Global patterns of thermal niche filling in ectotherms

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Abstract: Understanding how temperature determines the distribution of life is necessary to assess species' sensitivities to contemporary climate change. We test hypotheses about the importance of temperature in limiting geographic ranges of ectotherms by comparing the temperatures and areas species occupy to those they could potentially occupy based on their physiological thermal tolerances. While marine and low-latitude terrestrial ectotherms occupy temperatures that closely match their thermal tolerance limits, high-latitude terrestrial species under-occupy warm temperatures and are absent from thermally-tolerable areas towards the equator. These findings support the hypothesis that on land, temperature less often directly limits the warm range edge of high-latitude species because the historical range expansion of temperate species 'out of the tropics' resulted in biotic exclusion of these species within the tropics. Our findings also suggest that range edges of marine species and broad–ranging species, as well as cool range edges of terrestrial ectotherms at all latitudes, will respond more directly to climate warming.

One-Sentence Summary: The equatorward (warm) range edges of high-latitude ectotherms are limited by factors other than temperature.

Main Text:

Climate warming is already altering the distributions of species worldwide (*1*). Yet sensitivity to climate change varies considerably among species (*2*, *3*), calling into question the extent to which temperature directly limits species' geographic ranges. If a species occupies all accessible habitat where temperatures suit its tolerances (i.e., the species fills its potential thermal niche), then we expect the species' range limits to be sensitive to temperature change (*4*). In reality, species are often prevented from filling their potential thermal niche, since distributions are limited by factors other than temperature (*5–7*), such as dispersal (*8*), species interactions (*9*), resource availability, and non-thermal abiotic factors like moisture (on land, *10*) or oxygen (in water, *11*). Understanding where and when temperature directly constrains species ranges can help elucidate hypotheses about historical range shifts and improve projections of species' sensitivities to contemporary climate warming.

A long-standing hypothesis posits that abiotic factors (like temperature) are relatively more limiting at species' poleward range edges compared to their equatorward edges (*12*, *13*). This hypothesis is supported by a recent synthesis of empirical studies of the ecological limits to species ranges, which shows that biotic interactions consistently influence species' low-latitude and low-elevation range edges more often than their high-latitude and high-elevation edges (*9*). One possible cause for this pattern is an increased intensity of species interactions toward the tropics (*9*, *12*, *13*), for which empirical evidence is strong (*14–16*), owing to the increased biodiversity, density, or activity levels in the more productive, warmer, and more seasonally stable tropics (reviewed by ref *17*). However, the way in which temperature limitation might be superseded by biotic limitation in the tropics is not well articulated and could be informed by testing two alternative hypotheses regarding the drivers of species distributions.

The first hypothesis posits that the role of abiotic factors in limiting species ranges gradually decreases towards the tropics because of a superseding role of biotic interactions (*14–16*). Under this hypothesis, which we term the *Reduced-Abiotic-Limitation-in-the-Tropics Hypothesis,* we would expect both poleward and equatorward range limits to be more abiotically-limited at higher latitudes compared to lower latitudes. The second hypothesis posits that the reduction of abiotic limitation at warm range edges is more pronounced for species outside of the tropics that evolved tolerance to colder and more variable climates. This second hypothesis is an extension of the Out of the Tropics hypothesis (*18*, *19*), which posits that tropical species evolved greater tolerance to cold temperatures that allowed them to expand their ranges poleward. If this resulted in a trade-off between performance and thermal tolerance breadth (i.e., 'jack-of-all-trades is master of none', Principle of Allocation, refs *1*, *2*), then temperate species would fare worse in antagonistic species interactions (e.g., competition, predation, disease) compared to tropical species, potentially leading to greater biotic exclusion at the equatorward range edges of higher-latitude species. We call this the *Out-of-the-Tropics-Trade-Off Hypothesis*.

