

Unifying climate change biology across realms and taxa

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Abstract

A major challenge in modern biology is to understand extinction risk from climate change across all realms. Recent research has revealed that physiological tolerance, behavioral thermoregulation, and small elevation shifts are dominant coping strategies on land, while large-scale latitudinal shifts are more important in the ocean. Freshwater taxa may face the highest global extinction risks. Nevertheless, some species in each realm face similar risks because of shared adaptive, dispersal, or physiological tolerances and abilities. Taking a cross-realm perspective offers unique research opportunities because confounding, physical factors in one realm are often disaggregated in another realm. Cross-realm, across taxa, and other forms of climate-change biology synthesis are needed to advance our understanding of emergent patterns of risk across all life.

The need for cross-realm synthesis

Climate change poses an existential risk to species and ecosystems worldwide [1,2]. While there is broad consensus that the number of species at risk is large [3], there is substantially less consensus about which regions and **realms** (see Glossary) face the greatest risks or how species will cope with ongoing and future changes [4–6]. Terrestrial animals and plants from temperate regions are the most well-studied [7,8], and yet evidence suggests the most vulnerable taxa may lie outside these groups [4,9–11]. Ultimately, there are simply too many species to assess each individually. Instead, there is a need to understand the emergent patterns of climate responses so as to identify broadly analogous conditions across realms and taxa, understand processes of community re-assembly and changing ecosystem function, compare against past biotic upheavals in earth history [12], and guide more targeted conservation efforts.

Recent research has made great strides in understanding some of the similarities and differences among taxa, but there is a need to synthesize this progress in the emerging field of climate change biology (Box 1). Terrestrial, freshwater, and marine realms present fundamentally different physical settings within which species respond to climate change and within which they have evolved substantially different life history strategies (Box 2). We focus here on recent research progress, further research needs, and the benefits of synthesizing across realms and across taxa. Relatively few analyses cross the divisions among the terrestrial, freshwater, and marine realms, and of those that do, most studies focus on single climate change coping mechanisms, e.g., range shifts or adaptive evolution [3,9,10,13–25]. Focusing on single mechanisms leaves the emergent responses, including **extinction risk**, obscured. Because dominant mechanisms can differ across species and across realms, a broad rather than reductionist perspective is needed to understand how and why biodiversity changes in response to climate. Broad perspectives can also reveal unexpected similarities. For instance, if certain tropical montane species face a constellation of risks similar to certain temperate freshwater species, then understanding these parallels could inform strategies to mitigate those risks [2,8]. In an era of increasing scientific specialization, identifying similarities across disconnected research communities is important for innovation and progress [26].

By working from first principles across realms, regions, and species, we provide a conceptual synthesis to inform an understanding of macroscale climate change risks and to support global conservation strategies across all realms. We then identify research needs and changes in research practice to further integrate knowledge across realm boundaries.

Coping with climate change

Attempts to compare climate risk across species have focused on particular and often disparate processes [3,5,6,9,15,27]. Various authors have identified tropical forest [11,28], polar [29], freshwater [30], endemic [31], or tropical reef [32] species as those at great or even the greatest risk for reasons that include low physiological tolerance for warming, loss of climatically suitable habitat, and barriers to dispersal to newly suitable regions. A common framework to reconcile these risks and integrate these processes is important (Fig. 1).

At the **trailing range edge**, a suite of mechanisms allows organisms to cope with environmental changes *in situ* and avoid **extirpation**. Processes that reduce the risk of extirpation range from physiological tolerance to plasticity and evolutionary adaptation [27,33–36]. Behavior and development allow organisms to avoid stressful conditions by altering when and where to be active over the daily or seasonal cycle, including **phenological shifts** by plants and animals [17,37]. Genomic factors like mutation load or inbreeding may make extirpation more likely [35,36].

In contrast, expansion to newly suitable locations at the **leading range edge** is mediated by dispersal and subsequent establishment (Fig. 1). The first step (dispersal), results from both the dispersal ability of an organism and the suitability of the environment through which it disperses. Short-distance dispersal events can allow species to access substantially new microclimates in regions with sharp physical gradients across slope, aspect, or habitat structure, including differences in water stress on north vs. south-facing slopes or across forest-edge to interior [38,39] (Fig. 1). Somewhat more substantial shifts move species along elevation or depth gradients. Long-distance dispersal events are important in allowing

species to access new environments in regions with mild physical gradients, such as latitudinal shifts in terrestrial regions with low topographic variation, and for dispersal among insular habitats [40].

Processes important for *in situ* persistence and for expansion also interact in important ways. For example, plasticity or evolution can generate faster dispersal or establishment [36]. Likewise, adaptation to new biotic or abiotic conditions experienced during range expansion can be important for subsequent establishment [18,41]. Indirect effects mediated through interactions with other species can increase or decrease the risk of range contraction or expansion [42].

The hierarchy of mechanisms illustrated in Fig. 1 and the relative importance of each mechanism is mediated by the interaction between species traits and environments. Together, these response mechanisms determine the manner in which species survive and the relative climate risk they face. Some species, for instance, will tolerate climate change in place, while others will experience **range shifts** to new locations. The spectrum of outcomes is summarized by the relative degree of trailing-edge range contraction and leading-edge range expansion (Fig. 2). The risk, however, may also depend on transient dynamics [43], including temporal lags like **immigration credits** and **extinction debts** [44,45].

Predicting limits to survival in place

Many species cannot persist at the trailing edges of their ranges as climate continues to change (Fig. 1, Fig. 2) [46]. Marine organisms, in particular, appear to have less physiological tolerance for warmer conditions than species in other realms [9], though this sensitivity is offset slightly by greater **thermal plasticity** in marine and freshwater species than in species on land [16] (Fig. 1 and Text S1). On land, species with the most limited physiological tolerance for further warming occur at intermediate latitudes (20-30°), while those in the ocean are found near the equator [9]. Latitudinal patterns in physiological tolerance are more intermediate in freshwater species [10]. The greater habitat heterogeneity on land, in the intertidal zone, and in freshwater (Box 2) also suggest greater opportunities for **behavioral thermoregulation** and moving to nearby microclimate refugia than in fully marine environments (Fig. 1), which may explain the higher frequency and rate of latitudinal contractions in the

ocean than on land [9,14,37]. Despite recent synthesis, it remains unclear the extent to which species across realms can use phenological shifts to persist in place and whether such abilities differ among realms (Fig. 1) [25].

