TITLE

Reimagining species on the move across space and time

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ABSTRACT

Climate change is already leaving a broad footprint of impacts on biodiversity, from an individual caterpillar emerging earlier in spring to an entire plant community migrating poleward. Despite the various modes of how species are on the move, we primarily document shifting species along only one gradient (e.g., latitude or phenology) and along one dimension (space or time). Here we present a unifying framework for integrating the study of species on the move over space and time and from micro to macro scales. Future conservation planning and natural resource management will depend on our ability to use this framework to improve understanding, attribution, and prediction of species on the move.

HIGHLIGHTS

- Distributional shifts and phenological trends are hallmarks of contemporary climate change, yet these responses are generally considered in isolation of one another.
- Our pervasive inability to accurately predict climate change responses may result from the failure to consider that organisms have multiple pathways to climate-driven redistribution that can occur simultaneously.
- We advocate a more holistic approach that appraises how organisms are shifting along multiple spatiotemporal gradients simultaneously.
- Such an approach has the potential to reveal more complete climate tracking and could pave the way to more accurate projections of "species on the move" into the future.

OUTSTANDING QUESTIONS

1. Can more fully accounting for the thermal gradients available to species at various temporal and spatial scales enhance our understanding of species on the move?
2. Will reimagining species on the move resolve outstanding issues in global change biology such as the chronically low predictive power of species traits?
3. How will this novel framework reshape our management of species on the move?

INTRODUCTION

Climate change is having diverse impacts on ecosystems, from birds shifting to higher elevations to bud bursting earlier and earlier each year [1–3]. These various phenomena occur across a broad range of spatial and temporal scales, and are typically recorded as **range shifts** or **phenological shifts** (see **Glossary**). Collectively, species that are shifting their spatial distributions and/or timing of behavior and life history in response to climate change have come to be known as **species on the move** (SOTM). These phenomena have profound consequences for humanity and the natural world. Natural resource management must now address species shifting in and out of protected areas or across management boundaries, and human societies may lose species of cultural or economic importance or be exposed to novel species or diseases [4].

Detecting SOTM, attributing their shifts to human impacts, and predicting their future dynamics is a key challenge for ecology in the Anthropocene [5]. This challenge is magnified by the complexity of studying range and phenological shifts at multiple scales. Yet, the studies that have confronted this complexity have typically found greater insight into species' responses to climate change. For example, Nearctic birds have shifted spatial distributions and breeding phenology, but have tracked temperatures more through phenological shifts [6], while in Lepidoptera, species that have shifted both their ranges and phenology have shown more resilient population trends [7].

These promising studies aside, scientists primarily document shifting species by focusing on only a single temperature **gradient** (e.g., seasonal phenology or latitude) along one **dimension** (space or time). A pervasive inability to accurately predict the magnitude and/or direction of species shifts remains [5], despite extensive methodological improvements [8–10] including sampling advances and the incorporation of **biotic interactions** and **dispersal limitations**. We contend that, to make progress toward understanding and forecasting SOTM, we must embrace the idea that species' responses to climate change are happening simultaneously across multiple spatial and temporal gradients and at different **scales**. This represents a paradigm shift in how SOTM are monitored, modeled, and managed.

To achieve this paradigm shift, we develop a conceptual framework (Fig. 1) of responses to directional climate change where organisms can shift simultaneously along two dimensions – space and time – and along multiple thermal gradients that exist at various scales, from macro to micro. We base this framework on temperature because temperature changes due to climate change are more uniform and predictable than other changes (e.g., precipitation regimes [11]) and because thermal gradients are ubiquitous and diverse across the land, sea, inland waters, and sky. Yet, we acknowledge the fundamental importance of other components of species' niches (e.g., rainfall, biotic interactions) and hope that our framework can be applied to other abiotic gradients (e.g., oxygen, humidity, pH, etc.). Unified, this framework can lead us to a more holistic and accurate understanding of how species are, or are not, on the move.

A UNIFYING FRAMEWORK FOR SHIFTING SPECIES

The **thermal niche** is a fundamental component of species' Grinnellian niche, a range of temperatures in which a species can survive and reproduce [12]. In a warming world, we expect species to shift in order to conserve their thermal niche, but they can only do so if there are thermal gradients along which they can shift. Critically, there exists a multitude of thermal gradients at various spatial and temporal scales along which species could shift (Fig. 1), but we need to examine these potential avenues for shifting if we are to properly quantify SOTM.

