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Species better track climate warming in the oceans than on land

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Brief editorial summary of the paper: “Compiling a global geo-database of >30,000 range shifts, the authors show that marine species closely track shifting isotherms whereas terrestrial species lag behind, likely due to wider thermal safety margins and movement constraints imposed by human activities.”

22 **There is mounting evidence of species redistribution as climate warms. Yet, our knowledge**
23 **of the coupling between species range shifts and isotherm shifts remains limited. Here we**
24 **introduce** BioShifts, a global geo-database of 30,534 range shifts. Despite a spatial
25 **imbalance towards the most developed regions of the northern hemisphere and a**
26 **taxonomic bias towards the most charismatic animals and plants of the planet, data shows**
27 **that marine species are better at tracking isotherm shifts, and move towards the pole six**
28 **times faster than terrestrial species.** More specifically, we find that marine species closely
29 **track shifting isotherms in warm and relatively undisturbed waters (e.g. Central Pacific**
30 **Basin) or in cold waters subject to high human pressures (e.g. North Sea). On land, human**
31 **activities impede the capacity of terrestrial species to track isotherm shifts in latitude, with**
32 **some species shifting in the opposite direction to isotherms. Along elevational gradients,**
33 **species follow the direction of isotherm shifts but at a pace that is much slower than**
34 **expected, especially in areas with warm climates. Our results suggest that terrestrial**
35 **species are lagging behind shifting isotherms more than marine species, which is likely**
36 **related to the interplay between wider thermal safety margin of terrestrial vs. marine**
37 **species and more constrained physical environment for dispersal in terrestrial vs. marine**
38 **habitats.**

39 The redistribution of life on Earth in response to climate change¹⁻⁴ is now considered a
40 global change driver on its own with far-reaching implications for ecosystem and human health⁵.
41 Managing the consequences of climate-driven species redistributions requires a better
42 understanding of the capacity of species of various taxonomic groups and from different habitats
43 to shift their distribution ranges and track shifting isotherms. As climate warms, isotherms are
44 shifting poleward and upslope to cooler latitudes and elevations in most parts of the world,
45 generating spatially-structured patterns in the velocity of isotherm shifts^{6,7}. Marine organisms

46 seem to closely track this complex mosaic of climate velocities⁸. However, the pattern is less
47 clear for terrestrial organisms². Evidence suggests that biotic responses on land are lagging
48 behind the velocity of climate change, particularly for long-lived species and poor-dispersers^{9,10}.
49 To date, a comprehensive analysis of the coupling between the velocity of species range shifts
50 and the velocity of isotherm shifts across biological systems (i.e. terrestrial *vs.* marine) and life
51 forms (e.g. ectotherms *vs.* endotherms) is still lacking^{11,12}.

52 To fill this knowledge gap, we compiled data on range shifts for marine and terrestrial
53 species in both the northern and southern hemispheres from an exhaustive literature review
54 building on and updating the most recent syntheses on climate-related range shifts²⁻⁴
55 (BioShifts¹³; see Data Availability for download) ([Supplementary Fig. 1](#)). The BioShifts geo-
56 database encompasses 30,534 range shifts documented from 258 peer-reviewed studies¹³,
57 spanning a total of: 12,415 harmonized species names; four kingdoms (Bacteria, Plantae, Fungi
58 and Animalia); 20 phyla; and 56 classes. It also contains several methodological attributes (e.g.
59 study area, study period, sampling effort, data quality), that can be used to account for
60 methodological variations in meta-analyses or quantitative reviews such as ours¹⁴. Based on this
61 geo-database, we first carefully assessed the geographical and taxonomic biases^{4,15} impeding our
62 knowledge of climate change effects on species redistribution ([Extended Data 1-3](#)). We then
63 provided robust estimates of the velocity of latitudinal and elevational range shifts for the 20
64 most studied taxonomic classes (Fig. 1), with the aim to compare our estimates with former
65 estimates from the existing literature¹⁻³ while accounting for potential methodological biases¹⁴.
66 To do so, we fitted several linear mixed-effects models (LMMs) with methodological attributes
67 treated as random effects¹⁴, all arranged in a full factorial design of geographical gradient
68 (latitude *vs.* elevation)^{1,2} × biological system (marine *vs.* terrestrial)¹⁵ × hemisphere (North *vs.*
69 South)⁴ × positional parameter (centroid *vs.* margins)^{3,4} ([Supplementary Table 1](#)). We expected

70 (1) faster velocities of latitudinal range shifts in the oceans than on land³, (2) faster velocities of
71 range shifts in the northern hemisphere than in the southern hemisphere due to the inter-
72 hemispheric asymmetry in the rate of climate warming over the twentieth century¹⁶ and (3)
73 different velocities of shifts across the distribution range. For each taxonomic class, we thus
74 estimated the velocity of range shift separately for the centroid and the margins of the range,
75 making the distinction between the trailing and leading edge to test for different types of range
76 shifts^{3,4,17,18}: trailing-edge contractions; leading-edge expansions; **lockstep** shifts involving both
77 trailing-edge contractions and leading-edge expansions together with a displacement at the
78 centroid of the range; and lean range shifts involving stable margins with the centroid shifting
79 within the existing range.

80 Then, we assessed the coupling between the velocity of isotherm shifts and the velocity of
81 range shifts at the species level, along the latitudinal gradient in marine systems and separately
82 for the latitudinal and elevational gradients in terrestrial systems (**Extended Data 4-6**). As before,
83 we controlled for varying methodologies¹⁴, using LMMs, and tested for two-way interaction
84 terms between the velocity of isotherm shifts and: (i) life-form categories (ectotherms,
85 endotherms, phanerogams, cryptogams); (ii) baseline temperatures (the historical mean annual
86 temperature regime prior to the baseline survey); and (iii) the standardized human footprint index
87 (a scaled variable summarizing the direct and indirect human pressures on both terrestrial and
88 marine environments: human population density; buildings; roads; agricultural lands; pollution;
89 commercial shipping; industrial fishing; ocean acidification; etc.)^{19,20}. Among animals, we
90 distinguished ectotherms from endotherms to test the hypothesis that ectotherms better track
91 shifting isotherms than endotherms. Theory and evidence suggest that ectotherms are more
92 sensitive to temperature fluctuations than endotherms²¹ and conform more closely to their
93 physiological limits of thermal tolerance, especially so for marine ectotherms²², and are thus

94 more likely to closely track shifting isotherms⁸. For chlorophyllous organisms, we distinguished
95 phanerogams or seed-bearing plants (angiosperms and gymnosperms) from cryptogams
96 reproducing by spores (ferns, mosses, lichens and algae) to test the hypothesis that greater
97 dispersal abilities in cryptogams allows to better track shifting isotherms²³. As historical
98 temperature regime may affect the rate at which species are shifting their distributions^{24,25}, we
99 tested whether the coupling between species range shifts and isotherm shifts varied with baseline
100 temperatures. Similarly, we accounted for potential effects of anthropogenic disturbances on the
101 magnitude of the coupling. We expected that land-use intensity in terrestrial systems may impede
102 species range shifts through habitat fragmentation²⁶, while exploitation of marine resources (e.g.
103 demersal or bottom trawling) may accelerate the relocation of exploited stocks through massive
104 population die-offs and crashes followed by local extinctions²⁷.

105 **Results and discussion**

106 *Geographical, taxonomic and methodological biases matter*. We found a strong spatial
107 imbalance in the data towards the most developed regions of the northern hemisphere ([Extended](#)
108 [Data 1-2](#)) and a clear taxonomic bias towards the most charismatic animals (*Aves*, *Actinopterygii*,
109 *Amphibia*, *Mammalia*) and plants (*Magnoliopsida*, *Liliopsida*) ([Extended Data 3](#)). This supports
110 former claims that global meta-analyses on species range shifts are not truly global^{4,15} and that
111 most species remain understudied, while others attract most of the public, scientific and
112 government attention²⁸. In addition to these geographic and taxonomic biases, differences in
113 methodological attributes among studies play a key role in the observed variation in the velocity
114 of range shifts among the 12,415 species included in BioShifts¹³ (Fig. 2). Most of this variation
115 was explained by methodological attributes, which contributed from 6 to 82% (mean = 36%,
116 median = 35%) of the total variation ([Supplementary Table 1](#)). By contrast, differences among
117 taxonomic classes and positions at range margins (trailing edge *vs.* leading edge) contributed

118 only 0 to 50% (mean = 10%, median = 7%) of the total variation. These findings confirm the
119 importance of accounting for varying methodologies in meta-analyses¹⁴. However, contrary to
120 former meta-analyses arguing against the use of studies reporting range shifts for a single or a
121 handful number of species because such studies are more likely to select responsive species¹⁻³,
122 we found no relationship between sample size and the velocity of range shifts ([Supplementary](#)
123 [Fig. 2](#)). Hence, we recommend future meta-analyses on range shifts to consider all available
124 information instead of constraining the analyses to the set of studies that focused on multiple
125 species (e.g. more than 3 species).

126 *Marine organisms move faster than terrestrial organisms.* Once methodological attributes were
127 accounted for, the variation in the estimated velocity of range shifts among taxonomic classes
128 and positions at range margins was still fairly large, ranging from 3.20 m.yr⁻¹ downslope for
129 freshwater fishes (trailing edge, northern hemisphere) to 12.39 m.yr⁻¹ upslope for amphibians
130 (trailing edge, southern hemisphere) and from 6.52 km.yr⁻¹ equatorward for reptiles (trailing
131 edge, northern hemisphere) to 18.54 km.yr⁻¹ poleward for insects (centroid of the range, northern
132 hemisphere) (Fig. 3). Marine species (~80% being ectotherms in the database, [Extended Data 2](#))
133 have moved towards the poles at a mean (\pm s.e.m.) pace of 5.92 \pm 0.94 km.yr⁻¹ (one-sample
134 Student's *t*-test: $t = 6.26$; df residuals = 23; $P = 2.20 \times 10^{-6}$), almost six times faster than
135 terrestrial species (one-way ANOVA: $F = 12.68$; df factor = 1; df residuals = 45; $P = 8.88 \times 10^{-4}$).
136 This mean velocity far exceeds the one reported by the first synthesis (0.61 \pm 0.24 km.yr⁻¹)¹ but
137 is very similar in magnitude and direction to the mean velocity reported by a more recent
138 synthesis focusing exclusively on marine species (7.20 \pm 1.35 km.yr⁻¹)³. Importantly, the mean
139 velocity of latitudinal range shifts we found for terrestrial systems (1.11 \pm 0.96 km.yr⁻¹) was non-
140 significantly different from zero (one-sample Student's *t*-test: $t = 1.15$; df residuals = 22; $P =$
141 0.25). This contradicts a former synthesis from 2011 reporting a mean positive velocity of

142 latitudinal range shifts across a wide range of taxonomic groups ($1.76 \pm 0.29 \text{ km.yr}^{-1}$)². Although
143 the authors of this synthesis chiefly focused on terrestrial taxonomic groups, they also included
144 data on range shifts from several marine taxonomic groups (molluscs and algae) in their
145 analyses, which could explain the discrepancy. Along the elevation gradient, we found that
146 terrestrial species have shifted upslope at a mean pace of $1.78 \pm 0.41 \text{ m.yr}^{-1}$ (one-sample Student's
147 *t*-test: $t = 4.33$; *df* residuals = 36; $P = 1.13 \times 10^{-3}$), slightly faster than what was previously
148 reported ($1.22 \pm 0.18 \text{ m.yr}^{-1}$)².