Despite these general differences among realms, at least a few species facing the same types of limits to survival can be found in all realms (Fig. 2, Table S2). Species from more climatically stable environments often lack the physiological tolerance, plasticity, behavioral mechanisms, or standing genetic variation (evolutionary capacity) to cope with ongoing change *in situ*. Theory predicts that evolutionary processes may be most important near the equator, where fewer new and expanding species are likely to emerge as competitors [47] or in marine species with especially large population sizes [48,49]. The thermal heterogeneity of tropical coral reefs and mountainsides may provide corals and alpine plants, respectively, with an important reservoir of standing genetic variation that could allow **evolutionary rescue** [50–52]. However, traits like upper thermal limits appear to have limited evolutionary potential [13,53], and anthropogenic stresses can further reduce evolutionary capacity [54].

An ongoing research challenge is to interpret and understand the ranges that have not contracted. Is the lack of contraction an indication that these species can persist through physiological tolerance, evolution, acclimation, use of microclimate refugia, or amelioration of other stressors (e.g., competition or predation)? Or does apparent stability simply indicate delayed contraction (extinction debt) or insufficient sampling?

Predicting impediments to range expansion

Natural impediments to range shifts and expansion are likely, perhaps counterintuitively, to operate in similar ways across realms (Fig. 2, Table S2), even if the relative frequency of these processes differs substantially (Fig. 1). Insular environments, characterized by physical conditions that vary from regional norms, often have rare or endemic taxa and these species will face similar challenges in range expansion—whether they reside on mountain peaks, in isolated freshwater lakes or marine lakes—as each has species that are unlikely to successfully disperse among these habitats (Box 2). Many species will

likewise be limited by continental or saltwater basin margins. Just as a terrestrial or freshwater species along the continental margin in South Africa cannot disperse southward, a marine species in the Mediterranean Sea cannot directly disperse northward to escape warming conditions [55].

Many species will also be limited by physical or biotic processes that impact propagule dispersal. Marine currents that flow predominately in one direction along a coastline (when propagules are released) will limit the directionality of range shifts in a similar way that animal movements limit range shifts of certain plants (Box 2) [56,57]. The east-west orientation of physical features, such as mountain ranges or coastlines, will also impede poleward shifts or even shift species towards lower latitudes at higher elevations or deeper depths [58,59]. Finally, habitat discontinuities are important across realms, including the absence of rocky habitat amid long stretches of sandy, marine habitat or the absence of upland forest at lower elevations.

In contrast, anthropogenic impediments to dispersal are likely to differ in importance among realms. Species abundance and trophic level have been heavily depleted in many marine ecosystems, but for the most part, the habitat types present historically still occur and there are few anthropogenic barriers to dispersal [21]. In contrast, freshwater environments have been dammed at staggering frequencies, e.g., more than 3,700 dams just in the northeast US [60], each of which blocks the dispersal of some species. In terrestrial environments, large contiguous blocks of anthropogenic habitats (such as agricultural land or urban sprawl) now impede the dispersal of many species (Box 2).

In marine environments, the higher frequency of species with long-distance dispersal abilities and the lower importance of natural and human impediments to dispersal (Box 2) help explain why leading-edge range expansions are more common and of larger magnitude relative to terrestrial and freshwater ones (Fig. 1) [14]. Marine taxa with planktonic dispersal, often allowing for broad and distant colonization, provide a sharp contrast to terrestrial species, like earthworms that shift their distributions by only tens of kilometers over millennia [61]. Dispersal in the freshwater realm is often constrained along dendritic watersheds and dispersal opportunities may be extremely heterogeneous depending on the taxa and physical gradients, e.g., whether riverine systems run north-south vs. east-west. An open

question is whether these differences in dispersal capacity and climate exposure are sufficient to explain observed differences in range edge expansions, or whether additional differences in establishment and subsequent population growth also contribute.

A research agenda for insights across realms

The cross-realm research to date suggests that climate responses may occur at fundamentally different biological scales in different realms. Population-scale range expansions and contractions are better-documented in the ocean, but individual-scale responses through physiological tolerance and behavior are more commonly observed on land (Fig. 1). Understanding the future of global biodiversity will therefore require an integrative approach that links across biological scales from organismal to populations and communities. For which species is individual-scale adaptation sufficient to offset limited expansion of leading edges on land? Are range shifts sufficient for all but polar species in the ocean to offset a lack of persistence *in situ*? How do these processes interact in freshwater? Without this integration, climate biology will remain fragmented and lack the ability to forecast the future of biodiversity on earth.

The differences in observed climate responses across realms (Fig. 1) also raises fundamental questions about how species traits interact with a changing environment. Species across realms have evolved somewhat but not entirely different sets of traits and life histories, shaped in part by the spatial and temporal heterogeneity of each realm. Are these trait differences sufficient to explain the differences in observed climate responses? Or are there other fundamental differences among realms? To date, difficulties in making equivalent comparisons across realms have prevented a clear answer. Answering this question will be critical for building climate biology on a solid foundation of species traits that can be generalized across the tree of life.

Research across realms also provides important advantages, including for ecological synthesis efforts that test macroecological processes. Many environmental factors and species traits are colinear in one realm, making it difficult to untangle causal factors, but are disaggregated in other realms. For

instance, seasonality increases with latitude and with decreasing average temperatures on land, but not in the oceans. Likewise, different types of anthropogenic threats generally coincide on land, but not in the ocean [20]. Trophic level increases with body size in the ocean and freshwater environments, but not in terrestrial ones [22]. Ultimately, by integrating data and analyses across realms, researchers can better identify causal mechanisms and disentangle the factors mediating species' responses to climate change.