These two hypotheses make contrasting, testable predictions about how species interactions alter the relative importance of temperature in limiting ranges, which affects the expected sensitivities of range edges under ongoing climate change. The *Reduced-Abiotic-Limitation-in-the-Tropics Hypothesis* predicts greater exclusion of low-latitude species from environments with tolerable temperatures at all range edges compared to high-latitude species, whereas the *Out-of-the-Tropics-Trade-Off Hypothesis* predicts greater exclusion of high-latitude species at their equatorward range edges.

We tested these hypotheses by synthesising information on how ectothermic metazoa fill their potential thermal niche. For each species (n = 426), we defined the fundamental thermal niche using thermal tolerance limits from experimental assays (fig. 1). We delineated a species' potential thermal niche as the predicted extreme warm and cool body temperatures (based on the operative temperature of an ectotherm in its environment, *20*, outside of dormancy periods) within its fundamental thermal niche and encounterable within accessible habitat (see *Materials and Methods*). To assess how well species fill their potential thermal niches, we compared each species' potential thermal niche to its realized thermal niche, defined by the warm and cool extreme body temperatures across its current estimated geographic distribution (i.e., its realized range). We used the difference between the potential and realized thermal niche extremes to define warm and cool niche filling; negative thermal niche-filling values denote niche underfilling (fig. 1a,c) and positive values denote niche overfilling (i.e., cases in which species' realized ranges extend to more extreme temperatures than their thermal tolerance limits appear to allow; fig. 1a,c). We used these metrics to test the two hypotheses described above, as well as three additional hypotheses about factors that could simultaneously affect thermal range filling, namely that thermal niche underfilling is greater (i) in terrestrial compared to marine realms (*3, 21, 22*), (ii) in species with less dispersal potential (*4*), and (iii) in species that are more ecologically specialized (*23*, table S1). In all cases, we test the sensitivity of results to simulations of species' capacity to thermoregulate and to adjust their thermal limits with short-term acclimation.

Results and Discussion

Most terrestrial species could live in places with warmer extreme temperatures than those they currently experience across their range according to their thermal tolerance limits, hence they underfill the warm ends of their potential thermal niche (dashed red lines in fig. 2, fig. 3a). In terrestrial species, this warm niche underfilling was greater in higher latitude species than low-latitude species, whereas it was smaller (closer to zero, i.e., perfect filling), and did not change with latitude in intertidal and subtidal marine species (fig. 2 and 3, fig. S1, table S2).

At the cool extremes of the thermal niche, we found that most species occupy ranges where temperature extremes are colder than their cold tolerance limits appear to allow (solid blue lines in fig. 2, fig. 3b), hence by definition they 'overfill' the cool ends of their potential thermal niche. However, given that species must tolerate the climates in which they occur, we explore variation in overfilling values as a means to understand the mechanisms (e.g., cold season dormancy) that lead to these findings. Cool niche overfilling increased with latitude in terrestrial and intertidal species, but not in subtidal marine species, where cool niche overfilling was smaller (closer to zero, i.e., perfect filling) and did not change with latitude (fig. 2 and 3, fig. S1, table S2).

Whereas niche filling describes offsets between occupied and tolerable temperatures, how these offsets play out in geographic space depends on the spatial distribution of thermal gradients (*24*) (fig. 1b,d). We therefore additionally assessed how patterns of potential thermal niche filling differ when thermal niches are projected into geographical space (fig. 1b,d). We measured range filling as the proportion of a species' potential thermal range that it occupies and assess how range underfilling differs between species' equatorward and poleward range halves.

Although total range filling did not change with latitude (fig. 4a, fig. S1, table S3), there was a clear increase in equatorward bias in the portion of the potential thermal range that was

underfilled in terrestrial species, with an overall bias towards equatorward thermal range underfilling that increased with the latitudinal midpoint of a species' range (fig. 4b and red-blue color scale, fig. S1, fig. S2, table S3). By contrast, there was virtually no asymmetry in intertidal and subtidal marine species (white points and model fits close to zero, fig. 4b, fig. S1, table S3). Although marine species underfilled large proportions of their potential thermal ranges, indicating they do not occupy all thermally-tolerable areas, this range underfilling showed little latitudinal or thermal bias.

