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Climatic-niche evolution follows similar rules in plants and animals

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Climatic niches are essential in determining where species can occur and how they will respond to climate change. However, it remains unclear if climatic-niche evolution is similar in plants and animals or is intrinsically different. For example, previous authors have proposed that plants have broader environmental tolerances than animals but are more sensitive to climate change. Here, we test ten predictions about climatic-niche evolution in plants and animals, using phylogenetic and climatic data for 19 plant clades and 17 vertebrate clades (2,087 species total). Surprisingly, we find that for all ten predictions, plants and animals show similar patterns. For example, in both groups, climatic niches change at similar mean rates and species have similar mean niche breadths, and niche breadths show similar relationships with latitude across groups. Our results suggest that there are general 'rules' of climatic-niche evolution that span plants and animals, despite the fundamental differences in their biology. These results may help to explain why plants and animals have similar responses to climate change and why they often have shared species richness patterns, biogeographic regions, biomes and biodiversity hotspots.

T he realized climatic niche of a species ('climatic niche' here-after) is the large-scale temperature and precipitation conditions where it occurs[1,2]. Climatic niches, and the abiotic tolerances and biotic factors underlying them, may help determine where species can occur over space and time[1,2]. Therefore, they may be critically important for answering the most fundamental and urgent questions in ecology and evolution. For example, why are there more species in the tropics[3–5]? How do new species originate[5–7]? Why are some clades so species rich[8]? Where can an exotic species become established[9,10]? Will species persist under climate change[11,12]?

Two important properties of climatic niches are their widths and rates of change. From first principles and theory[1–3,6], if a species' niche is wide and/or can change rapidly, then it may be broadly distributed and resistant to climatic change. Conversely, if niches are narrow and change slowly, species may be narrowly distributed, unable to successfully disperse between habitats and regions, and vulnerable to climate change.

Several studies have analysed the correlates of variation in rates of climatic-niche evolution and climatic-niche widths among species[13–18]. However, these studies have generally focused on particular clades of animals or plants. Here, we test if there are general 'rules' of climatic-niche evolution across organisms. As an initial step towards answering this question, we compare plants and animals. These groups have very different biologies but are both relatively tractable (for example, species in both groups have relatively well-known geographic ranges, taxonomies and phylogenies).

Should we expect climatic-niche evolution to be similar between plants and animals or to be different? This is part of a broader question: do plants and animals evolve differently or similarly[19–22]? Huey and colleagues[20] reviewed how plants and animals respond to environmental stress, especially regarding physiology and climate. They suggested that plants should have broader tolerance ranges (because individuals generally cannot move to avoid stresses) but should be more sensitive to climate change. Thus, given their arguments, it

may be reasonable to expect differences in climatic-niche evolution between plants and animals. However, climatic niches seem to evolve at similar rates in plant and animal populations[18] with similar frequencies of climate-related local extinctions[23]. Furthermore, much variation in climatic niches among animal species may involve latitude (for example, broader temperature niche breadths at higher latitudes[15,24]) but it is unclear whether similar patterns occur across plants. Overall, it is unknown whether climatic-niche evolution in plants and animals is similar or shows distinct patterns in each group.

Here, we evaluate if there are general patterns of climatic-niche evolution that span plants and animals. To do this, we test ten predictions related to rates of niche evolution and evolution of niche widths. We test these predictions across 19 well-sampled plant clades (mostly angiosperms) and 17 well-sampled animal clades (all vertebrates), using published phylogenetic and climatic data.

We test the following ten predictions (Supplementary Table 1). Most were proposed and described in earlier studies but were often tested only in animals (hypotheses H4–H10). These vary from well-justified hypotheses to mere predictions. We number them as hypotheses (H1–H10) for simplicity. H1–H6 involve rates whereas H6–H10 involve niche widths. H1: Climatic niches evolve slowly. Slow rates are consistent with niche conservatism, a pattern with several potential causes (for example, stabilizing selection, limited genetic variation, gene flow, trade-offs and competition[25,26]). Previous studies estimated rates using phylogenetic approaches (for example, among vertebrates[16], grasses[27], and plant and animal populations[18]) and found that niches changed much more slowly than projected climate change (~1 °C per Myr[16,18]). H2: Climatic niches change more rapidly among recently diverged species. Previous analyses found strong negative relationships between species ages and rates[16,18,27]. This relationship may reflect a general tendency for phenotypic rates to be faster over shorter timescales[28]. H3: Temperature-related niche variables evolve faster at higher latitudes, whereas precipitation variables

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evolve faster at lower latitudes. This overall pattern was found among bird species[29] and among plant and animal populations[18]. This pattern might reflect positive relationships between niche widths and rates and relationships between latitude and niche widths (negative for precipitation and positive for temperature[24]), which we test below. H4: Minimum temperatures evolve faster than maximum temperatures. Previous authors[30] suggested that physiological tolerances to heat evolve more slowly than those to cold in both plants and animals (on the basis of physiological principles) and that 'heat freezes niche evolution'. However, no studies have tested if this hypothesis includes the relevant niche variables (hottest yearly temperatures (Bio5) and coldest yearly temperatures (Bio6)). H5: Species values for precipitation during the wettest yearly quarter (Bio16) evolve faster than those for the driest quarter (Bio17). To our knowledge, this prediction has not been tested. We propose this pattern given that it may be more difficult to adapt to drier conditions in the driest part of the year than to wetter conditions in the wettest part (since plants and animals both need water), which may lower rates in driest-quarter values. H6: Niches evolve faster in species with wider niches. Although it is unclear from theory whether wider niches should accelerate or decelerate niche evolution[14], there is some evidence that niches evolve faster in species with wider niches[14]. H7: Temperature niches are wider in temperate climates[5,31] whereas precipitation niches are wider in the tropics[24]. This pattern was supported in some studies[5,15] and is expected if species-level niche widths depend largely on seasonal variation within localities. H8: Species-level niche breadths are related to within-locality breadths. This prediction was supported in three vertebrate clades[15]. For temperature, the difference between coldest and hottest yearly temperatures at a locality (within-locality niche breadth) spanned most of the difference between coldest and hottest temperatures across the species' range (species-level niche breadth). This prediction tests whether species consist of divergent populations adapted to a narrow range of conditions or if individuals tolerate a broad range of conditions that largely span the species' niche breadth. H9: Temperature and precipitation niche breadths are positively related to each other. Previous authors[32] tested for trade-offs (negative relationships) between temperature and precipitation niche breadths in amphibians but found significant positive relationships instead. This pattern may arise if broadly distributed species have wide niches on both axes, whereas narrowly distributed species are narrow on both axes. H10: Species niche breadths are related to the position of each species on a given niche axis, with different relationships for temperature and precipitation. In amphibians[32], temperature niche widths are negatively related to species mean values for mean annual temperature and precipitation niche widths are positively related to annual precipitation. These patterns could be related to latitudinal niche-width patterns but niche position can be unrelated to latitude (for example, precipitation can be low or high across many latitudes).

Results

Our primary test for each prediction was a single analysis across all plants and then all animals (Supplementary Table 2). However, we also performed separate analyses within each animal and plant clade, to test for consistency with the overall pattern in each group (summary in Fig. 1 and see Supplementary Table 3).