To better illustrate our framework, imagine a canopy-dwelling frog species in a warming world. Long-term occurrence data might be used to detect a latitudinal range shift toward the poles; yet this range shift lags behind changing isotherms, suggesting the species is incompletely tracking climate change. Concurrently, a separate study might find that this frog is failing to also shift upslope in elevation despite marked warming. Yet another project might note that these frogs are shifting in time by advancing their breeding phenology earlier in the year when the weather is cooler. Additional studies of this species on other gradients may produce new, independent interpretations of whether the frog is tracking climate change or not. While these responses may seem disparate and inconsistent when studied in isolation, when placed together in context, a simple truth emerges: the frog is maintaining its niche within a complex, dynamic, hierarchically-nested thermal environment.

Here, we define two dimensions through which species can shift: space and time (Fig. 1). For each of these dimensions there exists multiple thermal gradients that occur at different scales. In space, latitude is the largest thermal gradient, stretching from the equator to the poles. Elevation (on land) and depth (in water) provide thermal gradients at intermediate scales while, at small scales there are thermal gradients in **microhabitat**, such as from canopy to forest floor

[13], down into soil, or within kelp forests. Temporally, temperature fluctuates in multi-annual cycles, across seasons, and across the day, all of which provide thermal gradients for changes in activity or development.

Seen within a two-dimensional, multiscale framework of potential temperature tracking, single-gradient studies may not accurately represent how well species are successfully adapting to climate change. Thus, assigning shifts as "lagging", "counter-intuitive", or "individualistic" [14–17] may not represent nature itself, but rather a limitation of how climate change impacts have been studied so far. To move beyond this myopia, we need to study species across multiple dimensions and along gradients at multiple scales (Fig. 2, [6]).

THE AVAILABILITY AND RELEVANCE OF DIFFERENT THERMAL GRADIENTS

Despite the potential for organisms to shift in multiple ways, the availability of different thermal gradients varies across the globe (Fig. 2). At large spatial scales, the latitudinal thermal gradient appears consistent, but actually changes with latitude. In temperate forests, for example, a steady thermal gradient may facilitate northward shifts [18], but this gradient is almost entirely absent across large swathes of the tropics (Fig. 2A). At intermediate scales, the availability of elevational gradients is far more heterogeneous (Fig. 2B). The Andes and Himalayas present sharp elevational thermal gradients allowing upslope shifts [19], yet organisms in the middle of the Amazon or Congo basin are hundreds of miles from the nearest foothill forest (Fig. 2B; [20]). Similarly, in the ocean, benthic species on wide continental plates or the abyssal plane do not have the same bathymetric opportunities as those on the continental shelf (Fig. 2B). Zooming in further still, thermal gradients exist within habitats. Lowland forests exhibit a striking thermal gradient from the forest floor to canopy [21], contrasting with the stunted forests of high elevation ridgelines (Fig. 2C).

Temporal thermal gradients also vary markedly across scales and geographies. Populations in boreal and temperate forest experience great swings in temperature between summer and winter (Fig. 2E), producing sharp seasonal gradients along which species can shift their phenology [7]; the tropics, meanwhile, have famously stable year-round temperatures. Humid forests also have buffered temperatures from day to night, while xeric deserts undergo extreme heat and cold across the daily cycle ([22]; Fig. 2D). Thus, for every ecosystem, we must consider which thermal gradients are available, and some places may have more options than others (Fig. 3): in the tropics, shifting upslope may be the most efficient strategy [20], while in the temperate north, shifts in phenology may negate the need for shifts in space [6,23].

Besides extrinsic availability, there are also intrinsic factors that can differentially affect species' ability to shift along different thermal gradients. Chief among these factors is dispersal ability. Shifts in latitude require covering the largest distances, a feat most likely for species with high dispersal ability [24]. For example, migratory butterflies may find it much easier to shift with latitude than non-volant millipedes. This contrast becomes even more stark when considering taxa that *cannot* physically move, like trees and kelp, that can only expand their range via recruitment of new individuals. Dispersal ability itself is also affected by factors such as landscape connectivity or ocean currents. Upslope elevational shifts may be more likely along continuously forested mountains than fragmented ones [25], latitudinal shifts may be impeded by ecological barriers such as coastlines [26], and oceanic shifts may be influenced by prevailing currents [27].