Thus, in terrestrial species, both warm niche and equatorward range underfilling are greatest *in* the tropics, at the warm range edge of species that live *outside* of the tropics (i.e., temperate species). This provides support for the *Out-of-the-Tropics-Trade-Off Hypothesis*. By contrast, we did not find empirical support for the *Reduced-Abiotic-Limitation-in-the-Tropics Hypothesis* since the observed pattern was opposite to the expectation of increased underfilling at the warm end of the potential thermal niche or range in species closer to the tropics (fig. 4b). Although these two hypotheses are not mutually exclusive, our findings provide more support for hypothesis 1 than for hypothesis 2.

The observed latitudinal patterns were generally robust to taxonomic non-independence, variation in thermal limit assay method, acclimatization to local conditions, and simulations of phenotypic plasticity and more complex thermoregulation behaviours (see *Materials and Methods - Analyses*). Simulating acclimatization of species to seasonal temperatures across the landscape (see *Supplementary Methods*) led generally to broader potential thermal niches and reduced both warm and cool niche overfilling (grey shadow compared to coloured density distributions in fig. 3a-b, fig. S3a; warm niche overfilling on land reduced by ~10 °C, cool niche overfilling reduced by ~5 °C). However, the relationships with latitude were robust to this acclimatization simulation (fig. S3b-e, table S4). Additionally, while simulating more refined thermoregulatory behaviour in a subset of terrestrial species (n = 219) did account for some portion of warm niche underfilling (see *Supplementary Methods*), patterns of warm niche underfilling across latitude remained (fig. S5a-c, table S5).

Remaining instances of cool niche overfilling and its increase with latitude might be explained by organisms' abilities to become seasonally dormant, to seek extremely buffered habitats (e.g., through burrowing), or via physiological plasticity and/or adaptation not accounted for in the acclimatization simulation. Although we attempted to use only temperatures during active time periods for species with known dormancy, limited information on the timing and duration of dormancy may have led to an underestimation of dormancy periods (see *Supplementary Methods*). Additionally, cooling rates used in cold tolerance studies are typically much faster than those experienced in microhabitats (*25*), potentially weakening the connection between laboratory-assayed cold tolerance and *in situ* survival. Further, cold tolerance plasticity (*26*) and local adaptation are expected to be greater in cooler parts of the range relative to locations where laboratory specimens were collected (fig. S4). Population differentiation in cold tolerance might be expected to be greater on land where gene flow across cold-temperature gradients are likely less than in the ocean (*27, 28*), hence greater overfilling in terrestrial species might be attributed to more extreme cold-tolerance of range-edge individuals relative to individuals sampled in laboratory assays. Importantly, these same mechanisms (acclimatization, seasonal dormancy, and local adaptation) cannot reasonably explain why terrestrial species underfill their warm thermal niche, as accounting for these mechanisms is not expected to reduce underfilling.

Thermal niche filling was greater in species with larger geographic range sizes, consistent with the hypothesis that larger-ranged species are less ecologically-specialised and thus more temperature-limited (*23*). This result (fig. S1, table S2) was robust to simulations of acclimatization and thermoregulatory behaviour (fig. S3, fig. S5, table S4, table S5). We found no relationship between dispersal distance and potential thermal niche or thermal range filling (fig. S1, table S2, table S3). We similarly found no relationship with body size, in contrast to expectations (*23*, fig. S1, table S2, table S3). We note that our analysis did not explicitly consider extrinsic barriers to dispersal (other than the land/sea interface), which might help to further articulate any relationships between niche underfilling and dispersal limitation. However, the present evidence suggests underfilling is not explained by dispersal ability or factors related to body size.