H1. Absolute rates of climatic-niche evolution were estimated for all 952 sampled plant species and all 1,135 animal species (Fig. 2). Mean rates in each group were similarly low (for example, 1.44 ± 4.01 (mean $\pm$ s.d.) and $0.82 \pm 2.50\,^{\circ}\mathrm{C}\,\mathrm{Myr}^{-1}$ for mean annual temperature for plants and animals; 226.0 ± 899.6 and $126.0 \pm 392.0\,\mathrm{mm}\,\mathrm{Myr}^{-1}$ for annual precipitation). No significant differences in rates were found between plants and animals for any of the six variables examined,
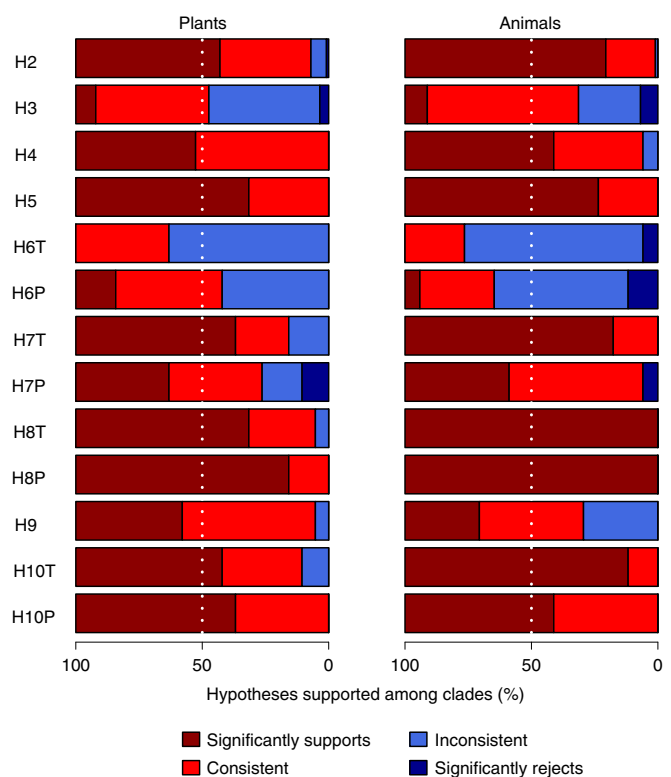

Fig. 1 | Support for ten hypotheses about climatic-niche evolution among 19 plant clades and 17 animal clades. These predictions/hypotheses are explained in Supplementary Table 1. H1–H6 involve rates of niche evolution. H6–H10 involve evolution of niche breadths. T and P indicate temperature- and precipitation-related hypotheses, respectively. For H2 and H3, the values shown are mean proportions across the six climatic variables tested for each prediction. For H4 and H5, the values shown are mean proportions of LRT and phylogenetic paired t-tests for each prediction. Mean slopes and R^2 values for H2–H10 are given in Supplementary Table 2. We classify results for each clade into four groups: significantly supporting the prediction ($P < 0.05$, dark red); consistent with the prediction but not significantly supporting (red); inconsistent but not significantly rejecting (blue); significantly rejecting ($P < 0.05$, dark blue). We consider a clade as consistent with a given prediction if the slope or difference in rates is in the predicted direction (regardless of P value) and as inconsistent with the prediction if the slope or difference in rates is in the opposite direction. Note that our primary test of each prediction is based on a combined analysis that includes all species of plants or animals and not these patterns of variation among clades.

based on phylogenetic analysis of variance (pANOVA; Fig. 2, Supplementary Tables 4 and 5 and Supplementary Appendix 1). These estimates were based on ancestral reconstructions using the best-fitting model and mean values across localities for each species and variable. Rates were similar using different models and different summaries across localities (Supplementary Appendix 2).

H2. Niche variables change faster in younger species in both plants and animals (Fig. 3 and Supplementary Fig. 1). Using rate estimates from H1 and phylogenetic regression, relationships were significantly negative between rates and species ages for both plants and animals ($n = 952$ and $1,135$, respectively) for all six variables. Regression slopes ranged from -0.69 to -0.86 and R^2 from 0.23 to 0.38 (Supplementary Table 2). Results within each of the 19 plant clades and 17 animal clades were similar, with negative relationships in >92% of the clades (Fig. 1 and Supplementary Dataset 1).
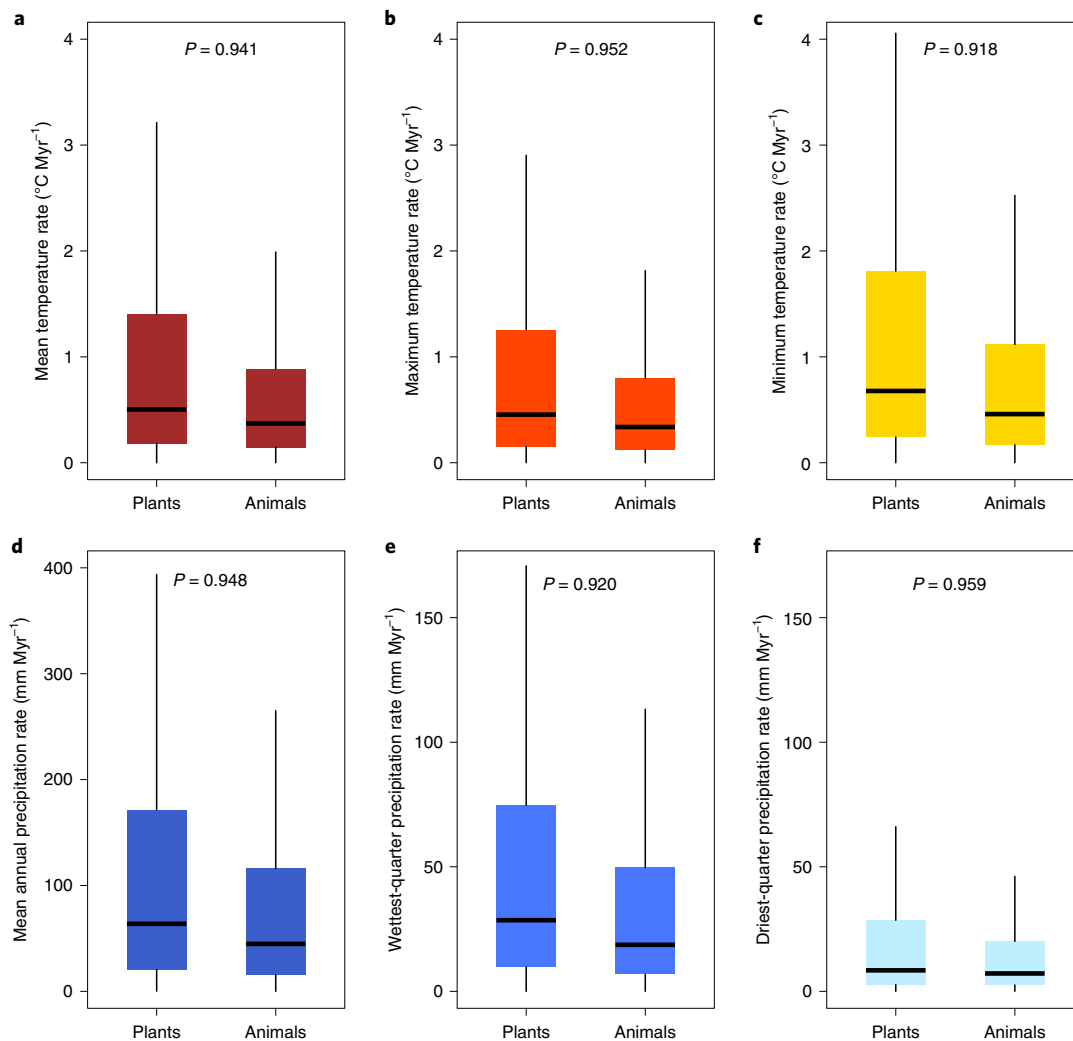
Fig. 2 | Rates of climatic-niche evolution in plants and animals (H1). a–f, Rates are based on mean annual temperature (**a**), maximum annual temperature (**b**) and minimum annual temperature (**c**) for each species of plant ($n=952$) and animal ($n=1,135$), and annual (**d**), wettest-quarter (**e**) and driest-quarter (**f**) precipitation for each species. The black horizontal line is the median rate; upper and lower limits of the box indicate first and third quartiles, respectively; whiskers are ranges of species values. *P* values are based on phylogenetic ANOVA (Supplementary Table 5).

H3. Rates of niche evolution are not significantly related to latitude (Supplementary Fig. 2) in plants or animals ($n=952$ and 1,135). Relationships between niche rates for each species (as in H1) and mean absolute latitude among localities for each species had slopes and R^2 near zero and were non-significant (except Bio17 in animals; Supplementary Table 5). Tests within each plant and animal clade showed similar patterns (Fig. 1 and Supplementary Dataset 2).