In addition to dispersal ability, other traits may enhance or hinder a species' ability to shift along particular gradients [28]. A fish that specializes on feeding from the surface of a lake cannot switch to a demersal lifestyle any more than an earthworm can climb to the canopy, and a species cannot alter its phenology without in-built mechanisms for plasticity. The relevance of different thermal gradients can even vary depending on an organism's life stage. Tadpoles in bromeliads and sea anemones clinging to rocks are clearly unable to shift in space, but their more vagile life stages – adult frogs and planktonic larvae – can potentially travel much greater distances. Thus, one must also consider the thermal gradients that each organism is *most likely* to employ for shifting, given its traits and life history.

HOW TO STUDY SHIFTING SPECIES

A greater recognition that species may simultaneously be shifting along multiple dimensions and at different scales requires ecologists to reimagine how to test for, evaluate impacts of, and forecast future species shifts. Field observations have been integral to building understanding of SOTM [1], but the high effort required of most field sampling has limited ecology's extent and scope of dimensions to-date [29]. While it may be possible to expand the scope (e.g., spatial or temporal) or supplement sampling (e.g., add sampling at finer scales) within traditional monitoring programs, we expect this option to be rare. However, combining existing data with emerging technologies and new tools will still provide great insight into SOTM [30].

The study of SOTM has long relied on tools like species distribution models (SDMs) for forecasting range shifts, but these models are often criticized for their low predictive power, which has been attributed to a multitude of factors [31–33]. Looking forward, process-based (i.e., mechanistic) models provide a more theoretically motivated integration of organismal physiology with population-level phenology and distribution [34,35]. Process-based models have a long history of applications to plant and animal phenology, sometimes integrating experiments and remotely sensed data with field observations [36]. Process-based models of range shifts and "hybrid SDMs" that include physiology or other processes have emerged much more recently and show great promise (e.g., [37]).

Modeling frameworks are emerging that can formally bridge multiple scales and dimensions [30]. For example, mechanistic models can be fitted to movement data from individual animals, informed with bioenergetics, and used to gain inference into population-level processes, including geographical distribution and seasonal behavior [38]. These and other flexible modeling frameworks may integrate traditional biodiversity surveys (which typically occur on a seasonal or annual basis) with novel technologies that operate at scales from minutes to days (e.g., next-generation sensors, environmental DNA [39]).

These models can also use experimental results as informative priors, underscoring the importance of experiments in clarifying mechanisms of shifting species in order to make robust predictions across scales. SOTM scientists increasingly use transplant experiments to study range expansions [40] and physiological experiments to collect critical parameters for biophysical models such as thermal performance [41,42]. Massive distributed experiments may be particularly useful because they can detect range and phenological shifts and shed light on mechanisms across dimensions and scales; for example, the International Tundra Experiment (ITEX) manipulated temperature in tundra plots and recorded the resulting rates of phenological shifts in plants [43]. In summary, all of the pieces—laboratory and field-based experimental data, long-term biodiversity monitoring, novel technologies, and complex spatiotemporal models—exist for the SOTM field to operationalize the theoretical integration that we propose.

PLANNING FOR A FUTURE ON THE MOVE

The management of SOTM also exists at several spatio-temporal scales. Interventions include allowing species to naturally respond, local habitat restoration or preservation, population supplementation, long-distance translocation, and/or assisted adaptation via selective breeding for beneficial genotypes/phenotypes [44–46]. Each of these management actions are sensitive spatially to the location of populations within the range (trailing edge, core or leading edge) as well as temporally to the circadian rhythm, phenology, and life-cycle of a species (Fig 4).

Our framework is purposefully univariate (temperature) to highlight the importance of dimension and scale in understanding SOTM, but management of species must consider all pressures on species populations (e.g., land-use and change, offtake and harvest, among other human disturbances), and how these pressures mediate SOTM. Understanding the multidimensionality of SOTM necessarily reduces existing uncertainty ([47], but see [48]), helping to explain, for example, why some species are not shifting along a given gradient by providing context from other gradients (Fig. 3; [6,7]). Such knowledge will help inform short- and long-term species risk or vulnerability assessments as well as guide priorities and discussions between managers and scientists in how, where, and when species are monitored. Thus, conservation practitioners can confidently direct resources towards select species or towards longer-term strategic goals that may be more proactive than reactive [49].