Our analysis distinguished between two hypotheses of how biotic interactions might limit species ranges. The interpretation that warm niche underfilling is linked to biotic interactions is consistent with the finding that the probability that biotic drivers limit the distribution of a species at its warm range boundaries increased with latitude in terrestrial modelling and experimental studies (*9*). Under this interpretation, it is interesting to think about why marine species show less thermal niche underfilling than terrestrial species. Indeed, trophic interactions in marine systems are often thought to be more size-based than species-based (*29*), potentially altering species-level impacts of negative biotic interactions. Additionally, although there are examples of biotic interaction intensity decreasing with latitude in marine systems, these are mostly intertidal (reviewed in *14*), indicating biotic interactions are less limiting to marine species ranges (also supported in *9*).

However, mechanisms other than biotic exclusion could be responsible for warm niche underfilling. Underfilling of the warm end of the niche might occur because other abiotic niche requirements are more limiting or are co-limiting in warm areas (e.g., moisture in the hot desert belts, oxygen at warmer ocean regions). If biotic limitation or other limiting abiotic niche requirements are responsible for warm niche underfilling, then species might have extra heat tolerance to buffer climate warming at their warm range edge. Yet if warm underfilling occurs because species' ecological limits to population growth are more limiting than an individual organisms' capacity to function under heat stress (as generally measured in experiments), species could have high heat sensitivity at their warm range edge despite these findings. Temporal variability in temperatures and a history of thermal stress can, for example, reduce heat tolerance at the population scale (*30–32*). Similarly, if early life stages are more heat-sensitive than the adults typically assayed (e.g., *33*, *34*), or if sublethal temperatures limit critical life-history functions (e.g., mate-finding), wild populations might not be able to persist in sublethal temperatures.

Observational evidence of variation in species' range shifts in response to climate warming already support the general marine-terrestrial differences predicted by these findings, indicating greater sensitivities in marine species (*3*, *22*), and can be used to test more refined hypotheses generated here about latitudinal and range-size gradients in sensitivities. Namely, if thermal niche underfilling is associated with lower climate sensitivity, we predict species in the terrestrial tropics to be more sensitive to climate change generally, and warm range edges of extra-tropical species to be less sensitive, with contractions more tied to drought or climate-related increases of antagonistically interacting species. Results presented here show that general patterns of temperature limitation among species emerge despite the existence of many complex factors that

likely shape individual distributions; the shared evolutionary history of biodiversity might likewise lead to general patterns in how biodiversity and ecosystem services respond to contemporary climate change.

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thermal tolerance plasticity data. All authors participated in consultations about how to run analyses, while J.G.R. and F.V. were additionally consulted about specific analyses. N.A.M. created all figures in consultation with J.M.S. Authors J.M.S. and N.A.M. wrote the manuscript and all authors provided feedback, edits, and revisions to the manuscript. A.L.H. provided thorough feedback on the manuscript and helped majorly with revisions. J.M.S. supervised the project.

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Data and materials availability: Data and code needed for analyses associated with the current submission are available in the public Living Up to Thermal Potentials GitHub repository ((*1*)), with large data files downloadable from Figshare (figshare.com/s/83bba4f780f53b6f21f5). Upon publication, the full repository and associated files will be archived and made available.