The full range of processes (Fig. 1) operate in each realm but, as August Krogh argued in the context of physiology, there is often a particularly convenient study system with which to address each question [62]. When a given process cannot be tractably studied in a given realm, we suggest a modified version of Krogh's principle: cross-realm-inspired studies that leverage advantages from one realm to inform our understanding of another realm. For example, local adaptation and gene flow are vital to understanding how corals respond to climate change [63], but a carefully controlled experiment may be easier to implement in plants with common gardens and reciprocal transplants; the experiment could be designed to mimic coral-like dispersal and other demographic characteristics. Evolution through time may be important in all realms, but most amenable to study in short-lived species [64]. With collaboration to ensure that studies cover the range of conditions relevant across realms, such single-realm studies could provide broad insight.

Towards a unified climate change biology across realms

We believe that there are at least four structural and cultural changes that would enable and facilitate this work. First, although there are special funding calls for research that works across broad disciplines (such as sociology and ecology) and across disciplines within biology (such as ecology and physiology or evolution), there is little effort in many places, such as the USA, to explicitly encourage and fund research that works across silos by taxonomic group (e.g., fishes and plants), regions (e.g., temperate, polar and tropical), or realms (marine, freshwater and terrestrial). Focused funding calls that fostered work across these silos would help overcome the inertia of working across realms, provide a nearly immediate increase in the amount of across-realm work, and improve long-term dialogue among

sub-fields. Second, integration could be facilitated by creating explicit opportunities for cross-silo synthesis and research at the interface between realms at scientific conferences, which currently tend to segregate along subdisciplinary lines. Examples like the International Biogeography Society meetings or the Species on the Move conferences have begun to do this. Third, graduate student training could be broadened to include more across-realm and across-taxonomic group exposure. Approaches for accomplishing this could include field courses that integrate across current silos, as well as a return to the broader natural history training that was common in the past. Fourth, but integrally related to the last point, this unification would be facilitated by changes in academic culture that enable students to invest in the time needed for across-realm (or taxon or region) experience. Our current culture strongly incentivizes immediate specialization and research narrowing, enabling publications to be produced more quickly. While changing this aspect of our current culture would be difficult, it would probably also be the most impactful.

Concluding remarks

As illustrated in this paper, a rapid acceleration of research attention in the last decade has begun to bring key similarities and differences among realms into focus [3,9,10,13,14,16–24]. These emergent patterns contain substantial gaps and uncertainties (Table S1), but also begin to point towards the types of species most at risk from climate change. However, our synthesis also highlights that substantially more research is needed to bridge gaps in understanding between scales of biological organization, among taxonomic groups, and across environmental realms.

Climate change and climate variability impact all levels of biological diversity, from genes to ecosystems. One of the greatest challenges facing scientists now is to understand how these impacts, and responses to those impacts, will scale across levels of biological organization and how the emergent responses will differ across species and ecosystems in all realms on Earth (see Outstanding Questions Box). Developing and fostering the emerging field of climate change biology can help us to meet this

231 challenge, advance our basic understanding of the natural world, and provide the basis needed for making
232 informed decisions about how best to safeguard biological diversity globally.
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Box 1: A need for synthesis in global change biology

We document the need and promise of developing a greater synthesis across realms and taxa, but this effort is illustrative of a broader need for synthesis in climate change biology across a diverse set of axes. Here we provide examples of other areas of climate change biology that would benefit from synthesis.

Within taxon, across realm synthesis – Many taxa, particularly when considered across broader phylogenetic levels, are found in multiple realms. Examples include vascular plants, arthropods, mammals, and others. Leveraging the physical differences among realms (Box 2), while controlling for shared biological characteristics (i.e., of closely related species), offers the potential to identify the relative importance of intrinsic species traits and extrinsic habitat properties in facilitating climate change responses.

Within realm, across region or across taxa synthesis – Much of the existing synthesis in climate change biology has focused at this level, e.g., comparing the rate at which species shift their distribution. However, more work is needed, as we still lack clear answers to basic questions, e.g., which regions of the world will experience the highest extinction rates [3]. Synthesis across biomes (e.g. dispersal-mediated range shifts in deserts vs. tropical rain forests) is largely unaddressed. Here too, differences in the physical setting offer research opportunities and points of leverage for increased understanding.

Across time responses – Integrating biological responses to changes in climate across different time scales is another topic that would benefit from synthesis. For instance, how the relative importance of processes illustrated in Fig. 1 varies across disparate time scales, from geological to contemporary, is not well understood [65,66]. Basic, albeit counterintuitive questions, like when might evolutionary rescue operate more quickly than dispersal-mediated range shifts, haven't been placed into a synthetic framework – one that can guide subsequent inquiry and contextualize existing knowledge.

256 Function across novel to historic ecosystems – As climate changes drive changes in the composition of
257 species assemblages, there is increasing need for synthesis across ecosystem functions. Is there a
258 predictable sign or magnitude of change for ecosystem functioning of increasingly novel assemblages?
259 Do novel ecosystems composed primarily of species that have shifted their distributions in response to
260 climate change differ in functioning from novel assemblages dominated by inter-continental invaders?
261 Answering these and related questions pose tremendous opportunities to advance the field of climate
262 change biology.

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Box 2: Differing physical characteristics across realms

Differences in the physical characteristics and structural properties of each realm influence how organisms are exposed to and respond to climate change (Fig. I). Air has a quarter the heat capacity, twenty-three times lower thermal conductivity, and dramatically higher transparency to solar radiation than water, which creates an environment on land with much greater exposure to high frequency thermal variability through time and space than in the water [67,68]. These differences in thermal variability influence the evolution of physiological tolerance and plasticity [16,69] and also create much faster rates of isotherm shifts in the ocean than on land [70,71]. The higher habitat and thermal heterogeneity in terrestrial and, to a lesser extent, freshwater systems compared to their less heterogeneous marine counterparts also provides more opportunities to persist in place through behavioral thermoregulation and shifts to nearby climate refugia [48] (Fig. I A-C). However, these differences in fluid media among realms also introduce stressors that can interact synergistically with temperature, including precipitation on land (where water is scarce) or acidification and deoxygenation in aquatic environments (where oxygen is scarce).

