

1 **Title page**

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3 **SHORT TITLE:** Coexistence dynamics in squamates

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5 **GEOGRAPHICAL AND ECOLOGICAL DRIVERS OF COEXISTENCE DYNAMICS IN**

6 **SQUAMATE REPTILES**

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29 **CONFLICT OF INTEREST STATEMENT**

30 The authors declare no competing of interests.

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52 **RUNNING TITLE:** Coexistence dynamics in squamates

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54 **GEOGRAPHICAL AND ECOLOGICAL DRIVERS OF COEXISTENCE DYNAMICS IN**

55 **SQUAMATE REPTILES**

56

57 **ABSTRACT**

58 **Aim:** Species richness varies widely across space. To understand the processes behind
59 these striking patterns, we must know what are the relevant drivers underlying species
60 coexistence. Several factors can potentially shape species coexistence such as the
61 speciation process, the time since divergence between lineages, environmental effects,
62 and intrinsic properties of the organisms. For the first time, we model the coexistence
63 dynamics of lizards and snakes across broad temporal and spatial scales, investigating
64 the role of species interactions, dispersal ability, and geographic area.

65 **Location:** Global

66 **Time period:** Last 20 million years

67 **Major taxa studied:** Squamata (lizards and snakes)

68 **Methods:** We used 448 closely related species pairs and their age since divergence
69 across 100 dated phylogenies. We categorized each pair as sympatric or allopatric and
70 as occurring on islands or continents. We measured morphological traits to quantify
71 niche divergence and used range and body size as proxies for dispersal ability. We
72 applied a model-comparison framework in lizards and snakes separately to evaluate
73 which factors best explained their coexistence dynamics.

74 **Results:** We found that distinct factors drive the coexistence dynamics in lizards and
75 snakes. In snakes, species pairs that coexist tend to occur on islands and are more
76 different in body size, suggesting that both geographical setting and species interactions

77 might be relevant factors. In contrast, we only found evidence that dispersal ability
78 shaped the coexistence of lizards, where species coexist when they have higher
79 dispersal abilities.

80 **Main conclusions:** Lizards and snakes greatly differ in coexistence dynamics. Higher
81 heterogeneity in coexistence dynamics within lizards and group-specific life-history
82 aspects might help to explain these findings. Our results emphasize that the interaction
83 between where organisms are and who they are, ultimately shapes biodiversity patterns.
84 We also highlight interesting avenues for further studies on species coexistence in deep
85 time.

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87 **KEY WORDS** dispersal ability, competition, niche divergence, snakes, lizards, islands,
88 continents

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102 **INTRODUCTION**

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104 Biodiversity is heterogeneously distributed across the Earth, and to explain why
105 certain regions comprise more species than others has been one of the major challenges
106 in Ecology and Biogeography (Gaston, 2000; Ricklefs, 2004). At global and regional
107 scales, the number of species is determined by speciation, extinction and migration
108 (Wiens & Donoghue, 2004; Ricklefs, 2006). However, to fully understand such spatial
109 variation in species richness we also need to know the mechanisms that ultimately
110 promote species coexistence and generate the observed species richness patterns at finer
111 spatial scales (Weber & Strauss, 2016; Pigot et al., 2018). How and why the distribution
112 of species changes across space and time has been the focus of intense debate in the
113 literature (e.g. Jackson & Overpeck, 2000; Sexton et al., 2009; Louthan et al., 2015).

114 Several factors can potentially shape the distribution of organisms and
115 consequently shape species coexistence (Hutchinson, 1957; Vamosi et al., 2009; Wisz
116 et al., 2013). Distinct speciation modes, for example, are linked to distinct predictions
117 regarding the patterns of coexistence between two closely related species. Sympatric
118 speciation assumes that two species will coexist since their emergence (Grossenbacher
119 et al., 2014), whereas allopatric speciation will produce geographically isolated species
120 (Kozak & Wiens, 2006) that can eventually expand their distributions and subsequently
121 coexist (Pigot & Tobias, 2015; Weber & Strauss, 2016; Pigot et al., 2018). In this case,
122 the time since divergence between lineages can play an important role in determining
123 coexistence patterns.

124 Biotic interactions and the intrinsic properties of organisms, such as their
125 dispersal ability, can also affect the process of geographic expansion, either accelerating
126 or preventing species coexistence over time (Johnson & Stinchcombe, 2007; Vamosi et

127 al., 2009; Lowe & McPeck, 2014; Jønsson et al., 2016; Weber & Strauss, 2016). From
128 an ecological perspective, the importance of competition in shaping coexistence is
129 based on the “principle of competitive exclusion”, which suggests that species
130 occupying similar ecological niches would not be able to coexist because they require
131 the same limited resources to survive (Hutchinson, 1957; Hardin, 1960). The outcome
132 of these ecological processes on an evolutionary time-scale could be character
133 displacement among populations or a pair of species (Brown & Wilson, 1956; Schluter,
134 2000), species sorting where only species with different ecological niches will coexist
135 (Anderson & Weir, 2021), or even the extinction of an entire lineage (e.g. Silvestro et
136 al., 2015). Indeed, the number of studies suggesting that competition is a relevant factor
137 in shaping the distribution of organisms at global and macroevolutionary scales has
138 rapidly increased (Gotelli et al., 2010; Pigot & Tobias, 2013; Silvestro et al., 2015;
139 Pigot et al., 2018). Pigot and Tobias (2013) for example, found that the coexistence of
140 closely related species of birds seems to be mediated by differences in their ecological
141 niche. On the other hand, other factors might play a role, and these same authors later
142 found that dispersal ability also determine how fast two species might expand their
143 distributions and coexist (Pigot & Tobias, 2015; Pigot et al., 2018). Dispersal is indeed
144 widely suggested to play a central role in the redistribution of organisms, contributing to
145 the colonization of new areas and range shifts, representing a potentially important
146 component driving coexistence dynamics (Lowe & McPeck, 2014; Jønsson et al., 2016;
147 Weber & Strauss, 2016).

148 Although biotic interactions and dispersal ability have been frequently invoked to
149 explain both spatial and temporal biodiversity patterns, the geographical scenario where
150 species thrive is another important aspect to be considered. Islands are widely known
151 for producing unique biodiversity patterns given their smaller size and geographic

152 isolation compared to continental settings (MacArthur & Wilson, 1967; Losos &
153 Ricklefs, 2009; Baeckens & Van Damme, 2020). Changes in body size like gigantism
154 and dwarfism are frequently reported in insular vertebrates ("island rule", Foster, 1964;
155 Van Valen, 1973; see also Benítez-López et al., 2021 but see Meiri, 2007). Patterns like
156 these are suggested to be the result of several mechanisms characterizing insular
157 systems, such as reduced predation, relaxed inter-specific competition and resource
158 limitation (Losos & Ricklefs, 2009; Baeckens & Van Damme, 2020; Benítez-López et
159 al., 2021). However, the consequences of these insular particularities on the coexistence
160 dynamics of species are less clear (Ricklefs, 2010; Pigot et al., 2018). On one hand, it is
161 feasible to expect that coexistence might be achieved faster on islands compared to
162 continents given that the first comprise smaller geographical limits and is usually
163 characterized by a relaxation of biotic constraints. On the other hand, islands harbor
164 populations that might be more likely to suffer stochastic extinctions or introgression
165 possibly erasing any signs of sympatry (Pigot et al., 2018).

