TITLE

Reimagining species on the move across space and time

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KEY WORDS

Range shift; phenological shift; biogeography; temporal ecology; spatial ecology

ABSTRACT

Climate change is already leaving a broad footprint of impacts on biodiversity, from an individual caterpillar emerging earlier in spring to dominant plant communities 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.

OUTSTANDING QUESTIONS

1. To date, studies of species on the move that are focused on a single gradient (such as elevation or seasonal phenology) in a single dimension (space or time) often find evidence for partial or no "climate tracking". Can we enhance our understanding of species on the move by more fully accounting for thermal gradients available to species at multiple temporal and spatial scales?
2. While they are hypothesized to be key drivers of species' range and phenological shifts, traits rarely emerge from synthesis studies as strong statistical predictors. Will reimagining species on the move resolve the chronically low predictive power of species traits?

3. Conservation interventions for shifting species also vary in scale and have rarely been matched to empirical evaluations of the gradient(s) along which species are actually shifting. How will this novel framework reshape our management of species on the move?

SPECIES MOVING IN TIME AND SPACE

Climate change is having diverse impacts on ecosystems, from birds shifting to higher elevations to buds bursting earlier each year [1–4]. 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 in response to climate change have come to be known as **species on the move** (SOTM), to which we also include species shifting their timing of behavior and life history. 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 [5].

Detecting SOTM, attributing their shifts to human impacts, and predicting their future dynamics is a key challenge for ecology in the Anthropocene [6]. This challenge is magnified by the complexity of studying range and temporal 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 [7], while in Lepidoptera, species that have shifted both their ranges and phenology have shown more resilient population trends [8].

These exemplar 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 responses to climate change remains [6], despite extensive improvements in methods and modeling [9–11] including sampling advances and the incorporation of **biotic interactions** and **dispersal limitations** into predictive models [12,13]. 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** [14,15]. 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 shifts due to climate change are more uniform and predictable than other changes (e.g., precipitation regimes [16]) and because thermal gradients are ubiquitous and diverse across land and water. Yet, we acknowledge the fundamental importance of other components of species' niches (e.g., rainfall, biotic interactions) and believe that our framework can be extended to other abiotic gradients (e.g., oxygen, humidity, pH, etc.) and the explicit incorporation of biotic interactions [17]. Thus, 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 critical component of a species' fundamental niche – the range of temperatures in which a species can survive and reproduce [18]. In a warming world, we expect species to **shift** in order to conserve their thermal niche, but this potential only exists 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). We need to examine these potential avenues for shifting if we are to properly quantify SOTM.

To 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 focusing on other gradients, like the vertical temperature cline produced by tall trees, may lead to 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, perhaps a simple truth would emerge: the frog is maintaining its fundamental 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 exist multiple thermal gradients that occur at different scales. In space, latitude is the largest thermal gradient, stretching from the equator to the poles while elevation (on land) and depth (in water) provide thermal gradients at intermediate scales. At small scales there are thermal gradients in **microhabitats** created by abiotic features like geological formations (e.g., boulder fields), as well as biotic structures or features that directly modify temperature clines (e.g., canopies and coral heads) [19]. 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, such as shifting daily activity patterns or altering breeding phenology.

Of course, tracking thermal gradients may also be mediated by biotic interactions [20] which can constrain range shifts – such as upslope shifts of birds limited by the rate of treeline expansion [21] – or facilitate them – such as parasites and pathogens shifting poleward in latitude enabled through shifts of hosts [22]. Our framework can thus be extended to describe these SOTM that are tracking temperature gradients indirectly via other species, but with caution, given the dynamic nature of species interactions.

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” [23–26] may not represent nature itself, but rather a limitation of how climate change impacts have been studied so far. To move forward, we need to study species responses to climate change across multiple dimensions and along gradients at multiple scales [7] (Fig. 2).

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 poleward shifts [27], 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 Eastern Rift mountains present sharp elevational thermal gradients allowing upslope shifts [28], yet organisms in the middle of the Amazon or Congo basin are hundreds of miles from the nearest foothill forest [29] (Fig. 2B). Similarly, in the ocean, benthic species on wide continental plates or the abyssal plain 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 where the change in temperature from a 1-meter increase in height equates to shifting hundreds of kilometers in latitude [30] (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 [8]; 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 [31] (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 [29], while in temperate ecosystems, shifts in phenology may negate the need for shifts in space [7,32]. Ultimately, the availability of these climatic gradients are further filtered and mediated through biotic interactions, which can both impede and facilitate the accessibility of gradients to species.

