

Review

Matching climate to biological scales

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Recent advances in climate modeling and remote sensing have increased the expectation that finer-grained climate data will improve biological relevance. However, the appropriate scale for biology depends on the system and the question posed, and finer-grained data do not always improve inference in ecology and evolution. In this review we synthesize knowledge from micrometeorology, physiology, and landscape ecology to develop a framework integrating climatic and biological lenses for understanding the scales of climate exposure. This framework can aid multiscale investigation of microclimate effects on individuals, populations, and communities. We newly conceptualize systems of climate scale, provide recommendations for trait-based approaches to determine the scales relevant to climate–biology interactions, and highlight opportunities offered by novel methods and technologies.

Contrasting lenses for viewing climate scale for ecology and evolution

Climate and biology are both dynamic and vary with **scale** (see [Glossary](#)). Almost all ecological and evolutionary phenomena are driven by fundamental biochemical reactions that are temperature- and water-dependent and operate at fine scales [1]. Broad-scale biological responses to climate, such as latitudinal diversity gradients, are the aggregate of processes operating within and upon individual organisms, such as cellular respiration, which tend to scale nonlinearly in space or time [2]. Two approaches have emerged to investigate climate–biology linkages, which we call ‘climate-first’ and ‘biology-first’, and they have generated different lenses of viewing scale ([Figure 1](#)).

Climate-first approaches, associated with the fields of geography and macroecology, measure or model climate and other environmental variables to best represent a region and duration of interest, independently of any particular species ([Figure 1A](#)). Frequently, this includes weather station data, or premanufactured spatial grids of averaged climate. Climate-first research emphasizes the **resolution** and **extent** of such grids. Biological observations – for example, presence, abundance, or trait data – are then overlaid on these climate grids. These biological values are considered as responses to the climate data. For instance, species distribution models (SDMs) link environmental grids (e.g., air temperature, precipitation, or elevation) to species occurrences to infer what climatic conditions are suitable, and therefore predict the likelihood of occurrence elsewhere [3]. Some demographic models use the nearest weather station or surface buoy to predict population dynamics [4]. Because such climate data are not species-specific, climate-first approaches can be easily applied across multiple systems and species, especially with the increasing availability of gridded remote sensing data [5].

Biology-first approaches, popular among ecophysiologicals, begin by considering the traits of a focal organism, such as its activity period, body mass, home range, reproductive phenology, and thermal physiology [6]. Climate is then measured or modeled based upon such traits to best capture that organism’s climate exposure ([Figure 1B](#)). Biology-first research thus

Highlights

Climate’s fingerprint on ecology and evolution is pervasive, yet the identification of causal relationships between climate and eco–evo dynamics remains evasive. This is due partly to a mismatch between the questions posed by scientists and how we represent climate and biology with data.

Popular methods estimate biological responses to gridded climate data from weather stations. Yet many organisms determine their microclimate exposure via behavior, morphology, and physiology. This means that most climate grids do not represent the conditions that organisms actually experience and therefore determine ecology and evolution.

Advancing ecological and evolutionary studies requires the integration of paradigms from contrasting research traditions for a better understanding of the scales relating climate to biology.

Capturing causal mechanisms entails recognizing the feedbacks between organismal biology and organismal microclimates.

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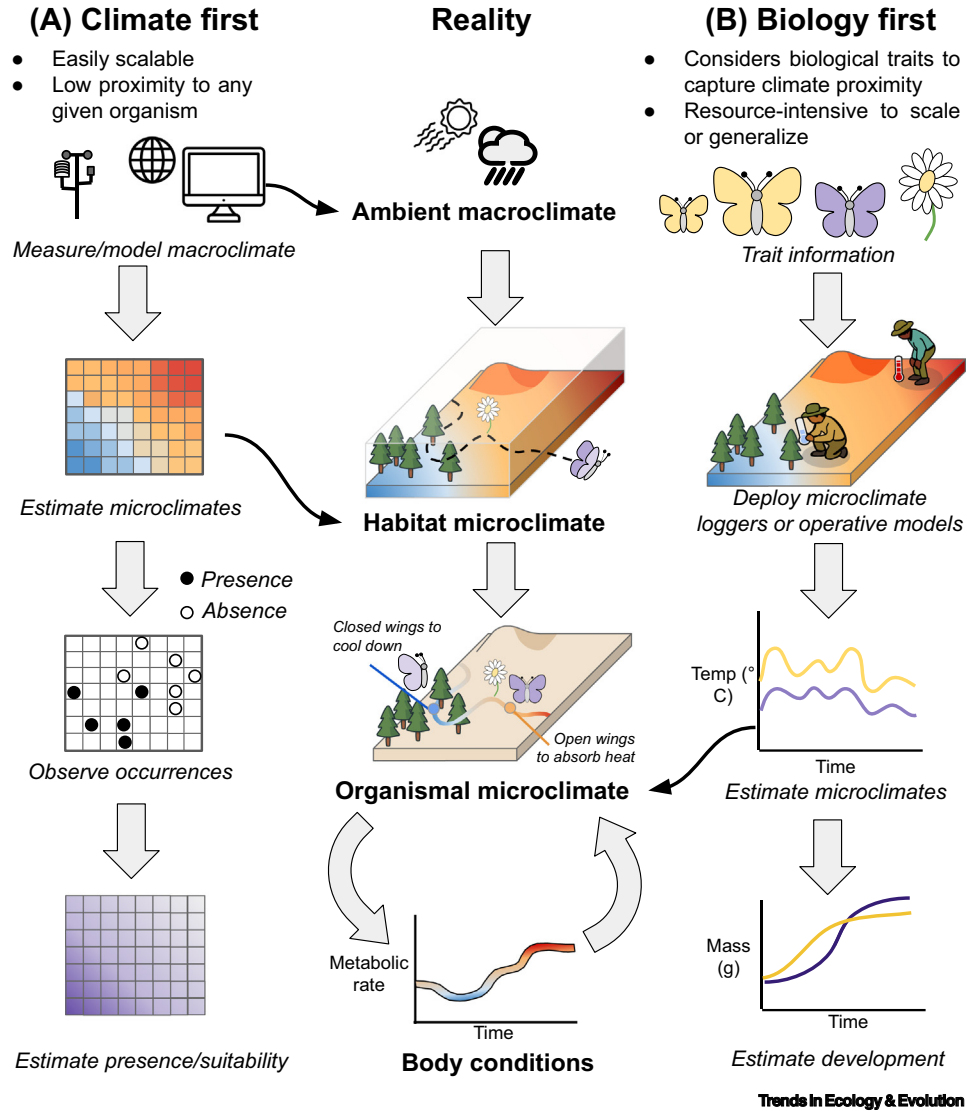
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Glossary

Bogert effect: the capacity for homeostatic behaviors (e.g., thermoregulation) to limit selective exposure across environmental gradients and therefore limit local adaptation.

