

Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia

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Microclimates have played a critical role in past species range shifts, suggesting that they could be important in biological response to future change. Terms are needed to discuss these future effects. We propose that populations occupying microclimates be referred to as holdouts, stepping stones and microrefugia. A holdout is a population that persists in a microclimate for a limited period of time under deteriorating climatic conditions. Stepping stones successively occupy microclimates in a way that facilitates species' range shifts. Microrefugia refer to populations that persist in microclimates through a period of unfavorable climate. Because climate projections show that return to present climate is highly unlikely, conservation strategies need to be built around holdouts and stepping stones, rather than low-probability microrefugia.

A small revolution in climate-change biology

Mounting evidence from paleoecology suggests that small pockets of vegetation occupying microrefugia played a pivotal role in plant responses to rapid climate change during the transition from the Last Glacial Maximum (LGM) [1]. Pioneering work suggests that microclimates will have a similar role under future, human-induced climate change [2,3]. Modeled estimates of range shifts, population dynamics, and extinctions may all need to be reassessed in light of such fine-grain effects, with important policy and conservation implications. However, research in this emerging field is limited by the resolution of climate simulations and because terminology and conceptual frameworks for understanding future fine-grain effects are not yet fully developed.

Here, we suggest that physical–natural science collaborations can revolutionize understanding of how plants and animals may respond to human-induced climate change. Joining physical models of microenvironments

(Figure 1) with fine-grain models of plant and animal response to climate change is needed to produce these new insights. Such work is already underway for some regions [2–5], and is shifting the resolution of analyses in climate-change biology by orders of magnitude. We describe the recent advances in this revolution and provide terminology to help frame the insights from the research.

Organism–environment interactions at fine scales

Environmental factors, including air and surface temperature, precipitation, radiation, and wind speed, interact with organismal phenotypes to create complex mosaics of temperature and water balance [6]. The interaction of multiple environmental factors can cause unexpected biotic responses to climate change, such as plants moving downhill in response to cold-air pooling [7]. Differences in microhabitat affinity can influence the strength of species interactions [8].

Environmental interactions also determine the incidence of extreme physiological stress events, which are an important biogeographic determinant for both plants and animals [9]. For example, evaporative water loss during heat waves can result in avian mortality events [10] and the incidence of thermal stress events for intertidal mussels depends from the latitudinal gradient in air temperatures based on whether tidal cycles coincide with the warmest part of the day [11].

The physiological details of organisms responding to their environment at subhourly temporal scales and spatial scales of meters can be crucial to predicting responses to climate change, but are often obscured by coarse climatic data [12]. The 1–100-km grid lengths of climate data generally used to predict distributions of plants and animals are three to four orders of magnitude coarser than the size of focal species being studied [12]. Climate simulations are typically applied in research using 20- or 30-year averages, rather than the full temporal resolution of the global climate model [General Circulation Model (GCM)].

Organismal responses can correspond either to averaged climate conditions or short timeframe variation, where

