

Regularities in species niches reveal the World's climatic regions

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Although classifications of the Earth's climates date back to the ancient Greeks, the climatic regions shaping the distribution of animals remain poorly resolved. Here we present a classification of global climates based on regularities in realised niches of 3657 amphibians, 7204 reptiles, 10684 birds and 4574 mammals. We found 16 main climatic regions that are mostly consistent across groups and previous plant expert-based classifications, confirming the existence of major climatic restrictions for life. The results also suggest that differences among groups likely relate to their particular adaptations and dispersal capabilities. We further show how the integration of species niche classifications with geographical information provides valuable information on potential mechanisms shaping the climatic regions. Our climate classification has applications in several disciplines, including conservation planning and ecological and evolutionary studies.

INTRODUCTION

Climate governs the basis for life on Earth. Besides historical contingencies and geographical barriers, abiotic conditions determine species ranges [1–3] and derived diversity patterns [4, 5]. On a global scale, distinctive climatic regimes impose generalised restrictions, leading to the formation of species pools adapted to them and ultimately to the generation of biomes [6]. Identifying the boundaries of these climate regimes is, therefore, a fundamental challenge to understand how life organizes on Earth.

Already Pythagoras proposed a classification of climate regimes of the known world in the sixth century BC [7]. However, it was not until the 19th century when geographers laid the foundations for such classifications [8]. By that time, researchers noticed the close relationship between the distribution of various life forms, especially vegetation types, and climate [8]. For instance, Köppen built his long-standing climate classification from pioneer plant classifications, assuming that vegetation forms carry information about climatic conditions [9, 10]. This assumption has received considerable support [11], and the Köppen classification system is widely used nowadays as the standard classification of climates in a range of disciplines, including climatology [12], geography [13], conservation planning [14], and ecology [15]. However, the fact that plant species are good indicators of general climatic conditions does not necessarily imply that such conditions restrict the distribution of other organisms in the same manner. If different taxa have different climatic adaptations, the boundaries defining climate types will vary among them. Following Thornthwaite [10], the “truly active factors” describing a climate type may vary among organisms. Thus, while Köppen's climate classification can indicate the active climatic factors for plants, it remains unknown whether they are also appropriate for other organisms.

Despite several attempts to refine or propose alternative climatic regions [16–19], quantitative studies defining climatic regions for other organisms are still lacking.

The current information on species distributions and global climatic variables, together with recent advances in niche modelling and classification techniques provide an unprecedented opportunity to identify the climatic boundaries shaping the distribution of faunas and floras across the globe. The last decades have witnessed a tremendous collective effort to record occurrences of a large number of species [20], which has resulted in comprehensive datasets with the distributional ranges of several groups [21–23]. Also, data on climatic variables at a global scale have been developed at high spatial resolutions [24, 25]. This information allows to characterise the realised climatic niches of diverse species and to find regularities among them. For example, projecting these realised climate niches into a climatic space [26] should, if climatic boundaries exist, reveal co-occurring groups of species across particular portions of the climatic space. Thus, identifying these portions, or niche domains, should uncover the main climatic boundaries shaping the organization of life (Fig. 1).

Besides climate shaping niche domains, dispersal barriers and historical contingencies may also influence their shape [3, 27, 28]. Therefore, similar climates may have different effects across geographic regions [29]. For instance, while a given climate may lead to specific species pools in some parts of the Earth, the same climate in other parts of the Earth may not hold specific species pools. Such lack of specific species can occur, for example, because the required adaptations have not appeared [30], the adapted species have been not able to disperse [31], or the area is too small to hold large species pools [32]. Thus, studying the signature of these historical and geographical processes, the geographical signal for short, in niche domains can provide valuable information about the potential mechanisms behind them and their associated climatic regions.

Here we explore the global climate regions of Tetrapoda by characterising the climatic niche domains of amphibians, birds, mammals and reptiles. Tetrapoda

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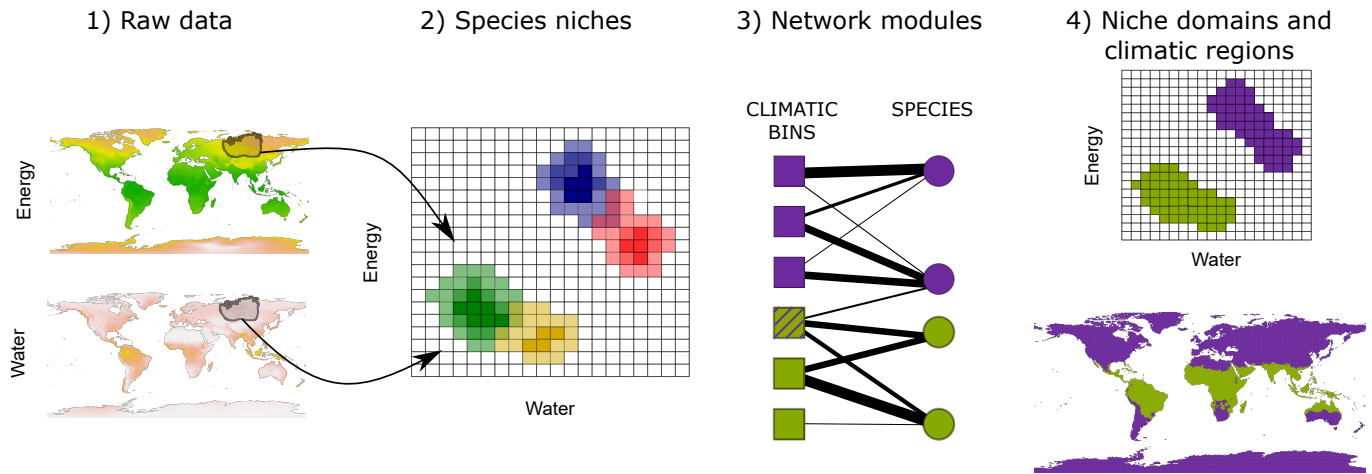