Besides extrinsic availability, there are also intrinsic factors that can differentially affect species' ability or need 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 [33]. 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, and can only expand their range via reproduction and 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 [34], latitudinal shifts may be impeded by ecological barriers such as coastlines [35], and oceanic shifts may be influenced by prevailing currents [36].

In addition to dispersal ability, other traits may enhance or hinder a species' ability to shift along particular gradients [37]. 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 easily alter its phenology without an evolved mechanism of phenotypic 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

Our framework necessitates a reimagination of how we test for, evaluate the impacts of, and forecast future species shifts. Field observations have been integral to building understanding of SOTM [1–4] but the high effort required of most field sampling has limited the extent and scope of ecological data and thus inference [38]. We strongly advocate for the expansion of these monitoring programs. For example, annual surveys could be conducted twice in the same season to detect phenological shifts, and regional surveys could include elevational or depth transects to detect finer-scale spatial shifts.

Given that biodiversity monitoring is already sparse and its expansion is resource-intensive, we expect that researchers will also need to merge disparate datasets collected across dimensions and scales. This will only be possible for datasets that are published with sufficient metadata and code [39]. To fully capture available gradients for shifting species, researchers will likely need to incorporate non-standardized data (e.g., opportunistic observations), which introduces substantial spatiotemporal bias that is currently challenging to overcome analytically [40]. However, next-generation sensors including acoustic devices and GPS trackers and new technologies such as environmental DNA are making biodiversity monitoring faster and cheaper than ever before [41]. We hope that these technologies will produce data at many spatial and temporal scales while reducing the sampling bias inherent in traditional biodiversity monitoring.

The best forecasts of SOTM will couple field data with laboratory experiments to reveal how species may respond to future temperature change. SOTM scientists increasingly use experiments to collect critical parameters of biophysical models such as thermal performance, metabolic rate, and behavior [42,43], and transplant experiments across thermal gradients to study the likelihood of range expansions [44]. Distributed experiments across regions and continents 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 [45]. As we expand process-based models (see below), a huge investment in conducting thermal response experiments for many species is imperative to parameterize multi-scale spatiotemporal models.

The analysis of SOTM data to-date has also been piecemeal, with models fitted at individual, population, or community scales, to explore the roles of dozens of processes from bioenergetics to dispersal limitation [46]. While we do not expect a single modeling approach to emerge that can capture all SOTM across all dimensions and scales, it is still possible to gain insight into SOTM with new modeling approaches. First, "hybrid" models are already integrating data types to make inference across scales – by, for example, combining animal movement estimates (modeled from individual-level tag data) with species distribution models (based on regional surveys) [47]. We advocate for the expansion of these coupled modeling approaches across spatial and temporal scales, which will require adhering to best practices in reporting and interoperability to ensure that the outputs (including uncertainty) of one model can be input into another [48]. Second, while the study of SOTM has historically relied on tools like species distribution models for forecasting range shifts [49–51], process-based (i.e., mechanistic) models provide a more theoretically motivated integration of organismal physiology with population-level phenology and distribution [52,53]. Fitting process-based and hybrid models and coupling them across dimensions and scales should be a clear focus of the SOTM field in the coming years, in order to use the newly-collected data that we encourage above to advance predictive power and skill. We also expect widespread application of the rapidly-growing suite of machine learning and artificial intelligence tools to SOTM, both in forecasting across dimensions and scales and in processing the vast quantities of incoming data.

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 adaptive genotypes/phenotypes [54–56]. 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. Notably, this framework can reveal whether a species not shifting along a given gradient is compensating via shifts along other gradients or is, more concerningly, stymied by a lack of available gradients [7,8] (Fig. 3). 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 [57].

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 [58], 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 [59] (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 will get there [60]. Moreover, it is possible that if species are not shifting in absolute distance or time as expected, then existing conservation and management may be more effective for SOTM than we thought – and novel, and possibly unnecessary, interventions could lead to maladaptation or deleterious outcomes.

