 factors, such as the effects of fire events (*Marengo et al., 2018*), will undoubtedly contribute to
529 harsher scenarios for these lizard species.
530

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Figure 1

The conceptual model used to evaluate the joint effects of habitat loss and climate change in the potential distribution of Amazonian lizards.

(A) Modeling suitability surfaces and defining potential distribution. (B) Division into landscape samples and habitat area quantification. (C) Density plots to evaluate changes in the frequency distribution of landscape covers within the predicted distribution for each climatic/deforestation scenario. The red arrow represents the high concentration of landscapes with about 30% of habitat area cover below the critical threshold, while the blue arrow represents the high concentration of landscapes with > 75% of habitat area cover. (D) Concentration maps of predicted habitat areas.

(A) Suitability maps

(B) Landscapes

(C) Landscape density plots according to the habitat area

Current
Pessimistic-Future
Optimistic-Future

(D) Concentration maps of predicted habitat areas

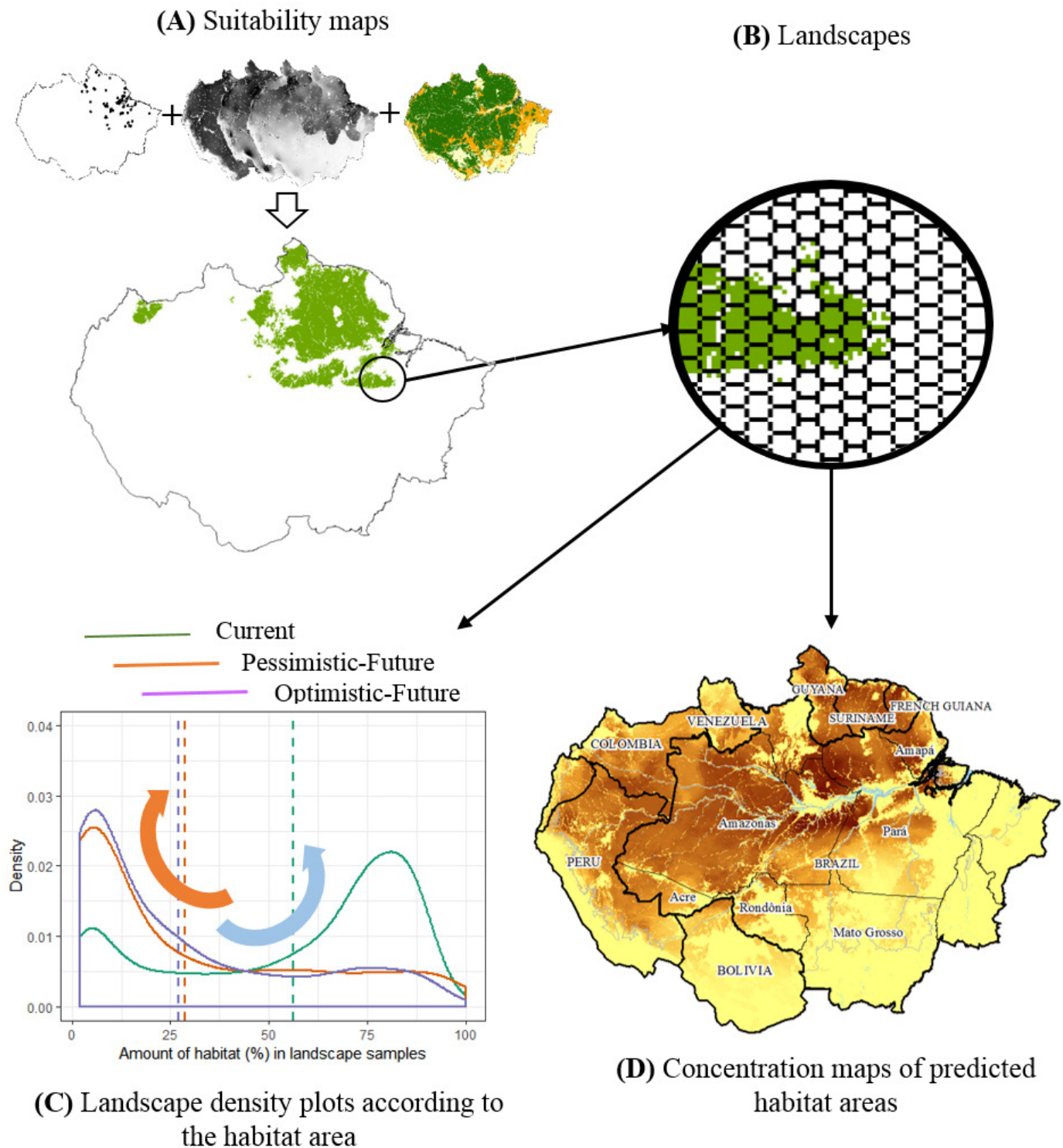



Figure 2

Concentration maps of predicted habitat areas.

(A) Species richness based on the sum of habitat areas for all Brazilian species in the current and (B) in a future pessimistic scenario, depicted by a gradient of colours, from yellow (no overlap) to brown (maximum overlap of species). The same approach only considering thermoconformers' vulnerable species classified on (C) pattern 3 and (D) pattern 5. Blue highlight corresponds to the Amazon river.