Boundary layer: the layer of fluid in the immediate vicinity of a surface within which friction and other surface effects impact exchange of energy and matter, assuming laminar flow. The planetary boundary layer influences macroclimates, while additional boundary layers at landscape, meter, and millimeter scales shape nested microclimates.

Climate proximity: the degree to which climate data represent the actual conditions that an organism or process is exposed to, distinct from the spatiotemporal resolution of the climate data. Varies from distal to proximal.

Dispersal kernel: a probabilistic function representing the population-averaged likelihood of dispersal-related movement across spatial distances.

Extent: the total volume encompassed by a dataset, such as the spatial area or the temporal duration.

Habitat microclimate: the physical atmospheric conditions (e.g., air temperature, air/vapor pressure, wind speed, radiation) within several meters above the highest land or water surface down to several meters below ground. Energy and matter exchange are influenced by vegetation, topography, soil composition, and human development.

Jensen's inequality: for nonlinear functions, the output in response to the mean input does not equal the mean output across all inputs. For nonlinear climate-biology relationships, this entails that the mean biological response to a climatic time series does not equal the biological response to the time-averaged climate.

Macroclimate: the physical atmospheric conditions within the lowest few meters of the troposphere relatively unaltered by local vegetation, topography, human developments, or water features, as weather stations attempt to measure.

Mean field approximation: the approximation of a high-dimensional process by averaging over degrees of freedom. For studying climate exposure, this can include assuming that coarse grid-cell average climatic variables, and/

Figure 1. Contrasting approaches to represent climate impacts on ecology and evolution. Climate-first and biology-first approaches attempt to capture reality via different means, with an illustrative example of each approach shown. (A) One climate-first approach may begin with representing macroclimates via weather station observations or gridded predictions, from which 2D microclimates are estimated in space and/or time; these typically estimate 'habitat microclimates' (Box 1), which in reality vary in 3D space. Using presence/absence observations, the likelihood of presence or suitability is predicted conditional on climate. (B) One biology-first approach may begin with consideration of the traits of a focal organism (e.g., body size, host plant); conditional on these traits, microclimates are then measured at times and locations considered important for the focal organism (e.g., via temperature loggers placed in the field); these typically estimate 'organismal microclimates', which in reality track a given organism through space and time. From these estimates of organismal microclimates, some biological response of interest is inferred, such as individual growth. Climate-first and biology-first approaches offer contrasting avenues to understand climate-biology relationships.

emphasizes how organismal biology, rather than data resolution, shapes the scale of climate exposure. Such approaches require species- and system-specific knowledge, and are thus information-intensive to apply across broad spatial, temporal, or biological scales [7]. Examples of biology-first research are use of physical operative models placed in an organism's microhabitats [8,9], and mechanistic ecophysiological modeling [10].

In recent decades, climate-first approaches have increased in popularity, associated with the proliferation of gridded environmental datasets [11] and global biodiversity records [12,13]. Even fine-grained microclimate data are increasingly available [14,15]. Much of the resulting research has been based on the assumption, either tacit or explicitly stated, that increasing resolution of climate or environmental data improves their biological relevancy [16–18]. Correspondingly, the literature has been mixed on whether the term ‘microclimate’ refers to fine resolution, biological relevance, or both. Yet increasing spatial grain or timestep may introduce irrelevant noise, or even cause misleading findings, if not linked to the processes by which organismal biology shapes the scale of climate exposure. For instance, organisms select and manipulate their environments, acting according to their perceptual range [19] and spatial configuration of features [20] dynamically across life stages [2]. Thus, higher climate data quantity (spatial or temporal resolution) does not always entail higher data quality (adequacy for capturing biological responses to climate), whether or not the data are labeled as microclimates [21]. While biology-first approaches more often recognize this, they require natural history and trait knowledge that is not available for most species, curtailing their broad applicability. A key objective is thus to harmonize climate-first and biology-first approaches for sound and scalable insights.

In this review we provide a set of core principles that conceptualize the scale of climate exposure. Drawing upon these principles, we develop a framework integrating information on climatic and biological scales to understand climate exposure for important processes in ecology and evolution. Our framework emphasizes that there is no best scale for all studies. Rather, the motivating questions, and how insights are intended to be generalized, should determine the selection of relevant scales of inquiry.

Core principles for understanding the scale of climate exposure

Principle 1: microclimates vary at fine spatial and temporal scales

Micrometeorology varies across fine vertical, horizontal, and temporal scales given gradients of topography, vegetation, and soil [22–24]. Accurately representing microclimates, however, relies not so much on climate data resolution as it does on adequately representing relevant near-surface processes. Across meters and hours, drivers of microclimate are dominated by **boundary layer** conditions, as terrain and vegetation affect turbulence and the energy balance between the air, substrates, and water [24]. Most organisms function within this zone of near-surface climate variation, with environmental conditions influencing body temperatures, water balance, and other states via morphology, physiology, and behavior [6,7]. Researchers should study which microclimate processes are most relevant for their ecosystems and taxa of interest. For more in-depth attention, we highlight classic overviews of micrometeorology [24,25] and physiology [10,26], and recent literature reviews on microclimate [27–29].

Principle 2: climate exposure reflects nested processes across atmospheric, habitat, and organismal scale systems

For conceptualizing the scale of climate exposure as useful for ecology and evolution, we suggest three nested scale systems: **macroclimate**, **habitat microclimate**, and **organismal microclimate** (Box 1). These systems differ in **climate proximity**: from distal (indirect biological relevance) to proximal (mechanistic relation to a specific organism’s biology) [21]. Distal macroclimate may only be useful when organismal microclimates and macroclimates are closely coupled, so macroclimates serve as an adequate **mean field approximation** for experienced conditions [30]. Climate-first approaches historically have used macroclimate, and more recently have moved towards representing habitat microclimate. Biology-first approaches typically focus on representing organismal microclimate (Figure 1).

or distal macroclimate, are statistically meaningful predictors of the microclimate exposure within the grid cells.

Organismal microclimate: the range of climate conditions to which a specific organism is exposed, filtered according to the organism’s behavior, movement, and other traits.

Resolution: the minimum distance between two adjacent data values, such as the area of a single spatial grid cell or the amount of time surpassed between points in temporal data.

Roughness length: a quantitative measure of the aerodynamic roughness of the ground that causes drag or displacement; lengths typically differ for wind (momentum) relative to the length for transfer of heat and vapor, which are typically equal to one another.

