



Species better track climate warming in the oceans than on land

Jonathan Lenoir ^{1,8}✉, Romain Bertrand ^{2,3,8}, Lise Comte ^{4,5}, Luana Bourgeaud ³, Tarek Hattab ⁶, Jérôme Murienne ³ and Gaël Grenouillet ^{3,7}

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

The redistribution of life on Earth in response to climate change^{1–4} is now considered a global change driver on its own with far-reaching implications for ecosystem and human health⁵. Managing the consequences of climate-driven species redistributions requires a better understanding of the capacity of species of various taxonomic groups and from different habitats to shift their distribution ranges and track shifting isotherms. As climate warms, isotherms are shifting poleward and upslope to cooler latitudes and elevations in most parts of the world, generating spatially structured patterns in the velocity of isotherm shifts (VIS)^{6,7}. Marine organisms seem to closely track this complex mosaic of climate velocities⁸. However, the pattern is less clear for terrestrial organisms². Evidence suggests that biotic responses on land are lagging behind the velocity of climate change, particularly for long-lived species and poor dispersers^{9,10}. To date, a comprehensive analysis of the coupling between the velocity of species range shifts and the VIS across biological systems (that is, terrestrial versus marine) and life forms (for example, ectotherms versus endotherms) is still lacking^{11,12}.

To fill this knowledge gap, we compiled data on range shifts for marine and terrestrial species in both the Northern Hemisphere and Southern Hemisphere from an exhaustive literature review, building on and updating the most recent syntheses on climate-related range shifts^{3–4} (BioShifts¹³; see ‘Data availability’ for download) (Supplementary Fig. 1). The BioShifts geo-database encompasses 30,534 range shifts documented from 258 peer-reviewed studies¹³, spanning a total of 12,415 harmonized species names, four kingdoms (Bacteria, Plantae, Fungi and Animalia), 20 phyla and 56 classes. It also contains several methodological attributes (for example, study area, study period, sampling effort and data quality)

that can be used to account for methodological variations in meta-analyses or quantitative reviews such as ours¹⁴. Based on this geo-database, we first carefully assessed the geographical and taxonomic biases^{4,15} impeding our knowledge of climate change effects on species redistribution (Extended Data Figs. 1–3). We then provided robust estimates of the velocity of latitudinal and elevational range shifts for the 20 most studied taxonomic classes (Fig. 1), with the aim to compare our estimates with former estimates from the existing literature^{1–3} while accounting for potential methodological biases¹⁴. To do so, we fitted several linear mixed-effects models (LMMs) with methodological attributes treated as random effects¹⁴, all arranged in a full factorial design of geographical gradient (latitude versus elevation)^{1,2} × biological system (marine versus terrestrial)¹⁵ × hemisphere (Northern versus Southern)¹ × positional parameter (centroid versus margins)^{3,4} (Supplementary Table 1). We expected: (1) faster velocities of latitudinal range shifts in the oceans than on land³; (2) faster velocities of range shifts in the Northern Hemisphere than in the Southern Hemisphere due to the inter-hemispheric asymmetry in the rate of climate warming over the twentieth century¹⁶; and (3) different velocities of shifts across the distribution range. For each taxonomic class, we thus estimated the velocity of range shift separately for the centroid and the margins of the range, making the distinction between the trailing and leading edge to test for different types of range shift^{3,4,17,18}: trailing-edge contractions, leading-edge expansions, lockstep shifts involving both trailing-edge contractions and leading-edge expansions together with a displacement at the centroid of the range, and lean range shifts involving stable margins with the centroid shifting within the existing range.

¹Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), UMR7058, CNRS and Université de Picardie Jules Verne, Amiens, France. ²Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, UMR5321, CNRS and Université Toulouse III - Paul Sabatier, Moulis, France. ³Laboratoire Evolution et Diversité Biologique, UMR5174, Université Toulouse III - Paul Sabatier, CNRS, IRD and UPS, Toulouse, France. ⁴School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA. ⁵Department of Ecology and Evolutionary Biology, The University of Tennessee, Knoxville, TN, USA. ⁶MARBEQ, Univ Montpellier, CNRS, IFREMER and IRD, Sète, France. ⁷Institut Universitaire de France, Paris, France.

⁸These authors contributed equally: Jonathan Lenoir, Romain Bertrand. ✉e-mail: jonathan.lenoir@u-picardie.fr

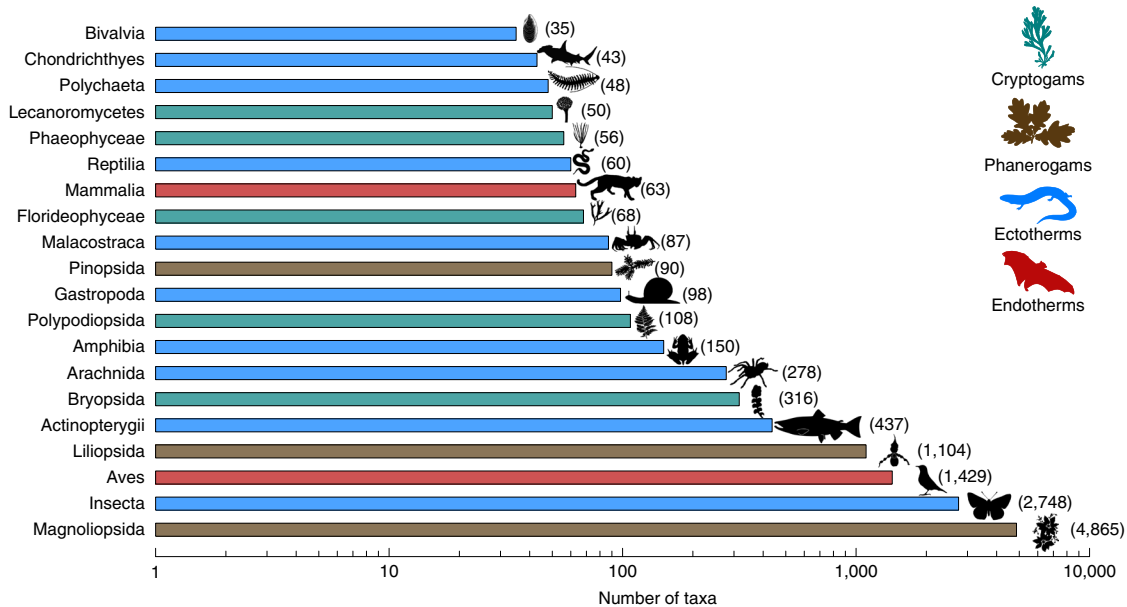


Fig. 1 | Taxonomic coverage. Number of taxa (in parenthesis), on a log scale, per taxonomic class. Taxonomic classes are shown from the least (top) to the most studied (bottom). Only taxonomic classes with >30 observations per factorial model are displayed. Credit: Sarah Werning / PhyloPic (frog silhouette) under a Creative Commons licence [CC BY 3.0](https://creativecommons.org/licenses/by/3.0/).

Then, we assessed the coupling between the VIS and the velocity of range shifts at the species level, along the latitudinal gradient in marine systems, and separately for the latitudinal and elevational gradients in terrestrial systems (Extended Data Figs. 4–6). As before, we controlled for varying methodologies¹⁴ using LMMs and tested for two-way interaction terms between the VIS and: (1) life form categories (ectotherms, endotherms, phanerogams and cryptogams); (2) baseline temperature (the historical mean annual temperature regimen before the baseline survey); and (3) the standardized human footprint index (HFI; a scaled variable summarizing the direct and indirect human pressures on both terrestrial and marine environments: human population density, buildings, roads, agricultural land, pollution, commercial shipping, industrial fishing, ocean acidification, and so on)^{19,20}. Among animals, we distinguished ectotherms from endotherms to test the hypothesis that ectotherms track shifting isotherms better than endotherms. Theory and evidence suggest that ectotherms are more sensitive to temperature fluctuations than endotherms²¹ and conform more closely to their physiological limits of thermal tolerance (especially so for marine ectotherms²²) and are thus more likely to closely track shifting isotherms⁸. For chlorophyllous organisms, we distinguished phanerogams or seed-bearing plants (angiosperms and gymnosperms) from cryptogams reproducing by spores (ferns, mosses, lichens and algae) to test the hypothesis that greater dispersal abilities in cryptogams allows better tracking of shifting isotherms²³. As historical temperature regimens may affect the rate at which species are shifting their distributions^{24,25}, we tested whether the coupling between species range shifts and isotherm shifts varied with baseline temperature. Similarly, we accounted for potential effects of anthropogenic disturbances on the magnitude of the coupling. We expected that land use intensity in terrestrial systems may impede species range shifts through habitat fragmentation²⁶, while exploitation of marine resources (for example, demersal or bottom trawling) may accelerate the relocation of exploited stocks through massive population die-offs and crashes followed by local extinctions²⁷.

Results and discussion

Geographical, taxonomic and methodological biases matter. We found a strong spatial imbalance in the data towards the most

developed regions of the Northern Hemisphere (Extended Data Figs. 1 and 2) and a clear taxonomic bias towards the most charismatic animals (Aves, Actinopterygii, Amphibia and Mammalia) and plants (Magnoliopsida and Liliopsida) (Extended Data Fig. 3). This supports former claims that global meta-analyses on species range shifts are not truly global^{4,15} and that most species remain understudied while others attract most of the public, scientific and government attention²⁸. In addition to these geographic and taxonomic biases, differences in methodological attributes among studies play a key role in the observed variation in the velocity of range shifts among the 12,415 species included in BioShifts¹³ (Fig. 2). Most of this variation was explained by methodological attributes, which contributed from 6–82% (mean = 36%; median = 35%) of the total variation (Supplementary Table 1). In contrast, differences among taxonomic classes and positions at range margins (trailing edge versus leading edge) contributed only 0–50% (mean = 10%; median = 7%) of the total variation. These findings confirm the importance of accounting for varying methodologies in meta-analyses¹⁴. However, in contrast with former meta-analyses arguing against the use of studies reporting range shifts for a single species or handful of species because such studies are more likely to select responsive species^{1–3}, we found no relationship between sample size and the velocity of range shifts (Supplementary Fig. 2). Hence, we recommend that future meta-analyses on range shifts consider all of the available information instead of constraining the analyses to the set of studies that focused on multiple species (for example, more than three species).

Marine organisms move faster than terrestrial organisms.

Once methodological attributes were accounted for, the variation in the estimated velocity of range shifts among taxonomic classes and positions at range margins was still fairly large, ranging from 3.20 m yr⁻¹ downslope for freshwater fishes (trailing edge; Northern Hemisphere) to 12.39 m yr⁻¹ upslope for amphibians (trailing edge; Southern Hemisphere) and from 6.52 km yr⁻¹ equatorward for reptiles (trailing edge; Northern Hemisphere) to 18.54 km yr⁻¹ poleward for insects (centroid of the range; Northern Hemisphere) (Fig. 3). Marine species (~80% being ectotherms in the database; Extended

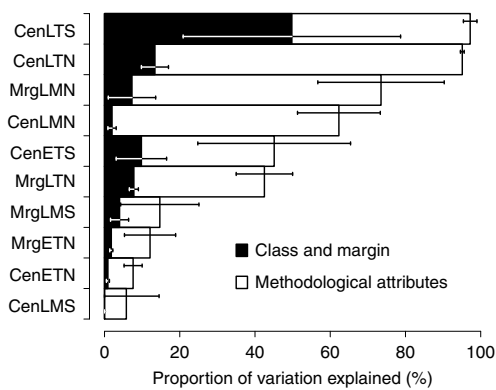


Fig. 2 | Sources of variation in species range shifts. Proportion of explained variation related to either the taxonomic class and position at the range margin (fixed-effect terms in the models) or methodological attributes (random-effect terms in the models) for each of the ten factorial models for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

Data Fig. 2) have moved towards the poles at a mean (\pm s.e.m.) pace of $5.92 \pm 0.94 \text{ km yr}^{-1}$ (one-sample Student's t -test: $t = 6.26$; d.f. residuals = 23; $P = 2.20 \times 10^{-6}$), which is almost six times faster than terrestrial species (one-way analysis of variance (ANOVA): $F = 12.68$; d.f. factor = 1; d.f. residuals = 45; $P = 8.88 \times 10^{-4}$). This mean velocity far exceeds the one reported by the first synthesis ($0.61 \pm 0.24 \text{ km yr}^{-1}$)¹ but is very similar in magnitude and direction to the mean velocity reported by a more recent synthesis focusing exclusively on marine species ($7.20 \pm 1.35 \text{ km yr}^{-1}$)³. Importantly, the mean velocity of latitudinal range shifts we found for terrestrial systems ($1.11 \pm 0.96 \text{ km yr}^{-1}$) was non-significantly different from zero (one-sample Student's t -test: $t = 1.15$; d.f. residuals = 22; $P = 0.25$). This contradicts a former synthesis from 2011 reporting a mean positive velocity of latitudinal range shifts across a wide range of taxonomic groups ($1.76 \pm 0.29 \text{ km yr}^{-1}$)². Although the authors of this synthesis chiefly focused on terrestrial taxonomic groups, they also included data on range shifts from several marine taxonomic groups (molluscs and algae) in their analyses, which could explain the discrepancy. Along elevational gradients, we found that terrestrial species have shifted upslope at a mean pace of $1.78 \pm 0.41 \text{ m yr}^{-1}$ (one-sample Student's t -test: $t = 4.33$; d.f. residuals = 36; $P = 1.13 \times 10^{-3}$), which is slightly faster than what was previously reported ($1.22 \pm 0.18 \text{ m yr}^{-1}$)².

Although we found a tendency towards faster latitudinal range shifts in the Northern Hemisphere ($4.24 \pm 0.70 \text{ km yr}^{-1}$; one-sample Student's t -test: $t = 4.66$; d.f. residuals = 36; $P = 4.28 \times 10^{-5}$) as opposed to the Southern Hemisphere ($1.07 \pm 0.34 \text{ km yr}^{-1}$; one-sample Student's t -test: $t = 1.43$; d.f. residuals = 9; $P = 0.19$), the difference was not significant (one-way ANOVA: $F = 3.08$; d.f. factor = 1; d.f. residuals = 45; $P = 0.09$). More data on species range shifts are thus clearly needed in the Southern Hemisphere (see geographical biases in Extended Data Figs. 1 and 2) to be able to confirm or infirm our hypothesis of faster range shifts in the Northern Hemisphere related to its faster rates of climate warming compared with the Southern Hemisphere¹⁶.

Regarding the position within the range, terrestrial taxa seem to have relatively stable latitudinal distributions, showing no clear signal of range shift at the trailing edge ($-0.17 \pm 1.61 \text{ km yr}^{-1}$; one-sample

Student's t -test: $t = -0.10$; d.f. residuals = 5; $P = 0.92$), the centroid of the range ($2.41 \pm 2.45 \text{ km yr}^{-1}$; one-sample Student's t -test: $t = 0.98$; d.f. residuals = 7; $P = 0.36$) or the leading edge ($0.81 \pm 0.65 \text{ km yr}^{-1}$; one-sample Student's t -test: $t = 1.24$; d.f. residuals = 8; $P = 0.25$). In contrast, marine species seem to be very sensitive to warming, showing trailing-edge contractions ($6.49 \pm 2.13 \text{ km yr}^{-1}$; one-sample Student's t -test: $t = 3.04$; d.f. residuals = 7; $P = 0.02$), leading-edge expansions ($6.02 \pm 1.77 \text{ km yr}^{-1}$; one-sample Student's t -test: $t = 3.40$; d.f. residuals = 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-sample Student's t -test: $t = 12.54$; d.f. residuals = 6; $P = 1.57 \times 10^{-5}$). Our results also indicate that the leading and trailing edges of marine species are equally sensitive to warming (one-way ANOVA: $F = 0.03$; d.f. factor = 1; d.f. residuals = 15; $P = 0.87$), which is consistent with expectations from thermal tolerance limits of marine ectotherms²² (although in contrast with a previous report³). In turn, this suggests that marine species are moving in lockstep⁴ towards the poles. Similarly, along elevational gradients, the trailing and leading edges of terrestrial species have moved towards the summits at comparable mean paces of 2.34 ± 0.67 and $2.15 \pm 0.60 \text{ m yr}^{-1}$, respectively (one-way ANOVA: $F = 0.03$; d.f. factor = 1; d.f. residuals = 23; $P = 0.87$). This indicates that terrestrial species are moving in lockstep towards mountain summits, which is very consistent with two recent syntheses concluding on symmetrical boundary shifts in mountains^{17,18}. Note, however, that the mean upslope shift was significant at the leading edge (one-sample Student's t -test: $t = 6.19$; d.f. residuals = 12; $P = 4.65 \times 10^{-5}$), but only marginally significant at both the trailing edge (one-sample Student's t -test: $t = 2.07$; d.f. residuals = 11; $P = 0.06$) and the centroid of the range (one-sample Student's t -test: $t = 2.13$; d.f. residuals = 11; $P = 0.06$).

Marine species are better at tracking isotherm shifts. Assessing the degree of coupling between species range shifts and isotherm shifts (Extended Data Figs. 4–6), we found that marine species track isotherm shifts in latitude better than terrestrial species (Figs. 4 and 5). For marine systems, our best model explained 33% of the total variation in the velocity of species range shifts (Fig. 4a). Only 4% of the total variation was related to fixed effects; namely, VIS, standardized HFI, baseline temperature, life form and synergistic effects between the VIS and HFI or baseline temperature (Fig. 4b), whereas 29% was explained by random effects or methodological attributes (Supplementary Table 2). Again, this strongly supports the idea that varying methodologies in estimates of climate-driven biological responses can contribute to most of the explained variation and need to be explicitly considered in quantitative reviews¹⁴. Of note, we found that faster climate velocities, combined with higher human pressures in the oceans (for example, commercial shipping, industrial fishing and ocean acidification) or warmer sea surface temperatures during the baseline survey, increase the velocity of species range shifts along the latitudinal gradient for both marine ectotherms and cryptograms (Fig. 5c,d, Extended Data Fig. 7 and Supplementary Table 2). More specifically, we found that marine species closely track shifting isotherms either in initially warm and undisturbed waters (for example, the Central Pacific Basin)¹⁹ or in initially cold waters where human activities are more pronounced (for example, the Norwegian Sea, North Sea and English Channel) (Fig. 6c and Extended Data Fig. 8). This pattern is unlikely to result from a collinearity issue between the VIS and standardized HFI ($R^2 = 0.05$) (Supplementary Fig. 3). Instead, it may stem from the combination of two processes. First, marine species are living closer to their upper thermal limits in the tropics, where sea surface temperatures are the highest, thus increasing the likelihood of local extirpations at their trailing edges as climate warms¹¹. Second, lower constraints on dispersal and colonization in the oceans (as opposed to terrestrial habitats)³ may help species to rapidly shift their distribution towards the newly available habitats. In contrast, at high

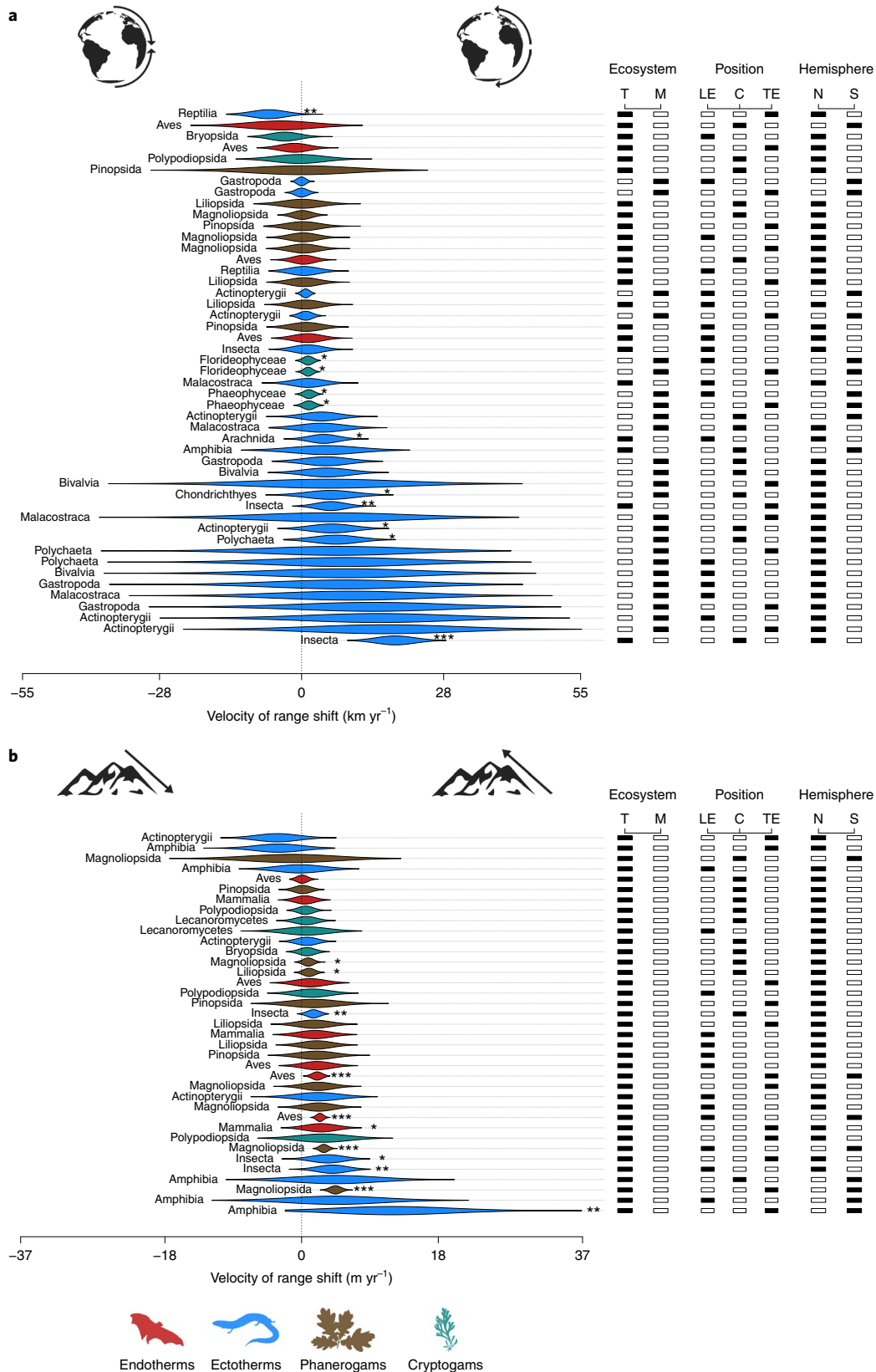


Fig. 3 | Mean velocity of species range shifts per taxonomic class. **a, b**, Estimated velocity of range shift per taxonomic class (that is, effect size) for latitudinal (**a**) and elevational range shifts (**b**), after accounting for methodological variation. Outputs are displayed for all of the possible combinations of positional parameter (TE: trailing edge; CE: centroid; LE: leading edge) \times hemisphere (N: Northern Hemisphere; S: Southern Hemisphere) \times biological system (M: marine; T: terrestrial). Violin plots represent the distribution of 5,000 bootstrap iterations. Asterisks show significant deviations from zero shift (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Credit: Icon Library (mountain silhouette) under a CC0 Public Domain Licence.