166 Several other ecological, physiological, and behavioral aspects can also influence
167 species coexistence dynamics (Gaston, 2000; Buckley et al., 2012). Squamate reptiles
168 (i.e. lizards and snakes) are ectothermic animals and their distributions will frequently
169 be limited by their physiological requirements (Buckley et al., 2012; Vitt & Caldwell,
170 2014). As a result, their distributions can be strongly determined by climatic conditions
171 (e.g. Buckley et al., 2012). Lizards and snakes, however, comprise more than 10.000
172 species ranging across a wide spectrum of latitudes and biomes (Roll et al., 2017; Uetz
173 & Hosek, 2017). While the species richness of snakes shows the typical latitudinal
174 gradient similar to endothermic organisms, lizards show a pattern distinct from any
175 other tetrapod group, with a higher richness in Australia (see Roll et al., 2017).
176 Furthermore, although closely related, snakes and lizards differ greatly in their

177 morphology and in several aspects of their natural history (Sites et al., 2011; Vitt &
178 Caldwell, 2014). Generally speaking, snakes have a slower metabolism and lower
179 population density compared to lizards (Vitt & Caldwell, 2014); lizards comprise more
180 diverse diet habits, including insectivorous, carnivorous and even herbivorous species
181 (Pianka & Vitt, 2003; Meiri, 2008), whereas snakes are strictly carnivorous (Greene,
182 1997). This impressive diversity is actually an indication that species distributions in
183 squamates might not be regulated by the same processes, and that aspects not related to
184 climate might also play an important role in shaping species distributions (e.g. Algar et
185 al., 2013; Cunningham et al., 2015). *Anolis* lizards, for example, comprise a classic
186 example of squamate reptiles among which species coexistence is strongly determined
187 by interspecific competition (Losos, 2011).

188 To reveal the relevant factors shaping the coexistence dynamics of a diverse group
189 such as squamates, and whether snakes and lizards share or not these factors, we need
190 investigations across broader taxonomic and spatial contexts. Here we take this
191 approach by investigating the role of biotic interactions, dispersal ability and different
192 geographical settings in shaping the coexistence dynamics across closely related species
193 of squamate reptiles. To do that, we use a model-comparison framework to (1) evaluate
194 the main speciation mode (i.e sympatric or allopatric) in lizards and snakes; (2) test if
195 the tendency to geographically overlap over time increases in species that are
196 ecologically distinct, (3) have high dispersal abilities, and/or (4) occur on islands. Our
197 study is the first to explicitly model the coexistence dynamics of squamates over time in
198 broad temporal and spatial scales. On top of that, we take into account the possible
199 effects of different ecological and geographical scenarios in driving coexistence. Our
200 results provide insights into the factors shaping species distributions and the dynamics
201 of coexistence, contributing to a better understanding of the processes shaping

202 biological communities and, at a broader scale, of those that modulate the evolution of
203 biodiversity.

204

205 **METHODS**

206

207 **Closely related species pairs**

208

209 To explore coexistence dynamics in squamates, we used one of the most
210 complete molecular phylogenies (Tonini et al., 2016) to define a pool of species pairs
211 ("sister" species), representing the most closely related species in the maximum-
212 likelihood topology. Our pool included only species from well sampled genera (70% or
213 more of all described species of a given genus had to be in the phylogeny) and for
214 which the phylogenetic placement of species pairs was highly supported (equal to or
215 higher than 0.95). To calculate genus sampling, we followed the taxonomy of the
216 Reptile Database up to January 2017 (Uetz et al., 2017). We were able to identify 538
217 species pairs (161 of snakes and 377 of lizards).

218

219 **Geographical ranges**

220

221 To determine if species comprising a given species pair coexist, we used species
222 polygon range maps mostly from Roll et al. (2017). For an additional 20 species, whose
223 maps were not available in Roll et al. (2017), we used those provided by the IUCN Red
224 List Assessment. We used the range map provided by Birskis-Barros et al. (2019) for
225 the South American rattlesnake *Crotalus durissus*, given the outdated distribution for
226 this species in the previous two databases. From the 538 species pairs, we could not

227 obtain range maps for four pairs given that at least one of the species did not have a map
228 available.

229 From the 534 species pairs for which we had range maps, we excluded species
230 that occur in marine or mangrove environments (10 pairs) and terrestrial pairs where
231 species are separated by marine barriers (species occurring on different landmasses or
232 islands, see Pigot & Tobias, 2015) (those represent 57 pairs). The dispersal dynamics
233 characterizing these species pairs might potentially differ from those where species are
234 terrestrial and occur on the same landmass and would potentially add noise to our
235 analyses.

236

237 **Age since divergence**

238

239 To model coexistence over time, we used the age since divergence of each
240 species pair estimated by Tonini et al. (2016) as our temporal measurement.
241 Given that estimates of age since divergence can be highly uncertain, we randomly
242 chose 100 different phylogenies from those generated by Tonini et al. (2016) to obtain a
243 range of possible age estimates for our species pairs. It is important to mention that
244 these 100 phylogenies were generated using the same backbone molecular phylogeny
245 and, therefore, the relationships between species pairs remain the same, but the age
246 estimates differ (see Tonini et al. 2016 for details). Therefore, we incorporated in our
247 analyses 100 different age since divergence estimates for each species pair (see below).

248 To avoid including species pairs for which evolutionary history might have been
249 strongly influenced by extinction we set a divergence time limit to our species pairs. We
250 first took the median of the 100 ages since divergence estimates for each pair and kept
251 those pairs comprising a median equal to or lower than 20 million years ago. After all

252 curatorial work, our final pool comprised 448 pairs of species (132 of snakes and 316 of
253 lizards) that we used to investigate the coexistence dynamics in squamates (see
254 Appendix I). These 448 pairs span a wide diversity of taxonomic groups and
255 geographical areas representing the vast diversity observed in squamates (see Figure 1).
256 We also ran additional analyses using only those pairs for which the median of the age
257 since divergence was equal to or lower than 10 million years ago (124 of snakes and
258 243 of lizards), a more conservative way to include species pairs with respect to
259 potential loss of history to extinction.

260

261 **Geographical overlap**

262

263 We considered a species pair as sympatric or allopatric based on the spatial
264 overlap of their geographical ranges. We considered a pair as sympatric when more than
265 30% of the smaller species range overlapped with the range of the other species. We
266 also ran additional analyses considering a given pair as sympatric when the smaller
267 range overlapped more than 70%. These additional analyses allowed us to explore if our
268 results on the coexistence dynamics of squamates would differ depending on how we
269 define sympatry. We quantified geographic overlap using the Raster package in R
270 (Hijmans, 2019). We should note that we choose a simpler geographical categorization
271 for methodological purposes (see Statistical analyses), considering as “allopatric”
272 species pairs that might have been originated under processes such as vicariance,
273 parapatric speciation, or founder events (see Skeels & Cardillo, 2019).