H4. Minimum annual temperatures change faster among species than maximum annual temperatures (Fig. 4a) in both plants and animals ($n=952$ and 1,135). We first used maximum-likelihood rate estimates including all species of animals and plants (instead of rate estimates for each species). We observed significantly higher rates (σ^2, unitless) for minimum than maximum temperatures for both plants (6.53 versus 3.33, $P<0.001$ from a likelihood-ratio test, LRT) and animals (5.54 versus 2.56, $P<0.001$). We also compared species-level rate estimates (as for H1) and phylogenetic paired *t*-tests showed higher mean rates for minimum than maximum temperatures for both plants (1.79 versus 1.31, $P=0.005$) and animals (1.19 versus 0.87, $P=0.021$). Results within each clade were similar. For plants, 100% of the clades had faster rates for minimum than maximum temperatures for both methods, with 63% and 32%

significantly higher for the LRT and *t*-test, respectively. For animals, 94% had faster maximum than minimum temperature rates for both methods, with significant differences in 71% and 47% for each method (Fig. 1 and Supplementary Dataset 3).

H5. Wettest-quarter precipitation (Bio16) changes faster among species than driest-quarter precipitation (Bio17) in both plants and animals (Fig. 4b; $n=952$ and 1,135). Using LRT across all species, the wettest-quarter rate was significantly higher than the driest-quarter rate for plants (15,485.7 versus 1,916.6, $P<0.001$ for LRT) and animals (11,265.0 versus 2,000.6, $P<0.001$). Phylogenetic paired *t*-tests based on species-level rates also showed higher rates for the wettest quarter for plants (100.6 versus 30.0, $P<0.001$) and animals (51.8 versus 22.3, $P=0.003$). Analyses of both methods within each clade showed that 100% of plant and animal clades have higher rates for Bio16 than Bio17, with significant differences in 84% and 53% of plant clades and 94% and 59% of animal clades for each method (Fig. 1 and Supplementary Dataset 3).

Niche breadths. Species niche breadths for temperature (SNBT) and precipitation (SNBP) were broadly similar between plants and animals. SNBT is based on the difference between the maximum
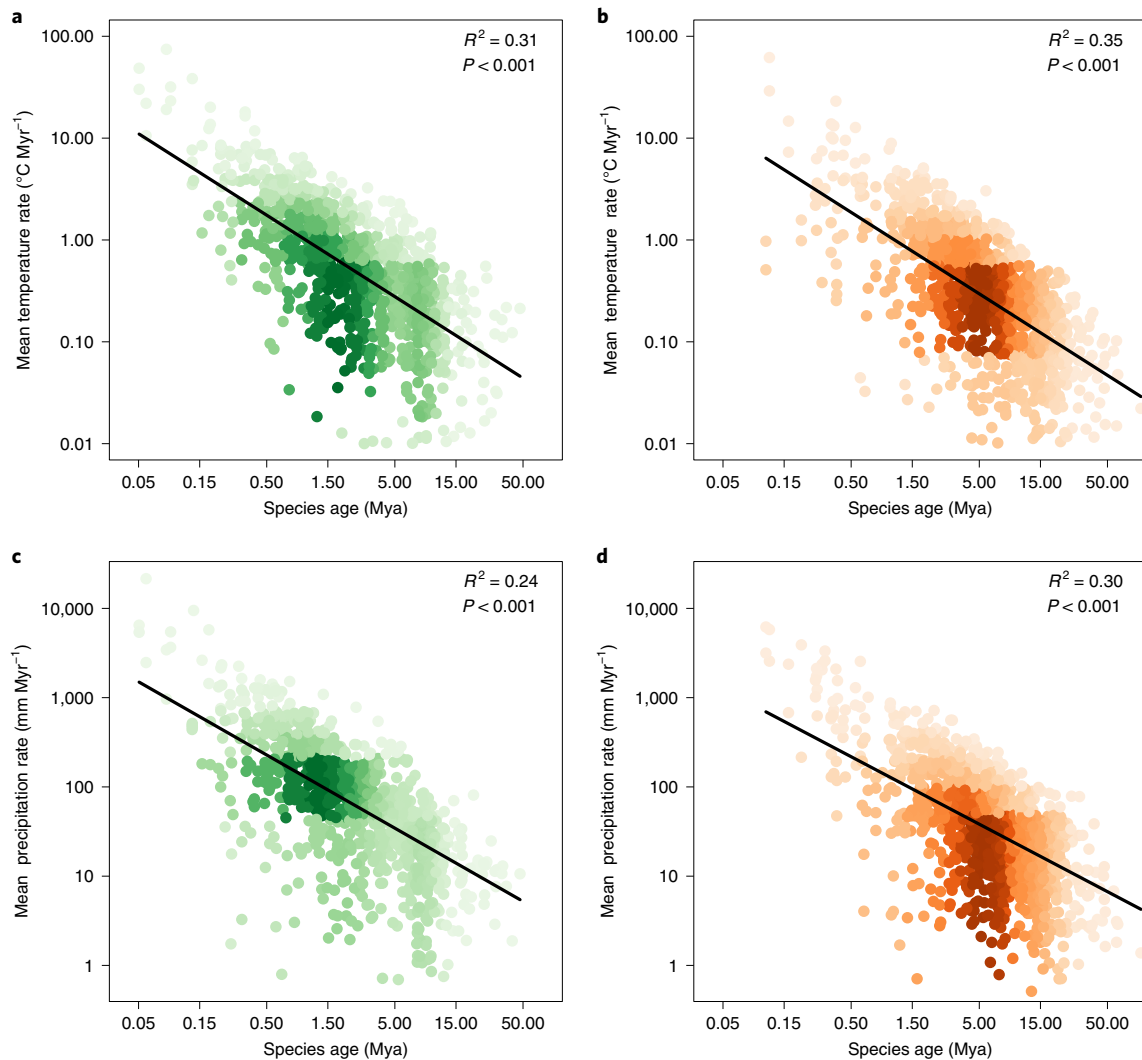
Fig. 3 | Relationships between rates of climatic-niche evolution and species age (H2). a,b, Rates based on mean annual temperatures for plants ($n = 952$, green (**a**)) and animals ($n = 1,135$, orange (**b**)). **c,d,** Rates based on annual precipitation for plants (**c**) and animals (**d**). Data are ln-transformed and darker colours indicate greater overlap of data points. Regression lines, R^2 and P values are based on PGLS (Supplementary Table 2). Results for maximum and minimum annual temperatures and wettest- and driest-quarter precipitation are similar and shown in Supplementary Fig. 1.

value of the hottest temperatures (Bio5) across localities and the minimum value of the coldest temperatures (Bio6) across localities. SNBP is the difference between the highest value (across localities) of wettest-quarter precipitation (Bio16) and lowest driest-quarter precipitation (Bio17). Within-locality niche breadths for temperature are based on differences between Bio5 and Bio6 for each locality and Bio16 and Bio17 for precipitation.

After excluding species known from single localities, the mean SNBT for 931 plant species and 1,053 animals were $34.79 \pm 12.11\,°C$ and $32.72 \pm 12.15\,°C$. The mean within-locality niche breadths for temperature for each species (WLNBT), averaged across species, were also similar (23.23 ± 8.07 and $22.75 \pm 8.50\,°C$). The mean ratios of within-locality to species-level niche breadths for temperature (ratioT) were also similar in plants and animals (0.68 ± 0.15 and 0.71 ± 0.16).

Results were similar for precipitation variables. Mean SNBP for plants and animals were 783.9 ± 500.4 and $859.5 \pm 611.9\,mm\ year^{-1}$, with mean within-locality niche breadths (WLNBP) of 348.2 ± 240.8 and $439.7 \pm 315.1\,mm$, and mean ratio of within-locality to species niche breadth for precipitation (ratioP) of 0.48 ± 0.21 and 0.55 ± 0.22 (Supplementary Tables 4–6). No significant differences were found

between plants and animals for any niche-breadth variables using phylogenetic methods (Supplementary Table 5).