149 Although we found a tendency towards faster latitudinal range shifts in the northern
150 hemisphere ($4.24 \pm 0.70 \text{ km.yr}^{-1}$; one-sample Student's *t*-test: $t = 4.66$; *df* residuals = 36; $P = 4.28$
151 $\times 10^{-5}$) as opposed to the southern hemisphere ($1.07 \pm 0.34 \text{ km.yr}^{-1}$; one-sample Student's *t*-test: t
152 $= 1.43$; *df* residuals = 9; $P = 0.19$), the difference was not significant (one-way ANOVA: $F =$
153 3.08 ; *df* factor = 1; *df* residuals = 45; $P = 0.09$). More data on species range shifts are thus clearly
154 needed in the southern hemisphere (see geographical biases in [Extended Data 1-2](#)) to be able to
155 confirm or infirm our hypothesis of faster range shifts in the northern hemisphere related to the
156 faster rates of climate warming over there compared with the southern hemisphere¹⁶.

157 Regarding the position within the range, terrestrial taxa seem to have relatively stable
158 latitudinal distributions, showing no clear signal of range shift at the trailing edge (-0.17 ± 1.61
159 km.yr^{-1} ; one-sample Student's *t*-test: $t = -0.10$; *df* residuals = 5; $P = 0.92$), the centroid of the
160 range ($2.41 \pm 2.45 \text{ km.yr}^{-1}$; one-sample Student's *t*-test: $t = 0.98$; *df* residuals = 7; $P = 0.36$) or the
161 leading edge ($0.81 \pm 0.65 \text{ km.yr}^{-1}$; one-sample Student's *t*-test: $t = 1.24$; *df* residuals = 8; $P =$
162 0.25). By contrast, marine species seem to be very sensitive to warming, showing trailing-edge
163 contractions ($6.49 \pm 2.13 \text{ km.yr}^{-1}$; one-sample Student's *t*-test: $t = 3.04$; *df* residuals = 7; $P = 0.02$),
164 leading-edge expansions ($6.02 \pm 1.77 \text{ km.yr}^{-1}$; one-sample Student's *t*-test: $t = 3.40$; *df* residuals =
165 8; $P = 9.32 \times 10^{-3}$) and poleward shifts at the centroid of the range ($5.13 \pm 0.41 \text{ km.yr}^{-1}$; one-

166 sample Student's t -test: $t = 12.54$; df residuals = 6; $P = 1.57 \times 10^{-5}$). Our results also indicate that
167 the leading and trailing edge of marine species are equally sensitive to warming (one-way
168 ANOVA: $F = 0.03$; df factor = 1; df residuals = 15; $P = 0.87$), which is consistent with
169 expectations from thermal tolerance limits of marine ectotherms²² (though in contrast to a
170 previous report³). **In turn, this suggests that marine species are moving in lockstep⁴ towards the**
171 **poles.** Similarly, along elevational gradients, the trailing and leading edge of terrestrial species
172 have moved towards the summits at a comparable mean pace of 2.34 ± 0.67 m.yr⁻¹ and 2.15 ± 0.60
173 m.yr⁻¹, respectively (one-way ANOVA: $F = 0.03$; df factor = 1; df residuals = 23; $P = 0.87$). **This**
174 **indicates that terrestrial species are moving in lockstep towards mountain summits,** which is very
175 consistent with two recent syntheses concluding on symmetric boundary shifts in mountains^{17,18}.
176 Note, however, that the mean upslope shift was significant at the leading edge (one-sample
177 Student's t -test: $t = 6.19$; df residuals = 12; $P = 4.65 \times 10^{-5}$), but only marginally significant at
178 both the trailing edge (one-sample Student's t -test: $t = 2.07$; df residuals = 11; $P = 0.06$) and the
179 centroid of the range (one-sample Student's t -test: $t = 2.13$; df residuals = 11; $P = 0.06$).

180 ***Marine species are better at tracking isotherm shifts.*** Assessing the degree of coupling between
181 species range shifts and isotherm shifts (**Extended Data 4-6**), we found that marine species better
182 track isotherm shifts in latitude than terrestrial species (Figs. 4-5). For marine systems, our best
183 model explained 33% of the total variation in the velocity of species range shifts (Fig. 4a). Only
184 4% of the total variation was related to fixed effects, namely the velocity of isotherm shifts (*VIS*),
185 standardized human footprint index (*HFI*), baseline temperatures (*BT*), life forms (*LF*) and
186 synergistic effects between *VIS* and *HFI* or *BT* (Fig. 4b), whereas 29% was explained by random
187 effects or methodological attributes (**Supplementary Table 2**). Again, this strongly supports the
188 idea that varying methodologies in estimates of climate-driven biological responses can
189 contribute to most of the explained variation and need to be explicitly considered in quantitative

190 reviews¹⁴. Noteworthy, we found that faster climate velocities combined with higher human
191 pressures in the oceans (e.g. commercial shipping, industrial fishing, ocean acidification) or
192 warmer sea surface temperatures during the baseline survey increases the velocity of species
193 range shifts along the latitudinal gradient for both marine ectotherms and cryptograms (Figs. 5c-
194 d, [Extended Data 7](#), [Supplementary Table 2](#)). More specifically, we found that marine species
195 closely track shifting isotherms either in initially warm and undisturbed waters (e.g. Central
196 Pacific Basin)¹⁹ or in initially cold waters where human activities are more pronounced (e.g.
197 Norwegian Sea, North Sea and English Channel) (Fig. 6c, [Extended Data 8](#)). This pattern is
198 unlikely to result from a collinearity issue between the velocity of isotherm shifts and the
199 standardized human footprint index ($R^2 = 0.05$) ([Supplementary Fig. 3](#)). Instead, it may stem
200 from the combination of two processes. First, marine species are living closer to their upper
201 thermal limits in the tropics, where sea surface temperatures are the highest, thus increasing the
202 likelihood of local extirpations at their trailing edges as climate warms¹¹. Second, lower
203 constraints on dispersal and colonization in the oceans (as opposed to terrestrial habitats)³ may
204 help species to rapidly shift their distribution towards the newly available habitats. By contrast,
205 at high latitudes where the thermal safety margin of marine species is larger¹¹, climate warming
206 alone is unlikely to explain isotherm tracking. Instead, anthropogenic activities (e.g. fishing
207 pressure and pollution in the North Sea) may render populations more sensitive to climate
208 change by reducing abundance and density, truncating the age distribution and leading to the
209 depletion of fish stock at the trailing edge of their range²⁷. In parallel, successful management
210 actions at higher latitudes, such as along the Norwegian's coastlines in the Norwegian Sea and
211 the Barents Sea, combined with climate warming, may increase population sizes of commercial
212 fishes at the leading edge of their range²⁹, thus promoting successful colonization.

213 Unlike in the oceans, the degree of coupling between the velocity of species range shifts
214 and the velocity of isotherm shifts is comparatively poor on land (Fig. 4). Again, this
215 inconsistency with a former synthesis² from 2011 may stem from the fact that we here analyzed
216 the coupling separately for the marine and terrestrial systems, a distinction that was not possible
217 in 2011 due to a lack of data at that time, for marine systems. Our best model explained 47% of
218 the total variation in the velocity of species range shifts along the latitudinal gradient on land
219 (Supplementary Table 2), of which the largest proportion was explained by varying
220 methodologies among studies (Fig. 4a). Among fixed effects, we found that range shifts were
221 best explained by differences between life forms and a negative interaction term between the
222 velocity of isotherm shifts and the standardized human footprint index (explaining 8% of the
223 total variation; Fig. 4b). Such antagonistic effect between climatic and human-related drivers
224 suggests that habitat loss and fragmentation – associated with high population densities and other
225 human activities such as agricultural practices – in the lowlands, combined with limited species'
226 dispersal abilities – relative to the speed at which isotherms are shifting along the latitude
227 gradient³⁰ – likely impede the capacity of terrestrial taxa to track shifting isotherms. Again, this
228 pattern is unlikely to result from a collinearity issue between the velocity of isotherm shifts and
229 the standardized human footprint index ($R^2 = 0.09$) (Supplementary Fig. 3). Interestingly, we
230 found that when exposed to a high degree of anthropogenic disturbances ($HFI > 0.3$), terrestrial
231 species tend to shift in the opposite direction to isotherms (i.e. HFI conditions for which both
232 velocities show opposite signs in Fig. 5b and Extended Data 9), most likely due to local
233 extinction processes at the leading edge. For instance, a previous study showed that during 1970-
234 1999, habitat loss and degradation led to a decline in the distribution sizes of three-quarters of
235 butterfly species that approach their northern climatic range margins in Britain, outweighing the
236 climate-induced species range shifts that were expected from climate warming²⁶. This is

237 consistent with the general idea that land-use and climate change may act as opposing forces on
238 species distribution changes. In addition, air conducts heat 25 times less effectively than water¹²,
239 which makes terrestrial species, in general, less sensitive than marine species to temperature
240 fluctuations and thus less likely to move as a direct response to climate warming¹¹. The
241 availability of thermal microrefugia (e.g. shaded environments) on land may also allow species
242 to more easily regulate their body temperature (e.g. microhabitats may allow terrestrial
243 ectotherms to increase their thermal safety margin by 3°C on average as compared with marine
244 ectotherms¹¹). Hence, we confirm that isotherm tracking is very unlikely for terrestrial taxa
245 living in the lowlands^{9,25}.

246 Along elevational gradients, the best model explained 11% of the total variation in the
247 velocity of range shifts (Fig. 4a; [Supplementary Table 2](#)) and showed that the velocity of
248 isotherm shifts interacts with both baseline temperatures and life forms (explaining 2% of the
249 total variation; Figs. 5a-6a, [Extended Data 9-10](#)). [Contrary to the latitudinal gradient, the](#)
250 [standardized human footprint index was not selected as a meaningful explanatory variable in the](#)
251 [best model](#). Noteworthy, we found a better coupling between the velocity of species range shifts
252 and the velocity of isotherms shifts for ectotherms in cold environments (i.e. close to
253 mountaintops). The geographic isolation and habitat area constraints specific to mountaintops
254 (e.g. sky islands) may exacerbate local extinction events through reduced population sizes as
255 climate warms and habitat area shrinks, thus paying off part of the climatic debt for ectotherms
256 living close to mountaintops. For instance, mass extinction events associated with climate
257 warming and pathogen outbreaks have already been reported for several amphibian species
258 endemic to mountainous regions³¹. For endotherms, phanerogams and cryptogams, the slope of
259 the relationship between the velocity of species range shifts and the velocity of isotherm shifts in
260 mountainous systems is negative, especially under warm climates ([Extended Data 9](#)). However,

261 we found that velocity values for range shifts along elevational gradients are always positive,
262 except under very warm baseline temperature conditions ($BT > 20^{\circ}\text{C}$). This indicates that
263 endotherms, phanerogams and cryptogams are in general shifting their elevational ranges
264 upslope to track shifting isotherms but are consistently lagging behind climate change. Isotherms
265 may be shifting upslope at a pace that is simply too fast for species with limited dispersal
266 abilities and long life spans, such as trees, to keep pace. Additionally, in the tropics, the higher
267 importance of biotic interactions³² may further impede the rate of range shifts over what is
268 expected from climate change alone³³. But most importantly, the global climatic grids that are
269 currently available, and that we used here, may still be too coarse in spatial resolution (1 km² at
270 best) to allow a reliable assessment of the true velocity of isotherm shifts experienced along
271 mountain slopes. Indeed, the topoclimatic and microclimatic heterogeneity that is available
272 across few metres in mountain systems, something that is not accounted for here, may provide a
273 strong spatial buffer against climate warming³⁴, allowing species to shift at relatively small
274 spatial distances and seemingly “stay”³⁵ relative to the velocity of isotherm shifts that is
275 measured at a coarser spatial resolution. Hence, the slow velocities of species range shifts that
276 we observed in mountainous areas could also be the result of local compensation effects
277 involving short distance escapes and species persistence within microrefugia.

