

1 Title page

2 **Article title:** The realised velocity of climate change reveals remarkable idiosyncrasy of species' distri-
3 butional shifts

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10 To date, our understanding of how species have shifted in response to recent climate warming has
11 been based on a few studies with a limited number of species. Here we present a comprehensive,
12 global overview of species' distributional responses to changing climate across a broad variety of
13 taxa (animals, plants, and fungi). We characterise species' responses using a metric that describes
14 the realised velocity of climate change: how closely species' responses have tracked changing cli-
15 mate through time. In contrast to existing 'climate velocity' metrics that have focused on space,
16 we focus on species and index their responses to a null expectation of change in order to examine
17 drivers of inter-specific variation. Here we show that species are tracking climate on average, but not
18 sufficiently to keep up with the pace of climate change. Further, species responses are highly idiosyn-
19 cratic, and thus highlight that projections assuming uniform responses may be misleading. This is
20 in stark contrast to species' present-day and historical climate niches, which show strong evidence
21 of the imprint of evolutionary history and functional traits. Our analyses are a first step in exploring
22 the vast wealth of empirical data on species' historic responses to recent climate change.

23 The natural environment is changing rapidly. Over the last century, habitats have become increasingly
24 fragmented and isolated¹, the climate has become warmer, and extreme climate events more frequent².
25 Biological diversity—the species of plants and animals with which we cohabit the Earth—has responded
26 predictably. Present-day extinction rates are estimated to be up to three orders of magnitude greater than
27 background rates³ and are projected to increase further over the next several decades⁴. Current estimates
28 suggest that over one million species may be threatened with extinction⁵, and that we have experienced a
29 50% decline in animal diversity in the past 40 years⁶.

30 The main direct human-induced drivers that impact biodiversity now are habitat loss⁷ and fragmentation¹,
31 but climate change is likely to become a dominant driver in the next few decades^{8–10}. Projected impacts
32 of climate change on biodiversity have attracted much attention, but the uncertainty around the magnitude
33 of future extinctions (e.g., 7.9%¹⁰ vs. 37%¹¹ of species) highlights the inadequacy of current forecasts. In
34 the face of changing climate species must either shift in space, to track favourable conditions, or time, for
35 example, flowering and breeding earlier. Evidence suggests they are doing both^{8,12–14}, but not all species
36 are responding equally. Some species are expanding their distributions, sometimes invasively¹⁵, and some
37 species are flowering later¹⁶; species may also be simply becoming less predictable¹⁷, perhaps as evolved

38 responses to environmental cues break down. Simply quantifying species' mean responses ignores the
39 important variability in responses among species¹⁸. Developing robust predictions of ecological responses
40 to climate change thus requires data from diverse species, ecosystems, and climates to account for this
41 large inter-specific variation.

42 The velocity of temperature change—the rate a species would have to shift its range to maintain constant
43 temperature—has been calculated at an average of 0.42 km/yr¹⁹. A meta-analysis of taxonomic groups
44 estimated the average pole-ward shift in species' distributions has been approximately 1.69 km/yr¹⁴, sug-
45 gesting that species might be capable of keeping pace with shifting climate. Yet even this estimate is
46 derived from just 21 studies with limited taxonomic coverage (361 birds, 9 mammals, and no plants), and
47 critically any single point estimate does not reflect the large variation in responses among species or within
48 taxa. Here we leverage the vast volume of distributional data stored in digital data repositories²⁰, repre-
49 senting over 10,000 species of plants, fungi, mammals, birds, reptiles, amphibians, and insects, to provide
50 the first global synthesis of species distributional responses to climate change. By contrasting historical
51 niche dimensions with those of the present day, we can characterise the realised biotic velocity of climate
52 change, which represents the relative degree to which species track climate across space.

53 We show that, on average, species' historical (pre-1980) ranges have warmed significantly, and that species
54 have generally shifted their distributions to ameliorate this warming, but not sufficiently to keep pace with
55 climate change. Yet this general pattern masks a remarkably degree of variability in species responses, and
56 many species' ranges are now even warmer than if their distributions had remained static. Further, we find
57 that, while species' niche dimensions are strongly predicted by their evolutionary history and functional
58 traits, the same is not true of their degree of tracking. Thus while species' distributions are reasonably
59 predictable, their changes in distributions are not.