274

275 **Geographical and ecological traits**

276

277 *Size of the geographical area*

278

279 To explore if the size of the geographical area affects the tendency by which
280 closely related species coexist over time, we categorized each species pair as occurring
281 on islands or continents. We considered as islands all geographically isolated land
282 masses smaller than Madagascar (the largest island considered). When the species
283 comprising a given pair occurred both on islands and continents, we considered the
284 geographical area as the one where both species occur. We did not have any cases
285 where both the species occurred on islands and continents.

286

287 *Ecological similarity*

288

289 To quantify how ecologically similar two species are and, thus, to explore the
290 importance of species interactions in affecting the tendency of closely related species to
291 coexist over time, we measured specimens deposited in several scientific collections
292 between the years of 2017 and 2019 (see supplementary methods). This massive data
293 collection allowed us to obtain measurements for more than 2000 specimens of lizards
294 and snakes comprising 300 and 152 species, respectively (150 and 76 sister pairs of
295 lizards and snakes; Appendix II and III). Therefore, we were able to obtain
296 morphological data for 47% and 57% of the pairs from our total pool (lizards and
297 snakes, respectively). On average, we were able to measure 6 specimens per species of
298 lizards and 5.7 specimens per species of snakes. For additional details on how we
299 determined the sex and the sexual maturity of the specimens see the supplementary
300 methods.

301 We focused on measuring morphological traits known to be associated with
302 different axes of the ecological niches of squamates. Additionally, we aimed to include
303 only males in our dataset as a way to decrease any noise caused by morphological
304 differences resulting from sexual dimorphism. Measurements for lizards comprised
305 snout-vent length (SVL), head length, width and height, jaw length, mid-body
306 circumference, the length of the humerus, ulna, femur and tibia, and the distance
307 between fore and hind limbs. Measurements for snakes comprised snout-vent length,
308 head length, width and height, mid-body circumference, tail length and eye diameter.
309 This dataset was combined with the morphological dataset for snakes of the family
310 Viperidae generated by Alencar et al. (2017), and with a few measurements for snout-
311 vent length taken from the literature (see Appendix II and III), all measurements from
312 adult males only.

313 To explore the role of species interactions in driving the tendency of species to
314 geographically overlap over time, we used two different metrics as proxies for
315 ecological similarity of a given species pair. First, we calculated the absolute difference
316 between the average of the log-transformed SVL of the species comprising each pair.
317 The larger the difference between the SVL, the less ecologically similar species are
318 expected to be (Wilson 1975; Ricklefs & Miles, 1994). We chose to use SVL as our
319 metric for body size given it is traditionally used by herpetologists as a proxy for size
320 (see Meiri, 2008). As a next step, we generated one morphospace for snakes and another
321 for lizards but excluding legless lizards, and a second one for all lizards including
322 legless lizards but excluding the distance between the fore and hind limbs measurement.
323 To generate these morphospaces we first size-corrected the morphological variables
324 (log-shape ratios) for each species by dividing each variable by the geometric mean
325 calculated for each species (see below) and log-transforming the resulting value (Price

326 et al., 2019; Friedman et al., 2020). The geometric mean was calculated for lizards as
327 the cube root of the product of species average SVL, mid-body circumference and
328 length of the limbs, and for snakes as the cube root of the product of species' average
329 SVL, tail length and mid-body circumference. We chose not to calculate the geometric
330 mean across all morphological variables because most of them are inclusive measures
331 of these dimensions of size (see Price et al., 2019). We chose to apply this size-
332 correction method because it allows us to produce a metric that preserves the allometric
333 component of shape (see Price et al., 2019). We performed phylogenetic principal
334 component analyses using the R package phytools (Revell, 2009; Revell, 2012) to
335 generate these morphospaces using the consensus phylogenetic tree from Tonini et al.
336 (2016). Using these morphospaces, we calculated the Euclidean distance between
337 species comprising each pair across all Phylogenetic axes combined. The larger the
338 euclidean distance, the less ecologically similar species are expected to be. In the end,
339 we had two proxies for ecological similarity, (1) differences in SVL and (2) the
340 Euclidean distance between species pairs within the morphospace.

341 To explore if the proxies for ecological similarity, that is, differences in SVL
342 and differences in shape (Euclidean distance) were correlated, we performed PGLS
343 analyses using ten phylogenetic trees from Tonini et al. (2016). These analyses
344 suggested that despite being significantly correlated in lizards (R^2 0.59 – 0.77, $p <$
345 0.05), differences in the SVL and Euclidean distances are not correlated in snakes ($R^2 <$
346 0.01, $p > 0.1$). In the subsequent analyses, we decided to use only the SVL differences
347 for lizards and keep both the differences in SVL and the Euclidean distance as proxies
348 for ecological similarity in snakes.

349

350 *Dispersal ability*

351

352 Despite often being considered a species trait, here we assess dispersal ability as
353 a trait characterizing a given species pair due to methodological reasons (see statistical
354 analyses below). To do this, we used two different metrics. First, we used the log-
355 transformed ratio between the average range size of each pair and the age since the
356 divergence of that pair. Range size can be a good proxy for dispersal ability because
357 larger ranges might reflect a higher ability of lineages to geographically expand (Brown
358 et al., 1996; Pigot et al., 2018). We decided to take into account the age since
359 divergence between species comprising each pair because older lineages might have
360 larger geographical ranges simply because they had more time to expand geographically
361 and not as a result of dispersion ability. Therefore, the ratio between range size and age
362 of divergence reflects the rate at which a given species pair was able to geographically
363 expand. We calculated this ratio 100 times for each pair using the different age
364 estimates obtained previously. As a next step, we used the average SVL for each pair.
365 Because larger animals might also have larger home ranges and/or territories (Brown et
366 al., 1996; Bonner, 2011), we expect that larger squamates might have higher dispersal
367 ability. It is important to note that the analyses using average SVL as a proxy for
368 dispersal ability included less species pairs compared to our first proxy given we
369 measured a smaller number of species than our total species pool (see above).

370 To explore if the two proxies were correlated with each other, we performed
371 PGLS analyses on the average snout-vent length and the average range size/age ratio,
372 using ten randomly sampled sets of the latter and the ten corresponding phylogenetic
373 trees from Tonini et al. (2016). Interestingly, all these analyses suggested that despite
374 being significantly correlated ($p < 0.05$), the relationships have either very low R^2 (0.06

375 – 0.08, for lizards) or moderate R^2 (0.14 – 0.18, for snakes). For this reason, we decided
376 to keep both proxies in our subsequent analyses (see below).