FIG. 1: Workflow to identify niche domains and climatic regions. Using the climatic conditions a given species experiences within its range (1), we project the species's niche into a climatic space discretised in an optimal number of bins (Appendix S1) (2). We translate the binned data into a weighted bipartite network, where climatic bins and species form the nodes and the probabilities of finding the species in the bins form the weighted links (3). Using a network community detection algorithm, we identify domains of the climatic space with similar species (4, upper). The climatic conditions defining these domains delineate the corresponding climatic regions of the Earth (4, lower). The striped climatic bin is linked to species classified in both climatic domains and, therefore, it represents a diffuse transition with low specificity.

84 is a well-suited group for our purpose. First, comprehensive
 85 databases are available, including the distributional
 86 ranges of most species in the group [21–23]. Second,
 87 the different classes within Tetrapoda possess diverse
 88 capabilities to disperse and withstand abiotic conditions.
 89 Therefore, we can investigate if various capabilities influ-
 90 ence climatic niche domains, and possibly generalise the
 91 climatic regions to other groups. Third, there is accumu-
 92 lated evidence on the main climatic factors controlling
 93 the distribution of these species, which simplifies the se-
 94 lection of appropriate climatic variables. In particular,
 95 the distribution of tetrapods is strongly determined by
 96 water and energy aspects of climate [4, 33–37]. Finally,
 97 researchers study Tetrapoda species in several disparate
 98 fields – from animal husbandry [38] to ecological [39] and
 99 evolutionary studies [40] – where a description of their
 100 climatic regions can be especially useful.

101 In our classification approach, we first approximate the
 102 realised niche of each species as the probability of finding
 103 the species across a two-dimensional space that repre-
 104 senting water and energy aspects of climate (Fig. 1). We
 105 then use a community-detection algorithm from network
 106 theory to simultaneously find portions of the climatic
 107 niche space holding similar species, the niche domains,
 108 and the species grouped into these domains. Mapping
 109 back to the Earth's surface gives for each climatic niche
 110 domain a climatic region. We then examine the transi-
 111 tion zones and the geographical signal in the climatic re-
 112 gions. The novel climatic regions confirm the existence of
 113 generalised climatic constraints across life forms. There-
 114 fore, the climatic regions provide valuable information
 115 for conservation and ecological and evolutionary studies

116 of Tetrapoda in particular and animals in general.

117 RESULTS

118 Major climatic niche domains of Tetrapoda

119 We first identified the niche domains of each Tetrapoda
 120 class independently. We calculated the proportion of ob-
 121 servations of each species within each bin of a climatic
 122 space defined by potential evapotranspiration (PET) and
 123 annual precipitation (AP; Fig. 1, Methods and Appendix
 124 S1). We represented this data as a weighted bipartite
 125 network where climatic bins and species form two dis-
 126 junct sets of nodes, and the probabilities of finding the
 127 species in the bins form the link weights. Using a hierar-
 128 chical network clustering algorithm [41, 42], we obtained
 129 groups of climatic bins holding similar species (i.e. niche
 130 domains) and the species most associated with them.

131 We found similarities among Tetrapoda classes in the
 132 detected niche domains, but also observed some differ-
 133 ences (Fig. 2). For instance, the number of major do-
 134 mains with 50 or more species in the lower hierarchical
 135 level is similar across Tetrapoda classes, ranging from 13
 136 to 15. However, mammals and birds show a domain of
 137 low energy, whereas reptiles present some domains across
 138 arid conditions, that is with elevated energy inputs and
 139 low water availability (Fig. 2). These differences seem
 140 to be related to the particular adaptations of each group
 141 to withstand climatic conditions. Nevertheless, the clas-
 142 sification of most domains was largely congruent across
 143 classes, and hence we classified the climatic space of the