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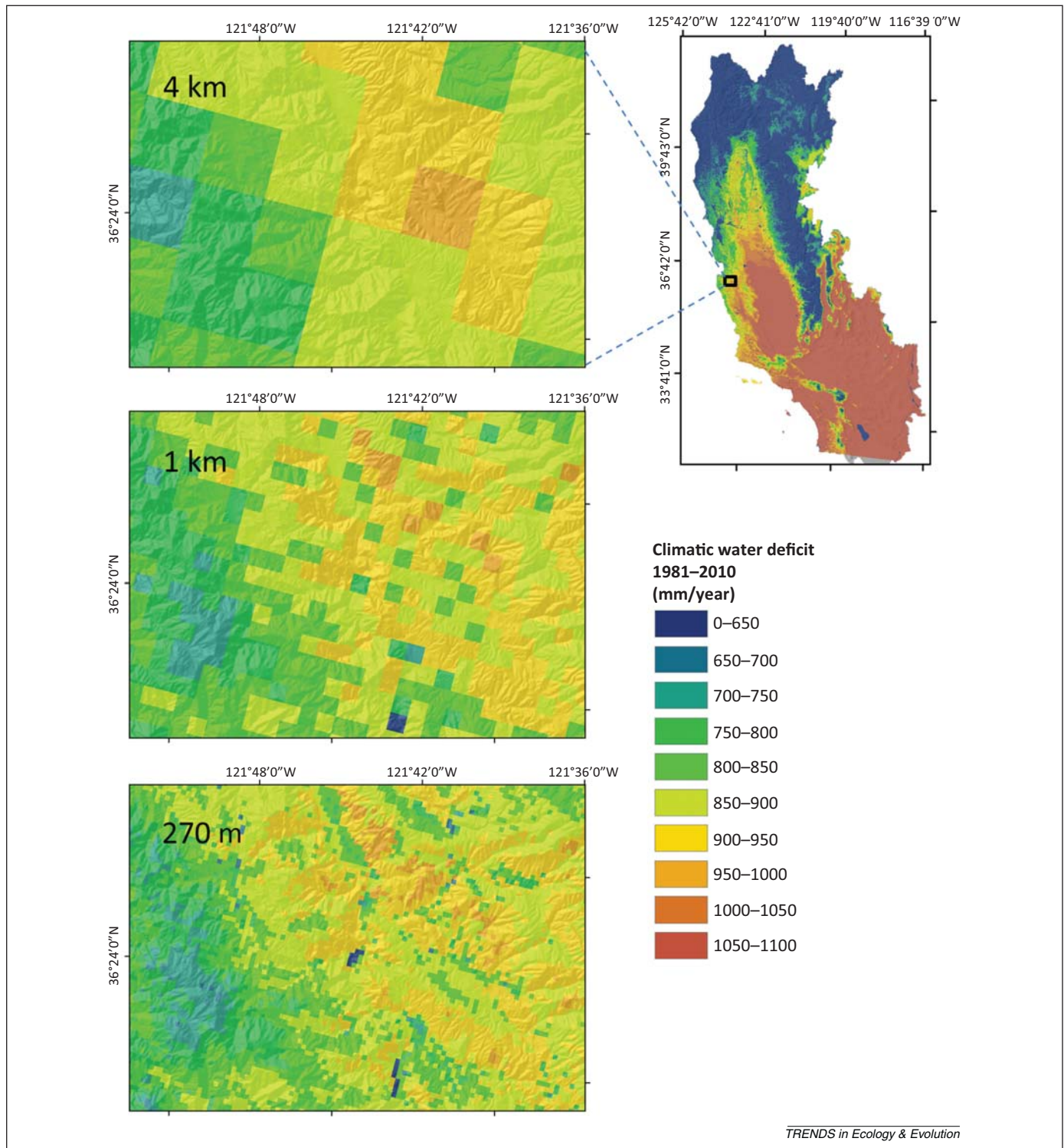


Figure 1. Fine-grain, large-domain modeling. Climatic water deficit calculated at three grain sizes for a domain covering the California Floristic Province (CFP) and desert outside of the CFP. Climatic water deficit can be a major limiting factor in plant distributions. The domain covers all of political California and encompasses the ranges of more than 2000 plant species that are endemic to the CFP. The insets contrast climatic water deficit calculated at the commonly used scales of 4 km and 1 km with calculation at finer grain 270 m. The fine-grain model is calculated using high-resolution temperature interpolation, detailed soil information, and a solar radiation model, capturing climatic and hydrologic effects of hill-slope shading, elevation, and soil properties that are not represented in the coarser models.

physiological responses to climate extremes are important. Two processes setting the distributional limits of intertidal mussels illustrate this point: southern limits in North America are set by mortality associated with acute thermal stress events, whereas southern limits in Europe are set by an energy budget integrated across the year [13]. Thus,

both coarse and fine-grain processes can be biologically important, but to date most climate and/or biological models have explored only relatively coarse temporal and spatial influences.

Biological models are now being constructed to capture fine-grain influences on the response of species to climate

change. Mechanistic biological models, which explicitly model how environmental conditions influence physiological processes on short time-steps and/or over limited spatial extents, are one strategy for appropriately integrating organismal responses to climate over time and space [14,15]. These models have demonstrated how coarse climatologies can bias estimates of biological change [16]. To build mechanistic models, body temperatures associated with microclimates can be assessed through constructing models of heat flow (i.e., biophysical models) or using physical models of organisms [6,13].

Correlative species distribution models (SDM) can be implemented at high spatial resolutions, if species occurrence data required as inputs are georeferenced with precision measured in meters or tens of meters and high resolution climatologies are available. The advent of Global Positioning System (GPS) data has made occurrence records accurate to scales of meters commonplace [17]. SDMs require only data on species occurrences and environmental (climatic) conditions, so they have the advantage of simplicity and wide applicability, but face several well-recognized limitations, including questionable transferability across time and space [18].

How do we talk about it?

'Microrefugia' is a term borrowed from paleoecology that describes isolated populations surviving in unusual microclimates relative to the surrounding landscape [19] or the places in which such populations persist [20]. As we describe below, the population-centered definition is more useful for analysis of the future. Such populations may help a species endure a period of unfavorable climate [19–21], or a glacial or interglacial climate excursion [1].

However, future climates are likely to be characterized by continuous warming in the long term, or relative stability (Figure 2). So, although 'microrefugia' is useful in describing some future situations, additional terms are needed to describe fully the effects of future climate change on biological systems.

'Microholdouts' (hereafter 'holdouts') is a term that describes isolated populations that survive in unusual microclimates for a limited duration (Figure 3). A holdout as proposed here is similar to a microrefugium, but without climatic conditions reversing to 'rescue' the population occupying the microclimate. Holdouts can be important in moderating species dispersal and population dynamics in response to future climate change.