377

378 **Statistical analyses**

379

380 We explored the coexistence dynamics of squamates over time by using
381 different probabilistic models of species co-occurrence (Figure 2, Pigot et al., 2013,
382 2015). In this framework, the dynamic of coexistence is modelled as a constant rate
383 Markov process, and maximum likelihood is used to perform model fitting and
384 parameter estimates. In a general manner, the models allow us to calculate the
385 probability that a species pair exists in its current geographical state (i.e. allopatry or
386 sympatry) given their age since divergence and the parameters controlling the rates of
387 transition from allopatry to sympatry (σ) and from sympatry to allopatry (ϵ) (Figure 2,
388 see also Pigot & Tobias, 2015). Therefore, we were able to model how coexistence
389 possibly changed over time by using a given set of species pairs. We fitted four
390 different models to our dataset using the R package *msm* (Jackson, 2011): 1) allo-one-
391 way, which assumes that lineages diverged in allopatry and then undergo a transition to
392 sympatry ($\gamma = 1$, $\sigma > 0$, and $\epsilon = 0$); 2) symp-one-way, which assumes that lineages
393 diverged in sympatry and then undergo a transition to allopatry ($\gamma = 0$, $\sigma = 0$, and $\epsilon > 0$);
394 3) allo-two-way, assumes that lineages diverged in allopatry, become sympatric but
395 became allopatric again ($\gamma = 1$, $\sigma > 0$, $\epsilon > 0$); Symp-two-way, which assumes that
396 lineages diverged in sympatry, undergo a transition to allopatry but come back to
397 sympatry later ($\gamma = 0$, $\sigma > 0$, and $\epsilon > 0$).

398 A schematic workflow of the model comparisons we performed is presented in
399 Figure S1. First, we fitted all four models 100 times across species pairs of lizards and

400 snakes separately using their age since divergence obtained from 100 different
401 topologies (see above). We then evaluated how many times a given model was favored
402 over the others using the Akaike Information Criterion (Burnham & Anderson, 2002)
403 (see Table S1-S4). We considered the best model to be the one with the lowest AIC
404 value and with a ΔAIC higher than two. To evaluate the effects of geographical position
405 (island vs continent), ecological similarity (body size difference and euclidean distance)
406 and dispersal ability (ratio of range area and age, average body size) in shaping the
407 coexistence dynamics of squamates, we ran another set of analyses comparing all four
408 models but also including the allo-one-way and the allo-two-way models with each
409 candidate factor as a covariate of σ (the parameter describing the transition rate to
410 sympatry). We decided not to include the Symp-two-way model with candidate factors
411 as covariates in our model comparison because transitions to coexistence occur at a
412 distinct stage in the symp-two-way model relative to those in the allopatric models. In
413 summary, we performed model comparisons across the six models (allo-one-way,
414 symp-one-way, allo-two-way, symp-two-way, allo-one-way with covariate, allo-two-
415 way with covariate) five times for snakes and four times for lizards, including one
416 distinct candidate driver in each of them (Table S1-S4, see summary in Figure S1). We
417 performed model comparisons separately using each candidate factor as they frequently
418 involved distinct species pairs datasets (e.g. morphology based proxies comprise fewer
419 species pairs than range size, for example).

420 When candidate drivers significantly improved a model over the others, we
421 quantified the hazard ratio to evaluate the direction of the relationship between
422 transition rates to sympatry and the driver of coexistence (Table S5). To illustrate how
423 transition rates to sympatry are affected by the drivers of coexistence, we extracted
424 estimates of transition rates to sympatry under the best models selected and the

425 corresponding hazard ratios for different values of the drivers (Figure 3). We performed
426 posterior predictive simulations to evaluate how well the best models could actually
427 predict the empirical data (see supplementary methods).

428

429 **RESULTS**

430

431 For our main dataset that considered sympatric species pairs as those with at least
432 30% of the smallest distribution overlapping and included pairs that diverged 20 million
433 years ago or less, 37% and 48% of the species pairs are sympatric in snakes and lizards,
434 respectively (Table S6). Proportions were very similar when considering only the
435 species pairs with a median age since divergence of less than 10 mya (see Table S6).
436 However, as expected, the number of sympatric pairs decreased when we considered as
437 sympatric only those pairs with more than 70% of the smallest distribution overlapping
438 (Table S6). Regardless of the dataset, however, lizards consistently show a higher
439 proportion of sympatric pairs compared to snakes (Table S6). In general, sympatric
440 pairs tend to be older than allopatric pairs among snakes (Table S7). In lizards,
441 however, sympatric and allopatric species pairs have very similar ages of divergence,
442 with sympatric pairs still being slightly older across datasets comprising pairs that have
443 diverged 20 mya or less (see Table S7).

444

445 Coexistence dynamics in squamates

446

447 *Model selection without covariates*

448 When comparing only the four models without adding any candidate traits that
449 could potentially be driving coexistence dynamics, the “allo-two-way-model” was

450 considered the best model for about 75% of the age datasets analyzed for snakes either
451 when considering species pairs that diverged less than 20 or 10 mya (Table S1-S2).
452 These results suggest that snakes generate species mainly via allopatric speciation with
453 transitions to sympatry over time and back to allopatry as lineages become older. On the
454 other hand, by comparing the four models without adding the covariates, we could not
455 recover a unique best model for lizards (Figure S1-S2). The symp-two-way-model and
456 the allo-two-way-model are equally likely, which suggests that geographical overlap in
457 lizards changed considerably through time. Additionally, no best model was detected
458 when performing model comparison with an overlap cut-off of 70% either in lizards or
459 snakes (see Table S3-S4).

460

461 *Model selection with the geographical setting as covariate*

462

463 Being on an island or continent seems to be an important driver of species
464 coexistence in snakes but not necessarily in lizards. When considering the two
465 additional models that include the geographical setting as a covariate on the transition
466 rate to sympatry, model comparisons suggested that the allo-two-way model with the
467 covariate was the best model across all age datasets in snakes, regardless of only
468 including younger pairs or not (Table S1-S2). According to this model, transition rates
469 to sympatry substantially increase in species pairs of snakes occurring on islands
470 compared to those occurring on continents (Figure 3, Table S5). When performing
471 model comparison under the 70% overlap cut-off, the allo-two-way model with the
472 covariate was still recovered as the best model across 76% of the age datasets in snakes.
473 However, no single best model was recovered when considering only the younger pairs
474 (Table S3-S4), although the model with geographical setting as covariate was still

475 among the best models (it was tied with another model in 99 out of 100 comparisons).
476 In contrast, no best model was selected for lizards and, therefore, we do not have
477 evidence that being on an island or continent is relevant in driving their coexistence
478 dynamics (Table S1-S4). It is also worth mentioning that, in general, the model that
479 includes geographical setting as a covariate was frequently not among the best tied
480 models in lizards, with the exception of when considering the 70% overlap threshold
481 and species pairs that diverged less than 10 mya (33, 26, 56, or 97 out of 100 model
482 comparisons depending on the dataset, see Tables S1-S4).