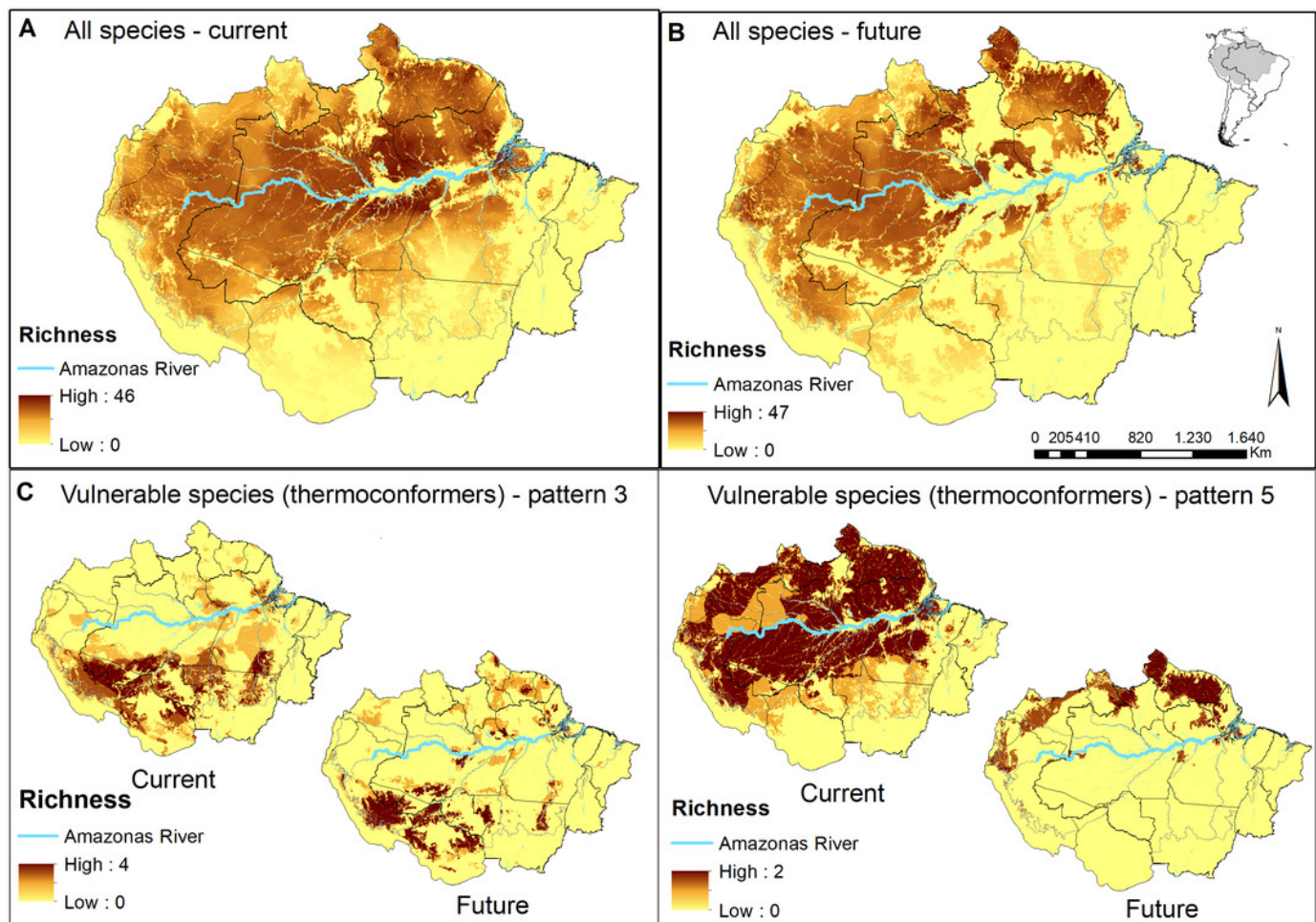
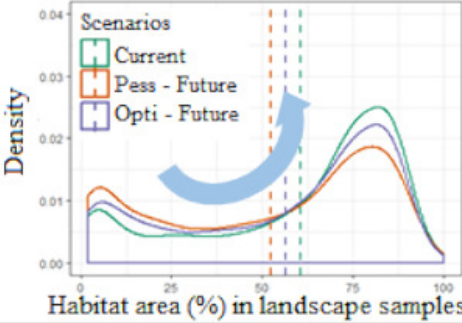
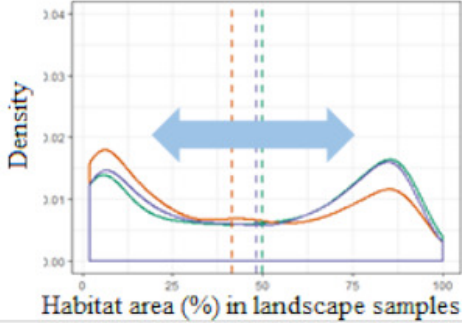
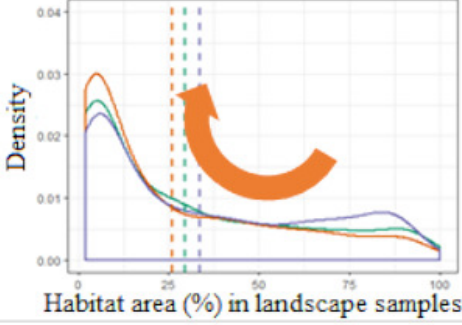
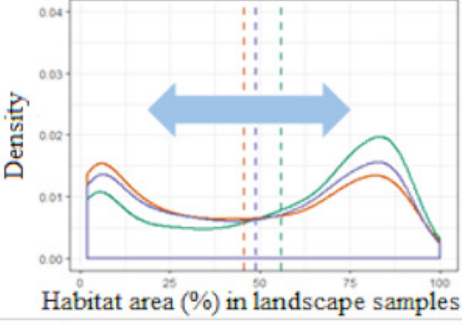
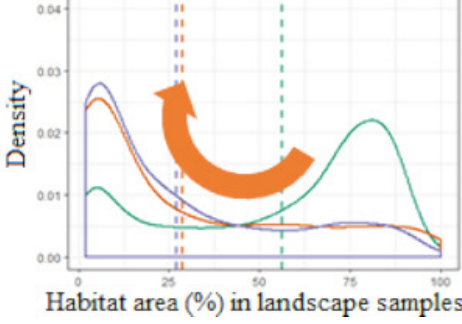



Figure 3

Infographic representing the five general patterns recognized in the distribution of Brazilian Amazonian lizard species.