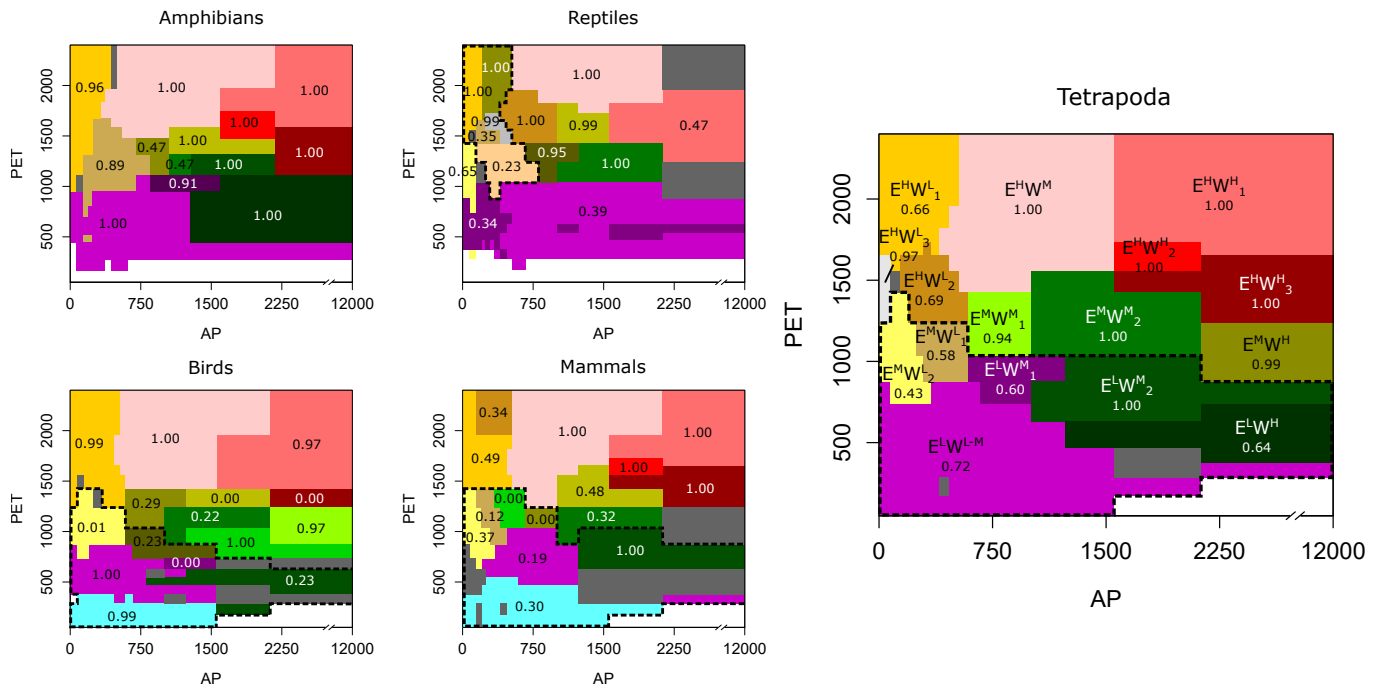


FIG. 2: **Tetrapoda niche domains across the climatic space.** The climatic niche domains of each group shown across a space defined by potential evapotranspiration (PET) as a surrogate of energy and annual precipitation (AP) as a surrogate of water inputs. Tetrapoda superclass domains labelled so that E and W represent energy and water, respectively, and superscripts H, M and L mean high, medium and low, respectively. Numerical subscripts differentiate domains of similar climates. Bootstrap support between 0 and 1. The dotted line represents the domains at the highest hierarchical level. Domains formed of less than 50 species coloured in dark grey.

144 Tetrapoda superclass by using all species jointly. The
 145 niche space of Tetrapoda divided into 16 main domains
 146 that were similar to those of the independent classes, and
 147 some of the above-explained particularities did not ap-
 148 pear (Fig. 2).

149 Since uncertainties related to the ranges of species ex-
 150 ist, we employed a bootstrap and a significance clustering
 151 procedure [43, 44] to assess the domain robustness (Ap-
 152 pendix S2). While several domains were well supported,
 153 we found that the niche domains corresponding to inter-
 154 mediate energy (between approximately 1000 and 1500
 155 PET units; E^M climates in Fig. 2) and low to moderate
 156 water (up to approximately 800 m.m.l.l.; W^L to W^M)
 157 were among the least supported. This robustness analy-
 158 sis shows that these niche domains are more challenging
 159 to classify.

160 Tetrapoda vs Köppen's climatic regions

161 With delineated niche domains, we studied the geo-
 162 graphic location of their climatic conditions, the climatic
 163 regions in Fig. 1 and 3, which allowed for a more pre-
 164 cise comparison between groups and Köppen's regions.
 165 The similarities among the regions of Tetrapoda classes
 166 measured as Adjusted Mutual Information (AMI) ranged
 167 from 0.57 to 0.68, with mean AMI = 0.62 (Table S1).

168 Moreover, the regions based on the niche domains of the
 169 superclass Tetrapoda were mostly congruent with the re-
 170 gions of its independent classes (mean AMI = 0.71, rang-
 171 ing from 0.66 to 0.77). Köppen's regions were more dis-
 172 similar both to the regions of Tetrapoda (AMI = 0.44)
 173 and the ones of Tetrapoda classes (mean AMI = 0.44,
 174 ranging from 0.40 to 0.47).

175 Focusing on particular regions, we saw that climates
 176 of high energy (E^H) were consistent among groups and
 177 Köppen's classification. Desert climates (high energy and
 178 low water, $E^H W^L$, BWh and BWk according to Köppen's
 179 system) were the most similar across all classifications.
 180 Tropical savanna and steppe climates (high energy and
 181 medium water, $E^H W^M$, Aw and BSh respectively follow-
 182 ing Köppen) were also consistently defined, though both
 183 of these Köppen regions were often classified together
 184 in all groups but reptiles (Fig. 3). Similarly, Köppen's
 185 tropical rainforest (Af) and tropical monsoon (Am) cli-
 186 mates were for the most part well recovered. However,
 187 we found three different tropical-humid regions, each one
 188 mostly corresponding to one of the three largest masses of
 189 tropical rainforests: Amazonian, African and Southeast
 190 Asian rainforests; $E^H W^H_1$, $E^H W^H_2$ and $E^H W^H_3$, respec-
 191 tively (Fig. 3). Regarding regions of low energy (conti-
 192 nental, E, and polar climates, D, corresponding to the
 193 highest hierarchical level in Köppen's system), we found
 194 a slightly higher level of disagreement between Köppen's

195 and Tetrapoda classifications (Fig. 3). Finally, temper-
196 ate climates (medium energy E^M) were the least congru-
197 ent between groups and Köppen's regions. Regions of
198 medium energy were at the same time the least congru-
199 ent among the different classifications and the least sup-
200 ported by the bootstrap analyses, suggesting that these
201 climates impose less restrictive conditions.