483

484 *Model selection with ecological similarity as covariate*

485

486 Ecological similarity seems to be an important driver of species coexistence in
487 snakes but not in lizards. Model selection suggested that the allo-two-way model with
488 body size difference as the covariate was the best model across all age datasets for
489 snakes (all 100 model comparisons), regardless of whether the data were restricted to
490 younger pairs (Table S1-S2). According to this model, transition rates to sympatry
491 increase with increasing differences in body size between species pairs (Figure 3, Table
492 S5). Despite always suggesting the same positive relationship, transition rates to
493 sympatry and the hazard ratio have unreliably high values when estimated using ages of
494 divergence extracted from some phylogenies (Figure 3, Table S5). This suggests that
495 model fitting might have failed to converge in these datasets. However, simulations
496 using parameter estimates under the best model are still able to recover proportions of
497 sympatric and allopatric pairs similar to the empirical data (see below). When analyzing
498 species pairs of snakes under the 70% overlap cut-off no model was preferred, but the
499 model with body size difference as the covariate tied with another model about 60% of

500 the time (Table S3-S4). In contrast, we did not recover a best model when adding the
501 differences in shape (measured by the Euclidean distance, see Methods) of species pairs
502 as the covariate on transition rates to sympatry in snakes, although this model is
503 frequently tied with other models (see Tables S1-S4). Additionally, we did not find
504 strong evidence of ecological similarity being an important driver of coexistence in
505 lizards (Table S1-S4). It is important to mention, however, that although we did not
506 recover a best model for lizards, the model with body size difference as the covariate is
507 among the best models in several of the model comparisons performed (Table S1-S4).

508

509 *Model selection with dispersal ability as covariate*

510

511 Contrary to the analyses above, dispersal ability seems to be a relevant driver of
512 coexistence dynamics in lizards but not snakes (Table S1-S2). Model selection
513 suggested that the allo-two-way model with the ratio of range size and age as the
514 covariate was the best model across more than 80% of the age datasets of lizards when
515 considering the overlap threshold of 30%, regardless of whether only younger pairs
516 were included (Table S1-S2). According to this model, transition rates to sympatry
517 increase with faster rates of geographic expansion (i.e. the larger the ratio between
518 geographical range and time; Figure 3, Table S5). We did not recover a single best
519 model when analyzing species pairs of lizards under the 70% overlap cut-off (Table S3-
520 S4), but the model with dispersal as a covariate was usually among the tied models
521 (above 80% of the comparisons). When performing model selection with mean body
522 size (the other proxy for dispersion ability) as the covariate, we recovered the allo-two-
523 way model that included the covariate as the best model for 57% of the age datasets but
524 only in our main analyses (30% overlap and all species pairs, Table S1). Surprisingly,

525 however, according to this model transition rates to sympatry increase the smaller the
526 species (Figure 3, Table S5). We did not find a single best model for these model
527 comparisons using species pairs of snakes but models with dispersal proxies as
528 covariates usually tied with other models (Table S1-S4).

529

530 Posterior predictive simulations

531

532 For all best models with covariates selected in our main analyses (30% overlap
533 between species and including all species pairs), simulated proportions of sympatric
534 pairs frequently recovered the empirical proportions (Figure S2).

535

536 **DISCUSSION**

537

538 In lizards and snakes, neither time or sympatric speciation alone can explain the
539 coexistence patterns observed among extant species. On the other hand, by performing
540 extensive data collection and comparing statistical models, we found evidence for
541 completely distinct drivers underlying the coexistence dynamics of these two closely
542 related groups. In general, our results suggest that the species' geographical setting,
543 ecologically similarity, and dispersal ability might play different roles in shaping the
544 coexistence dynamics within each taxonomic group analyzed.

545 By taking a first look at the patterns of geographical overlap, we found that most
546 species pairs of snakes are allopatric. Allopatric speciation is indeed the rule across
547 vertebrates, with many vertebrate groups having more allopatric than sympatric sister
548 species (Barraclough & Vogler, 2000; Pigot & Tobias, 2015; García-Navas et al., 2020;
549 see review in Hernández-Hernández et al., 2021). In lizards, however, allopatric and

550 sympatric pairs had similar proportions. Allopatric pairs of snakes tend to be younger
551 than sympatric ones, which conforms to a scenario where coexistence would be
552 achieved with time. Indeed, without adding any covariates, the coexistence dynamics in
553 snakes are best described by allopatric speciation with lineages eventually becoming
554 sympatric as time goes by and becoming allopatric again as they get older (allo-two-
555 way model, Table S1-S2). In lizards, on the other hand, sympatric species and allopatric
556 pairs tend to have very similar ages, with allopatric pairs being older in some cases
557 (Table S7). This result might suggest two scenarios: (1) sympatric speciation plays an
558 important role in the diversification of lizards; (2) allopatric speciation is still the rule,
559 but time alone does not explain the coexistence dynamics of lizards. In any case, we
560 indeed could not recover a single best model in the first set of model comparisons for
561 the group (Table S1-S4). It is worth noting that when a single model is chosen in
562 lizards, the sympatric model is the one selected (19 vs 1, Table S1), and when two
563 models are equally likely (80% of the time), the sympatric model is also among them
564 (Table S1).

565 Taken together, these first results suggest that lizards might be more
566 heterogeneous and have more dynamic distributions compared to snakes, either because
567 their lineages are influenced by different processes and/or because their distributions
568 change more through time. A wider array of processes acting simultaneously could
569 potentially mask coexistence signals when we include all species in the same category
570 “Lizards”. Indeed, lizards occurring in the same islands can show completely distinct
571 patterns of diversification. At the Socotra Archipelago, for example, closely related
572 species of the genera *Hemidactylus* and *Haemodracon* show sympatric distributions
573 with marked differences in body size, whereas those of the genus *Pristurus* tend to be
574 allopatric or parapatric with no apparent divergence in body size (see García-Porta et

575 al., 2016). Furthermore, species richness can indeed be achieved via distinct pathways
576 in distinct lizard clades and geographic regions. High species richness is associated with
577 low functional divergence in agamids and gekkoes but with high functional diversity in
578 varanids and scincids (Skeels et al., 2020). Exploring whether distinct clades are also
579 characterized by distinct coexistence dynamics might be an interesting next step.
580 However, we would need a much higher number of phylogenetically well-supported
581 species pairs within each of the distinct clades to explore group-specific coexistence
582 dynamics.

583 When adding covariates to the transition rates to sympatry, the allo-two-way
584 model is frequently recovered as the best model across the analyses for which we were
585 able to recover a single best model. In contrast to previous findings in birds (Pigot et al.,
586 2018), islands seem to promote species coexistence in snakes. Surprisingly, however,
587 this effect was not evident in lizards. In other words, the model with the geographical
588 setting as covariate does not have higher support compared to those without the
589 covariate in lizards. Indeed, in this set of analyses for lizards, ties were mainly between
590 the allo-two-way and symp-two-way models that lack covariates (Table S1). In general,
591 snakes have a slower life history and lower energetic demands compared to lizards
592 (Pough, 1973; Vitt & Caldwell, 2014). Therefore, resources on islands might appear
593 less scarce for snakes than lizards, potentially allowing snakes to more easily coexist in
594 insular environments given the relaxation of some biotic constraints (e.g. predation, and
595 perhaps less intense competition) and the smaller geographical limits of islands
596 compared with continental settings. Lizards, on the other hand, have high population
597 densities on islands (Novosolov et al., 2015) and the resultant scarcity of resources
598 might lead to much more intense competition. Hence, the smaller geographical limits

599 would not increase coexistence in insular lizards at least when compared with
600 continental settings.