Habitat dimensionality—such as the surface of terrestrial ecosystems, dendritic river networks, and three-dimensional environments in oceans—delimit how organisms can redistribute to track changing climatic conditions (Fig. I D-F). On land, species can track shifting climates by moving upward, poleward, or a combination of both as dictated by the underlying topography [72]. Similarly, marine species can move deeper rather than latitudinally, especially in regions with strong temperature gradients, though in ways not as limited by topography [73]. In contrast, redistribution in fresh waters is more likely to be constrained by network structure and the availability of upstream habitat [74].

Habitat directionality that arises from atmospheric winds, stream flows and ocean currents restricts movement patterns that can facilitate or inhibit species capacity to track shifting climates [75] (Fig. I G-I). The higher degree of anthropogenic habitat fragmentation in terrestrial and freshwater systems reduces dispersal opportunities [76], whereas human activities in the ocean (especially

overfishing) erode species ability to persist in place and reduce biotic barriers to colonization and establishment [54,77] (Fig. I J-L).

Some organisms inhabit multiple realms, including certain aquatic insects, intertidal organisms with sessile adults, and diadromous species. These species often move between realms during developmental transitions in complex life cycles, exposing them to stressors and limits in each environment. These transitions may impose a form of double jeopardy, putting these species at particularly high risk of extinction. Alternatively, cross-realm transitions may provide opportunities for escape from stressful climate conditions and opportunities to mitigate the dispersal limitations imposed by individual realms. Either way, understanding the realms in which these species reach limits to survival may provide greater insight into cross-realm differences in climate vulnerability.

303 **Glossary**

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305 **Behavioral thermoregulation:** behavioral adjustments to regulate body temperature (e.g., to minimize
306 climate exposure) by capitalizing on accessible microhabitats, modifying activity periods, and adopting
307 different thermo- and environmental stress-regulatory strategies.

308 **Immigration credit:** time lags in colonization events after an environmental change (e.g., in climate),
309 resulting in delayed shift or expansion of a species range into areas that are newly suitable.

310 **Extinction debt:** time lags in extirpation events after an environmental change (e.g., in climate), resulting
311 in delayed loss of populations and range contraction from areas that are newly unsuitable.

312 **Extinction risk:** likelihood of a species going globally extinct throughout all of its range within the
313 foreseeable future.

314 **Extirpation:** local extinction of a species at a particular geographic location within its range.

315 **Evolutionary rescue:** genetic adaptation that allows the recovery and persistence of a population under
316 otherwise unsuitable conditions.

317 **Leading range edge:** current limit of species distribution (often coldest) where populations are expanding
318 into increasingly suitable habitats under climate change.

319 **Phenological shifts:** changes in the timing of life-history events, including timing of migration or
320 reproduction.

321 **Range shifts:** changes in the distribution limits of a species, often along altitudinal, latitudinal or depth
322 gradients.

323 **Realm:** a broad classification of biological environments, used here in the sense of marine, terrestrial, or
324 freshwater environments.

325 **Thermal plasticity:** phenotypic changes in response to changes in climate that allow organisms to rapidly
326 adjust their thermal tolerance without evolutionary change.

327 **Trailing range edge:** current limit of species distribution (often warmest) where populations are
328 contracting from increasingly unsuitable habitats under climate change.

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Figure Legends

Figure 1. Hierarchy of climate change coping mechanisms within species. Species cope with climate change and variability through a hierarchy of processes across scales of time and space, from the physiology and behavior of individual organisms to the spatial dynamics and evolution of populations and species. The relative importance of different mechanisms for coping with changing climates differ on average across terrestrial, freshwater, and marine realms (as represented by the size of the icons), resulting in differences in the overall degree of trailing edge persistence, leading edge expansion, and, ultimately, species survival. Relative positions of the different mechanisms and ratings were based on existing literature to represent broad patterns and do not apply to all species. Confidence in the relative ratings (as represented by the degree of transparency) indicates our qualitative assessment of the degree of support from the scientific literature (see also Text S1 and Table S1 for references).

Figure 2. Climate change consequences for species survival. Response to climate change and implications for global extinction risk, expressed as the relative rates of leading edge expansion and trailing edge contraction. These spatio-temporal dynamics lead to divergent outcomes for species survival and some species in each realm are likely to fall in each category. (i) Species likely to adapt in place have limited dispersal ability/opportunity and broad climatic tolerance/adaptive capacity such as Osage orange (*Maclura pomifera*), *Daphnia spp.*, and spiny chromis (*Acanthochromis polyacanthus*). (ii) Species likely to expand their range have high dispersal capacity and expanding climatically suitable habitat such as bark beetles, smallmouth bass (*Micropterus dolomieu*), and parrotfish (Scaridae). (iii) Species likely to contract their range are locally distributed, climate sensitive, and have limited adaptive capacity and dispersal capacity such as montane tropical epiphytes, freshwater mussels, and *Acropora* coral. (iv) Species likely to shift to new locations have high dispersal capacity and are sensitive to climate such as many butterflies, aquatic pondweeds, and black sea bass (*Centropristis striata*). See Table S2 for details and Table S3 for photo credits.

522 **Fig. I. Environmental differences across realms set the stage for different climate change responses.**

523 Realms differ substantially in the habitat heterogeneity, dimensionality, directionality, and human
524 impacts, which together influence how organisms persist and redistribute in response to variation and
525 change in climate. See [Table S4](#) for photo credits.