202 Climatic transition zones

203 A complete understanding of niche domains and their
204 associated climatic regions entails exploring whether the
205 domains have hard or diffuse transitions. Climatic condi-
206 tions corresponding to diffuse transitions should present
207 low specificity levels to the domain where they belong
208 (Fig. 1). Our network approach allows to calculate this
209 specificity by the dual classification of climatic bins and
210 species into same niche domains (Fig. 1). We com-
211 puted the specificity of each climatic bin as the ratio
212 between the link weights of the species classified in the
213 same domain and the total link weights [3, 45]. Then,
214 we projected these values geographically. As expected,
215 lower specificity values were in general associated with
216 the boundaries of the climatic regions (Fig. 4a and S1).
217 Our results also revealed that harsh conditions, such
218 as desert and continental-polar climates ($E^H W^L$ and
219 $E^L W^L$), present the highest specificity levels, regardless
220 of the group (Fig. 4a and S1), reflecting the difficulties
221 to colonise these climates. Contrarily, temperate regions
222 showed the lowest levels of specificity. These regions were
223 also weakly supported in the bootstrap analysis; we found
224 that bootstrap p -values and mean specificity were signif-
225 icantly correlated (stand. Glmm. coeff. 6.21; $P < 0.001$;
226 R^2 conditional = 0.29, see Material and Methods). To-
227 gether with the higher variability of these regions across
228 groups, this result further supports the idea that these
229 climatic conditions could impose less restrictive condi-
230 tions to Tetrapoda.

231 Geographical signal in climatic regions

232 Historical and geographical processes can produce the
233 detection of climates leading to specific species pools in
234 some regions of the Earth but not in others. Thus,
235 to explore for this geographical signal, we first com-
236 pared the distribution of the climatic conditions and
237 species grouped within the same niche domain. A ge-
238 ographic mismatch between species and climate distri-
239 butions would point to portions of the climatic regions
240 that are defined by species occurring in other geographic
241 areas. Exploring these patterns for each niche domain
242 revealed notable geographic agreement between species
243 and climatic conditions of the same domain (Figs. 4b
244 and S2-6). Nevertheless, we found some differences across
245 groups and regions. More extreme climates showed larger
246 mismatches between species and climates distributions.

247 For instance, for all groups but reptiles, desert climate
248 ($E^H W^L$) was mostly defined by species inhabiting Aus-
249 tralia and to a lesser extent by species from the Namib-
250 ian desert and The horn of Africa, with few or none
251 species inhabiting the Sahara desert (Figs. 4c and S2-
252 S6). Similarly, the northern climatic regions of amphib-
253 ians and reptiles were defined by species at lower lat-
254 itudes (Figs. S2-3). Approaching the geographical sig-
255 nal more quantitatively (see Material and Methods), we
256 found a stronger signal for the worse dispersers amphib-
257 ians and reptiles than for mammals and birds (Fig. 4d),
258 suggesting that dispersal capabilities can contribute to
259 the geographical signal in the niche domains. Finally,
260 the Tetrapoda superclass showed the lowest geograph-
261 ical signal, which suggests that, beyond dispersion, an
262 increased evolutionary time can reduce the geographical
263 signal.

264 DISCUSSION

265 We detected 16 climatic regions governing the distri-
266 bution of Tetrapoda. Despite the substantial physiolog-
267 ical and functional differences among the groups, most
268 of their niche domains and climatic regions are consis-
269 tent. Some of these climatic regions resemble Köppen's
270 regions, which supports the idea that general climatic
271 constraints organise the distribution of life on Earth.

272 While we found a high general congruence across
273 groups, some niche domains and climatic regions were
274 more consistent than others. In general, more extreme
275 climates, such as arid or low-energy continental areas,
276 were well defined in all groups. These climates also
277 presented high levels of specificity, showing that species
278 adapted to other climates have more difficulties to with-
279 stand these conditions. Both of these results suggest that
280 extreme climates impose strong adaptive barriers [46, 47],
281 even across distinctive evolutionary lineages.

282 Contrarily, milder climatic conditions, especially tem-
283 perate climates, showed the lowest specificity, statisti-
284 cal support, and congruence across groups. These cli-
285 mates are more difficult to classify due to the overlap
286 in the climatic space of species pools with different cli-
287 matic optima. Two complementary reasons can explain
288 this ambiguity: First, while we used two variables widely
289 recognised to shape Tetrapoda distributions, alternative
290 variables, such as seasonal changes of energy and precip-
291 itation [48], may also influence species inhabiting tem-
292 perate regions. Including these variables might help to
293 further separate temperate species pools across the cli-
294 matic space. Second, the climatic conditions of these do-
295 mains may not prevent the colonisation of species with
296 other realised optima or preferences, which would gen-
297 erate the observed overlap in the climatic space across
298 milder conditions. Questions remain about the relative
299 contribution of each factor.