Scale: the measure of an element that describes its size, volume, or complexity in relation to other elements within the same spectrum. Elements may take any measurable form that is subdivisible and combinable, including spatial, temporal, biological, physical, chemical, and geographical spectra.

Scale domain: a portion of the scale spectrum (e.g., from 100 m² to 1000 m² for spatial extent, or from 1 day to 3 months for temporal duration) within which a given process-pattern relationship is generally of the same form. Identifying the limits of a scale domain helps determine across what scales a finding can be generalized or extrapolated.

These scale systems are not defined by their spatial resolution or temporal timestep; macroclimate data can be high resolution in space or time, while organismal microclimate or even body temperature estimates can be coarse resolution. For example, popular global databases such as WorldClim and CHELSA [31,32] offer relatively fine-resolution interpolations of macroclimate, yet do not represent the proximal below-vegetation, aquatic, or soil microclimates relevant for most species. While increasing data resolution across a certain part of the scale spectrum (e.g., from years to months) may be beneficial for most research inquiries, increasing resolution across other parts of the scale spectrum (e.g., from hours to minutes) may not improve representation of climate–biology processes [21]. Instead, understanding mechanisms that generate the microclimates experienced by a focal organism, and how physiology and behavior respond to such microclimates, is key to capturing climate–biology processes; resolution then determines how variation in such processes can be expressed. Increasing resolution of climate data that are distal to focal organisms (e.g., macroclimate, or irrelevant microclimates) may in fact reduce the accuracy of biological predictions derived from such climate data [21]. Researchers should endeavor to quantify climate variation for macroclimate, habitat microclimate, and organismal microclimate, and consider how these scale systems determine **scale domains** for a process of interest [17]. Modeling biological responses to multiple climate datasets spanning distal to proximal then helps determine an adequate level of detail to represent [21,33].

Principle 3: biological responses to climate at one place and time are sensitive to a broader climatic context

Many correlative studies link biological responses to meteorological conditions at the same time and location as the response itself [3]. However, an organism has accumulated experience of

Box 1. Conceptualizing systems of climate scale

Definitions of climate scales, including ‘macroclimate’ and ‘microclimate’, have often been couched in the spatial extents across which meteorological processes operate: macroclimate at ~50 km, mesoclimate at ~100 m to 50 km, and microclimate at ~100 m [27,111]. Yet understanding organismal climate exposure requires a species-centric view of scale beyond meteorological processes, accounting for how organisms filter their climate exposure [6,22]. We therefore propose three nested systems of scale characterizing organismal climate exposure: macroclimates, habitat microclimates, and organismal microclimates.

With few exceptions (e.g., pressure fronts), macroclimates (Figure 1A) vary smoothly in space and time because the atmosphere mixes rapidly. Although widely used in ecological studies, macroclimates are rarely an adequate approximation of climate exposure for any organism or community. Habitat microclimates (Figure 1B) vary horizontally and vertically at millimeter to meter scales and across minutes to hours [24,28], contingent on topographic, vegetative, and edaphic features. Like macroclimates, habitat microclimates may lack direct mechanistic ties to a species’ ecology or evolution, instead describing the physical landscape. For a focal organism, such as a *Phelsuma* gecko (Figure 1), unoccupied habitat microclimates in the forest canopy may be poorer predictors of body temperature even than macroclimate. Quantifying variation in habitat microclimates, however, helps identify conditions that organisms avoid. Although species-agnostic, habitat microclimates are still influenced by biotic features: plant canopies create microclimates, and megafauna such as elephants reshape them by clearing vegetation [54]. Some mechanistic [102,103] and correlative [14] microclimate models provide useful representations of habitat microclimates without reference to specific species.

Organismal microclimates (Figure 1C) are the subset of habitat microclimates to which an individual is directly exposed and define the climatic variables of its multivariate niche. Following the proposition that habitats are descriptive while niches are mechanistic [112], organismal microclimates are mechanically tied to growth, survival, and reproduction. Even individuals of the same species may experience different organismal microclimates due to distinct microhabitat use or thermoregulation. Moreover, organismal microclimates track an individual’s movement through time, often spanning multiple habitat microclimates. For instance, a gecko may experience sun-exposed branch temperatures in the morning and, at night, the buffered conditions within an *Asplenium* fern (Figure 1C). Some locations may be irrelevant because they are never occupied due to abiotic or biotic constraints (gray pixels in Figure 1C). For both mobile and sessile organisms, behavior (e.g., leaf angle, mollusk valve opening), morphology (e.g., posture, mass), and physiology (e.g., skin moisture) alter experienced organismal microclimates. Thus, a feedback loop exists between organismal traits shaping selected organismal microclimates, which in turn shape organismal biology. The spatial and temporal scales over which organismal microclimates affect ecology and evolution depend on an organism’s ‘ecological neighborhood’ [17,113], determined by body size [52], development [34,37], perceptual range [19], activity periods [20], and home range [8]. Measuring or modeling organismal microclimates therefore requires acute knowledge of species’ natural history and traits [104,105], or sensors placed on organisms themselves [100].

Physiological and morphological traits mechanically translate organismal microclimates into organismal states (Figure 1D), such as body temperatures or plant hydration, which vary across life stages and species (Figure 1E). These organismal conditions then propagate through ecological and evolutionary scales. Understanding emergent climate–biology patterns (some examples in Figure 1F) typically requires mechanistic representation of links between fine climate scales and fine biological scales [7].