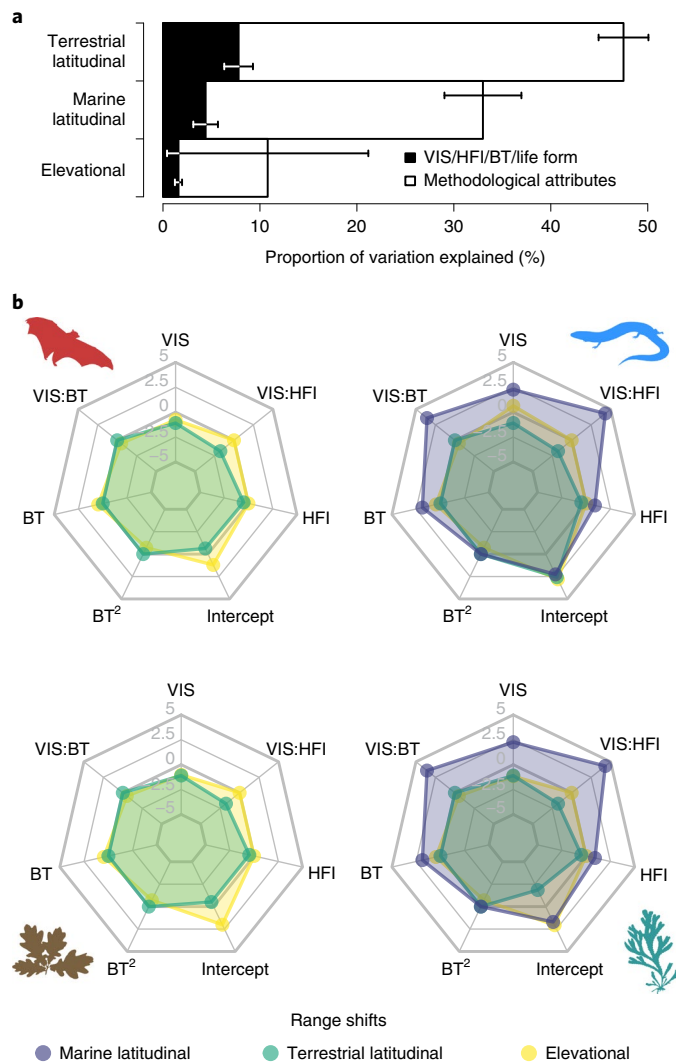


Fig. 4 | Degree of coupling between species range shifts and isotherm shifts. a, b. Model outputs in terms of the proportion of explained variation (**a**) and effect size related to the VIS, baseline temperature (BT), BT^2 , standardized HFI and two-way interaction terms (VIS:HFI and VIS:BT) for each of the four studied life forms (endotherms, ectotherms, phanerogams and cryptogams) (**b**). Intercept refers to the effect size of the focal life form. Error bars represent the distribution of 5,000 bootstrap iterations. Model outputs are displayed separately for marine latitudinal range shifts, terrestrial latitudinal range shifts and elevational range shifts.

latitudes where the thermal safety margin of marine species is larger¹¹, climate warming alone is unlikely to explain isotherm tracking. Instead, anthropogenic activities (for example, fishing pressure and pollution in the North Sea) may render populations more sensitive to climate change by reducing abundance and density, truncating the age distribution and leading to the depletion of fish stock at the trailing edge of their range²⁷. In parallel, successful management actions at higher latitudes, such as along the Norwegian coastlines in the Norwegian Sea and the Barents Sea, combined with climate warming, may increase population sizes of commercial fishes at the leading edge of their range²⁹, thus promoting successful colonization.

Unlike in the oceans, the degree of coupling between the velocity of species range shifts and the VIS is comparatively poor on land (Fig. 4). Again, this inconsistency with a former synthesis² from 2011 may stem from the fact that here we analysed the coupling

separately for the marine and terrestrial systems—a distinction that was not possible in 2011 due to a lack of data at that time, for marine systems. Our best model explained 47% of the total variation in the velocity of species range shifts along the latitudinal gradient on land (Supplementary Table 2), of which the largest proportion was explained by varying methodologies among studies (Fig. 4a). Among fixed effects, we found that range shifts were best explained by differences between life forms and a negative interaction term between the VIS and standardized HFI (explaining 8% of the total variation; Fig. 4b). Such an antagonistic effect between climatic and human-related drivers suggests that habitat loss and fragmentation (associated with high population densities and other human activities such as agricultural practices) in the lowlands, combined with limited dispersal abilities of species (relative to the speed at which isotherms are shifting along the latitudinal gradient³⁰) probably impede the capacity of terrestrial taxa to track shifting isotherms. Again, this pattern is unlikely to result from a collinearity issue between the VIS and standardized HFI ($R^2 = 0.09$) (Supplementary Fig. 3). Interestingly, we found that when exposed to a high degree of anthropogenic disturbances ($HFI > 0.3$), terrestrial species tend to shift in the opposite direction to isotherms (see HFI conditions under which both velocities show opposite signs in Fig. 5b and Extended Data Fig. 9), probably due to local extinction processes at the leading edge. For instance, a previous study showed that during 1970–1999, habitat loss and degradation led to a decline in the distribution sizes of three-quarters of butterfly species that approach their northern climatic range margins in Britain, outweighing the climate-induced species range shifts that were expected from climate warming²⁶. This is consistent with the general idea that land use and climate change may act as opposing forces on species distribution changes. In addition, air conducts heat 25 times less effectively than water¹², which makes terrestrial species, in general, less sensitive than marine species to temperature fluctuations and thus less likely to move as a direct response to climate warming¹¹. The availability of thermal microrefugia (for example, shaded environments) on land may also allow species to more easily regulate their body temperature (for example, microhabitats may allow terrestrial ectotherms to increase their thermal safety margin by 3°C on average compared with marine ectotherms¹¹). Hence, we confirm that isotherm tracking is very unlikely for terrestrial taxa living in the lowlands^{9,25}.

Along elevational gradients, the best model explained 11% of the total variation in the velocity of range shifts (Fig. 4a and Supplementary Table 2) and showed that the VIS interacts with both baseline temperature and life forms (explaining 2% of the total variation; Figs. 5a and 6a and Extended Data Figs. 9 and 10). In contrast with the latitudinal gradient, the standardized HFI was not selected as a meaningful explanatory variable in the best model. Of note, we found a better coupling between the velocity of species range shifts and the VIS for ectotherms in cold environments (that is, close to mountaintops). The geographic isolation and habitat area constraints specific to mountaintops (for example, sky islands) may exacerbate local extinction events through reduced population sizes as the climate warms and the habitat area shrinks, thus paying off part of the climatic debt for ectotherms living close to mountaintops. For instance, mass extinction events associated with climate warming and pathogen outbreaks have already been reported for several amphibian species endemic to mountainous regions³¹. For endotherms, phanerogams and cryptogams, the slope of the relationship between the velocity of species range shifts and the VIS in mountainous systems is negative, especially under warm climates (Extended Data Fig. 9). However, we found that velocity values for range shifts along elevational gradients are always positive, except under very warm baseline temperature conditions (baseline temperature $> 20^\circ\text{C}$). This indicates that endotherms, phanerogams and cryptogams are in general shifting their elevational ranges

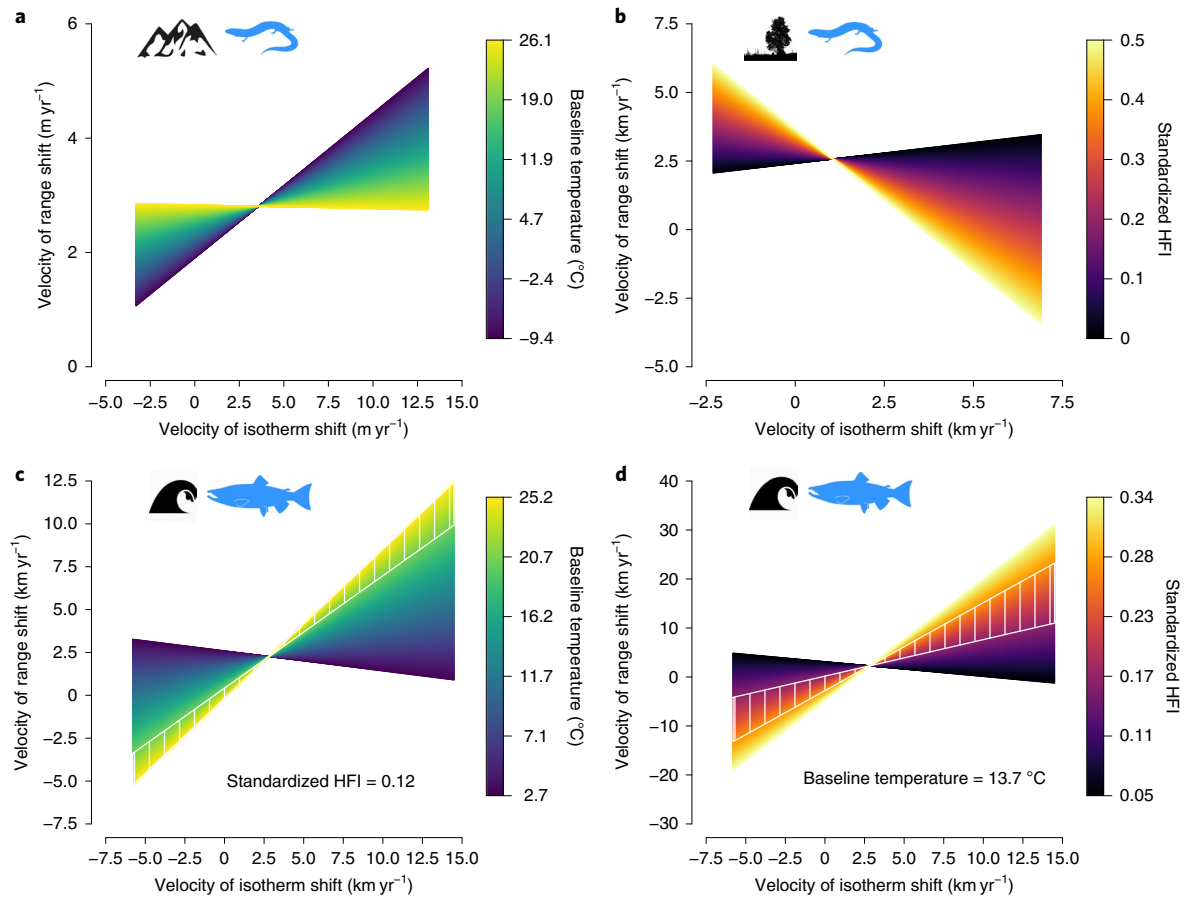


Fig. 5 | Main determinants of the velocity of species range shifts. a–d, Results are displayed along elevational (**a**) and latitudinal gradients (**b–d**) for both terrestrial (**a** and **b**) and marine realms (**c** and **d**). **a**, Interaction effect between baseline temperature and the VIS in elevation for ectotherms. **b**, Interaction effect between the standardized HFI and VIS in latitude for terrestrial ectotherms. **c**, Interaction effect between baseline temperature and the VIS in latitude for marine ectotherms while setting the standardized HFI to its median value in the database. **d**, Interaction effect between the standardized HFI and VIS in latitude for marine ectotherms while setting the baseline temperature to the median value in the database. The two white lines and the white hatching represent the range of conditions under which marine ectotherms closely track the shifting isotherms in latitude (that is, the slope parameter is not significantly different from 1 based on 5,000 bootstrap iterations). Note that negative slopes do not necessarily indicate species range shifts in the opposite direction to isotherm shifts, unless the signs of the two estimates (for a given combination of baseline temperature and standardized HFI) are opposite. Credit: Icon Library (mountain and seascape silhouettes) under a CC0 Public Domain Licence.

upslope to track shifting isotherms but are consistently lagging behind climate change. Isotherms may be shifting upslope at a pace that is simply too fast for species with limited dispersal abilities and long life spans, such as trees, to keep pace. Additionally, in the tropics, the higher importance of biotic interactions³² may further impede the rate of range shifts over what is expected from climate change alone³³. Most importantly, the global climatic grids that are currently available, and that we used here, may still be too coarse in spatial resolution (1 km² at best) to allow a reliable assessment of the true VIS experienced along mountain slopes. Indeed, the topoclimatic and microclimatic heterogeneity that is available across a few metres in mountain systems (something that is not accounted for here) may provide a strong spatial buffer against climate warming³⁴, allowing species to shift relatively small spatial distances and seemingly stay³⁵ relative to the VIS that is measured at a coarser spatial resolution. Hence, the slow velocities of species range shifts that we observed in mountainous areas could also be the result of local compensation effects involving short-distance escapes and species persistence within microrefugia.

General implications. To conclude, the coupling between species range shifts and isotherm shifts is not uniform across biological

systems, confirming the lags observed in the biotic responses of terrestrial organisms to climate change^{9,10}. Of note, we demonstrate complex interactions between the velocity of climate warming, the degree of human pressures on the environment, historical temperature regimens and species characteristics. We suggest that commercial fishing may speed up the displacement of marine species distribution through resource depletion and population crashes at the trailing edge, whereas low constraints on dispersal in the oceans may allow marine species living close to their upper thermal limits to better track climate warming at the leading edge. On land, habitat loss and fragmentation due to land use changes may impede the ability of terrestrial species to track shifting isotherms. These complex interactions need to be accounted for to improve scenarios of biodiversity redistribution and its consequences on human well-being⁵ under future climate change. The fact that marine species track climate warming better than terrestrial species also suggests that biodiversity redistribution will have more immediate and far-reaching consequences in the oceans than on land. For instance, community reshuffling^{9,25} and the tropicalization of temperate ecosystems^{36,37} is likely to happen much faster in marine than terrestrial systems, with more direct and rapid consequences on ecosystem health and functioning (for example, increasing fish herbivory in kelp forests³⁸), as

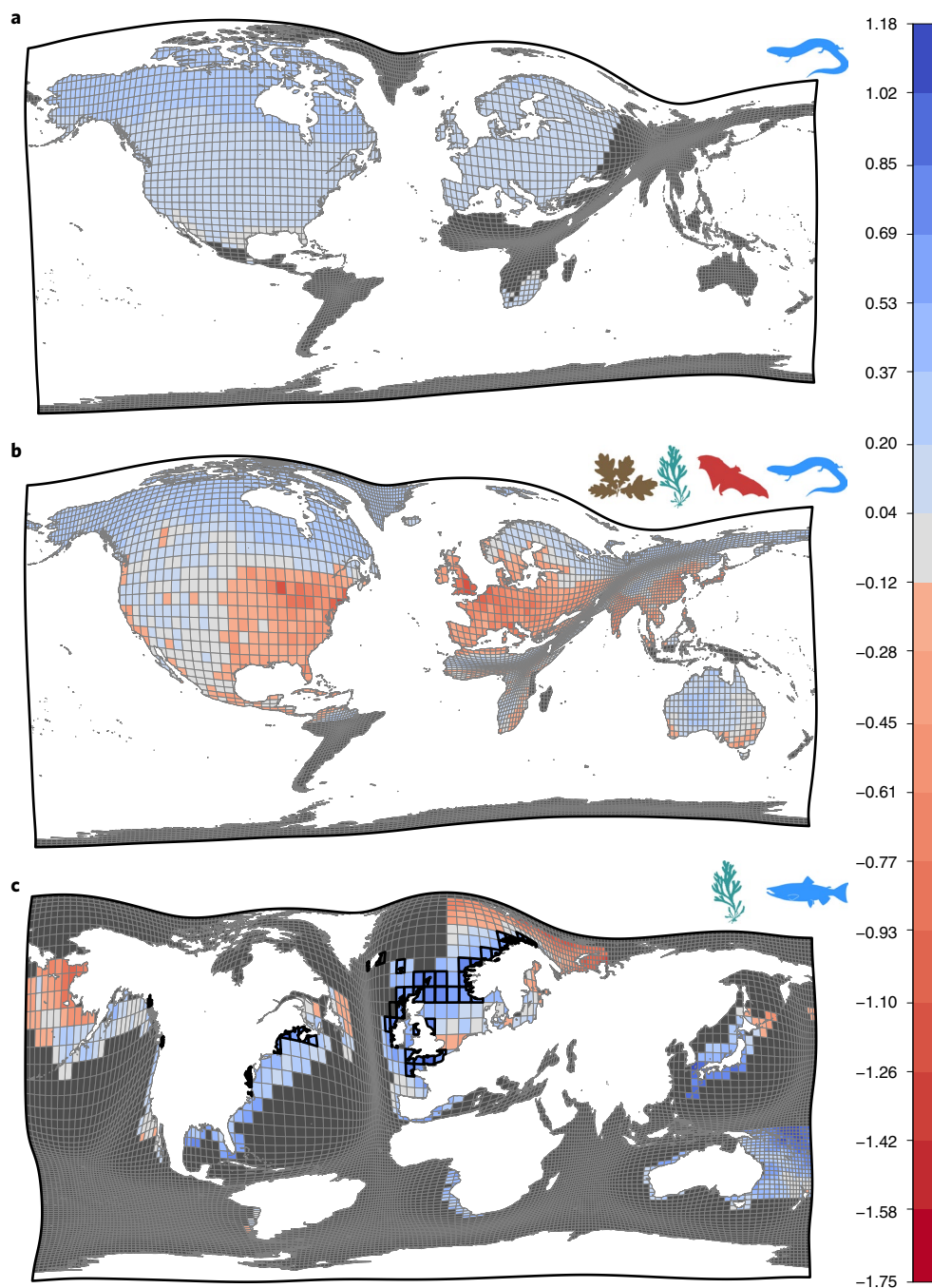


Fig. 6 | Maps of the degree of coupling between species range shifts and isotherm shifts. a–c, Cartograms show the predicted slope coefficient between the velocity of species range shifts and the VIS per $2^\circ \times 2^\circ$ grid cell along elevational (**a**) and latitudinal gradients (**b** and **c**) for both terrestrial (**b**) and marine realms (**c**). Note that panel **a** only displays the predicted slope coefficient for ectotherms. Positive slope values (bluish colours) close to 1 suggest perfect isotherm tracking while negative values (reddish colours) suggest that species are not tracking the shifting isotherms. Note that negative slopes do not necessarily mean that species are shifting in the opposite direction to isotherm shifts (see Fig. 5). The number of range shift estimates (that is, sample size) in each grid cell was used to distort the map: the bigger the grid cell, the larger the sample size. Grid cells with a black and bold border display areas where species are closely tracking the shifting isotherms (that is, the slope parameter is not significantly different from 1 based on 5,000 bootstrap iterations).

well as on the valuable services (for example, fishery) and disservices (for example, coastal erosion) oceans can provide.