300 We also found some domains that were well supported
301 but unique for each group. These differences between

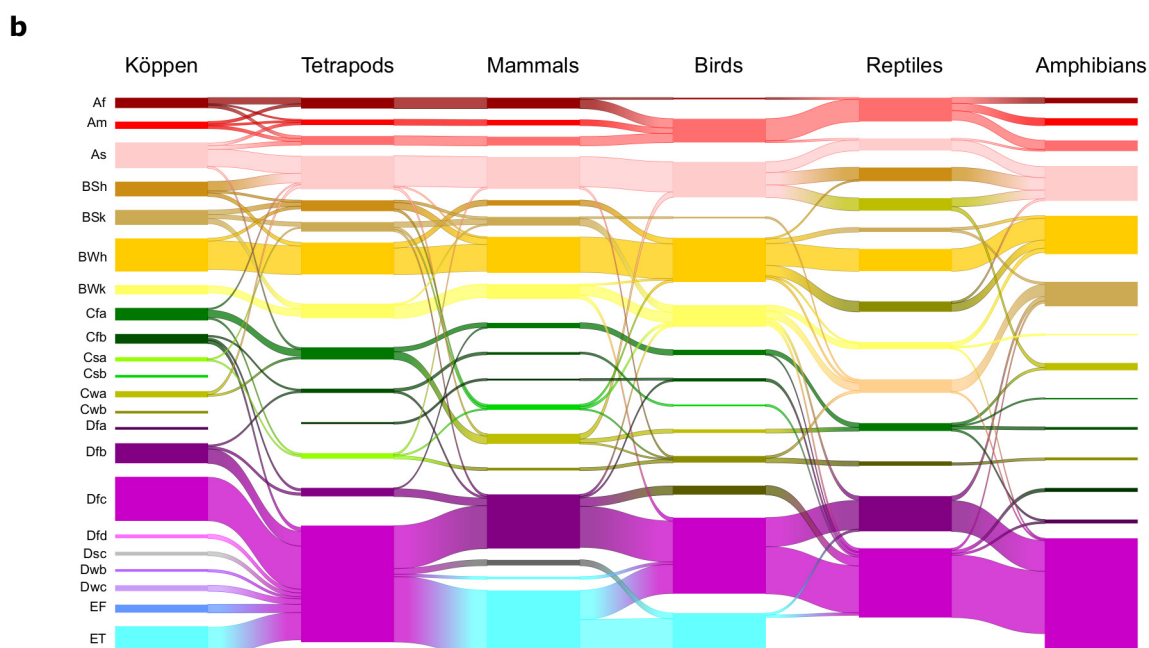
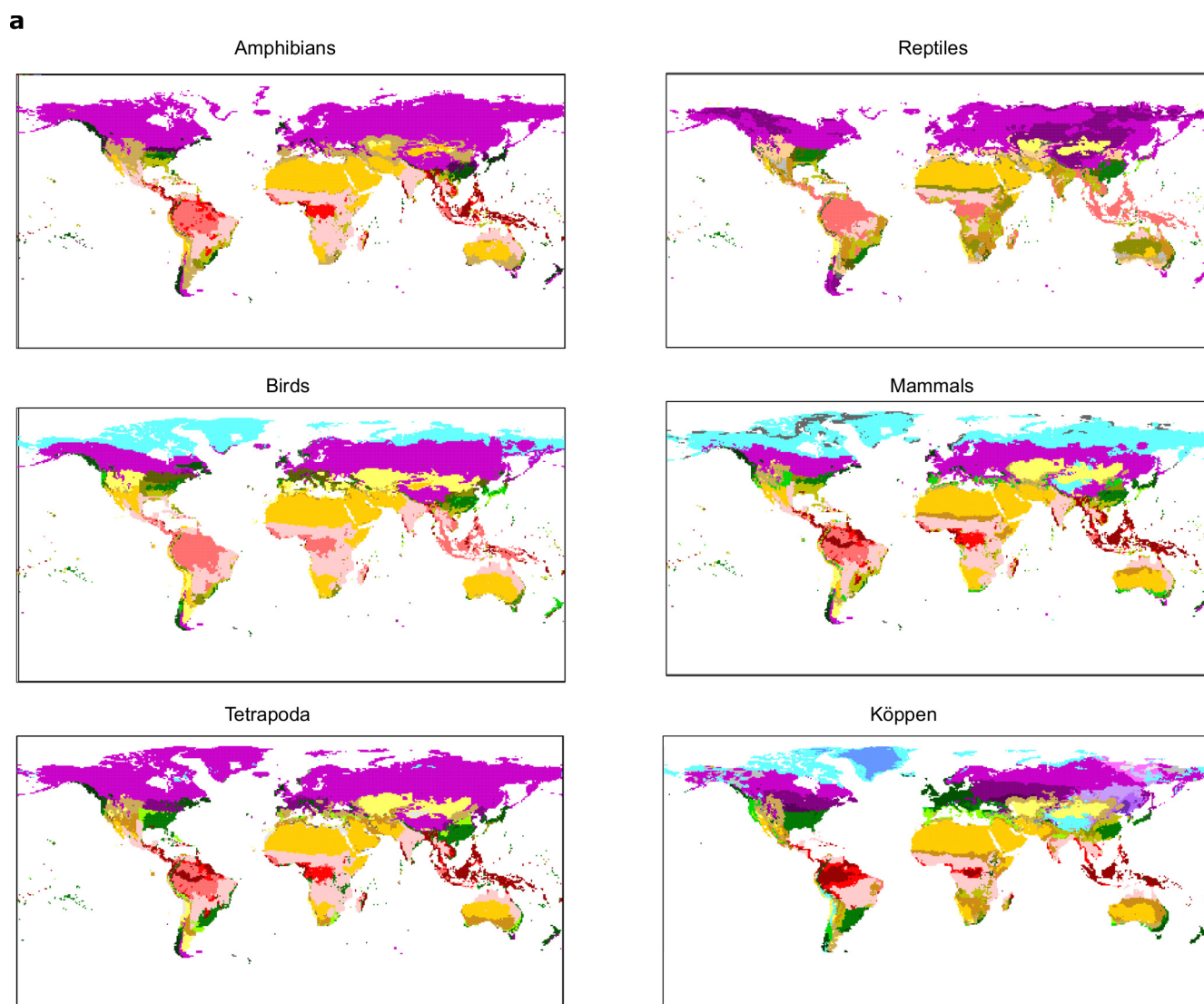


FIG. 3: Tetrapoda groups and Köppen's climatic regions are largely congruent. **a** Geographic location of Tetrapoda niche domains and Köppen's climatic regions. **b** Alluvial diagram showing the similarities among the climatic regions. Colours according to Fig. 2.

302 groups seem to relate to the particular physiological
303 adaptations of each group. For instance, homeothermic
304 birds and mammals defined a region of low energy, con-
305 sistent with Köppen’s polar climates, that reptiles and
306 amphibians lacked. Similarly, reptiles, a group holding
307 several species adapted to arid environments [36], de-
308 fined some regions of low precipitation and high PET.
309 Hence, despite the high similarities among groups, our
310 results stress that caution is needed when generalising
311 the climatic regions to other groups of organisms.