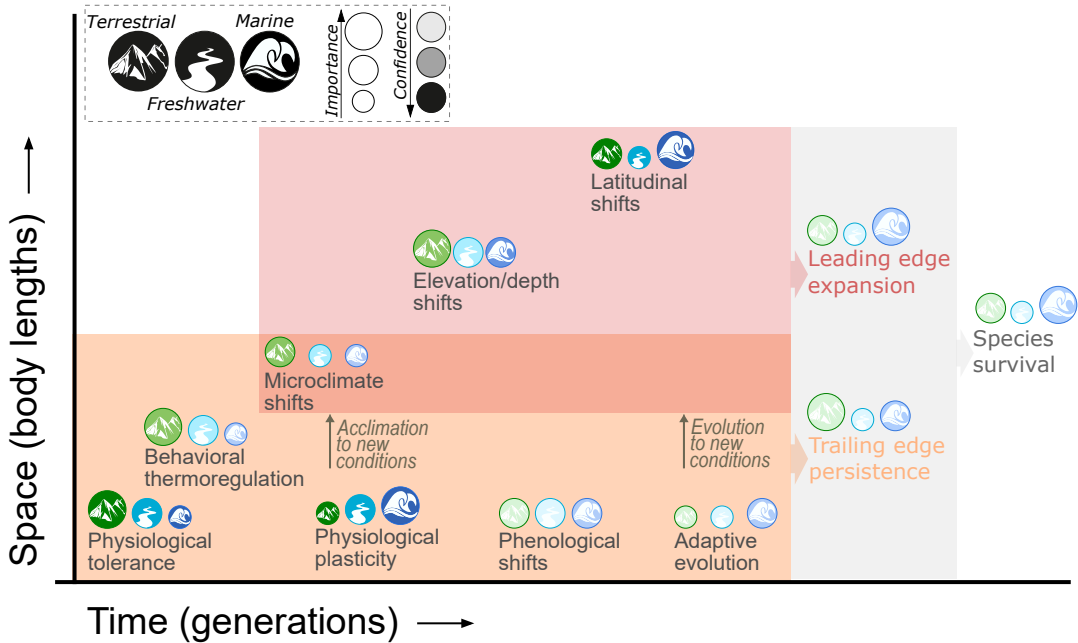
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Highlights

- An integrated perspective crossing terrestrial, freshwater, and marine realms is essential to understand where and why species are most vulnerable to climate change.
- The dominant eco-evolutionary processes for coping with climate change differ across realms.
- Cross-taxa and cross-realm research can provide unique insights and opportunities to advance our understanding of the processes and mechanisms threatening species survival.
- Academic culture and practice often impedes cross-realm research, such that structural and cultural transitions are needed to advance a more unified field of climate change biology.

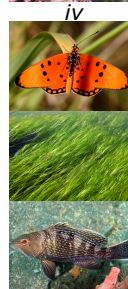
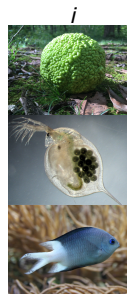
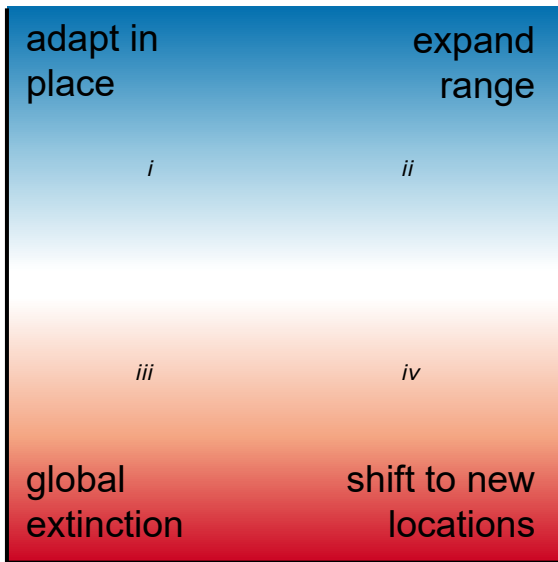
Box -- Outstanding research questions

- To what extent does climate-related extinction risk differ across terrestrial, freshwater, and marine realms?
- To what extent do species that live across multiple realms or at the interfaces between realms face amplified or mitigated extinction risk from climate change?
- How do indirect climate change effects through altered biotic interactions affect species climate responses across realms?
- In which realms and taxa do immigration credits and extinction debts manifest most strongly?
- Can species traits explain differences in range shifts across taxa and realms?
- How does the role of adaptive evolution to climate change differ across realms?
- When do stationary trailing edges indicate successful adaptation to novel conditions?
- Do non-climatic human impacts interact with climate change similarly or differently across realms?
- Do species range shifts scale up similarly across realms to affect community reorganization, macroecological biodiversity patterns, and ecosystem function?



Trailing edge contraction

Adaptive capacity
and tolerance

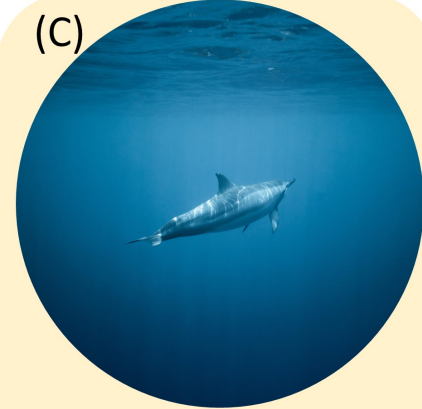
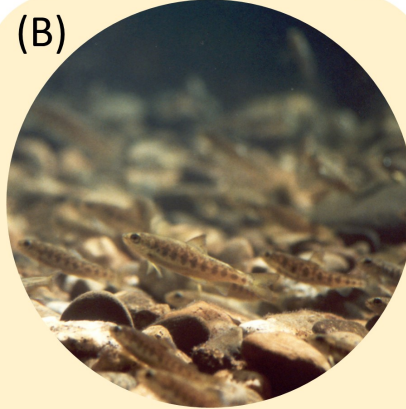
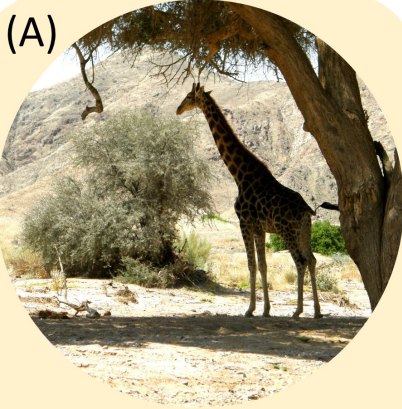