Density plots depict the frequency of landscapes along an axis of habitat area (%) observed for that pattern, a short description of the observed pattern, the number of species recognized within this pattern, and the threat category assigned to this pattern. The plots represent the distribution of Norops fuscoauratus (D'Orbigny, 1837 in Duméril & Bibron, 1837) (pattern 1), Neusticurus bicarinatus (Linnaeus, 1758) (pattern 2), Colobosaura modesta (Reinhardt & Luetken, 1862) (pattern 3), Kentropyx striata (Daudin, 1802) (pattern 4) and of Copeoglossum nigropunctatum (Spix, 1825) (pattern 5), used as examples of each general pattern.

Graph	Pattern	Responses	Amount of species	Threat level
	1	High density of landscapes >75% of habitat area	34	Low
	2	Landscapes <30% and >75% in similar proportions	4	Low
	3	High density of landscapes <30%.	10	High
	4	Small reduction of landscapes >75% in future scenarios	10	Low
	5	High reduction of landscapes >75% in future scenarios	5	High

Climate + Forest Cover scenarios.

Scenarios combining effects of climate and landscape change and how they were defined in this study, and the observed response patterns depicting how habitat availability in the landscape changes in each scenario, for each pattern.

1 **Table 1:**
2 **Climate + Forest Cover scenarios.**
3 Scenarios combining effects of climate and landscape change and how they were defined in this study, and the observed response
4 patterns depicting how habitat availability in the landscape changes in each scenario, for each pattern.

Moment	Climate change scenarios	Deforestation scenarios	Observed response patterns				
			Pattern 1	**Pattern 2**	**Pattern 3**	**Pattern 4**	**Pattern 5**
Current (2019)	SDMs based on 8 uncorrelated bioclimatic variables derived from the monthly temperature and rainfall values describing local, current climatic trends (BIO01, BIO02, BIO03, BIO04, BIO12, BIO14, BIO18, BIO19*)	Forest cover projections on a governance scenario (GOV - 2019): environmental governance scenario projecting deforestation similar to the actual rates of the present days**	Higher density of landscapes with >75% habitat area	Similar density of landscapes with >75% and <30% habitat area	Higher density of landscapes with <30% habitat area	High density of landscapes with >75% habitat area	High density of landscapes with >75% habitat area
Future (2050)	Consensual SDMs based on the same 8 bioclimatic variables, derived from 17 AOGCMs, considering the most pessimistic CO_2 emission perspective (RCP 8.5). (BIO01, BIO02, BIO03, BIO04, BIO12, BIO14, BIO18, BIO19*)	Forest cover projections on a governance scenario (GOV - 2050): Optimistic, environmental governance scenario projecting 17% forest loss in the year 2050 **	Higher density of landscapes with >75% habitat area	Similar density of landscapes with >75% and <30% habitat area	Higher density of landscapes with <30% habitat area	Similar density of landscapes with >75% and <30% habitat area	Higher density of landscapes with <30% habitat area
		Forest cover projections on a "business-as-usual" scenario (BAU - 2050): Pessimistic, low environmental compliance scenario, projecting 37% forest loss in the year 2050**	Higher density of landscapes with >75% habitat area	Similar density of landscapes with >75% and <30% habitat area	Higher density of landscapes with <30% habitat area	Similar density of landscapes with >75% and <30% habitat area	Higher density of landscapes with <30% habitat area

6 * Bioclimatic variables extracted from WorldClim (Hijmans et al., 2005; http:\\www.worldclim.org)

7 ** Forest cover rasters extracted from SimAmazonia project (Soares-Filho et al., 2006 - https://csr.ufmg.br/simamazonia)