However, it is important to bear in mind that our findings, as well as former syntheses on the topic, are still dependent on data availability and thus suffer from severe taxonomic and geographic biases. Despite a broad taxonomic coverage of the tree of life (Extended Data Fig. 3), species range shifts recorded in

BioShifts¹³ cover only 0.6% of the described biodiversity on Earth ($n=2,094,892$ taxa). Besides, it is noteworthy that species range shifts in the Southern Hemisphere and in tropical regions in general are under-represented. These limitations may affect our perception of species redistribution, and by consequence challenge global biodiversity conservation efforts^{4,15}. It is thus more important now than ever to continue to study and document range shifts in areas and

for taxonomic groups that have been so far somewhat neglected. Our database on species range shifts provides solid foundations on which to build a truly global monitoring of species redistribution. We thus call for future research perspectives linking our database on species range shifts with existing but scattered databases on species traits^{39–44}, to improve our ability to anticipate biodiversity redistribution under climate change.

Methods

Literature search. We reviewed the scientific and peer-reviewed literature reporting climate-driven range shifts under contemporary climate change. By contemporary climate change, we refer to the period stretching from the beginning of the nineteenth century and onwards. As a general approach, we started from the reference lists of the most recent meta-analyses and syntheses on the topic^{2–4}, which we completed by regularly searching the scientific literature published between 2014 and 2018, following the same protocol as in Lenoir and Svenning⁴ (Supplementary Fig. 1). Because of the clear focus on latitudinal and elevational range shifts in the scientific literature and the lack of information on the other geographical dimensions¹, we excluded several reports focusing exclusively on bathymetric or longitudinal range shifts. Broad inclusion criteria comprised studies: (1) focusing on relatively recent distribution changes (since the 1850s); (2) based on the occurrence or abundance data of at least one species; and (3) that were based on assessments covering at least two historical censuses with a minimum of 10 years between censuses. Hence, we excluded studies reporting distribution range changes from a single census (that is, using a synchronous approach comparing data from different ontogenetic life stages of the same species, such as seedlings versus adult trees) or based on historical patterns of species mortality obtained from climatic reconstructions only, without real occurrence or abundance data from at least two different time periods to confirm model outputs. We also excluded studies focusing exclusively on distributional range changes of invasive alien species. This selection procedure led to a total of 258 published and peer-reviewed studies for which we could extract data on species range shifts^{8,27,45–300}.

We used Google Sheets to store the raw data on species range shifts in a dynamic and common file that we shared among co-authors, while always keeping a regular copy of the database saved on several computers to ensure backups. Once studies were clearly identified and stored as .pdf files in a common folder in Google Docs, each co-author picked studies, one by one, and entered data manually in the database. Some of the .pdf files were carefully annotated to help us quickly identify and recover any meaningful information in the main text or display items (for example, tables or figures). When data on species range shifts were not directly available in the main text, in tables or in the appendices of the publication, we first contacted the corresponding authors and requested the data. In cases of no positive response from the original authors and when data on range shifts could be extracted from published figures, we used the WebPlotDigitizer program (<https://automeris.io/WebPlotDigitizer/>). When range shifts were reported for more than one geographically distinct survey area or between more than two censuses (for example, more than one resurvey of historical data), we considered them as independent case studies ($n = 325$). This data entry procedure led to a total of 30,534 range shift estimates at the species level (see 'Data availability' to access the database: BioShifts¹³).

Range shift estimates, as reported by the original authors, were coded as positive values if they were poleward in latitude or upward in elevation, and negative otherwise (equatorward and downward). When the authors reported horizontal range shifts with both the magnitude and direction (that is, azimuth) values, we used trigonometric relationships to transform these values into latitudinal range shifts for consistency with the main bulk of data available in the scientific literature. Next, we divided each range shift estimate by the study duration between two consecutive censuses (ending year – starting year + 1) to assess the rate or velocity of range shift (in km yr^{-1} along the latitudinal gradient and in m yr^{-1} along elevational gradients). In addition to the velocity of range shift at the species level, we also retrieved information at the case study level ($n = 325$), including methodological attributes known to potentially affect the velocity of range shift¹⁴: the starting year of the study (start); the ending year of the study (end); the size of the study area (area); the number of taxa in a study (N_{taxa} ; a continuous variable ranging from 1–4,426; median = 21; mean = 122); the frequency of sampling (sampling; a factor variable with four levels: continuous, irregular or a comparison of two or multiple periods); whether range shift estimates were generated from occurrence or abundance data (PrAb) (a factor variable with two levels: Pr for presence or occurrence data and Ab for abundance data); the spatial resolution of the raw data used to estimate range shifts (grain; a factor variable with three levels: fine for data based on GPS coordinates with a spatial resolution lower than 10 km; coarse for data based on range maps or atlas grids with a spatial resolution greater than 100 km; and medium for intermediate situations); the quality of the approach used to estimate range shifts (quality; a factor variable with four levels: low when no data cleaning procedures were performed before computing range shifts; balanced when data cleaning or

resampling procedures were carried out to calculate range shifts on a balanced dataset; modelled when range shifts were obtained by computing the difference in the position of a given range parameter estimated from species distribution models (SDMs) independently calibrated during at least two different time periods (note that in this case SDM outputs represent the realized and not the potential species distribution for a given time period); and resurveyed when range shifts were calculated from paired designs such as permanent plots); and whether the significance levels of range shift estimates were assessed or not in the original study (signif; a factor variable with two levels). To improve the balance in the number of observations among levels of a given factor variable, we merged some levels with poor data coverage together for the sampling and quality variables. For instance, the levels continuous and irregular were merged together with the level multiple, such that sampling was used in our analyses as a factor variable with two levels: two versus multiple. Regarding the quality variable, we merged the level resurveyed together with the level balanced, such that quality was used in our analyses as a factor variable with three levels: low; balanced; and modelled. Still at the case study level ($n = 235$), we digitized the study region in Google Earth and used the resulting polygons to retrieve spatial information such as the total area covered by the study. If no clear maps delineating the study area were reported in the original study (for example, maps displaying the study region), we used national geographic boundaries or any meaningful spatial information from the text to delineate the study area. All spatial polygons were used to produce a geo-database (Extended Data Figs. 1 and 2).

Taxonomic harmonization. Before undertaking any taxonomic harmonization procedure, the last version of our database, dated April 2018, contained 13,570 entries of taxa at any taxonomic rank up to the genus level (that is, subspecies, species and genus). Using the R programming language⁴⁰¹, we assembled an R script to retrieve, for each taxonomic entry, the most recent accepted name and its associated classification. After a visual inspection for obvious syntax correction, three steps of taxonomic verification were performed. First, names were searched in the National Center for Biotechnology Information (NCBI) taxonomy database using the function classification from the R package taxize⁴⁰². Then, in the same way, any remaining taxonomic entity not found in the NCBI database was verified with the Integrated Taxonomic Information System (ITIS) database. The full taxonomic classification was also retrieved during these two steps. Third, the last remaining taxonomic entities not found in the NCBI and ITIS databases were checked using the Global Biodiversity Information Facility database, using the function name_backbone in the R package rgbif. If we found a match, the corrected taxonomic entity was checked again in the NCBI and ITIS databases by undergoing the previously mentioned procedure once again to retrieve a reliable taxonomic classification. Finally, only names at the species and genus level were kept for the analyses (subspecies being aggregated at the species level). Following this taxonomic harmonization procedure, the final number of taxa names in the database was reduced to 12,415.

Climate velocity. Using the spatial information obtained from the digitized polygons, as well as the temporal information (start and end years) available from each of the 258 publication sources, we retrieved basic temperature information to calculate the velocity of temperature change throughout the study period. Terrestrial climate data were obtained from WorldClim version 1.4 (<http://www.worldclim.org/>) and the Climate Research Unit (CRU) TS version 3.23 (<https://crudata.uea.ac.uk/cru/data/hrg/>), whereas marine climate data were obtained from Bio-ORACLE (<http://www.bio-oracle.org/>) and the Met Office Hadley Centre observation datasets (<https://www.metoffice.gov.uk/hadobs/hadisst/>).

Because marine and terrestrial taxa shift at different rates and directions, to potentially track the complex mosaic of local climate velocities⁸, we calculated the observed local velocity of temperature change (that is, the spatial shift of isotherms over time)^{6,7} for each case study, following the approach used by Burrows et al.⁷. We divided the temporal change in annual mean temperature observed over the studied period ($^{\circ}\text{C yr}^{-1}$) by the corresponding spatial gradient ($^{\circ}\text{C km}^{-1}$ or $^{\circ}\text{C m}^{-1}$) as a measure of the velocity of temperature change (km yr^{-1} or m yr^{-1})⁶. The temporal gradient was calculated using time-series data from the CRU covering the period 1901–2016 at a spatial resolution of 0.5° (~ 55 km at the equator) and from the Met Office Hadley Centre observation datasets covering the period 1870–2018 at a spatial resolution of 1° (~ 111 km at the equator) for the terrestrial and marine studies, respectively. To do so, we regressed annual mean temperature ($^{\circ}\text{C}$) values for all years throughout the study period, as well as the two preceding years, against time (yr) using linear regressions. When the starting year was before 1901 or 1870 for terrestrial and marine systems, respectively, we started the time series in 1901 or 1870 depending on the climate series. The slope parameter ($^{\circ}\text{C yr}^{-1}$) of this model was then used as an estimate of the temporal gradient. For the sake of comparison with the rate of range shift usually calculated along the latitudinal and elevational gradients, we calculated the spatial gradient of annual mean temperature along the latitudinal (km yr^{-1}) and elevational (m yr^{-1}) gradients separately. This allowed us to assess both the latitudinal and elevational velocity of temperature change (LatVeloT and EleVeloT). To assess the latitudinal spatial gradient of annual mean temperature across land and sea, we used spatial grids from WorldClim and Bio-ORACLE, respectively, at a spatial resolution of 5 arcmin

(~ 9.2 km at the equator). The WorldClim grid of annual mean temperature was downloaded at the finest spatial resolution, which is 30 arcsec (~ 1 km at the equator), but aggregated at 5 arcmin to be consistent with the spatial resolution of sea surface temperatures. Latitudinal spatial gradients were calculated as in Burrows et al.⁷ based on a 3×3 neighbourhood sub-grid with the centre cell being the focal cell to which the computed value of average latitudinal spatial gradient was attributed. The average latitudinal spatial gradient for each focal centre cell was computed as follows. Identifying the nine cells of the 3×3 neighbourhood sub-grid as *a, b, c, d, e, f, g, h* and *i*, with *a–c* being the top row, *d–f* the middle row and *g–i* the bottom row, the focal centre cell is *e*. Within this sub-grid centred on *e*, there are six possible pairs of north–south differences in temperature between direct neighbouring cells in the Northern Hemisphere: *a–d*; *b–e*; *c–f*; *d–g*; *e–h*; and *f–i*. In the Southern Hemisphere, south–north differences in temperature are computed instead of north–south differences: *d–a*; *e–b*; *f–c*; *g–d*; *h–e*; and *i–f*. All six pairs of temperature differences per sub-grid were then divided by the spatial distance separating the two neighbouring cells belonging to the same pair (about 111 km) before computing the mean across all six values, excluding any missing values (usually along coastlines), using weightings: 1; 2; 1; 1; 2; and 1. For elevational gradients, we used the temperature data from the WorldClim grid of annual mean temperature at the finest spatial resolution (30 arcsec, which is ~ 1 km at the equator) and calculated the spatial gradient across each case study using a linear model relating annual mean temperature (the response variable) to both elevation and latitude (the explanatory variables). We used latitude as a covariate in this model to account for the latitudinal variation in temperature observed within studies covering large spatial extents (that is, elevation values close to the equator are not directly comparable, in terms of temperature, to elevation values close to the poles). The coefficient parameter along elevational gradients ($^{\circ}\text{C m}^{-1}$) was then used as an estimate of the local adiabatic lapse rate. For the study areas that were larger in extent than the spatial resolution of the temperature grids, we computed the mean values of LatVeloT or EleVeloT throughout the entire study area by averaging values across all spatial grid cells overlapping with the polygons delineating the study area.

Additional drivers of range shifts. As baseline temperature conditions may affect the rate at which species are shifting their distributions²⁴, we extracted annual mean temperature values during the year of the initial census (start), as well as the two preceding years, and calculated the mean (hereafter, the baseline temperature in $^{\circ}\text{C}$). For terrestrial and marine systems, we used time-series data from the CRU and the Met Office Hadley Centre observation datasets, respectively. When the initial census of a given publication source was before 1901 or 1870 for terrestrial and marine systems, respectively, we used the oldest years available from the time series to compute baseline temperature conditions. Similar to climate velocity variables, when the study areas were larger in extent than the spatial resolution of the temperature grids, we computed the mean values of baseline temperature throughout the entire study area by averaging values across all spatial grid cells overlapping with the polygons delineating the study area.

As anthropogenic disturbances such as land use intensity or industrial fishing may act as confounding factors on the velocity of range shift²⁴, we retrieved information on anthropogenic impacts for both the terrestrial and marine environment. For terrestrial systems, we downloaded the Global Terrestrial Human Footprint maps for the year 2009³⁰. These maps, at a spatial resolution of 30 arcsec (~ 1 km at the equator), provide remotely sensed and bottom-up survey information on eight variables measuring the direct and indirect human pressures on the environment: (1) the extent of built environments; (2) human population density; (3) electric infrastructure (night-light time); (4) crop lands; (5) pasture lands; (6) roads; (7) railways; and (8) navigable waterways acting like roads for people to access natural resources. All eight pressure variables were scaled by the original authors based on their degree of influence on the terrestrial environment. For instance, human population density and night-time lights were scaled between 0 and 10 while roads were scaled between 0 and 8. Scores for each of the eight individual threats were then summed and weighted by the original authors to make a composite map of the global HFI ranging from 0–50. For marine systems, we used the Global Map of Human Impact on Marine Ecosystems¹⁹, also available at a spatial resolution of 30 arcsec (~ 1 km at the equator). This gridded dataset provides a cumulative impact score ranging from 0.01–90.1 for the minimum and maximum value, respectively. It was developed on the basis of expert judgement, to estimate ecosystem-specific impacts with respect to 17 anthropogenic drivers of ecological change (for example, commercial shipping, demersal and pelagic fishing, ocean acidification and pollution). To allow comparison between terrestrial and marine systems, we rescaled both indices between 0 and 1 (standardized HFI) and computed the mean per study area. The original authors have extensively validated HFI values against satellite imagery, yielding high confidence that they represent conditions of human pressure on the environment²⁰.

Assessing geographic and taxonomic biases. To evaluate spatial biases in the reporting of species range shift, we built $2^{\circ} \times 2^{\circ}$ gridded maps, on top of which we overlaid the digitized polygons associated with the observations gathered in the database for both the terrestrial and marine realms, and separately for latitudinal and elevational range shifts. For each $2^{\circ} \times 2^{\circ}$ grid cell, we also computed the

relative proportion of ectotherms versus endotherms for animals and phanerogams versus cryptogams for plants and plant-like life forms (for example, lichens and algae). We distinguished ectotherm from endotherm life forms due to their contrasting sensitivity to temperature fluctuations in the environment, with ectotherms being unable to physiologically regulate their body temperature in contrast with endotherms. The distinction between phanerogam and cryptogam life forms allowed a contrast between two different reproduction strategies among chlorophyllous organisms: the evolved seed-bearing plants (angiosperms and gymnosperms) versus the other plant-like life forms reproducing by spores (ferns, mosses, lichens and algae). We then generated cartograms using the diffusion-based method for producing density-equalizing maps³⁰³. The number of range shift rates per $2^{\circ} \times 2^{\circ}$ grid cell (that is, sample size) was used to distort the map: the bigger the grid cell, the larger the sample size (Extended Data Fig. 1). We additionally estimated the phylogenetic coverage of the range shift database with respect to the whole tree of life described in the Open Tree of Life (<https://tree.opentreeoflife.org>), collapsed at the level of taxonomic classes and the total number of species recorded in the Catalogue of Life (<http://catalogueoflife.org/>).

Estimating the velocity of range shifts per taxonomic class. Data coverage in our database is very unbalanced between: the marine versus terrestrial realm; the Northern Hemisphere versus the Southern Hemisphere; and the margins versus centroid of the species range (Supplementary Table 1). Besides, data on species range shifts do not even exist for some taxonomic classes in some of the combinations of realm \times hemisphere \times position in the species range. For instance, dicots (Magnoliopsida) are exclusively terrestrial organisms while cartilaginous fishes (Chondrichthyes) almost exclusively live in marine habitats, except for a few sharks and rays living in freshwater habitats during all or part of their lives. Thus, a single model to estimate the velocity of range shifts per taxonomic class while accounting for methodological biases^{14,15} would be inappropriate. Hence, we divided latitudinal range shifts ($n = 16,952$) into a full factorial design³⁰⁴ with eight experimental units based on all of the possible combinations of levels across three factor variables: biological system (marine versus terrestrial); hemisphere (Northern versus Southern); and range position (centroid versus margins). We did the same for elevational range shifts ($n = 13,582$) except that there were only four possible experimental units (that is, terrestrial systems only). To ensure a robust fit, we further focused on taxonomic classes with >30 observations per experimental unit ($n = 20$ taxonomic classes fulfilled this sample size criterion) (Fig. 1 and Supplementary Table 1), which reduced our sample size to 16,399 and 13,341 observations for latitudinal and elevational range shifts, respectively. Among the 12 possible combinations, only one combination (latitude \times margins \times terrestrial \times Southern Hemisphere) could not be fulfilled due to a lack of range shift data ($n = 8$). This resulted in a total of 11 sub-models (that is, factorial models) (Supplementary Table 1).

For each of the 11 factorial models for which the data were available, we built an LMM relating the velocity of species range shift for a given taxon (that is, the response variable) against taxonomic class, a factor variable with as many levels as the number of taxonomic classes within the focal experimental unit (for example Amphibia versus Aves for latitudinal range shifts at the centroid of the distribution in terrestrial systems of the Southern Hemisphere) (Supplementary Table 1). Note that if a given factorial model only had data for one unique taxonomic class (for example, Actinopterygii for latitudinal range shifts at the centroid of the distribution in marine systems of the Southern Hemisphere) (Supplementary Table 1), the variable class was not included in the fixed effects of the LMM. For the five LMMs focusing on the rate of range shift at the margins of the distribution, we added an extra factor variable (margin) with two levels (leading versus trailing edge) in the fixed effects, to provide robust estimates of the rate of range shift at both the leading and trailing edges. Given the complex structure of the database, involving repeated observations per taxonomic unit (for example, family or genus) or methodological level, linear mixed-effects modelling is the most appropriate modelling approach³⁰⁴. This allowed us to provide estimates of the velocity of range shifts per taxonomic class that are representative across all levels of a given methodological variable rather than providing estimates for each level separately, while accounting for taxonomic non-independence. More specifically, we included genus as a random intercept term nested (or not, in cases of singularity fit) within family to account for potential taxonomic autocorrelation in the residuals of the models. In addition, because the different methodological approaches used in the scientific studies may also contribute to a non-negligible fraction of the variation in range shifts¹⁴, we considered several methodological variables as random intercept terms in the LMMs (area, start, N_{taxa} , sampling, PrAb, grain, quality and signif). To be included in the random part of our LMMs, the continuous variables area, start and N_{taxa} were first transformed into factor variables with four levels each, using the respective quantiles as cutting points. Then, for each factorial model separately, we selected only the set of uncorrelated variables with at least two levels having more than four observations. We used the lmer function from the lme4 package³⁰⁵ in the R programming language³⁰¹.

We used a model selection procedure where the best random-effect structure was identified by testing all of the combinations of random factors and selecting the one with the lowest Akaike information criterion with small-sample correction (AICc). To compare AICc values among candidate models, we set the

restricted maximum likelihood argument to FALSE in the lmer function (that is, REML = FALSE for maximum likelihood)³⁰⁵. To ensure robust estimations, all of the singular fits were removed from the list of candidate models before model selection. In cases of singular fits across all candidate models, we used case study (source) as the unique random intercept term. If the random intercept term source also led to a singular fit, we used a linear regression model. For each of the LMMs (or linear regression models in cases of singular fits for all of the candidate models) focusing on the velocity of range shift at the margins of the distribution, we also included an interaction between margin and class that we tested against a model without the interaction term in the fixed effects based on the AICc value. When the absolute difference in AICc value between these two candidate models was >2, we selected the model with the lowest AICc value. Otherwise, in cases of equivalent competing models, we selected the one with the interaction effect between margin and class, considering that it allows flexible range shift estimations at the trailing and leading edge. Once the best LMM was selected for each factorial model (Supplementary Table 1), we set REML to TRUE³⁰⁵ to extract coefficient estimates among the different levels of the factor variables class and margin. To test whether the estimated rate of range shift for a given taxonomic class and at a given position within the range was significantly different from 0, we re-ran each of the 11 selected best models using a bootstrap approach ($n = 5,000$ iterations). From these 5,000 estimates, we computed the mean and median velocity of range shift as well as the standard deviation and 95% confidence interval per taxonomic class. Finally, to assess the overall goodness of fit of the different factorial models, as well as to compare the relative importance of biological versus methodological effects on the rate of range shift, we computed the marginal (that is, variance explained by the fixed effects) and conditional (that is, variance explained by both the fixed and random effects) R^2 values³⁰⁶ of each bootstrap iteration and for each factorial model using the rsquaredGLMM function from the MuMIn package in the R programming language³⁰¹.