Terrestrial

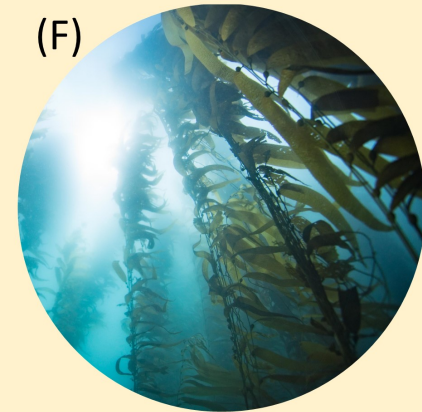
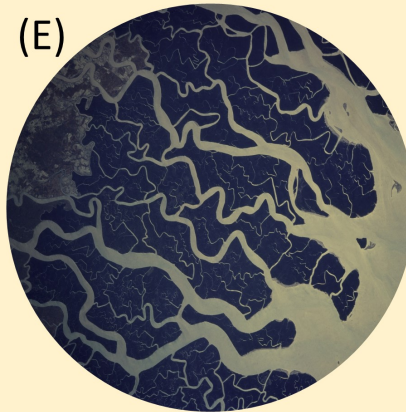
Freshwater

Marine

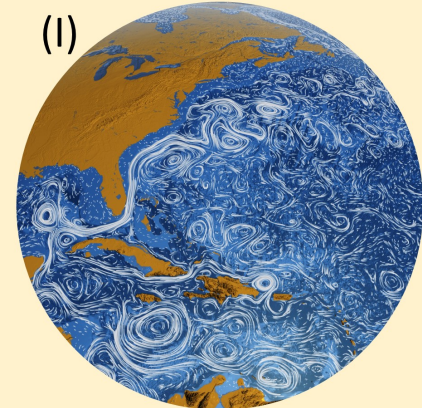
Habitat
heterogeneity



Habitat
dimensionality



Habitat
directionality



Human
impacts



Supplementary Material

Unifying climate change biology across realms and taxa

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Text S1: Climate change response comparisons across realms

The last decade has seen a rapid increase in cross-realm studies, providing key insights into the mechanisms by which species are exposed and respond to climate change (Fig. 1, Table S1). For instance, a comparison of climate change velocity across realms over recent decades revealed uneven climate exposure due to fundamental differences in the physical characteristics and structural properties of each realm [S1]. Even though temperature trends have been twice as fast on land as compared to aquatic systems due to the higher heat capacity of water, the velocity of climate change was higher in the ocean than in inland standing waters or over land because spatial temperature gradients were three times less pronounced in the ocean. This velocity difference suggests that marine species will have to move greater distances to follow isotherm shifts. In addition, lower dispersal opportunities for freshwater and terrestrial species (due to a combination of natural and human-induced fragmentation) may impede their redistribution, especially for species with poor dispersal abilities [S2,S3].

Differences in habitat heterogeneity among realms also create important differences in climate responses. Habitat heterogeneity is higher on land, where differences between air and near-surface (sub-canopy) air temperature can be as high as 25°C [S4]. This heterogeneity also makes behavioral thermoregulation a more important potential mechanism for terrestrial species to cope with current and future climatic conditions as compared to marine species [S5,S6]. Similarly, microclimatic refugia providing cooler and more stable thermal regimes are likely to be more readily available on land, especially in forested landscapes with sharp topographic gradients [S7], where they could both enhance trailing edge persistence (‘holdouts’ *sensu* [S8]) and leading edge expansion (‘stepping stones’ *sensu* [S8]) [S9–S11]. Nonetheless, bathymetric range shifts in the ocean can, to a certain degree, offer alternatives to long-distance latitudinal shifts, especially in regions with strong temperature gradients [S12,S13].

In the freshwater realm, the degree of thermal heterogeneity (and thus the potential for behavioral thermoregulation) is expected to be intermediate between that of terrestrial and marine systems but varies in complex ways across scales of space and time from the interplay between topography, stream channel complexity, and groundwater inputs [S14]. Tributaries can also represent important short-distance microclimatic refugia for some species that allow persistence under deteriorating climatic conditions or provide slower climate velocity pathways that facilitate redistribution [S2]. Understanding the emerging spatio-temporal complexity of microclimate and thermal exposure across realms and their implications for

future biodiversity responses under changing climates represent important avenues for future research [S15].

Beyond environmental differences, macro-physiological studies have also helped uncover striking differences and similarities regarding the spatial variation and evolution of thermal sensitivity across realms. Notably, large-scale patterns in thermal tolerance have repeatedly shown a near-invariance of heat tolerance with latitude in terrestrial species (both plants and animals), but a steeper decline for freshwater and especially marine species towards the poles [S16–S19]. Although primarily generated from the study of ectothermic animals, these findings point to the key role of environmental variability in shaping the evolution of thermal tolerance, where the spatial variability in thermal tolerance broadly reflects spatial variation in thermal extremes [S18]. However, spatial differences in climate extremes are generally larger than spatial differences in thermal tolerance, such that species live closer to their thermal limits at mid-latitudes on land and in the tropics in the ocean [S6,S20]. Freshwater systems have more variable and intermediate patterns [S21]. Further accounting for the availability of thermal refugia (e.g., shaded habitats on land or deeper waters in the ocean) revealed that marine ectotherms live on average 20% closer to their thermal limits than do their terrestrial counterparts [S6]. Despite some inherent limitations of thermal vulnerability indices [S22], these results suggest that species in the ocean may be more sensitive to future temperature increases, especially in the tropics where populations currently display narrower thermal safety margins.