The difference between a microrefugium and a holdout is defined by climate trajectory in the landscape. If regional climate continues to change, microclimates eventually become unsuitable for persisting populations, resulting in holdouts that eventually disappear (Figure 2B). If regional climate returns to an historic reference point, regional climate ameliorates potential adverse effects, and microrefugial populations may expand. Almost all GCM simulations using the Intergovernmental Panel on Climate Change (IPCC) RCPs indicate warmer end-century temperatures than at present (Figure 2B), so this may be the century of the holdout.

'Microstepping-stones' (hereafter 'stepping-stones') (Figure 4) is a term that we propose to denote a series of

populations occupying successive microclimates that have a role in mediating the range shift of a species in response to climate change. Stepping-stones may be important at the leading edge, trailing edge, or center of the range of a species.

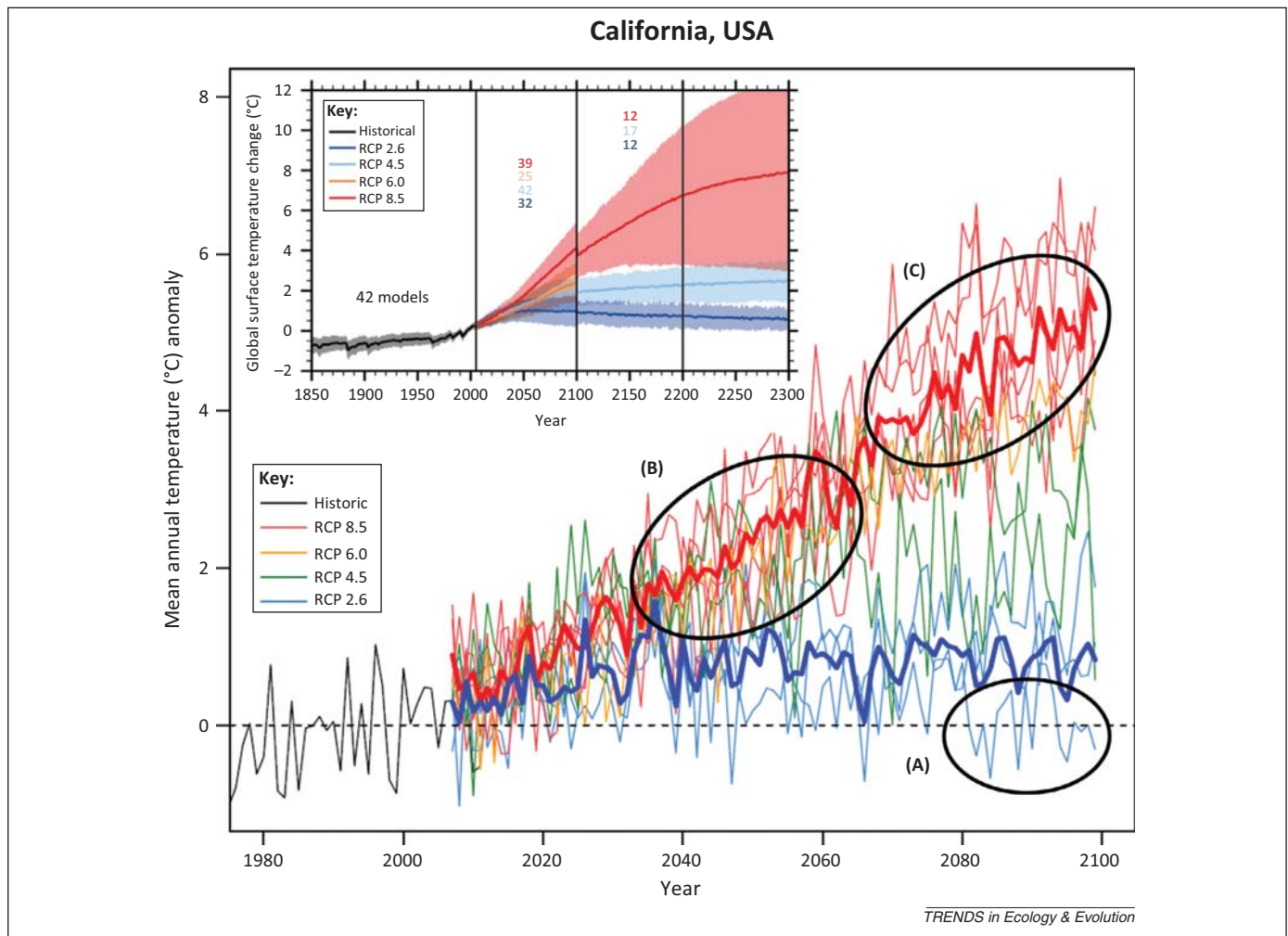
Microrefugia, holdouts, and stepping-stones are all species specific. We know from paleoecology that the responses of species to climate change are individualistic [22]. Thus, a microclimate is host to a microrefugium, holdout, or stepping-stone only with respect to individual species. This does not preclude occupation by multiple species, but species will persist, move on, or become locally extinct based on individual climatic tolerances in relation to microclimates and climate in the surrounding landscape, rather than as a group.

The dual criteria of both a microclimate and an occupying population are particularly important for simulations of the future, which is why simply borrowing terms from paleoecology may cause confusion. In paleoecology, microclimates are usually inferred from biological evidence (fossils of organisms or fossil pollen). Therefore, paleoecologists have often defined microrefugia as places that harbor species as surrounding climate deteriorates [20,21]. However, places (microclimates) do not always equate to populations. Definitions that focus on populations, rather than place, are therefore more useful for analyses of biological change, both past and future [19]. For the future, it is important not only to know if there is a microclimate in a location, but also whether that microclimate is biologically relevant and will be occupied by populations of one or more species. In population-centered terminology, microclimates are isolated, relatively small places in which climatic conditions are different than in the surrounding landscape; holdouts, stepping-stones, and microrefugia are populations that occupy microclimates. Populations that gradually disappear as climate change progresses are holdouts, whereas populations rescued by a climate reversal are microrefugia, and a series of holdouts that facilitate a range shift are stepping-stones.

This set of terminology can help biologists communicate with policymakers and stakeholders while helping clarify evolving usage in the paleoecological literature [1,19,20]. Given that global climate is likely to be warming throughout this century and beyond, it is important to have terms such as holdout and stepping-stone to indicate the impermanence of any static conservation solutions, and to dispel any notion that climate is returning to 'normal' or current conditions anytime in our lifetimes or those of our children.

What scale is appropriate?

Identifying holdouts, stepping-stones, and microrefugia requires models of future climate and models of biological response. Climate models are needed that can resolve microclimates capable of harboring small populations, areas as little as a few tens of square meters for insects and understory plants, to hundreds of square meters for dominant tree species. Biological models are needed to resolve the intersection of the environmental niche requirements of species with microclimates, the ability of species to disperse to suitable microclimates, and population dynamics that may occur in the suitable habitat patches provided by microclimates.



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Figure 2. Microrefugia, holdouts, and stepping-stones in global (inset) and regional (main panel) climate space. Holdouts, microrefugia, and stepping-stones are distinguished from one another by the trajectory of surrounding climate. Global climate projections (inset) show that Representative Concentration Pathway (RCP) 4.5, 6.0, and 8.5 models project continuous warming with no return to historical conditions through 2300, the climate context that characterizes holdouts. Global RCP 2.6 projections show temperatures that return to near-historical levels but only in simulations that extend to 2300, indicating that climate context for microrefugia may exist, if at all, only in a subset of RCP 2.6 models. Regional differences may deviate from these global averages, but regional projections for California (main panel) indicate that only one (GISS RCP2.6) of 11 models shows a return to historical temperature levels that would create the context necessary for microrefugia (A). Other scenarios show either continual warming in which holdouts will gradually disappear (B) or sustained strong warming (C) in which context stepping-stones become increasingly important. The main panel represents time series of annual mean surface air temperature anomalies ($^{\circ}\text{C}$) for California from 11 CMIP5 models through 2099, with RCP indicated by line color (8.5 red; 2.6 blue). Thick red and blue lines represent multimodel means for RCP 8.5 and 2.6, respectively. The broken line represents baseline 1981–2010 mean annual temperature for California. The inset is Figure 12.5 from the Fifth Assessment of the Intergovernmental Panel on Climate Change (IPCC) [4], showing a time series of global annual mean surface air temperature anomalies (relative to 1986–2005) from CMIP5 concentration-driven experiments. Projections are shown for each RCP for the multimodel mean (unbroken lines) and the 5–95% range (± 1.64 standard deviation) across the distribution of individual models (shading). Discontinuities at 2100 are due to different numbers of models performing the extension runs beyond the 21st century, and have no physical meaning. Only one ensemble member is used from each model and numbers in the figure indicate the number of different models contributing to the different time periods. No ranges are given for the RCP 6.0 projections beyond 2100 because only two models were available [56].

Focal organisms and their habitat requirements are a starting point for informing the choice of appropriate scales for modeling. Fine-grain spatial data may be less important for organisms in spatially homogeneous environments or those that can move to buffer their environment. High temporal resolution data may be less important in environments where diurnal or seasonal variability is limited, at least relative to the environmental tolerances of organisms [12]. Consequently, research on plants has emphasized spatial resolution, whereas research on animal thermoregulation has emphasized temporal resolution. The biological question also influences choice of climate data; temporal resolution may be more crucial for studies of survival and reproduction than for studies of distribution [15]. High temporal or spatial resolution may not be important for wide-ranging species or those that will find

suitable climate space expanding. Where fine-grain spatial processes are important, small populations associated with microclimates may have key roles in determining the abilities of species to track suitable climatic conditions.

For biologists, perhaps the greatest challenge is in the availability of high-resolution climate surfaces, because constructing these surfaces requires new physical modeling skills or new collaborations with climate scientists. Establishing these skills and collaborations is critical to improved understanding of holdouts, stepping-stones, and microrefugia.

A first step in physical modeling of microclimates is simulating temperature variation with elevation. Global climate grids are typically only available at horizontal resolutions of 1–5 km, downscaled from GCMs using interpolations from weather stations that have been adjusted for

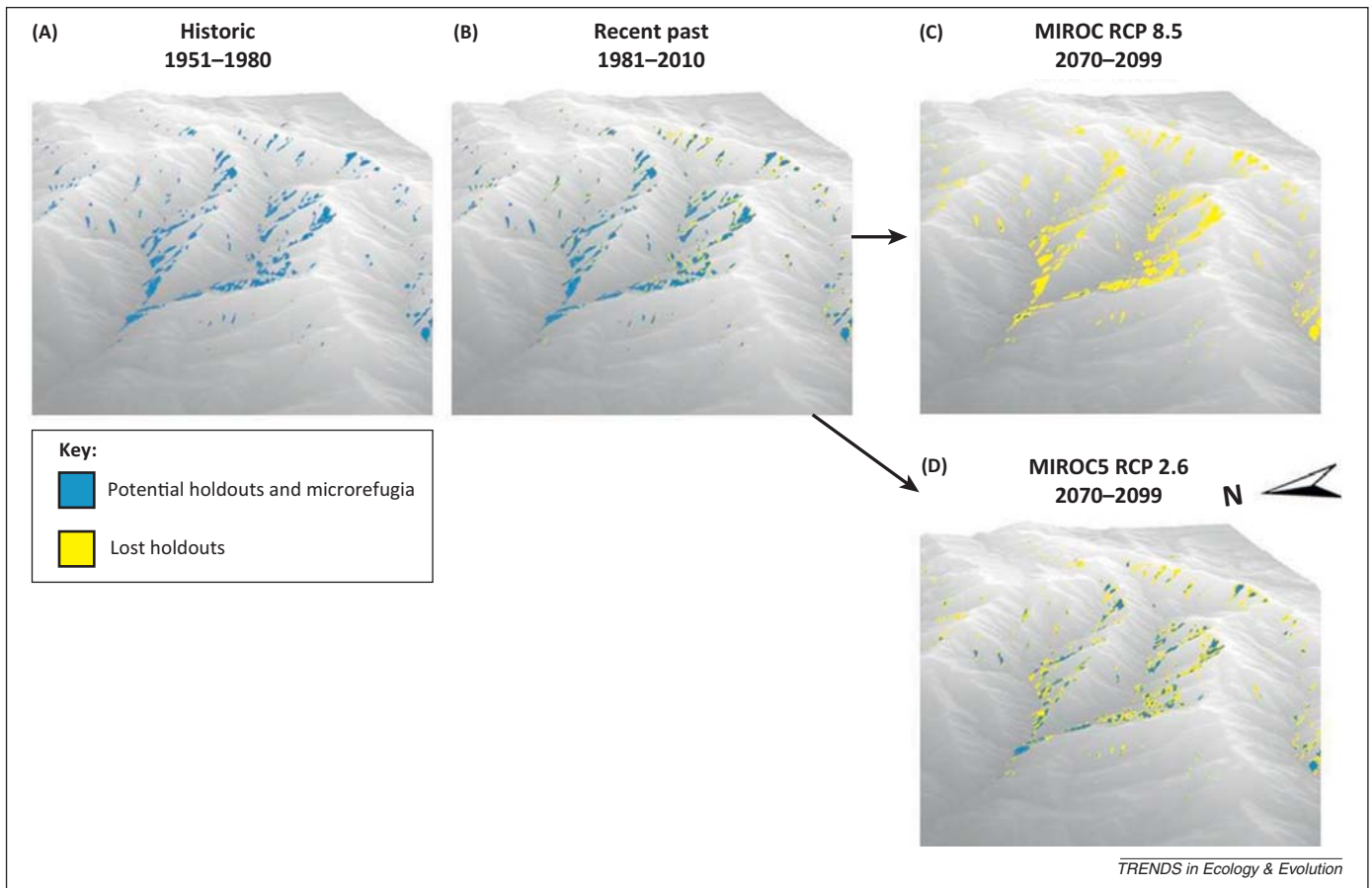


Figure 3. Holdouts and microrefugia. Holdouts are populations that persist in microclimates while climate deteriorates in the surrounding landscape, whereas microrefugia are isolated populations that persist through periods of deteriorating climate until favorable conditions return. (A–D) show potential holdouts and microrefugia (blue) and loss of holdouts (yellow) across two representative concentration pathways (RCPs) by the end of the 21st century. Microrefugia are evident only in RCP 2.6. Maps are based on 30-m statistical downscales of water year climatic water deficit (mm) in the Tehachapi Mountains, California and are overlaid on a 30-m digital elevation model (DEM). Water deficit is a determinant of range limits for many plants, and is used here as a surrogate for microclimates likely to be occupied by plant populations. Blue and yellow patches represent relatively wet conditions less than two standard deviations from 1951–1980 historical mean. Contemporary period consists of historic data from 2001–2010 and future projected water deficit is from MIROC RCP 8.5 or 2.6 simulations.

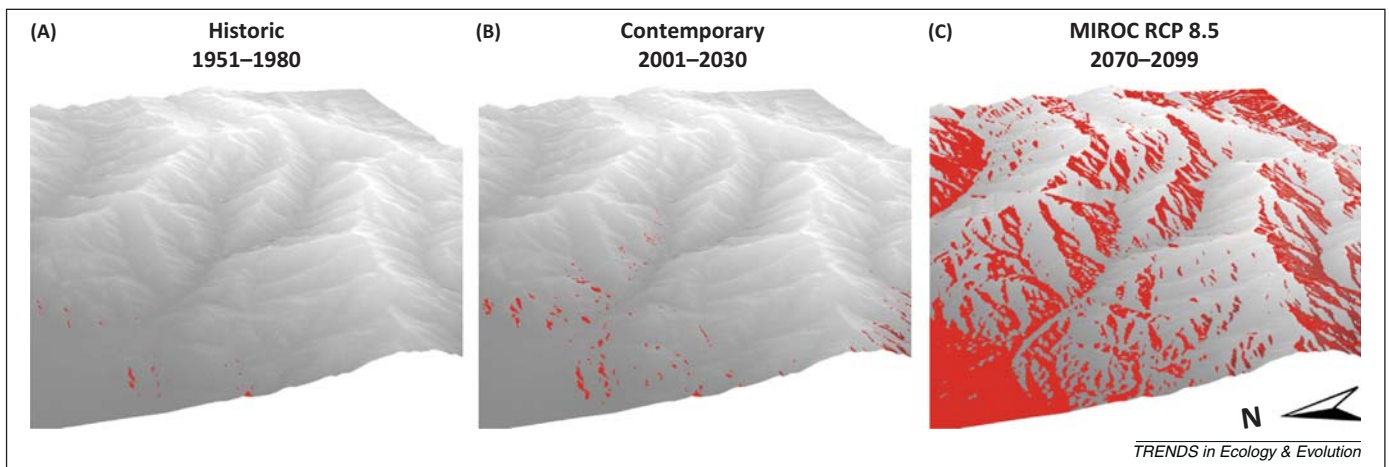


Figure 4. Stepping-stones. Stepping-stones (red) are populations that occupy successively changing microclimates, facilitating a species range shift in response to climate change. Maps are based on 30-m statistical downscales of water year climatic water deficit (mm) in the Tehachapi Mountains, California and are overlaid on a 30-m digital elevation model (DEM). Red represents relatively dry areas more than two standard deviations from the 1951–1980 historical mean (A). Contemporary period (B) comprises historic data from 2001 to 2010 and future projected water deficits from MIROC RCP 8.5 simulations from 2011 to 2030. (C) End-century MIROC RCP 8.5 projections.

temperature variation with elevation [23]. Further temperature correction for elevation is now possible using high-resolution digital elevation models (DEM), available for many regions at horizontal resolutions of 30 m or finer. Extending elevation-corrected interpolations to higher

resolutions can offer important biological insights. Temperature variability calculated at sub-kilometer scales has been demonstrated to be substantially greater than variability among coarser grids [23–25]. This means that species may be able to adjust to warming by moving

Box 1. Holdouts, stepping-stones and range shifts

The role of holdouts and stepping-stones in mediating range shifts depends on whether they are at the leading edge, trailing edge, or center of the species range. Leading-edge stepping-stones may undergo purging of alleles due to small population size [19] facilitating the expression of recessive traits that favor rapid dispersal to track climate change. Examples are long-winged morphs of bushcrickets (*Cynocephalus discolor* and *Metrioptera roeselii*) in England and long-winged seed morphs of lodgepole pine (*Pinus contorta*) in western North America. In these cases, the highly dispersed form is found at leading edges of range shifts past (lodgepole pine) and present (bushcrickets) [58,59].

Central holdouts may be important in providing genes beneficial for adaptation to leading edge populations. Central populations receive genes from both the leading edge (least adapted to novel conditions) and trailing edge (most adapted to novel conditions) populations and so are valuable conduits of adaptive traits toward the leading edge [60]. As climate change causes conditions to deteriorate, populations in the range center will decline, but holdouts will decline last, helping to prolong gene transfer that enhances adaptation at the leading edge.

Trailing-edge populations harbor important genetic information accumulated during glacial–interglacial range shifts of the past [22]. Although trailing-edge holdouts will eventually disappear, their existence can be prolonged through management. For instance, control of predators can reduce predation and maintain holdouts of small mammals. This type of management to maintain holdouts may allow genetic information to persist *in situ* for decades until *ex situ* or other long-term conservation strategies are worked out.

The effective role of holdouts and stepping-stones in range-shift dynamics depends on climate change velocity relative to landscape position, as well as other biotic and abiotic factors. The ability of species to track climate change is a function of topography and species' traits such as dispersal, competitive advantage, life history and resistance to disturbance. Connectivity among isolated populations within metapopulations is more likely when species are small bodied, reproduce asexually, and carry light genetic loads [19]. Whereas holdouts and stepping-stones at any one location most likely cannot maintain populations by themselves, they can have key roles in mediating range shifts when connected to other subpopulations. In addition, successive groups of stepping-stones may be central to avoiding extinction for some species whose climatic tolerances dictate long-distance, rapid range shifts in response to climate change.

shorter distances than would be suggested by studies using multi-kilometer climate grids, increasing estimated probabilities of persistence and decreasing the probability of local extinction [26].

A second major determinant of microclimates is variation in solar radiation due to landscape shading, slope, and aspect. Radiation models available from the physical sciences are limited by DEM resolution, so the newer high-resolution DEMs enable simulation of microclimates related to radiation effects, as well as correction of temperature for elevation. Radiation microclimates can have strong biological relevance, especially in temperate and high-latitude settings, acting through temperature, potential evapotranspiration, and soil moisture. For example, radiation on equator-facing temperate slopes can greatly accentuate climatic water deficit, a key determinate of tree distributions [27,28]. Similarly, the bottom of a steep east–west trending gorge would be predicted to experience daytime temperatures warmer than surrounding higher areas based only on elevation-corrected interpolation, but may in fact be much cooler than surrounding uplands because of the shading effects of steep side walls. This topographic shading of incoming solar radiation can create microclimates in

gorges that shelter isolated populations of species, such as Wollemi pine (*Wollemia nobilis*) in Australia [17].

Other biologically relevant microclimatic effects include cold air drainage, rainshadows, wind, influences of small and medium-sized lakes and rivers on precipitation and temperature, fog formation, local inversions, and convective effects of land cover and topography [29,30]. These dynamic processes are more difficult to simulate at high resolution, but a new generation of algorithms (e.g., for cold air drainage [31]) and high-resolution regional climate models (e.g., of local winds and fire weather corridors [32]) are coming online to inform biological modeling [12].

Given computational limits, modelers face a trade-off between spatial and temporal resolution of climate data. A 100-km GCM grid cell contains 10 billion 1-m² cells, whereas a 30-year climate normal represents over 10 950 individual monthly means. This makes simulation of climate at scales relevant to populations or individual plants and animals a huge computational challenge, because many organisms are smaller than 1 m and may respond to weather events, such as freezes, that unfold on timescales of minutes or hours. This challenge is sometimes addressed by simulating only a portion of the range of a species, but conservation planning and estimates of extinction risk will usually require simulations of whole ranges, often of multiple species. Therefore, fine-grain modeling is defined by the phenomena being studied, balanced by computational constraints, but always at finer spatial or temporal scales than the 1–4-km monthly averaged 30-year normals that are commonly used in species distribution modeling.

Conservation consequences

Conservation planners need to be aware that microrefugia are unlikely under all but a few future climate scenarios, so that planning for holdouts and stepping-stones should be the major focus of protected areas and species plans. Continuing climate change produces fading holdouts, whereas climate reversal produces persistent microrefugia. All RCP scenarios project continuing climate change without reversal, except for a few RCP2.6 simulations (Figure 2). This indicates that microrefugia will be rare, resulting only if global mitigation policy is aggressive or geoengineering is used to change the trajectory of climate change.

Planning for holdouts and stepping-stones focuses on whether and how species can keep pace with changing climate, in the context of continuing change. Conserving holdouts may maintain sources of dispersal, genetic information, and populations involved in stepping-stone effects (Box 1). Management levers might include limiting disturbance to allow holdouts of mature trees to persist even after climate suitability has declined, because deeply rooted trees may be less affected by surface conditions compared with seedlings or immature trees [33]. At the same time, the trailing edge for some species may be the leading edge for others, so monolithic management may suppress stepping-stones at the expense of holdouts, or vice versa.

Mosaics of landscape management may be the best way to meet multiple species and ecosystem conservation goals simultaneously. For instance, stand-replacing fire might be controlled in one part of a landscape to help holdouts of one species persist, whereas promotion of stand-replacing

fire in other parts of the same landscape could facilitate vegetation transitions to help other species range shifts keep pace with climate change [34]. Consideration of novel and disappearing climates and the velocity of climate change may help in designing landscapes that harbor both holdouts and stepping-stones to meet conservation goals [35].

Holdouts and stepping-stones need to be understood not only in landscape context, but also in the context of regional climate change and the entire ranges of species. For instance, efficient protected area plans for climate change require consideration of range shifts and changes in range sizes for species within the planning region [36,37]. Given that range changes may be mediated by holdouts and stepping-stones, analyses that are both large domain and fine grain are required. Biological models are needed that can provide the link between microscale changes and macroscale impact. How to best incorporate microclimatic effects into biological models is an important avenue of ongoing research (Box 2).

One approach that speaks to conservation endpoints is the integration of correlative SDMs and population models

Box 2. Tools for fine-grain, large-domain studies

Several tools are emerging for assessing fine-grain processes at spatial extents that are relevant to assessing changes in the distribution of species. Among the new tools are microsensors that measure temperature, relative humidity, and other variables; airborne and hand-held imaging devices that enable fine-grain recognition of vegetation and temperature in landscapes; and distributed experiments that sample climate-change effects on individual organisms across biogeographic spatial domains.

Fine-grain sensor networks can be used to better understand the distribution of microclimates in a landscape and from ground level into the air column [33]. These are important advances, because standard climatologies report air temperature at a 2-m elevation, whereas many biologically important processes are being mediated at or near the ground surface [12]. For instance, a seedling may experience radiative warming of the ground surface that is not captured in 2-m air temperatures, but that may be a critical factor in determining survival in times of summer water stress [33].

Microsensors combine sensors for temperature, relative humidity, or other variables with a solid-state data logger in a package little bigger than a wristwatch, costing a fraction of a traditional weather station (around US\$100 versus several thousand dollars). These sensors deployed at multiple levels (e.g., 20-cm intervals above the ground surface) can be used to construct temperature profiles that enable surface conditions important to plants and small animals to be estimated from standard 2-m climatologies [33]. Sophisticated networks linking hundreds of sensors can be used to characterize microclimates across landscapes and in vertical profile.

High-resolution remote sensing is an important complement to sensor measurements. Hand-held thermal imagery can be used to identify temperature patterns in landscapes with more spatial detail than all but the most dense microsensor networks [24]. Airborne multispectral imaging platforms provide spatial and spectral resolution finer than satellite-borne sensors, some enabling identification of individual trees and other plants to the level of genus or species [57]. Flight paths for these instruments, such as the NEON multispectral airborne sensor in the USA, are being programmed to sample large enough areas to be informative at macroecological scales [57].

Experiments, sensor networks, and modeling can be combined to scale-up effects measured at the level of individual organisms to landscapes or ranges of species. For example, common garden trials of seeds transplanted to lower (warmer) sites can be used to estimate the establishment niche of a plant species, with sensor networks measuring microclimates appropriate for recruitment at ground level. These measurements on landscape scales can be translated to broader domains by modeling.

to better account for demographic processes [38]. Holdouts and the main distribution of species are analogous to islands and mainlands in metapopulation theory [19]. This means that metapopulation models and newer coupled metapopulation–climate models [38] can be used to assess possible impacts of holdouts, stepping-stones, and microrefugia.

Stochastic population models incorporate variation and uncertainty in demographic and environmental parameters to provide population trajectories that are used to calculate extinction risk [37,39–45]. Dynamic vegetation models (DVMs) are process based, often incorporate eco-physiology, and have also been parameterized to the level of species at fine spatial grains, to simulate range shifts, refugia in paleoecological studies, and to explore ramifications of future climate change [37,46–49]. These existing modeling tools can be applied to improve understanding of how populations exploit microclimates.

What's next?

Next-generation models are emerging that can address the effects of dispersal, species interactions, population dynamics, and disturbance on holdouts and stepping-stones. LANDIS-II [50] and BioMove [51], for example, provide flexible, modular model architecture that allows users to vary spatial and temporal grain and extent and to select custom extensions to simulate a range of mechanistic detail, depending on the study objective. Climatic effects on fire regimes can be simulated, and species successional (and, thus, range) dynamics can be explored through climate-mediated rates of growth, decay, and establishment [52,53]. In LANDIS-II, soil carbon and nitrogen can also vary with climate change [54].

Conservation-planning frameworks for the application of these models are still being elaborated. Some conservationists have despaired of the uncertainty in climate projections and in understanding of the response of species, advocating instead the conservation of abiotic land facets as a surrogate to understanding climate-change biology [55]. However, planning for the long-term persistence of biodiversity in the face of climate change will not be accomplished by ignoring biology. Much of the biology of change may be occurring at finer scales than most current climate or biological models can resolve. Conserving the biodiversity of the world over the coming centuries of change requires a crash course in holdouts, stepping-stones, and microrefugia.

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