278 *General implications.* To conclude, the coupling between species range shifts and isotherm
279 shifts is not uniform across biological systems, confirming the lags observed in the biotic
280 responses of terrestrial organisms to climate change^{9,10}. Noteworthy, we demonstrate complex
281 interactions between the velocity of climate warming, the degree of human pressures on the
282 environment, historical temperature regimes and species characteristics. We suggest that
283 commercial fishing may speed up the displacement of marine species distribution through
284 resource depletion and population crashes at the trailing edge, whereas low constraints on

285 dispersal in the oceans may allow marine species living close to their upper thermal limits to
286 better track climate warming at the leading edge. On land, habitat loss and fragmentation due to
287 land-use changes may impede the ability of terrestrial species to track shifting isotherms. These
288 complex interactions need to be accounted for to improve scenarios of biodiversity redistribution
289 and its consequences on human well-being⁵ under future climate change. The fact that marine
290 species better track climate warming than terrestrial species also suggests that biodiversity
291 redistribution will have more immediate and far-reaching consequences in the oceans than on
292 land. For instance, community reshuffling^{9,25} and the “tropicalisation” of temperate
293 ecosystems^{36,37} is likely to happen much faster in marine than in terrestrial systems, with more
294 direct and rapid consequences on ecosystem health and functioning (e.g. increasing fish
295 herbivory in kelp forests³⁸) as well as on the valuable services (e.g. fishery) and disservices (e.g.
296 coastal erosion) oceans can provide.

297 However, it is important to bear in mind that our findings, as well as former syntheses on
298 the topic, are still dependent on data availability and thus suffer from severe taxonomic and
299 geographic biases. Despite a broad taxonomic coverage of the tree of life (Extended Data 3),
300 species range shifts recorded in BioShifts¹³ cover only 0.6% of the described biodiversity on
301 Earth (N = 2,094,892 taxa). Besides, it is noteworthy that species range shifts in the southern
302 hemisphere and in tropical regions in general are underrepresented. These limitations may affect
303 our perception of species redistribution, and by consequence challenge global biodiversity
304 conservation efforts^{4,15}. It is thus more important now than ever to continue to study and
305 document range shifts in areas and for taxonomic groups that have been so far somewhat
306 neglected. Our database on species range shifts provides solid foundations to build a truly global
307 monitoring of species redistribution. We thus call for future research perspectives linking our

308 database on species range shifts with existing but scattered databases on species traits³⁹⁻⁴⁴ to
309 improve our ability to anticipate biodiversity redistribution under climate change.

310

Methods

311 ***Literature search.*** We reviewed the scientific and peer-reviewed literature reporting climate-
312 driven range shifts under contemporary climate change. By contemporary climate change, we
313 here mean the period stretching from the beginning of the 19th century and onwards. As a
314 general approach, we started from the reference lists of the most recent meta-analyses and
315 syntheses on the topic²⁻⁴ that we completed by regularly searching the scientific literature
316 published between 2014 and 2018, following the same protocol as in Lenoir & Svenning⁴
317 (Supplementary Fig. 1). Because of the clear focus on latitudinal and elevational range shifts in
318 the scientific literature and the lack of information on the other geographical dimensions⁴, we
319 excluded several reports focusing exclusively on bathymetric or longitudinal range shifts. Broad
320 inclusion criteria comprised studies: (i) focusing on relatively recent (since 1850s) distribution
321 changes; (ii) based on occurrence or abundance data of at least one species; and (iii) only if
322 studies were based on assessments covering at least two historical censuses **with a minimum of**
323 **10 years between censuses**. Hence, we excluded studies reporting distribution range changes
324 from a single census (synchronous approach comparing data from different ontogenetic life
325 stages of the same species like seedlings vs. adult trees) or based on historical patterns of species
326 mortality obtained from climatic reconstructions only, without real occurrence or abundance data
327 from at least two different time periods to confirm model outputs. We also excluded studies
328 focusing exclusively on distributional range changes of invasive alien species. This selection
329 procedure led to a total of 258 published and peer-reviewed studies for which we could extract
330 data on species range shifts^{8,27,45-300}.

331 We used Google Sheets to store the raw data on species range shifts in a dynamic and
332 common file that we shared among co-authors, while always keeping a regular copy of the
333 database saved on several computers to ensure backups. Once studies were clearly identified and

334 stored as “.pdf” files in a common folder in Google Docs, each co-author picked studies, one by
335 one, and entered data manually in the database. Some of the “.pdf” files were carefully annotated
336 to help us quickly identify and recover any meaningful information in the main text or display
337 items (e.g. tables or figures). When data on species range shifts were not directly available in the
338 main text, in tables or in the appendices of the publication, we first contacted the corresponding
339 authors and requested the data. In case of no positive response from the original authors and
340 when data on range shifts could be extracted from published figures, we used the
341 “WebPlotDigitizer” program (<https://automeris.io/WebPlotDigitizer/>). When range shifts were
342 reported for more than one geographically distinct survey area or between more than two
343 censuses (e.g. more than one resurvey of historical data), we considered them as independent
344 case studies (N = 325). This data entry procedure led to a total of 30,534 range shift estimates at
345 the species level (see Data Availability to access the database: BioShifts¹³).

346 Range shift estimates, as reported by the original authors, were coded as positive values if
347 poleward in latitude, or upward in elevation, and negative otherwise (equatorward and
348 downward). When the authors reported horizontal range shifts with both the magnitude and
349 direction (i.e. azimuth) values, we used trigonometric relationships to transform these values into
350 latitudinal range shifts for consistency with the main bulk of data available in the scientific
351 literature. Next, we divided each range shift estimate by the study duration between two
352 consecutive censuses (ending year – starting year + 1) to assess the rate or velocity of range shift
353 (*ShiftR*), in kilometer per year along the latitudinal gradient and in meter per year along
354 elevational gradients. In addition to the velocity of range shift at the species level, we also
355 retrieved information at the case study level (N = 325), including methodological attributes
356 known to potentially affect the velocity of range shift¹⁴: the starting year of the study (*Start*); the
357 ending year of the study (*End*); the size of the study area (*Area*); the number of taxa in a study

358 (*Ntaxa*) (continuous variable ranging from 1 to 4426; median = 21; mean = 122); the frequency
359 of sampling (*Sampling*) (factor variable with four levels: “continuous”; “irregular”; or
360 comparison of “two”; or “multiple” periods); whether range shift estimates were generated from
361 “occurrence” or “abundance” data (*PrAb*) (factor variable with two levels); the spatial resolution
362 of the raw data used to estimate range shifts (*Grain*) (factor variable with three levels: “fine” for
363 data based on GPS coordinates with a spatial resolution lower than 10 km; “coarse” for data
364 based on range maps or atlas grids with a spatial resolution greater than 100 km; and “medium”
365 for intermediate situations); the quality of the approach used to estimate range shifts (*Quality*)
366 (factor variable with four levels: “low” when no data cleaning procedures were performed before
367 computing range shifts; “balanced” when data cleaning or resampling procedures were carried
368 out to calculate range shifts on a balanced dataset; “modeled” when range shifts were obtained
369 by computing the difference in the position of a given range parameter estimated from species
370 distribution models (SDMs) independently calibrated during at least two different time periods
371 (note that in this case SDM outputs represent the realized and not the potential species
372 distribution for a given time period); and “resurveyed” when range shifts were calculated from
373 paired designs such as permanent plots); and whether the “significance” of range shift estimates
374 were assessed or “not” in the original study (*Signif*) (factor variable with two levels). To improve
375 the balance in the number of observations among levels of a given factor variable, we merged
376 some levels with poor data coverage together for the *Sampling* and *Quality* variables. For
377 instance, the levels “continuous” and “irregular” were merged together with the level “multiple”
378 such that *Sampling* was used in our analyses as a factor variable with two levels: “two” vs.
379 “multiple”. Regarding the *Quality* variable, we merged the level “resurveyed” together with the
380 level “balanced” such that *Quality* was used in our analyses as a factor variable with three levels:
381 “low”; “balanced”; and “modeled”. Still at the case study level (N = 235), we digitized the study

382 region in Google Earth and used the resulting polygons to retrieve spatial information such as the
383 total area covered by the study. If no clear maps delineating the study area was reported in the
384 original study (e.g. map displaying the study region), we used national geographic boundaries or
385 any meaningful spatial information from the text to delineate the study area. All spatial polygons
386 were used to produce a geo-database ([Extended Data 1-2](#)).

387 ***Taxonomic harmonization.*** Before undertaking any taxonomic harmonization procedure, the
388 last version of our database, dated April 2018, contained 13,570 entries of taxa at any taxonomic
389 rank up to the genus level (i.e. subspecies, species and genus). Using the R programming
390 language³⁰¹, we assembled an R script in order to retrieve, for each taxonomic entry, the most
391 recent accepted name and its associated classification. After a visual inspection for obvious
392 syntax correction, three steps of taxonomic verification were performed. First, names were
393 searched in the National Center for Biotechnology Information (NCBI) taxonomy database using
394 the function “classification” from the R package “taxize”³⁰². Then, in the same way, any
395 remaining taxonomic entity not found in NCBI was verified with the Integrated Taxonomic
396 Information System (ITIS) database. The full taxonomic classification was also retrieved during
397 these two steps. Third, the last remaining taxonomic entities not found in NCBI and ITIS were
398 checked using the Global Biodiversity Information Facility (GBIF) database, using the function
399 “name_backbone” in the R package “rgbif”. If we found a match, the corrected taxonomic entity
400 was again checked in NCBI and ITIS by undergoing the previously mentioned procedure once
401 again to retrieve a reliable taxonomic classification. Finally, only names at the species and the
402 genus level were kept for the analyses (subspecies being aggregated at the species level).
403 Following this taxonomic harmonization procedure, the final number of taxa names in the
404 database was reduced to 12,415.