H6. Climatic niches do not evolve faster in species with wider niches (Supplementary Fig. 3), in plants or animals ($n = 931$ and $1,053$). Using species-level rate estimates, we found no significant relationships between rates for annual mean temperature and SNBT, nor between annual precipitation and SNBP ($P > 0.05$, all slopes and R^2 near zero). Few clades showed significant relationships (<20% of plant or animal clades) and neither positive nor negative relationships dominated (24–58% positive; Supplementary Dataset 4).

H7. In both plants and animals ($n = 931$ and $1,053$), temperature niches are wider at higher latitudes, whereas precipitation niches are wider at lower latitudes (Fig. 5). Based on phylogenetic regression, SNBT showed weak but significantly positive relationships with absolute latitude (mean across localities) for each species for both plants and animals ($R^2 = 0.10$ and 0.37). SNBP showed weak but significantly negative relationships with absolute latitude ($R^2 = 0.02$ and 0.08). For SNBT, 63% of plant and 82% of animal clades showed significant positive relationships. For SNBP, only 47% of plant and
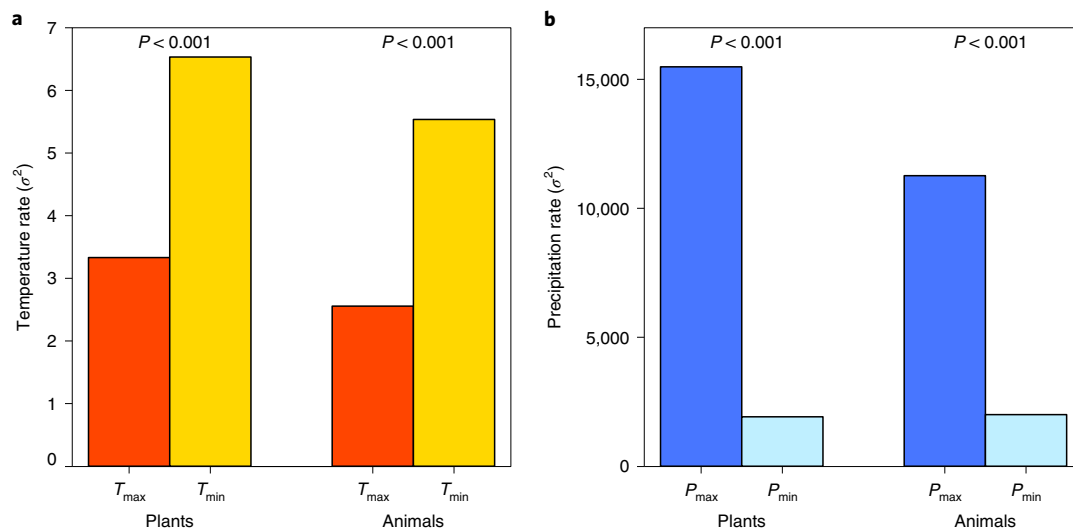
Fig. 4 | Comparison of evolutionary rates for maximum and minimum annual temperatures (H4) and wettest- and driest-quarter precipitation (H5).
a, Rates are based on maximum (T_{max}, red) and minimum (T_{min}, yellow) annual temperature for plants ($n = 952$) and animals ($n = 1,135$), respectively. **b**, Rates are based on wettest-quarter (P_{max}, blue) and driest-quarter (P_{min}, light blue) precipitation for plants and animals. Rates are maximum-likelihood estimates of σ^2 across all plant and animal species. P values are based on likelihood-ratio tests between models with different rates between variables or the same rate (Supplementary Table 2).

animal clades showed significant relationships but relationships were negative in 74% and 94% of plant and animal clades.

H8. For both plants and animals ($n = 931$ and 1,053), climatic-niche breadths are dominated by seasonal variation within localities (Fig. 6a–d). Based on phylogenetic regression, WLNBT were significantly, positively related to SNBT, in both plants and animals ($R^2 = 0.39$ and 0.49). Similarly, WLNBP were significantly, positively related to SNBP in both groups ($R^2 = 0.52$ and 0.57). There were strong, positive relationships across almost all clades in both plants and animals, for both temperature and precipitation (Fig. 1).

H9. Temperature and precipitation niche breadths are positively related in both plants and animals ($n = 931$ and 1,053), rather than showing trade-offs (Fig. 6e,f). These relationships were significant ($P < 0.001$) but weak in both groups ($R^2 = 0.09$ and 0.01; Supplementary Table 2) based on phylogenetic regression. Analyses within each clade revealed that 95% and 71% of plant and animal clades had positive relationships, with significant relationships in 42% and 29%.

H10. Climatic-niche breadths are significantly related to niche position for both temperature and precipitation (Fig. 6g–j). Based on phylogenetic regression, SNBT significantly decreased with mean annual temperature for both plants and animals ($n = 931$ and 1,053; $R^2 = 0.12$ and 0.30). SNBP increased with mean annual precipitation ($R^2 = 0.34$ and 0.36). Within each group, 90% and 100% of clades showed negative relationships for temperature, with 58% and 88% significant. For precipitation, 100% of plant and animal clades showed positive relationships, with 63% and 59% significant.

Discussion
In this paper, we find surprisingly similar patterns of climatic-niche evolution in plants and vertebrate animals. We test ten predictions about rates of niche evolution and evolution of niche widths and find similar results for each one in plants and animals. As one way of summarizing this similarity, the proportion of clades in which results are at least consistent with each prediction is strongly related between plants and animals ($R^2 = 0.85$, $P < 0.001$, $n = 13$; Fig. 1).

This overall similarity is surprising, given the fundamental differences in the biology of these two groups and the idea that plants have broader tolerances to environmental variation than animals but are more sensitive to climate change[20]. Overall, our study represents a step towards uncovering whether there are general rules of climatic-niche evolution that span all organisms. Next, we discuss why niche evolution is similar between plants and animals and the broader implications.

Why is niche evolution similar in plants and animals? We addressed two main aspects of niche evolution: rates and widths. We discuss these topics in the order of our ten predictions.

In both plants and animals, rates were slow and not significantly different for any variables (H1). Slow rates are consistent with the concept of niche conservatism. Several population-level mechanisms may underlie niche conservatism, including selection against invading different climates, competition and limited genetic variation and gene flow that impede local adaptation[25,26]. Our results also confirm that rates of past niche change are typically much slower than projected climate change, by 10,000-fold or more[16,18]. This disparity in rates is consistent with widespread local extinctions that have already occurred in plants and animals (at similar frequencies[23]). These patterns contrast with the idea that plants are more sensitive to climate change than animals[20].

We found faster rates in younger species (H2), supporting earlier studies[16,18]. This result may reflect a general pattern of faster phenotypic rates over shorter timescales[28]. Furthermore, if niches are constrained to remain similar over time (for example, from conservatism), then rates will appear slower over longer timescales (for example, if sister species differ by 2 °C, the rate will be rapid if they split 0.2 million years ago (Ma) but slow if it was 20 Ma).