By contrast, examining plasticity of heat tolerance across realms indicates that thermal plasticity is about twice as high for marine, and albeit to a lesser extent freshwater, than terrestrial species, but with no clear spatial patterns [S23]. These differences among realms presumably result from the comparatively higher potential for thermoregulation in terrestrial habitats, which creates lower selection pressure on the evolution of thermal plasticity (the Bogert Effect). Nonetheless, Gunderson et al. [S23] also demonstrated an overall limited acclimation ability among all ectotherms, indicating that plasticity alone will be unlikely to be a primary mechanism for species to cope with climate change, even in the most plastic marine groups. Interestingly, a recent meta-analysis of intraspecific thermal plasticity in ectotherms demonstrated that substantial variation in thermal acclimation capacity also exists within species, where populations with the highest heat tolerance display the lowest plasticity [S24]. The same study did not find any appreciable differences among realms [S24].

Theoretical models and experiments also suggest that evolutionary adaptations may enhance persistence and redistribution under changing climates; however, the potential for thermal adaptation is still unknown for most species in the context of variable natural environments [S25]. The often high standing genetic variation and large effective population sizes in marine species might provide the potential for evolutionary rescue in the ocean [S26,S27], though freshwater fishes have even higher diversity if between-population diversity is included [S28]. However, the high degree of phylogenetic conservatism and lower tempo of evolution in heat as compared to cold tolerance also suggests the existence of physiological constraints on the evolution of upper thermal limits and limited scope for further evolutionary adaptation across all realms and major life forms [S17,S29]. Further investigating these evolutionary constraints as well as the role of behavioral thermoregulation and thermal plasticity are needed to more accurately predict the consequences of climate change on species persistence.

Beyond differences in thermal exposure and sensitivity, cross-realm studies have advanced our understanding of the geography and taxonomy of biodiversity responses to ongoing climate change. For instance, shifts in phenology (seasonal timing of ecological events) have now been documented for a wide variety of species and habitats [S30–S32], and although the pace of shifting climates suggests a faster

shift in the seasonal timing of temperatures in the ocean than on land [S33], evidence to date suggests that phenological shifts are more variable across taxonomic groups than across realms [S34,S35]. There is also some indication that mismatches in thermal sensitivity and phenological shifts among interacting species may greatly influence species responses to climate change in all realms, especially in higher trophic level species (see [S36] for a comparison between terrestrial and freshwater species). However, these indirect effects resulting from altered biotic interactions are still poorly understood and deserve further examinations [S37,S38].

Numerous studies have also reported shifts in the distribution ranges of species in response to climate change that result from trailing edge contractions and leading edge expansions along latitudinal, elevation and depth gradients [S39]. Re-analysis of these climate-induced range shifts reveals that extirpations at the trailing edge of species distributions are more common in freshwater relative to marine and terrestrial species [S40] and are almost six times faster in the ocean than on land [S41]. These findings are consistent with overall faster declines in freshwater biodiversity than are observed in marine or terrestrial systems [S42] and with the greater thermal conformity of marine than terrestrial species [S43].

Patterns are similar at the leading edge of species distributions, where marine species follow isotherm shifts more closely than their terrestrial counterparts [S41]. This pattern is consistent with higher dispersal constraints on land, where human activities can strongly affect dispersal by altering the amount and distribution of habitats [S3]. Although evidence is very limited to date (e.g., [S44] reported broadly comparable magnitude of northern latitudinal shifts for terrestrial and freshwater groups in Britain), we hypothesize that habitat fragmentation may be an even stronger impediment to leading edge range expansions in the freshwater realm.

Because of these constraints, freshwater species may face on average a higher risk of extinction from climate change, displaying both a low ability to persist in place and to move in space. Extinction risk may be comparatively lower in the marine realm, where faster rates of colonization at the leading edge may at least partially compensate for the extirpations occurring at the trailing edge, except at the poles where further expansion is not possible [S45] or in rare, insular marine habitats like marine lakes [S46].

Despite the broad base of studies across hundreds of species and geographic locations, substantial gaps in knowledge persist in our understanding of species responses to climate change across realms. Comparison methods remain relatively rudimentary for cross-realm comparisons, lacking the sophistication possible with detailed single-taxon studies. In addition, sampling across regions and realms remains highly uneven. All of these limitations impede our understanding of the relative importance of different coping mechanisms across realms and thus call for urgent research attention.

Table S1. Climate change responses differ across realms. Table to complement Fig. 1. The relative importance of different mechanisms for coping with changing climates differ on average across terrestrial, freshwater, and marine realms. In the table, +++ represents a mechanism that is relatively more available, while + represents mechanisms least available to species within a realm. Ratings were chosen to represent broad patterns and do not apply to all species. Confidence indicates our qualitative assessment of the degree of support from the scientific literature for the relative ratings.

Consequence	Mechanism	Terrestrial	Freshwater	Marine	Confidence	References
Greater trailing edge persistence		+++	+	++	Low	[S40,S41]
	Physiological tolerance	+++	++	+	High	[S6,S18,S21]
	Plasticity	+	++	+++	High	[S23]
	Behavioral thermoregulation	+++	++	+	Medium	[S6,S12,S23,S47]
	Phenological shifts	++	++	++	Low	[S34,S35]
	Shifts among microclimates	++	+	+	Medium	
	Adaptive evolution	+	+	++	Low	[S27,S29]
Greater leading edge expansion		++	+	+++	Low	[S41]
	Elevation or depth shifts	+++	++	++	Medium	[S41,S48]
	Latitudinal shifts	++	+	+++	High	[S41]
Species survival		++	+	+++	Low	

Table S2. Examples of climate change responses across realms. Examples of species that fit each projected climate change outcome from Fig. 2.

Projected Outcome	Key Mechanism(s)	Terrestrial Example	Marine Example	Freshwater Example	Climate tolerance or adaptive capacity	Dispersal
Adapt in place (without expansion)	Limited dispersal ability or opportunity; broad climatic tolerance or adaptive ability	Osage orange (<i>Maclura pomifera</i>)	Spiny chromis (<i>Acanthochromis polyacanthus</i>)	<i>Daphnia spp.</i>	high	low
Expand distribution	High dispersal ability and expanding climatically suitable habitat	Bark beetles (Scolytinae)	Parrotfish (Scaridae)	Smallmouth bass (<i>Micropterus dolomieu</i>)	medium to high	high
Shift distribution	High dispersal capacity and sensitive to climate	Various butterfly species (Lepidoptera)	Black sea bass (<i>Centropristis striata</i>)	Aquatic pondweed	low or uncertain	high
Contract distribution/ Extinction	Locally distributed, climate sensitive, limited adaptive capacity and dispersal capacity	Tropical, montane epiphytes	<i>Acropora</i> coral	Freshwater mussels (Bivalvia)	low	low

Table S3. Credits for photos in Fig. 2.