Coupling between species range shifts and isotherm shifts. We assessed the coupling between the velocity of species range shifts and the VIS using LMMs built separately for the latitudinal and elevational gradients. We specified the velocity of species latitudinal (km yr^{-1}) or elevational (m yr^{-1}) range shifts as the response variable and either the latitudinal or elevational VIS (LatVeloT/ EleVeloT; continuous variables) as the main explanatory variable. To account for potential interacting effects on the relationship between the velocity of range shifts and the VIS, we added several covariates in our models: baseline temperature (a continuous variable); standardized HFI (a continuous variable representing human pressures on the environment bounded between 0 and 1); and life form (a factor variable with four levels: ectotherm, endotherm, cryptogam and phanerogam). As temperature regimens and human pressures on the environment are not directly comparable between lands and oceans, we further modelled the coupling between the velocity of species latitudinal range shifts and the VIS in latitude (LatVeloT) separately for the marine and terrestrial realm. We tested for all two-way interaction terms between each covariate (baseline temperature, HFI and life form) and the VIS (either LatVeloT or EleVeloT). We also tested for a unimodal relationship between the estimated rates of range shifts and baseline temperature conditions using a second-order polynomial term. The variables position within the range (a factor variable with three levels: trailing edge, centroid and leading edge) and hemisphere (a factor variable with two levels: Northern versus Southern) were not incorporated as covariates in the models as both variables had no effect to explain the variation in the rates of latitudinal and elevational range shifts per taxonomic class (Supplementary Table 2).

Similar to the LMMs developed at the taxonomic class level, the aforementioned explanatory variables were used as fixed effects in LMMs, whereas the methodological attributes (area, start, N_{tax} , sampling, PrAb, grain, quality and signif) were used as random intercept terms. Starting from the beyond optimal model (the full model with all of the fixed effects)³⁰⁵, separately for the velocity of latitudinal range shifts in marine and terrestrial systems as well as for the velocity of elevational range shifts, we tested all model combinations and selected the best model based on the lowest AICc value, setting REML to FALSE (that is, maximum likelihood) for model selection and then to TRUE to estimate the coefficients once the best model was selected³⁰⁵. We first selected the random-effect structure after removing singular fits, using the exact same procedure as for the models used to estimate the mean velocity of range shift per taxonomic class. We then selected the fixed-effect structure, keeping the previously identified random structure constant. All continuous variables (LatVeloT, EleVeloT, baseline temperature and HFI) were standardized to z scores using the gscale function³⁰⁷ from the jtools package in the R programming language³⁰¹. This function standardizes each value of a given variable by subtracting it from the mean and dividing it by two times the standard deviation of the focal variable (instead of one time as is more commonly done). This rescaling formula is recommended over the traditional formula of dividing by one times the standard deviation because it allows direct comparisons of model coefficients with untransformed binary predictors³⁰⁷. For the sake of consistency, we focused on the set of species belonging to the taxonomic classes with >30 observations, resulting in 16,521 (1,403 marine versus 15,118 terrestrial) and 13,459 observations for latitudinal and elevational range shifts, respectively. The 95% confidence intervals around each of the estimated coefficients were calculated

using bootstraps ($n = 5,000$ iterations), similar to the models used to estimate the mean velocity of range shift per taxonomic class.

Finally, to illustrate the capacity of species to track the shifting isotherms, we mapped the predicted slopes for each combination of the predictors identified in the best models, separately for latitudinal (marine or terrestrial) and elevational range shifts. A slope value of 1 between the velocity of species range shifts and the VIS indicates a perfect coupling, with species closely tracking the shifting isotherms. To do so, we built a $2^\circ \times 2^\circ$ gridded map, on top of which we overlaid the digitized polygons associated with each observation used in the previous models. We then generated cartograms using the diffusion-based method for producing density-equalizing maps³⁰⁸. As before (see 'Assessing geographic and taxonomic biases'), the number of range shift rates per grid cell (that is, sample size) was used to distort the map: the bigger the grid cell, the larger the sample size. Finally, we tested whether the slope estimated for each $2^\circ \times 2^\circ$ grid cell (that is, according to the grid-specific baseline temperature and standardized HFI) significantly differed from a value of 1 (indicating a perfect coupling), based on 5,000 bootstrap iterations.

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

Data availability

The data supporting the findings of this study are available in the BioShifts geo-database in the Figshare digital repository¹³ available at <https://doi.org/10.6084/m9.figshare.7413365.v1>.

Code availability

R scripts used in the analyses are available at <https://doi.org/10.6084/m9.figshare.7413365.v1>.

Received: 18 October 2019; Accepted: 3 April 2020;

Published online: 25 May 2020

References

- Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
- Poloczanska, E. S. et al. Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919–925 (2013).
- Lenoir, J. & Svenning, J.-C. Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* **38**, 15–28 (2015).
- Pecl, G. T. et al. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**, eaai9214 (2017).
- Loarie, S. R. et al. The velocity of climate change. *Nature* **462**, 1052–1055 (2009).
- Burrows, M. T. et al. The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655 (2011).
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L. & Levin, S. A. Marine taxa track local climate velocities. *Science* **341**, 1239–1242 (2013).
- Bertrand, R. et al. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**, 517–520 (2011).
- Devictor, V. et al. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* **2**, 121–124 (2012).
- Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L. & Sunday, J. M. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569**, 108–111 (2019).
- Pinsky, M. L., Selden, R. L. & Kitchel, Z. J. Climate-driven shifts in marine species ranges: scaling from organisms to communities. *Annu. Rev. Mar. Sci.* **12**, 153–179 (2020).
- Comte, L. et al. BioShifts: a global geo-database of climate-induced species redistribution over land and sea. *Figshare* <https://doi.org/10.6084/m9.figshare.7413365.v1> (2020).
- Brown, C. J. et al. Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Glob. Change Biol.* **22**, 1548–1560 (2016).
- Feeley, K. J., Stroud, J. T. & Perez, T. M. Most 'global' reviews of species' responses to climate change are not truly global. *Divers. Distrib.* **23**, 231–234 (2017).
- Friedman, A. R., Hwang, Y.-T., Chiang, J. C. H. & Frierson, D. M. W. Interhemispheric temperature asymmetry over the twentieth century and in future projections. *J. Clim.* **26**, 5419–5433 (2013).
- Rumpf, S. B., Hülber, K., Zimmermann, N. E. & Dullinger, S. Elevational rear edges shifted at least as much as leading edges over the last century. *Glob. Ecol. Biogeogr.* **28**, 533–543 (2019).

18. Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M. & Hargreaves, A. L. Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. *Glob. Ecol. Biogeogr.* **27**, 1268–1276 (2018).
19. Halpern, B. S. et al. A global map of human impact on marine ecosystems. *Science* **319**, 948–952 (2008).
20. Venter, O. et al. Global terrestrial human footprint maps for 1993 and 2009. *Sci. Data* **3**, 160067 (2016).
21. Paaijmans, K. P. et al. Temperature variation makes ectotherms more sensitive to climate change. *Glob. Change Biol.* **19**, 2373–2380 (2013).
22. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* **2**, 686–690 (2012).
23. Angert, A. L. et al. Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.* **14**, 677–689 (2011).
24. Guo, F., Lenoir, J. & Bonebrake, T. C. Land-use change interacts with climate to determine elevational species redistribution. *Nat. Commun.* **9**, 1315 (2018).
25. Bertrand, R. et al. Ecological constraints increase the climatic debt in forests. *Nat. Commun.* **7**, 12643 (2016).
26. Warren, M. S. et al. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69 (2001).
27. Engelhard, G. H., Righton, D. A. & Pinnegar, J. K. Climate change and fishing: a century of shifting distribution in North Sea cod. *Glob. Change Biol.* **20**, 2473–2483 (2014).
28. Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R. & Legendre, F. Taxonomic bias in biodiversity data and societal preferences. *Sci. Rep.* **7**, 9132 (2017).
29. Kjesbu, O. S. et al. Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proc. Natl Acad. Sci. USA* **111**, 3478–3483 (2014).
30. Schloss, C. A., Nuñez, T. A. & Lawler, J. J. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl Acad. Sci. USA* **109**, 8606–8611 (2012).
31. Pounds, J. A. et al. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167 (2006).
32. Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. & Roy, K. Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Syst.* **40**, 245–269 (2009).
33. HilleRisLambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R. & Theobald, E. J. How will biotic interactions influence climate change-induced range shifts? *Ann. NY Acad. Sci.* **1297**, 112–125 (2013).
34. Lenoir, J. et al. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Glob. Change Biol.* **19**, 1470–1481 (2013).
35. Graae, B. J. et al. Stay or go—how topographic complexity influences alpine plant population and community responses to climate change. *Perspect. Plant Ecol. Evol. Syst.* **30**, 41–50 (2018).
36. Vergés, A. et al. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc. R. Soc. B Biol. Sci.* **281**, 20140846 (2014).
37. Vergés, A. et al. Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. *Funct. Ecol.* **33**, 1000–1013 (2019).
38. Vergés, A. et al. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc. Natl Acad. Sci. USA* **113**, 13791–13796 (2016).
39. Kattge, J. et al. TRY—a global database of plant traits. *Glob. Change Biol.* **17**, 2905–2935 (2011).
40. Kissling, W. D. et al. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecol. Evol.* **4**, 2913–2930 (2014).
41. Meiri, S. Traits of lizards of the world: variation around a successful evolutionary design. *Glob. Ecol. Biogeogr.* **27**, 1168–1172 (2018).
42. Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C. & Costa, G. C. AmphiBIO, a global database for amphibian ecological traits. *Sci. Data* **4**, 170123 (2017).
43. Frimpong, E. A. & Angermeier, P. L. Fish Traits: a database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries* **34**, 487–495 (2009).
44. Wilman, H. et al. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027 (2014).
45. Agnihotri, P. et al. Climate change-driven shifts in elevation and ecophysiological traits of Himalayan plants during the past century. *Curr. Sci.* **112**, 595 (2017).
46. Aguirre-Gutiérrez, J., Kissling, W. D. & Carvalheiro, L. G. Functional traits help to explain half-century long shifts in pollinator distributions. *Sci. Rep.* **6**, 24451 (2016).
47. Akatov, P. V. Changes in the upper limits of tree species distribution in the Western Caucasus (Belaya River basin) related to recent climate warming. *Russ. J. Ecol.* **40**, 33–38 (2009).
48. Alofs, K. M., Jackson, D. A. & Lester, N. P. Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. *Divers. Distrib.* **20**, 123–136 (2014).
49. Amano, T. et al. Links between plant species' spatial and temporal responses to a warming climate. *Proc. R. Soc. Lond. B Biol. Sci.* **281**, 20133017 (2014).
50. Ambrosini, R. et al. Climate change and the long-term northward shift in the African wintering range of the barn swallow *Hirundo rustica*. *Clim. Res.* **49**, 131–141 (2011).
51. Angelo, C. L. & Daehler, C. C. Upward expansion of fire-adapted grasses along a warming tropical elevation gradient. *Ecography* **36**, 551–559 (2013).
52. Archaux, F. Breeding upwards when climate is becoming warmer: no bird response in the French Alps. *Ibis* **146**, 138–144 (2004).
53. Ash, J. D., Givnish, T. J. & Waller, D. M. Tracking lags in historical plant species' shifts in relation to regional climate change. *Glob. Change Biol.* **23**, 1305–1315 (2017).
54. Asher, J., Fox, R. & Warren, M. S. British butterfly distributions and the 2010 target. *J. Insect Conserv.* **15**, 291–299 (2011).
55. Assandri, G. & Morganti, M. Is the spectacled warbler *Sylvia conspicillata* expanding northward because of climate warming? *Bird Study* **62**, 126–131 (2015).
56. Auer, S. K. & King, D. I. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob. Ecol. Biogeogr.* **23**, 867–875 (2014).
57. Bässler, C., Hothorn, T., Brandl, R. & Müller, J. Insects overshoot the expected upslope shift caused by climate warming. *PLoS ONE* **8**, e65842 (2013).
58. Batdorf, K. E. *Distributional Changes in Ohio's Breeding Birds and the Importance of Climate and Land Cover Change*. MSc thesis, Ohio State Univ. (2012).
59. Battisti, A. et al. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.* **15**, 2084–2096 (2005).
60. Baur, B. & Baur, A. Snails keep the pace: shift in upper elevation limit on mountain slopes as a response to climate warming. *Can. J. Zool.* **91**, 596–599 (2013).
61. Beaugrand, G., Luczak, C. & Edwards, M. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Change Biol.* **15**, 1790–1803 (2009).
62. Bebber, D. P., Ramotowski, M. A. T. & Gurr, S. J. Crop pests and pathogens move polewards in a warming world. *Nat. Clim. Change* **3**, 985–988 (2013).
63. Beever, E. A., Ray, C., Wilkening, J. L., Brussard, P. F. & Mote, P. W. Contemporary climate change alters the pace and drivers of extinction. *Glob. Change Biol.* **17**, 2054–2070 (2011).
64. Bergamini, A., Ungricht, S. & Hofmann, H. An elevational shift of cryophilous bryophytes in the last century—an effect of climate warming? *Divers. Distrib.* **15**, 871–879 (2009).
65. Berke, S. K. et al. Range shifts and species diversity in marine ecosystem engineers: patterns and predictions for European sedimentary habitats. *Glob. Ecol. Biogeogr.* **19**, 223–232 (2010).
66. Betzholtz, P., Pettersson, L. B., Ryrholm, N. & Franzen, M. With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proc. R. Soc. B Biol. Sci.* **280**, 20122305 (2012).
67. Bhatta, K. P., Grytnes, J.-A. & Vetaas, O. R. Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere* **9**, e02084 (2018).
68. Biella, P. et al. Distribution patterns of the cold adapted bumblebee *Bombus alpinus* in the Alps and hints of an uphill shift (Insecta: Hymenoptera: Apidae). *J. Insect Conserv.* **21**, 357–366 (2017).
69. Bodin, J. et al. Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation? *J. Veg. Sci.* **24**, 269–283 (2013).
70. Boisvert-Marsh, L., Périé, C. & de Blois, S. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere* **5**, art83 (2014).
71. Botts, E. A., Erasmus, B. F. N. & Alexander, G. J. Observed range dynamics of South African amphibians under conditions of global change. *Austral Ecol.* **40**, 309–317 (2015).
72. Botts, E. A. *Distribution Change in South African Frogs*. PhD thesis, Univ. Witwatersrand (2012).
73. Bowman, J., Holloway, G. L., Malcolm, J. R., Middel, K. R. & Wilson, P. J. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Can. J. Zool.* **83**, 1486–1494 (2005).
74. Brommer, J. E. The range margins of northern birds shift polewards. *Ann. Zool. Fenn.* **41**, 391–397 (2004).
75. Brommer, J. E., Lehikoinen, A. & Valkama, J. The breeding ranges of central European and Arctic bird species move poleward. *PLoS ONE* **7**, e43648 (2012).

76. Brusca, R. C. et al. Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecol. Evol.* **3**, 3307–3319 (2013).
77. Bulgarella, M., Trewick, S. A., Minards, N. A., Jacobson, M. J. & Morgan-Richards, M. Shifting ranges of two tree weta species (*Hemideina* spp.): competitive exclusion and changing climate. *J. Biogeogr.* **41**, 524–535 (2014).
78. Büntgen, U. et al. Elevational range shifts in four mountain ungulate species from the Swiss Alps. *Ecosphere* **8**, e01761 (2017).
79. Campos-Cerqueira, M. & Aide, T. M. Lowland extirpation of anuran populations on a tropical mountain. *PeerJ* **5**, e4059 (2017).
80. Campos-Cerqueira, M., Arendt, W. J., Wunderle, J. M. & Aide, T. M. Have bird distributions shifted along an elevational gradient on a tropical mountain? *Ecol. Evol.* **7**, 9914–9924 (2017).
81. Cannone, N. & Pignatti, S. Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? *Clim. Change* **123**, 201–214 (2014).
82. Chen, I.-C. et al. Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Glob. Ecol. Biogeogr.* **20**, 34–45 (2011).
83. Chen, I. et al. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Natl Acad. Sci. USA* **106**, 1479–1483 (2009).
84. Chivers, W. J., Walne, A. W. & Hays, G. C. Mismatch between marine plankton range movements and the velocity of climate change. *Nat. Commun.* **8**, 14434 (2017).
85. Chust, G. et al. Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J. Mar. Sci.* **71**, 241–253 (2014).
86. Coals, P., Shmida, A., Vasl, A., Duguny, N. M. & Gilbert, F. Elevation patterns of plant diversity and recent altitudinal range shifts in Sinai's high-mountain flora. *J. Veg. Sci.* **29**, 255–264 (2018).
87. Comte, L. & Grenouillet, G. Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography* **36**, 1236–1246 (2013).
88. Cristine, L. E. & Kerr, J. T. Temperature-related geographical shifts among passerines: contrasting processes along poleward and equatorward range margins. *Ecol. Evol.* **5**, 5162–5176 (2015).
89. Courtin, F. et al. Updating the northern tsetse limit in Burkina Faso (1949–2009): impact of global change. *Int. J. Environ. Res. Public Health* **7**, 1708–1719 (2010).
90. Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T. & Mynsberge, A. R. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* **331**, 324–327 (2011).
91. Crozier, L. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia* **135**, 648–656 (2003).
92. Cubillos, J. et al. Calcification morphotypes of the coccolithophorid *Emiliania huxleyi* in the Southern Ocean: changes in 2001 to 2006 compared to historical data. *Mar. Ecol. Prog. Ser.* **348**, 47–54 (2007).
93. Currie, D. J. & Venne, S. Climate change is not a major driver of shifts in the geographical distributions of North American birds. *Glob. Ecol. Biogeogr.* **26**, 333–346 (2017).
94. Czortek, P. et al. Climate change, tourism and historical grazing influence the distribution of *Carex lachenalii* Schkuhr—a rare arctic-alpine species in the Tatra Mts. *Sci. Total Environ.* **618**, 1628–1637 (2018).
95. Dainese, M. et al. Human disturbance and upward expansion of plants in a warming climate. *Nat. Clim. Change* **7**, 577–580 (2017).
96. Danby, R. K. & Hik, D. S. Evidence of recent treeline dynamics in southwest Yukon from aerial photographs. *Arctic* **60**, 411–420 (2007).
97. Dawson, M. N., Grosberg, R. K., Stuart, Y. E. & Sanford, E. Population genetic analysis of a recent range expansion: mechanisms regulating the poleward range limit in the volcano barnacle *Tetraclita rubescens*. *Mol. Ecol.* **19**, 1585–1605 (2010).
98. Delava, E., Allemand, R., Léger, L., Fleury, F. & Gibert, P. The rapid northward shift of the range margin of a Mediterranean parasitoid insect (Hymenoptera) associated with regional climate warming. *J. Biogeogr.* **41**, 1379–1389 (2014).
99. DeLuca, W. V. *Ecology and Conservation of the Montane Forest Avian Community in Northeastern North America*. PhD thesis, Univ. Massachusetts (2013).
100. DeLuca, W. V. & King, D. I. Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. *J. Ornithol.* **158**, 493–505 (2017).
101. Dieker, P., Drees, C. & Assmann, T. Two high-mountain burnet moth species (Lepidoptera, Zygaenidae) react differently to the global change drivers climate and land-use. *Biol. Conserv.* **144**, 2810–2818 (2011).
102. Dobbertin, M. et al. The upward shift in altitude of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland—the result of climate warming? *Int. J. Biometeorol.* **50**, 40–47 (2005).
103. Dolezal, J. et al. Vegetation dynamics at the upper elevational limit of vascular plants in Himalaya. *Sci. Rep.* **6**, 24881 (2016).
104. Dou, H., Jiang, G., Stott, P. & Piao, R. Climate change impacts population dynamics and distribution shift of moose (*Alces alces*) in Heilongjiang Province of China. *Ecol. Res.* **628**, 625–632 (2013).
105. Duarte, L. et al. Recent and historical range shifts of two canopy-forming seaweeds in north Spain and the link with trends in sea surface temperature. *Acta Oecologica* **51**, 1–10 (2013).
106. Dulvy, N. K. et al. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* **45**, 1029–1039 (2008).
107. Dumais, C., Ropars, P., Denis, M., Dufour-Tremblay, G. & Boudreau, S. Are low altitude alpine tundra ecosystems under threat? A case study from the Parc National de la Gaspésie, Québec. *Environ. Res. Lett.* **9**, 094001 (2014).
108. Engelhard, G. H., Pinnegar, J. K., Kell, L. T. & Rijnsdorp, A. D. Nine decades of North Sea sole and plaice distribution. *ICES J. Mar. Sci.* **68**, 1090–1104 (2011).
109. Eskildsen, A. et al. Testing species distribution models across space and time: high latitude butterflies and recent warming. *Glob. Ecol. Biogeogr.* **22**, 1293–1303 (2013).
110. Feeley, K. J. et al. Upslope migration of Andean trees. *J. Biogeogr.* **38**, 783–791 (2011).
111. Fei, S. et al. Divergence of species responses to climate change. *Sci. Adv.* **3**, e1603055 (2017).
112. Felde, V. A., Kapfer, J. & Grytnes, J. Upward shift in elevational plant species ranges in Sikkildalen, central Norway. *Ecography* **35**, 922–932 (2012).
113. Fenberg, P. B. & Rivadeneira, M. M. Range limits and geographic patterns of abundance of the rocky intertidal owl limpet, *Lottia gigantea*. *J. Biogeogr.* **38**, 2286–2298 (2011).
114. Flousek, J., Telenský, T., Hanzelka, J. & Reif, J. Population trends of central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. *PLoS ONE* **10**, e0139465 (2015).
115. Forero-Medina, G., Terborgh, J., Socolar, S. J. & Pimm, S. L. Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS ONE* **6**, e28535 (2011).
116. Forsman, A., Betzholtz, P. & Franzén, M. Faster poleward range shifts in moths with more variable colour patterns. *Sci. Rep.* **6**, 36265 (2016).
117. Fox, R. et al. Moths count: recording moths for conservation in the UK. *J. Insect Conserv.* **15**, 55–68 (2011).
118. Franco, A. M. A. et al. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Glob. Change Biol.* **12**, 1545–1553 (2006).
119. Freeman, B. G. & Freeman, A. M. C. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proc. Natl Acad. Sci. USA* **111**, 4490–4494 (2014).
120. Frei, E., Bodin, J. & Walther, G.-R. Plant species' range shifts in mountainous areas—all uphill from here? *Bot. Helv.* **120**, 117–128 (2010).
121. Gamache, I. & Payette, S. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. *J. Biogeogr.* **32**, 849–862 (2005).
122. Gonzalez, P. Desertification and a shift of forest species in the West African Sahel. *Clim. Res.* **17**, 217–228 (2001).
123. Greenlee, E. S. *The Effects of a Warming Climate on the Migratory Strategies of a Putatively Non-migratory Bird, the Gray Jay (Perisoreus canadensis)*. PhD thesis, Ohio State Univ. (2012).
124. Greenwood, S., Chen, J.-C., Chen, C.-T. & Jump, A. S. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. *Glob. Change Biol.* **20**, 3756–3766 (2014).
125. Grewe, Y., Hof, C., Dehling, D. M., Brandl, R. & Brändle, M. Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. *Glob. Ecol. Biogeogr.* **22**, 403–409 (2013).
126. Groom, Q. J. Some poleward movement of British native vascular plants is occurring, but the fingerprint of climate change is not evident. *PeerJ* **1**, e77 (2013).
127. Hale, S. S., Buffum, H. W., Kiddon, J. A. & Hughes, M. M. Subtidal benthic invertebrates shifting northward along the US Atlantic Coast. *Estuar. Coasts* **40**, 1744–1756 (2017).
128. Hargrove, L. J. *Limits to Species' Distributions: Spatial Structure and Dynamics of Breeding Bird Populations Along an Ecological Gradient*. PhD thesis, Univ. California Riverside (2010).
129. Harris, J. B. C. et al. Using diverse data sources to detect elevational range changes of birds on Mount Kinabalu, Malaysian Borneo. *Raffles Bull. Zool.* **25**, 197–247 (2012).
130. Hassall, C. Odonata as candidate macroecological barometers for global climate change. *Freshw. Sci.* **34**, 1040–1049 (2015).
131. Hermes, C., Jansen, J. & Schaefer, H. M. Habitat requirements and population estimate of the endangered Ecuadorian Tapaculo *Scytalopus robbinsi*. *Bird Conserv. Int.* **28**, 302–318 (2018).