To clarify existing decision-making tools such as Resist-Accept-Direct (RAD) or Resistance-Resilience-Transition (RRT), which guide whether to resist or accept ecological changes or to direct species towards a desirable outcome [50], we must ensure the dimension and scale of the intervention matches the dimension and scale of the phenomenon. For example, management to restore or connect terrestrial landscapes often assumes that species will track increasing temperatures to higher elevations or latitudes. However, if a species adjusts its phenology, circadian rhythm, or microhabitat preferences it may not need to shift latitudinally to conserve its thermal niche (at least for the time being). Thus, practitioners could then prioritize preserving or enriching local habitat complexity rather than landscape connectivity (Fig. 4). Conversely, if species are indeed shifting broadly in space, then protecting or connecting habitat solely for current ranges ignores where species will be in the future or how they'll get there [51]. Moreover, it is possible that if species aren't shifting in absolute distance or time as expected, then the existing conservation and management may be more effective for SOTM than we thought—and thus novel, and possibly unnecessary, interventions may lead to maladaptation or deleterious outcomes.

CONCLUDING REMARKS

Embracing a multidimensional, scalable framework for conceptualizing climate-change responses will lead us to redefine our understanding of species' ability to track climate change. This paradigm shift could resolve the ongoing paradox that, while ecosystems on the whole are responding to climate change, few single-species responses can be predicted well with existing methods. Part of this puzzle is the recurring finding that ecological and life-history traits rarely predict single-species responses well, despite strong theoretical underpinnings, but our framework could be expanded to bring trait-based predictions into focus. Furthermore, this framework can inspire multidimensional thinking across all ecological disciplines, expanding our understanding of species distributions and anthropogenic responses beyond two-dimensional space. With new insights we are better able to ready society for SOTM [4], providing a more nuanced picture of which species may be more likely to shift into new territory, which may take up new daily activity patterns, which may adjust their phenology earlier in the year, and how all of these shifts affect humans.

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FIGURES

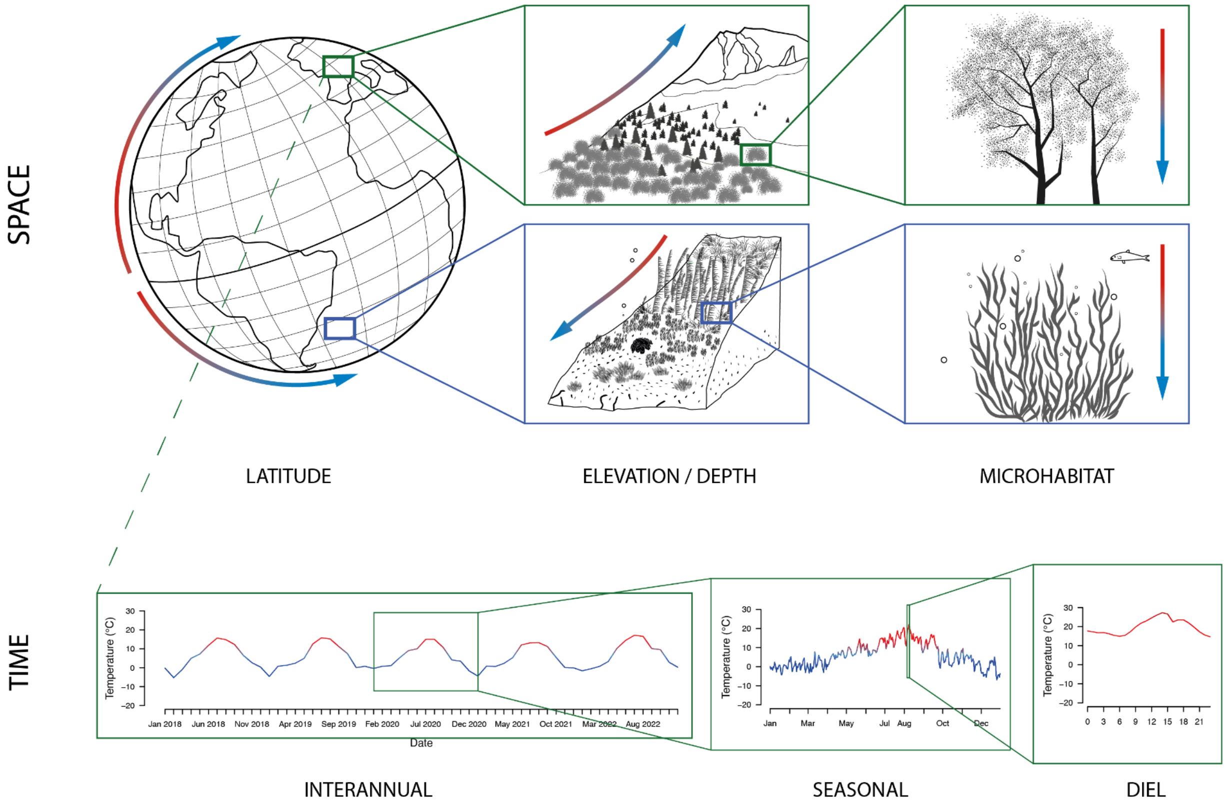

Figure 1.