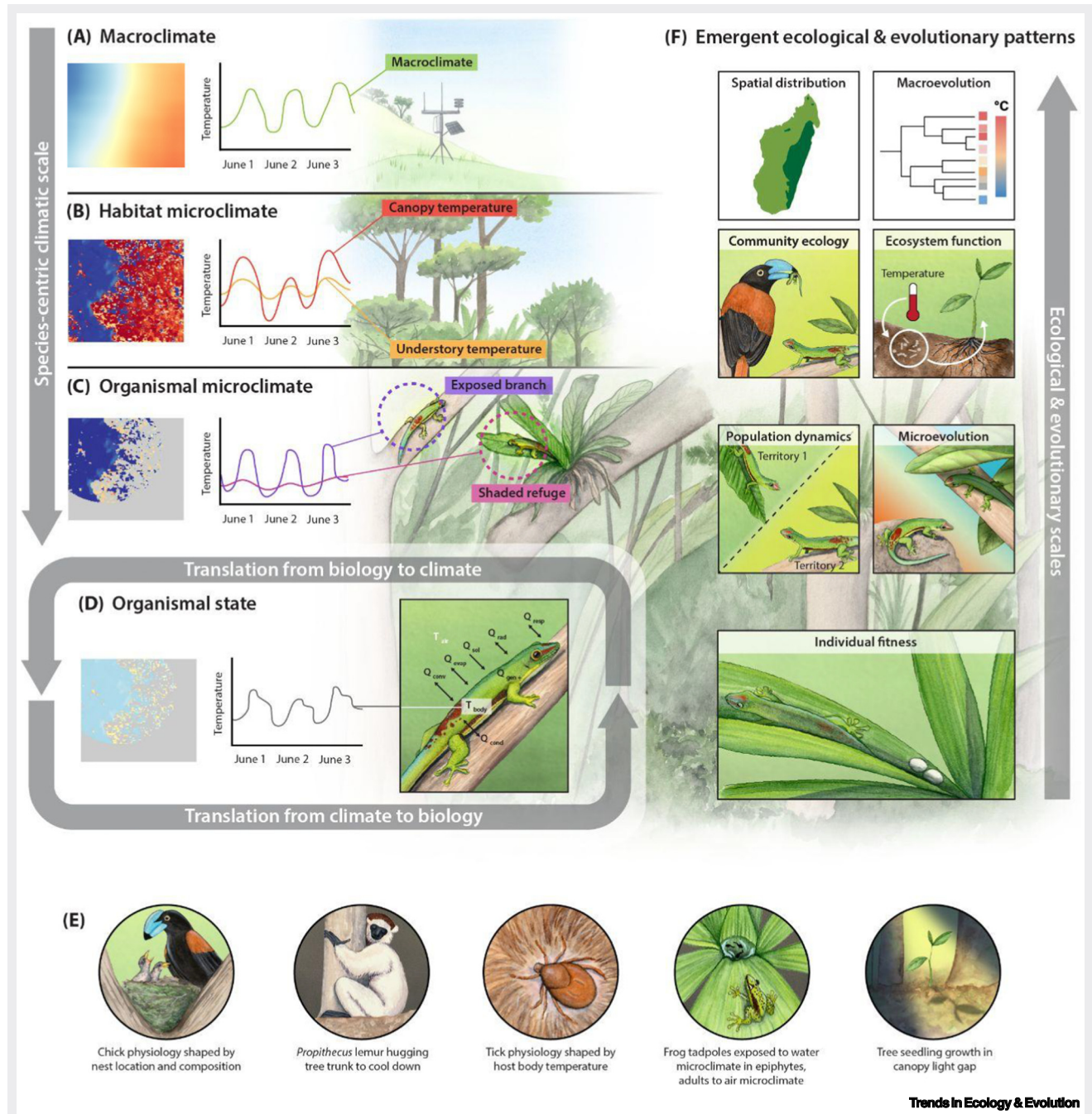


Figure 1. Nested systems of climate scale. Macroclimate, habitat microclimate, and organismal microclimate integrate downwards to shape organismal states. Organismal states feed back to influence organismal microclimates, and also propagate upwards to shape emergent ecological and evolutionary patterns.

physical conditions across space and time leading up to the moment of sampling, and populations occur at a location given past climates [34]. The role of these spatial contexts and climate histories are critical but not fully understood. Across space, organisms may preferentially select certain conditions (i.e., organismal microclimates) over other available conditions; why an

organism is found somewhere may therefore strongly depend on avoidance of microclimates elsewhere. Identifying why behavioral microclimate selection occurs is informative for understanding thermoregulatory capacity, niche limits, or non-climatic constraints on spatial distributions [35].

Across time, an organism's development, phenology, and fitness depend on prior climate exposure. Two organisms occupying the same microclimates today may have substantially different fitness given their differential historic climate exposure. The mean and variability in temperature and moisture experienced during formative life stages – such as during embryonic development or metamorphosis – can shift an organism's ontogenetic trajectory [36]. Temporal lags often exist in biological responses to climate due to metabolic latency, behavioral inertia or memory, population dynamics, or adaptation to past climates [34]. The sequence of thermal and hydric time series is also important, determining durations suitable for activity [20,37], physiological damage or repair [38], and dispersal distances [39].

Some approaches can help us to understand the effects of spatial context and prior climate exposure. Techniques from landscape ecology quantify spatial variability and scale-of-effect [40,41]. Modeling thermal load sensitivity, rather than critical thermal limits, accounts for cumulative stressful thermal exposure [38,42]. Rather than measure or model climate conditions just at locations and times of biological records, researchers can define climate data extent and duration according to the organism's home range and generation time (Figure 2). Open-source tools [43] can then aid in evaluating what climate windows are most strongly correlated with a biological response of interest. Generalizing knowledge of climate–biology processes may also be most mechanistically sound when scales are couched not just in absolute spatial units (e.g., meters) or temporal units (hours), but instead in biological traits and processes that consider how an organism experiences and filters its environment (e.g., perceptual range, phenological time, **dispersal kernel**) [44] (Figure 2).

Principle 4: interactions of organismal microclimate and organismal biology drive emergent ecological and evolutionary patterns

While macroclimate, and therefore habitat microclimates, sets boundaries on available conditions, organismal microclimates and species' traits interact to shape climate exposure. These fine-scale interactions propagate upward to influence ecological and evolutionary patterns [1,2]. For instance, organismal microclimates affect water transport within individual plants, which shapes individual growth and population viability. These local processes generate inter-population productivity patterns across a latitudinal precipitation gradient [1]. The phylogenetic diversity of thermal niches across animal clades also arises from microclimate heterogeneity experienced by individuals of each species [45]. While fine-scale phenomena may average out at larger scales to correlate with macroclimate, whether such patterns are mechanistically sound depends on the direction and structure of fine-scale processes [17,46]. For instance, many studies report little or no mean change in terrestrial range shifts towards cooler locations [47], yet individuals or populations may actually be tracking suitable microclimates in contrasting directions that cancel each other out in the aggregate [39,48]. Averaging climate can lead to misinterpretation of climate effects, given biological nonlinearities and **Jensen's inequality** [46,49]. Observations, simulations, and manipulations of climate–biology relationships conducted at different scales can provide insight into which individual-level processes shape emergent patterns (Box 2).