We found no consistent impact of latitude (H3) or niche widths (H6) on rates, contradicting earlier studies[18,29]. An earlier study[14] reviewed expected relationships between widths and rates but found no clear predictions. Hua[33] developed theory to explain how reduced tropical seasonality might influence temperature niche widths but did not include rates. Hua[33] suggested that reduced seasonality leads to narrower niche widths because of trade-offs between maintaining broad niche widths versus achieving higher
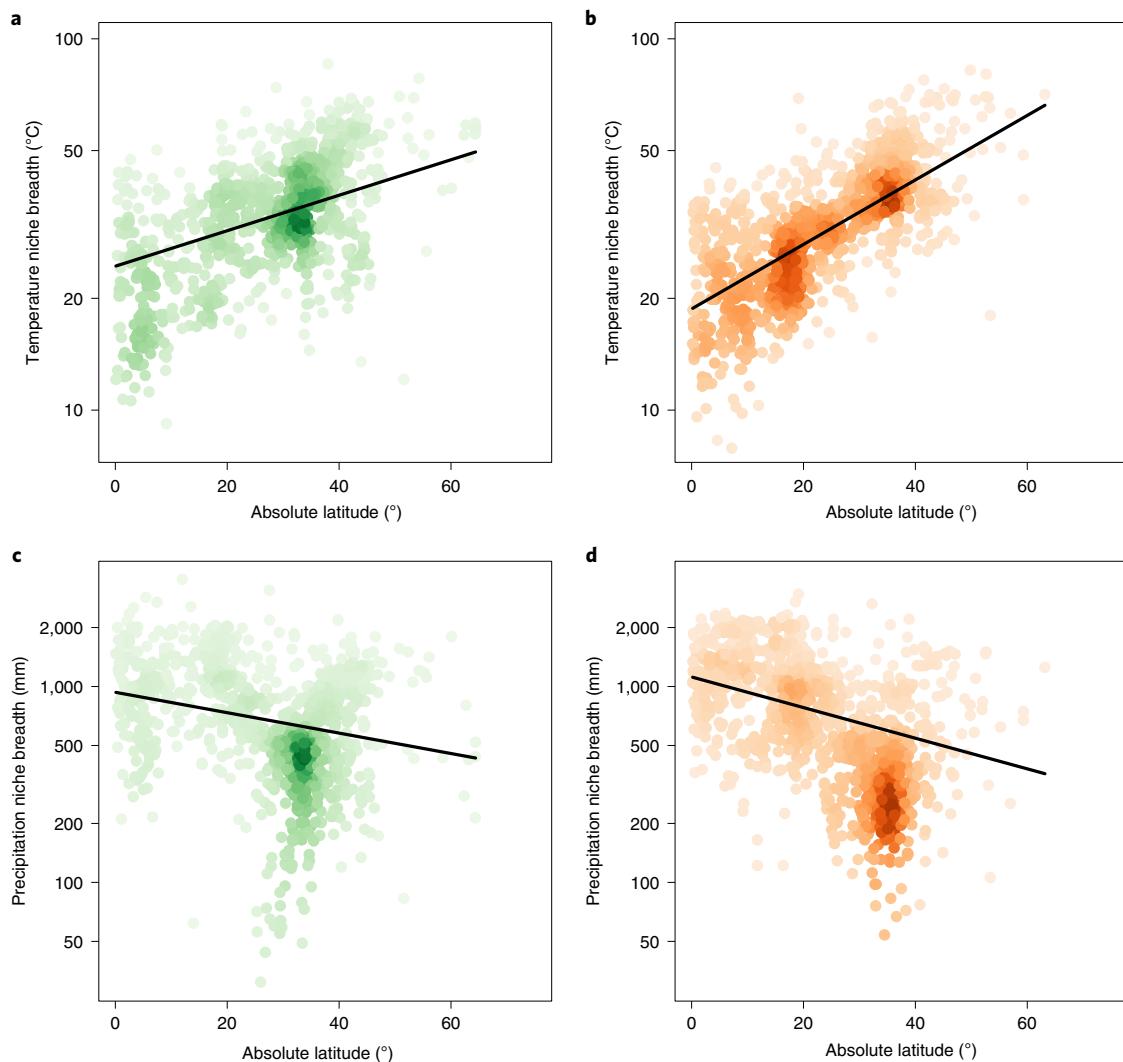
Fig. 5 | Relationships between niche breadths and absolute latitude of each species (H7). a,b, Temperature niche breadths for plants (n=931, green (**a**)) and animals (n=1,053, orange (**b**)). **c,d,** Precipitation niche breadths for plants (**c**) and animals (**d**). Rates are ln-transformed and darker colours indicate greater overlap of data points. Regression lines, R^2 and P values are based on PGLS (Supplementary Table 2).

performance at a narrower set of temperatures[33,34]. Importantly, the lack of a clear relationship between rates and latitude rejects the idea that latitudinal variation in rates drives the latitudinal richness gradient[5,14,33].

In both plants and animals, we found faster rates for minimum temperatures than for maximum temperatures (H4). Previous authors[30] suggested that physiological tolerances to cold evolve more quickly than tolerances to heat, given intrinsic physiological properties spanning both groups. Our results are consistent with this idea. However, these rate differences might also reflect that minimum temperatures generally decrease strongly from the equator to the poles, whereas maximum temperatures are more similar across latitudes[35]. This pattern might lead to more variability among species (and faster rates) for minimum than maximum temperatures. Future studies are needed to address whether these rate differences are related to physiology, geographic variability or both.

We also found faster rates among species in wettest-quarter precipitation than in driest-quarter precipitation (H5) in plants and animals. This prediction has not been proposed before. Like H4, this pattern might also be explained by physiological constraints or spatial variation in climate. Since all plants and animals require water, adapting to scarcer water in the driest quarter may be more

difficult than adapting to variation in precipitation in the wettest quarter[36], constraining the driest-quarter rate. Alternatively, spatial variability might explain the differences in rates instead. Specifically, driest-quarter precipitation (Bio17) can be similar between arid regions and mesic regions with more seasonal precipitation. In contrast, wettest-quarter precipitation (Bio16) may better reflect overall precipitation (Bio12), leading to more variation among habitats and species. For the species sampled here (n=2,087), the mean ratio of Bio16:Bio12 is 0.43 ± 0.11 whereas Bio17:Bio12 is 0.10 ± 0.06. Further research is needed to distinguish these explanations.

We also found that niche widths were generally similar between plants and animals. A previous study[20] predicted wider environmental tolerances in plants than in animals but did not test this prediction with climatic-niche data.

These similar niche widths may help explain some basic patterns in ecology and biogeography. Specifically, across regions and elevations, diverse biomes are defined by different climates, vegetation types and plant and animal species[37]. For example, in the southwestern United States, going from low to high elevations one finds desert, grassland, pine–oak forest and spruce–fir forest[37]. Although not all species in these life zones are confined to one zone, few occur in all zones. Similarly, there is extensive turnover in plant and
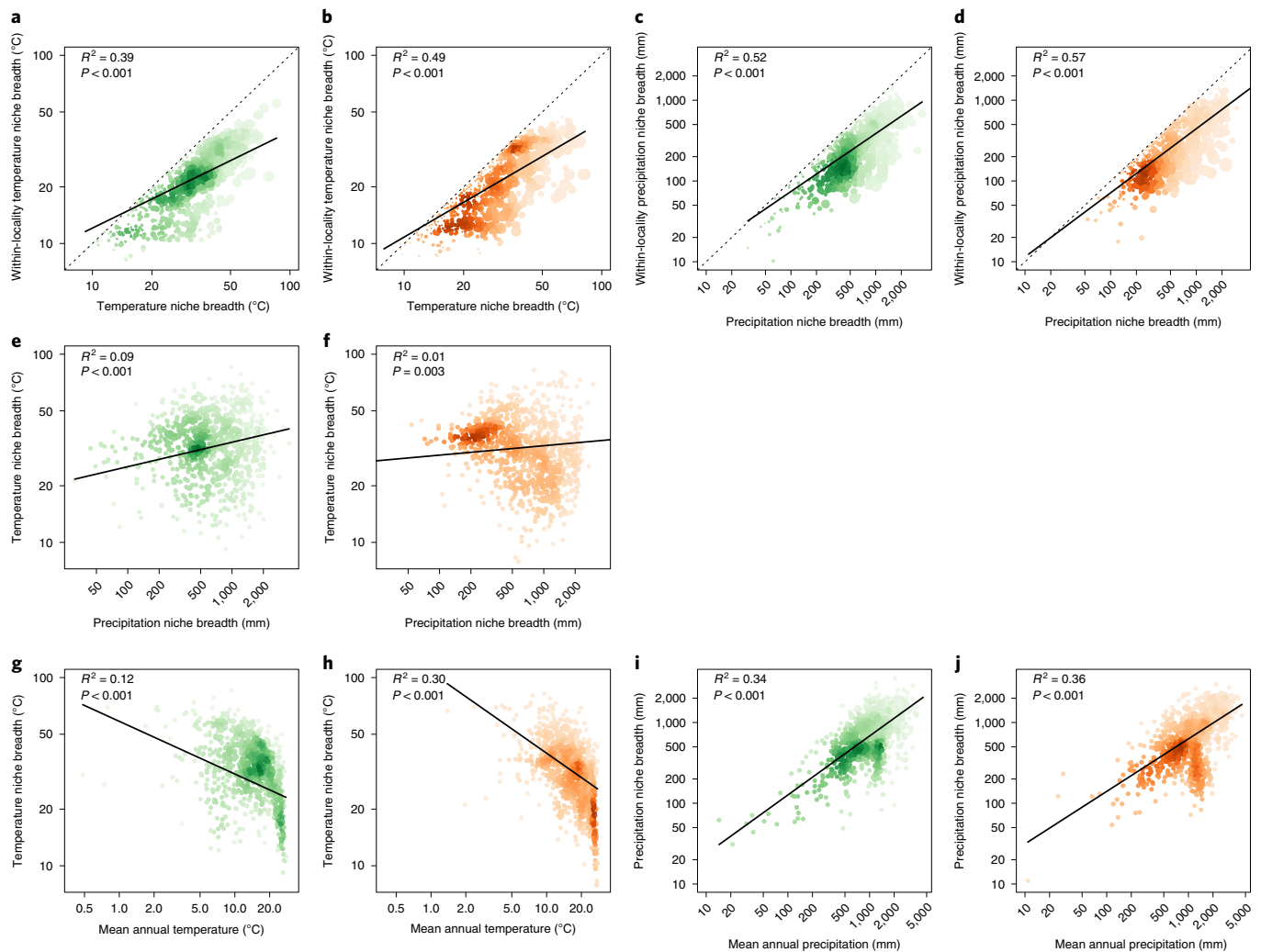
Fig. 6 | Relationships between mean within-locality and species-level niche breadths (H8), between temperature and precipitation niche breadths (H9) and between niche breadths and niche position (H10). a–d, H8: Temperature niche breadths for plants ($n = 931$, green (**a**)) and animals ($n = 1,053$, orange (**b**)). Precipitation niche breadths for plants (**c**) and animals (**d**). **e,f**, H9: Temperature and precipitation niche breadths for plants (**e**) and animals (**f**). **g–j**, H10: Temperature niche breadths and mean annual temperature for plants (**g**) and animals (**h**); precipitation niche breadths and annual precipitation for plants (**i**) and animals (**j**). In **a–d**, dashed lines show 1:1 reference lines, data points are scaled by the number of localities per species. Data are ln-transformed and darker colours indicate greater overlap of data points. Regression lines, R^2 and P values are based on PGLS (Supplementary Table 2).