Species track temperature in both space and time, at varying scales. (A) Species experiencing climate change have been documented shifting in space at a range of scales, taking advantage of latitudinal, elevational, and microhabitat gradients in temperature. (B) Species experiencing climate change have also exhibited shifts in time (phenological shifts), ranging from interannual phenomena to altered timing of seasonal behaviors and changing diel patterns. These spatial and temporal shifts at different scales and along different gradients can be conceptually unified: species shift in response to temperature change along spatial and temporal dimensions, and at any temporal or spatial scale, species may have different gradients available to them along which to shift.

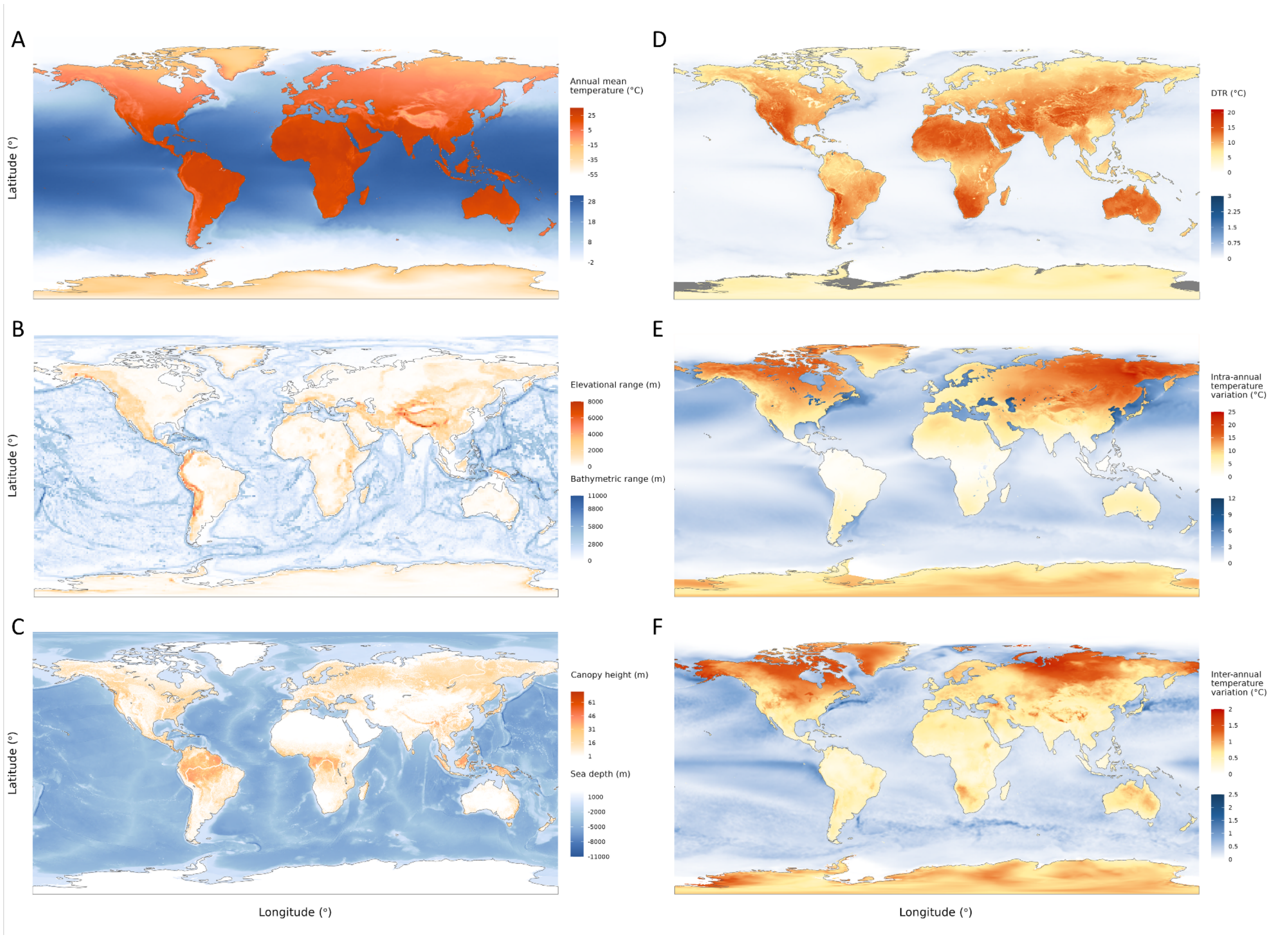

Figure 2.

The availability of thermal gradients differs across the world. We demonstrate the global distribution of thermal gradients via: (A) the latitudinal gradient in annual mean temperature, (B) elevational range on land and bathymetric range in the ocean (maximum-to-minimum range within 3-degree pixels), (C) forest canopy height on land and depth in the ocean, (D) daily