601 Species interactions also underlie species coexistence in snakes, and divergence
602 in body size (but not shape) seems to be the most likely route to avoid competition and
603 promote coexistence, similar to what has been suggested for birds (Pigot et al., 2018).
604 On the other hand, we found no definitive or clear evidence that ecological similarity is
605 a relevant driver of species coexistence in lizards. For 99% of the time when we had
606 more than one best model (a tie) the model involving ecological divergence (complex-
607 allo-two-way) was among them for lizards (Table S1). The prediction that the likelihood
608 of coexistence increases with increasing the ecological difference between species,
609 assumes that some species pairs would accumulate more morphological differences
610 allopatrically allowing them to coexist faster than others (i.e. species sorting, Grant,
611 1972; Davies et al., 2007). Although we did not find definitive support for this
612 prediction in lizards, morphological divergence could still be driving the coexistence
613 dynamics at the local scale. If this is the case, we would expect that sympatric
614 populations of a given species pair would be more morphologically distinct compared to
615 allopatric populations of these same species (character displacement, Brown & Wilson,
616 1956; Davies et al., 2007). We might not have been able to capture these smaller-scale
617 differences given our large-scale approach and goals. A fruitful next step would be to
618 apply recently developed and promising frameworks to detangle the role of species
619 sorting and character displacement in speciation and species coexistence dynamics (see
620 Anderson & Weir, 2021), and to increase the intra-specific morphological sampling
621 allowing us to compare morphological divergence at the population-level.

622 Even though competition has widely been seen as an important factor shaping
623 community structure (e.g. Darwin, 1859; Webb et al., 2002; Cavender-Bares et al.,

624 2009), a lack of strong evidence of competitive interactions shaping trait-divergence has
625 also been suggested (e.g. Meiri et al., 2011; Stuart & Losos, 2013; Shi et al., 2018,
626 Slavenko et al., 2021). Slavenko et al. (2021) suggested that environmental filtering
627 might be more important in driving morphological divergence in lizards than
628 competitive interactions, which could potentially explain why we did not find clear
629 evidence for morphological differences mediating coexistence dynamics in lizards.
630 Another possibility is that morphological divergence could be more relevant in some
631 geographical regions than others or within some groups of lizards (see Skeels et al.,
632 2020). Competition might be more prevalent in climatically stable areas (Dobzhansky,
633 1950; MacArthur, 1969; Henriques-Silva et al., 2019) or regions with lower resource
634 availability and, therefore, morphological divergence could be an important driver of
635 coexistence at lower compared with higher latitudes or on islands compared with
636 continents (e.g. García-Porta et al., 2016), respectively.

637 In contrast to what we found for competitive interactions, dispersal ability
638 (measured by the ratio between range size and age of divergence) seems to be a relevant
639 driver of species coexistence in lizards but not necessarily in snakes. It is worth
640 mentioning that our dispersal metric that uses range size/age has its limitations and
641 assumptions. For example, it is thought that species might both start and go extinct with
642 smaller range sizes (Foote, 2007). Hence we might be pulling together species at very
643 different stages which might mask the potential effect of dispersal and perhaps explain
644 the lack of dispersal effects in snakes. By restricting the time window of analysis, this
645 problem might be ameliorated but not explicitly taken into account. However, the lack
646 of an association is still present in snakes when considering species pairs that diverged
647 less than 10 Mya.

648 Lizards indeed have been suggested to have comparatively higher dispersal
649 abilities than snakes, at least regarding long-distance dispersal to oceanic islands (see
650 Pitta et al., 2013). It is important to note, however, that we are not able to disentangle
651 between the ability to move across geographical space and the ability to establish
652 populations in new geographical areas (see Jønsson et al., 2016), as we considered both
653 as being part of the “dispersal ability” of species. Simply being more mobile across
654 space would not necessarily mean that species would successfully establish populations
655 in new geographical areas, possibly allowing species coexistence. This scenario has the
656 potential to be especially true for snakes, for which our results suggest that competitive
657 interactions are relevant drivers of species coexistence. Therefore, in snakes, only those
658 species that are different enough might be able to rapidly coexist, even if others have
659 high dispersal abilities. The establishment of populations, and consequently coexistence
660 among species, might also be compromised if not enough time has elapsed for strong
661 reproductive barriers to emerge and prevent populations from fusing (Weir & Price,
662 2011). The interaction between dispersal and competition, as well as between
663 competition and geographical setting, in driving species coexistence deserves further
664 investigation (see Lowe & McPeck, 2014; Jønsson et al., 2016). Indeed, the statistical
665 framework to explore the interaction between coexistence drivers is already available
666 (Pigot et al., 2016, 2018). However, we would need a much higher number of
667 phylogenetically well-supported species pairs, as well as their morphological
668 information to be able to properly investigate these questions.

669 Despite being favored in some of the model comparisons, models with mean
670 body size as the covariate on the transition rates to sympatry suggested that the smaller
671 the lizard the higher these transition rates. This might look unexpected given that both
672 proxies for dispersal ability (ratio between range and age, and body size) were

673 positively, despite weakly, correlated (see Methods). However, the body size dataset
674 comprises a much smaller number of sister pairs compared to the range and age ratio
675 dataset, which could explain the differences in the coexistence dynamics depicted by the
676 models.

677 On the other hand, we cannot rule out the possibility that the preconception that
678 larger species would be better dispersers might not be totally true for lizards. Going
679 further, the reason for a negative relationship between body size and the transition rates
680 to sympatry could be interpreted in light of the well-known link between body size and
681 specific axes of the ecological niche in animals (Peters, 1986; Meiri, 2008; Clarke,
682 2021). Contrary to what has been suggested for several other organisms, Costa et al.
683 (2008) found that body size is negatively related to dietary niche-breadth in predatory
684 lizards and, therefore, the diversity of prey consumed decreases as body size increases.
685 Furthermore, several small lizard species are insectivorous (Pianka & Vitt, 2003) and
686 might face less severe pressures when dealing with the scarcity of food resources
687 compared to larger species that may rely on more limited food availability. This, in turn,
688 might enable smaller species to share the same resources and coexist. Although some
689 large bodied species of lizards are herbivorous, meaning that their food might be readily
690 available in some environments, the higher total metabolic rate of larger animals also
691 requires a greater caloric intake (Pough, 1973). Coupled with that, small insectivorous
692 lizards can be more mobile than larger herbivorous due to the higher energetic food
693 taken by the first (Pough, 1973). All of these factors could help to explain a higher
694 incidence of coexistence over time in smaller lizards.