Linking climatic and biological scales from individuals to communities

Stemming from these principles, we present a framework (Box 2) that guides researchers on how to integrate climate-first and biology-first approaches for scale-informed investigation of the role

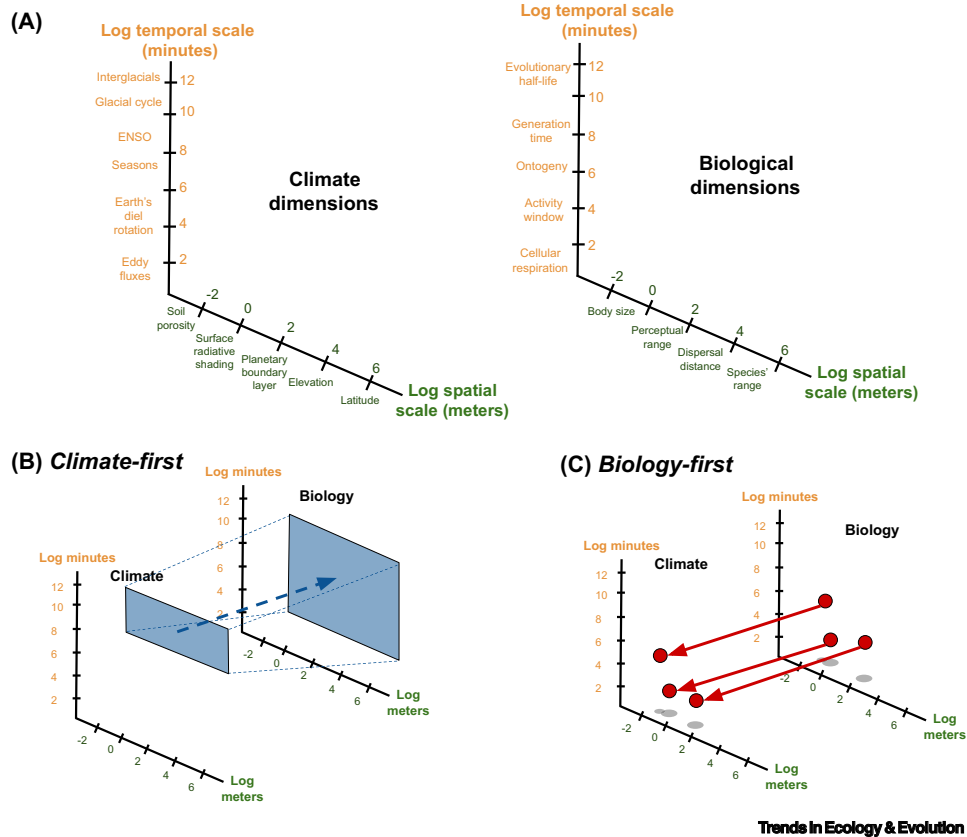


Figure 2. Deriving relationships between climate and biology across spatial and temporal scales. Climate and biology are both composed of processes nested in space and time, as represented here by Stommel diagrams (A). Climate scales are determined primarily by meteorological forcing, and biological scales are determined primarily by species' traits. Climate and biology at the same extent may correlate with each other (e.g., latitudinal clines and a species' range, both at broad scales), yet these correlations oftentimes are due to causal relationships at finer scales. (B) Climate-first approaches conceptualize climate as shaping ecology and evolution, exploring correlative patterns (dashed arrow) between climate and biology in a manner that seeks to extrapolate inference across scales (polygons). (C) Biology-first approaches explore how biological traits shape climate exposure, exploring causal mechanisms (solid arrows) in a manner that is specific to a species, system, and given scale (points). These approaches can be combined to capture dynamics between climate and biology at different spatiotemporal scales: for example, that fine-scale microclimates may influence broad-scale biology (see [Box 2](#) in the main text).

of climate in ecology and evolution. Complementing this framework, we synthesize insights on climate–biology interactions across four domains: individual traits, vertical and horizontal niches, biotic interactions, and biological communities.

Individual traits filter climate exposure

While the magnitude of environmental variation sets constraints on available habitat microclimates, organismal traits shape how available conditions translate into experienced climate [50]. For example, all else being equal, larger and more mobile organisms can perceive [19] and sample [51] a greater range of microclimates than smaller or more sedentary organisms [52] (Figure 3). Organism size also determines the height at which microclimate is experienced [53] and with what biophysical processes an organism interacts: megafauna experience microclimate gradients induced by tall plant canopies [28,54], while tiny organisms (<1 cm) are subject to the microscale boundary layer of air near surfaces [52,55]. Drawing from

landscape ecology [41], researchers can investigate how organismal traits cause variation in the scale-of-effect of climate on biological responses. This approach leverages gridded climate data with a biology-first lens of how traits filter an organism's climate exposure.

In addition to size and mobility, behavioral regulation and microhabitat preferences can define organismal microclimates, limiting exposure to climatic extremes [56]. Lungless salamanders, for example, are sensitive to desiccation, and remain underground when surface conditions are warm and dry [33]. Leaf area and stomatal control both influence plant hydroregulation via transpiration [1]. Buffering behaviors present an immediate line of defense against stressful climatic extremes, but such behaviors are not equally accessible to all organisms. In response to rising temperatures in the Mojave Desert, rodent communities retreat belowground to avoid hot extremes; most birds, however, cannot dig belowground and instead have experienced local extinctions (Box 2).

By reducing exposure to extremes, regulating behaviors can buffer natural selection and slow the pace of local adaptation, a phenomenon known as the **Bogert effect** [22,57,58]. For instance, despite the broad climate conditions experienced by the eastern fence lizard across 20° in latitude, its strong thermoregulatory capacity collapses experienced thermal variation to limit local physiological specialization across its range [59]. Likewise, behavioral thermoregulation limits physiological divergence of bees [60] in urban heat islands.

The instantaneous, microevolutionary, and macroevolutionary potential of buffering behaviors all hinge on the magnitude of climatic exposure in space and time. Spatial homogeneity of temperature at night provides nocturnal species with a low capacity to thermoregulate; correspondingly, the capacity for the Bogert effect is weaker in nocturnal than in diurnal species [61]. If understanding mechanisms shaping emergent patterns (e.g., phenotypes) is a priority, fine-resolution

Box 2. A framework unifying climatic and biological scales

To advance understanding of how climate links to biology, we present a framework integrating climate-first and biology-first approaches. The framework outlines tools and practices for an iterative research program, helping researchers position their work across these approaches. We map a case study by Riddell *et al.* [93] onto this framework to illustrate how both approaches can be combined.

Inquiry should begin by articulating research questions linking climate and biology (Figure 1A). The nature of these questions – such as scale of inquiry (species versus communities; local versus global) – guides the analytical path. Questions about correlations between climate and biological responses align with climate-first, whereas questions about mechanisms linking climate exposure to organismal function align with biology-first. Riddell *et al.* examined how macroclimate trends relate to demographic change in desert birds and mammals (climate-first) and which organismal traits explain variation in such relations (biology-first) [93].