Supplementary Materials

Materials and Methods

Figs. S1 to S9

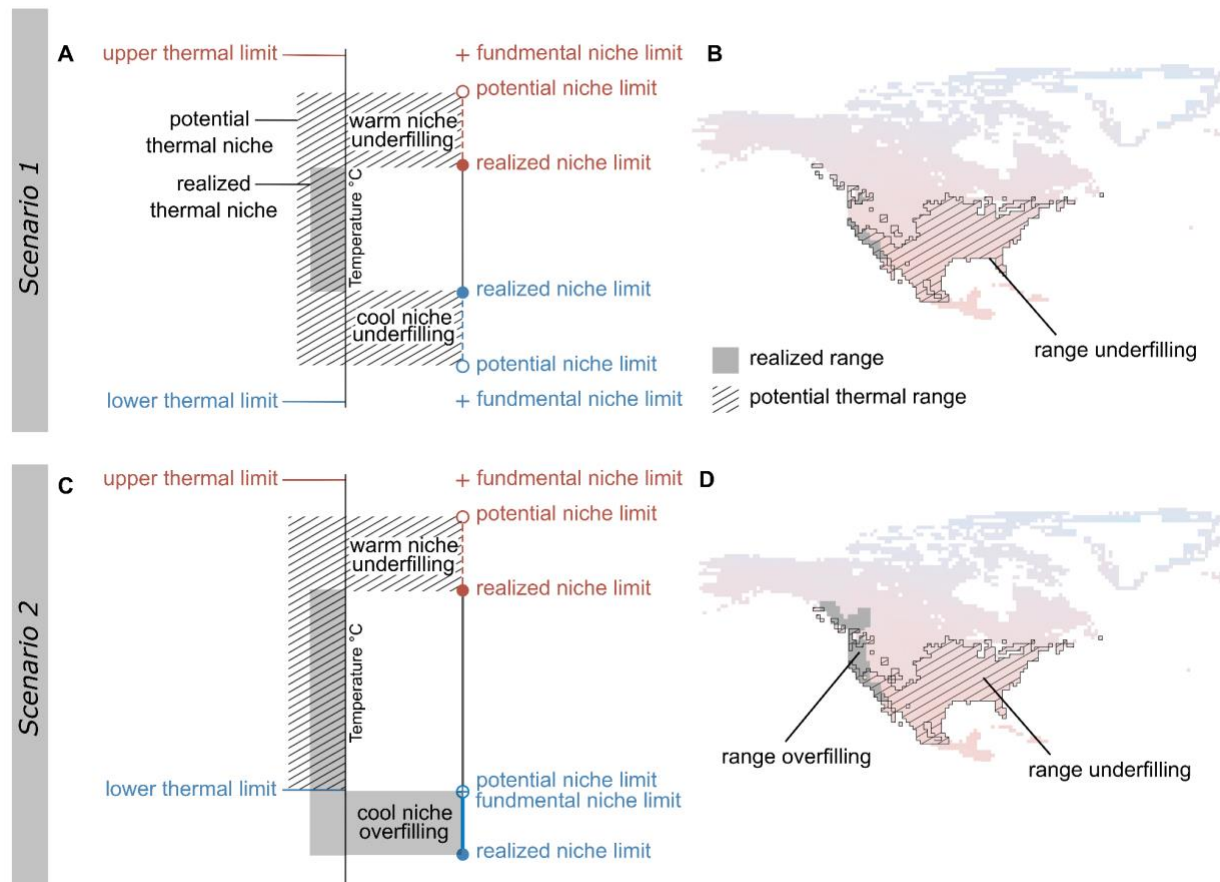Tables S1 to S7

Supplementary Methods

Fig. 1. Patterns of thermal niche filling projected in thermal and geographic space. Two explanatory scenarios (1: A-B; 2: C-D) illustrate potential and realized overlap in thermal space (A, C) and geographic space (B, D). (**A, C**) The fundamental thermal niche is defined by the physiologically-determined maximum (red) and minimum (blue) thermal limits. A species' potential thermal niche is the extreme body temperatures within its fundamental thermal niche that it can experience (given constrained thermoregulatory behaviour) across the available habitat (here defined as the landscape or seascape contiguous with the species' realized range). A species' realized