MOVING FORWARD WITH SOTM

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 will help 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 (see Outstanding Questions). With new insights we are better able to ready society for SOTM [5], providing a more nuanced picture of which species may be more likely to shift into new places, 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.

ACKNOWLEDGMENTS

This manuscript arose from discussions at a workshop funded by the University of Florida IFAS Office of the Dean for Research that followed the Species on the Move conference in Bonita Springs, Florida, USA in May 2023. Many different sources provided funding for individual authors to attend this workshop and we are grateful to them all.

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FIGURES

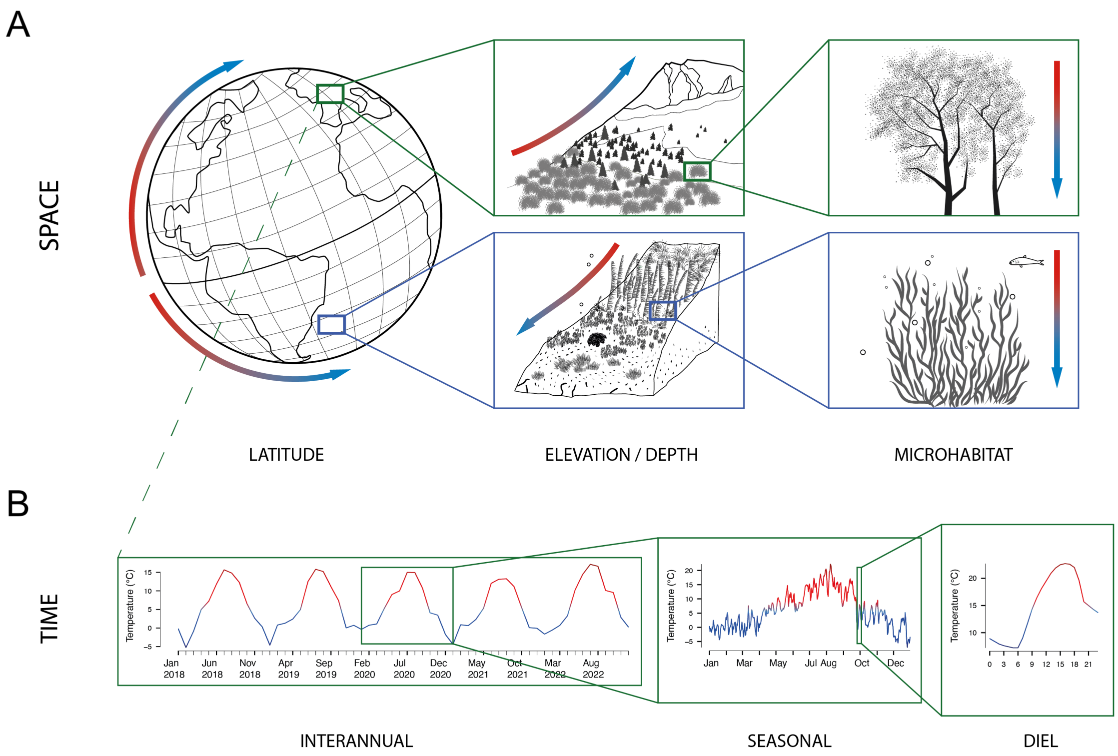

Figure 1.

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, ranging from interannual phenomena to altered timing of seasonal behaviors (phenological shifts) 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.