405 **Climate velocity.** Using the spatial information obtained from the digitized polygons as well as
406 the temporal information (*Start* and *End* years) available from each of the 258 publication
407 sources, we retrieved basic temperature information to calculate the velocity of temperature
408 change throughout the study period. Terrestrial climate data were obtained from WorldClim v.
409 1.4 (<http://www.worldclim.org/>) and the Climate Research Unit (CRU) TS v. 3.23
410 (<https://crudata.uea.ac.uk/cru/data/hrg/>) while marine climate data were obtained from BIO-
411 ORACLE (<http://www.bio-oracle.org/>) and the Met office Hadley Centre observations datasets
412 (<https://www.metoffice.gov.uk/hadobs/hadisst/>).

413 Because marine and terrestrial taxa shift at different rates and directions to potentially track
414 the complex mosaic of local climate velocities⁸, we calculated the observed local velocity of
415 temperature change (i.e. the spatial shift of isotherms over time)^{6,7} for each case study, following
416 the approach used by Burrows *et al.*⁷. We divided the temporal change in annual mean
417 temperature observed over the studied period ($^{\circ}\text{C}.\text{yr}^{-1}$) by the corresponding spatial gradient
418 ($^{\circ}\text{C}.\text{km}^{-1}$ or $^{\circ}\text{C}.\text{m}^{-1}$) as a measure of the velocity of temperature change ($\text{km}.\text{yr}^{-1}$ or $\text{m}.\text{yr}^{-1}$)⁶. The
419 temporal gradient was calculated using time-series data from the CRU covering the period 1901-
420 2016 at a spatial resolution of 0.5° (about 55 km at the equator) and from the Met office Hadley
421 Centre observations datasets covering the period 1870-2018 at a spatial resolution of 1° (about
422 111 km at the equator) for terrestrial and marine studies, respectively. To do so, we regressed
423 annual mean temperature ($^{\circ}\text{C}$) values for all years throughout the study period as well as the two
424 preceding years against time (yr) using linear regressions. When the starting year was prior to
425 1901 or 1870 for terrestrial and marine systems, respectively, we started the time series in 1901
426 or 1870 depending on the climate series. The slope parameter ($^{\circ}\text{C}.\text{yr}^{-1}$) of this model was then
427 used as an estimate of the temporal gradient. For the sake of comparison with the rate of range
428 shift usually calculated along the latitudinal and elevational gradients, we calculated the spatial

429 gradient of annual mean temperature along the latitudinal (km.yr^{-1}) and **along** elevational (m.yr^{-1})
430 gradients, separately. This allowed us to assess both the latitudinal and elevational velocity of
431 temperature change (*LatVeloT* and *EleVeloT*). To assess the latitudinal spatial gradient of annual
432 mean temperature across land and sea, we used spatial grids from WorldClim and BIO-
433 ORACLE, respectively, at a spatial resolution of 5 arc-minute (about 9.2 km at the equator). The
434 WorldClim grid of annual mean temperature was downloaded at the finest spatial resolution,
435 which is 30 arc-second (about 1 km at the equator), but aggregated at 5 arc-minute to be
436 consistent with the spatial resolution of sea surface temperatures. Latitudinal spatial gradients
437 were calculated as in Burrows *et al.*⁷ based on a 3×3 neighborhood sub-grid with the centre cell
438 being the focal cell and its eight neighboring cells used to calculate the difference in
439 temperatures for each northern and southern (resp. southern and northern in the southern
440 hemisphere) pairs divided by the distance between them. Average differences ($^{\circ}\text{C.km}^{-1}$) for the
441 focal centre cell were calculated, excluding any missing values (usually along coastlines), using
442 weightings of 1 and 2 for cells diagonal and adjacent, respectively, to the focal centre cell. For
443 the elevation gradient, we used the temperature data from the WorldClim grid of annual mean
444 temperature at the finest spatial resolution (30 arc-second which is about 1 km at the equator)
445 and calculated the spatial gradient across each case study using a linear model relating annual
446 mean temperature (the response variable) to both elevation and latitude (the explanatory
447 variables). We used latitude as a covariate in this model to account for the latitudinal variation in
448 temperature observed within studies covering large spatial extents, i.e. elevation values close to
449 the equator are not directly comparable, in terms of temperature, to elevation values close to the
450 poles. The coefficient parameter along elevational gradients ($^{\circ}\text{C.m}^{-1}$) was then used as an
451 estimate of the local adiabatic lapse rate. For the study areas that were larger in extent than the
452 spatial resolution of the temperature grids, we computed the mean values of *LatVeloT* or

453 *EleVeloT* throughout the entire study area by averaging values across all spatial grid cells
454 overlapping with the polygons delineating the study area.

455 ***Additional drivers of range shifts.*** As baseline temperature conditions may affect the rate at
456 which species are shifting their distributions²⁴, we extracted annual mean temperature values
457 during the year of the initial census (*Start*) as well as the two preceding years and calculated the
458 mean (hereafter *BT* in °C). For terrestrial and marine systems, we used time-series data from
459 CRU and the Met office Hadley Centre observations datasets, respectively. When the initial
460 census of a given publication source was prior to 1901 or 1870 for terrestrial and marine
461 systems, respectively, we used the oldest years available from the time series to compute
462 baseline temperature conditions. Similar to climate velocity variables, when the study areas were
463 larger in extent than the spatial resolution of the temperature grids, we computed the mean values
464 of *BT* throughout the entire study area by averaging values across all spatial grid cells
465 overlapping with the polygons delineating the study area.

466 As anthropogenic disturbances such as land-use intensity or industrial fishing may act as
467 confounding factors on the velocity of range shift²⁴, we retrieved information on anthropogenic
468 impacts for both the terrestrial and marine environment. For terrestrial systems, we downloaded
469 the Global terrestrial Human Footprint maps for the year 2009²⁰. These maps, at a spatial
470 resolution of 30 arc-second (about 1 km at the equator), provide remotely-sensed and bottom-up
471 survey information on eight variables measuring the direct and indirect human pressures on the
472 environment: (1) the extent of built environments; (2) human population density; (3) electric
473 infrastructure (night-light time); (4) crop lands; (5) pasture lands; (6) roads; (7) railways; and (8)
474 navigable waterways acting like roads for people to access natural resources. All eight pressure
475 variables were scaled by the original authors based on their degree of influence on the terrestrial
476 environment. For instance, human population density and night-time lights were scaled between

477 0 and 10 while roads were scaled between 0 and 8. Scores for each of the eight individual threats
478 were then summed and weighted by the original authors to make a composite map of the global
479 human footprint index ranging from 0 to 50. For marine systems, we used the Global Map of
480 Human Impact on Marine Ecosystems¹⁹, also available at 30 arc-second resolution (about 1 km
481 at the equator). This gridded dataset provides a cumulative impact score ranging from 0.01 to
482 90.1 for the minimum and maximum value, respectively. It was developed on the basis of expert
483 judgment, to estimate ecosystem-specific impacts with respect to 17 anthropogenic drivers of
484 ecological change (e.g. commercial shipping, demersal and pelagic fishing, ocean acidification,
485 pollution). To allow comparison between terrestrial and marine systems, we rescaled both
486 indices between 0 and 1 (standardized human footprint index or standardized *HFI*) and computed
487 the mean per study area. The original authors have extensively validated *HFI* values against
488 satellite imagery, yielding high confidence they represent conditions of human pressure on the
489 environment²⁰.

490 ***Description: assessing geographic and taxonomic biases.*** To evaluate spatial biases in the
491 reporting of species range shift, we built $2^\circ \times 2^\circ$ gridded maps, on top of which we overlaid the
492 digitized polygons associated with the observations gathered in the database for both the
493 terrestrial and marine realm, and separately for latitudinal and elevational range shifts. For each
494 $2^\circ \times 2^\circ$ grid cell, we also computed the relative proportion of ectotherms *vs.* endotherms for
495 animals and phanerogams *vs.* cryptogams for plants and plant-like life forms (e.g. lichens and
496 algae). We distinguished ectotherm from endotherm life-forms due to their contrasting sensitivity
497 to temperature fluctuations in the environment, with ectotherms being unable to directly regulate
498 their body temperatures as opposed to endotherms. The distinction between phanerogams and
499 cryptogam life-forms allowed to contrast between two different reproduction strategies among
500 chlorophyllous organisms: the evolved seed-bearing plants (angiosperms and gymnosperms) *vs.*

501 the other plant-like life forms reproducing by spores (ferns, mosses, lichens and algae). We then
502 generated cartograms using the diffusion-based method for producing density-equalizing
503 maps³⁰³. The number of range shift rates per $2^\circ \times 2^\circ$ grid cell (i.e. sample size) was used to
504 distort the map: the bigger the grid cell, the larger the sample size ([Extended Data 1](#)). We
505 additionally estimated the phylogenetic coverage of the range shift database with respect to the
506 whole tree of life described in the Open Tree of Life (<https://tree.opentreeoflife.org>) collapsed at
507 the level of taxonomic classes and the total number of species recorded in the Catalogue of Life
508 (<http://catalogueoflife.org/>).

509 ***Detection: estimating the velocity of range shifts per taxonomic class.*** Data coverage in our
510 database is very unbalanced between: the marine vs. terrestrial realm; the northern vs. southern
511 hemisphere; and the margins vs. centroid of the species range ([Supplementary Table 1](#)). Besides,
512 data on species range shifts do not even exist for some taxonomic classes in some of the
513 combination of realm \times hemisphere \times position in the species range. For instance, dicots
514 (*Magnoliopsida*) are exclusively terrestrial organisms while cartilaginous fishes
515 (*Chondrichthyes*) almost exclusively live in marine habitats except for a few sharks and rays
516 living in freshwater habitats during all or part of their lives. Thus, a single model to estimate the
517 velocity of range shifts per taxonomic class while accounting for methodological biases^{4,14,15}
518 would be inappropriate. Hence, we divided latitudinal range shifts (N = 16,952) into a full
519 factorial design³⁰⁴ with eight experimental units based on all possible combinations of levels
520 across three factor variables: biological system (marine vs. terrestrial); hemisphere (north vs.
521 south); and range position (centroid vs. margins). We did the same for elevational range shifts (N
522 = 13,582) except that there were only four possible experimental units (i.e. terrestrial systems
523 only). To ensure robust fit, we further focused on taxonomic classes with more than 30
524 observations per experimental unit (N = 20 taxonomic classes fulfilling this sample size

525 criterion) (Fig. 1, [Supplementary Table 1](#)), which reduced our sample size to 16,399 and 13,341
526 observations for latitudinal and elevational range shifts, respectively. Among the 12 possible
527 combinations, only one combination (latitude \times margins \times terrestrial \times south) could not be
528 fulfilled due to a lack of range shift data ($N = 8$). This resulted in a total of 11 sub-models (i.e.
529 factorial models) ([Supplementary Table 1](#)).