thermal niche is the extreme body temperatures it can experience throughout its realized range. Potential thermal niche limits differ from fundamental thermal limits when temperatures within the fundamental niche are not found in the current climate across the habitat available. (**B, D**) A species' realized range encloses its observed extent of geographic occurrence, while its potential thermal range encloses the areas of available habitat where extreme body temperatures remain within the species' fundamental thermal niche limits. A species might not occur in all available niche space (niche underfilling, panel A; range underfilling, panel B) or might appear to occur beyond the available niche space (niche overfilling, panel C; range overfilling, panel D).
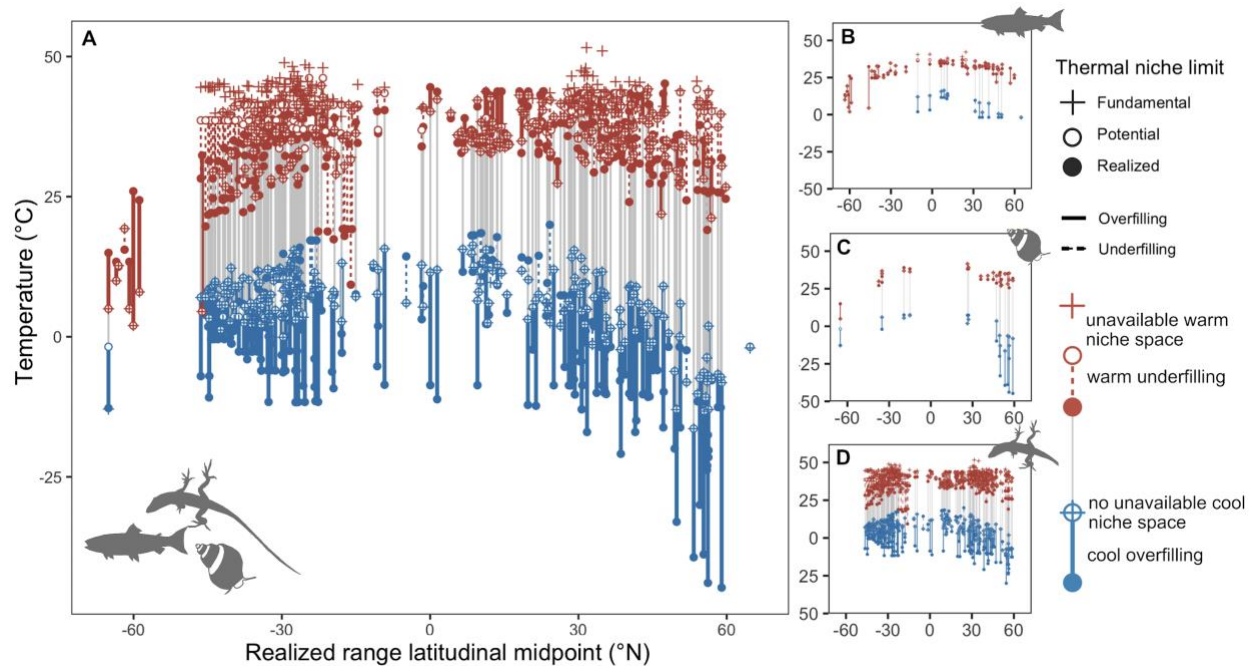