60 Results and discussion

61 **A comparative index of species' niche tracking.** We propose a measure that captures the extent to which
62 a species' distribution is tracking climate by standardising its observed niche change by the change it
63 would have experienced had it not shifted its distribution. Formally, we define this as:

$$track_{\tau} = \frac{current_{\tau} - past_{\tau}}{projected_{\tau} - past_{\tau}} \quad (1)$$

64 Where $current_{\tau}$ is a given quantile (τ) of a species' climatic distribution across its present-day range,
65 $past_{\tau}$ the same quantile of a species' range in the past, and $projected_{\tau}$ the same quantile of a species' past
66 range under present-day climatic conditions. This index should be calculated separately for temperature,
67 pollution, or whatever environmental variable is of interest. Thus a $track$ of 0 would indicate a species
68 that has tracked changing climate perfectly, while a $track$ of 1 would be consistent with a species that
69 had not moved whatsoever to track changing environmental conditions. Values between 0 and 1 suggest
70 moderate tracking, while values greater than 1 or less than 0 represent a change in climate relationship
71 greater than if the species had not moved at all. Uncertainty in either species' past or current ranges can
72 be accounted for through a bootstrap procedure, whereby the past and current distributions are re-sampled
73 to standardise sampling across time periods (see methods).

74 Our approach has two main innovations: its focus on (1) the whole of a species' distribution and (2) ex-
75 pected change. (1) When estimating species' range distributions we typically focus on species' limits²¹
76 (e.g., upper and lower quantiles) while in community ecological²² and macro-evolutionary²³ studies we
77 tend to focus on central tendencies (e.g., the median). However, there is no strong *a priori* reason that
78 species can, or must, track all quantiles equally. Indeed some evidence suggests different constraints on
79 species' warm-range limits versus their cool-range limits, with biotic interactions more influential in the
80 former, and climate determining the latter²⁴. It is possible, therefore, that the drivers of species' range
81 edges and centres may be diverging under climate change. Our approach is to check all quantiles of a
82 species' distribution. (2) The magnitude of experienced and projected climate change shows substantial
83 geographical variation¹⁹, and so species' responses might thus be expected to also vary in space. We sug-
84 gest that species' distributional responses should be measured on the basis of the magnitude of change

to which they are exposed, and the denominator of our index re-scales species' change around an expectation under distributional stasis. This change reflects the magnitude of ecological and evolutionary selection, and while there are many ways of addressing this, we suggest ours is perhaps the simplest and most transparent, so represents a fair starting point. We note that we could also rescale our index according to the distance that would need to be travelled to maintain climate stasis (*sensu* Loarie *et al.*¹⁹), but prefer to present here a unitless index of tracking, which is simpler to compare across taxa and between biogeographic regions.

Niche tracking across the tree of life throughout the past sixty years. To assess the extent to which species have tracked climate, we used the most comprehensively sampled time-series data for species' distributions (GBIF²⁰) and climate (UEA's CRU²⁵). This represents over 630 million raw occurrence records collected over the past century. We focus on five quantiles: the 5th, 25th, 50th (median), 75th, and 95th. Here, we present species' range data collected from 1955–2015 for 10,700 species (4,879 plants, 1,517 fungi, 273 mammals, 433 birds, 147 reptiles and amphibians, and 3,451 insects), each observation matched to one of nine climate variables in the year in which they were sampled (mean, minimum, maximum temperature, precipitation, 'rainy-day' frequency, vapour pressure, potential evapotranspiration, 'frost day' frequency, and cloud cover). In the methods we give more detail of our reproducible analysis pipeline, and in the supplementary materials provide instructions for repeating our analyses with different data curation and cleaning choices. Our metric was designed to account for known biases in the GBIF data²⁶, and in the methods we outline our simulations which address the influence of sampling uncertainty.

Almost all species are tracking some climate variable through time (99.5% have at least one $track_\tau$ between 0 and 1). Most species are, to some extent, tracking temperature (see Figure 1); 65% track at least one quantile and 43% track at least two. The three temperature indices are, however, the least-tracked of any climate variable, while precipitation is the most-tracked (86% of species track at least one of its quantiles). Notably, however, many taxa are not tracking climate through time, and many have experienced more change than if their distributions had remained static. Just as most species are tracking at least one quantile of one climate variable, 99.9% of species have 'overshoot' (have a $track_\tau$ less than 0; for example becoming colder in a warming region) in at least one quantile of at least one climate variable. As we show in Figure 1, these results are consistent with our null simulations where species' range change is a combi-

113 nation of essentially random movement and a moderate degree of subsequent climate filtering. Thus while
114 our results confirm that, by-and-large, species are tracking climate change, the magnitude of this varies
115 across species, taxa, and aspects of climate (see Figure 1). For example, while fungi and insects are, on
116 the whole, broadly tracking the median of temperature (median $track_{50\%}$ of 0.46 and 0.64, respectively),
117 plants and mammals track temperature (median $track_{50\%}$ of 1.16 and 1.07, respectively) more poorly than
118 precipitation (median $track_{5\%}$ of 0.79 and 0.89, respectively).