530 For each of the 11 factorial models for which the data were available, we built a linear
531 mixed-effects model (LMM) relating the velocity of species range shift (*ShiftR*) for a given taxon
532 (i.e. the response variable) against taxonomic *Class*, a factor variable with as many levels as the
533 number of taxonomic classes within the focal experimental unit (e.g. *Amphibia* vs. *Aves* for
534 latitudinal range shifts at the centroid of the distribution in terrestrial systems of the southern
535 hemisphere) ([Supplementary Table 1](#)). Note that if a given factorial model only had data for one
536 unique taxonomic class (e.g. *Actinopterygii* for latitudinal range shifts at the centroid of the
537 distribution in marine systems of the southern hemisphere) ([Supplementary Table 1](#)), then the
538 variable *Class* was not included in the fixed effects of the LMM. For the five LMMs focusing on
539 the rate of range shift at the margins of the distribution, we added an extra factor variable
540 (*Margin*) with two levels (“leading” vs. “trailing” edge) in the fixed effects, to provide robust
541 estimates of the rate of range shift at both the leading and trailing edges. Given the complex
542 structure of the database, involving repeated observations per taxonomic units (e.g. family,
543 genus) or methodological levels, LMM is the most appropriate modelling approach³⁰⁴. This
544 allowed to provide estimates of the velocity of range shifts per taxonomic class that are
545 representative across all levels of a given methodological variable rather than providing
546 estimates for each level separately, while accounting for taxonomic non-independence. More
547 specifically, we included *Genus* as a random intercept term nested (or not: in case of singularity
548 fit) within *Family* to account for potential taxonomic autocorrelation in the residuals of the

549 models. In addition, because the different methodological approaches used in the scientific
550 studies may also contribute to a non-negligible fraction of the variation in range shifts¹⁴, we
551 considered several methodological variables as random intercept terms in the LMMs (*Area*,
552 *Start*, *Ntaxa*, *Sampling*, *PrAb*, *Grain*, *Quality* and *Signif*). To be included in the random part of
553 our LMMs, the continuous variables *Area*, *Start* and *Ntaxa* were first transformed into factor
554 variables with four levels each, using the respective quantiles as cutting points. Then, for each
555 factorial model separately, we selected only the set of uncorrelated variables with at least two
556 levels having more than four observations. We used the “lmer” function from the “lme4”
557 package³⁰⁵ in the R programming language³⁰¹.

558 We used a model selection procedure where the best random effect structure was identified
559 by testing all the combinations of random factors and selecting the one with the lowest Akaike
560 information criterion with small-sample correction (AICc). To compare AICc values among
561 candidate models, we set the restricted maximum likelihood argument to “FALSE” in the “lmer”
562 function (i.e. REML = FALSE for maximum likelihood)³⁰⁵. To ensure robust estimations, all the
563 singular fits were removed from the list of candidate models prior to model selection. In case of
564 singular fits across all candidate models, we used case study (*Source*) as the unique random
565 intercept term. If the random intercept term *Source* also led to a singular fit, then we used a linear
566 regression model (LM). For each of the LMMs (or LMs in case of singular fits for all the
567 candidate models) focusing on the velocity of range shift at the margins of the distribution, we
568 also included an interaction between *Margin* and *Class* that we tested against a model without
569 the interaction term in the fixed effects based on the AICc value. When the absolute difference in
570 AICc value between these two candidate models was greater than two, we selected the model
571 with the lowest AICc value. Otherwise, in case of equivalent competing models, we selected the
572 one with the interaction effect between *Margin* and *Class* considering that it allows flexible

573 range shift estimations at the trailing and leading edge. Once the best LMM was selected for
574 each factorial model (Supplementary Table 1), we set REML to TRUE³⁰⁵ to extract coefficient
575 estimates among the different levels of the factor variables *Class* and *Margin*. To test whether
576 the estimated rate of range shift for a given taxonomic class and at a given position within the
577 range was significantly different from zero, we reran each of the 11 selected best models using a
578 bootstrap approach (N = 5,000 iterations). From these 5,000 estimates, we computed the mean
579 and median velocity of range shift as well as the standard deviation and 95% confidence interval
580 per taxonomic class. Finally, to assess the overall goodness-of-fit of the different factorial
581 models, as well as to compare the relative importance of biological versus methodological effects
582 on the rate of range shift, we computed the marginal (i.e. variance explained by the fixed effects)
583 and conditional (i.e. variance explained by both the fixed and random effects) R² values³⁰⁶ of
584 each bootstrap iteration and for each factorial model using the “r.squaredGLMM” function from
585 the “MuMIn” package in the R programming language³⁰¹.

586 ***Attribution: coupling between species’ range shifts and isotherms’ shifts.*** We assessed the
587 coupling between the velocity of species range shifts and the velocity of isotherm shifts (*VIS*)
588 using LMMs built separately for the latitudinal and elevational gradients. We specified the
589 velocity of species latitudinal (km.yr⁻¹) or elevational (m.yr⁻¹) range shifts as the response
590 variable and either the latitudinal or elevational *VIS* (*LatVeloT* / *EleVeloT*; continuous variables)
591 as the main explanatory variable. To account for potential interacting effects on the relationship
592 between the velocity of range shifts and *VIS*, we added several covariates in our models: baseline
593 temperature (*BT*; a continuous variable); standardized human footprint index (standardized *HFI*;
594 a continuous variable representing human pressures on the environment bounded between 0 and
595 1); and life forms (*LF*) (a factor variable with 4 levels: ectotherm, endotherm, cryptogam,
596 phanerogam). As temperature regimes and human pressures on the environment are not directly

597 comparable between lands and oceans, we further modeled the coupling between the velocity of
598 species latitudinal range shifts and *VIS* in latitude (*LatVeloT*) separately for the marine and
599 terrestrial realm. We tested for all two-way interaction terms between each covariate (*BT*, *HFI*
600 and *LF*) and *VIS* (either *LatVeloT* or *EleVeloT*). We also tested for a unimodal relationship
601 between the estimated rates of range shifts and baseline temperature conditions (*BT*) using a
602 second-order polynomial term. The variables *Position* within the range (a factor variable with 3
603 levels: trailing edge, centroid and leading edge) and *Hemisphere* (a factor variable with 2 levels:
604 North vs. South) were not incorporated as covariates in the models as both variables had no
605 effect to explain the variation in the rates of latitudinal and elevational range shifts per
606 taxonomic class (Supplementary Table 2).

607 Similar to the LMMs developed at the taxonomic class, the aforementioned explanatory
608 variables were used as fixed effects in LMMs, whereas the methodological attributes (*Area*,
609 *Start*, *Ntaxa*, *Sampling*, *PrAb*, *Grain*, *Quality* and *Signif*) were used as random intercept terms.
610 Starting from the beyond optimal model (full model with all fixed effects)³⁰⁵ separately for the
611 velocity of latitudinal range shifts in marine and terrestrial systems as well as for the velocity of
612 elevational range shifts, we tested all model combinations and selected the best model based on
613 the lowest AICc value, setting REML to FALSE (i.e. maximum likelihood) for model selection
614 and then to TRUE to estimate the coefficients once the best model was selected³⁰⁵. We first
615 selected the random effect structure after removing singular fits, using the exact same procedure
616 as for the models used to estimate the mean velocity of range shift per taxonomic class. We then
617 selected the fixed effect structure, keeping the previously identified random structure constant.
618 All continuous variables (*LatVeloT*, *EleVeloT*, *BT* and *HFI*) were standardized to *z*-scores using
619 the “gscale” function³⁰⁷ from the “jtools” package in the R programming language³⁰¹. This
620 function standardizes each value of a given variable by subtracting it from the mean and dividing

621 it by two times the standard deviation of the focal variable (instead of one time as more
622 commonly done). This rescaling formula is recommended over the traditional formula of
623 dividing by one time the standard deviation because it allows direct comparisons of model
624 coefficients with untransformed binary predictors³⁰⁷. For the sake of consistency, we focused on
625 the set of species belonging to the taxonomic classes with more than 30 observations, resulting in
626 16,521 (1,403 marine vs. 15,118 terrestrial) and 13,459 observations for latitudinal and
627 elevational range shifts, respectively. The 95% confidence intervals around each of the estimated
628 coefficients were calculated using bootstraps (N = 5,000 iterations), similar to the models used to
629 estimate the mean velocity of range shift per taxonomic class.

630 Finally, to illustrate the capacity of species to track the shifting isotherms, we mapped the
631 predicted slopes for each combination of the predictors identified in the best models, separately
632 for latitudinal (marine or terrestrial) and elevational range shifts. A slope value of one between
633 the velocity of species range shifts and the velocity of isotherm shifts indicates a perfect coupling
634 with species closely tracking the shifting isotherms. To do so, we built a $2^\circ \times 2^\circ$ gridded map, on
635 top of which we overlaid the digitized polygons associated with each observation used in the
636 previous models. We then generated cartograms using the diffusion-based method for producing
637 density-equalizing maps³⁰³. As before (see section entitled “*Detection: assessing geographic and*
638 *taxonomic biases*”), the number of range shift rates per grid cell (i.e. sample size) was used to
639 distort the map: the bigger the grid cell, the larger the sample size. Finally, we tested whether the
640 slope estimated for each $2^\circ \times 2^\circ$ grid cell (i.e. according to the grid-specific baseline temperature
641 and the standardized human footprint index) significantly differed from a value of one
642 (indicating a perfect coupling), based on 5,000 bootstrap iterations.

643

Author Contribution

644 JL, LC, JM and GG initiated and conceived the project idea. LC and JL built the general
645 structure of the database. GG, LC, RB, TH and JL reviewed the scientific literature and filled the
646 database throughout the project duration. GG ensured data curation. LB and LC carried out the
647 taxonomic harmonization of the database with help from JM. TH linked the taxonomic backbone
648 of the database to the Open Tree of Life (<https://tree.opentreeoflife.org>) and to Catalogue of Life
649 (<http://catalogueoflife.org/>) to produce a visualization of the phylogenetic coverage of the
650 database. GG, LC, JL and RB prepared the set of methodological variables included as
651 covariates in the subsequent analyses. RB and JL analyzed the data with help from LC, LB and
652 GG. TH, RB and JL produced all the figures. JL wrote the manuscript with contribution from all
653 co-authors. JL and RB contributed equally to this work.

654

Data Availability

655 The data supporting the findings of this study are available in the BioShifts geo-database in the
656 Figshare Digital Repository¹³ available at <https://figshare.com/s/ebd19485a00757ababb0>

657

Code Availability

658 R scripts used in the analyses are available at <https://figshare.com/s/ebd19485a00757ababb0>

659

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666

Competing Interests Statements

667 Authors declare no competing interests. Reprints and permissions information is available at

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Figure Legends

1409 **Fig. 1 | Taxonomic coverage.** Number of taxa (in parenthesis), in log scale, per taxonomic class:
1410 from the least (top) to the most (bottom) studied taxonomic class. Only taxonomic classes with
1411 more than 30 observations per factorial model are displayed.

1412 **Fig. 2 | Sources of variation in species range shifts.** Proportion of explained variation either
1413 related to the taxonomic class and position at the range margin (fixed-effect terms in the models)
1414 or to methodological attributes (random effect terms in the models) for each of the 10 factorial
1415 models for which we had data (Supplementary Table 1). Each factorial model represents a
1416 combination of positional parameter (Cen: centroid; Mrg: margins) \times spatial gradient (L:
1417 latitude; E: elevation) \times biological systems (M: marine; T: terrestrial) \times hemisphere (N: north; S:
1418 south). Note that the “Margin” factor variable with two levels (leading edge vs. trailing edge)
1419 was only tested in model combinations focusing on margins (Mrg). Error bars represent the
1420 distribution of 5,000 bootstrap iterations.