With questions defined, researchers should propose scale-explicit hypotheses about links between climate and biological processes (Figure 1B). Relevant scales may be guided by available data: for Riddell *et al.*, a multidecade Mojave Desert animal resurvey. They hypothesized that decadal macroclimate warming influenced abundances, and that two niche dimensions (vertical habitat use and diel activity) plus morphological traits (e.g., body size) shaped climate exposure and mediated abundance responses.

Research question(s) and study scales then point toward climate-first, biology-first, or combined approaches (Figure 1C). To explore demographic correlations with macroclimate, Riddell *et al.* modeled dynamic occupancy for birds and mammals using weather station data. To investigate trait-based origins of climate responses, they estimated thermal conductance and morphology using museum specimens.

Cross-scale research benefits from pairing climate-first and biology-first approaches to address complementary questions, or integrating them to scale up proximal mechanisms [106] (Figure 1D). Exemplifying the latter, Riddell *et al.* parameterized mechanistic microclimate and biophysical models for each species (biology-first), then used those models to simulate behavior and physiology responding to dynamic climate grids (climate-first). A biology-first approach alone would limit inference to individual responses; a climate-first approach alone would yield population-level patterns divorced from organismal biology.

Integrating climate-first and biology-first approaches yields cross-scale discoveries that neither approach could provide independently (Figure 1E). Such insights clarify scales at which climate and biology are causally linked, to refine questions on climate–biology relationships. Riddell *et al.* found that mammals avoided daytime heat by using belowground refugia, whereas most birds lacked burrowing abilities and thus faced greater heat exposure. These fine-scale mechanisms explain why mammals remained stable across decades of warming while birds declined. Subsequent questions can then seek to identify limits of scale domains or better represent fine-scale processes at broader scales.

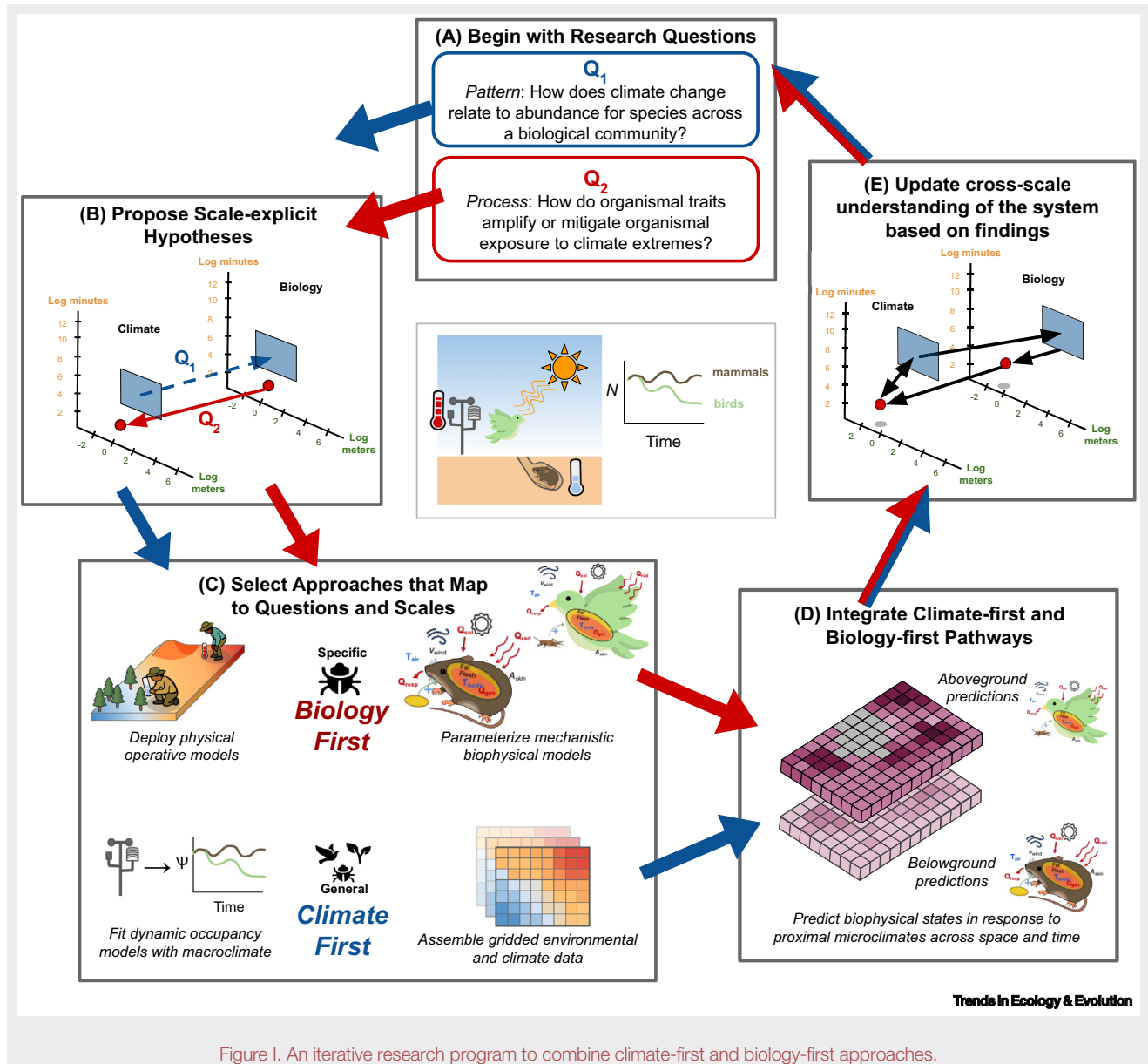
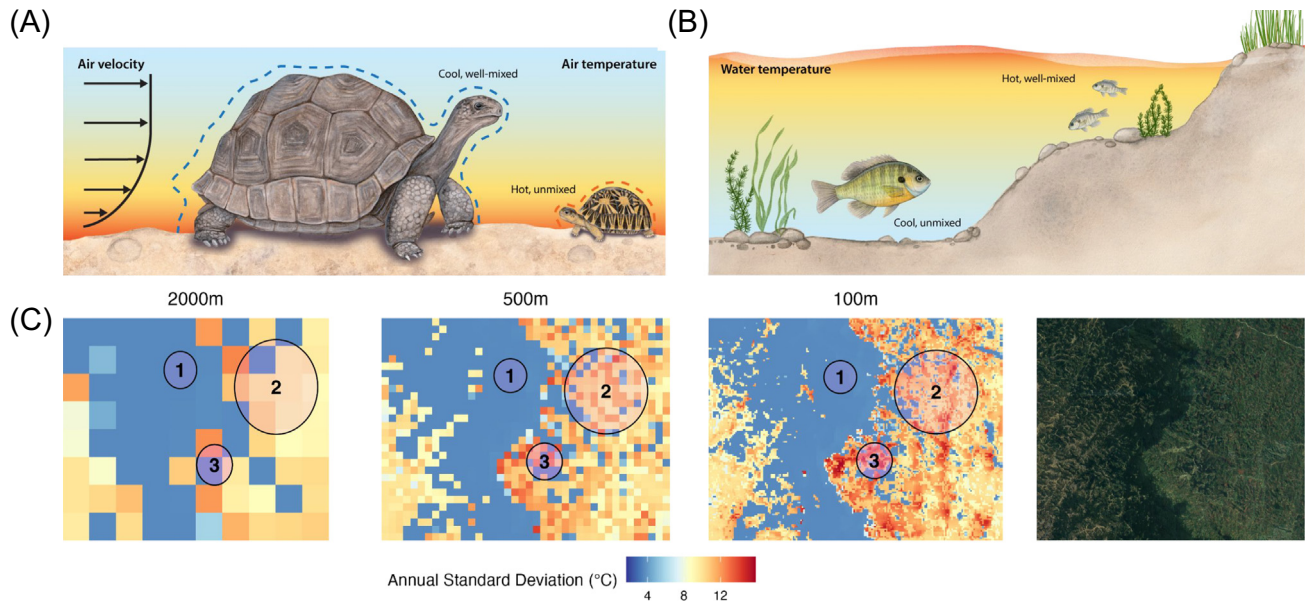