119 **Idiosyncratic drivers of species' tracking.** To examine the potential drivers of species' ranges and range
120 tracking, we first examined the phylogenetic signal of species' climate quantiles. We focused on mammals,
121 birds, reptiles, and plants, since we were able to find broadly inclusive, dated phylogenies for these taxa.
122 We found strong evidence of phylogenetic signal in species' past (median Pagel's λ^{27} of 0.60) and current
123 (median λ of 0.57) distributions, but limited signal in our index (median λ of <0.001). Past climate showed
124 stronger phylogenetic signal than our index in 158 of all 180 (4 taxa, 5 quantiles, and 9 climate variables)
125 possible taxon-climate-quantile combinations (144 for current climate; see Figures 2 and 3). This confirms
126 the known result that species' current-day and past ranges are strongly influenced by evolution²⁸, but
127 suggests that species' realised velocity of change (our tracking index) may be associated with different
128 factors.

129 We additionally examined species' traits as potential drivers of species' distributions and potential to track
130 changing environment. We focused on mammals, birds, and plants, since global, openly-released trait
131 datasets exist for these taxa. Again, we found statistically significant associations between traits and
132 past distributions of 191 of 270 (at $\alpha_{5\%}$; 6 traits, 9 climate variables, and 5 quantiles) taxon-climate-
133 quantile combinations (193 for current distributions), but not between the traits and our tracking index (13
134 combinations or 5%; see Figure 3). While the traits we used are strongly associated with species' climate
135 responses^{29,30} (hence their strong predictive power of species' distributions, but not degree of tracking),
136 we emphasise that we could not find sufficient data to assess the potential impact of dispersal ability³¹.
137 These findings, while surprising, are in keeping with emerging evidence that species' traits are a relatively
138 poor predictor of change at range edges³².

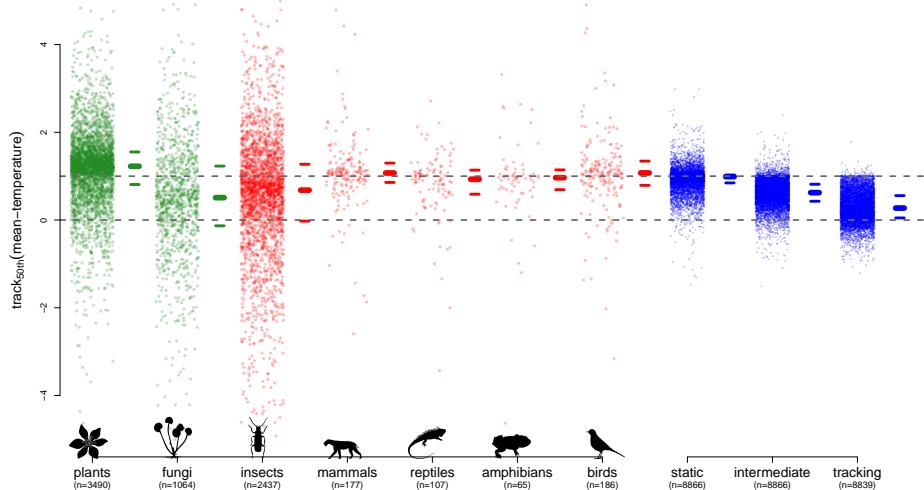
139 **Species' movement through climate space is disconnected from their position within it.** Given our
140 index is poorly predicted by traditionally important variables, we now consider whether index values are

141 predictive of each other. It is well known that the axes of global climate are not independent and that
142 they are not changing independently^{2,25}, and so we would expect species' relative tracking of climate
143 to show similar patterns. As we show in Figure 4, principal components analysis of species' current
144 and past climate distributions, which we refer to as their climate space, shows strong correlations across
145 climate variables. Yet our index does not; species' relative degree of tracking is both of much higher
146 dimension (the amount of variance explained by each principal component axis is similar) and shows
147 relatively less correlation across climates axes . We argue, therefore, that while species' positions in
148 climate space show strong associations, species' relative tracking of their position in climate space does
149 not. This result explains the poor predictive power of species' traits and evolutionary history for our index:
150 the ecological and evolutionary rules that determine species' climate relationships are changing. Thus, in
151 our analysis, we can explain species' current distributions only by the degree to which they resemble past
152 distributions.