1421 **Fig. 3 | Mean velocity of species range shifts per taxonomic class.** Estimated velocity of range
1422 shift per taxonomic class (i.e. effect size) in km.yr^{-1} and m.yr^{-1} for (a) latitudinal and (b)
1423 elevational range shifts, respectively, after accounting for methodological variation. Outputs are
1424 displayed for all possible combinations of positional parameter (TE: trailing edge; CE: centroid
1425 vs. LE: leading edge) \times hemisphere (N: north; S: south) \times biological systems (M: marine; T:
1426 terrestrial). Violin plots represent the distribution of 5,000 bootstrap iterations. Stars show
1427 significant deviations from zero shift (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

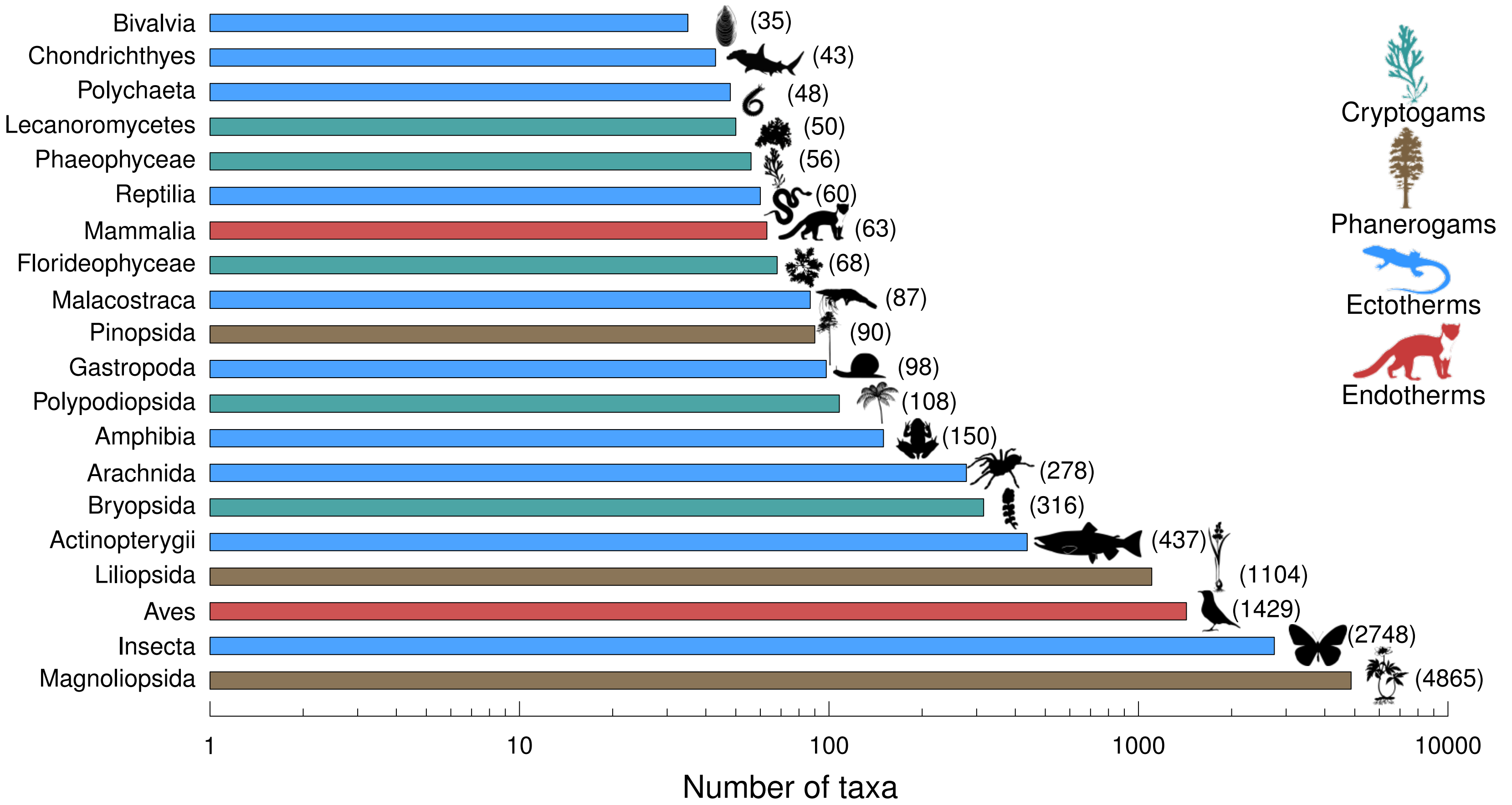
1428 **Fig. 4 | Degree of coupling between species range shifts and isotherm shifts.** Models outputs
1429 in terms of (a) proportion of explained variation and (b) effect size related to the velocity of
1430 isotherm shifts (VIS), baseline temperatures ($BT + BT^2$), standardized human footprint index

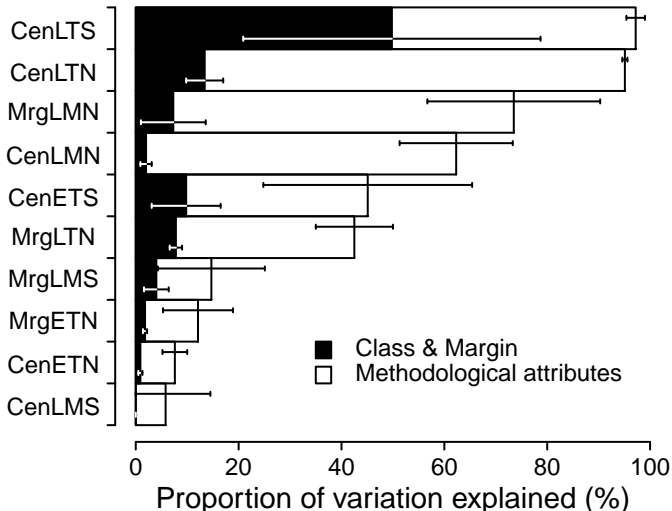
1431 (*HFI*) and two-way interaction terms (*VIS:HFI* and *VIS:BT*) for each of the four studied life
1432 forms (*LF*: endotherms, ectotherms, phanerogams and cryptogams). Intercept refers to the effect
1433 size of the focal life form. Error bars represent the distribution of 5,000 bootstrap iterations.
1434 Model outputs are displayed separately for marine latitudinal range shifts, terrestrial latitudinal
1435 range shifts and elevational range shifts.

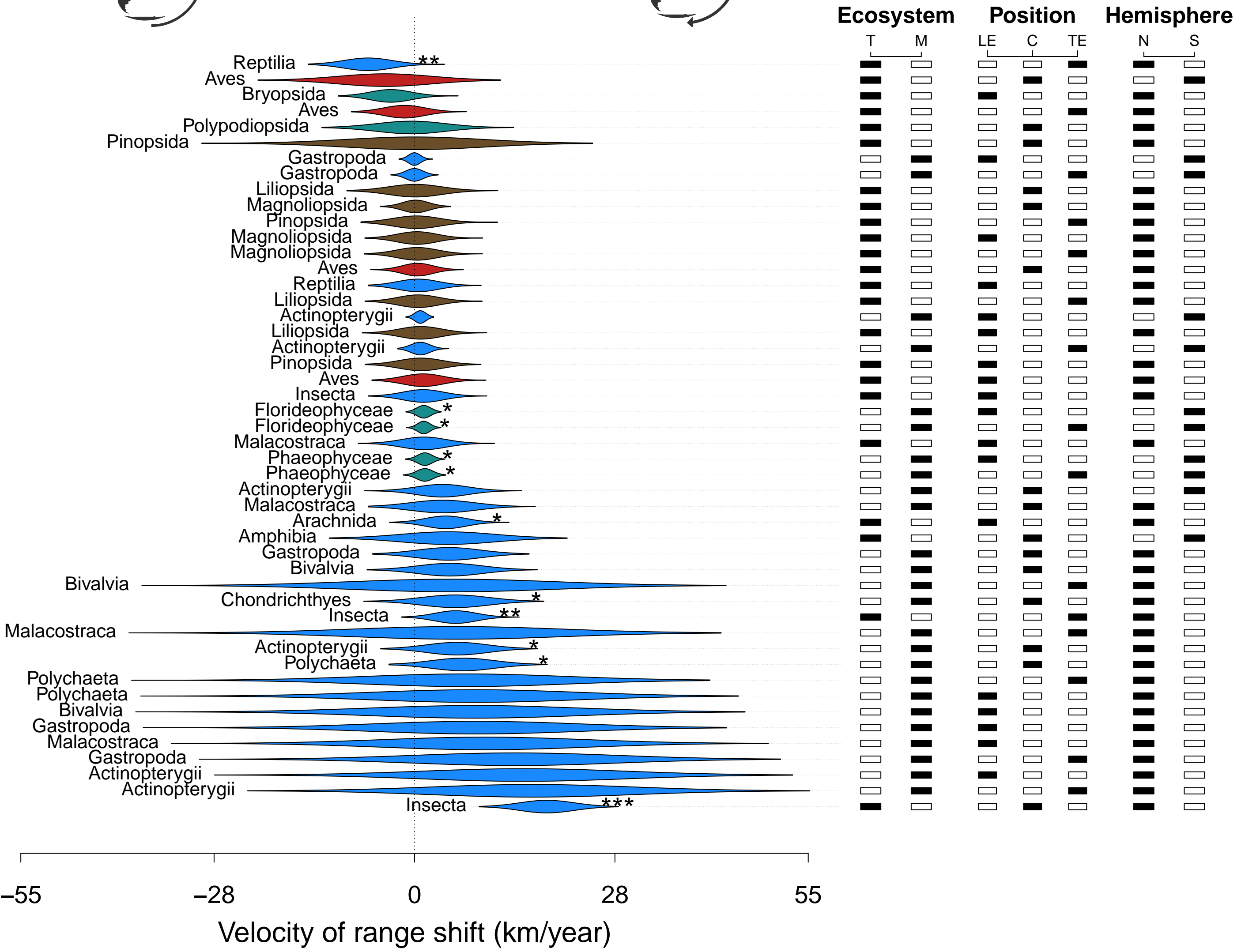
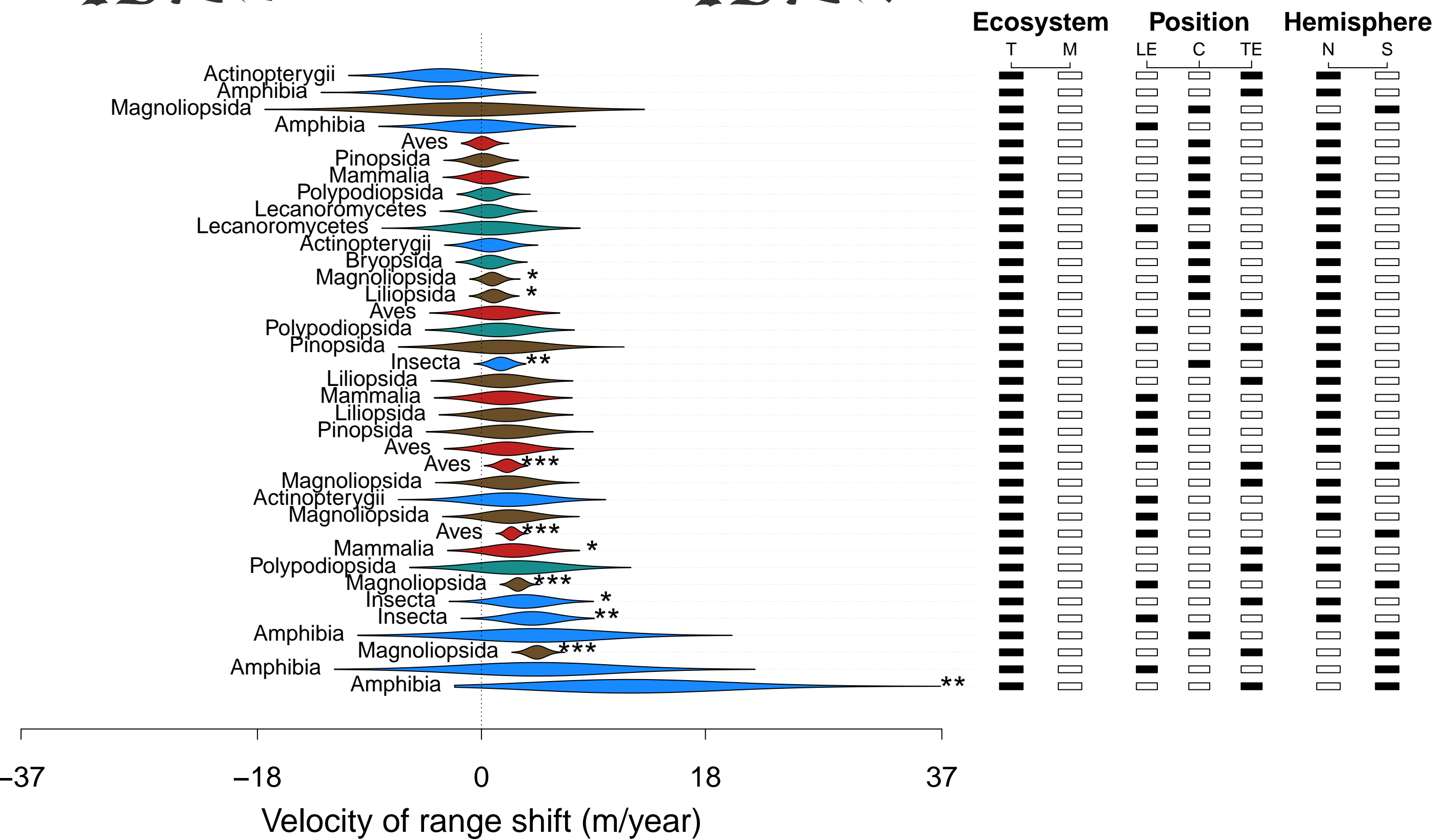
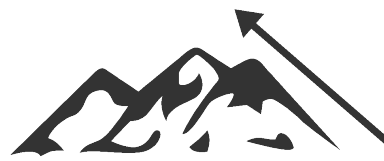
1436 **Fig. 5 | Main determinants of the velocity of species range shifts.** Results are displayed along
1437 (a) elevational and (b, c, d) latitudinal gradients for both the (a, b) terrestrial and (c, d) marine
1438 realms. Panel a shows the interaction effect between baseline temperatures and the velocity of
1439 isotherm shifts in elevation for ectotherms. Panel b shows the interaction effect between the
1440 standardized human footprint index and the velocity of isotherm shifts in latitude for terrestrial
1441 ectotherms. Panel c shows the interaction effect between baseline temperatures and the velocity
1442 of isotherm shifts in latitude for marine ectotherms while setting the standardized human
1443 footprint index to its median value in the database. Panel d shows the interaction effect between
1444 the standardized human footprint index and the velocity of isotherm shifts in latitude for marine
1445 ectotherms while setting baseline temperatures to the median value in the database. The two
1446 white lines and the white hatching represent the range of conditions for which marine ectotherms
1447 closely track the shifting isotherms in latitude (i.e. slope parameter not significantly different
1448 from 1 based on 5,000 bootstrap iterations). Note that negative slopes do not necessarily indicate
1449 species range shifts in the opposite direction to isotherm shifts, unless the signs of the two
1450 estimates (for a given combination of baseline temperatures and standardized human footprint
1451 index) are opposite.