312 Beyond niche domains, our results also show differ-
313 ences in the geographical signal across groups. That
314 amphibians – species with the lowest dispersal capac-
315 ity – showed the highest geographical signal suggests
316 that dispersal processes play an essential role: worse dis-
317 perser species have more difficulties tracking their pre-
318 ferred climates [49], limiting the colonisation of disjoint
319 areas with similar climates. Moreover, the Tetrapoda
320 superclass shows the lowest geographical signal, which
321 suggests that a increased evolutionary time can reduce
322 this effect. Thus, evolutionary history – through the ap-
323 pearance of convergent adaptations to similar climates in
324 different geographic regions[50] – may also influence the
325 geographical signal in niche domains. In any case, the
326 ultimate causes and consequences of this signal require
327 further attention. Why are some amphibians able to in-
328 habit arid conditions in the Australian desert but not
329 in the Sahara desert (Fig. S2)? Why can some reptiles
330 withstand cold climates in and around the Himalayan
331 mountains but not at the high latitudes of the northern
332 hemisphere (Fig. S3)? These are some of the emerging
333 fundamental questions whose answers require historical
334 biogeographical and evolutionary approaches.

335 Our results bring us closer to a definition of climatic
336 regions that represent active factors for the organisation
337 and evolution of life. Nevertheless, it would be interesting
338 to improve some aspects in future studies. First, while
339 we used a large number of species (about 26,000), they
340 are taxonomically biased and only represent a small frac-
341 tion of the terrestrial organisms. Similarly, we used two
342 climatic variables widely known to affect the distribution
343 and diversity patterns of animals and plants in general
344 [4, 33], but other climatic variables might refine some of
345 the least supported regions. Finally, our domains repre-
346 sent portions of the realised climatic niche space, and this
347 space may be influenced by historical, geographical, and
348 biotic factors beyond pure climate [3, 27, 51]. Although
349 the geographical signal was rather low, identifying po-
350 tential niches may also improve the accuracy of climatic
351 regions. At the current pace of biological data accumula-
352 tion and computational development, it is reasonable to
353 expect that some of these limitations will soon be over-
354 come. Meanwhile, the considerable congruence of several
355 climatic regions across the studied groups and Köppen’s
356 system provides confidence in their robustness. Hence, it
357 is likely that using more and better data would not pro-
358 duce regions substantially different from those presented
359 here.

360 Regardless of how generalisable the results are, the
361 niche domains and their associated species pools and cli-
362 matic regions can be used as a basis for ecological and
363 evolutionary studies, as well as for conservation planning
364 concerning Tetrapoda. Some of the many questions that
365 the results reported here (data available in Appendix S3)
366 can help to answer include : Are all the climatic regions
367 similarly conserved and/or protected? Do the species
368 forming each niche domain differ functionally or phy-
369 logenetically? Is the adaptation to niche domains evo-
370 lutionary constrained? Do diversification, extinction or
371 speciation rates differ among the species associated with
372 different domains?

373 In conclusion, our data-driven climate classification re-
374 veals major climatic boundaries organising the distribu-
375 tion of life on Earth. Questions remain regarding the
376 mechanism underlying differences between groups in the
377 climatic regions and the geographical signal. Neverthe-
378 less, the regions that are consistent across groups can
379 help answer questions in a diverse array of fields, includ-
380 ing climatology, geography, ecology, evolution and con-
381 servation.

382 MATERIAL AND METHODS

383 Data

384 We obtained the distribution ranges of mammals and
385 amphibians from The IUCN Red List of Threatened
386 Species [21], of birds from Bird species distribution maps
387 of the world [22] and of reptiles from ref. [23]. We in-
388 cluded only the native range of terrestrial species in the
389 analyses in all instances. In the case of birds, we only
390 used the breeding ranges. Moreover, since there is a
391 higher uncertainty when determining the realised niches
392 of narrow-ranging species [52], we removed the species
393 whose ranges were less than 5 grid cells of 0.5 degrees.
394 After this cleaning of the data, we used 3657 amphibians,
395 7204 reptiles, 4574 mammals and 10684 birds, for a total
396 of 26119 Tetrapoda species.

397 We approximated the species’ Grinnellian niches[51]
398 with two climatic variables that represent energy and wa-
399 ter inputs. While we could have used several other vari-
400 ables, we chose energy and water since they best explain
401 climatic effects on species distributions [4]. As surrogates
402 of energy and water inputs, we used mean annual poten-
403 tial evapotranspiration (PET) and annual precipitation,
404 respectively. Both variables have been shown to be im-
405 portant factors for Tetrapoda species distributions [33–
406 35]. Moreover, they have also been used in previous cli-
407 mate classifications [18] and are regularly used to derive
408 other drivers of species distributions such as the UNEP
409 aridity index [53, 54]. We obtained PET from ref. [25]
410 and annual precipitation from ref. [24], both at a 0.08°
411 resolution. Finally, we obtained Köppen’s climatic re-
412 gions from refs. [9, 55].