132. Hernández, L., Cañellas, I., Alberdi, I., Torres, I. & Montes, F. Assessing changes in species distribution from sequential large-scale forest inventories. *Ann. Sci.* **71**, 161–171 (2014).
133. Hernández, L. et al. Exploring range shifts of contrasting tree species across a bioclimatic transition zone. *Eur. J. Res.* **136**, 481–492 (2017).
134. Hersteinsson, P. & Macdonald, D. W. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**, 505–515 (1992).
135. Hickling, R., Roy, D. B., Hill, J. K. & Thomas, C. D. A northward shift of range margins in British Odonata. *Glob. Change Biol.* **11**, 502–506 (2005).
136. Hiddink, J. G., Burrows, M. T. & García Molinos, J. Temperature tracking by North Sea benthic invertebrates in response to climate change. *Glob. Change Biol.* **21**, 117–129 (2015).
137. Hill, N. J., Tobin, A. J., Reside, A. E., Pepperell, J. G. & Bridge, T. C. L. Dynamic habitat suitability modelling reveals rapid poleward distribution shift in a mobile apex predator. *Glob. Change Biol.* **22**, 1086–1096 (2016).
138. Hitch, A. T. & Leberg, P. L. Breeding distributions of North American bird species moving north as a result of climate change. *Conserv. Biol.* **21**, 534–539 (2007).
139. Hofgaard, A., Tømmervik, H., Rees, G. & Hanssen, F. Latitudinal forest advance in northernmost Norway since the early 20th century. *J. Biogeogr.* **40**, 938–949 (2013).
140. Holzinger, B., Hülber, K., Camenisch, M. & Grabherr, G. Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecol.* **195**, 179–196 (2008).
141. Hovick, T. J. et al. Informing conservation by identifying range shift patterns across breeding habitats and migration strategies. *Biodivers. Conserv.* **25**, 345–356 (2016).
142. Hsieh, C.-H., Kim, H. J., Watson, W., Di Lorenzo, E. & Sugihara, G. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Glob. Change Biol.* **15**, 2137–2152 (2009).
143. Hsieh, C., Reiss, C. S., Hewitt, R. P. & Sugihara, G. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. *Can. J. Fish. Aquat. Sci.* **65**, 947–961 (2008).
144. Huang, Q., Sauer, J. R. & Dubayah, R. O. Multidirectional abundance shifts among North American birds and the relative influence of multifaceted climate factors. *Glob. Change Biol.* **23**, 3610–3622 (2017).
145. Jepsen, J. U., Hagen, S. B., Ims, R. A. & Yoccoz, N. G. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *J. Anim. Ecol.* **77**, 257–264 (2008).
146. Jiménez-Alfaro, B., Gavilán, R. G., Escudero, A., Iriondo, J. M. & Fernández-González, F. Decline of dry grassland specialists in Mediterranean high-mountain communities influenced by recent climate warming. *J. Veg. Sci.* **25**, 1394–1404 (2014).
147. Jones, S. J., Lima, F. P. & Wethey, D. S. Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *J. Biogeogr.* **37**, 2243–2259 (2010).
148. Jones, S. J., Southward, A. J. & Wethey, D. S. Climate change and historical biogeography of the barnacle *Semibalanus balanoides*. *Glob. Ecol. Biogeogr.* **21**, 716–724 (2012).
149. Jore, S. et al. Multi-source analysis reveals latitudinal and altitudinal shifts in range of *Ixodes ricinus* at its northern distribution limit. *Parasit. Vectors* **4**, 84 (2011).
150. Jump, A. S., Huang, T. & Chou, C. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography* **35**, 204–210 (2012).
151. Juvik, J., Rodomsky, B., Price, J., Hansen, E. & Kueffer, C. ‘The upper limits of vegetation on Mauna Loa, Hawaii’: a 50th-anniversary reassessment. *Ecology* **92**, 518–525 (2011).
152. Kawakami, Y., Yamazaki, K. & Ohashi, K. Northward expansion and climatic factors affecting the distribution limits of *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae) in Japan. *Appl. Entomol. Zool.* **49**, 59–66 (2014).
153. Kelly, A. E. & Goulden, M. L. Rapid shifts in plant distribution with recent climate change. *Proc. Natl Acad. Sci. USA* **105**, 11823–11826 (2008).
154. Kerby, T. K., Cheung, W. W. L., van Oosterhout, C. & Engelhard, G. H. Wondering about wandering whiting: distribution of North Sea whiting between the 1920s and 2000s. *Fish. Res.* **145**, 54–65 (2013).
155. Kerr, J. T. et al. Climate change impacts on bumblebees converge across continents. *Science* **349**, 177–180 (2015).
156. Kirchman, J. J. & Van Keuren, A. E. Altitudinal range shifts of birds at the southern periphery of the boreal forest: 40 years of change in the Adirondack mountains. *Wilson J. Ornithol.* **129**, 742–753 (2017).
157. Kitahara, M., Iriki, M. & Shimizu, G. On the relationship between the northward distributional expansion of the great mormon butterfly, *Papilio memnon* Lineatus, and climatic warming in Japan. *Lepidoptero. Soc. Jpn* **52**, 253–264 (2001).
158. Kleisner, K. M. et al. The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. *PLoS ONE* **11**, e0149220 (2016).
159. Koide, D., Yoshida, K., Daehler, C. C. & Mueller-Dombois, D. An upward elevation shift of native and non-native vascular plants over 40 years on the island of Hawai‘i. *J. Veg. Sci.* **28**, 939–950 (2017).
160. Kopp, C. W. & Cleland, E. E. Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. *J. Veg. Sci.* **25**, 135–146 (2014).
161. Kotwicki, S. & Lauth, R. R. Detecting temporal trends and environmentally-driven changes in the spatial distribution of bottom fishes and crabs on the eastern Bering Sea shelf. *Deep-Sea Res. Pt II* **94**, 231–243 (2013).
162. Kreuser, J. M. *Climate Change, Range Shifts, and Differential Guild Responses of Michigan Breeding Birds*. MSc thesis, Michigan State Univ. (2013).
163. Kuhn, E., Lenoir, J., Piedallu, C. & Gégout, J.-C. Early signs of range disjunction of submountainous plant species: an unexplored consequence of future and contemporary climate changes. *Glob. Change Biol.* **22**, 2094–2105 (2016).
164. Kuletz, K. J., Renner, M., Labunski, E. A. & Hunt, G. L. Changes in the distribution and abundance of albatrosses in the eastern Bering Sea: 1975–2010. *Deep-Sea Res. Pt II* **109**, 282–292 (2014).
165. Kullman, L., Journal, T. & Feb, N. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.* **90**, 68–77 (2002).
166. Kullman, L. & Öberg, L. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *J. Ecol.* **97**, 415–429 (2009).
167. Kurihara, T. et al. Area-specific temporal changes of species composition and species-specific range shifts in rocky-shore mollusks associated with warming Kuroshio Current. *Mar. Biol.* **158**, 2095–2107 (2011).
168. Kwon, T., Lee, C. M. & Kim, S. Northward range shifts in Korean butterflies. *Clim. Change* **126**, 163–174 (2014).
169. La Sorte, F. A. & Thompson, F. R. III Poleward shifts in winter ranges of North American birds. *Ecology* **88**, 1803–1812 (2007).
170. Landa, C. S., Ottersen, G., Sundby, S., Dingsør, G. E. & Stiansen, J. E. Recruitment, distribution boundary and habitat temperature of an arcto-boreal gadoid in a climatically changing environment: a case study on Northeast Arctic haddock (*Melanogrammus aeglefinus*). *Fish. Oceanogr.* **23**, 506–520 (2014).
171. Larrucea, E. S. & Brussard, P. F. Shift in location of pygmy rabbit (*Brachylagus idahoensis*) habitat in response to changing environments. *J. Arid Environ.* **72**, 1636–1643 (2008).
172. Lättman, H., Milberg, P., Palmer, M. W. & Mattsson, J. Changes in the distributions of epiphytic lichens in southern Sweden using a new statistical method. *Nord. J. Bot.* **27**, 413–418 (2009).
173. Le Roux, P. C. & McGeoch, M. A. Rapid range expansion and community reorganization in response to warming. *Glob. Change Biol.* **14**, 2950–2962 (2008).
174. Lehto, A. & Virkkala, R. North by north-west: climate change and directions of density shifts in birds. *Glob. Change Biol.* **22**, 1121–1129 (2016).
175. Leidenberger, S., Harding, K. & Jonsson, P. R. Ecology and distribution of the isopod genus *Idotea* in the Baltic Sea: key species in a changing environment. *J. Crustac. Biol.* **32**, 359–381 (2012).
176. Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**, 1768–1771 (2008).
177. Leonelli, G., Pelfini, M., Morra di Cella, U. & Garavaglia, V. Climate warming and the recent treeline shift in the European Alps: the role of geomorphological factors in high-altitude sites. *Ambio* **40**, 264–273 (2011).
178. Lima, F. P., Ribeiro, P. A., Queiroz, N., Hawkins, S. J. & Santos, A. M. Do distributional shifts of northern and southern species of algae match the warming pattern? *Glob. Change Biol.* **13**, 2592–2604 (2007).
179. Lindley, J. & Daykin, S. Variations in the distributions of *Centropages chierchiaie* and *Temora stylifera* (Copepoda: Calanoida) in the north-eastern Atlantic and western European shelf waters. *ICES J. Mar. Sci.* **62**, 869–877 (2005).
180. Ling, S. D., Johnson, C. R., Ridgway, K., Hobday, A. J. & Haddon, M. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Glob. Change Biol.* **15**, 719–731 (2009).
181. MacLaren, C. A. Climate change drives decline of *Juniperus seravchanica* in Oman. *J. Arid Environ.* **128**, 91–100 (2016).
182. MacLean, I. M. D. et al. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Glob. Change Biol.* **14**, 2489–2500 (2008).
183. Mair, L. et al. Temporal variation in responses of species to four decades of climate warming. *Glob. Change Biol.* **18**, 2439–2447 (2012).

184. Málíš, F. et al. Life stage, not climate change, explains observed tree range shifts. *Glob. Change Biol.* **22**, 1904–1914 (2016).
185. Martinet, B. et al. Forward to the north: two Euro-Mediterranean bumblebee species now cross the Arctic Circle. *Ann. Soc. Entomol. Fr.* **51**, 303–309 (2015).
186. Mason, S. C. et al. Geographical range margins of many taxonomic groups continue to shift polewards. *Biol. J. Linn. Soc.* **115**, 586–597 (2015).
187. Massimino, D., Johnston, A. & Pearce-Higgins, J. W. The geographical range of British birds expands during 15 years of warming. *Bird Study* **62**, 523–534 (2015).
188. Mathisen, I. E., Mikheeva, A., Tutubalina, O. V., Aune, S. & Hofgaard, A. Fifty years of tree line change in the Khibiny Mountains, Russia: advantages of combined remote sensing and dendroecological approaches. *Appl. Veg. Sci.* **17**, 6–16 (2014).
189. Melles, S. J., Fortin, M. J., Lindsay, K. & Badzinski, D. Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Glob. Change Biol.* **17**, 17–31 (2011).
190. Menéndez, R., González-Megías, A., Jay-Robert, P. & Marquéz-Ferrando, R. Climate change and elevational range shifts: evidence from dung beetles in two European mountain ranges. *Glob. Ecol. Biogeogr.* **23**, 646–657 (2014).
191. Merrill, R. M. et al. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *J. Anim. Ecol.* **77**, 145–155 (2008).
192. Mieszzkowska, N. et al. Changes in the range of some common rocky shore species in Britain—a response to climate change? *Hydrobiologia* **555**, 241–251 (2006).
193. Molina-Martínez, A. et al. Changes in butterfly distributions and species assemblages on a Neotropical mountain range in response to global warming and anthropogenic land use. *Divers. Distrib.* **22**, 1085–1098 (2016).
194. Monahan, W. B. & Hijmans, R. J. Ecophysiological constraints shape autumn migratory response to climate change in the North American field sparrow. *Biol. Lett.* **4**, 595–598 (2008).
195. Morelli, T. L. et al. Anthropogenic refugia ameliorate the severe climate-related decline of a montane mammal along its trailing edge. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 4279–4286 (2012).
196. Moreno-Fernández, D., Hernández, L., Sánchez-González, M., Cañellas, I. & Montes, F. Space–time modeling of changes in the abundance and distribution of tree species. *Ecol. Manag.* **372**, 206–216 (2016).
197. Moreno-Rueda, G., Pleguezuelo, J. M., Pizarro, M. & Montori, A. Northward shifts of the distributions of Spanish reptiles in association with climate change. *Conserv. Biol.* **26**, 278–283 (2012).
198. Moret, P., Araújo, M., de los, A., Gobbi, M. & Barragán, A. Climate warming effects in the tropical Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador. *Insect Conserv. Divers.* **9**, 342–350 (2016).
199. Moritz, C. et al. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264 (2008).
200. Morueta-Holme, N. et al. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proc. Natl Acad. Sci. USA* **112**, 12741–12745 (2015).
201. Moskwik, M. Recent elevational range expansions in plethodontid salamanders (Amphibia: Plethodontidae) in the southern Appalachian Mountains. *J. Biogeogr.* **41**, 1957–1966 (2014).
202. Mueter, F. J. & Litzow, M. A. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* **18**, 309–320 (2008).
203. Myers, P., Lundrigan, B. L., Hoffman, S. M. G., Haraminac, A. P. & Seto, S. H. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. *Glob. Change Biol.* **15**, 1434–1454 (2009).
204. Neukermans, G., Oziel, L. & Babin, M. Increased intrusion of warming Atlantic water leads to rapid expansion of temperate phytoplankton in the Arctic. *Glob. Change Biol.* **24**, 2545–2553 (2018).
205. Nicastro, K. R. et al. Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga *Fucus vesiculosus*. *BMC Biol.* **11**, 6 (2013).
206. Nicolas, D. et al. Impact of global warming on European tidal estuaries: some evidence of northward migration of estuarine fish species. *Reg. Environ. Change* **11**, 639–649 (2011).
207. Niven, D. K., Butcher, G. S. & Bancroft, G. T. Christmas bird counts and climate change: northward shifts in early winter abundance. *Am. Birds* **63**, 10–15 (2010).
208. Nye, J. A., Link, J. S., Hare, J. A. & Overholtz, W. J. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* **393**, 111–129 (2009).
209. Orensanz, J. L., Ernst, B., Armstrong, D. A., Stabeno, P. J. & Livingston, P. Contraction of the geographical range of distribution of snow crab (*Chionoecetes opilio*) in the Eastern Bering Sea: an environmental ratchet? *Cal Coop. Ocean Fish* **45**, 65–79 (2004).
210. Ottosen, K. M., Steingrund, P., Magnussen, E. & Payne, M. R. Distribution and timing of spawning Faroe Plateau cod in relation to warming spring temperatures. *Fish. Res.* **198**, 14–23 (2018).
211. Overholtz, W. J., Hare, J. A. & Keith, C. M. Impacts of interannual environmental forcing and climate change on the distribution of Atlantic mackerel on the U.S. northeast continental shelf. *Mar. Coast. Fish.* **3**, 219–232 (2011).
212. Pakeman, R. J. et al. Species composition of coastal dune vegetation in Scotland has proved resistant to climate change over a third of a century. *Glob. Change Biol.* **21**, 3738–3747 (2015).
213. Paprocki, N., Heath, J. A. & Novak, S. J. Regional distribution shifts help explain local changes in wintering raptor abundance: implications for interpreting population trends. *PLoS ONE* **9**, e86814 (2014).
214. Parolo, G. & Rossi, G. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic Appl. Ecol.* **9**, 100–107 (2008).
215. Pateman, R. M., Hill, J. K., Roy, D. B., Fox, R. & Thomas, C. D. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science* **336**, 1028–1030 (2012).
216. Peñuelas, J. & Boada, M. A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. Change Biol.* **9**, 131–140 (2003).
217. Perissinotto, R., Pringle, E. L. & Giliomee, J. H. Southward expansion in beetle and butterfly ranges in South Africa. *Afr. Entomol.* **19**, 61–69 (2011).
218. Pitt, N. R., Poloczanska, E. S. & Hobday, A. J. Climate-driven range changes in Tasmanian intertidal fauna. *Mar. Freshw. Res.* **61**, 963–970 (2010).
219. Pernollet, C. A., Korner-Nievergelt, F. & Jenni, L. Regional changes in the elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis* **157**, 823–836 (2015).
220. Péron, C. et al. Interdecadal changes in at-sea distribution and abundance of subantarctic seabirds along a latitudinal gradient in the Southern Indian Ocean. *Glob. Change Biol.* **16**, 1895–1909 (2010).
221. Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915 (2005).
222. Peterson, T. A. Subtle recent distributional shifts in Great Plains bird species. *Southwest. Nat.* **48**, 289–292 (2003).
223. Ploquin, E. F., Herrera, J. M. & Obeso, J. R. Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. *Oecologia* **173**, 1649–1660 (2013).
224. Poloczanska, E. S. et al. Little change in the distribution of rocky shore faunal communities on the Australian east coast after 50 years of rapid warming. *J. Exp. Mar. Biol. Ecol.* **400**, 145–154 (2011).
225. Popy, S., Bordignon, L. & Prodon, R. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. *J. Biogeogr.* **37**, 57–67 (2009).
226. Potvin, D. A., Välimäki, K. & Lehtikoinen, A. Differences in shifts of wintering and breeding ranges lead to changing migration distances in European birds. *J. Avian Biol.* **47**, 619–628 (2016).
227. Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M. & Saarinen, K. Species traits explain recent range shifts of Finnish butterflies. *Glob. Change Biol.* **15**, 732–743 (2009).
228. Precht, W. F. & Aronson, R. B. Climate flickers and range shifts of reef corals. *Front. Ecol. Evol.* **2**, 307–314 (2004).
229. Pyke, G. H., Thomson, J. D., Inouye, D. W. & Miller, T. J. Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere* **7**, e01267 (2016).
230. Quero, J. Changes in the Euro-Atlantic fish species composition resulting from fishing and ocean warming. *Ital. J. Zool.* **65**, 493–499 (1998).
231. Rannow, S. Do shifting forest limits in south-west Norway keep up with climate change? *Scand. J. Res.* **28**, 574–580 (2013).
232. Rappole, J. H., Glasscock, S., Goldberg, K., Song, D. & Faridani, S. Range change among new world tropical and subtropical birds. *Bonn. Zool. Monogr.* **57**, 151–167 (2011).
233. Raxworthy, C. J. et al. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Glob. Change Biol.* **14**, 1703–1720 (2008).
234. Reid, S. B. & Goodman, D. H. Pacific lamprey in coastal drainages of California: occupancy patterns and contraction of the southern range. *Trans. Am. Fish. Soc.* **145**, 703–711 (2016).
235. Reif, J. & Flousek, J. The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. *Oikos* **121**, 1053–1060 (2012).
236. Renner, M. et al. Modeled distribution and abundance of a pelagic seabird reveal trends in relation to fisheries. *Mar. Ecol. Prog. Ser.* **484**, 259–277 (2013).
237. Riley, M. E., Johnston, C. A., Feller, I. C. & Griffen, B. D. Range expansion of *Aratus pisonii* (mangrove tree crab) into novel vegetative habitats. *Southeast. Nat.* **13**, N43–N48 (2014).
238. Rivadeneira, M. M. & Ferna, M. Shifts in southern endpoints of distribution in rocky intertidal species along the south-eastern Pacific coast. *J. Biogeogr.* **32**, 203–209 (2005).