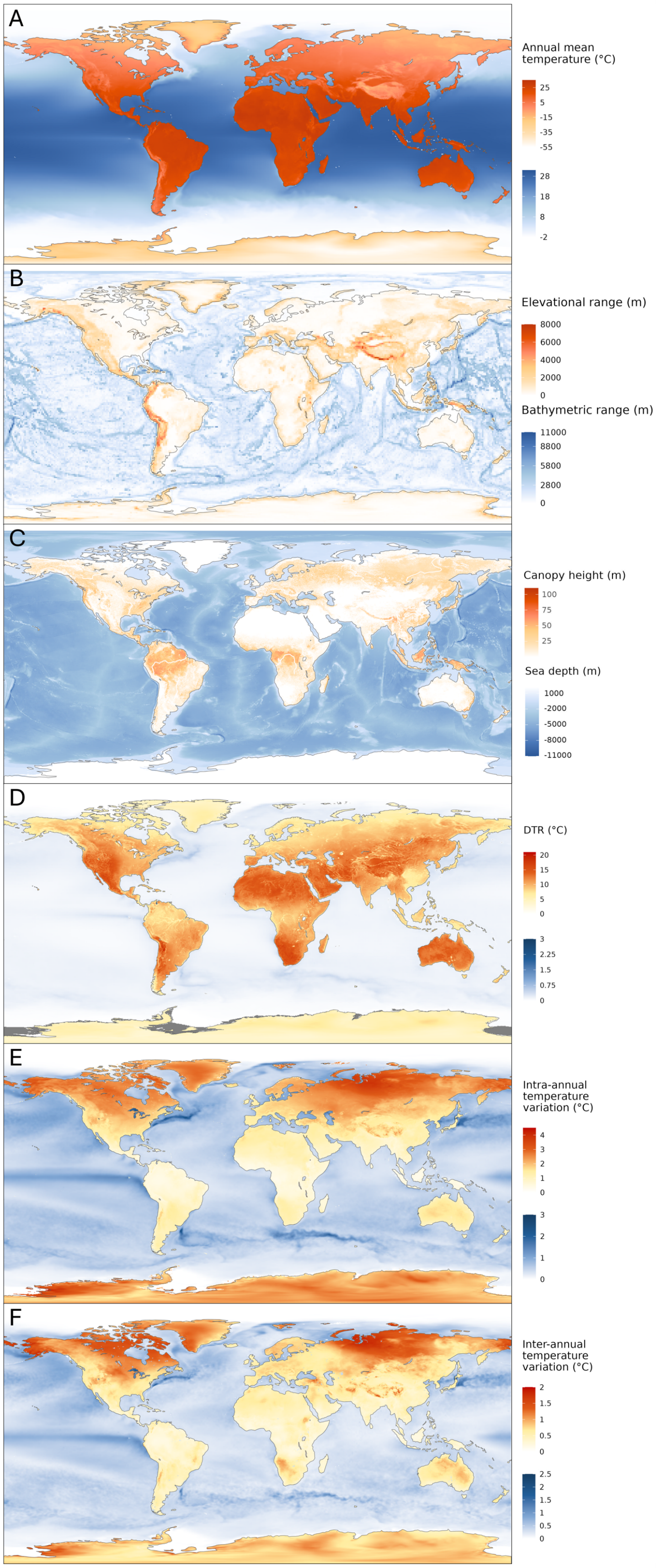
A
Annual mean temperature (°C)
25
5
-15
-35
-55
28
18
8
-2
B
Elevational range (m)
8000
6000
4000
2000
0
Bathymetric range (m)
11000
8800
5800
2800
0
C
Canopy height (m)
100
75
50
25
Sea depth (m)
1000
-2000
-5000
-8000
-11000
D
DTR (°C)
20
15
10
5
0
3
2.25
1.5
0.75
0
E
Intra-annual temperature variation (°C)
4
3
2
1
0
3
2
1
0
F
Inter-annual temperature variation (°C)
2
1.5
1
0.5
0
2.5
2
1.5
1
0.5
0

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.