Picture	Name	URL	License	Credit
(i)	Osage orange (<i>Maclura pomifera</i>)	https://www.flickr.com/photos/vastateparksstaff/32499331354	CC BY 2.0	Virginia State Parks / flickr
	<i>Daphnia magna</i>	https://commons.wikimedia.org/wiki/File:Daphnia_magna_asexual.jpg	CC BY-SA 4.0	Dieter Ebert/Wikimedia Commons
	Tropical fish	https://www.flickr.com/photos/74504731@N00/3355351945	CC BY 2.0	Nikita / flickr
(ii)	European spruce bark beetle (<i>Ips typographus</i>)	https://en.wikipedia.org/wiki/Dendroctonus_micans#/media/File:Dendroctonus_micans_(21931043154).jpg	CC BY-SA 2.0	Gilles San Martin / Wikimedia Commons
	Smallmouth Bass (<i>Micropterus dolomieu</i>)	https://en.wikipedia.org/wiki/Smallmouth_bass#/media/File:Detailed_underwater_photo_of_smallmouth_bass_fish_micropterus_dolomieu.jpg	CC0 Public Domain	Engbretson Eric / Wikimedia Commons
	<i>Cetoscarus bicolor</i>	https://upload.wikimedia.org/wikipedia/commons/d/dd/Bicolor_parrotfish.JPG	CC BY-SA 3.0	Richard Ling / Wikimedia Commons
(iii)	Epiphytes (Dominica)	https://en.wikipedia.org/wiki/Epiphyte#/media/File:Epiphytes_(Dominica).jpg	CC BY-SA 3.0	Hans Hillewaert / Wikimedia Commons
	Freshwater pearl mussel	https://en.wikipedia.org/wiki/Freshwater_pearl_mussel#/media/File:Group of Margaritifera margaritifera.jpg	CC BY-SA 3.0	Boldie / Wikimedia Commons
	<i>Acropora</i> (Acroporidae)	https://en.wikipedia.org/wiki/Acropora#/media/File:Acropora_coral_reefs.jpg	CC0 Public Domain	NOAA / Wikimedia Commons
(iv)	<i>Acraea acrita</i>	https://en.wikipedia.org/wiki/Acraea_(butterfly)#/media/File:Acraea_acrita_male.jpg	CC0 Public Domain	Dominique Bernaud / Wikimedia Commons
	Vue subaquatique de la rivière La course à Estrée Potamot pectiné	https://commons.wikimedia.org/wiki/File:Vue_subaquatique_de_la_riviere%20La_course_%20Estr%C3%A9e_Potamot_pectin%C3%A9_2017.jpg#/media/File:Vue_subaquatique_de_la_riviere%20La_course_%20Estr%C3%A9e_Potamot_pectin%C3%A9_2017.jpg	CC BY-SA 4.0	Lamiot / Wikimedia Commons
	Black Sea Bass (<i>Centropristis striata</i>)	https://www.flickr.com/photos/mentalblock/34700700461	CC BY-NC-SA 2.0	Kevin Bryant / flickr

Table S4. Credits for photos in Box 2, Fig. I.

Picture	Name	URL	License	Credit
(a)	Giraffe (<i>Giraffa</i>) and Oryx (<i>Oryx</i>)	https://www.publicdomainpictures.net/en/view-image.php?image=46025&picture=giraffe-and-oryx-under-tree	CC0 Public Domain	Lilla Frerichs
(b)	Atlantic salmon (<i>Salmo salar</i>)	https://www.flickr.com/photos/usfwsnortheast/5198591082/in/photostream	CC0 Public Domain	E. Peter Steenstra/USFWS / flickr
(c)		https://www.piqsels.com/en/public-domain-photo-zvqwa	CC0 Public Domain	--
(d)	Kilimanjaro from Amboseli	https://commons.wikimedia.org/wiki/File:Kilimanjaro from Amboseli.jpg	CC BY-SA 4.0	Sergey Pesterev / Wikimedia Commons
(e)	Ganges River Delta	https://www.flickr.com/photos/nasamarshall/14610275771	CC BY-NC 2.0	NASA's Marshall Space Flight Center / flickr
(f)	Fish Sounds - Kelp Forest	https://www.flickr.com/photos/caseagrants/46267906622	CC BY 2.0	Camille Pagniello / flickr
(g)	Windblown trees, Humphrey Head, UK	https://en.wikipedia.org/wiki/File:Windblown trees, Humphrey Head - geograph.org.uk - 48659.jpg	CC BY-SA 2.0	Dave Dunford / Wikimedia Commons
(h)	Mexico Agua Azul Cascades	https://www.needpix.com/photo/607726/mexico-agua-azul-cascades-rapids-water-river-waterfalls-yellow-sandstone-water-courses	CC0 Public Domain	DEZALB / Pixabay
(i)	Perpetual Ocean	https://www.nasa.gov/topics/earth/features/perpetual-ocean.html	May use NASA content without needing explicit permission	Scientific Visualization Studio at NASA's Goddard Space Flight Center
(j)	Shanghai interchange	https://unsplash.com/photos/7nrsVjvALnA	Free to use under the Unsplash License	Jeremy Bishop / Unsplash
(k)	Glen Canyon Dam AZ	https://commons.wikimedia.org/wiki/File:Glen Canyon Dam AZ.jpg	CC BY-SA 4.0	Justjeffaz (Jeff Brunton) / Wikimedia Commons
(l)	Crab boat working the North Sea	https://en.wikipedia.org/wiki/Fishing_vessel#/media/File:Krabbenkutter Ivonne Pellworm P5242390jm.JPG	CC BY-SA 2.0 de	Joachim Müllerchen / Wikimedia Commons

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