239. Rowe, K. C. et al. Spatially heterogeneous impact of climate change on small mammals of montane California. *Proc. R. Soc. Lond. B Biol. Sci.* **282**, 20141857 (2014).
240. Rowe, R. J., Finarelli, J. A. & Rickart, E. A. Range dynamics of small mammals along an elevational gradient over an 80-year interval. *Glob. Change Biol.* **16**, 2930–2943 (2010).
241. Rubal, M., Veiga, P., Cacabelos, E., Moreira, J. & Sousa-Pinto, I. Increasing sea surface temperature and range shifts of intertidal gastropods along the Iberian Peninsula. *J. Sea Res.* **77**, 1–10 (2013).
242. Rumpf, S. B. et al. Range dynamics of mountain plants decrease with elevation. *Proc. Natl Acad. Sci. USA* **115**, 1848–1853 (2018).
243. Sabatés, A., Martín, P., Lloret, J. & Raya, V. Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurata*, in the western Mediterranean. *Glob. Change Biol.* **12**, 2209–2219 (2006).
244. Santos, M. J., Thorne, J. H. & Moritz, C. Synchronicity in elevation range shifts among small mammals and vegetation over the last century is stronger for omnivores. *Ecography* **38**, 556–568 (2015).
245. Savage, J. & Vellend, M. Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* **38**, 546–555 (2015).
246. Serrano, E. et al. Rapid northward spread of a Zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean. *PLoS ONE* **8**, e52739 (2013).
247. Sheldon, A. L. Possible climate-induced shift of stoneflies in a southern Appalachian catchment. *Freshw. Sci.* **31**, 765–774 (2012).
248. Shiyatov, S. G., Terent'ev, M. M., Fomin, V. V. & Zimmermann, N. E. Altitudinal and horizontal shifts of the upper boundaries of open and closed forests in the Polar Urals in the 20th century. *Russ. J. Ecol.* **38**, 223–227 (2007).
249. Sittaro, F., Paquette, A., Messier, C. & Nock, C. A. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Glob. Change Biol.* **23**, 3292–3301 (2017).
250. Solow, A. et al. A test for a shift in the boundary of the geographical range of a species. *Biol. Lett.* **10**, 20130808 (2014).
251. Song, X. et al. Climate warming-induced upward shift of Moso bamboo population on Tianmu Mountain, China. *J. Mt. Sci.* **10**, 363–369 (2013).
252. Speed, J. D. M., Austrheim, G., Hester, A. J. & Myrsterud, A. Elevational advance of alpine plant communities is buffered by herbivory. *J. Veg. Sci.* **23**, 617–625 (2012).
253. Stafford, R., Hart, A. G. & Goodenough, A. E. A visual method to identify significant latitudinal changes in species' distributions. *Ecol. Inform.* **15**, 74–84 (2013).
254. Stuart-Smith, R. D., Barrett, N. S., Stevenson, D. G. & Edgar, G. J. Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Glob. Change Biol.* **16**, 122–134 (2010).
255. Stueve, K. M., Isaacs, R. E., Tyrrell, L. E. & Densmore, R. V. Spatial variability of biotic and abiotic tree establishment constraints across a treeline ecotone in the Alaska Range. *Ecology* **92**, 496–506 (2011).
256. Sultaire, S. M. et al. Climate change surpasses land-use change in the contracting range boundary of a winter-adapted mammal. *Proc. R. Soc. Lond. B Biol. Sci.* **283**, 20153104 (2016).
257. Swaby, S. E. & Potts, G. W. The sailfin dory, a first British record. *J. Fish Biol.* **54**, 1338–1340 (1999).
258. Tape, K. D., Gustine, D. D., Ruess, R. W., Adams, L. G. & Clark, J. A. Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. *PLoS ONE* **11**, e0152636 (2016).
259. Tayleur, C. et al. Swedish birds are tracking temperature but not rainfall: evidence from a decade of abundance changes. *Glob. Ecol. Biogeogr.* **24**, 859–872 (2015).
260. Telwala, Y., Brook, B. W., Manish, K. & Pandit, M. K. Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre. *PLoS ONE* **8**, e57103 (2013).
261. Thorson, J. T., Ianelli, J. N. & Kotwicki, S. The relative influence of temperature and size-structure on fish distribution shifts: a case-study on walleye pollock in the Bering Sea. *Fish Fish.* **18**, 1073–1084 (2017).
262. Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C. & Beissinger, S. R. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Change Biol.* **18**, 3279–3290 (2012).
263. Tougou, D., Musolin, D. L. & Fujisaki, K. Some like it hot! Rapid climate change promotes changes in distribution ranges of *Nezara viridula* and *Nezara antennata* in Japan. *Entomol. Exp. Appl.* **130**, 249–258 (2009).
264. Tryjanowski, P., Sparks, T. H. & Profus, P. Uphill shifts in the distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality. *Divers. Distrib.* **11**, 219–223 (2005).
265. Tu, C., Tian, Y. & Hsieh, C.-H. Effects of climate on temporal variation in the abundance and distribution of the demersal fish assemblage in the Tsushima Warm Current region of the Japan Sea. *Fish. Oceanogr.* **24**, 177–189 (2015).
266. Urli, M. et al. Inferring shifts in tree species distribution using asymmetric distribution curves: a case study in the Iberian mountains. *J. Veg. Sci.* **25**, 147–159 (2014).
267. Vällimäki, K., Lindén, A. & Lehikoinen, A. Velocity of density shifts in Finnish landbird species depends on their migration ecology and body mass. *Oecologia* **181**, 313–321 (2016).
268. Van Bogaert, R. et al. A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *J. Biogeogr.* **38**, 907–921 (2011).
269. Van Hal, R., Smits, K. & Rijnsdorp, A. D. How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. *J. Sea Res.* **64**, 76–84 (2010).
270. VanDerWal, J. et al. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nat. Clim. Change* **3**, 239–243 (2013).
271. Veech, J. A., Small, M. F. & Baccus, J. T. The effect of habitat on the range expansion of a native and an introduced bird species. *J. Biogeogr.* **38**, 69–77 (2011).
272. Virkkala, R., Heikkinen, R. K., Lehikoinen, A. & Valkama, J. Matching trends between recent distributional changes of northern-boreal birds and species-climate model predictions. *Biol. Conserv.* **172**, 124–127 (2014).
273. Virkkala, R. & Lehikoinen, A. Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. *Glob. Change Biol.* **20**, 2995–3003 (2014).
274. Virkkala, R. & Lehikoinen, A. Birds on the move in the face of climate change: high species turnover in northern Europe. *Ecol. Evol.* **7**, 8201–8209 (2017).
275. Virtanen, R. et al. Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Glob. Ecol. Biogeogr.* **19**, 810–821 (2010).
276. Vittoz, P., Bodin, J., Ungricht, S., Burga, C. A. & Walther, G. One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *J. Veg. Sci.* **19**, 671–680 (2008).
277. Walters, G. E. & Wilderbuier, T. K. Decreasing length at age in a rapidly expanding population of northern rock sole in the eastern Bering Sea and its effect on management advice. *J. Sea Res.* **44**, 17–26 (2000).
278. Walther, G.-R., Beißner, S. & Burga, C. A. Trends in the upward shift of alpine plants. *J. Veg. Sci.* **16**, 541–548 (2005).
279. Wehtje, W. The range expansion of the great-tailed grackle (*Quiscalus mexicanus* Gmelin) in North America since 1880. *J. Biogeogr.* **30**, 1593–1607 (2003).
280. Weinberg, J. Bathymetric shift in the distribution of Atlantic surfclams: response to warmer ocean temperature. *ICES J. Mar. Sci.* **62**, 1444–1453 (2005).
281. Wells, C. N. & Tonkyn, D. W. Range collapse in the Diana fritillary, *Speyeria diana* (Nymphalidae). *Insect Conserv. Divers.* **7**, 365–380 (2014).
282. Wen, Z. et al. Heterogeneous distributional responses to climate warming: evidence from rodents along a subtropical elevational gradient. *BMC Ecol.* **17**, 17 (2017).
283. Wernberg, T. et al. Seaweed communities in retreat from ocean warming. *Curr. Biol.* **21**, 1828–1832 (2011).
284. Wethey, D. S. & Woodin, S. A. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* **606**, 139–151 (2008).
285. Wilson, R. J. et al. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**, 1138–1146 (2005).
286. Wilson, S., Anderson, E. M., Wilson, A. S. G., Bertram, D. F. & Arcese, P. Citizen science reveals an extensive shift in the winter distribution of migratory western grebes. *PLoS ONE* **8**, e65408 (2013).
287. Wolf, A., Zimmerman, N. B., Anderegg, W. R. L., Busby, P. E. & Christensen, J. Altitudinal shifts of the native and introduced flora of California in the context of 20th-century warming. *Glob. Ecol. Biogeogr.* **25**, 418–429 (2016).
288. Wright, D. H., Nguyen, C. V. & Anderson, S. Upward shifts in recruitment of high-elevation tree species in the northern Sierra Nevada, California. *Calif. Fish Game* **102**, 17–31 (2016).
289. Wu, J. Detecting and attributing the effects of climate change on the distributions of snake species over the past 50 years. *Environ. Manag.* **57**, 207–219 (2016).
290. Wu, J. Can changes in the distribution of lizard species over the past 50 years be attributed to climate change? *Theor. Appl. Climatol.* **125**, 785–798 (2016).
291. Wu, J. & Shi, Y. Attribution index for changes in migratory bird distributions: the role of climate change over the past 50 years in China. *Ecol. Inform.* **31**, 147–155 (2016).
292. Yamano, H., Sugihara, K. & Nomura, K. Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophys. Res. Lett.* **38**, L04601 (2011).

293. Yang, D.-S., Conroy, C. J. & Moritz, C. Contrasting responses of *Peromyscus* mice of Yosemite National Park to recent climate change. *Glob. Change Biol.* **17**, 2559–2566 (2011).
294. Yang, L. et al. Long-term ecological data for conservation: range change in the black-billed capercaillie (*Tetrao urogalloides*) in northeast China (1970s–2070s). *Ecol. Evol.* **8**, 3862–3870 (2018).
295. Yemane, D. et al. Assessing changes in the distribution and range size of demersal fish populations in the Benguela Current Large Marine Ecosystem. *Rev. Fish Biol. Fish.* **24**, 463–483 (2014).
296. Yukawa, J. et al. Distribution range shift of two allied species, *Nezara viridula* and *N. antennata* (Hemiptera: Pentatomidae), in Japan, possibly due to global warming. *Appl. Entomol. Zool.* **42**, 205–215 (2007).
297. Zhang, R. et al. Geographic characteristics of sable (*Martes zibellina*) distribution over time in Northeast China. *Ecol. Evol.* **7**, 4016–4023 (2017).
298. Zhang, Y., Xu, M., Adams, J. & Wang, X. Can Landsat imagery detect tree line dynamics? *Int. J. Remote Sens.* **30**, 1327–1340 (2009).
299. Zhu, K., Woodall, C. W. & Clark, J. S. Failure to migrate: lack of tree range expansion in response to climate change. *Glob. Change Biol.* **18**, 1042–1052 (2012).
300. Zuckerberg, B., Woods, A. M. & Porter, W. F. Poleward shifts in breeding bird distributions in New York State. *Glob. Change Biol.* **15**, 1866–1883 (2009).
301. R Core Development Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2019).
302. Chamberlain, S. A. & Szöcs, E. taxize: taxonomic search and retrieval in R. *F1000Res* **2**, 191 (2013).
303. Gastner, M. T. & Newman, M. E. J. Diffusion-based method for producing density-equalizing maps. *Proc. Natl Acad. Sci. USA* **101**, 7499–7504 (2004).
304. Zuur, A. F., Ieno, E. N. & Elphick, C. S. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**, 3–14 (2010).
305. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2014).
306. Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142 (2013).
307. Gelman, A. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873 (2008).

Acknowledgements

We acknowledge the authors who kindly sent us their data on species range shift estimates. In particular, we are thankful to K. Kleisner and C. Hassall, who kindly provided data on behalf of the NOAA Northeast Fisheries Science Center, The Nature Conservancy, the British Arachnological Society and the Spider Recording Scheme. Finally, we acknowledge grants from the Agence Nationale de la Recherche (TULIP ANR-10-LABX-41 and CEBA ANR-10-LABX-25-01).

Author contributions

J.L., L.C., J.M. and G.G. initiated and conceived the project idea. L.C. and J.L. built the general structure of the database. G.G., L.C., R.B., T.H. and J.L. reviewed the scientific literature and filled the database throughout the duration of the project. G.G. ensured data curation. L.B. and L.C. carried out the taxonomic harmonization of the database with help from J.M. T.H. linked the taxonomic backbone of the database to the Open Tree of Life (<https://tree.opentreeoflife.org>) and Catalogue of Life (<http://catalogueoflife.org/>) to produce a visualization of the phylogenetic coverage of the database. G.G., L.C., J.L. and R.B. prepared the set of methodological variables included as covariates in the subsequent analyses. R.B. and J.L. analysed the data with help from L.C., L.B. and G.G. T.H., R.B. and J.L. produced all of the figures. J.L. wrote the manuscript with contributions from all co-authors.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-020-1198-2>.

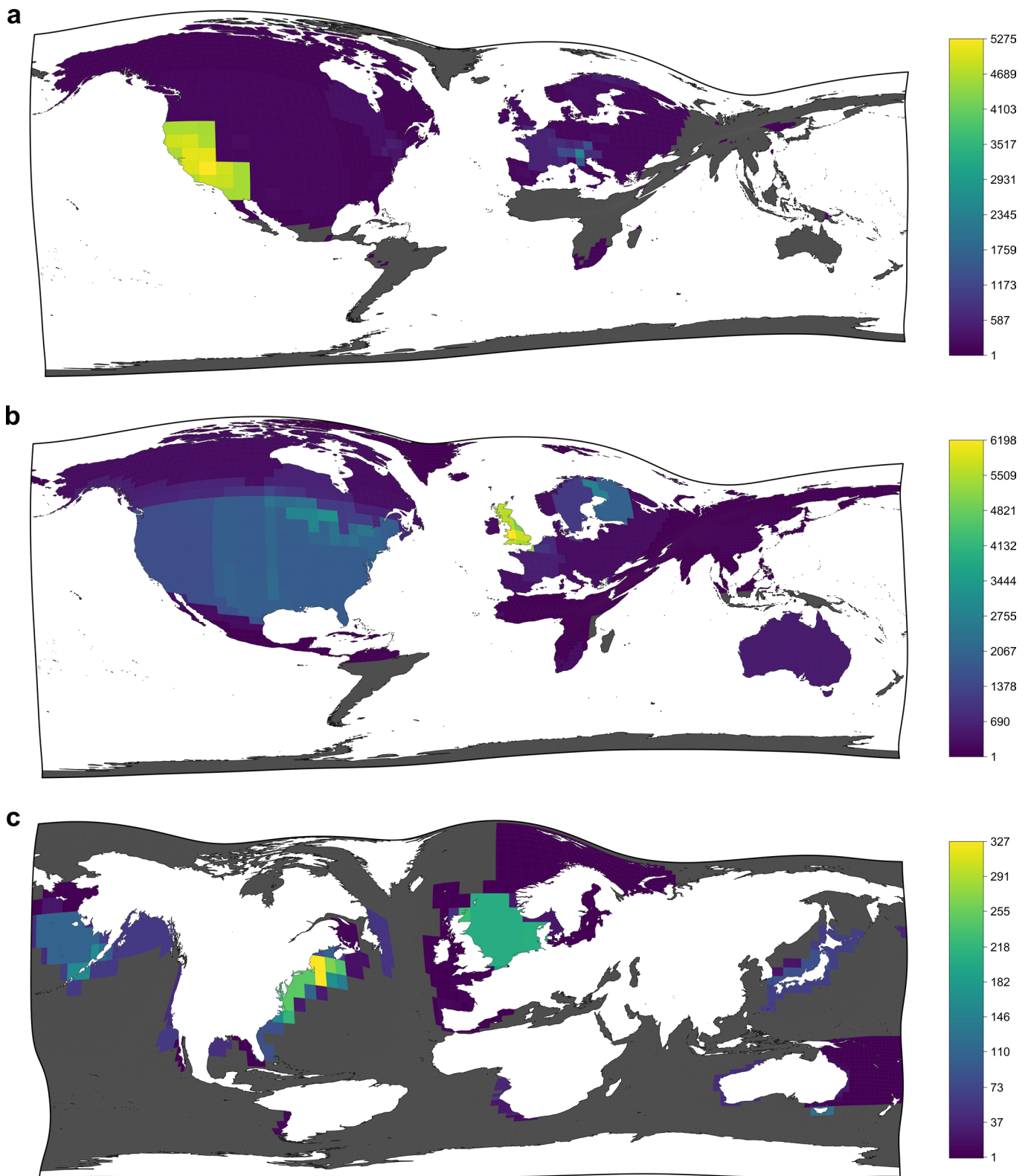
Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-020-1198-2>.

Correspondence and requests for materials should be addressed to J.L.