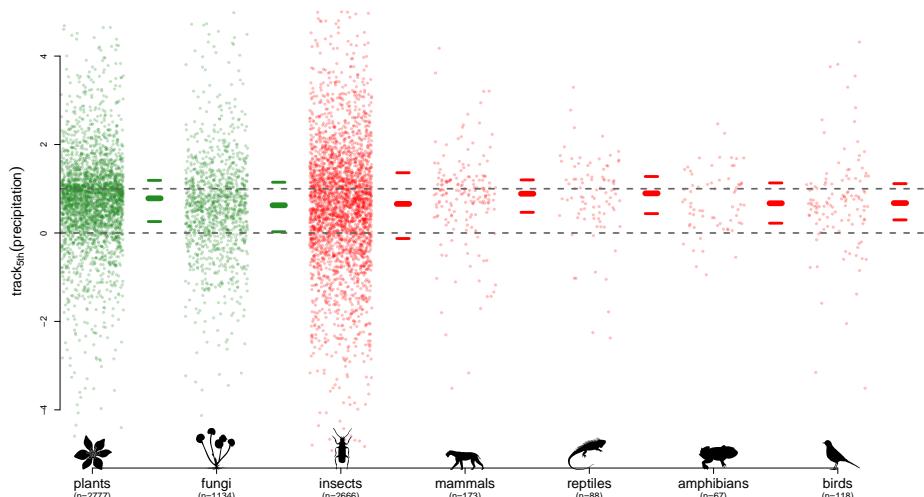
153 There are alternative explanations for our results, of which we highlight three: (1) we are ignoring im-
154 portant niche axes, (2) we are ignoring biotic interactions, and (3) our index highlights random variation
155 in distribution. (1) Our climate variables are not all-encompassing, and we ignore other drivers such as
156 geology and habitat-type. Yet we do detect strong pattern in current and past distributions, suggesting that
157 the absence of pattern in our indices is meaningful. (2) Competition and facilitation among species are
158 likely strong drivers of species' ability to track climate³³. Yet, again, they are surely also likely to have
159 driven species' past distributions, and so it is unclear to us why only our metric, and not also current and
160 past distributions, is so poorly predicted by our trait and phylogenetic data. (3) If species were perfectly
161 tracking climate, $current_{\tau}$ would be equal to $past_{\tau}$ and so our index values could reflect sampling error
162 or some other purely stochastic input. Yet such noise, if truly random, would mean our empirical index
163 values would be centred at 0 or resemble our simulated data, neither of which is the case (see Figure
164 1).

165 Conclusion

166 Our results are consistent with the processes underlying species' responses to climate change being distinct
167 from those that generated their distributions in the past. This is in keeping with emerging evidence from the
168 paleo-ecological literature that species' historic ranges were more variable than previously thought, and
169 seemingly influenced by different environmental factors than today^{34,35}. During and after the last ice-age,
170 for example, 'no-analogue' conditions generated previously-unseen species assemblages³⁶. Equally, our
171 observation of idiosyncrasy in species' degree of tracking is consistent with species' population crashes
172 (and so extinctions) becoming less predictable during previous mass extinction events^{37,38}. We call upon
173 others to examine the additional drivers of our metric of relative change, and to extend its definition to
174 include more nuanced definitions of climate space. We predict, however, that if the current mass extinction
175 event continues, it is likely that patterns of idiosyncrasy among species' declines and distributional changes
176 will become more common.



(a) $track_{50\%}(\text{mean-temp})$



(b) $track_{5\%}(\text{precipitation})$

Figure 1: Most species are tracking some aspect of climate, but there is pronounced variation among species and clades. In (a) we show the 50th quantile (median) of our tracking index of mean annual temperature, and in (b) the 5th quantile of our index of precipitation. On the left of each plot, our seven major taxonomic groups plotted (in green for plants and fungi, and in red for animals). At the far-right of (b), we show the output from our simulations of species that are perfectly tracking, imperfectly tracking, or not tracking climate at all (in blue; see Methods for details). To the right of each distribution of points the median (thickest line) and inter-quartile range (thinner lines) are shown as horizontal lines for each distribution. While the majority of species are tracking global climate to some extent, there is profound variation among species and clades. Figure 1a makes clear the variation among and within taxonomic groups; the distributions of fungi, insects, and reptiles are, broadly, tracking changes in mean temperature well, while other taxa (*e.g.*, mammals and plants) are not. Comparing Figures 1a and 1b makes clear how different taxonomic groups and species may be tracking different aspects of climate; plants are broadly tracking the lower-limit of precipitation, for instance.