Figure 1. An iterative research program to combine climate-first and biology-first approaches.

microclimate data can help [9], but only if such data are filtered to an organism’s microclimate exposure.

Vertical, not just horizontal, microclimate heterogeneity and configuration influences species’ exposure
Most spatially explicit analyses have focused upon climate variation horizontally, but not vertically, given the convenience of horizontal gridded layers [11]. Yet there can exist sharp, and predictable, vertical gradients of wind and temperature within a few meters above and below aquatic and terrestrial surfaces, contingent upon the density of vertical layers, amount of topographic shading, and the **roughness length** for heat and wind of the surface, among other factors [24]. Changes in microclimate variance across meters of vertical space can equal the magnitude of changes in



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Figure 3. Scale of climate exposure is a function of morphology, biotic context, environmental heterogeneity, and the grain of the sampled environment. (A) Organismal morphology impacts the experienced microclimates (larger organisms tend to be farther above the ground, and thus more exposed to freely exchanging air, than smaller organisms) and body temperatures (size influences the inertia of energy and hydric transfer). (B) Size and biotic interactions can also determine microclimate availability; larger bluegill fish may occupy preferable oxygenated pelagic waters, relegating smaller fish to littoral (near-shore) waters. (C) The extent to which organisms sample their environments influences the need for fine spatial resolution. An organism with restricted mobility, perceptual range, or territory size occupying a homogeneous environment (⊙) may experience a narrow range of climatic conditions, which can be adequately represented with either coarse-(2000 m) or fine-resolution (100 m) microclimatic temperature predictions. Thus, coarse resolution maps here offer an adequate mean field approximation for fine resolution maps. Yet for organisms with either small or broad home ranges in heterogeneous environments (⊗, ⊚), fine-resolution maps are necessary to represent accessible thermal heterogeneity. How the organism interacts with such heterogeneity is contingent on behavior and morphology. The vertical habitat range of a species (i.e., how readily a species can move vertically below- and aboveground) should also determine the height(s) at which climate exposure is represented. Microclimate predictions derived from [114].

microclimate variance across hundreds of kilometers of horizontal space [62]. This vertical gradient creates microclimatic niche variation that influences key fitness-related processes – such as foraging, nesting, and hydric and thermal regulation – in frogs [61,63], fishes [64], insects [65,66], and epiphytic plants [67]. Estimates of climate exposure are thus highly sensitive to the resolution and spatial extent at which vertical microclimate profiles are characterized [53].

Spatial configuration – how features are arranged relative to one another – has long been central in landscape ecology [17,68], yet it has received relatively less attention in climate change ecology. However, the configuration of microclimates may prove more consequential than their mean conditions or overall variability [69]. Fine-grained microclimate configuration can influence the thermoregulatory capacity of individual organisms [20,53,55], and how mobile organisms navigate landscapes. For tiny insects this may include the orientation and morphology of leaves and rocks, which can change surface temperature by up to 20°C over a few centimeters [70]. Thermoregulatory costs decline when thermal variation is high compared with the size of an individual’s territory (i.e., a ‘fine-grained’ thermal habitat) than when variation is low relative to territory size (i.e., a ‘coarse-grained’ thermal habitat) [8,35] (Figure 3). Correspondingly, thermoregulation is more common in lizard species from forest edges (a more fine-grained habitat) than in their counterparts from closed-canopy forests (a more coarse-grained habitat) [45]. At landscape scales, land cover and topography shape microclimate configuration [69], which determines thermal connectivity and how organisms disperse to track suitable conditions [71]. Consequently,

overlooking microclimate heterogeneity may undermine estimates of species' ranges and range shifts [5,39,48,72]. Landscape resistance modeling [73,74] can predict the likelihood of movement while accounting for microclimate configuration, and is well poised to capture meaningful climate exposure if resistance maps represent biological responses to organismal microclimate (e.g., biophysical stress).

Feedbacks between climate exposure and biotic interactions

In Hutchinsonian niche theory, climate constrains niches broadly, while biotic interactions refine them locally [64,75]. Yet, biotic interactions such as competition and predation also shape organismal microclimates by influencing access to preferred microhabitats and resources [76,77]. For instance, dominant bluegill fish exclude smaller individuals from thermally optimal sites [78] (Figure 3). Similarly, lizards compete for microhabitats providing favorable thermal and radiative conditions [77], while plants and corals vie for optimal light conditions [79,80]. Plant community composition shapes vertical thermal and light gradients in forests [28], and total biomass determines oxygen gradients in lakes [64]. Cross-scale relationships also exist: macroclimate trends (e.g., warming/drying) can influence the strength of biotic interactions, thereby determining microclimate availability [81]. For example, under historic macroclimate conditions, treefrogs occupy preferred microclimates, but simulated drying enables invaders to outcompete resident species, displacing poor competitors into less favorable thermal and hydric conditions [82]. Accordingly, biotic context strongly mediates access to specific microclimates.

The grain and extent of climate data may determine detection of competition or niche overlap between species. Coarse-scale climate data may suggest niche overlap or competition where none exists, whereas finer-scale organismal microclimate data can reveal niche partitioning [8,58,83]. Accurately interpreting interspecific niche overlap requires consideration of the biotic dimensions alongside climatic conditions [76].