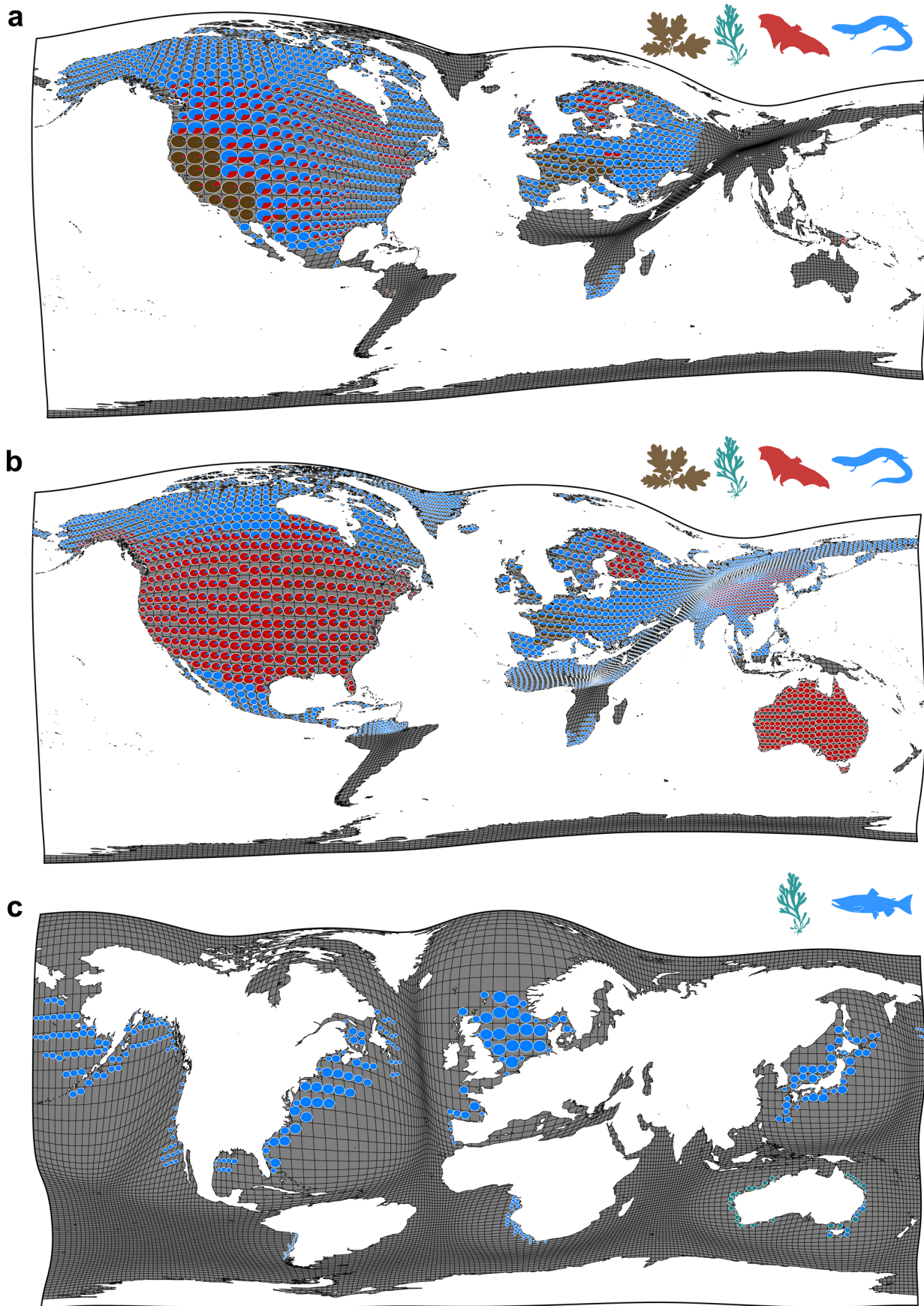
Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

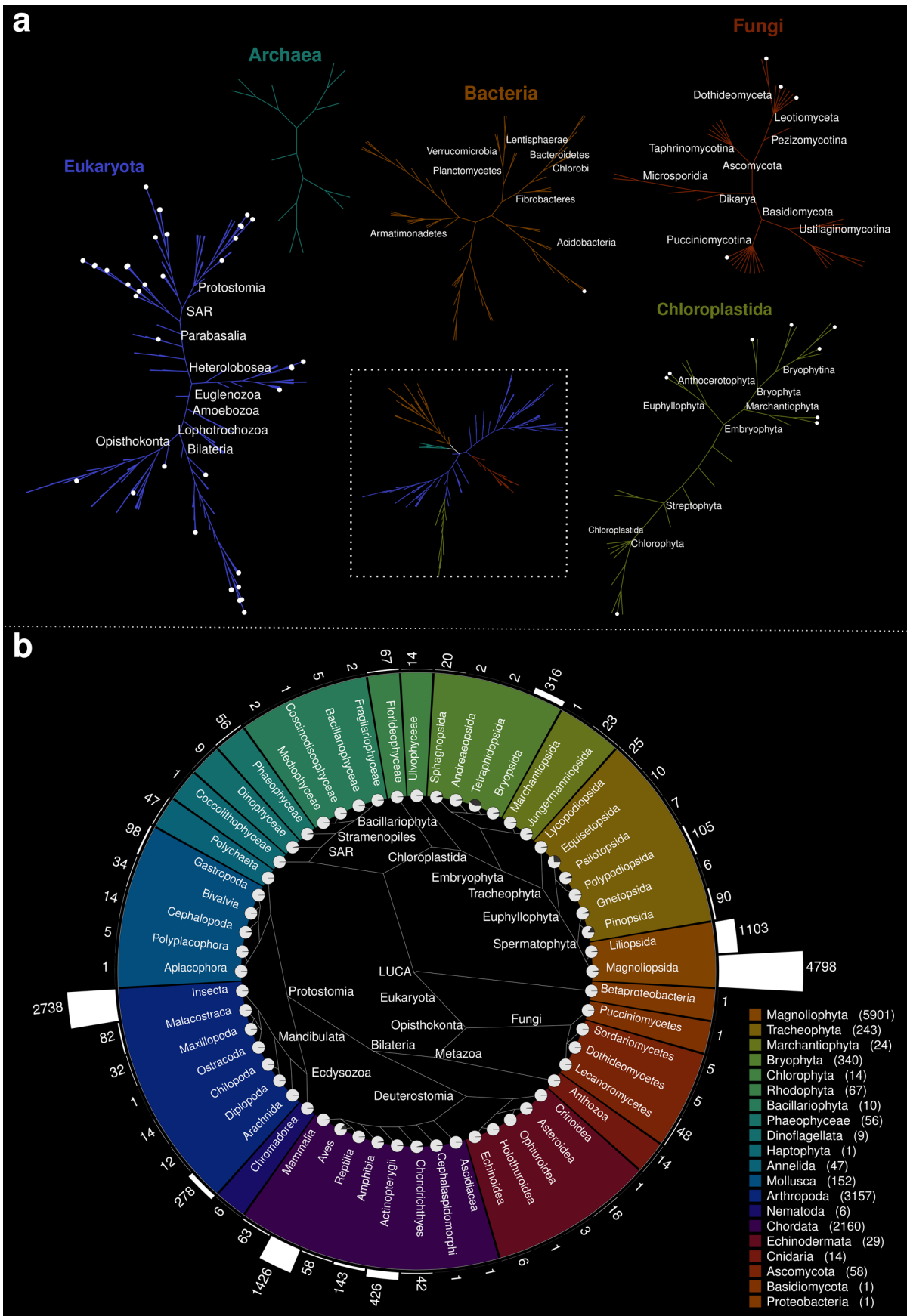
© The Author(s), under exclusive licence to Springer Nature Limited 2020



Extended Data Fig. 1 | Cartograms of the spatial sampling effort in the geo-database. Number of taxa per $2^\circ \times 2^\circ$ grid cell for **a**, elevational and **b, c**, latitudinal range shifts across the terrestrial (**a, b**) and (**c**) marine realm.

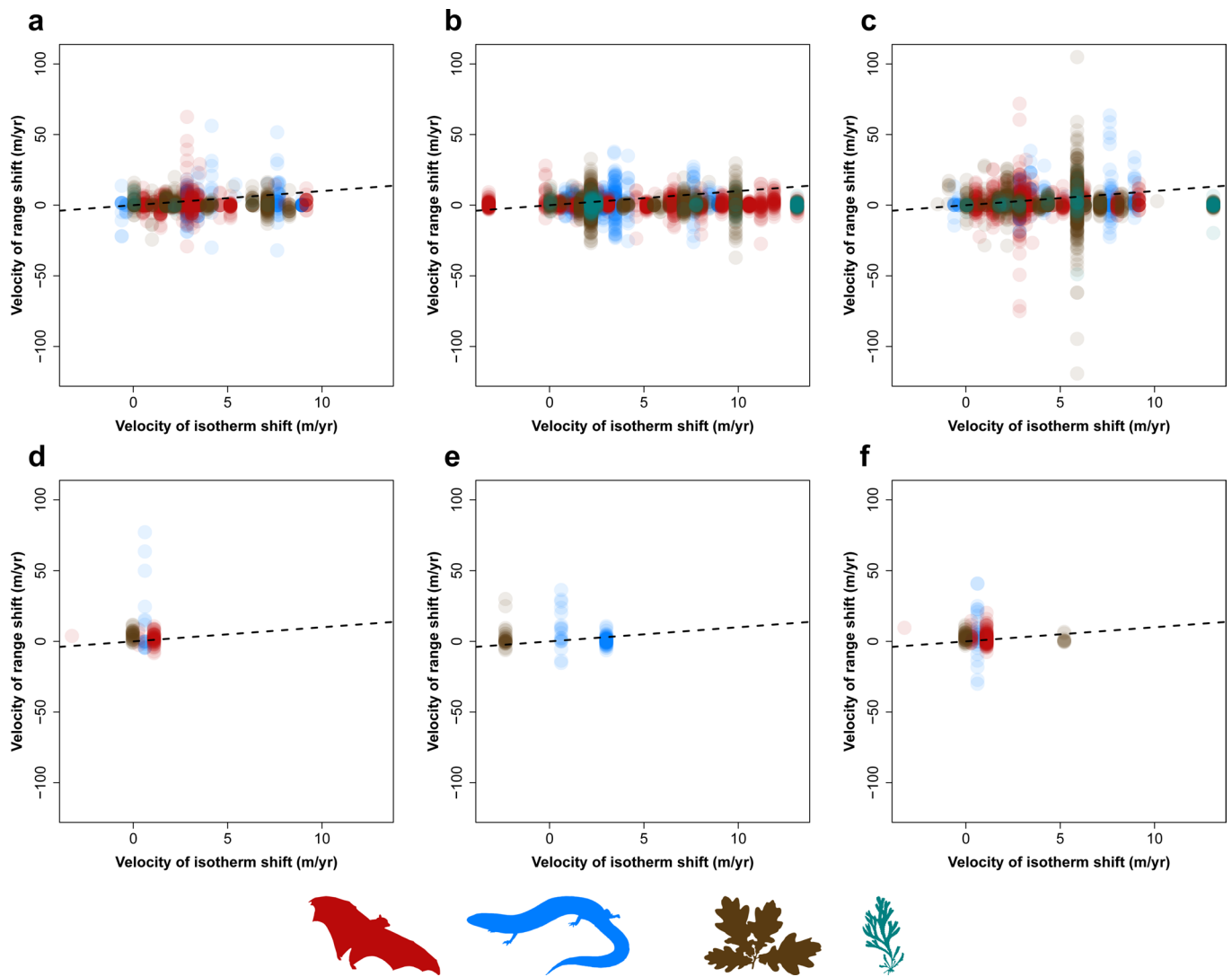


Extended Data Fig. 2 | Cartograms of the relative proportion of ectotherms, endotherms, phanerogams and cryptogams in the geo-database. Relative proportion of data per taxonomic group per $2^\circ \times 2^\circ$ grid cell for **a**, elevational range shifts and **b, c**, latitudinal range shifts across the terrestrial (**a, b**) and (**c**) marine realm. Ectotherms, endotherms, phanerogams and cryptogams are displayed in blue, red, brown and cyan, respectively.

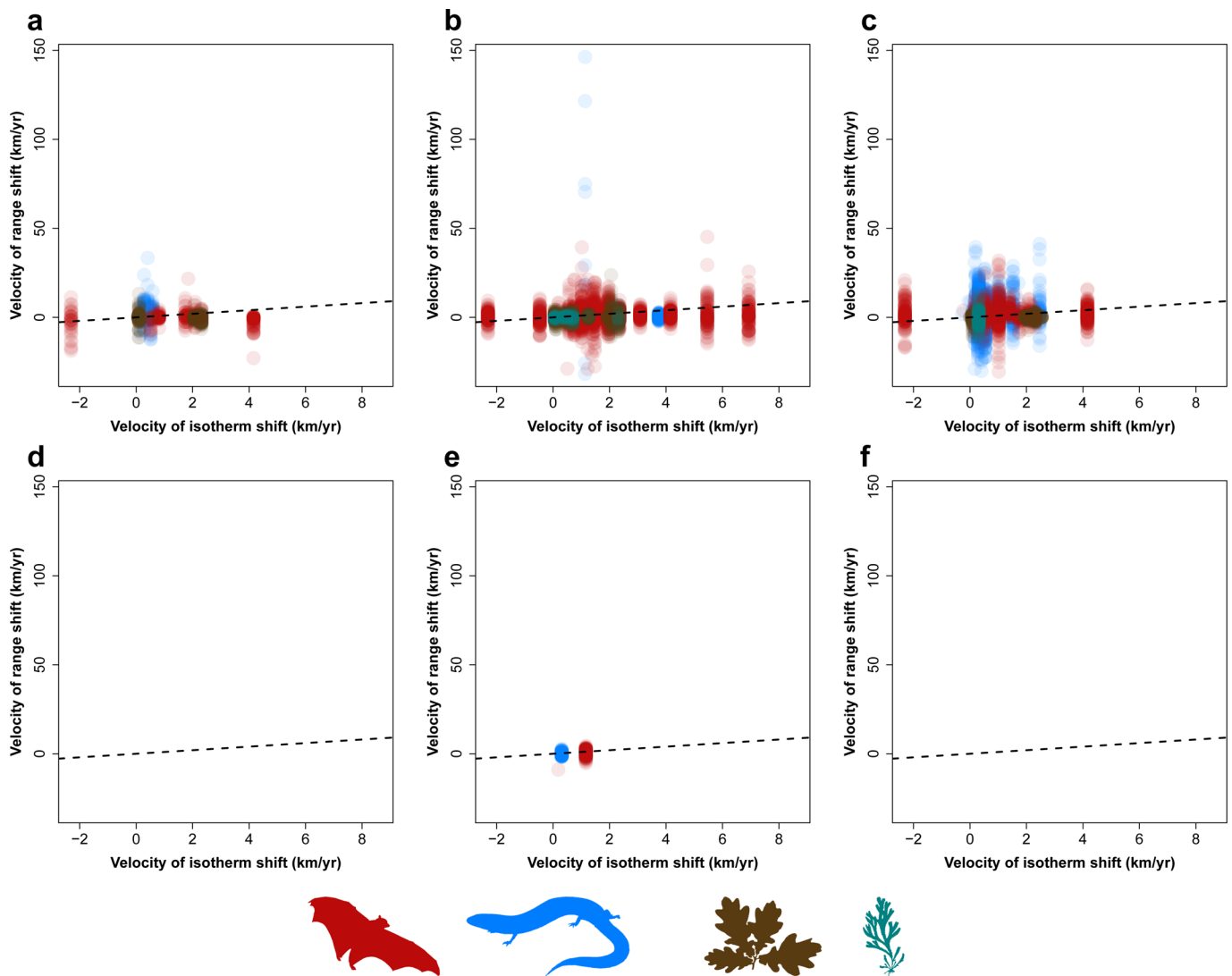


Extended Data Fig. 3 | See next page for caption.

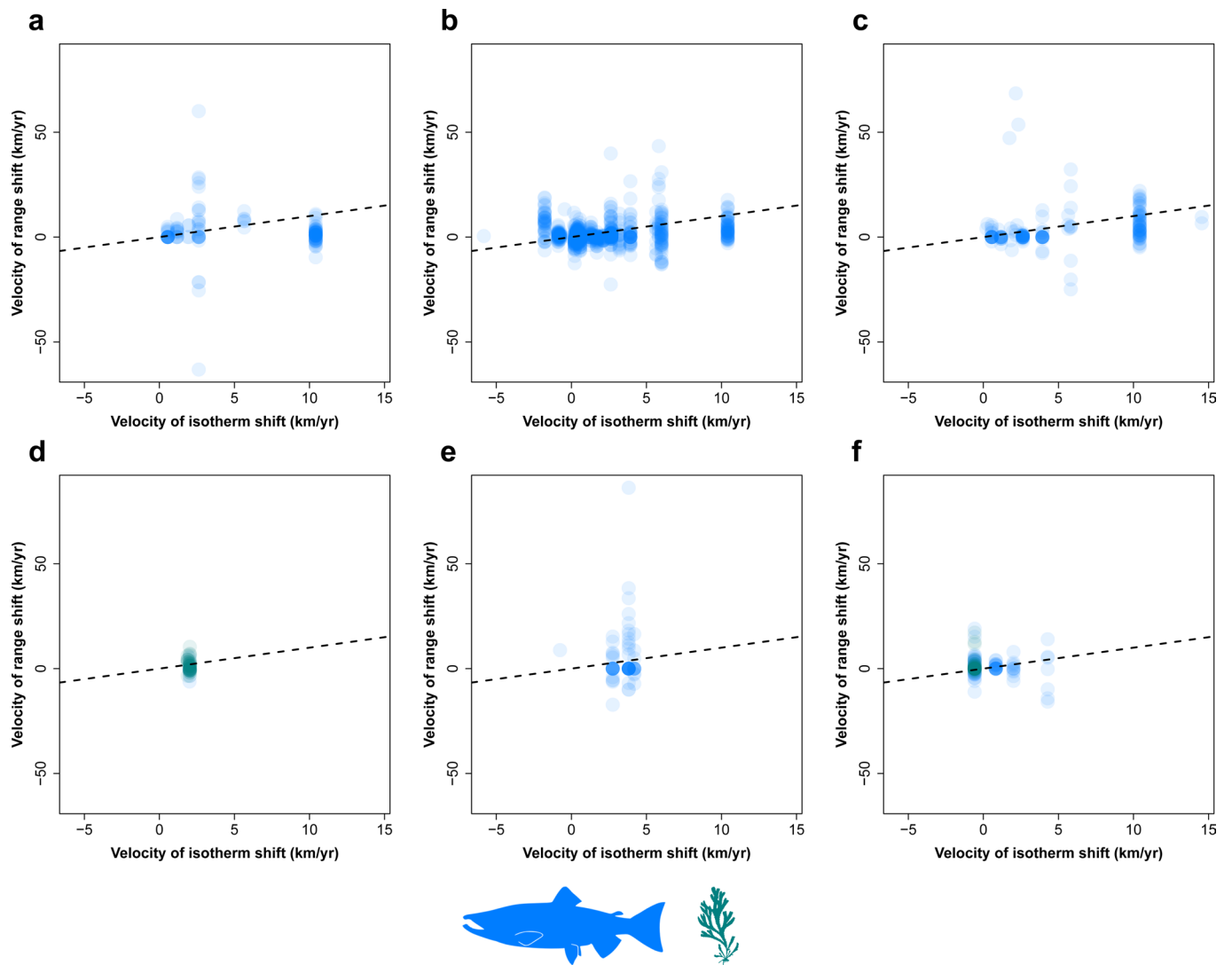
Extended Data Fig. 3 | Phylogenetic coverage of the geo-database. Data on species range shifts throughout **a**, the whole tree of life with a focus on **b**, the phylogenetic relationships among the 56 taxonomic classes included in BioShifts. Simplified representation of the Open Tree of Life (<https://tree.opentreeoflife.org>) collapsed at the level of taxonomic classes. Clades included in BioShifts are highlighted by white dots at the tips. Branches' colors indicate the taxonomic phylum to which classes belong. Bars show the number of species registered in BioShifts per taxonomic class. Pie charts at the tips of the phylogeny represent the proportion of species recorded in BioShifts (in black) compared to the total number of species recorded in Catalogue of Life (<http://catalogueoflife.org/>). The white part in the pie charts represent the proportion of species not covered in BioShifts. Colors represent the 20 phyla occurring in BioShifts (the number of species per phyla is provided in parentheses).



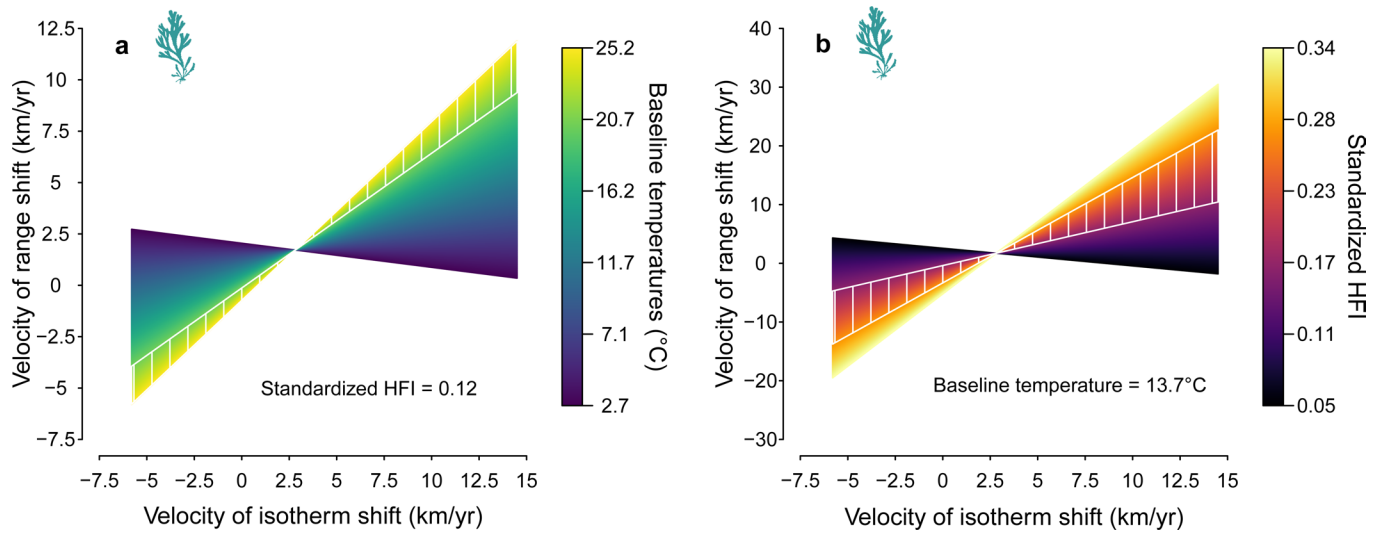
Extended Data Fig. 4 | Degree of coupling between species elevational range shifts (m yr^{-1}) and isotherm shifts in elevation (m yr^{-1}). The degree of coupling is displayed separately for the **a-c**, Northern and **d-f**, Southern Hemisphere and separately for the **a, d**, trailing edge, **b, e**, centroid and **c, f**, leading edge of the range. The dotted line represents the 1:1 relationship of perfect match, meaning that organisms are closely tracking the shifting isotherms. Ectotherms, endotherms, phanerogams and cryptogams are displayed in blue, red, brown and cyan, respectively.