Fig. 2. Species underfill their warm thermal niche and overfill their cool thermal niche.
(**A-D**) Species' fundamental (crosses), realized (solid circles) and potential (open circles) thermal niche limits versus the latitudinal midpoint of their realized range for (A) all realms, and separately for (B) subtidal marine, (C) intertidal marine, and (D) terrestrial species. Warm and cool niche limits are shown in red and blue respectively. Dashed lines connecting the potential and realized niche limits indicate breadth of warm or cool niche underfilling, while thick connecting lines indicate breadth of warm or cool niche overfilling.
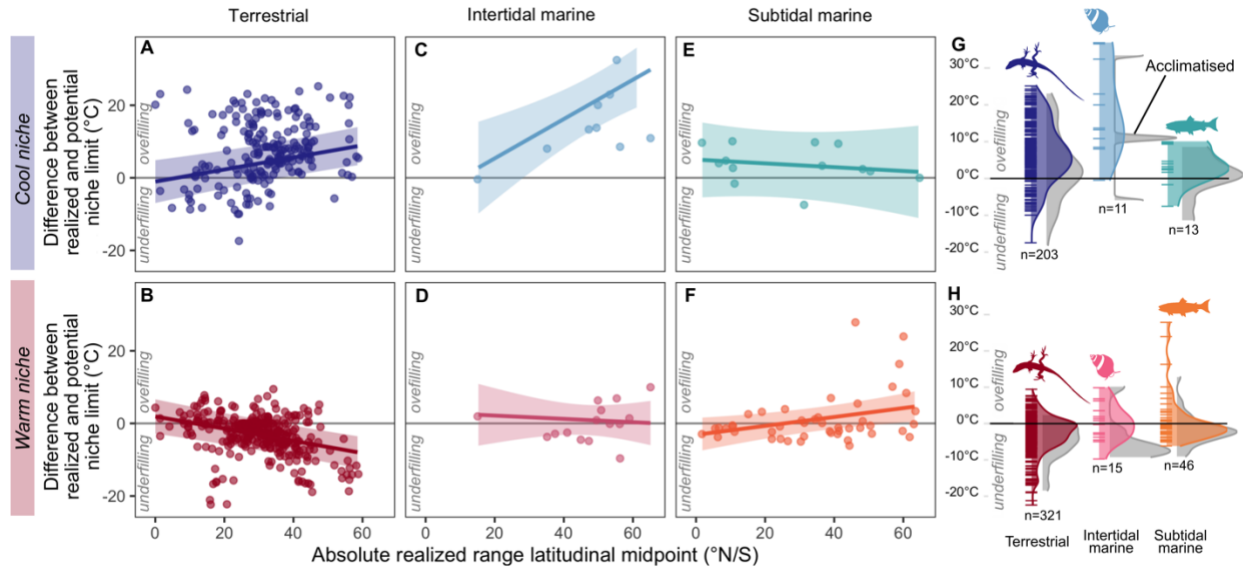
Fig. 3. Warm and cool niche filling vary with the latitude of a species' range, realm, and acclimatisation. (**A-F**) Warm (warm shades, below) and cool (cool shades, above) filling of the potential thermal niche across the absolute latitudinal midpoint of a species' realized range, showing model fitted relationships (lines) and associated confidence intervals (shaded areas) from separate models of warm and cool niche filling as a function of variables in table S1. Each point represents the shortfall (negative, underfilling) or excess (positive, overfilling) of temperatures occupied beyond the potential niche limit at either the warm or cool edge of a species' potential thermal niche. Warm niche underfilling and cool niche overfilling increase with latitude in terrestrial species (A-B), while only cool niche overfilling increases with latitude in intertidal