temperature range (hottest hour - coldest hour each day, averaged over 5 years), (E) intra-annual temperature variation (average standard deviation of monthly temperatures over 20 years), and (F) inter-annual temperature variation (standard deviation of annual mean temperatures over 20 years). Temperature data were extracted from ERA5 (2004-2023); elevation and depth data were extracted using a DEM from NOAA's ETOPO 2022 at 60 Arc Second Resolution.

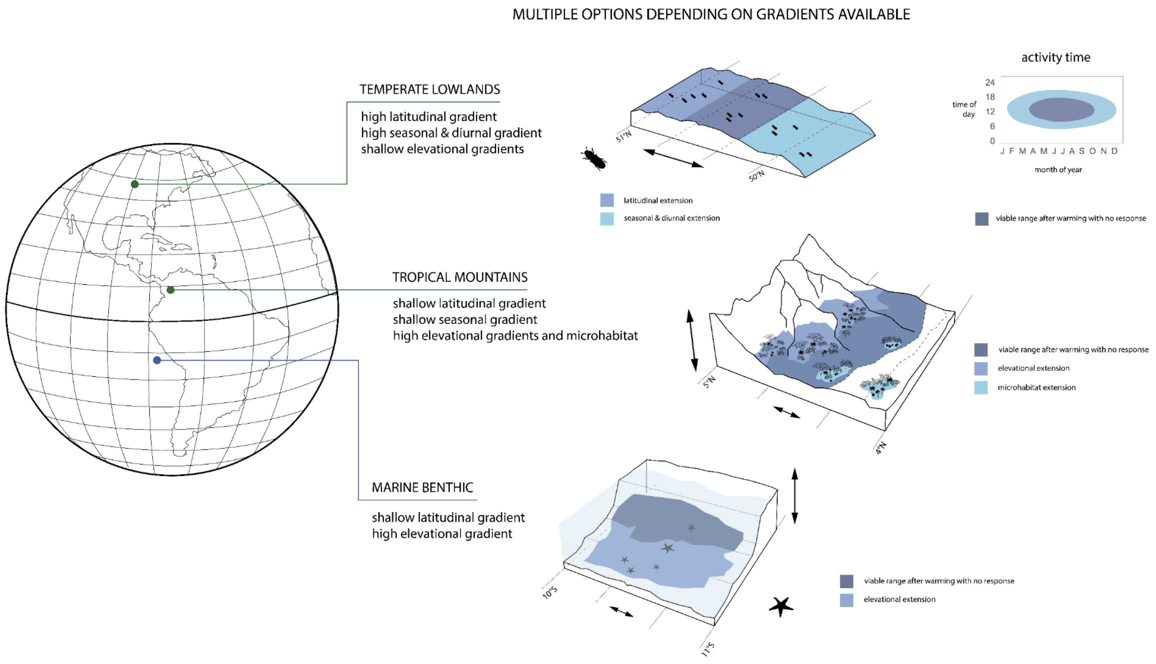

Figure 3.

Varying availability of gradients around the world gives rise to differential opportunities for species to track thermal niches over space and time. Three different example environments – temperate lowlands (top), tropical mountains (middle), and marine seafloor (bottom) – show variable access to thermal gradients across multiple dimensions. Differing available gradients may, in turn, shift expectations about the type and magnitude of spatial or temporal shift following climate warming for given species – with each species (e.g., a beetle [top] or a sea star [bottom]) having its own ability or limitations to effectively track temperature given its life history and traits.