695 Going further, the relative importance of each coexistence driver in distinct
696 stages of the coexistence process is an aspect that deserves to be explored in squamates.
697 As found by Pigot et al. (2018), patterns of narrow geographic overlap in birds seem to

698 be driven by dispersal abilities and age, whereas wider coexistence patterns are mainly
699 driven by ecosystem productivity and niche-divergence. For several of the analyses
700 performed here, especially when considering as sympatric the species pairs with a
701 geographic overlap higher than 70% of the smallest distribution, model comparisons
702 were not able to choose between models. This probably occurs because using the 70%
703 cut-off inevitably decreases the number of sympatric pairs, probably affecting the
704 ability of these analyses to discern between models. Therefore, the addition of more
705 well-supported species pairs coupled with their morphological information is essential
706 to detangle between the differential drivers of species coexistence in distinct moments
707 in the past.

708

709 **Conclusions**

710 This study shows that lizards and snakes, although closely related, differ greatly
711 in the drivers of species coexistence. Speciation seems to predominantly occur via
712 allopatric speciation in snakes. Lizards, on the other hand, seem to be more
713 heterogeneous and have more dynamic distributions, which likely prevented us from
714 recovering a single best model without the addition of covariates (see Results). In
715 snakes, species that occur on islands or have different body sizes are more likely to
716 coexist. In contrast, lizard species are more likely to co-occur when they have higher
717 dispersal abilities.

718 Indeed, it has been widely shown that lizards tend to exhibit unique diversity
719 patterns that frequently do not follow the “rules” that usually apply to snakes or other
720 vertebrate groups (Meiri, 2007; Powney et al., 2010; Roll et al., 2017; Novosolov et al.,
721 2018). These differences might have profound consequences either for community
722 structure and lineage diversification, and care should be taken when analyzing these two

723 taxonomic groups together (see also Slavenko et al., 2019; Whiting & Fox, 2020).
724 Beyond this, our results emphasize that when analyzing biogeographical,
725 macroecological or macroevolutionary patterns and processes, one should take into
726 account not only the geographical scenario but also who these organisms are (see also
727 White, 2016; Skeels et al., 2020). It is the interaction between where and who that will
728 ultimately shape biodiversity patterns.

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1033 **DATA AVAILABILITY**

1034 Data used in this study are part of the supplementary material or have been published
1035 elsewhere.

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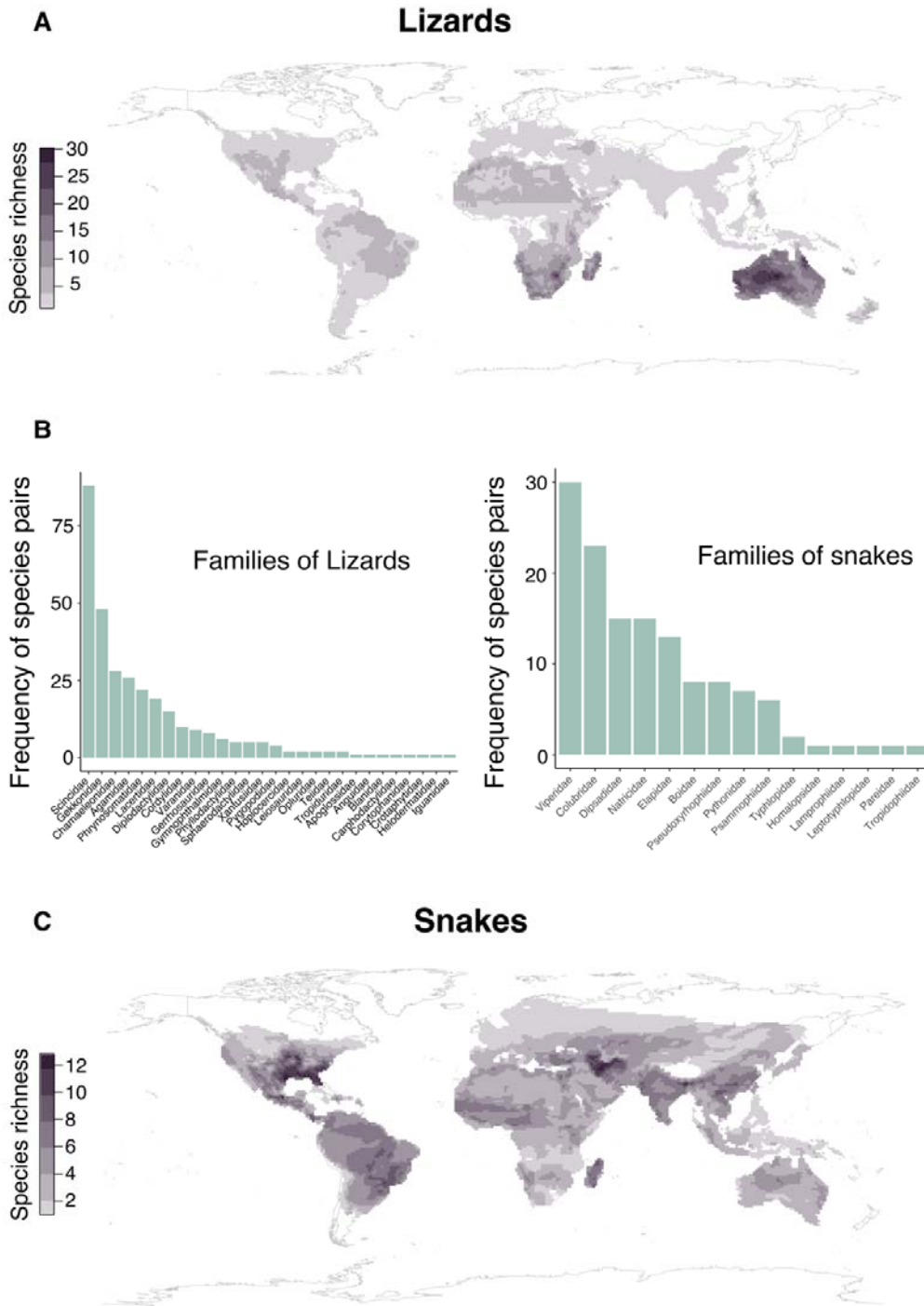
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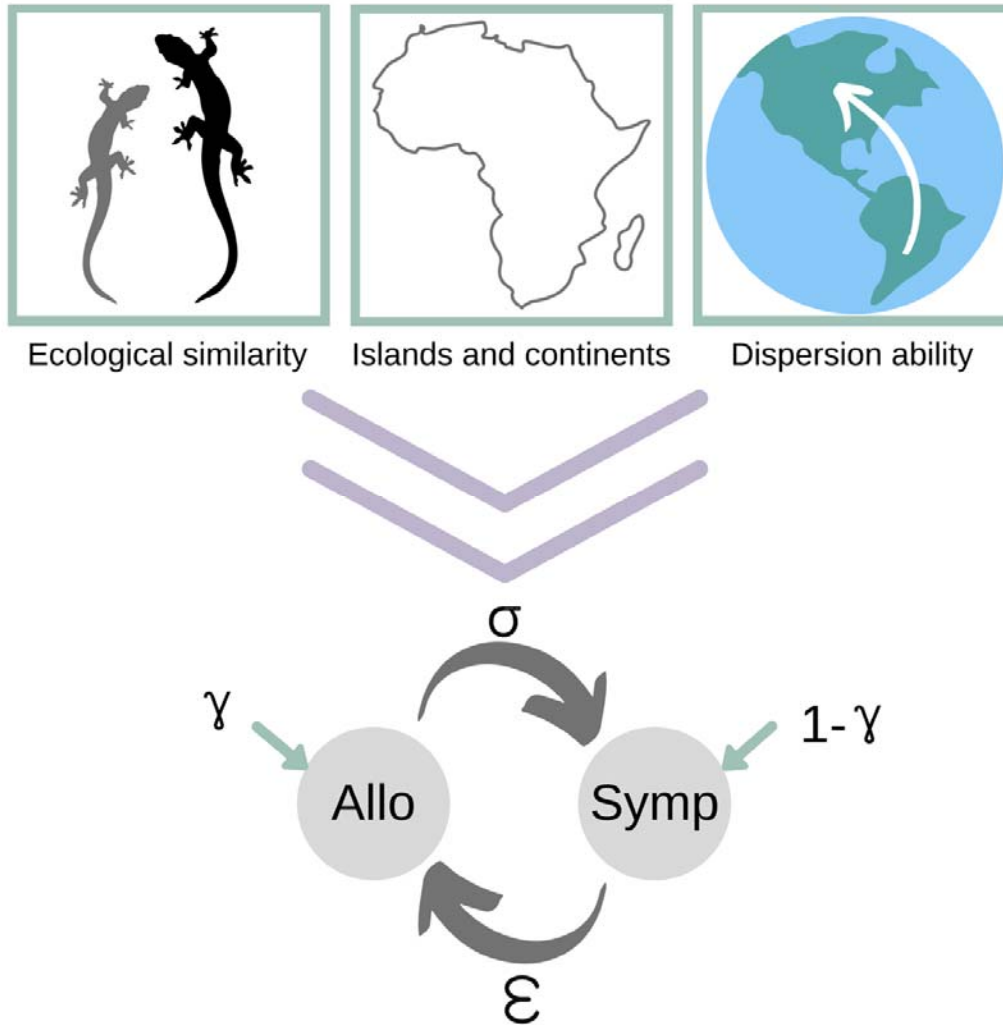
FIGURE LEGENDS