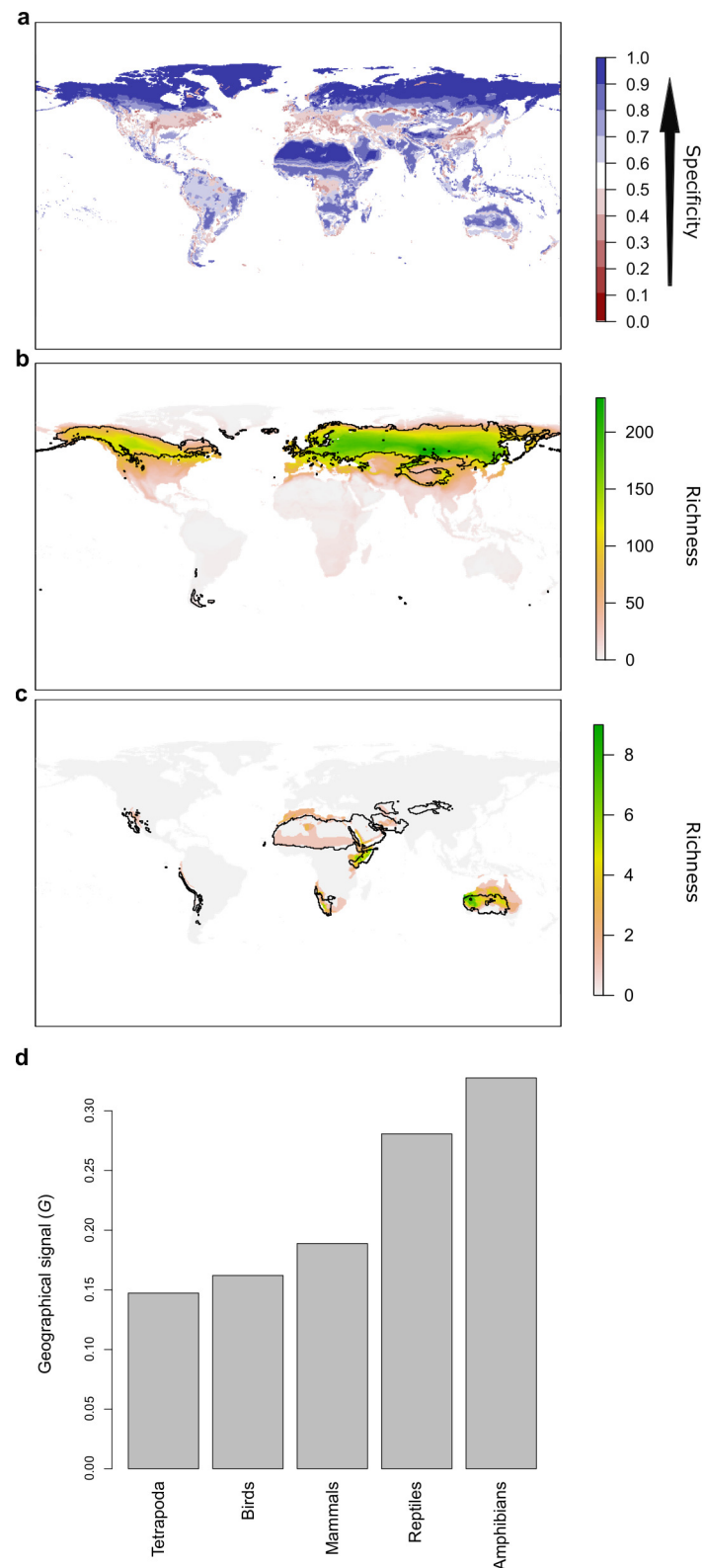


FIG. 4: The geographic location of climatic domains and their associated species provide insights into the mechanism underlying the climatic regions. **a** Geographic projection of the specificity of climatic bins to their niche domain. **b** An example showing a bird's niche domain with a low geographical signal. The distribution of the climatic conditions (black line) and the species (coloured richness values) belonging to the same niche domain were mostly congruent. **c** An example of an amphibian's niche domain showing a high geographical signal, reflected in a substantial mismatch between the distribution of climatic conditions and species belonging to the same domain. **d** A quantitative approximation of the geographical signal, ranging between 0 and 1, for the different taxonomic groups (see Materials and Methods).

413

Niche characterisation

414 We characterised the realised climatic niche of each
415 species using an approach similar to the one proposed in
416 ref.[26]. We divided the climatic space formed by PET
417 and annual precipitation into bins and calculated the pro-
418 portion of occurrences a given species has in each climatic
419 bin. Both the shape of the divisions and the number of
420 divisions of each climatic axis affect the result. For in-
421 stance, dividing the axis into regular intervals can destroy
422 critical information if the climatic values more restrictive
423 are skewed toward any extreme of the distribution or if
424 the climatic values are represented non-uniformly across
425 the globe (as for annual precipitation, Fig. S7). Also
426 dividing the space into too few intervals destroys infor-
427 mation, whereas using too many divisions can generate
428 niche domains with only a few species. To overcome the
429 first issue, we divided the axes in quantiles based on the
430 distribution of climatic values across the Earth. By do-
431 ing so, we obtained an almost uniformly divided PET
432 axis (Fig. S7). Contrarily, the number of divisions of the
433 annual precipitation axis was skewed towards low values,
434 which resulted in a higher resolution over the presumably
435 more relevant low-precipitation conditions (Fig. S7). To
436 solve the second issue, we selected the lowest number of
437 divisions that maximised the gain in information (see Ap-
438 pendix S1). The optimal number of axis divisions was 17
439 in all cases but amphibians, where it was 18 (Fig. S8).

440 Next we accounted for potential commission errors,
441 which may affect the different climates a species experi-
442 ences. Specifically, range maps can overestimate the
443 area occupied by a species, which directly influences the
444 niche characterisation [56]. Extracting the climatic val-
445 ues that a species range covers from a high-resolution
446 climatic raster (such as 0.08°) may reduce commission
447 errors at the borders of the species range, but increases
448 this error otherwise. Extracting climatic values from a
449 coarser raster can reduce the influence of commission er-
450 rors over the areas inside of a range but increases them
451 over the borders. To alleviate the effects of these poten-
452 tial errors, we first extracted the climatic values from the
453 high-resolution rasters (0.08°). Then, we computed the
454 average climatic values among selected raster pixels lo-
455 cated within cells of 0.5 degrees. In this way, we reduced
456 the effects of commission errors both at the borders of
457 and inside species ranges. Moreover, we also conducted
458 a bootstrap significance test that takes uncertainty of
459 species ranges into account (see below).