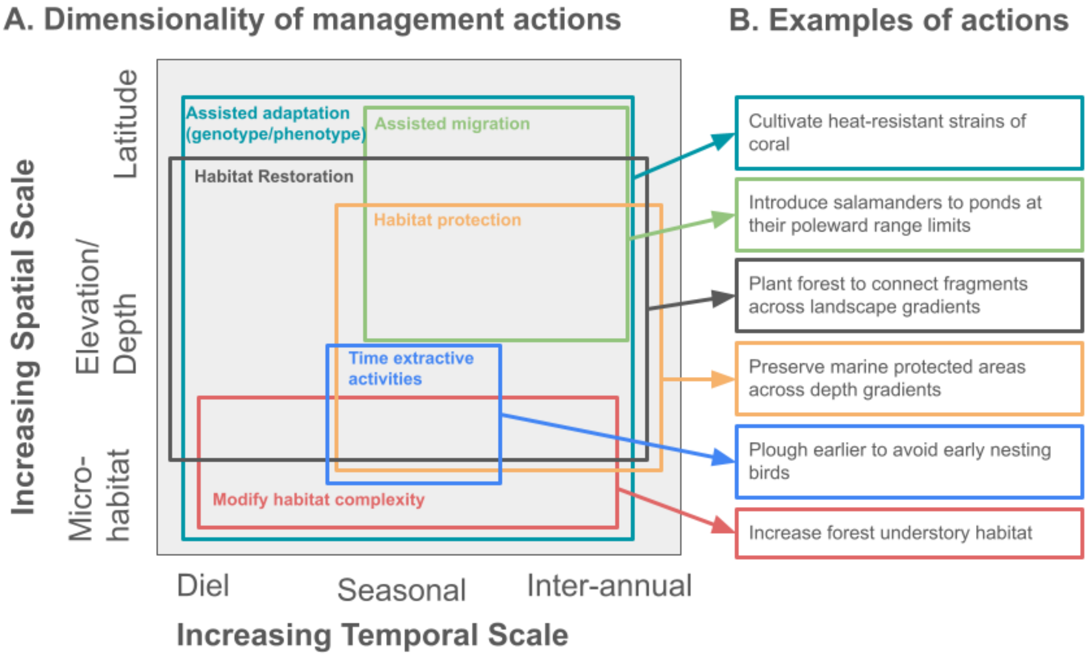

Figure 4.

With opportunities for shifting species differing across dimensions and scales, management and conservation actions logically also have varying influence across scales and gradients. Here, we highlight six different types of management actions (A) each of which – with specific examples (B) [52–57] – has an approximate zone of influence across different aspects of spatial and temporal scale. For example, assisted migration generally helps species cope with range shifts across broader spatial scales (e.g., latitude) and is effective across multi-annual time scales, whereas increasing habitat complexity through understory restoration primarily provides microhabitat buffering that can also facilitate thermal tracking across many time scales, from daily to long-term.

GLOSSARY

- **Biotic Interaction**: The association – whether facilitative, antagonistic, or neutral in outcome – between two living creatures. Biotic interactions can either hinder or facilitate range shifts depending on the nature of the relationship.
- **Circadian Rhythm:** Biological processes over a 24 hour time period; influenced by environmental variables such as temperature or day length.
- **Dimension**: Distinct axes or aspects from which a species can respond to climate change with two primary dimensions of space (e.g., microhabitat to latitude) and time (e.g., diel to inter-annual).
- **Gradient**: A range of environmental conditions in space or time such as temperature change across habitat types or from one season to the next.
- **Microhabitat**: The fine scale, localized environment where an organism lives, which often has unique attributes that differ from the surrounding environment.
- **Phenological shift**: Changes in the timing of life-cycle processes such as breeding, migration or flowering, in response to climate change.
- **Range shift**: The expansion or contraction of species geographic ranges, typically assumed poleward or upslope, in response to changing environmental conditions.
- **Scale**: Temporal and spatial extent of environmental change or ecological response ranging from broad (macro) to fine (micro) levels of scale.
- **Species on the Move (SOTM)**: Species that are shifting their geographic ranges and/or timing of their life history/life-cycle processes in response to climate change.
- **Thermal niche**: The range of temperatures experienced by a species across space and time in which it can survive, reproduce, and perform vital ecological functions.