1452 **Fig. 6 | Maps of the degree of coupling between the velocity of species range shifts and the**
1453 **velocity of isotherm shifts.** Cartograms show the predicted slope coefficient between the
1454 velocity of species range shifts and the velocity of isotherm shifts per $2^\circ \times 2^\circ$ grid cell along (a)

1455 elevational and **(b, c)** latitudinal gradients for both terrestrial **(b)** and **(c)** marine realms. Note that
1456 panel **a** only displays the predicted slope coefficient for ectotherms. Positive slope values (bluish
1457 colors) close to 1 suggest a perfect isotherm tracking while negative values (reddish colors)
1458 suggest that species are not tracking the shifting isotherms. Note that negative slopes do not
1459 necessarily mean that species are shifting in the opposite direction to isotherm shifts (see Fig. 5).
1460 The number of range shift estimates (i.e. sample size) in each grid cell was used to distort the
1461 map: the bigger the grid cell, the larger the sample size. Grid cells with a black and bold border
1462 display areas where species are closely tracking the shifting isotherms (i.e. slope parameter not
1463 significantly different from 1 based on 5,000 bootstrap iterations).



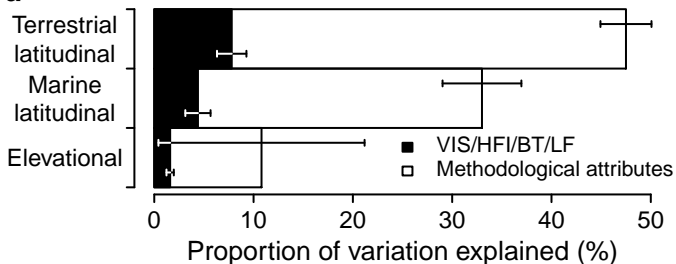


a**b**

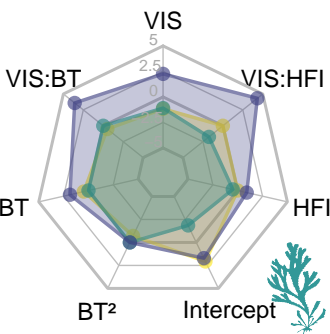
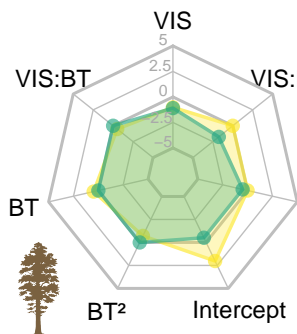
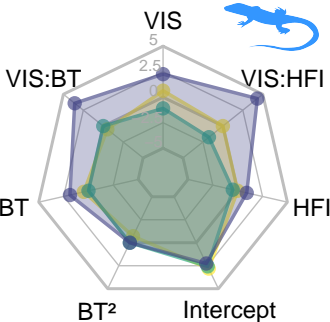
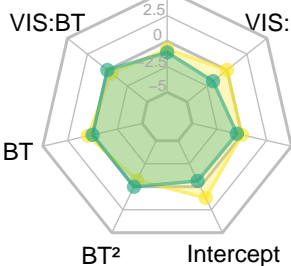





 Endotherms Ectotherms Phanerogams Cryptogams

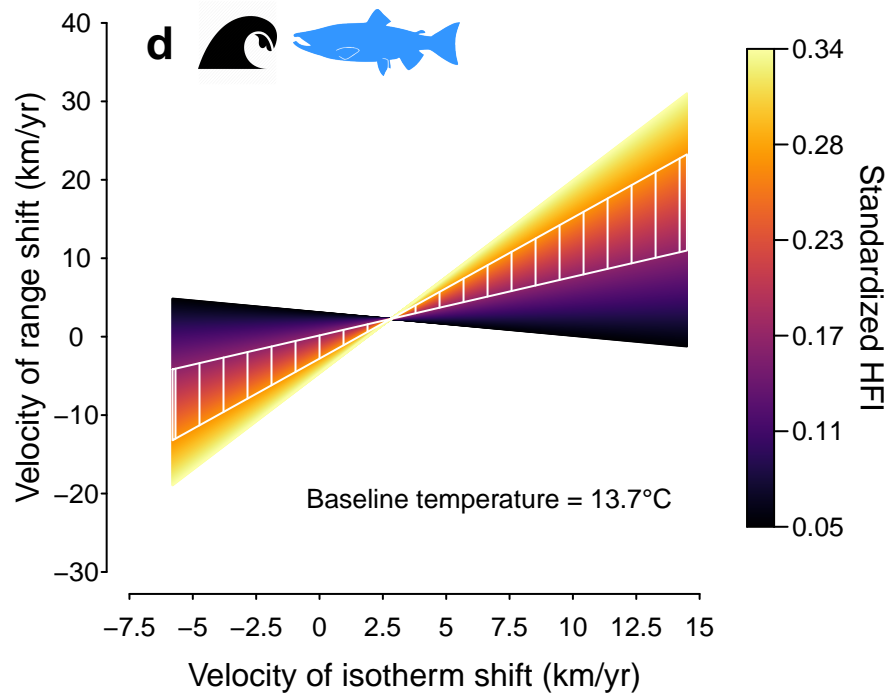
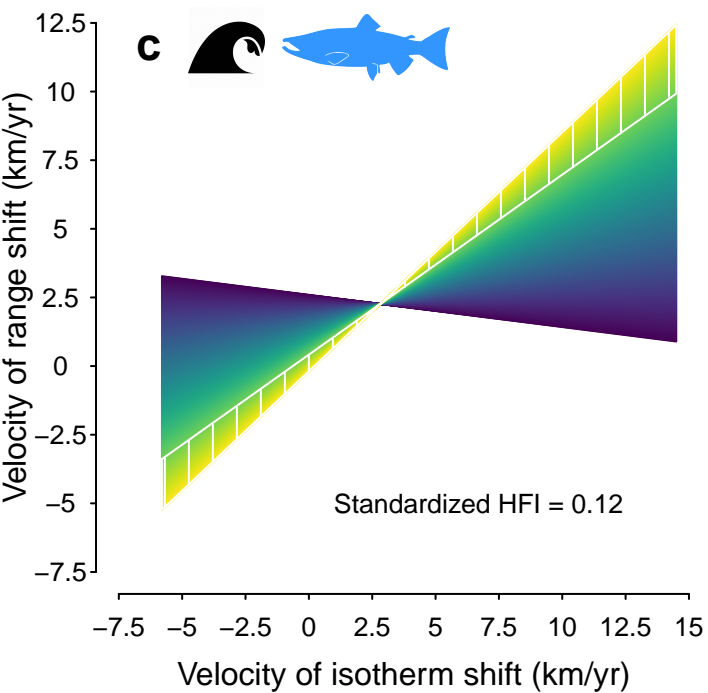
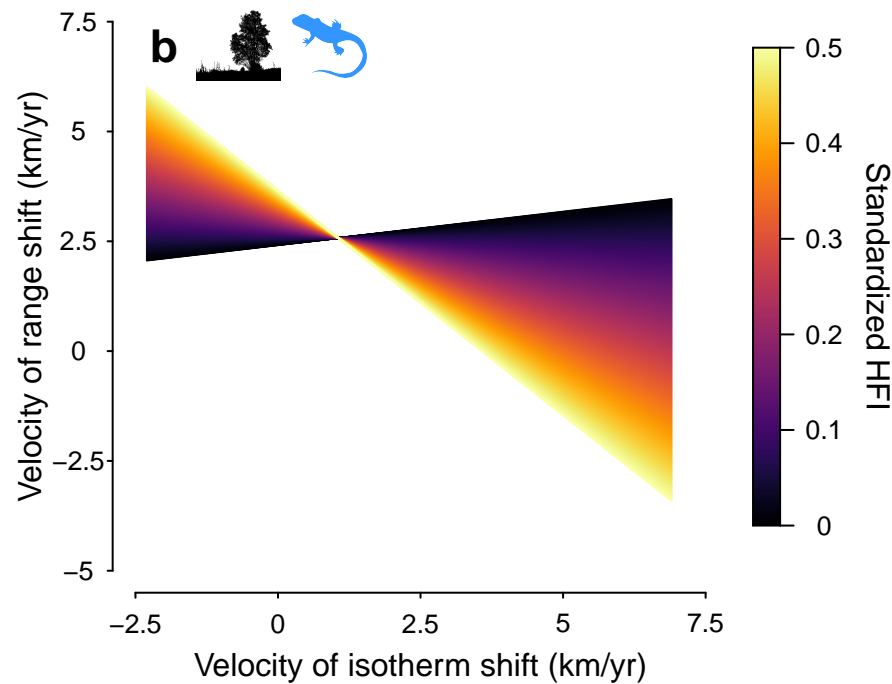
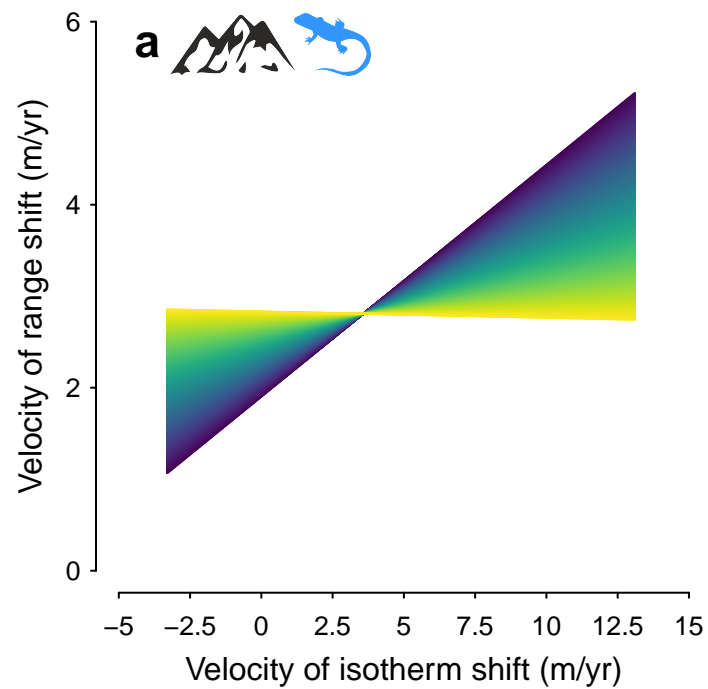