460 Niche domains and climatic regions identification

461 We employed a network community detection ap-
462 proach to identify the niche domains and the species
463 mainly associated with them. For each group of species,
464 we first generated a weighted bipartite network where
465 species and climatic bins formed the disjoint sets of
466 nodes, and the proportion of occurrences of species in

467 intervals of the climatic values corresponding to the cli-
468 matic bins formed the weighted links. We then used
469 the hierarchical version of the community detection al-
470 gorithm known as Infomap [41, 42] to identify the niche
471 domains. We ran the algorithm 1000 times, selecting the
472 network partition with the best quality.

473 To consider the uncertainty associated with both the
474 species ranges and the community detection, we con-
475 ducted a bootstrap analysis. For each species, we resam-
476 pled with replacement from the distribution of climatic
477 values within species ranges at a resolution of 0.08° . We
478 averaged climatic values laying within 0.5° cells and cal-
479 culated the proportion of occurrences in each climatic
480 bin. With resampled data from all species, we generated
481 a bootstrapped network and ran Infomap 1000 times us-
482 ing this network. Given the high computational cost of
483 this analysis, we only generated 100 bootstrap networks.
484 We followed the approach proposed in ref. [44] to calcu-
485 late the support of the niche domains. For each identified
486 domain, we calculated the proportion of bootstrap net-
487 works with a domain more similar than Jaccard index
488 0.5 [44].

489 With obtained niche domains, we detected the climatic
490 regions by identifying areas across the Earth's surface
491 that hold the climatic conditions grouped within each
492 niche domain. Finally, to compare climatic regions across
493 Tetrapoda groups and with Köppe's classification, we cal-
494 culated the adjusted mutual information (AMI) [57].

495 Climatic transition zones

496 The joint classification of climatic bins into domains
497 and the species most associated to them allowed us to
498 calculate the specificity of the bins to the domain where
499 they belong, which indicates zones of transitions between
500 domains (Fig. 1). That is, a bin acting as a transition
501 between two domains should contain species from both
502 domain and, therefore, a low specificity to the domain
503 where it is classified [3, 45]. To consider the link weights,
504 we calculated this specificity S_i^D of a climatic bin i in
505 domain D as the sum of link weights $w_{i,j}$ of the species j
506 present in the bin and also belonging to the same domain
507 as the bin, divided by the sum of link weights of all the
508 species present in the bin, such that

$$S_i^D = \frac{\sum_{j \in D} w_{i,j}}{\sum_j w_{i,j}}. \quad (1)$$

509 This index is 1 when the bin has only species of the
510 same domain as the bin, and tends to 0 otherwise. We
511 then projected these specificity values into the geographic
512 space by assigning these values to the geographical raster
513 cells q that hold the climatic conditions represented by
514 the bins, thus obtaining the projected specificity S_q^D . Fi-
515 nally, we explored the relationship between average S^D
516 and bootstrap support. We fitted a logistic GLMM of
517 bootstrap p -values as function of mean S^D as fixed term

518 and the taxonomic group as a random intercept term.
519 GLMM was conducted using the lme4 [58] package in
520 R [59].

521 Geographical signal

522 To investigate the geographical signal, we first ob-
523 served the match between the geographic location of the
524 species and the climatic conditions associated with the
525 corresponding niche domain. Then, we quantified the
526 geographical signal by comparing the geographically pro-
527 jected specificity S^P with a measure of specificity based
528 on the actual pool of species co-occurring geographically.
529 That is, the specificity of a climatic bin S^D is based on
530 the species that co-occur in the climatic space and then
531 it is projected geographically to obtain S^P (see above).
532 Hence, S^P does not considered the actual pool of species
533 co-occurring in the geographic space. In case of a large
534 geographical signal, we would expect large differences be-
535 tween the species co-occurring in the climatic and geo-
536 graphic spaces. For instance, the geographic mismatch
537 between species and climates belonging to the same do-
538 main is produced by species co-occurring in a given por-
539 tion of the climatic space but not in all geographical areas
540 with the climate represented in such portion of the cli-
541 matic space. In this sense, in case of geographical signal
542 we would expect differences between the projected speci-
543 ficity S^P and a value of specificity based on the species
544 pool occurring in given geographical areas, for short the
545 actual specificity S^A . A higher actual specificity than the
546 projected indicates areas that host most of the species
547 associated with a niche domain, while the opposite in-
548 dicates areas not, or only scarcely, colonised by these

549 species.

550 Using Eq. 1, we calculated the actual specificity of a
551 geographical raster cell q , whose corresponding climatic
552 bin i is in domain D , as the ratio between the link weights
553 of species in raster cell q that belong to its associated
554 domain and the total link weights of species in q ,

$$S_{q,i}^A = \frac{\sum_{j \in D,q} w_{i,j}}{\sum_{j \in q} w_{i,j}}. \quad (2)$$

555 To calculate the geographical signal G , we computed
556 the projected and actual specificity for each climatic
557 raster cell q at 0.5° resolution. Then, we calculated the
558 average differences between projected and actual speci-
559 ficity in absolute terms, such that

$$G = \frac{1}{N} \sum_{q=1}^N |S_q^A - S_q^P|, \quad (3)$$

560 where N is the total number of raster cells. This index
561 is 0 when there is no geographical signal and tends to 1
562 for high signals.

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