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1060 **Figure 1.** Species diversity analyzed in the present study across geographical regions (a,
 1061 c) and the taxonomic diversity of the species pairs (b) of lizards and snakes included in
 1062 our analyses.

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1065 **Figure 2.** Summary of the statistical models compared in the present study and their

1066 parameters. γ = relative frequency of allopatric speciation, σ = transition rate from

1067 allopatry to sympatry, ϵ = transition rate from sympatry to allopatry. We included

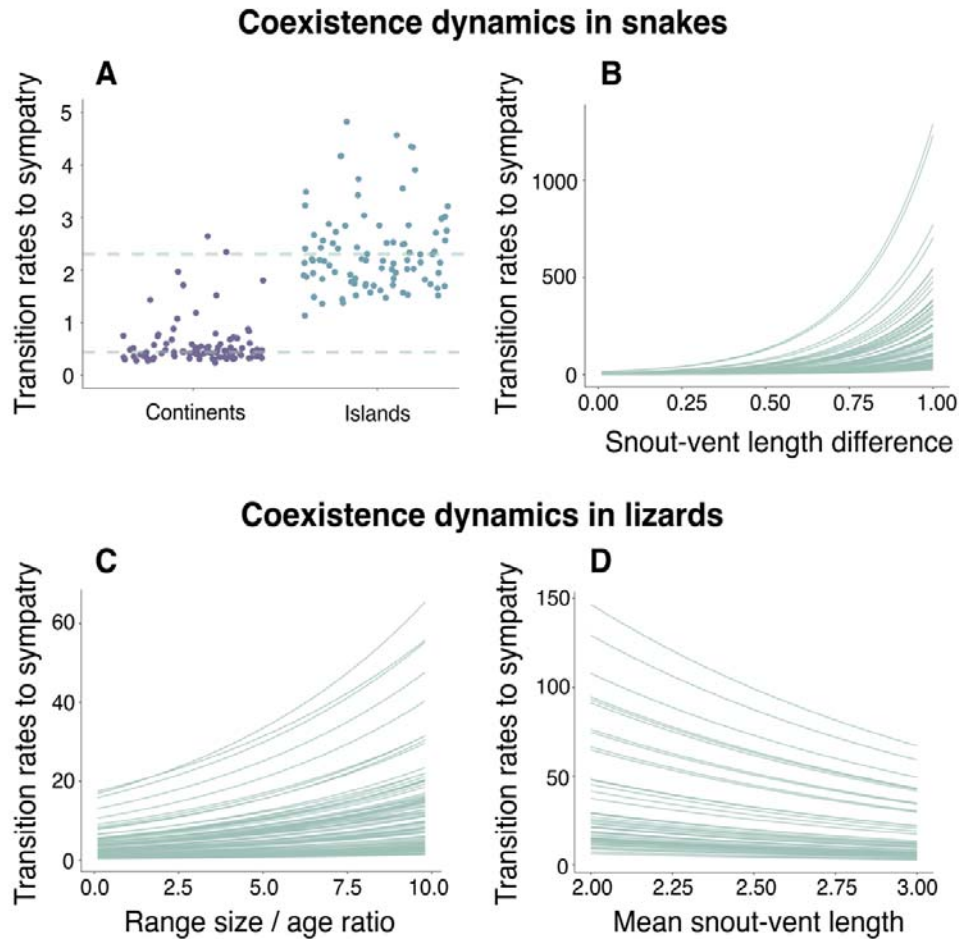
1068 ecological similarity (i.e. body size and shape differences), occurrence on islands or

1069 continents, and the dispersion ability (i.e. range size/age ratio and mean body size)

1070 separately as covariates on the transition rate to sympatry. Modified from Pigot &

1071 Tobias (2015).

1072



1073

1074 **Figure 3.** Estimates of transitions rates to sympatry relative to (a) species pairs
1075 occurrence on islands or continents, (b) snout-vent length difference, and (c) dispersal
1076 ability (range size / age ratio and mean snout-vent length), under the best model selected
1077 for snakes (a, b) and lizards (c, d). Multiple dots and lines represent estimates when
1078 using distinct age datasets (see Methods). Dashed lines in panel (a) represent medians of
1079 transition rates taken across all estimates. Given the extremely high values of 12 of
1080 these estimates (1 continent and 11 island), we excluded these from the plot for
1081 visualization purposes.

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