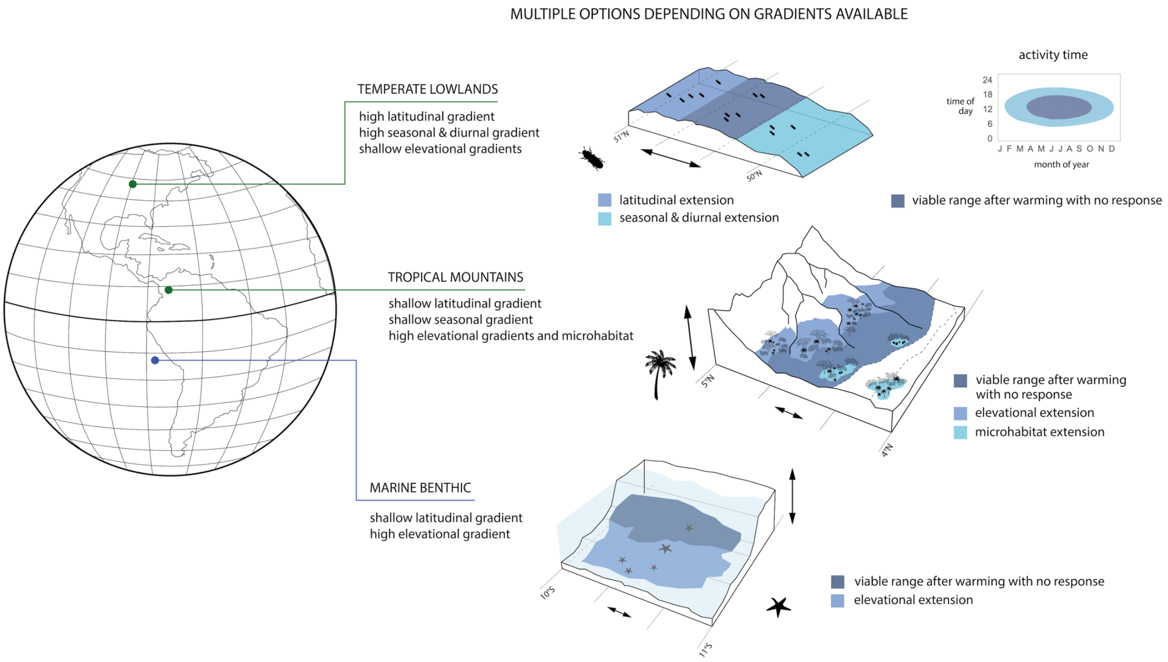

Figure 3.

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 grassland lowlands (top), tropical forested 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], an understory palm [middle], or a sea star [bottom]) having its own ability or limitations to effectively track temperature given its life history and traits.

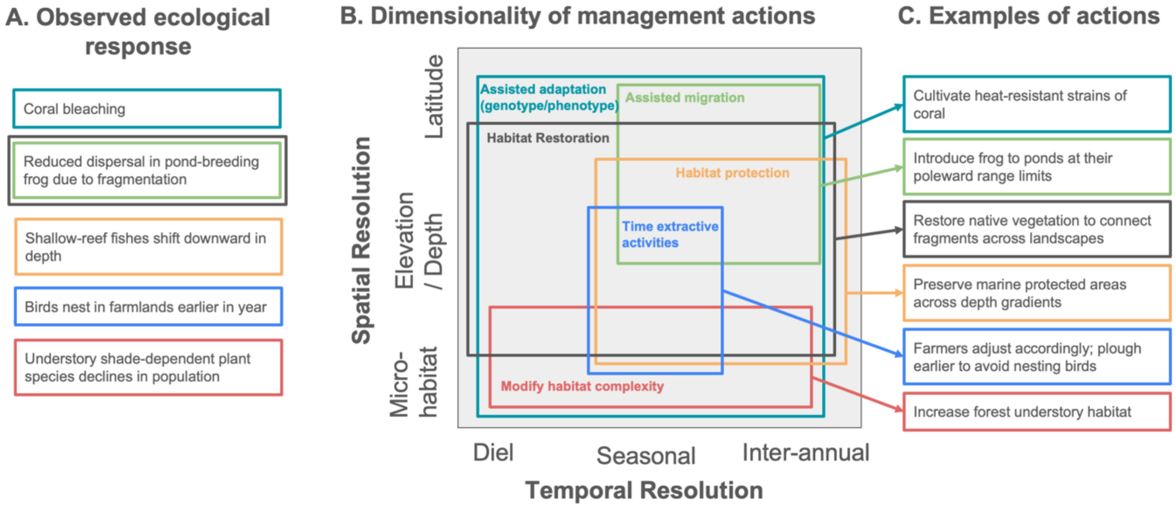

Figure 4.

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 common ecological responses to climate change (A) and six different types of management actions (B) each of which – with specific examples (C) [61–66] – 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 along which a species can respond to climate change, with two primary dimensions: space (e.g., microhabitat to latitude) and time (e.g., diel to inter-annual).
- **Gradient**: A cline in 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 seasonal 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 in response to changing environmental conditions.
- **Shift**: Referencing broadly to changes in distribution and/or phenology; thus ‘shifts’ in space and/or time.
- **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 spatial distributions 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.