marine species (C). In subtidal species, neither warm nor cool niche filling change with latitude (E-F). (**G-H**) Distribution of warm and cool niche filling measurements across ecological realms with (grey) and without (coloured) simulating acclimatization to the local thermal environment. Sample sizes for acclimatized distributions from left to right, top to bottom are n = 117, n = 5, n = 12, n = 163, n = 8, n = 41.
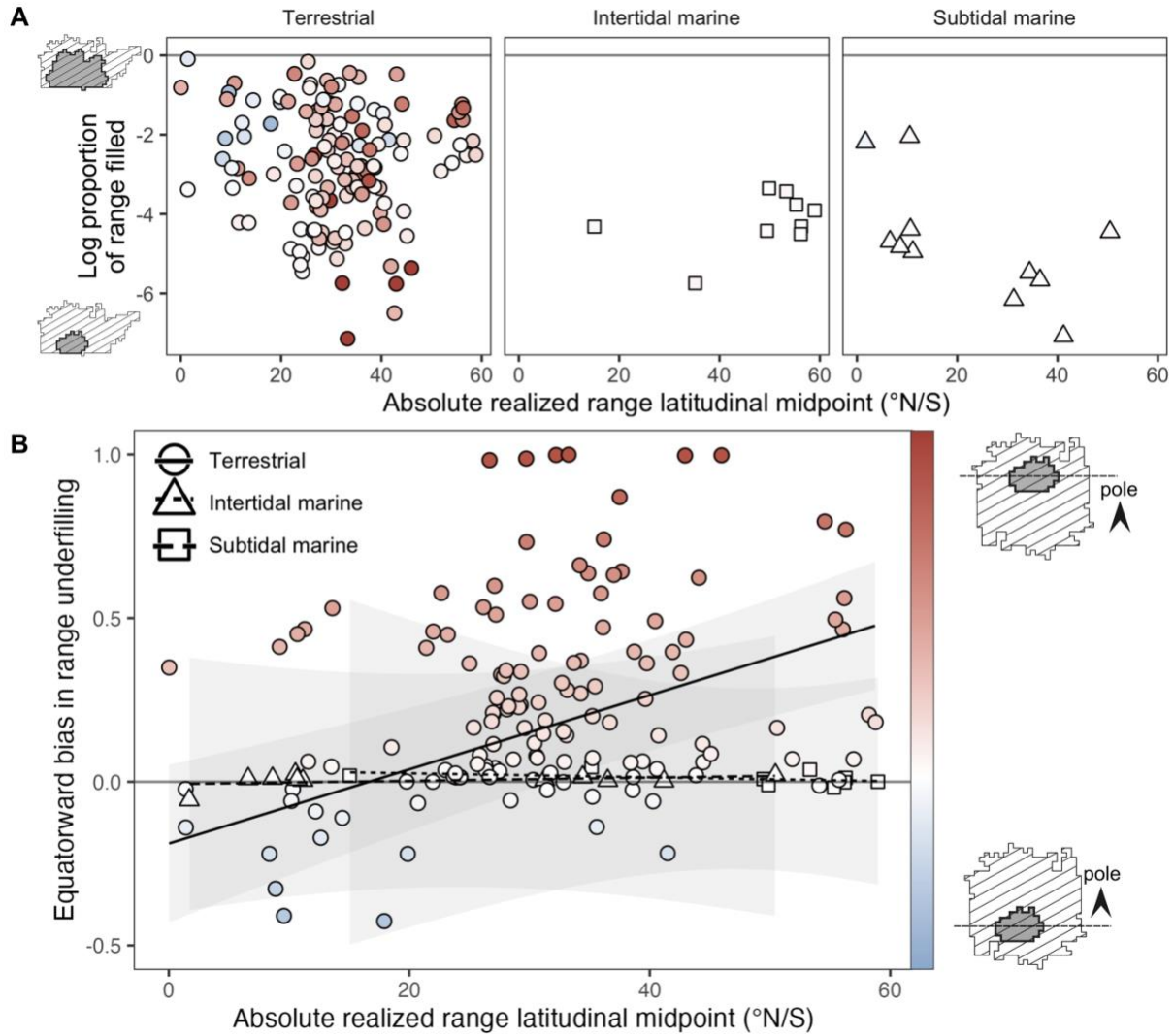
Fig. 4. Range underfilling does not differ among species at different latitudes but is biased towards the equator within species. (**A**) Across all realms (shapes) the proportion of geographic area in the potential thermal range that a species occupies does not change with the absolute latitude of its range. (**B**) Equatorward bias in range underfilling within a species' range (i.e., the difference between the proportion of a species' equatorward and poleward potential range that is underfilled) increases with the absolute latitude of a species' range in terrestrial species. Positive values (red) indicate underfilling is greater in the equatorward range half of a species' range, while negative values (blue) indicate underfilling is greater in its poleward range half. Intertidal and subtidal marine species showed no latitudinal asymmetry in underfilling (white points) at any latitude. Lines show best-fit relationships and shaded areas indicate 95% confidence intervals from the model of equatorward bias in range underfilling as a function of variables in table S1.