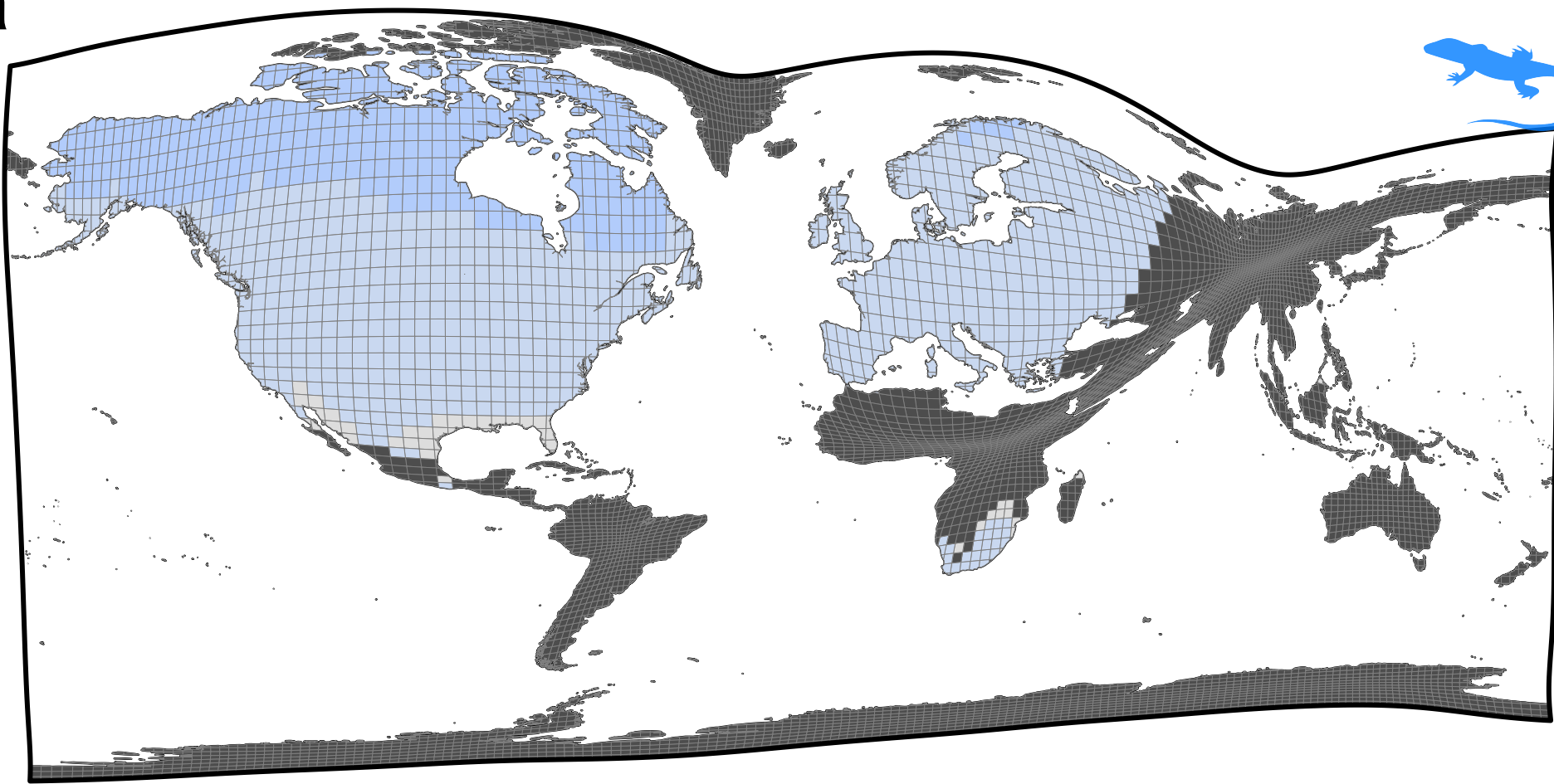
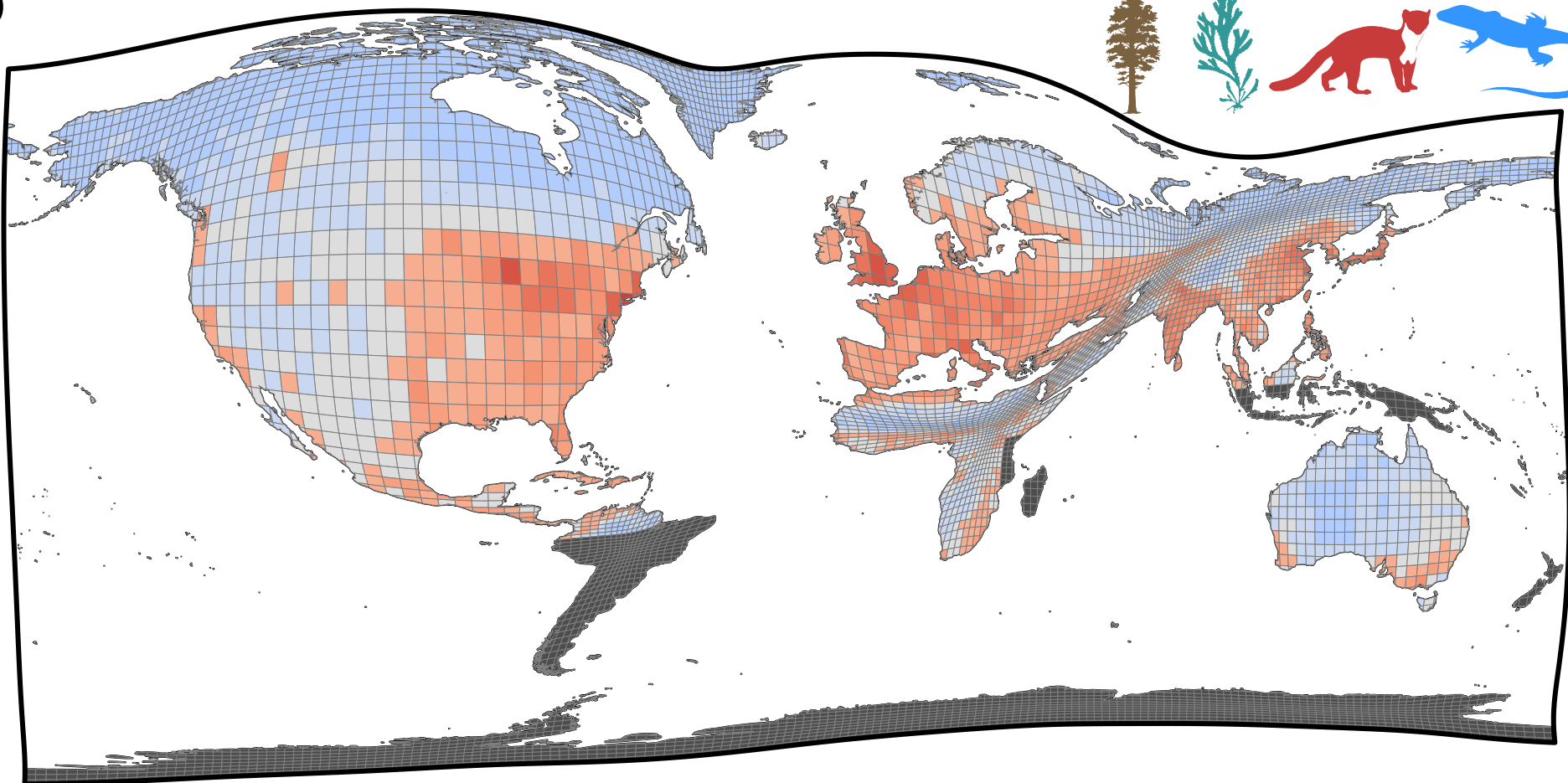
b



Range shifts

● Marine latitudinal ● Terrestrial latitudinal ● Elevational



a**b****c**