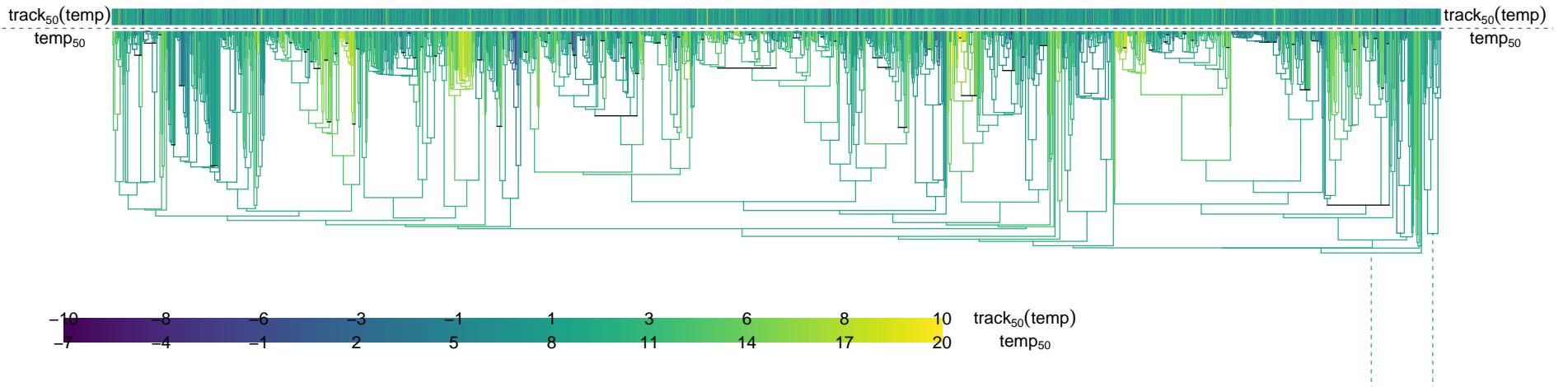


Figure 2: Despite strong phylogenetic signal in species' static distributions, species' changes in distributions are not phylogenetically patterned. Here we show the plant tree of life, with the two oldest branches shortened for compactness (emphasised with dashed lines). Internal branches are shaded by ancestral state reconstructions, assuming Brownian motion, of species' median mean-temperature in the past. Phylogeny tips are coloured according to the track index of the same underlying data (compare with Figure 1). This general pattern of strong phylogenetic signal of climate (shown by the coloured pattern to the internal branches), but not of degree of tracking, is characteristic of almost all of our underlying climate data (see also Figure 3).