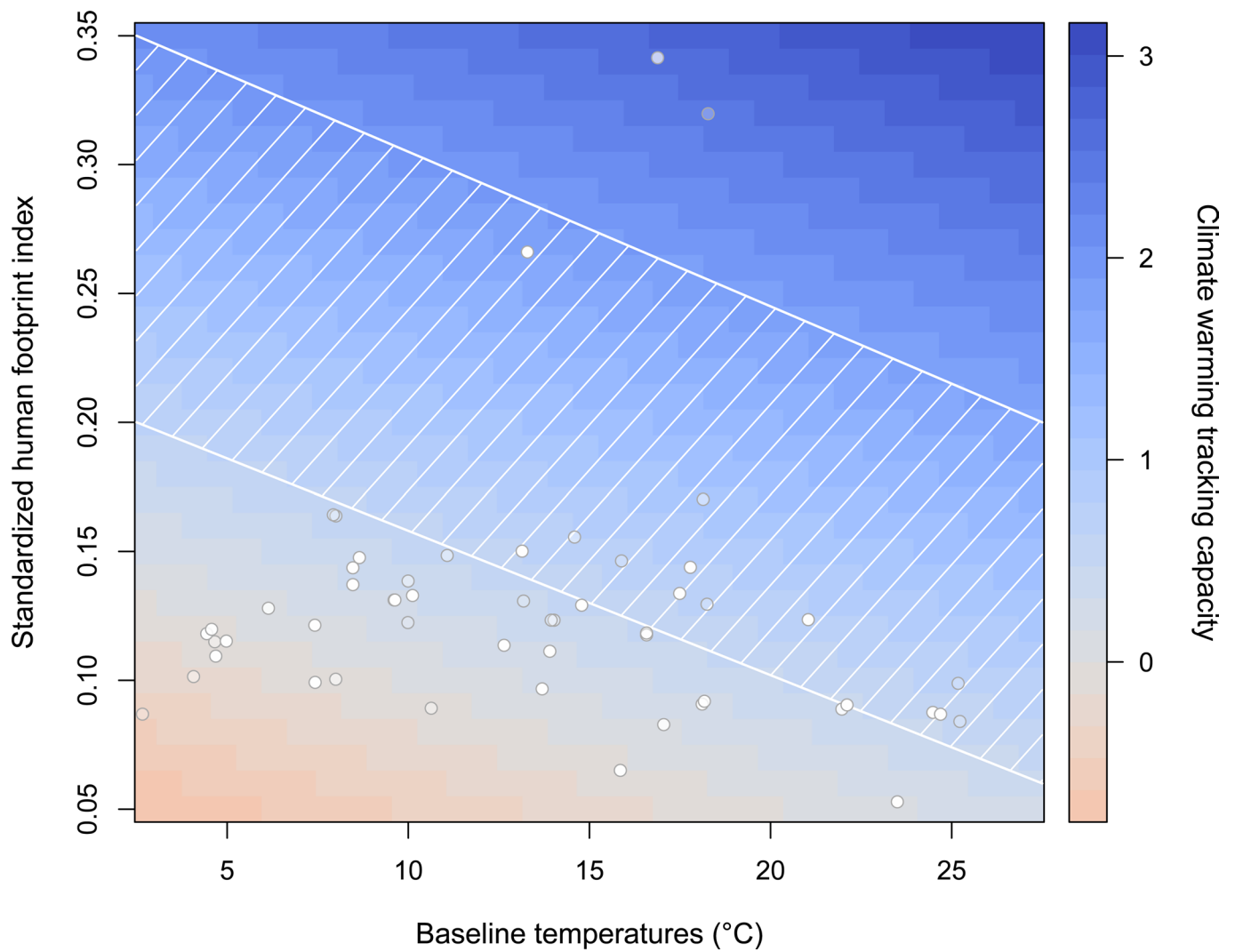
Extended Data Fig. 5 | Degree of coupling between terrestrial species latitudinal range shifts (km yr^{-1}) and isotherm shifts in latitude (km yr^{-1}). The degree of coupling is displayed separately for the **a-c**, Northern and **d-f**, Southern Hemisphere and separately for the **a, d**, trailing edge, **b, e**, centroid and **c, f**, leading edge of the range. The dotted line represents the 1:1 relationship of perfect match, meaning that organisms are closely tracking the shifting isotherms. Ectotherms, endotherms, phanerogams and cryptogams are displayed in blue, red, brown and cyan, respectively. Note that there are no data on the velocity of terrestrial latitudinal range shifts at the trailing and leading edge of range shifters for the Southern Hemisphere.



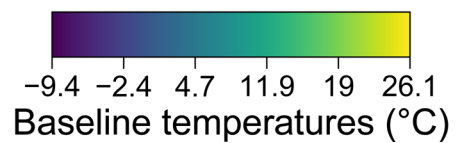
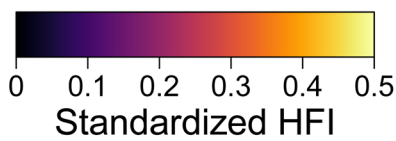
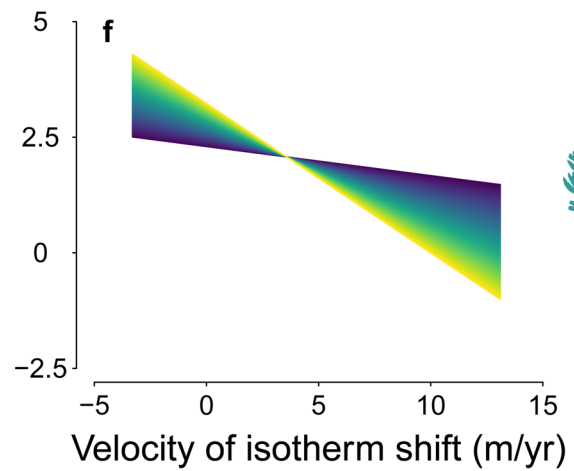
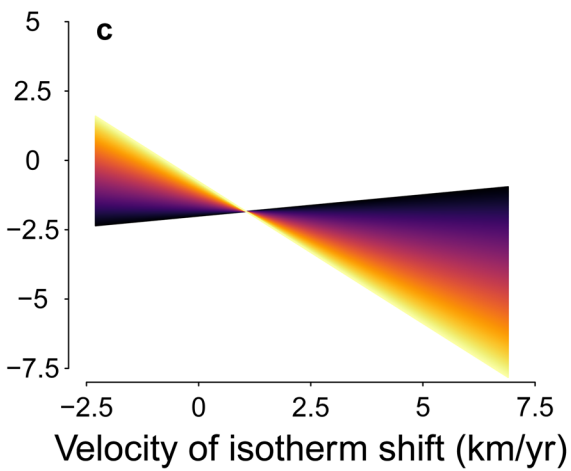
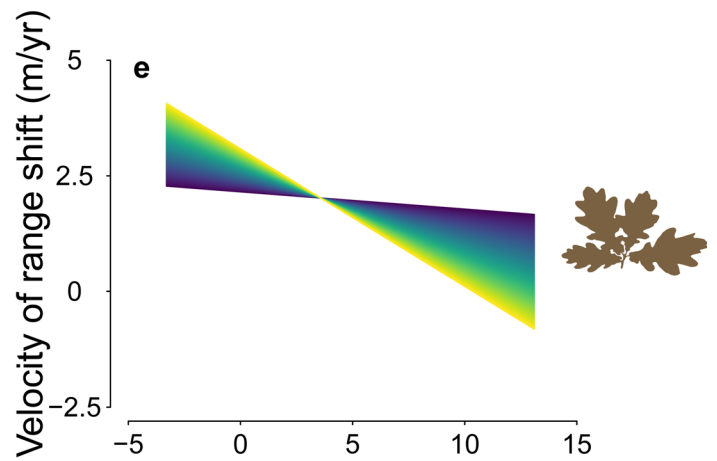
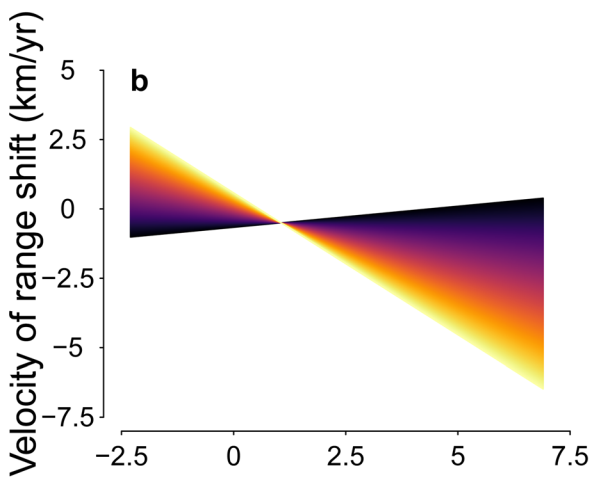
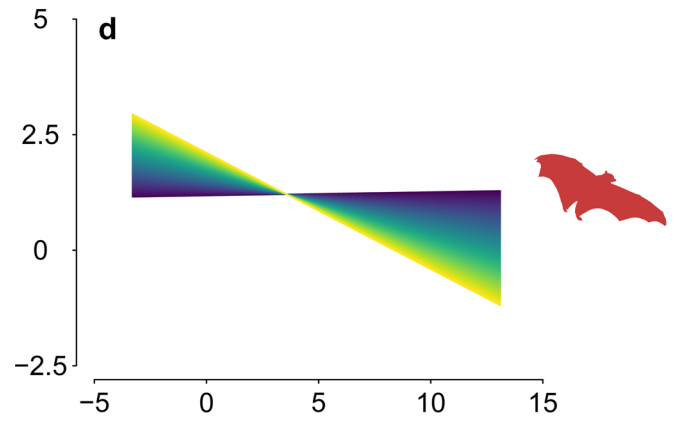
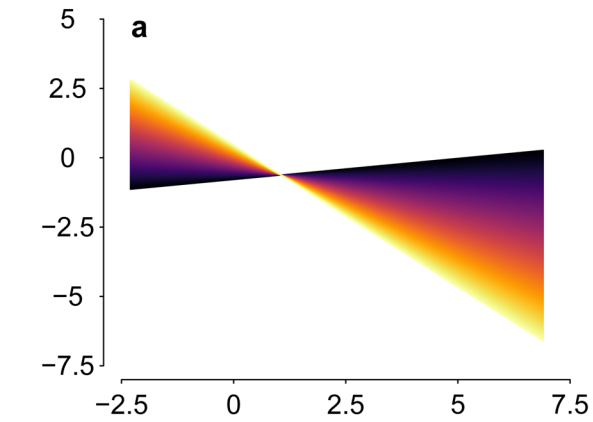
Extended Data Fig. 6 | Degree of coupling between marine species latitudinal range shifts (km yr^{-1}) and isotherm shifts in latitude (km yr^{-1}). The degree of coupling is displayed separately for the **a–c**, Northern and **d–f**, Southern Hemisphere and separately for the **a, d**, trailing edge, **b, e**, centroid and **c, f**, leading edge of the range. The dotted line represents the 1:1 relationship of perfect match, meaning that organisms are closely tracking the shifting isotherms. Ectotherms and cryptogams are displayed in blue and cyan, respectively.



Extended Data Fig. 7 | Degree of coupling between species range shifts and isotherm shifts for marine cryptogams. Interaction effects between the VIS and **a**, baseline temperatures or **b**, the standardized HFI on the velocity of species range shifts along the latitudinal gradients for marine cryptogams. The two white lines and the white hatching represent the range of conditions for which marine cryptogams closely track the shifting isotherms in latitude (that is slope parameter not significantly different from 1 based on 5,000 bootstrap iterations).



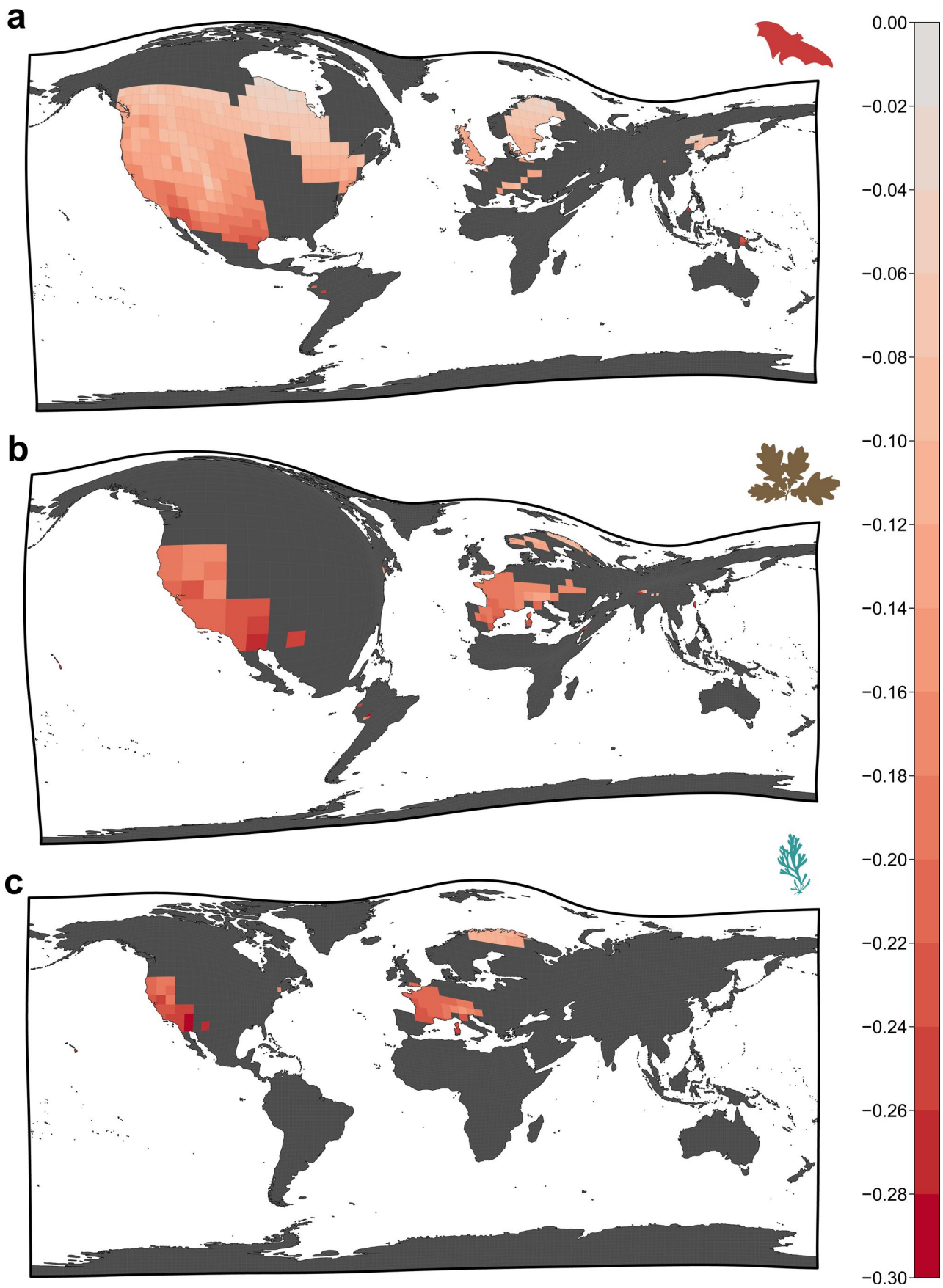
Extended Data Fig. 8 | The climate warming tracking capacity of marine organisms. Combined effect of mean annual sea surface temperature prior to the baseline survey (baseline temperatures) and human pressures on the environment (the standardized HFI) on the slope of the relationship between the velocity of marine species range shifts and the VIS along the latitudinal gradient in the oceans (climate warming tracking capacity). The white lines and hatching represent the range of conditions for which marine taxa closely track the shifting isotherms in latitude (that is slope parameter not significantly different from 1 based on 5,000 bootstrap iterations). White transparent dots show the distribution of the raw data ($N = 1,403$ range shift estimates) used to fit the model. This plot includes both marine ectotherms and cryptogams.



Extended Data Fig. 9 | See next page for caption.

Extended Data Fig. 9 | Degree of coupling between species range shifts and isotherm shifts for terrestrial endotherms, phanerogams and cryptogams.

Interaction effects between **a-c**, the VIS along the latitudinal gradient and the standardized HFI as well as between **d-f**, the VIS along elevational gradients and baseline temperatures on the velocity of species range shifts for terrestrial (**a, d**) endotherms, (**b, e**) phanerogams and (**c, f**) cryptogams. Note that negative slopes do not necessarily indicate species range shifts in the opposite direction to isotherm shifts, unless the signs of the two estimates (for a given combination of baseline temperatures and standardized HFI) are opposite. Credit: Icon Library (mountain silhouette) under a CCO Public Domain Licence.



Extended Data Fig. 10 | See next page for caption.

Extended Data Fig. 10 | Cartograms of the predicted slope coefficient between the velocity of species range shifts and the velocity of isotherm shifts along elevational gradients for terrestrial endotherms, phanerogams and cryptogams. Slope estimate per $2^\circ \times 2^\circ$ grid cell along elevational gradients for **a**, endotherms, **b**, phanerogams and **c**, cryptogams. The number of range shift estimates (that is sample size) in each grid cell was used to distort the map: the bigger the grid cell, the larger the sample size. Note that negative slopes do not necessarily mean that species are shifting in the opposite direction to isotherm shifts (see Extended Data Fig. 9).

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection

Range shift measures were obtained from a literature search as described in the Methods section. Climatic data were obtained from WorldClim v. 1.4, the Climate Research Unit (CRU) TS v. 3.23, BIO-ORACLE and the Met office Hadley Centre observations datasets. We used global terrestrial human footprint maps for the year 2009 (Venter et al. 2016) as well as a global map of human impact on marine ecosystems (Halpern et al. 2008).

Data analysis

R code used to perform the analyses are available together with the underlying data at <https://figshare.com/s/ebd19485a00757ababb0>.

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

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

WorldClim, CRU, BIO-ORACLE, Met office Hadley Centre and human footprint datasets (Halpern et al. 2008; Venter et al. 2016) are freely available. Links to datasets are included in the Methods and References sections in the manuscript.

Field-specific reporting

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

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

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

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

Study description	In this study, we introduce BioShifts, a global geo-database which includes 30,534 range shift measures. We provide robust estimates of the velocity of latitudinal and elevational range shifts for the 20 most studied taxonomic classes. We also assess the coupling between the velocity of isotherm shifts and the velocity of range shifts and evaluate the influence of life-form categories, historical mean annual temperature regime and the standardized human footprint index on range shifts.
Research sample	The BioShifts dataset contains 30,534 range shifts obtained from 258 published and peer-reviewed papers. The dataset includes 12,415 species following taxonomic harmonization.
Sampling strategy	For statistical reasons, we focused on the set of species belonging to the taxonomic classes with more than 30 observations. For our analyses to assess the velocity of species range shift at the taxonomic class level (see section entitled 'Detection: estimating the velocity of range shifts per taxonomic class' of the Methods for more information), this criteria resulted in 16,399 and 13,341 observations for latitudinal and elevational range shifts, respectively. Regarding our analyses of the coupling between the velocity of range shifts at the species level vs. the velocity of isotherm shifts, this criteria of more than 30 observations per taxonomic class resulted in 16,521 and 13,459 observations for latitudinal and elevational range shifts, respectively (see section entitled 'Attribution: coupling between species' range shifts and isotherms' shifts' of the Methods for more information).
Data collection	The BioShifts database was built from a literature review as described in the Methods section of the manuscript. Other freely available datasets were obtained from the sources mentioned above and in the Methods and References sections in the manuscript.
Timing and spatial scale	The literature search was performed between 2014 and 2018. The spatial scale is global.
Data exclusions	No data were excluded from the dataset provided at https://figshare.com/s/ebd19485a00757ababb0 .
Reproducibility	R code used to perform the analyses are available at https://figshare.com/s/ebd19485a00757ababb0 .
Randomization	Data on species range shifts were allocated to groups depending on methodological attributes used as covariates in the analyses (see Methods section of the manuscript for more information on the factor variables we used as covariates in the analyses). Randomization procedures were carried out to assess the statistical significance of the velocity of range shifts per taxonomic class as well as when analysing the coupling between the velocity of species range shifts and the velocity of isotherm shifts (see Methods section of the manuscript for more details on the randomization procedure we used).
Blinding	Blinding was used during data analysis by simply allocating a unique running ID to each of the study from which we extracted data on species range shifts (see Methods section of the manuscript for more information).
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

Reporting for specific materials, systems and methods

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

Materials & experimental systems

n/a	Included in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

Methods

n/a	Included in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging