



# Changing Thermal Landscapes: Merging Climate Science and Landscape Ecology through Thermal Biology

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## Abstract

Climate change and habitat modification both alter thermal environments and species distributions. However, these drivers of global change are rarely studied together, even though many species are experiencing climate change and habitat modification simultaneously. Here we review existing literature and propose avenues for merging the largely disparate lines of climate and landscape ecological research using temperature exposure and species' thermal sensitivity as a shared framework. The integration of research on climate and landscape change is in the early stages and lags behind research focused solely on the ecological effects of climate change. Recent studies highlight important mismatches between the resolution of widely used climate datasets and ecological processes, which can be addressed through detailed mapping of thermal landscapes and the microclimates within them. Furthermore, the thermal niches of species, evolved under past climates, can predict the responses of species to changing microclimates associated with habitat modification; this suggests that microclimates and thermal niches may together act as a common filter, reassembling communities in response to both climate and landscape change. There is a need to further integrate microclimate and thermal niche data into landscape ecological research to advance our basic understanding of the combined effects of landscape and climate change and to provide actionable data for climate adaptation strategies that largely focus on activities at landscape scales.

**Keywords** Thermal niche · Temperature · Microclimate · Connectivity · Redistribution · Climate change

## Introduction and Overview

Habitat modification and climate change are among the primary threats to global biodiversity. Ameliorating catastrophic species losses will require concerted research and management strategies that target the combined effects of these threats [1], including processes that occur at landscape scales [2].

Current climate change research, however, disproportionately uses regional and global scale data [3, 4], whereas many population management and climate change adaptation strategies occur at local and landscape scales (e.g., wetland restoration, adaptive land use management, reforestation, and ecological corridors) [5]. Therefore, rapid integration of climate science and landscape ecology is needed to generate information that is actionable for conservation practitioners who must plan for climate change resilience when managing populations, reserves, and corridors.

Although species are experiencing both habitat modification and climate change simultaneously, these threats are typically studied independently [6, 7]. Many studies have documented recurrent landscape patterns and processes resulting from habitat modification, including habitat area effects [8, 9], altered connectivity [10, 11], land-use matrix effects [12–14], metapopulation dynamics [15], and changes to ecosystem services [16, 17]. In the last 20 years, a growing literature on the ecological consequences of climate change has also identified emergent trends [4, 18], including range shifts [19], changes in

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phenology and morphology [20, 21], physiological responses [22], mass mortality [23], and changes in abundance and community composition [24, 25]. Successfully integrating both fields will be critical as habitat modification continues and climate change intensifies.

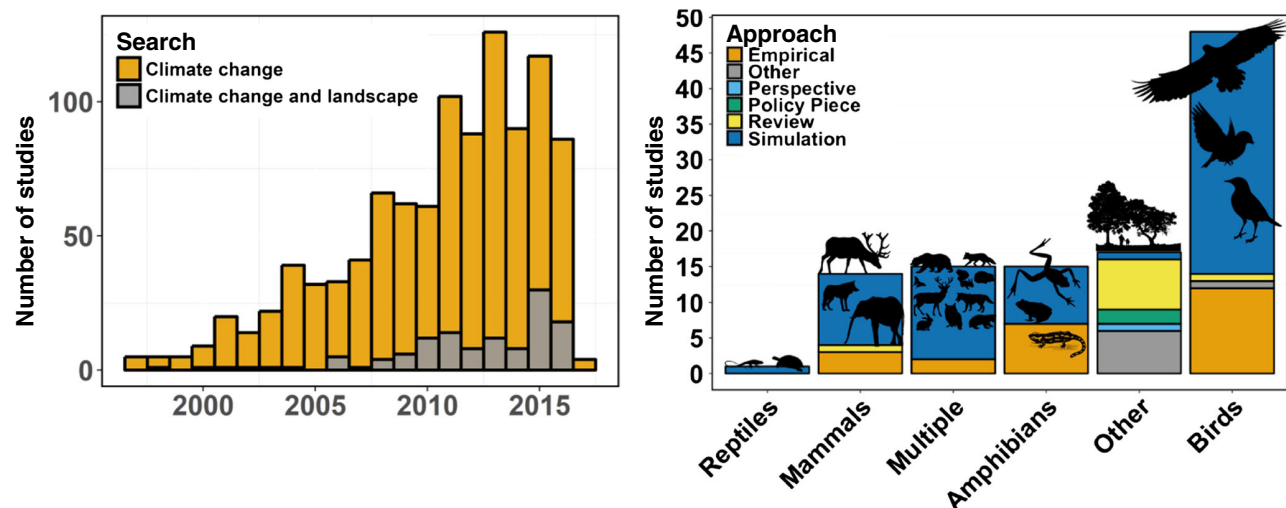
Fortunately, signs of a nascent paradigm at the nexus of climate change and habitat modification research is emerging. Recent work highlights the centrality of microclimate variation and climatic niches to understanding species responses to climate change [26–29]. Because habitat modification also affects thermal landscape variation [14, 30, 31], integration of data on microclimates and climatic niches will likely accelerate insights into the vulnerability of organisms to the combined effects of climate and landscape change. The two principle components for assessing vulnerability of organisms to environmental changes are a species' exposure and sensitivity [32]. In changing thermal environments, temperature variation across space and time determines an animal's exposure, whereas its sensitivity is largely governed by climatic niche—as well as the traits, population dynamics, and adaptive capacity associated with that climatic niche.

The aims of this review were to examine (1) how an animal's *exposure* to novel temperature regimes is mediated by microhabitats and landscape features and (2) how species-specific *sensitivity*—determined by thermal niches—can directly and indirectly shape species distributions and filter animal communities in changing thermal landscapes. We focus primarily on aspects of the thermal niche as potential mechanisms underlying species sensitivity to both climate and landscape change; however, other niche axes could similarly mediate responses to these threats, including tolerance of changing moisture and salinity regimes. To provide context for this discussion, we first give a brief overview of trends in the

number of studies of terrestrial vertebrates that integrate climate and landscape variables. We then discuss how microclimate variation and thermal niches can be further integrated into landscape-scale studies to address problems related to climate change adaptation, providing an example of thermal landscape connectivity. Here, we define “landscape scale” as a spatial extent at which local populations (and communities) belonging to a regional species pool can be structured across multiple (macro-) habitat types. We expect that continued integration of fine-scale climate data and thermal biology into landscape ecological research will provide advances in management of at-risk species and communities through better understanding of species distributions at the landscape scale.

### Trends in Research Efforts to Merge Climate Science with Landscape Ecology

To examine trends in the number of studies focused on climate change effects on landscape patterns and processes of terrestrial vertebrates, we searched the Web of Science (WOS) database on February 14, 2017, using the following search terms: TITLE (“climate” change) AND TOPIC (“vertebrate\*” OR “amphibian\*” OR “reptile\*” OR “bird\*” OR “mammal\*”) AND TOPIC (“landscape\*”) from 1997 to 2017. For comparison, we then performed the same search after dropping the search term TOPIC (“landscape\*”). We obtained 1153 total articles, 1029 that were unique to the “climate change-only” search and 124 articles from the “climate change” AND “landscape” search (Fig. 1). This comparative search provided an index of research effort focused on climate change at all scales versus climate change effects at landscape scales; however, results may be subject to errors of omission such that some studies could focus on



**Fig. 1** Despite the rapid growth in climate change publications since 1997, relatively few studies have examined climate change effects in an explicitly landscape-level context as shown by Web of Science® search

results (left panel). Simulation studies and studies on birds tended to be the most common articles returned from the search for “climate change and landscape” keywords (right panel)

landscape-scale processes but not include the word “landscape” in the title, abstract, or keywords. Therefore, we also performed a complementary search in the journal *Landscape Ecology*, which is focused almost exclusively on landscape patterns and processes, between 1997 and 2017 using the search term “climate change.” We refined this search by (1) excluding reviews and perspectives, (2) retaining only articles that had climate\* OR warm\* OR temperature OR “global change” in the title, and (3) manually checking these articles and retaining only those that focused on terrestrial vertebrates, which yielded 19 articles out of 2131 articles published in the journal during the search period.

These complementary literature searches both suggest that the integration of climate change and landscape ecological research on terrestrial vertebrates is underway but makes up only a small percentage of the literature on climate change or landscape ecology (~ 11%, based on WOS search—Fig. 1a; ~ 1%, based on *Landscape Ecology* search). These trends are consistent with a contemporaneous survey of the literature that identified only 12 studies that fully integrated land use and climate change into study designs when analyzing change in species distributions [7]. Our examination of trends here shows that, among terrestrial vertebrates, studies have focused disproportionately on birds and that simulation or modeling studies far outnumber field-based studies (Fig. 1b, based on the more comprehensive WOS results). The literature was also biased toward temperate systems, with only 27% of studies occurring in the tropics.

Studies returned by these searches varied considerably in conceptual focus, but authors typically used one of several approaches: they (1) examined shifts in observed distributions using climate and landscape variables as predictors or expected distributions using species distribution models (SDMs) [33–39], (2) modeled changes in functional connectivity under climate change [40, 41], or (3) examined the value of current reserve networks for ameliorating the effects of climate change [42, 43]. Most studies did not, however, explicitly incorporate potential mechanisms underlying species responses to both land-cover and climate change, such as species’ fundamental thermal niches [31], desiccation risk [44], behavior [45], or the buffering potential of microhabitats [27]. These mechanisms are becoming widely incorporated into climate change research and can provide a common currency for understanding the combined effects of habitat modification and climate change on landscape-scale patterns and processes. Below, we summarize how these mechanisms may determine species’ vulnerability, via their exposure and sensitivity, as land-cover and climate change reshape thermal landscapes.

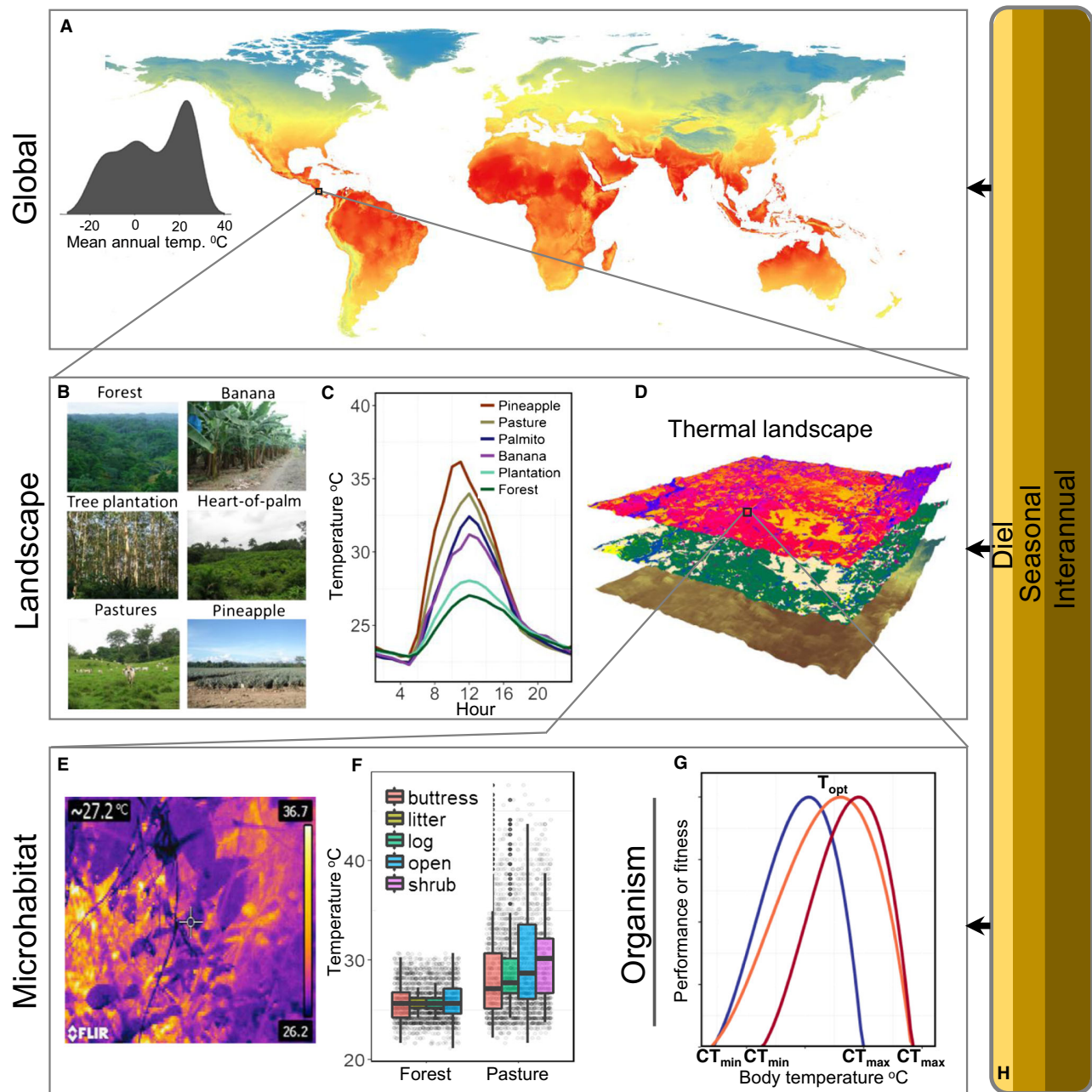
## Exposure: Landscape Features and Climate Change Shape Thermal Landscapes

The environmental temperatures that animals experience vary as a function of location and time, and the factors driving

temperature variation are highly scale-dependent (Fig. 2). Quantifying temperature exposure, therefore, requires understanding the spatial scale relevant to the daily and seasonal life history processes of the focal organisms as well as the factors that contribute to spatial structuring of thermal variation at that scale. Many terrestrial vertebrates experience spatial temperature variation on the scale of several to 100s of meters per day, depending on body size and mobility [47]. Therefore, an animals’ vital life-history processes (e.g., foraging, mate searching, and dispersal) are often responding to temperature variation at microscales (among microhabitats) to mesoscales (among landscape features). This temperature variation is largely mediated by microhabitat structure at the microscale, land-cover composition and topography at the mesoscale (i.e., landscape scale), and latitude at the global scale. Importantly, the climatic conditions at each scale are nested within, modified by, and variously decoupled from the conditions at coarser scales (Fig. 2). Below we discuss sources of temperature variation across scales, the organism’s role in exposure, and important considerations when measuring temperature exposure.

## Microhabitats and Microscale Thermal Heterogeneity

At microscales, various microhabitats, such as tree gaps, rocks, logs, and phytotelmata, provide a spatial and temporal mosaic of temperatures, which animals exploit to thermoregulate and to buffer themselves from extreme temperatures [27]. Microhabitats buffer temperatures in a consistent manner within forest systems across the globe and can reduce extreme heat exposure by up to 10 °C [48]. However, the availability of microhabitats and the magnitude of their buffering effects depend on the specific land-cover type in which they are found, such that daytime temperatures of microhabitats increase with decreasing canopy cover [49]. In the tropical Andes of Colombia, for example, thermally buffered microhabitats increased in abundance and changed in composition with forest succession, from young-secondary forest to primary forest [50]. The orientation of microhabitats also contributes to the variation in temperatures experienced by organisms [51, 52]. For example, the shape and aspect of individual boulders generates temperature gradients of 11 °C across rock surfaces, within just 2 m<sup>2</sup>, allowing animals such as lizards to track a narrow range of preferred body temperatures [53, 54]. Similarly, thermal variation along the vertical strata of habitats provides thermoregulatory opportunities for arboreal species that can climb or descend to track preferred temperatures [55]. In many instances, the buffering capacity of microhabitats is closely tied to water availability and so may change in time, depending on rainfall. For example, *Asplenium* bird’s nest ferns, found throughout the Paleotropics, can buffer ambient temperature by several degrees Celsius, but this difference diminishes as ferns dry [56].



**Fig. 2** Variation in thermal exposure and sensitivity. At the global scale, (a) mean annual temperature increases with decreasing latitude [46]. Within this global context, temperature variation at the landscape scale is driven largely by macrohabitat types (i.e., land-cover types; b, c; Nowakowski et al. 2017b) and topography (d). At any given point on the landscape, there can be considerable microclimate variation (e; Scheffers et al. 2017b) that in turn is mediated by macrohabitat type (f; Nowakowski et al. *unpubl.*). Organisms typically experience spatial

temperature variation at the microhabitat and landscape scales. The temperature-dependent performance or fitness of organisms varies among species, resulting in thermal performance curves with different shapes and breadths, as determined by parameters such as critical thermal minimum ( $CT_{min}$ ) and maximum ( $CT_{max}$ ) and thermal optimum ( $T_{opt}$ ) temperatures (g). Temperature variation at diel, seasonal, and interannual temporal scales interacts with spatial temperature variation (h)

### Landscape-Scale Thermal Variation

At the landscape scale, temperature variation is determined extensively by land-cover type (and associated vegetation structure). Adjacent land-cover types (e.g., forest vs

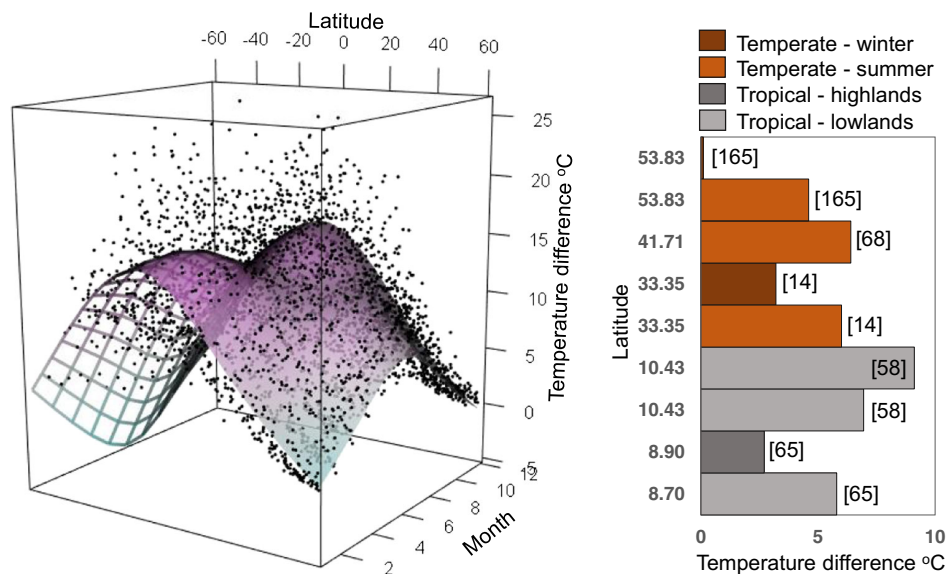
pasture) can differ in maximum, near-ground air temperatures by  $> 10$  °C, resulting from differences in height and cover of vegetation that intercepts direct solar insolation (i.e., shade) [14, 49, 57]. The extent and magnitude of thermal edge effects along land-cover ecotones can depend

on the presence of streams and the structure of vegetation, which may transition gradually or abruptly between land-cover types [30, 31]. Anthropogenic land-cover types, such as agricultural and urban land uses, are typically hotter and drier than forests during the day [58], suggesting that daytime thermal conditions may represent a strong environmental filter shaping assemblages in human-modified landscapes [59, 60].

The thermal suitability of different land-cover types will also depend on the underlying topography [61]. The amount of direct solar radiation reaching substrates varies with aspect and slope (in addition to canopy cover), such that flat substrates and equatorial-facing slopes receive more direct radiation at solar noon [51, 61]. Therefore, topographical features like polar-facing coves and low-lying ravines may function as topographical refugia for cool-adapted species [29, 62]. Moreover, flat landscapes are often preferentially cleared for cultivation, frequently leaving forest remnants on steep slopes and rugose terrain that are less suitable for agriculture [63, 64]. Changes in elevation also modulate local temperatures through adiabatic lapse rates [65], modify temperature differences between adjacent habitats [66], and affect the movement of cold air—depending on inclination, cold air can drain from the uplands to form cold air pools in the lowlands [67].

### Temporal and Spatial Variation Interact

Temporal and spatial variation in temperature interact such that the difference in daytime temperatures between adjacent land-cover types varies across latitudes, seasons, and times of day. For example, differences between closed-canopy and open habitats are greatest in the tropics but these differences vary seasonally, especially in temperate zones (Fig. 3) [71]. Daily temperature fluctuations also depend on geographic location and habitat, with daytime temperature ranges often being greater in unshaded microhabitats, open land-cover types, and at high elevations [50, 52, 59, 69]. High daily temperature fluctuations in open habitats, for example, are due not only to extreme daytime temperature but also to low nighttime temperatures; at night, open habitats may be slightly cooler than forests because they radiate more long-wave radiation back to the atmosphere than forests [72]. Although most studies focus on extreme daytime and summer temperatures in limiting activity and causing thermal stress, cool nighttime and winter temperatures also affect thermal habitat quality [73]. In temperate zones, winter temperatures along a fragmentation gradient were coldest in highly fragmented landscapes, which may increase energetic expenditures and associated mortality for overwintering animals such as birds [74]. Species that live within dynamic thermal landscapes require buffered refugia



**Fig. 3** Left panel shows estimates of temperature differences between closed-canopy (100% shade) and open-canopy habitats (0% shade) across latitudes and season from a mechanistic microclimate model [68]. Kearney et al. [68] used the model NicheMapper to develop a global, gridded dataset of hourly microclimates (temporally downscaled) at different heights, levels of shade, and for different substrate types. This dataset indicates that near-ground temperature differences between closed- and open-canopy habitats tend to be greatest in the tropics, but the magnitude of differences varies seasonally and across latitudes. The color ramp corresponds to

temperature differences on the vertical axis, to aid visualization of fit surface. Right panel shows temperature differences between mean maximum daytime temperatures in forest and open-canopy habitats, as measured in the field and reported in the literature. Numbers in brackets indicate source studies as listed in references, from which we extracted habitat-specific temperatures from text, tables or figures [14, 59, 66, 69, 70]. Note that in addition to latitude, season, and elevation, other factors, such as precipitation, vegetation type, sensor type, and height of sensors, can contribute to the observed variation across studies

capable of mediating the loss of thermally-suitable habitat from concurrent land-cover and climate change.

### The Organism Is the Final Arbiter of Exposure

Ultimately, organisms mediate the microclimate variation they experience through their physical characteristics (e.g., body size, shape, color) [75], physiology (e.g., evaporative cooling), and behavior (i.e., thermoregulation) [76]. Although organismal traits can decouple environmental and body temperatures, largely through metabolic control in endotherms and behavioral thermoregulation in ectotherms, the thermal conditions individuals are exposed to constrain the range of potential metabolic costs and realized body temperatures. Importantly, the spatial scale at which air temperatures are most relevant to body temperatures will depend on the size and shape of the organism relative to the boundary layer (layer of air delineated by size and shape of the focal surface structure, such as a single leaf or entire forest canopy, and wind speed) [51]. For instance, surface and near-surface air temperatures across several to 10s of meters are relevant to the movement behavior of desert tortoises [77]; in contrast, leaf-surface temperatures across several centimeters are relevant to small insects [78].

### Integrating Climate Data into Landscape-Scale Research

Ongoing climate change operates on each source of temperature exposure (e.g., land-cover type) by increasing mean regional temperatures, temperature extremes [79], and altering regional patterns of precipitation [80]. As a result, landscape features that were once suitable, such as grasslands and pastures, can become too hot or too dry for some organisms [59] while increasing in suitability for others (e.g., heliothermic reptiles that bask in direct sunlight) [81].

These complex, spatiotemporal changes in thermal landscapes affect physical and biological processes that are of interest to climate scientists and landscape ecologists alike but cannot be adequately captured at the coarse resolution of most existing climate datasets [82]. The grid size of climate datasets used to predict species distributions is 10,000-fold greater, on average, than the animal's body length [3]. For example, the WorldClim datasets, widely used in species distribution models, interpolate temperature and precipitation data from often far flung weather stations that are typically placed in open areas [46, 83]. This results in a substantial mismatch between the climate grid (at a scale of  $\sim 1 \text{ km}^2$ ) and microclimates experienced by most species. To remedy this spatial mismatch, researchers are now developing high resolution microclimate maps that capture biologically relevant temperature variation.

### Making Microclimates from Macroclimates

Methods for downscaling coarse climate grids to landscape- and microscales generally make use of mechanistic or statistical approaches [3, 61, 84]. Mechanistic methods draw on equations from environmental biophysics to model local microclimate conditions, such as air and substrate temperatures, as a function of atmospheric and geographic parameters (e.g., latitude, azimuth of sun, slope and aspect of substrates, and attenuating effects of atmosphere and vegetation) [61, 85, 86]. Mechanistic microclimate models have also been coupled with biophysical models that iteratively solve energy-mass equations to estimate biologically relevant body temperatures and energy budgets [61, 76, 87]. In contrast, statistical downscaling involves regressing coarse climate data and environmental variables onto fine-scale microclimate measurements (e.g., using machine learning algorithms) and then projecting that model onto a spatial grid [88, 89]. Depending on the desired resolution, this process may proceed in hierarchical stages, first generating statistical associations between climate and topographic features and vegetation types and then downscaling to microhabitats within these features [29, 84]. For development and validation, both mechanistic and statistical downscaling requires measurements of local microclimates.

To measure temperature at fine spatial scales, researchers are increasingly deploying arrays of small sensors in the field [50, 88, 90]; attaching sensors to animals [77, 91]; or directly measuring body temperatures using implanted data loggers, infrared thermometers, and thermography [53, 92, 93]. The use of next-generation technologies, including improved infrared cameras deployed on the ground or on drones as well as LiDAR data to model topoclimate, provides unprecedented spatial resolution, and is rapidly being incorporated into ecological datasets [29, 94–96]. There are important tradeoffs among these methods, however; for example, infrared images measure substrate surface temperatures, whereas sensor arrays can better capture air temperatures. Thermal infrared images provide data at ultra-high spatial resolutions (e.g., 78,800 pixels per image), whereas thermal sensors provide high temporal resolution at the cost of spatial resolution relevant to small organisms [94]. The choice of appropriate method will depend on the size, mobility, thermoregulatory strategy, and the relative importance of direct and reflected solar radiation and conduction for the organism of study [3, 97].

### Microclimates Decoupled from Macroclimates

Perhaps one of the greatest hurdles to integrating climate data into landscape ecology is the uncertainty in how the rates of regional temperature changes will translate to temperature increases within specific landscape features and microhabitats. When projecting future temperatures using global circulation models, studies assume that rates of temperature increase will

either be uniform across habitats—equivalent to projected regional increases—or that there will be non-uniform rates of increase in different land-cover types [59] and microhabitats [27]. It is most likely, however, that topographic features and microhabitats will vary in the degree to which their temperatures are decoupled from regional temperature changes [29, 98, 99]. Improving predictions of microclimate stability over time will, therefore, be critical for mapping thermal refugia and predicting range shifts.

### Sensitivity: Thermal Niches, Behavior, and Water Loss in Heterogeneous Thermal Landscapes

Sensitivity to changing environments will be largely determined by a species' evolved niche, which describes how individuals' vital rates change as a function of environmental conditions. An area is within a species' fundamental niche if a population can maintain positive population growth rates under the prevailing environmental conditions, prior to effects of interspecific competition, predation, or mutualisms [100]. Typically, the realized niche, after taking into account biotic interactions and dispersal limitation, is more confined than the fundamental niche. Climate change ecologists increasingly use information on fundamental and realized thermal niches to predict the effects of climate change on species range shifts and extinction risk at broad spatial scales [76, 101–103]. These approaches can be adapted to research areas within landscape ecology to better explain organisms' distributions, metapopulation dynamics, and functional connectivity at the landscape scale. If the underlying assumptions are met (see below), quantifying organisms' niches can be a useful way to translate species' fundamental biology into mechanistic predictions of changes in population dynamics and species distributions under thermal landscape change.

### Correlative Approaches and the Realized Thermal Niche

The realized thermal niches of species—the range of temperature conditions where a species occurs—is often inferred using bioclimatic envelope models or other methods of relating species presences/absences to the climates in which they occur [104]. Species' climatic envelopes are useful in that they can predict species' responses to both habitat and climate change as a result of niche tracking. Cool-adapted species and climate specialists are likely to be more sensitive to future climate change than warm-adapted species and climate generalists [105–107]. In fact, there is an emerging link between the climatic conditions a species is associated with across their geographic range and how they use habitats available at the micro- and landscape scales [66, 105]. For example, in SE Costa Rica, amphibians and reptiles with warmer thermal niches (as assessed from their range-wide climatic conditions), were more likely to occur in

deforested habitats of a forest-agriculture landscape [66]. Although bioclimatic models are widely-used in climate change research, often requiring large, coarse climate datasets, landscape-scale studies may better define realized thermal niches by modeling variation in occupancy, abundance, or other population parameters as a function of fine-scale temperature variation across thermal landscapes [e.g., 66].

### Mechanistic Approaches and the Fundamental Thermal Niche

In contrast to the realized thermal niche, the fundamental thermal niche is typically measured using experiments to determine the range of temperatures under which growth (of populations or individuals), locomotion, or physiological processes can occur [108]. The most common approach is to generate a thermal performance curve (TPC) by measuring some aspect of physical performance across a range of temperatures that is assumed to correlate with fitness (e.g., sprint speed) [108–110]. One of the strengths of TPCs is that they estimate biologically meaningful quantities, such as thermal tolerance breadths and thermal optima. Thermal optima are temperatures at which performance (or fitness) is maximized, and performance (or fitness) decreases as body temperatures deviate from thermal optimum toward lower or upper thermal tolerances ( $CT_{min}$  or  $CT_{max}$ , respectively). Differences between habitat-specific field body temperatures and thermal optima (or preferred temperatures) provide a measure of thermal habitat quality [111] (but see [112]), which can be used to predict species distributions and population dynamics in heterogeneous landscapes. Although there is no single theoretically or empirically justified parameterization of a thermal performance curve [108], the parameters of TPCs provide direct measurements of species–temperature relationships that represent mechanistic predictions of responses to changing thermal landscapes.

The lower and upper bounds of the TPC,  $CT_{min}$ , and  $CT_{max}$ , are easily estimated parameters for many ectotherms and represent physiological limits beyond which organisms cannot function ecologically [113]. Thermal tolerance breadths of endotherms, however, are typically measured as upper and lower limits of the thermal neutral zone, the range of environmental temperatures beyond which organisms must raise their resting metabolic rate to maintain body temperatures [114]. Within the context of warming induced by climate and land-cover change, species-specific thermal tolerances may impose a hard-physiological boundary on habitat associations [113]. Importantly, performance will generally decrease steeply as a species approaches its upper critical temperature (Fig. 2g). As a result, organisms may experience severe fitness costs even at temperatures below  $CT_{max}$ , thereby limiting their distributions. As body temperatures approach  $CT_{max}$ , animals experience increased levels of corticosterone, production of

heat shock proteins, and decreased blood-oxygen concentrations [113, 115]. As climate and land-cover change increase risk of chronic or acute exposure to dangerously high temperatures, natural populations may experience elevated mortality risk [116], reduced foraging efficiency, increased metabolic rate and energy demands (in nocturnal species as well), or reduced activity in order to avoid thermal stress [117, 118]. However, avoiding thermal stress by reducing activity comes with opportunity costs of time spent foraging and searching for mates, which may lead to population declines and shifts in landscape distributions [119].

Thermal tolerances, especially  $CT_{max}$ , have been widely used to predict sensitivity of species to climate warming [28, 101, 120], and recently have been used to predict species' sensitivity to habitat modification [66, 121]. In forest-agriculture landscapes, for example, ectotherms with low heat tolerances were more likely to be restricted to cool, intact forests, whereas species with high heat tolerances were more likely to maintain high abundances in altered habitats, such as pastures and forest fragments [59, 121]; across multiple systems,  $CT_{max}$  alone explained 24–66% (mean = 38%) of the variation in species sensitivity to habitat modification. The difference between  $CT_{max}$  and habitat-specific body temperatures (i.e., the thermal safety margin) can provide a useful measure of vulnerability—combining exposure and sensitivity—to both climate warming and landscape change [28, 59] and may provide a means for mapping current and future distributions of thermally-suitable habitat.

### Changing Thermal Niches?: Assumptions, Adaptation, and Plasticity

Although thermal niches play a role in shaping species responses to thermal landscape change [31], integrating thermal biology with landscape ecology requires addressing the assumptions and limitations of these measures [108]. For example, correlative measures of realized thermal niches can differ substantially from fundamental thermal niches, in part, because areas of climatically suitable habitat often remain unoccupied due to dispersal limitation, competition, or resource distributions [114]. Furthermore, thermal traits derived from TPCs can vary substantially depending on the measure of performance used (e.g., locomotion, growth, or oxygen consumption), the method of measurement [122], prior temperature exposure [123], life stage [124], the presence of stressors (e.g., pollutants; [108]), and disease [125]. Importantly, commonly-used measures of the thermal niche do not provide details on actual population level vital rates, but instead assume that these measures correlate with population-level fitness. Future work must examine the links between the thermal traits of interest and the mechanisms by which populations persist or decline to determine the ultimate value of thermal niches for mapping species distributions at the landscape scale.

Predicting the effects of thermal landscape change on species distributions and population dynamics depends not only on characterizing species' thermal niches, but also on the degree to which thermal niches can change because of evolutionary adaptation and physiological plasticity. There is evidence for both adaptation and acclimation of thermal tolerances to local conditions in ectotherms such as lizards and frogs [126, 127]. However, thermal tolerances, especially upper thermal tolerances, are often highly conserved across species [128, 129] and exhibit limited acclimation potential (e.g.,  $CT_{max}$  increased on average by  $\sim 0.13$  °C per 1 °C increase in acclimation temperature for frogs and lizards; [123, 130]. Both acclimation and adaptation are generally more pronounced in cold tolerance [131], which probably provides only marginal benefits under climate change and habitat conversion because these threats likely often affect species at the upper end of their thermal tolerance range. The relatively low capacity for plasticity or adaptation to heat stress in many terrestrial ectotherms studied to date may lead to rapidly increasing mismatches between organisms' thermal niches and their thermal environment, especially for groups with longer generation times [18].

Examining individual variation in thermal traits among landscape features may provide clues to how organisms will adapt or fail to adapt to thermal landscape change. For example, strawberry poison frogs (*Oophaga pumilio*) occurring in forest and pastures showed no significant differences in  $CT_{max}$  even though individuals from pasture experienced warmer field body temperatures (often nearing mean  $CT_{max}$ ) and had higher preferred body temperatures than individuals from forest (Rivera-Ordoñez et al., *unpubl.*). In contrast,  $CT_{max}$  of ant populations in urban environments was higher than those in nearby rural areas [132]. By substituting space for time, thermally contrasting habitats (e.g., forest-agriculture or rural-urban gradients) represent “natural” experiments in which local populations are exposed to temperature differences across space that are equivalent to those expected over decades of climate warming.

### Thermoregulation and Behavioral Landscape Ecology

Thermoregulation—the ability to behaviorally track preferred temperatures by moving among microhabitats—can buffer terrestrial animals from extreme temperatures resulting from land-cover and climate change [76]. For example, during hot days, koalas adopt cooling postures pressed against tree trunks that are up to 9 °C cooler than surrounding air temperature [133]. However, during periods of extreme heat or drought, even cool microclimates may be insufficient to prevent mortality [134]. Importantly, as periods of extreme heat become more common in the future [135], it may not be within a species behavioral repertoire to use new microhabitats (e.g.,



burrows) when commonly used microhabitats become thermally unsuitable [136].

The variation and configuration of thermal environments across a landscape determines how effectively organisms can thermoregulate [112]. Models and field experiments suggest that dispersed rather than clumped thermal environments better allow ectotherms to maintain optimum body temperatures while using less energy to shuttle between adjacent suitable microclimates [112, 137]. In altered landscapes, organisms could incur greater energetic costs moving across converted habitats and secondary forests if spatial-microhabitat heterogeneity is lower in these habitats, as is the case in areas of the tropics [50]. In contrast, for heliothermic species, the establishment of plantations and reforestation efforts could limit their opportunities for thermoregulation [81]. The dependence of thermoregulation on landscape structure and associated microclimate heterogeneity could, therefore, affect the magnitude and timing of species responses to climate change.

The size, mobility, and perceptual range of an organism relative to the spatial grain of thermal landscape heterogeneity will ultimately determine the ability of species to thermoregulate effectively and buffer themselves from temperature increases [45]. Body size determines which microhabitats and what spatial and temporal scales are relevant for thermoregulation and highly mobile animals will be able to sample larger spatial extents than more sedentary species. When navigating heterogeneous landscapes, perceptual range of an organism will limit ability to detect available microhabitats, increasing search times, and thereby modify relative costs of thermoregulation [137–139]. However, few comprehensive examinations of the energetic costs of thermoregulation in human-altered landscapes exist, and quantifying these costs remains necessary for predicting the consequences for populations in changing thermal landscapes.

### Evaporative Water Loss in Changing Thermal Landscapes

Environmental moisture is often strongly and inversely correlated with temperature across landscapes, which means organisms in warm habitats are more likely to be challenged with minimizing water loss [60, 140, 141]. When exposed to high temperatures, organisms typically maintain body temperatures below lethal physiological limits by dissipating heat through evaporative cooling. Amphibians, for example, lose water through their highly permeable skin, which can reduce body temperatures by  $> 10$  °C below air temperatures [142]. However, this strategy may be effective for only a matter of minutes in open, dry habitats before individuals are at risk of lethal dehydration. If physiological constraints on either body temperature or dehydration are exceeded, mortality results, which can scale to mass die-offs at the population level during periods of extreme heat [23, 136].

As climate change increases the frequency of extreme temperatures and droughts, desiccation-prone species could cross thresholds at which they are unable to maintain viable local populations and metapopulations. In desert habitats of the Southwest USA, models project a fourfold increase in risk of lethal dehydration for small passerine birds by the end of the century [141], and dehydration risk will likely be mediated by the composition of land-cover and availability of suitable microclimates. Dehydration risk also depends on a variety of species traits. Within and among taxa, mass-specific water loss is greatest for small-bodied individuals [141, 143, 144], suggesting that small individuals (i.e., juveniles) and species may be most susceptible to dehydration resulting from climate change and habitat alteration. Microhabitat use, such as living in hot, dry forest canopies, can also prime species to deal with dehydration via physiological adaptations (e.g., cutaneous resistance in canopy frogs [143]).

Species resistance to water loss and variation in moisture gradients may interact to shape abundance and community structure across the landscape [145]. In a temperate forest, for example, water loss measured using physical models was significantly affected by topography and in turn predicted above-ground abundances of a plethodontid salamander [146]. In fragmented forests, desiccation-prone species may be less likely to persist in small forest patches due to increased winds, temperatures, and reduced humidity resulting from high edge-to-area ratios [60]. Species with low resistance to water loss may also be susceptible to isolation effects [10, 44], resulting from reduced survival and movement in the matrix and the influence of maintaining water balance on space use and movement behavior [144, 147, 148]. For example, desiccation-prone amphibian species in Bolivia were less likely to occupy isolated forest patches surrounded by a warm savannah than were other amphibians with lower rates of water loss [44]. Measures of realized moisture niche can also predict habitat affiliations. In Central America, for example, bird species that are associated with dry biomes throughout their ranges tended to be associated with relatively dry agricultural habitats at the landscape scale [149, 150].

## Research Frontiers in Thermal Landscape Ecology: Landscape-Scale Redistributions and Thermal Connectivity

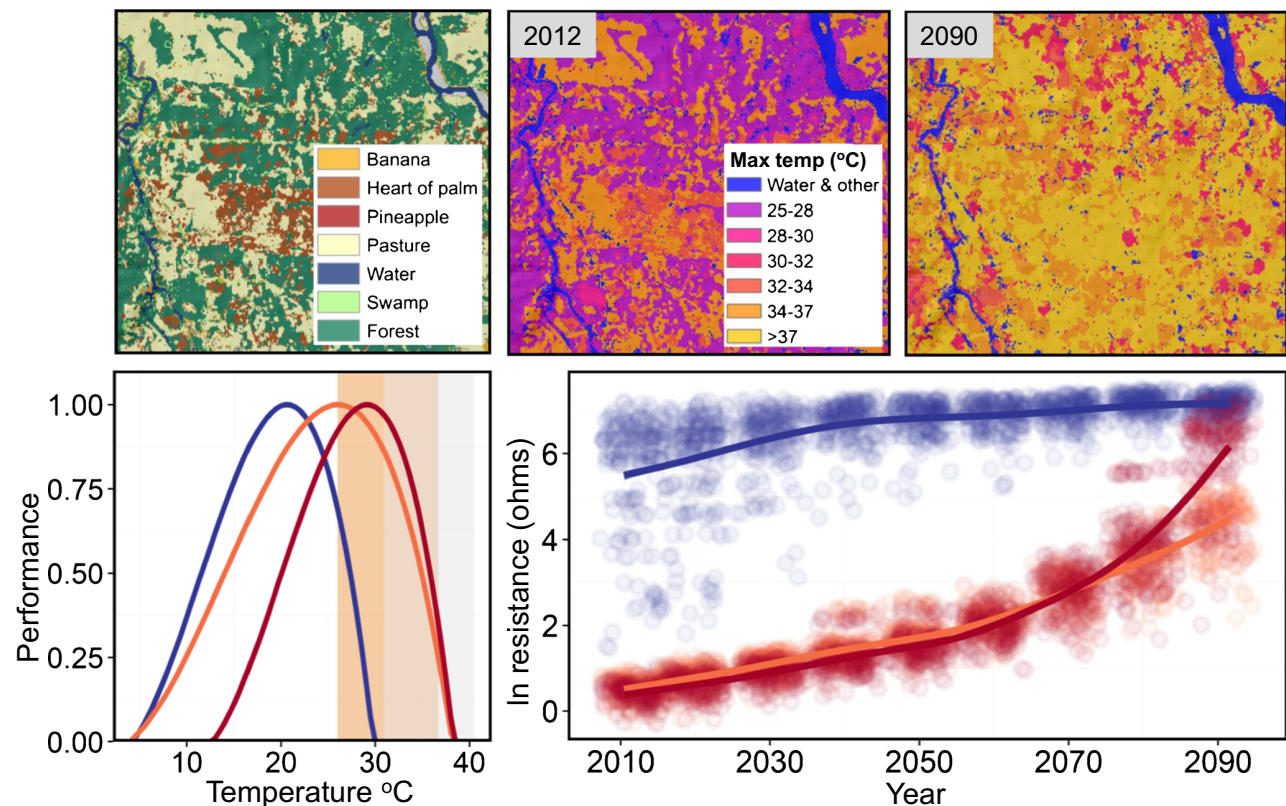
### Species Redistributions at the Landscape Scale

In response to climate change, species are expected to shift their distributions, adapt in place, or go extinct [18, 151]. There is extensive evidence of rapid latitudinal and elevational range shifts as well as variation among taxa in the pace of distributional shifts [19, 152]. However, global and regional studies of species redistribution rarely account for thermal landscape heterogeneity

and microclimates [7, but see 37], even though the fingerprints of climate change should first be apparent at local and landscape scales. The effects of habitat conversion on the thermal environment may mask, accentuate, or if not properly accounted for, be falsely attributed to global climate change [6, 153, 154]. Recent mechanistic approaches suggest that accounting for microclimate, thermoregulatory behavior, adaptation, and dispersal can considerably reduce the magnitude of projected range shifts compared to traditional approaches relying on coarse climate grids [29, 155]. By focusing on landscape-scale processes and linking

analyses across spatial scales, we may better predict lag times and the magnitude of species' responses at large spatial extents.

Some of the lag times in observed latitudinal and elevational shifts in species distributions may result from use of buffering microhabitats [48], topographical refugia [61, 62], and vertical and horizontal shifts in habitat use [55, 66]. For examples, scansorial and arboreal animals have the option of selecting habitat in vertical space to dynamically respond to changes in temperature by simply shifting downward toward cooler, wetter microclimates on or in the ground [55]. Horizontal shifts among



**Fig. 4.** We examined the potential for species-specific thermal biology and thermal landscape change (combined temperature changes from land-cover and climate change projections) to alter connectivity (effective distances) among 20 random points on a  $5 \times 5$  km landscape in NE Costa Rica. We modeled effective distances using circuit theory models [167], and examined changes in these distances into the future, simultaneously under a business-as-usual land-cover change scenario and a moderate  $\text{CO}_2$  emissions climate change scenario (A1B scenario; [168]). We modeled resistances for three hypothetical diurnal amphibian species: one cool-adapted species with low  $\text{CT}_{\text{max}}$  and two warm-adapted species with high  $\text{CT}_{\text{max}}$ , but with different shaped thermal performance curves (lower-left panel). The primary input for circuit models are resistance surfaces—raster grids in which cell values represent relative resistance to movement associated with landscape features. Here, resistance values were calculated as the inverse of thermal performance. We estimated habitat-specific body temperatures with a biophysical model [87, 169] and interpolated these values along the hypothetical TPCs to assign habitat-specific resistance values to grid cells. Microclimate data, measured in the field, for each land-cover type were projected into the future and used as inputs for the biophysical model. Detailed methods of land-cover change and climate projections,

biophysical modeling, and microclimate measurements can be found in Nowakowski et al. [59]. Top panels: changes in the distribution of thermal habitats under combined land-cover and climate change projections, from 2012 to 2090. Bottom panels: Landscape resistances were calculated for three hypothetical species from TPCs and used as input for circuit models (bottom left). Shaded rectangles indicate shifts in the range of maximum, habitat-specific body temperatures modeled for three hypothetical species, from 2012 to 2090. Resistance distances (effective ecological distances) among sites were modeled for each species into the future (bottom right). As both climate and land-cover change progressed, the effective distances among sites ( $\ln$  resistance in ohms in the bottom-right panel) were greatest for the cool-adapted species and increased only gradually for this species into the future, primarily as a result of forest loss and decreasing thermal suitability of forest with regional temperature increases. In contrast, the effective distances among sites were initially low for warm-adapted species that encountered little thermal resistance in the contemporary thermal landscape, but effective distances increased at a greater rate than for the cool-adapted species, as once-suitable land-cover types became thermally unsuitable over time as a result of climate warming

habitats (e.g., from open- to closed-canopy) may also allow species to persist in landscapes without apparent range shifts at broader scales. In Costa Rica, amphibian species change their affiliation from natural forested habitats in the lowlands to deforested pasture habitats upslope in order to track their thermal niche, suggesting that with climate change these species will become ever more reliant on forest [66]. Adopting a thermal landscape approach to understand how thermal conditions determine the distribution of species at the landscape scale will allow managers and conservationists to better support species through climate adaptation strategies.

Land-cover and climate change can also reshuffle species occurrence in space and time, giving rise to novel communities and the breakdown of long-standing interactions [4, 156–158]. These indirect effects may be equally or more important than direct abiotic effects, and can stem from altered distributions of predators, food resources, competitors, and pathogens [157]. Endotherms, especially, may respond more quickly to indirect effects than direct effects of changing thermal landscapes if redistributions are driven by shifts in availability of thermally-sensitive food species (e.g., insects and plants). Competition is generally expected to increase lags in species redistributions, in part, by reducing population growth rates in newly-colonized habitats [159]. These lags depend also on dispersal abilities of interacting species; good dispersers may escape predators, pathogens, and competitors by colonizing new habitat patches and better track their climatic niche. Pathogen dynamics are likely to change drastically across thermal landscapes as warming temperatures affect virulence [160] and as climate, landscape configuration, and thermal biology of hosts and pathogens all interact to modify disease risk [161]. Mutualistic plant-pollinator interactions can also break down; for example, fragmentation limits movement of hummingbirds and thereby disrupts their pollination of *Heliconia* plants in isolated forest remnants [162], a phenomenon that may be exacerbated by warming matrix habitat. Although much work has examined the effects of landscape modification on species interactions [9, 156, 158, 163], providing a solid foundation for future integrative research, we are just beginning to understand the potential role of climate change [4, 157]; the interactive effects of climate and landscape change on species interactions, however, remain largely unknown.

### Thermal Connectivity

Under climate change, the ability of species to track their thermal niches and shift distributions toward future climate analogs may be facilitated or impeded by the composition of intervening landscapes [164, 165]. Functional connectivity is the degree to which landscape features channel or impede the movement of organisms and depends on the interaction between species traits and landscape features. Connectivity is a key parameter, determining long-term persistence of metapopulations and contributing to the maintenance of local genetic

diversity, viable populations, and species richness [15, 166]. Maintaining connectivity in changing thermal landscapes may require integrating information on microclimates and species-specific thermal traits into modeling approaches and their applications (see Fig. 4). Even if natural habitat fragments are sufficiently buffered against rising temperatures to avoid species extinctions, loss of connectivity among fragments may cause populations to become isolated. As temperatures rise globally, landscapes with intervening open habitats that were previously available for dispersal for cool-adapted forest species may become too warm, turning natural habitats into islands cut off from nearby populations and ultimately limiting opportunities for range shifts (see Fig. 4). Thermal connectivity—animal movement mediated by thermal landscape variation and thermal traits—may therefore affect the maintenance of genetically-diverse local populations [10] and the ability of species to track their climatic niches under land-cover and climate change [164, 170].

### Conclusions

Land-cover and climate change are reshaping thermal landscapes, creating novel templates on which population dynamics, community assembly, and evolutionary processes unfold. A thermal landscape approach offers a way forward, but substantial knowledge gaps remain. We highlight several core research questions that need to be addressed before an understanding of thermal landscapes can be fully applied to the ecological challenges facing the globe:

1. Which thermal traits and associated mechanisms are most closely linked to population-level fitness and viability under changing thermal environments?
2. What are the consequences of thermal–environmental filtering for community reassembly and interactions under thermal landscape change?
3. To what extent do individual variation and lability in thermal traits, through acclimation or selection, buffer species from thermal landscape change, thereby delaying shifts in distribution?
4. How does spatial configuration and heterogeneity of thermal landscapes interact with temporal thermal variability to promote or diminish population persistence?

We expect continued climate warming will exacerbate effects of habitat modification in coming decades (and vice versa; [2]), species will vary markedly in their responses to both threats [152, 171, 172], and species' niches, evolved under past climates, will help predict current and future sensitivity to thermal landscape change [106, 121, 149]. These species-thermal landscape interactions will likely modify (1) matrix suitability and consequences for dispersal, resource

subsidies in habitat patches, and disturbance regimes; (2) the amount of thermally-suitable habitat and consequences for species distributions; (3) functional connectivity and consequences for gene flow, metapopulation maintenance, disease dynamics, and range shifts; (4) and interspecific competition and consequences for community assembly [173]. The integration of climate change and thermal biology into landscape ecology, however, is in the early stages, and many of these questions remain unexplored, despite the imminent challenges these threats pose for conservation [7].

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### Compliance with Ethical Standards

**Conflict of Interest** The authors declare that they have no conflict of interest.

**Human and Animal Rights and Informed Consent** This article does not contain any studies with human or animal subjects performed by any of the authors.

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