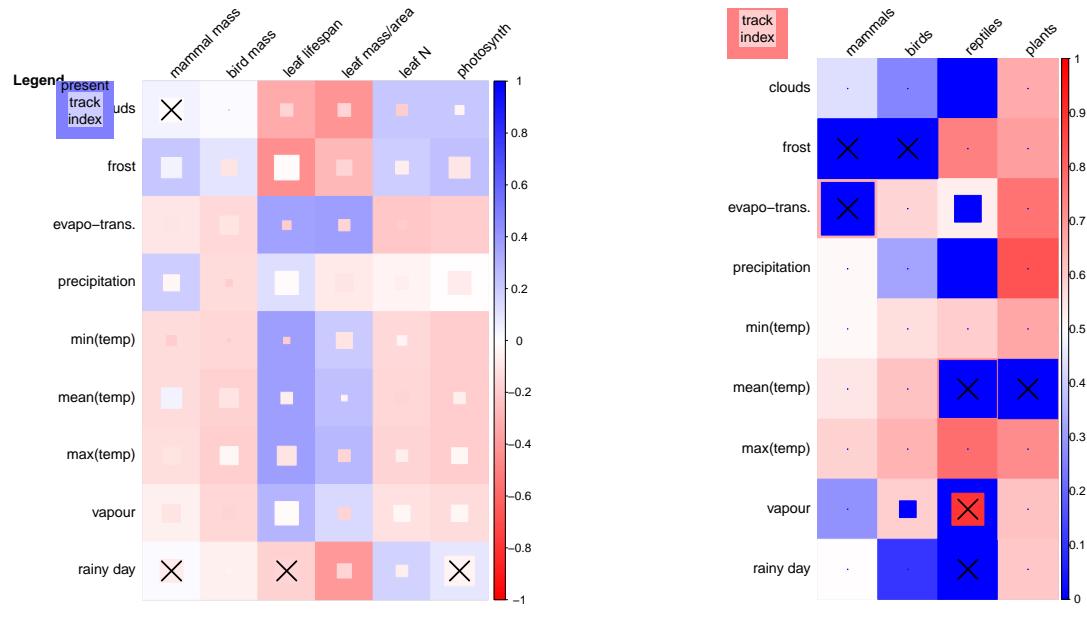


Figure 3: Species' static climate variables show strong trait correlations and phylogenetic signal, but their relative degree of tracking does not. In (a), we show the correlation (Pearson's ρ) between the median of each climate variable (rows) with each of our included traits (columns) using colour (see legend at the right). In each cell, the outer, larger box depicts the correlation between species' present-day climate and the trait, while the smaller, inner box the correlation for species' relative tracking (whose size is proportional to intensity of correlation). The 4 (of 54) track-index correlations that are statistically significant (at $\alpha_{5\%}$) are highlighted with crosses. In (b), we show, for each taxon, the phylogenetic signal (Pagel's λ^{27}) of major climate variables and relative tracking indices (rows) using colour (see legend at the right). As with (a), in each cell the outer, larger box depicts the correlation between species' present-day climate and the trait, while the smaller, inner box the correlation for species' relative tracking (whose size is proportional to phylogenetic signal strength). The single track-index metric for which phylogenetic signal was stronger than the underlying data is highlighted with a cross.