animal species between adjacent biogeographic regions with divergent climates (for example, Nearctic versus Neotropical)[37]. An obvious explanation for these patterns is that most plant and animal species can occupy only a limited (and similar) range of climatic conditions. Our results here support this idea.

Why do plants and animals have similar niche widths? One explanation is that plant and animal species generally have similar physiological tolerance ranges, despite their divergent biology. Some physiological data[30] are potentially consistent with this idea, although they also suggest that many plants can tolerate somewhat hotter (>40 °C) and much colder conditions (<0 °C) than most vertebrates. An important challenge for future studies is to find comparable physiological measurements for plants and animals that are relevant to their climatic distributions for both temperature and precipitation.

Trade-offs in tolerances may be even more relevant for explaining similar niche widths. Plant and animal species can collectively tolerate very hot, cold, wet and dry climates. However, fewer species can tolerate all four extremes, especially if this requires conflicting adaptations[37,38]. Such trade-offs might confine most plant and

animal species to limited portions of the overall range of climates across the globe, even if the specific adaptations are very different in each group. Theory suggests that such trade-offs may generally underlie climatic-niche widths[33,34]. However, climatic niches may differ from physiological tolerances[30] and many other factors may influence climatic distributions (for example, competition), either alone or together[38].

Some predictions tested here were related to latitudinal variation in niche widths (H7, H8 and H10). Temperature niche widths were wider at higher latitudes and precipitation widths were wider at lower latitudes (H7), consistent with latitudinal patterns in seasonality[24]. Thus, species-level niche widths were dominated by within-locality niche widths (H8) and within-locality niche widths were dominated by seasonal variation[15]. This pattern suggests that most species are not composed of populations that are each adapted to a narrow range of conditions. Instead, each individual tolerates a broad range of conditions, similar to the species-level niche breadth. We also found that niche position and widths were related (H10), with wider temperature and precipitation niches associated with lower temperatures and higher precipitation. This pattern might

also have a latitudinal component (for example, both temperature and precipitation are high along the equator). These latitudinal patterns of seasonality and niche widths have been discussed for decades[24,31] but few studies (if any) documented them broadly in plants. We found similar latitudinal patterns in plants and animals.

Importantly, although some similarity in niche widths between plants and animals might be explained by latitudinal seasonality patterns, those patterns do not make this similarity inevitable or trivial. Imagine ten plant and ten animal species, all on the same mountain slope. In theory, each plant species could be restricted to a narrow range of elevations and temperatures (yielding narrow temperature niche widths), while each animal species occurred from the lowest to highest elevations (yielding wide niche widths). Thus, species niche widths depend partly on seasonal variation at each locality but also on the range of conditions that species occur in across localities (H8).

Moreover, we found positive relationships between temperature and precipitation niche breadths (H9), even though latitudinal seasonality patterns would predict a negative relationship[32]. This positive relationship presumably arises because widely distributed species have broader niches on both axes, whereas narrowly distributed species are narrower on both. These results reject the idea of a general trade-off between widths on different axes. However, since these positive relationships are weak, most variation on each axis is unrelated to the other.

Finally, relationships between niche position and niche width (H10) may be influenced by latitudinal seasonality patterns but these may not be the sole explanation. For example, arid and mesic habitats occur in both tropical and temperate regions. Species in drier regions had narrower niche widths for precipitation. These species will experience low precipitation during both the wettest and driest quarters, leading to narrow niche widths[32]. In contrast, species in the wettest environments may experience very different annual precipitation values over short spatial scales (leading to wide species-level niche widths) but still occur in very similar habitat[32]. Overall, niche position and niche width show different relationships for temperature and precipitation but similar patterns in plants and animals.

In summary, patterns of niche evolution are very similar in plants and animals despite obvious differences in their biology. The possible causes of these similar patterns include niche conservatism, physiological constraints, trade-offs and latitudinal patterns of seasonality. Disentangling these causes should be an exciting area for future research.

Conclusions and implications. In this study, we test ten predictions about climatic-niche evolution in plants and animals. We find very similar patterns between groups, despite fundamental differences in their biology. These results may help explain why plants and animals have similar responses to climate change and why biogeographic regions, biodiversity hotspots, biomes and species richness patterns are often similar between these groups[37,39–41]. Finally, our study represents another step towards finding general rules of ecology and evolution that span plants and animals.

Methods

Phylogenetic and climatic data collection. We focused on analysing patterns among closely related species in well-sampled clades. We searched for studies with both time-calibrated molecular phylogenies and matching climatic data for clades of plants and animals (Supplementary Dataset 5). For animals, we used 17 tetrapod clades that were analysed in a previous study on niche evolution[16]. These clades had trees with relatively complete species sampling (mean = 86.2% of described species included; median = 87.1%, s.d. = 16.2%, range = 50.3–100%). For plants, we searched Google Scholar (https://scholar.google.com) from August to October 2018, using three keywords: 'phylogeny', 'WorldClim' and the name of a clade or angiosperm family (for example, bryophyte, fern, conifer and Asteraceae). We searched within all major land plant groups, including angiosperms and six major non-angiosperm clades (bryophytes, cycadophytes, gnetophytes, lycophytes, pinophytes (conifers) and pteridophytes (ferns)). In addition to searching for

studies within these major clades, we also conducted searches within many angiosperm orders and families. There are 64 angiosperm orders, 34 with less than five families[42]. The other 30 orders have 339 families in total[42]. We searched all 77 families among the 34 smaller orders. For the 30 larger orders, we searched all families having more than the median number of species. In total, separate searches were conducted within ~250 of the 416 angiosperm families[42]. We found 37 studies with relatively complete species sampling for phylogenetic and climatic data (>45% of described species in the clade). We then contacted the authors and were able to obtain locality and/or climatic data for 19 plant clades (very few studies had all their relevant data publicly available). These 19 clades were also well sampled (mean = 74.5% of described species, median = 77.3%, s.d. = 17.5%, range = 45.9–100%).