Fine-scale microclimates are subject not just to biotic context, but can feed back to shape biotic interactions. Microclimatic heterogeneity shapes patterns of butterfly oviposition on host plants, driving more egg-laying variation within than among populations [84]. Similarly, microclimate-informed models alter predictions of parasitic impacts, such as bark beetle infestations [85]. Organisms may leverage microclimatic heterogeneity to enhance fitness by mitigating thermal, hydric, or pathogenic stress; amphibians that use warmer microhabitats garner greater resistance to chytridiomycosis [86]. Understanding how organismal microclimates may impact biotic interactions requires the identification of appropriate climate resolution and extent based on organisms' habitat selection behaviors and local climate heterogeneity (Figure 3).

Furthermore, the structure of biotic interactions and associated climatic exposure can change through an organism's life stages. Rapid growth or ontogenetic shifts can alter predator-prey dynamics, opening access to novel microclimates [87]. If such novel microclimates are more variable, then finer temporal sampling may be necessary. Ideally, each interacting species' organismal microclimates and physiology are represented, yet examples of such work are few (but see [83,88]). Practical alternatives include biotic rescaling, which simplifies multiple climatic and biotic factors into fewer proxies (e.g., using tree canopy structure to simultaneously represent microclimate and primary productivity) [89]. Such simplified representations facilitate modeling, albeit potentially with low transferability to new contexts.

Representing scale-appropriate climate across biological communities

Community assembly both shapes and responds to scale-dependent climate effects on organisms. The resolution of climate data affects how strongly and clearly community-level patterns

emerge; in birds, community dissimilarity and turnover appear lower when macroclimate data are spatially coarser [90]. Higher spatial resolution, however, may only improve explanatory power of community responses if accompanied by increasing climate proximity, as found with plant communities [72,91,92]. Thus, climate data resolution becomes meaningless, and even misleading, if not capturing the right time periods, heights, or environmental features relevant to each species in a community (Figure 2).

Differences among species in morphology, activity timing, and movement make it difficult to characterize community-wide climate exposure [7]. But progress is more readily made when those communities share similar microclimates, such as understory plants in closed-canopy forest [92] or graminoids and bryophytes in tundra [89]. For other systems, disparities in vertical niches (arboreal versus terrestrial) or organismal mass can cause substantial differences in microclimate exposure, and thermal niches, across a community [61,63]. Accurately assessing climate impacts on most communities will require the difficult but important task of representing organismal microclimates and their biophysical consequences, rather than applying a single habitat microclimate for all species [93].

Concluding remarks: the frontiers of scaling climate to organisms

Environmental change and organismal traits jointly determine organisms' microclimate exposure. Many ecological and evolutionary studies have taken either a climate-first approach and prioritized obtaining high-resolution climate data, or a biology-first approach and focused on climate exposure for specific taxa. These two approaches are in fact explicitly measuring different climate scale systems: habitat microclimate or organismal microclimate, respectively. With this recognition, we can better leverage each approach, and our framework (Box 2) demonstrates how to integrate these two traditions to identify appropriate scales for climate data collection and analysis. This integration requires quantitative assessments of when mean field approximations – often inherent in coarse-scale data – fail.

SDMs in particular can benefit from incorporating feedbacks between climate and biology. Although SDMs have widespread utility for basic science and conservation [3], their capacity for out-of-sample prediction and for identifying causal mechanisms is limited, partly because they inadequately represent how organismal biology interacts with environmental exposure [94]. Recent advances can address these shortcomings. Examples include incorporating hypothesized causal relationships into SDM structures [95] using spatially varying covariates that implicitly capture variation in species–environment relationships [96], or setting SDM predictions as initial conditions for process-based movement and demographic models [97].

Integrating physiological, behavioral, and landscape ecology, and using next-generation technologies, can refine our understanding of climate–biology relationships (see Outstanding questions). Combining insights across disciplines can clarify how spatial environmental patterns and organismal decision-making jointly shape individual fitness through energetic and fear landscapes [98]. Remote sensing and big data can highlight large-scale patterns and anomalies that guide targeted observational and experimental studies [99]. Recent guidelines on microclimate monitoring also advance standardization of practice [29]. Animal-mounted sensors directly measure organismal microclimates [100] in tandem with body conditions. Sensor technologies could involve brain implants that manipulate physiological responses or behavior (e.g., testing the importance of thermoregulation), or 'Internet of Things' sensor networks that track ecological interactions (e.g., testing microclimate dependency of pollination events [101]). Mechanistic microclimate [102,103] and biophysical niche models [104,105] bridge climate-first and biology-first approaches, linking spatial microclimate data with organismal traits to model dynamic exposure

Outstanding questions

What organismal traits (e.g., size, activity window, generation time) are most important in shaping the scale at which organismal microclimates are experienced, and what is the degree to which they are decoupled from habitat microclimates?

What landscape features (e.g., vegetation, topography, human-built structures) are most important to represent in order to help distinguish habitat microclimates from macroclimates?

What grain of spatial and temporal resolution in trait information, such as field body temperature or heat tolerance, is sufficient or most appropriate for scaling biology-first approaches to meet climate-first approaches?

For comparing across species and systems, should the scale of climate–biology processes be expressed in absolute spatiotemporal units (e.g., meters and hours) or in organism-relative units (e.g., body lengths, generation times)?

How does consideration of both climate and biological scales aid understanding of intraspecific niche conservatism versus phylogenetic niche conservatism?

For what systems, species, and ecological or evolutionary processes is a mean field approximation best upheld, so that macroclimate may be a suitable proxy for climate exposure?

Are there generalizable statistical properties (e.g., spatial autocorrelation, fractal dimensions) that can distinguish climate variation at macroclimate, habitat microclimate, and organismal microclimate levels?

How can novel sensor technologies help measure organismal microclimates and quantify the roles of physiology and behavior in shaping climate exposure?

[7,106]. Although current niche models rarely incorporate biotic interactions or density dependence, they can be integrated with models that do represent these processes [107].

Nevertheless, many such approaches are only as reliable as the biological data brought to bear. In this regard, natural history and physiological data acquisition are as essential as ever. Large-scale trait databases are becoming increasingly available [108–110], and are critical for developing reliable generalizations between organismal traits, environmental contexts, and climate exposure. Clearly acknowledging assumptions and uncertainties in climate–biological relationships will promote transparency, facilitate effective research, and highlight gaps needing future investigation.

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Declaration of interests

The authors declare no competing interests.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work we used ChatGPT 5.0 to simplify some parts of author-generated text, using only author-identified references. After using this tool, we carefully reviewed and edited the content and we take full responsibility for the content of the published article.

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