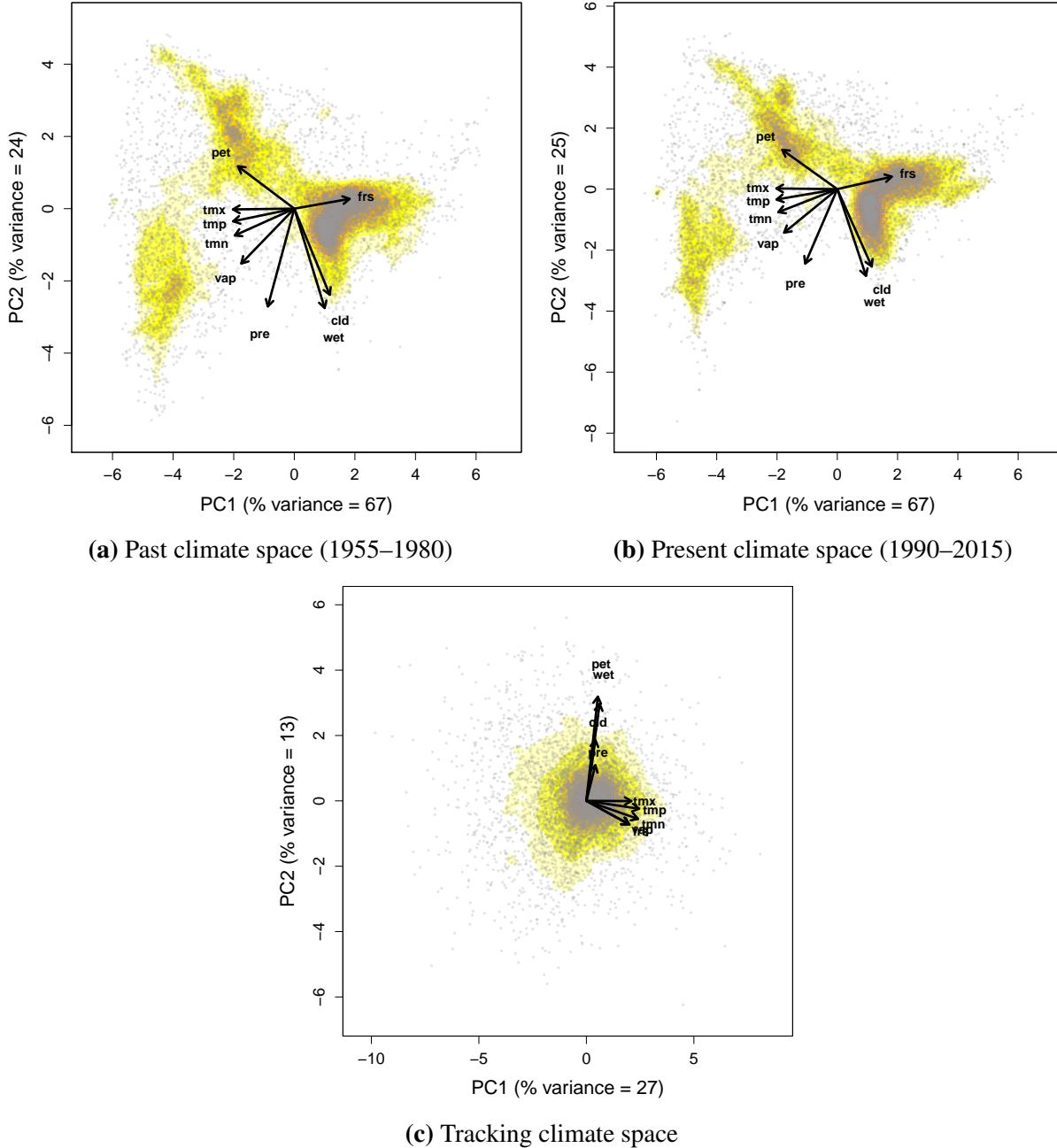


Figure 4: Species' movement through climate space differs from their current and past positions within it. Principal component analysis (PCA) biplots of (a) species' median past climate values, (b) median current climate, and (c) the median track-index of all climate variables. Each PCA axis explains some amount of variation in the underlying data (labelled on the axes themselves). In (a) and (b), species' climate variables are correlated with one-another, and the space reflects global patterns in climate. In (c), this pattern has broken down: while some associations among climate axes still remain (notably temperature), the general pattern is one of uncorrelated shifts through climate space.

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180 are under the Public Domain Dedication 1.0 license and uncredited unless otherwise stated below. The
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182 mammal by Scott Hartman (used under the Creative Commons Attribution 3.0 Unported license), and the
183 amphibian by Nobu Tamura (used under the Creative Commons Attribution 3.0 Unported license).

184 **Author Contributions** WDP and TJD contributed to all aspects of the study.

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187 **Competing interests** The authors declare no competing financial interests

188 Methods

189 All analyses were conducted in *R* version 3.6.1⁴⁰, and all names in *italics* refer to *R* packages. Code to
190 reproduce all analyses in their entirety is available in the online supplementary materials and online at
191 <https://github.com/willpearse/track-index>. In the supplementary materials, we provide extended figures
192 summarising all tracking index quantiles and climate variables in the same detail as presented in the main
193 text.

194 Data collation

195 Species' distribution data were downloaded from the Global Biodiversity Information Facility (GBIF)^{20,41}.
196 We downloaded only data highlighted by GBIF as not having any spatial issues, meaning they contained
197 no obvious location errors (*e.g.*, latitude/longitude swaps or rounded coordinates). These occurrence data
198 include records that were flagged as having potential issues and corrected by GBIF; our results were
199 qualitatively identical if we excluded these records and so we include them here for completeness. We
200 used 'human observation' occurrences (*e.g.*, records from surveys), and not vouchered specimens (*e.g.*,
201 pressed specimens in a herbarium) because preliminary analysis revealed qualitatively identical results
202 across the two methods, but with many fewer observations vouchered observations.

203 We only worked with species that had at least 1000 records on GBIF within our focal time periods (1955–
204 1980 and 1985–2015). We focused on these time periods because they contain sufficient observations
205 for large-scale analysis. Since climate change was underway within the 1980s², this also allows us to
206 have reasonably large (if naïvely defined) 'pre-change' and 'post-change' periods. Our 1000 observation
207 threshold limits us to better-studied species, but our results are robust to increases (*e.g.*, 10,000 observa-
208 tions) in this threshold. We only made use of data for which species identity was known, and we ignored
209 variation among sub-species. The GBIF taxonomy is, itself, to some extent checked and harmonised, and
210 so we retained in our analysis any species within GBIF that was not present in another datasets (see Corn-
211 well *et al.*⁴² for a discussion of the GBIF taxonomy for plants). In the supplementary materials, we give
212 instructions for re-running our analysis with differing curation thresholds to verify our choices.

213 Climate data were downloaded from Harris *et al.*²⁵'s nine global time-series. We split the data into yearly
214 (averaged) 0.5° cells, from which we estimated each of our nine climate variables for each species observa-
215 tion using *raster*⁴³. Plant trait data were taken from Wright *et al.*²⁹ (leaf lifespan, leaf mass-per-unit-area,
216 leaf Nitrogen mass, and leaf photosynthetic capacity), mammal body mass data from the Amniote Trait
217 Database⁴⁴, and bird body mass data from EltonTraits⁴⁵. We were unable to find sufficient coverage of the
218 other taxa in this study in open-access trait databases to facilitate further analysis. We used existing global
219 mammal⁴⁶, bird⁴⁷, amphibian⁴⁸, plant ('ALLOTB' phylogeny³⁹), and reptiles⁴⁹ phylogenies, and in cases
220 where posterior distributions of trees were available we used a single draw from that distribution. Missing
221 species were added into the phylogenies using *congeneric.merge* in *pez*⁵⁰.

222 Calculating and testing our track index

223 As we describe in the main text, we quantify the realised velocity of climate change using a simple index of
224 climate tracking. Our index, $track_{\tau}$, scales the observed magnitude of species' shift in climate ($current_{\tau} -$
225 $past_{\tau}$) according to the degree of change to which that species was exposed ($projected_{\tau} - past_{\tau}$). Our
226 metric is comparable across species, and can also be calculated in such a way as to control for changes
227 in sampling. The sampling of species through time and across space is known to be uneven across the
228 data in GBIF^{26,51}. To ensure our method was statistically robust to such changes, we employed a bootstrap
229 procedure during the calculation of $track_{\tau}$. To do this we randomly re-sampled, with replacement, the
230 occurrences making up $current_{\tau}$ and $projected_{\tau}$ to be of the same number as $past_{\tau}$, and vice-versa for
231 $past_{\tau}$ and $current_{\tau}$. We repeated this process 999 times, and calculated a $track_{\tau}$ value for each re-sample,
232 generating 999 $track_{\tau}$ values whose medians we report here. This process accounts for uneven sampling
233 by generating a pseudo-posterior distribution of conservatively-estimated values. In each bootstrap, the
234 better-sampled time period is sub-sampled to match the poorer-sampled period, accounting for differences
235 in sampling. Equally, the poorer-sampled period is re-sampled in order to increase the variance around the
236 index, essentially cross-validating our estimate. When applied to empirical data, our bootstrap approach
237 reveals that the certainty differing tracking quantiles (and climate variables) is uneven. We therefore
238 excluded uncertain (*i.e.*, estimates with high variation across pseudo-posteriors) and outliers from figures
239 within the main text, and so report sample sizes within Figure 1 (and its counterparts in the supplementary

240 materials).

241 To assess the performance of our (bootstrapped) track index, we simulated species' with ranges that
242 tracked climate to varying extents through time. Using the climate data from above in the years 1962
243 and 2002 (the mid-points of the ranges of our data), we simulated species with varying maximum possible
244 range sizes (2x2, 5x5, 10x10, or 20x20 grid-cell extents) and varying latitudinal shifts in range through
245 time (-4, -3, ..., 3, or 4 grid-cells). We also varied species' degree of environmental tracking (α ; taking
246 a value of 0, 0.5, or 1) and probability of occupancy(σ ; taking a value of 0.5, .75, or 1). Together, these
247 latter two parameters define a species' probability of being present in a particular cell within its range:
248 $(1 - \alpha) \times \text{sigma} + \alpha \times \mathcal{N}$. \mathcal{N} is defined as a scaled Normal probability density function with a mean
249 equal to the median of the species' distribution in 1962 and a variance of 1. Thus a species with an α of
250 1 is present only in cells within its range that resemble its climatic centre (*i.e.*, are similar to the median
251 value of the species' climatic distribution), and a species with an α of 0 is present in proportion σ of the
252 cells within its potential range. We simulated all possible combinations of parameters across 100 possible
253 centre-points of species' ranges, providing a full range of potential range shifts and 26,598 total simulation
254 runs. As with our empirical data, in simulation runs where, by chance, simulated species were not present
255 in the past or current time-period, they were excluded from the analysis.

256 Trait, phylogenetic, and PCA analyses

257 We calculated the Pearson's correlation between all estimated climatic niche variables (current_τ , past_τ ,
258 projected_τ , track_τ and the bootstrapped track_τ). While we show only a handful of these correlations
259 in Figure 3, we provide all correlations in the supplementary figures (and note that the qualitative results
260 of all correlations are the same). For the phylogenetic signal analyses, we likewise calculated Pagel's λ
261 (using *phytools*⁵²) for all indices, reporting all results in full in the supplementary materials (results are,
262 again, qualitatively identical to the results in the main text). Principal component analyses were performed
263 on all current, past, and track indices across all variables for a given quantile (*i.e.*, the 5th, 25th, 50th, 75th,
264 and 95th). While we report only the 50th quantiles in the main text, in the supplementary materials we
265 give results for all quantiles, which are qualitatively identical to the results in the main text.

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