For climatic data, we only used studies that included georeferenced localities from throughout each species' range (not studies focusing on one region). For most studies, the authors obtained locality data from GBIF (https://www.gbif.org) and indicated that they carefully checked localities for each species. Thus, they excluded localities outside the species' natural range. These authors extracted their climatic data from the WorldClim database[43], which was also used for all animal clades. Therefore, climatic data were comparable across all studies. The WorldClim database is based on average values from 1950 to 2000 from weather station data at ~1 km^2 resolution. If only localities were available from the authors (13 of 19 clades), we extracted the climatic data from the WorldClim database using the function extract in the R package raster[44] in R (v.3.5.1)[45].

Our predictions (Supplementary Table 1) involved six climatic variables: mean annual temperature (Bio1), highest and lowest annual temperatures (Bio5, Bio6; or maximum temperature of the warmest month and minimum temperature of the coldest month), annual precipitation (Bio12) and precipitation of the wettest and driest quarters of the year (Bio16 and Bio17). These variables include yearly extremes that can potentially set species' range limits and reflect climatic tolerances (Bio5, Bio6, Bio16 and Bio17), along with standard averages (Bio1 and Bio12).

The 17 animal clades (1,135 species) included all major clades of terrestrial vertebrates (tetrapods), including amphibians, squamates (lizards and snakes), turtles, crocodilians, birds and mammals. Sample sizes of localities per species ranged from 1 to 114,888 (mean = 405). The 19 plant clades (952 species) included conifers, monocots and eudicots, with sample sizes from 1 to 35,199 (mean = 350). We followed two plant studies in treating certain subspecies as distinct species, given their phylogenetic, geographic and ecological distinctness. The two clades were *Cucurbita*[46] (19 taxa sampled, including seven subspecies) and *Cremastosperma* and *Mosannona*[47] (35 taxa sampled, including three subspecies). We did not estimate new phylogenies for this study but methods of tree estimation and time calibration are briefly summarized in Supplementary Dataset 5. This dataset also includes the proportion of species sampled (relative to the total richness of the clade) for each study.

Estimating absolute rates of niche change. To estimate rates, we first calculated mean, maximum (90th percentile) and minimum (10th percentile) values among localities for each variable for each species (Supplementary Dataset 6). We performed analyses using all three values. We then estimated absolute rates of niche change for each species[16,18], to facilitate comparisons between groups. To find the best-fitting likelihood model of evolution for each climatic variable for each clade, we used the R packages ape v.5.2 and Geiger v.2.0.6 (refs. [48] and [49], respectively). We compared four models: white noise (WN; no phylogenetic signal, $\lambda = 0$), Brownian Motion (BM; strong phylogenetic signal, $\lambda = 1$), Ornstein–Uhlenbeck (OU; single optimum) and estimated lambda (LA; λ between 0 and 1). The best-fitting model had the lowest Akaike information criterion (AIC) score (Supplementary Dataset 7). The WN model is inappropriate for ancestral reconstructions and may be erroneously selected when there are few species sampled[18] (see Supplementary Appendix 2). Therefore, if the WN model had the best fit, we used the second-best model instead (Supplementary Dataset 7). Next, we transformed trees based on the best-fitting model and then reconstructed ancestral values for each node using phylogenetic generalized least squares (PGLS) in the R package caper[50]. To estimate the rate for each species for each variable, we took the absolute difference between the estimated value at its most recent ancestral node and the value for that species and divided this difference by the age of that node[16]. Rates were estimated using BM, OU and LA models. The mean, maximum and minimum values across localities for each variable for each species were also used (Supplementary Table 7 and Supplementary Dataset 8). The main results used the mean values and best-fitting models but alternative approaches yielded similar rates (Supplementary Appendix 2).

Within the 17 animal clades, we used all 1,135 species to infer rates. A previous study[16] used only selected sister-species pairs to estimate rates (540 species) from subclades with >80% of known species sampled. We found only slightly higher mean rates for these 540 species (Supplementary Table 9). Therefore, we used all 1,135 species here. For plants, selecting actual sister species was more difficult, given the lower proportional sampling of species in trees. Therefore, we estimated rates for all 952 plant species and then tested for a relationship between mean rates and sampling proportions across clades. We found no significant relationships (Supplementary Table 10). Therefore, we assumed that using all the species in each plant clade would not strongly bias the analyses.

Calculation of niche breadth. Six indices were used to describe niche breadths[15] as follows. (1) The within-locality niche breadth for temperature (WLNBT) is the difference between the maximum temperature of the warmest month (Bio5) and the minimum temperature of the coldest month (Bio6) for each locality. The mean WLNBT across localities for each species was calculated. (2) The species niche breadth for temperature (SNBT) is the difference between the maximum Bio5 and the minimum Bio6 across all the species' sampled localities. (3) The ratioT is the mean WLNBT divided by SNBT for each species. (4) The within-locality niche breadth for precipitation (WLNBP) is the difference between the wettest-quarter precipitation (Bio16) and driest-quarter precipitation (Bio17) for each locality. The mean across localities was used as each species' WLNBP. (5) The species niche breadth for precipitation (SNBP) is the difference between the maximum Bio16 and the minimum Bio17 across all localities. The ratioP is the mean WLNBP divided by SNBP for each species. The ratioT and ratioP estimate how much within-locality niche breadth contributes to species niche breadth.

For these indices, we removed species with only one locality (given that their ratioT and ratioP must be 1.00). Resampling analyses[15] indicate that including species with five or fewer localities should not bias ratioT or ratioP. Therefore, we excluded only species with single localities, leaving data for 931 plant species (21 single-locality species removed) and 1,053 animal species (82 species removed). We did not otherwise correct for differences in range size or numbers of localities among species. Given that niche breadth might determine range size and range size might determine the number of localities[51], excluding species with few localities might bias the overall sample of niche breadths. Data on niche widths for these 1,984 species are given in Supplementary Dataset 9.

Combining trees. We performed statistical analyses within each clade. We also performed the same analyses across all sampled plants and across all sampled animals. To generate large-scale trees spanning clades within each group, we assembled higher-level time-calibrated phylogenies from previous studies (see below). We then included only one species per clade and then replaced that species with the species-level tree for that clade. The 19 plant clades were from 15 families, with two, two and three clades from Bignoniaceae, Cucurbitaceae and Annonaceae, respectively. We used a tree for land plant families[52] to represent conifers. We also used a recent tree of angiosperm families[53]. At the genus level, we used 11 species to represent the 11 sampled genera in Bignoniaceae, Cucurbitaceae and Annonaceae. We extracted this 11-genus tree using the R package S.Phylomaker[54]. This package uses a large-scale angiosperm tree[55] as a backbone and is updated for species-level trees. We used the function bind.tree in ape to combine trees across genera and families.

We combined the 17 animal clades using a time-calibrated tetrapod tree[56]. We then combined the animal and plant trees using a time-calibrated kingdom-level tree[57]. This final tree contained 2,087 species. All trees are given in Supplementary Dataset 10, including the tree for each clade, for all plants, all animals and the combined animal–plant tree.

Data analyses. To test most hypotheses (H2, H3 and H6–H10), we used PGLS regression in caper[50]. For the six rate variables, six niche-breadth variables and four other variables tested (species age, absolute latitude, Bio1 and Bio12), we tested whether each variable was normally distributed (within plants and animals) using the Shapiro–Wilks test in R. The raw data were not normally distributed for any variable but most variables (12 of 16) were after ln-transformation (Supplementary Figs. 4 and 5 and Supplementary Table 11). For the remaining four variables (absolute latitude, WLNBT, ratioT and ratioP), we examined whether histograms of their distributions fit normal distribution curves (bell shaped with small gaps and few outliers[58]). Three of the four fit this pattern (all but latitude) and small deviations from normality (potentially caused by large sample sizes) should not strongly impact the results[58]. We used ln-transformed variables in H2–H10. However, neither the original nor ln-transformed values of absolute latitude were normally distributed. Therefore, we also performed non-parametric Spearman's rank correlation for H3 and H7. These results were generally similar to those from PGLS (but see Supplementary Table 12 for details). These non-phylogenetic results are included in Supplementary Datasets 2 and 4.

If climatic niches evolve faster in younger clades (H2), we expect a negative relationship between a species' evolutionary rate and the node age of its most recent common ancestor. We predicted (H3) positive relationships between each species rates for temperature variables and the species absolute latitude (average latitude across localities in the species range, then transformed to the absolute value). We predicted negative relationships between latitude and precipitation rates (H3). If climatic niches evolve faster given wider species niche widths (H6), we expect positive relationships between rates and niche breadths for both SNBT and SNBP. For H7, temperature niches are expected to be wider in temperate climates, which should yield positive relationships between SNBT and absolute latitude. Similarly, precipitation niches are expected to be wider in the tropics, presumably yielding negative relationships between SNBP and absolute latitude. For H8, if niche breadths are dominated by seasonal variation within localities, we expect ratioT and ratioP to be >0.5. We also expect WLNBT to be positively related to SNBT and WLNBP to be positively related with SNBP. We tested if SNBT is positively related to SNBP (H9). We tested for relationships between niche breadths

and niche position (H10), by testing relationships between SNBT and Bio1 and between SNBP and Bio12.

H4 predicts that minimum annual temperatures (Bio6) evolve faster than maximum annual temperatures (Bio5). Similarly, H5 hypothesizes faster rates of evolution among species in wettest-quarter precipitation (Bio16) than driest-quarter precipitation (Bio17). For each pair of variables (using the raw data[59]), we performed a likelihood-ratio test (LRT) comparing the likelihood for the observed rates for each variable and for rates set to be equal between the two variables[59]. We used the Nelder–Mead method for function minimization for optimization convergence, using available R code[59]. We allowed trait covariation in each model. For H4 and H5, we estimated overall rates across each clade (using the maximum-likelihood estimate of σ^2; Supplementary Dataset 3). For our other analyses, we used rate estimates for individual species, which allowed us to relate these rates to attributes of species (for example, age, latitude and niche width), which was not possible using clade-wide values of σ^2. However, we also used phylogenetic paired t-tests to compare species-level rates (ln-transformed) for these two hypotheses (Supplementary Dataset 3). We used the function phyl.pairedttest in the R package phytools v.0.6–44 (ref. [60]).

We performed analyses for plants and animals overall and for each clade separately (Supplementary Datasets 1–4). We also compared (ln-transformed) rates and niche breadths between plants and animals directly using three methods, with group membership (plant versus animal) as a categorical factor (Supplementary Table 5). First, we used PGLS to test for differences between clades. Second, we used phylogenetic ANOVA to test if the observed F-values differed from null distributions (1,000 phylogeny-based simulation replicates). All residuals were normally distributed based on examination of histograms (Supplementary Fig. 6). Third, we used conventional two sample t-tests (in R), without phylogeny. Phylogenetic ANOVA was performed using the function phylANOVA in the R package phytools v.0.6–44 (ref. [60]).

The R codes used in these analyses are given in Supplementary Dataset 11. All the data used in these analyses are given in Supplementary Datasets 1–10. However, the full climatic data for each locality for each species (summarized in Supplementary Datasets 8 and 9) are given in Supplementary Dataset 12.

Potential caveats. We acknowledge several caveats about our analyses. First, our findings depend on the hypotheses we examined. We focused on predictions that were testable in both groups. For example, variables specific to a group might explain additional rate variation within that group (for example, endothermy in animals[18,61] and growth form in plants[17]). Our exclusion of these variables might explain some noise (for example, low R^2) in our analyses of rates within groups but these within-group patterns were not our primary interest here.

Second, our sampling of animal clades was limited. We included only terrestrial vertebrates, whereas most animal species (~80%) are arthropods[62]. However, we know of few datasets for arthropods (or other invertebrates) with climatic data and time-calibrated trees for well-sampled clades. Moreover, our sampling of vertebrate clades was broadly representative. Therefore, summarizing patterns among these clades should be meaningful (whereas inclusion of a few arthropod clades among 17 vertebrates clades might be problematic). Nevertheless, a previous analysis of rates among populations[18] included some arthropods and found broadly similar rates relative to vertebrates. Inclusion of arthropods should be a priority for future studies. Our sampling for plant clades (17/19 angiosperms) reflects the fact that most plant species (~90%) are angiosperms[63].

Third, our estimates of climatic-niche variables could be inaccurate in some species. For example, a species' niche width may be underestimated if the coldest, hottest, driest or wettest locality in a species' range was unsampled. However, this should not bias our conclusions, since this could happen in any or all species. Similarly, estimates of mean values across a species range may be biased by differences in access and collection efforts across the range[64,65]. However, this should apply across groups and our rate estimates were similar using different ways of summarizing rate variation across localities (means versus extremes; Supplementary Table 7).

Finally, we focused on realized climatic niches (climatic conditions where species occur), not the fundamental niche (conditions where they could occur given physiological tolerances alone[1]). Fundamental and realized niches can differ, given various abiotic and biotic factors that might prevent species from occurring in locations they can physiologically tolerate[1,2]. However, data on physiological tolerances do not directly estimate fundamental niches. For example, physiological tolerances might reflect when species are active (summer versus winter and day versus night) and microhabitats (shade versus sun), rather than large-scale climatic distributions. Plants and animals could still have very different physiological tolerances to heat, cold and drought. Intriguingly, our results suggest that such differences (if they occur) do not lead to consistent differences in their rates and patterns of climatic-niche evolution.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Supplementary Datasets 1–12 are available on Dryad (https://doi.org/10.5061/dryad.wh70rxwjm).

Code availability
All the R codes used in this study are available in Supplementary Dataset 11 on Dryad (https://doi.org/10.5061/dryad.wh70rxwjm).

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Author contributions

H.L. and J.J.W. designed the study and wrote the paper. H.L. performed analyses. All authors contributed to revisions.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-020-1158-x.

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Software and code

Policy information about availability of computer code

Data collection	Some data collection was performed using the R package raster version 2.8-19
Data analysis	Data analysis was conducted using R version 3.5.1, and the following R packages: ape version 5.2, Geiger version 2.0.6, caper version 1.01, S.Phylomaker, and phytools version 0.6-44

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data are available in the Supplementary Information as Datasets S1–S10. Additional data are in Dataset S12.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our study compares patterns of climatic niche evolution between plants and animals using phylogenetic methods and data from 19 clades of plants and 17 clades of animals (total of 2087 species).
Research sample	Our study used data from 19 clades of plants and 17 clades of animals and a total of 2087 species. The data were mostly taken from published studies, and included the phylogeny for each clade and data on geographic localities for each species and climatic niche data from each locality. In some cases, we extracted climatic niche data (from a public database) from localities from which climatic data were not available from the original study.
Sampling strategy	We included all plant and animal clades with the relevant information on phylogeny and climatic niches. We only included clades that were relatively complete, with >45% of the known species included in each clade. We searched for relevant clades using Google Scholar from August to October of 2018.
Data collection	The study compared climatic niche evolution in plants and animals. We used phylogenetic, climatic and/or locality data from previously published studies. For published studies with locality data but not climatic data, we downloaded climatic data for each locality from a public database (WorldClim).
Timing and spatial scale	Our data were on climatic niches of plants and animals. These were obtained from geographic localities. We did not perform field sampling ourselves to obtain these data: they were from thousands of species found all over the world.
Data exclusions	Data were excluded for species with only one locality when calculating the contribution of each locality to overall niche breadth.
Reproducibility	Our study is not based on experiments. It is based on comparisons of climatic niche evolution in plants and animals over macroevolutionary timescales.
Randomization	There was no random allocation into groups. We are comparing climatic niche evolution in plants and animals, not in random groups.
Blinding	Blinding was not relevant to our study. We are comparing climatic niche evolution in plants and animals.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology
☒	Animals and other organisms
☒	Human research participants
☒	Clinical data

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging