Effects of microclimate variation on insect persistence under global change

Authors: Jeremy T. Kerr[1, †, *], Susan C.C. Gordon[1*], I-Ching Chen[2](陳一菁), Gabrielle Ednie[1], Wendy Foden[3,4,5], Tim Newbold[6], Ashley R. Reynolds[1,7], Andrew J. Suggitt[8], John S. Terblanche[9], Matthew J. Watson[1]

[1] Department of Biology, University of Ottawa, Ottawa, Ontario, Canada

[2] Department of Life Sciences, National Cheng Kung University, Tainan, Taiwan

[3] Global Change Biology Group, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa

[4] South African National Parks, Cape Research Centre, Tokai Park, Cape Town, South Africa

[5]Climate Change Specialist Group, Species Survival Commission, International Union for Conservation of Nature, Gland, Switzerland

[6] Department of Genetics, Centre for Biodiversity and Environment Research, Evolution & Environment, University College London, London, UK

[7] Centre for Arctic Knowledge and Exploration, Canadian Museum of Nature, Ottawa, Ontario, Canada

[8] Department of Geography and Environmental Sciences, Northumbria University, Newcastle upon Tyne, UK

[9] Centre for Invasion Biology, Faculty of AgriSciences, Stellenbosch University, Stellenbosch, South Africa

*** These authors contributed equally as first authors**

† email: Jeremy.Kerr@uottawa.ca

Abstract

The direct and indirect effects of climate change expose insect populations to environmental conditions that can approach or exceed their physiological limits. The complex life cycles of many insect species, with their elaborate networks of biotic interactions, can add to their vulnerability. In this Perspective, we argue that the negative effects of extreme weather can be offset if insects are able to use favorable microclimates. Microclimatic diversity can be modelled, measured remotely, or measured *in situ* at scales relevant to insect life cycles. Microclimatic availability within habitats can improve opportunities for adaptive or plastic responses to extremes, potentially moving insect populations toward a more favorable balance between extinction and colonization which can allow species to maintain or shift their geographical ranges over time. Management plans for insects should promote microclimate heterogeneity, as well as the maintenance or creation of microclimates relevant to target species, such as shaded areas and variable topography that reduce temperature and increase moisture availability. Consideration of microclimates is a potentially useful way to advance insect conservation in this period of rapid climate change.

[H1] Introduction

Of the 2421 insect species listed as Threatened by the International Union for Conservation of Nature (IUCN), 27% face risks related to climate change[1], with many species experiencing increased temperatures and reduced precipitation[2]. The consequences of these changes for insect species are pervasive, leading to extensive population declines[3,4], geographical range shifts[5], and changes in seasonal timing[6]. Insect species respond rapidly to climate change[7,8] owing to their predominantly short generation times, multiple life stages with distinct climatic

and habitat requirements, and physiological and ecological dependence on external environmental conditions. Models of future insect responses to anticipated climate changes suggest that population and species declines will accelerate [9]. Strategies for insect conservation in this period of rapid climate change are urgently needed.

The resilience of insects to global change could depend, in part, on their ability to access favorable microclimates. Microclimates are combinations of temperature and moisture conditions at localized scales, which may deviate from macroclimatic averages (Figure 1). Local climate, topography and land use changes interact to determine microclimate characteristics and availability. For example, intact (typically forested) habitats maintain a higher complexity of microclimates than habitats that have been modified to have lower vertical and landscape-level heterogeneity[10]. This reduced complexity increases insects' exposure to direct sunlight, amplifying the daytime temperature extremes that they experience[11,12]. Such localized increases in temperature can also create drier microclimates, particularly if vegetation is removed[13].

Whether these microclimates exert meaningful biological effects depends on the extent to which conditions deviate from climatic conditions across broader areas, as well as the life histories of the organisms within such areas. Microclimates with conditions that are more moderate relative to a species' niche limits than those in surrounding areas can reduce insect species' exposures to both sustained increases in average temperatures (press events) and to short-term extreme events (pulse events), potentially improving the likelihood of local persistence. For example, atypical microclimates can be found on slopes oriented away from the equator or in forest understories that trap humidity. Conversely, some microclimates can be more extreme relative to species' niche limits than the surrounding area. For example, herbivory can

reduce leaf transpiration and increase temperatures of leaf surfaces, consequently exposing leaf-dwelling insect species to hotter and less tolerable temperatures[14].

With rapid technological developments facilitating *in situ* data collection, advances in modelling frameworks, and rapid growth in microclimate data availability, new interactions between microclimates and insect life histories are becoming increasingly clear[10]. However, the typical traits shared by many insect species make the role of microclimates in their ecology and evolution particularly challenging to elucidate. A small body size and limited mobility can mean that insects might respond to climatic conditions over very small spatial scales; for example, leaf-inhabiting insects might respond to millimeter-scale differences in temperatures[15]. The pronounced seasonality of many insect species, coupled with changes in activity patterns between different life stages, means that identifying the climatic parameters likely to have the greatest impact can be challenging[16,17].

Despite these challenges, rapid progress in the measuring and modeling of microclimates is enabling new understanding of how microclimate variation could affect insect species. In this Perspective, we first discuss the microclimate models and technologies that measure microclimates in unprecedented detail over relatively broad areas. We then identify how suitable microclimates affect insect species' niche space and key ecological and evolutionary processes (including colonization and extinction dynamics and range shifts). Identifying when, where, and for which species microclimate availability limits eco-evolutionary dynamics is both increasingly feasible and urgently needed[18] if we are to bend the curve for insect population declines, and ultimately, species-level extinction rates[19]. Coupled with knowledge of species' natural histories, incorporating microclimatic refugia into conservation strategies could improve conservation

outcomes, buying time for species to adapt, to move to more suitable areas, or to persist for longer in historically occupied areas.

[H1] Defining and quantifying insect-scale microclimates

Many insect species use a combination of aquatic, terrestrial, and aerial environments across different developmental stages. Each life stage is exposed and sensitive to distinct environmental factors[20], including ground surface temperature, soil temperature, air temperature, soil humidity, precipitation, and moisture[21]. Given their small body size and short, multi-stage life cycles, insects experience environmental variation at small spatial and temporal scales[21,22] relative to larger species, and microclimates are particularly powerful drivers of their ecology and evolution[23,24]. In this section, we discuss the ways that insects respond to small-scale variation in temperature and humidity, then summarize how such variations are quantified.

[H2] How insects respond to microclimates

Insects can perceive subtle shifts in temperature (<0.1°C) and humidity (~5-10%)[25,26], and continuously assimilate environmental information over their lifetimes, across generations, and through evolutionary adaptations[27]. Thus, insects readily assess and integrate environmental information with their internal state or condition (for example, mating, immune, or nutritional status), as they map their home ranges, track resources, and make decisions about habitat quality[28,29]. Insects can then select favorable microclimates and use them as microrefugia, although this ability is dependent on life stage and mobility (for example, mobile adults versus stationary eggs and pupae)[24].

Insect survival and activity are limited to specific ranges of temperature and humidity, referred to here as thermal and hydric tolerances, or collectively 'environmental tolerances'[30,31]. Thermal tolerance ranges are bound by species' lower and upper limits[32]; conditions beyond

these limits will reduce organismal performance or induce harm[33,34]. Compared to thermal tolerance ranges, less is known about hydric tolerance ranges. Exceeding species' lower (dry) or upper (wet) hydric tolerance limits causes physiological stress, such as dehydration[35]. Importantly, thermal and hydric limitations interact under increasingly extreme environments[36]. Substantial inter- and intra-specific variability in tolerances have been observed, reflecting species' unique evolutionary histories[37,38], including across different seasons and life stages[39].

Environmental tolerances can be inferred from species' biogeographical ranges[40] or measured directly[39,41]. Biogeographic studies of tolerances identify the upper and lower limits of environmental conditions that species experience across their geographical ranges, an approach that is most reliable for species that are widely observed. Such measurements can then be used to assess the extent of exposure to conditions that exceed species' realized niche limits through metrics like Thermal Position Index[42] (Figure 1), which can improve predictions of organismal responses to climate change[4]. Alternatively, lethal critical thermal limits (CT_{max} and CT_{min}) can be determined through controlled physiological experiments, although these can be costly and time-consuming, especially for large-bodied and rare species[43]. Other lab-based metrics, such as thermal performance curves, integrate variation in species' performance at temperatures between CT_{max} and CT_{min}, better capturing species-specific risks in variable climates than critical thermal limits alone[33]. Although both biogeographic and lab-based indices can improve predictions of species' responses to changes in climate[4,44], they estimate different aspects of environmental tolerance. Lab-based measurements rarely consider behavior or the complexities of species' responses to subtle spatial and temporal variation in conditions, and should be considered within target species' suite of ecological needs[45]).

[H2] Measuring microclimates

Identifying whether insects use favorable microclimates in a way that could increase their resilience to global change requires detailed measurements of microclimates at relevant scales. Microclimate measurements are derived from three methods—modelling, *in situ* measurements, and remote sensing[46] — which each have advantages and disadvantages (Figure 2).

Modelling combines meso-climatic (such as 30m resolution) and macro-climatic (such as 200km resolution) data with land cover information, leading to very high resolution predictions for localized conditions. Predictions are consistently available at less than 30m resolution, and can be as little as 1m, but rely on downscaling from relatively coarse resolution databases[47,48]. Such models, including *microclima*[49], *NicheMapR*[50], and *Microclimc*[51], are the most widely accessible tools for measuring microclimates, as they integrate diverse datasets with daily information. These models can be tailored to insect life histories by specifying predictions of soil or air temperature at set distances above ground and integrating vegetation and topography [47,48,50,52]. This approach provides flexibility in estimating different microclimates that insects experience throughout their lifecycles, for example temperature belowground and aboveground[49].

In contrast, *in situ* measurements, though resource-intensive, can achieve exceptionally high resolutions limited only by the size of the sensor (for example, an iButton measures temperature at the size of the sensor, which is 1.7cm), and its capacity to collect temporal data (one measurement per minute for iButtons). This flexibility permits measurements of additional environmental variation relevant to insect behavior. Microclimate sensors offer point-based measurements, a locally accurate but likely discontinuous representation of spatial variability in temperature and moisture availability[53]: spatially-continuous, direct measurements of temperatures using *in situ* sensors would require deployment of a carpet of sensors covering the

complete area of interest. Such a strategy would likely be unhelpful and impractical for many reasons. Nevertheless, *in situ* monitoring tools can be deployed flexibly to measure a wide array of environmental characteristics[46]. By standardizing measurement protocols[54] and combining local datasets into large databases (for example, SoilTemp[55]), *in situ* data could dramatically improve insights into insect-relevant microclimates.

Remote sensing data, collected by equipment mounted on satellites or small aircraft including drones (aerial imagery), in contrast, is restricted to variables observable through the electromagnetic spectrum or active sensing. These variables include ground surface temperature, soil moisture, and landscape heterogeneity, but exclude direct measurements of air temperature, soil temperature, and precipitation[56–59]. Additionally, for satellite remote sensing, revisit times (meaning, the interval at which satellites pass over an area) might not provide the temporal resolution required for certain studies[60]. However, remote sensing offers increasingly high-resolution thermal data, as modern satellites are equipped with sensors achieving resolutions of <5 m[61]. Many climate datasets are publicly available[62], although spatial resolutions are often too coarse for microclimate studies at insect scales, even when datasets are specifically targeted for microclimate research (for example, 15km resolution[52]).

Aerial imagery currently provides the only method for direct, centimeter-level measurements of ground surface temperature and landscape heterogeneity, offering unmatched customization by adjusting sensor type and flight altitude to balance spatial resolution versus spatial extent of measurement[63,64].This adaptability makes aerial imagery arguably the most effective tool for capturing insect-relevant microclimatic conditions[57,58]. Although this method can be spatially and temporally adjusted relative to research needs, it remains resource-intensive.

These measurement approaches are particularly valuable when they are integrated in complementary ways. While impractical for large-scale studies, tailored *in situ* data can significantly enhance the accuracy of microclimate models[53]. However, its limited spatial extent necessitates its integration into model-based approaches to bridge the gap between high resolution and broader coverage. Downscaling techniques can further refine existing satellite imagery to resolutions as low as 30 m, or <5m when combined with aerial imagery[65–68]. By combining *in situ* and remotely sensed data, microclimatic observations can be both accurate and sufficiently highly resolved to be relevant for insect-focused research. New remote sensing platforms are needed to expand access to microclimate observations over broad areas, and *in situ* measurements will remain vital for validation of remotely sensed or modelled environmental characteristics and to provide direct measurements of conditions that cannot be detected remotely or modelled reliably.

Across all of these approaches, microclimate measurements that focus on moisture are considerably more limited than thermal microclimates[47,69,70]. Tolerance to desiccation varies across insect life stages[20,71], making hydrologic microrefugia critical. This gap arises in part from a lack of high-resolution observational data on factors such as precipitation[72], soil moisture[73], and groundwater flow[69]. While *in situ* measurements provide the highest resolution data, vegetation indices from wet-dry season time series are commonly used as a substitute. Development of spatially-explicit hydrological microclimate data will improve understanding of how to manage insect populations as climatic conditions change.

[H1] Implications for species ecology and evolution

Insect species with broader thermal and hydric tolerance limits are likely to be more resilient to climate changes[74,75]. For species with more specialized requirements, microclimates will likely serve as vital refuges, mitigating some shifts in climates and rising frequency and severity of extreme weather[76]. The boundaries of species' realized niches, and their individual, population, or species-level responses[77], are more effectively identified by accounting for microclimates[78], and how they interact with species' ecological and evolutionary context (Box 1). For example, a species relying on grassy habitats might experience very different levels of temperature and humidity – with different effects on organismal performance – depending on whether the habitat is embedded in forested, agricultural, or urban landscapes[79]. Such understanding of realized niches can help predict variation in species occupancy within landscapes, an approach that also informs understanding of pest movement and abundance in agricultural and silvicultural settings[79,80].

While climate is changing at an unprecedented rate, microclimates can provide temporary refugia for individuals and populations to adapt to changing conditions or respond plastically (Figure 3). If adaptation and plasticity do not sufficiently enable species to tolerate shifting climates and extreme weather regimes, then it is likely that that the balance between population extinctions and colonizations will also change. Nevertheless, populations could use microclimates to reduce exposure to the most damaging forms of climate and weather change *in situ* (referred to here as micro-refugia) or could use emerging microclimates in new areas to 'escape' through colonization. Emergent patterns of extinction and colonization dynamics will become apparent through examinations of species range dynamics, as equatorial ranges shrink with extinction, and microclimates facilitate, or fail to facilitate, colonization and range

226 expansion. These ecological patterns, and the role of microclimates in shaping them, are
227 discussed in this section.

228 ***[H2] Adaptation and plasticity***

229 A diverse suite of life-history (timing and abundance of offspring), morphological (body
230 size and color), behavioral (activity times), and physiological (thermal tolerance, desiccation
231 and/or starvation resistance, locomotion performance) characteristics depend on the timing,
232 magnitude and persistence of environmental change, specifically both 'press' and 'pulse'
233 climatic events (Box 2)[27,81]. Insects can plastically adjust traits *in situ*, shift their geographic
234 ranges to track optimal conditions, or use some combination of both mechanisms to sustain local
235 populations[82]. To date, little consensus has been reached on which traits will respond most
236 strongly to changing environmental conditions in the field, but life-history plasticity is widely
237 expected to offset negative climate change impacts (such as changing phenology to match local
238 host plant flowering times, or accumulating sufficient development time above key growth
239 thresholds[83]). Yet, that plasticity is likely limited. For example, phenological asynchrony of the
240 brown argus butterfly (*Aricia agestis*) with its host plant imposes limits on local population
241 growth, influencing resource selection, evolutionary responses, and range dynamics[84].

242 In the short term, if environmental change is sufficient to trigger a plastic or
243 developmental response, insects can develop alternative phenotypes (traits) with adaptive
244 advantages for future environments, so long as environmental cue reliability is high (for instance,
245 the future environment matches the induced trait's response) relative to their generation
246 time[83,85,86]. Local weather shifts in the insect's occupied microsites could then translate to
247 differentially expressed phenotypes at the population level that are assimilated by genetic
248 changes to become evolved responses[83]. Examples include developmental polyphenisms such as

249 locust phase changes between solitary and gregarious forms, short- and long-winged crickets that
250 trade-off dispersal and reproduction, and color polymorphisms associated with seasonality in
251 some butterflies[87]. If induced trait responses fail to match future conditions, then this plasticity
252 can be viewed as maladaptive, and would usually be purged from the population over time
253 through selection. Numerous examples of population-level variation in functional traits, such as
254 upper thermal limits to activity and survival or desiccation resistance (drought survival), are
255 correlated with microclimate conditions, illustrating that these kinds of changes take place
256 frequently and extensively across insect taxa. A classic example is the local population
257 adaptation of chill coma temperature—the lower limit to activity—observed in a non-
258 overwintering crop pest in sub-Saharan Africa, the African sugarcane borer[88] (*Eldana*
259 *saccharina).*

260 Heat tolerance, however, shows far less variation among individuals, seasons,
261 populations and species than cold tolerance, suggesting fundamental evolutionary constraints on
262 rates of heat adaptation[83,85,86]. For example, pest fruit flies show some local adaptation of heat
263 tolerance[89], stoneflies living in different thermally distinct streams only differ in heat tolerance
264 by a small amount[90]. Similar patterns occur in butterflies[91], disease vectors such as mosquitoes
265 and tsetse[92] and have been reflected in global databases compilations[93,94] and comparisons across
266 26 species of rolled leaf beetles from diverse elevations and microenvironments[95]. However, the
267 among-population compensation of heat tolerance to local weather is likely insufficient to fully
268 buffer climate change impacts, since despite widespread plasticity of thermal limits, the
269 magnitude of an adaptive response is typically weak[96].

270 For some species, exposure to environmental extremes for a given amount of time will
271 induce a dramatic and persistent trait change, while that same experience will produce no lasting

(or even a negative effect) for another species[97]. In a comparative study of several *Drosophila* species, species from hotter and drier environments needed longer hardening treatments to elicit their maximum hardening response compared to species from less extreme environments [97]. While the reason(s) for a species' lack of plastic response remain unclear, it is widely assumed to be 'costly' (either biochemically at a cellular level or from an evolutionary Darwinian fitness perspective) to maintain greater tolerance[45]. Theoretical models of evolution that specifically include a focus on phenotypic plasticity leading to evolutionary change consider magnitude of environmental change relative to cue reliability, as well as trait plasticity and timing of new environmental conditions relative to trait change (in other words, cue reliability[85,86]).

Early work on the evolution of climate specialists versus generalists emphasized life-cycle duration relative to environmental change as moderators of fitness benefits of plastic responses[98]. However, meta-analyses and comprehensive reviews have largely focused on snap-shot approaches, rarely considering the time-course and relative persistence of trait responses, despite their importance to understanding the fitness benefits of any induced plastic response[96,99]. A daunting but critical task to produce robust predictive forecasting of climate change impacts at the microsite scale is to integrate these species- and trait-specific plastic time-courses into population dynamic models. Further, integration across approaches (bridging experimental manipulation and field observations), from multiple lines of evidence, are required to infer mechanisms of evolutionary adaptation for species persistence in an era of rapid change.

[H2] Colonization and extinction dynamics

With climate-driven population losses underway among insects[100,101], microclimates can create either localized opportunities or challenges for species' persistence and colonization. Among Lepidoptera and Coleoptera, local extinction was reduced by microclimate variation,

measured as the variability among quadrats in solar radiation reaching the earth's surface (mediated by topographic heterogeneity)[77]. The effect of buffering against extinction risk was strongest among species known to be negatively affected by climate change and species in areas with the highest levels of climate warming. In an analysis of 600 arthropod species over 150 years in Italy, taxonomic and functional loss were lower in areas with higher microclimate heterogeneity[102]. The strength of these and other findings suggest that microclimate heterogeneity can be an important driver of insect population dynamics.

A particularly well studied system is the range expansion of the silver-spotted skipper (*Hesperia comma*) in southern England (Figure 3). Survival, and consequently overall occupancy of this species within habitat patches, can be explained by microclimatic temperatures (derived from modelled solar radiation, which is mediated by aspect, slope, and other habitat characteristics at a 5m resolution), in addition to other factors[103,104]. Across a wider set of butterfly and moth species in England, local extinctions were more likely where microclimatic temperatures (using modelled estimates of temperature and aridity, also at a 5m resolution) were higher.

Dispersal is a key aspect of extinction and colonization dynamics, and although weather conditions have been shown to affect these processes[105], the role of microclimates has only rarely been considered. Identifying how microclimates affect movement through the landscape is critical to understanding the functional connectivity of patches (in other words, whether individuals can identify and disperse to favorable patches). Patch connectivity could vary dynamically with pulse and press events if favorable microclimates are distributed unevenly across the matrix.

Rare tests of the role of microclimate in colonization and extinction dynamics have come from mesocosm experiments. For example, in an experimentally controlled, semi-natural mesocosm of connected habitat patches (the Metatron, France), extreme heat increased the rate at which butterflies departed individual patches, while humidity reduced the departure rate[106]. In a grouping of unconnected indoor mesocosms (the Ecotron, Germany), microclimate availability reduced the movement of beetles, crickets, and true bugs under extreme heat, but only when suitable microclimates contained food resources[107].

Although the mesocosm approach can offer unique insights, field observations might be required to understand colonization-extinction dynamics among strong dispersers. In a rare example from a field setting, choice of oviposition location in butterflies reflected microclimate suitability[108]. Common techniques like mark-release-recapture studies do not intrinsically differentiate between behavioral responses to microclimates and variable mortality in the matrix, making radio and GPS telemetry particularly valuable[109,110]. Such techniques can be impractical for many insect species because of their body sizes or challenges related to sensor power and battery life[111].

[H2] Range shifts

Insect species' responses to localized changes, including to microclimates, will ultimately influence geographical range shifts at broad extents. Warm microclimates are expected to facilitate poleward colonization by warm-adapted species[112]. Conversely, cool microclimates (such as debris-covered glaciers, which maintain cooler temperatures than those that are uncovered[113]) are also expected to act as refugia and facilitate colonization outside of species' current ranges. In population and metapopulation models of *Hesperia comma,* the addition of

340 microclimate data (derived in the same way as [103,104]) allowed better predictions of changes in
341 occupancy across patches at the species' range edge, including the colonization of 156
342 previously unoccupied patches [104].

343 Shifts will include population extinctions from historically-occupied areas and dispersal
344 to, and colonization of, areas that were not. If rates of range loss exceed those of range
345 expansion, extinction will eventually result. Some species have been able to take advantage of
346 the additional opportunities that microclimatic variability provides to expand more rapidly than
347 expected (for example, *Hesperia comma*[104]), or to persist at their equatorward range edge despite
348 broad-scale climatic conditions becoming less tolerable[77]. Yet, ameliorative effects of
349 microclimatic variability will not apply equally to all insects, with anthropogenic climate change
350 already resulting in 'winners' and 'losers' in most taxa (for example, ref.[114], but see ref. [115]).
351 Some species have life history constraints (such as poor dispersal or specialism on a particular
352 host plant species) that prevent them from using beneficial microclimates. Research should
353 prioritize the identification of macro-climatic 'losers' at the coarser scale that are also poorly
354 placed to exploit meso- or micro-refugia in the landscape, either because they simply cannot
355 access them, or because species-specific resources are not available when they get there.

356 Studies of species' range responses to climate change are biased towards the
357 documentation of leading edge range expansions, despite a long-identified conservation need for
358 better information about species' trailing edges[116]. Meta-analytic estimates of shifts in species'
359 leading edges outnumbered trailing edge estimates by over 3 to 1[117], with a lack of data on
360 species' trailing edges[118]. This disparity often leads multispecies studies to conclude that
361 predictions of climate change responses are a good match to observations across taxa, for both
362 range shifting[119] and changes in overall extinction risk[120].

Detecting range losses of small-bodied organisms like insects can be a far more difficult task than that of range expansions. Range loss requires the provable absence of all populations from an area, while range expansions are inferred with the establishment and detection of a single population. Use of macroclimatic data can result in pessimistic, or inaccurate, predictions of range losses because those data can miss small areas that remain suitable for the target species. Microclimatic observations and modelling could overcome this challenge. When used to analyze data at finer scales, models built with microclimate data provide a much better fit to observed range shifts than do macroclimate models[121,122], and also tend to predict the presence of climatically-suitable alternatives closer to existing populations than the macroclimate models.

[H1] Managing for microclimates

Species plasticity, adaptation, and their extinction-colonization dynamics ultimately determine their persistence in this era of rapid climate change. Because species that specialize on a narrow range of climatic conditions are more vulnerable to climate change[123], access to favorable microclimates could increase their population growth rates. Moreover, how those localized population trends scale up to broader landscapes and associated macroclimatic conditions will affect species' susceptibilities to climate-driven extinction. Given a growing body of evidence that microclimates influence species persistence, it is now worth considering whether habitat management interventions could make use of this information.

Prioritizing sites with high microclimatic heterogeneity in area-based conservation planning is a valuable principle. Spatial datasets and models that identify heterogeneity hotspots can be used in conjunction with spatial conservation planning tools, such as Marxan[124]. For regions where these data are unavailable, topographic or habitat heterogeneity could provide a useful proxy for microclimate variation. In planning for landscape connectivity, care should be

386 taken to account for ‘stepping stones’ of suitable microclimates alongside broader-scale climate
387 connectivity[125].

388 Although existing examples are few, management interventions that either directly or
389 indirectly altered microclimates have benefitted insects of conservation concern (Figure 4). For
390 example, the large blue butterfly (*Maculinea arion*) became extinct from Britain in 1979 after
391 excess shrub growth cooled the soil below the thermal requirements of the red ant (*Myrmica*
392 *sabuleti*), a species that is parasitized by *M. arion* larvae[126]. In the 1980s, however,
393 conservationists removed shrubs and imposed intensive livestock grazing, which created warmer
394 microhabitats suitable for the ants and ultimately enabled the reintroduction of *M. arion*[127]. This
395 example highlights the importance of simultaneously managing non-climatic threats, such as
396 habitat degradation and invasive species, which interact with climate change to alter insect
397 microhabitats. Other management actions have targeted species groups or local communities
398 more broadly; a project to block artificial drainage in peatlands in the UK is predicted to prevent
399 summer drying, maintaining cool and wet microrefugia[128,129]. This should increase crane-fly
400 abundance, thereby increasing food availability for native birds[128].

401 Careful attention to—and indeed manipulation of—sites to create suitable microhabitats
402 and microclimates could help to extend both the assisted colonization range and the duration at
403 which species can persist within their historical ranges. Such ‘climate-targeted’ conservation
404 actions could include constructing shade structures to manage heat events, installing sprinklers
405 and engineering topography to create moist microclimates, managing water release and shading
406 to cool water temperatures and managing fire and grazing regimes to manipulate soil
407 temperatures[130]. While many management interventions have been suggested (for example,

shading streams to create cold-water refuges for aquatic species[131,132]), more research on the success of these interventions is needed to guide their use in providing microclimate refuges.

[H1] Outlook

Evidence that climate change is contributing to the sixth mass extinction is now very strong, and climate-driven extinctions or population declines are also apparent in insects[133]. Although less is known about insect responses to microclimate variation than to macroclimate variation, the evidence we have summarized here suggests that microclimates could be considered in insect conservation plans. Conservation scientists often grapple with the question of whether and when to act on incomplete knowledge. Further research into the role of microclimates in changing insect species' conservation trajectories is urgently needed, given the current pace of insect declines and the need for innovative solutions.

Making progress on this emerging research topic requires understanding whether and how microclimates could shelter species during press and pulse climate events. Knowledge of the relative roles of press and pulse events in altering species' capacity to adapt or respond phenotypically to recent climate changes can inform whether their extinction-colonization dynamics in the future will also change. Identifying the direction and magnitude of species responses to extreme temperatures will inform the extent to which access to favorable microclimates determines species persistence. Such an evidence base will guide whether interventions, such as maintenance or re-establishment of microclimatic heterogeneity within habitats and the surrounding matrix, could be part of the conservation plan for a species.

These actions will require integration of a range of measurement methods that enable sufficient spatial and temporal resolutions. The datasets that result from such efforts can provide

the key to understanding where microclimatic refugia are most reliably present in habitats. Modeling techniques have made rapid strides in this respect, as have remote sensing methods, but *in situ* monitoring provides direct evidence of variation and should not be disregarded. Currently, accurate distribution maps, let alone detailed observations of their responses to environmental change, are lacking for many species[134,135]. Such data gaps mean that many insect species' responses to climate change can be modelled but not measured.

Managing microclimates could balance extinction-colonization equilibria enough to delay anticipated rises in global extinctions from climate change. The key is “delay”. As business-as-usual emissions pathways could imperil a third of Earth’s species[136], deploying management strategies rapidly, but with appropriate precautions, must become a priority. The future of the world’s most diverse class of species, and potentially the indispensable services and functions they provide, depend on it.

References

1. IUCN. *The IUCN Red List of Threatened Species*. https://www.iucnredlist.org.
2. Wilson, R. J. & Fox, R. Insect responses to global change offer signposts for biodiversity and conservation. *Ecological Entomology* **46**, 699–717 (2021).
3. Outhwaite, C. L., McCann, P. & Newbold, T. Agriculture and climate change are reshaping insect biodiversity worldwide. *Nature* **605**, 97–102 (2022).
4. Soroye, P., Newbold, T. & Kerr, J. Climate change contributes to widespread declines among bumble bees across continents. *Science* **367**, 685–688 (2020).
5. Kerr, J. T. *et al.* Climate change impacts on bumblebees converge across continents. *Science* **349**, 177–180 (2015).
6. Stemkovski, M. *et al.* Disorder or a new order: How climate change affects phenological variability. *Ecology* **104**, e3846 (2023).
7. Outhwaite, C. L., Cooke, R., Millard, J. & Bladon, A. J. Pervasive and synergistic effects of climate change. in *Routledge Handbook of Insect Conservation* (Routledge, 2024).
8. Müller, J. *et al.* Weather explains the decline and rise of insect biomass over 34 years. *Nature* **628**, 349–354 (2024).
9. Ghisbain, G. *et al.* Projected decline in European bumblebee populations in the twenty-first century. *Nature* **628**, 337–341 (2024).
10. Kemppinen, J. *et al.* Microclimate, an important part of ecology and biogeography. *Global Ecology and Biogeography* **33**, e13834 (2024).

11. Schultz, N. M., Lawrence, P. J. & Lee, X. Global satellite data highlights the diurnal asymmetry of the surface temperature response to deforestation. *Journal of Geophysical Research: Biogeosciences* **122**, 903–917 (2017).
12. De Frenne, P. *et al.* Global buffering of temperatures under forest canopies. *Nat Ecol Evol* **3**, 744–749 (2019).
13. Wright, A. J. & Francia, R. M. Plant traits, microclimate temperature and humidity: A research agenda for advancing nature-based solutions to a warming and drying climate. *Journal of Ecology* **112**, 2462–2470 (2024).
14. Pincebourde, S. & Casas, J. Narrow safety margin in the phyllosphere during thermal extremes. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 5588–5596 (2019).
15. Pincebourde, S. & Woods, H. A. Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. *Functional Ecology* **26**, 844–853 (2012).
16. Stange, E. E. & Ayres, M. P. Climate Change Impacts: Insects. in *eLS* (John Wiley & Sons, Ltd, 2010). doi:10.1002/9780470015902.a0022555.
17. Kingsolver, J. G. *et al.* Complex Life Cycles and the Responses of Insects to Climate Change. *Integrative and Comparative Biology* **51**, 719–732 (2011).
18. Shah, A. A., Dillon, M. E., Hotaling, S. & Woods, H. A. High elevation insect communities face shifting ecological and evolutionary landscapes. *Current Opinion in Insect Science* **41**, 1–6 (2020).
19. Bridle, J. *et al.* How should we bend the curve of biodiversity loss to build a just and sustainable future? *Philosophical Transactions of the Royal Society B: Biological Sciences* **380**, 20230205 (2025).

20. Benk, G., Thompson, P. J., Hu, X. P. & Appel, A. G. Water Loss and Desiccation Tolerance of the Two Yearly Generations of Adult and Nymphal Kudzu Bugs, Megacopta cribraria (Hemiptera: Plataspidae). *Environmental Entomology* **49**, 651–659 (2020).
21. Klinges, D. H. *et al.* Proximal microclimate: Moving beyond spatiotemporal resolution improves ecological predictions. *Global Ecology and Biogeography* **33**, e13884 (2024).
22. Bowden, J. J. *et al.* High-Arctic butterflies become smaller with rising temperatures. *Biol Lett* **11**, 20150574 (2015).
23. Lembrechts, J. J., Nijs, I. & Lenoir, J. Incorporating microclimate into species distribution models. *Ecography* **42**, 1267–1279 (2019).
24. Greiser, C., von Schmalensee, L., Lindestad, O., Gotthard, K. & Lehmann, P. Microclimatic variation affects developmental phenology, synchrony and voltinism in an insect population. *Functional Ecology* **36**, 3036–3048 (2022).
25. Budelli, G. *et al.* Ionotropic Receptors Specify the Morphogenesis of Phasic Sensors Controlling Rapid Thermal Preference in Drosophila. *Neuron* **101**, 738-747.e3 (2019).
26. Enjin, A. Humidity sensing in insects — from ecology to neural processing. *Current Opinion in Insect Science* **24**, 1–6 (2017).
27. González-Tokman, D. *et al.* Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. *Biological Reviews* **95**, 802–821 (2020).
28. Kaun, K. R. *et al.* Natural variation in food acquisition mediated via a Drosophila cGMP-dependent protein kinase. *J Exp Biol* **210**, 3547–3558 (2007).
29. Simões, J. M. *et al.* Robustness and plasticity in Drosophila heat avoidance. *Nat Commun* **12**, 2044 (2021).
30. Parmesan, C. & Singer, M. C. Mosaics of climatic stress across species' ranges: tradeoffs cause adaptive evolution to limits of climatic tolerance. *Philosophical Transactions of the Royal Society B: Biological Sciences* **377**, 20210003 (2022).

31. Kazenel, M. R., Wright, K. W., Griswold, T., Whitney, K. D. & Rudgers, J. A. Heat and desiccation tolerances predict bee abundance under climate change. *Nature* **628**, 342–348 (2024).
32. Bennett, J. M. *et al.* The evolution of critical thermal limits of life on Earth. *Nat Commun* **12**, 1198 (2021).
33. Buckley, L. B., Huey, R. B. & Kingsolver, J. G. Asymmetry of thermal sensitivity and the thermal risk of climate change. *Global Ecology and Biogeography* **31**, 2231–2244 (2022).
34. Parks, S. A., Carroll, C., Dobrowski, S. Z. & Allred, B. W. Human land uses reduce climate connectivity across North America. *Global Change Biology* **26**, 2944–2955 (2020).
35. Benoit, J. B., McCluney, K. E., DeGennaro, M. J. & Dow, J. A. T. Dehydration Dynamics in Terrestrial Arthropods: From Water Sensing to Trophic Interactions. *Annual Review of Entomology* **68**, 129–149 (2023).
36. Sinclair, B. J., Saruhashi, S. & Terblanche, J. S. Integrating water balance mechanisms into predictions of insect responses to climate change. *Journal of Experimental Biology* **227**, jeb247167 (2024).
37. Sinclair, B. J., Williams, C. M. & Terblanche, J. S. Variation in Thermal Performance among Insect Populations. *Physiological and Biochemical Zoology* **85**, 594–606 (2012).
38. MacLean, H. J. *et al.* Evolution and plasticity of thermal performance: an analysis of variation in thermal tolerance and fitness in 22 Drosophila species. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180548 (2019).
39. Franken, O., Huizinga, M., Ellers, J. & Berg, M. P. Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* **186**, 311–322 (2018).
40. Kerr, J. T. Racing against change: understanding dispersal and persistence to improve species' conservation prospects. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20202061 (2020).

41. Bretzlaff, T., Kerr, J. T. & Darveau, C.-A. High temperature sensitivity of bumblebee castes and the colony-level costs of thermoregulation in *Bombus impatiens*. *Journal of Thermal Biology* **117**, 103710 (2023).
42. Watson, M. J. & Kerr, J. T. Climate-Driven Body Size Changes in Birds and Mammals Reveal Environmental Tolerance Limits. *Global Change Biology* **31**, e70241 (2025).
43. Rezende, E. L., Castañeda, L. E. & Santos, M. Tolerance landscapes in thermal ecology. *Functional Ecology* **28**, 799–809 (2014).
44. Diamond, S. E. *et al.* A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology* **93**, 2305–2312 (2012).
45. Clusella-Trullas, S., Garcia, R. A., Terblanche, J. S. & Hoffmann, A. A. How useful are thermal vulnerability indices? *Trends in Ecology & Evolution* **36**, 1000–1010 (2021).
46. Lembrechts, J. J. *et al.* Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography* **28**, 1578–1596 (2019).
47. Kearney, M. R., Gillingham, P. K., Bramer, I., Duffy, J. P. & Maclean, I. M. D. A method for computing hourly, historical, terrain-corrected microclimate anywhere on earth. *Methods in Ecology and Evolution* **11**, 38–43 (2020).
48. Kearney, M. R. *et al.* Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. *Methods in Ecology and Evolution* **5**, 273–286 (2014).
49. Maclean, I. M. D., Mosedale, J. R. & Bennie, J. J. Microclima: An r package for modelling meso- and microclimate. *Methods in Ecology and Evolution* **10**, 280–290 (2019).
50. Kearney, M. R. & Porter, W. P. NicheMapR – an R package for biophysical modelling: the microclimate model. *Ecography* **40**, 664–674 (2017).
51. Maclean, I. M. D. & Klinges, D. H. Microclimc: A mechanistic model of above, below and within-canopy microclimate. *Ecological Modelling* **451**, 109567 (2021).

52. Kearney, M. R., Isaac, A. P. & Porter, W. P. microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Sci Data* **1**, 140006 (2014).
53. Bramer, I. *et al.* Chapter Three - Advances in Monitoring and Modelling Climate at Ecologically Relevant Scales. in *Advances in Ecological Research* (eds. Bohan, D. A., Dumbrell, A. J., Woodward, G. & Jackson, M.) vol. 58 101–161 (Academic Press, 2018).
54. De Frenne, P. *et al.* Ten practical guidelines for microclimate research in terrestrial ecosystems. *Methods in Ecology and Evolution* **16**, 269–294 (2025).
55. Lembrechts, J. J. *et al.* SoilTemp: A global database of near-surface temperature. *Global Change Biology* **26**, 6616–6629 (2020).
56. Jayaramu, Y. *et al.* Sensing the dependable surficial signatures of temporal groundwater variations in arid coastal regions through geospatial techniques with respect to microclimate changes. *Environmental Research* **250**, 118483 (2024).
57. Ednie, G. & Kerr, J. T. High resolution thermal remote sensing and the limits of species' tolerance. *PeerJ* **10**, e13911 (2022).
58. Faye, E., Rebaudo, F., Yánez-Cajo, D., Cauvy-Fraunié, S. & Dangles, O. A toolbox for studying thermal heterogeneity across spatial scales: from unmanned aerial vehicle imagery to landscape metrics. *Methods in Ecology and Evolution* **7**, 437–446 (2016).
59. Li, Z.-L. *et al.* Soil moisture retrieval from remote sensing measurements: Current knowledge and directions for the future. *Earth-Science Reviews* **218**, 103673 (2021).
60. Rhodes, M. W., Bennie, J. J., Spalding, A., ffrench-Constant, R. H. & Maclean, I. M. D. Recent advances in the remote sensing of insects. *Biological Reviews* **97**, 343–360 (2022).
61. Kulu, E. Satellite Constellations - 2024 Survey, Trends and Economic Sustainability. *th International Astronautical Congress* (2024).
62. Suggitt, A. J. *et al.* Conducting robust ecological analyses with climate data. *Oikos* **126**, 1533–1541 (2017).

63. Duffy, J. P., Anderson, K., Fawcett, D., Curtis, R. J. & Maclean, I. M. D. Drones provide spatial and volumetric data to deliver new insights into microclimate modelling. *Landscape Ecol* **36**, 685–702 (2021).
64. Zellweger, F., Frenne, P. D., Lenoir, J., Rocchini, D. & Coomes, D. Advances in Microclimate Ecology Arising from Remote Sensing. *Trends in Ecology & Evolution* **34**, 327–341 (2019).
65. Bonafoni, S., Anniballe, R., Gioli, B. & Toscano, P. Downscaling Landsat Land Surface Temperature over the urban area of Florence. *European Journal of Remote Sensing* **49**, 553–569 (2016).
66. Pu, R. Assessing scaling effect in downscaling land surface temperature in a heterogenous urban environment. *International Journal of Applied Earth Observation and Geoinformation* **96**, 102256 (2021).
67. Zawadzka, J., Corstanje, R., Harris, J. & Truckell, I. Downscaling Landsat-8 land surface temperature maps in diverse urban landscapes using multivariate adaptive regression splines and very high resolution auxiliary data. *International Journal of Digital Earth* **13**, 899–914 (2020).
68. Zellweger, F. *et al.* Microclimate mapping using novel radiative transfer modelling. *Biogeosciences* **21**, 605–623 (2024).
69. McLaughlin, B. C. *et al.* Hydrologic refugia, plants, and climate change. *Global Change Biology* **23**, 2941–2961 (2017).
70. Lembrechts, J. J. *et al.* Global maps of soil temperature. *Global Change Biology* **28**, 3110–3144 (2022).
71. Thorat, L. & Nath, B. B. Insects With Survival Kits for Desiccation Tolerance Under Extreme Water Deficits. *Front. Physiol.* **9**, (2018).

72. Karger, D. N., Wilson, A. M., Mahony, C., Zimmermann, N. E. & Jetz, W. Global daily 1 km land surface precipitation based on cloud cover-informed downscaling. *Sci Data* **8**, 307 (2021).
73. Karthikeyan, L. & Mishra, A. K. Multi-layer high-resolution soil moisture estimation using machine learning over the United States. *Remote Sensing of Environment* **266**, 112706 (2021).
74. Diamond, S. E. & Yilmaz, A. R. The role of tolerance variation in vulnerability forecasting of insects. *Current Opinion in Insect Science* **29**, 85–92 (2018).
75. Riddell, E. A., Mutanen, M. & Ghalambor, C. K. Hydric effects on thermal tolerances influence climate vulnerability in a high-latitude beetle. *Global Change Biology* **29**, 5184–5198 (2023).
76. Vives-Ingla, M. *et al.* Interspecific differences in microhabitat use expose insects to contrasting thermal mortality. *Ecological Monographs* **93**, e1561 (2023).
77. Suggitt, A. J. *et al.* Extinction risk from climate change is reduced by microclimatic buffering. *Nature Clim Change* **8**, 713–717 (2018).
78. Storlie, C. *et al.* Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biology Letters* **10**, 20140576 (2014).
79. Mosedale, J. R. *et al.* Mechanistic microclimate models and plant pest risk modelling. *J Pest Sci* **97**, 1749–1766 (2024).
80. Ma, G. & Ma, C.-S. Potential distribution of invasive crop pests under climate change: incorporating mitigation responses of insects into prediction models. *Current Opinion in Insect Science* **49**, 15–21 (2022).
81. Ma, C.-S., Ma, G. & Pincebourde, S. Survive a Warming Climate: Insect Responses to Extreme High Temperatures. *Annual Review of Entomology* **66**, 163–184 (2021).

82. Harvey, J. A. *et al.* Scientists' warning on climate change and insects. *Ecological Monographs* **93**, e1553 (2023).
83. Sgrò, C. M., Terblanche, J. S. & Hoffmann, A. A. What Can Plasticity Contribute to Insect Responses to Climate Change? *Annual Review of Entomology* **61**, 433–451 (2016).
84. Stewart, J. E. *et al.* Phenological variation in biotic interactions shapes population dynamics and distribution in a range-shifting insect herbivore. *Proceedings of the Royal Society B: Biological Sciences* **291**, 20240529 (2024).
85. Chevin, L.-M., Lande, R. & Mace, G. M. Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLOS Biology* **8**, e1000357 (2010).
86. Leung, C., Grulois, D., Quadrana, L. & Chevin, L.-M. Phenotypic plasticity evolves at multiple biological levels in response to environmental predictability in a long-term experiment with a halotolerant microalga. *PLOS Biology* **21**, e3001895 (2023).
87. West-Eberhard, M. J. *Developmental Plasticity and Evolution*. (Oxford University Press, 2003).
88. Kleynhans, E., Mitchell, K. A., Conlong, D. E. & Terblanche, J. S. Evolved variation in cold tolerance among populations of ldana saccharina (Lepidoptera: Pyralidae) in South Africa. *Journal of Evolutionary Biology* **27**, 1149–1159 (2014).
89. Weldon, C. W., Nyamukondiwa, C., Karsten, M., Chown, S. L. & Terblanche, J. S. Geographic variation and plasticity in climate stress resistance among southern African populations of Ceratitis capitata (Wiedemann) (Diptera: Tephritidae). *Sci Rep* **8**, 9849 (2018).
90. Birrell, J. H., Frakes, J. I., Shah, A. A. & Woods, H. A. Mechanisms underlying thermal breadth differ by species in insects from adjacent but thermally distinct streams – A test of the climate variability hypothesis. *Journal of Thermal Biology* **112**, 103435 (2023).
91. Dongmo, M. A. K. *et al.* Local adaptation in thermal tolerance for a tropical butterfly across ecotone and rainforest habitats. *Biology Open* **10**, bio058619 (2021).

92. Terblanche, J. S., Klok, C. J., Krafsur, E. S. & Chown, S. L. Phenotypic plasticity and geographic variation in thermal tolerance and water loss of the tsetse Glossina pallidipes (Diptera: Glossinidae): Implications for distribution modelling. *The American Journal of Tropical Medicine and Hygiene* **74**, 786–794 (2006).
93. Bennett, J. M. *et al.* GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci Data* **5**, 180022 (2018).
94. Chown, S. L., Addo-Bediako, A. & Gaston, K. J. Physiological variation in insects: large-scale patterns and their implications. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* **131**, 587–602 (2002).
95. García-Robledo, C., Kuprewicz, E. K., Staines, C. L., Erwin, T. L. & Kress, W. J. Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proceedings of the National Academy of Sciences* **113**, 680–685 (2016).
96. Weaving, H., Terblanche, J. S., Pottier, P. & English, S. Meta-analysis reveals weak but pervasive plasticity in insect thermal limits. *Nat Commun* **13**, 5292 (2022).
97. van Heerwaarden, B., Sgrò, C. & Kellermann, V. M. Threshold shifts and developmental temperature impact trade-offs between tolerance and plasticity. *Proceedings of the Royal Society B: Biological Sciences* **291**, 20232700 (2024).
98. Gilchrist, G. W. Specialists and Generalists in Changing Environments. I. Fitness Landscapes of Thermal Sensitivity. *The American Naturalist* **146**, 252–270 (1995).
99. Rohr, J. R. *et al.* The complex drivers of thermal acclimation and breadth in ectotherms. *Ecology Letters* **21**, 1425–1439 (2018).
100. Forister, M. L. *et al.* Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science* **371**, 1042–1045 (2021).
101. Wagner, D. L. Insect Declines in the Anthropocene. *Annual Review of Entomology* **65**, 457–480 (2020).

102. Marta, S., Brunetti, M., Manenti, R., Provenzale, A. & Ficetola, G. F. Climate and land-use changes drive biodiversity turnover in arthropod assemblages over 150 years. *Nat Ecol Evol* **5**, 1291–1300 (2021).
103. Lawson, C. R., Bennie, J. J., Thomas, C. D., Hodgson, J. A. & Wilson, R. J. Local and landscape management of an expanding range margin under climate change. *Journal of Applied Ecology* **49**, 552–561 (2012).
104. Bennie, J. *et al.* Range expansion through fragmented landscapes under a variable climate. *Ecology Letters* **16**, 921–929 (2013).
105. DiLeo, M. F., Nonaka, E., Husby, A. & Saastamoinen, M. Effects of environment and genotype on dispersal differ across departure, transfer and settlement in a butterfly metapopulation. *Proceedings of the Royal Society B: Biological Sciences* **289**, 20220322 (2022).
106. Legrand, D. *et al.* Ranking the ecological causes of dispersal in a butterfly. *Ecography* **38**, 822–831 (2015).
107. Terlau, J. F. *et al.* Microhabitat conditions remedy heat stress effects on insect activity. *Global Change Biology* **29**, 3747–3758 (2023).
108. Eilers, S., Pettersson, L. B. & Öckinger, E. Micro-climate determines oviposition site selection and abundance in the butterfly Pyrgus armoricanus at its northern range margin. *Ecological Entomology* **38**, 183–192 (2013).
109. Alston, J. M., Joyce, M. J., Merkle, J. A. & Moen, R. A. Temperature shapes movement and habitat selection by a heat-sensitive ungulate. *Landscape Ecol* **35**, 1961–1973 (2020).
110. Knight, S. M., Pitman, G. M., Flockhart, D. T. T. & Norris, D. R. Radio-tracking reveals how wind and temperature influence the pace of daytime insect migration. *Biology Letters* **15**, 20190327 (2019).
111. Kissling, D. W., Pattemore, D. E. & Hagen, M. Challenges and prospects in the telemetry of insects. *Biological Reviews* **89**, 511–530 (2014).

112. Bell, F., Botham, M., Brereton, T. M., Fenton, A. & Hodgson, J. Grizzled Skippers stuck in the south: Population-level responses of an early-successional specialist butterfly to climate across its UK range over 40 years. *Diversity and Distributions* **27**, 962–972 (2021).
113. Tampucci, D. *et al.* Debris-covered glaciers as habitat for plant and arthropod species: Environmental framework and colonization patterns. *Ecological Complexity* **32**, 42–52 (2017).
114. Jackson, H. M. *et al.* Climate change winners and losers among North American bumblebees. *Biology Letters* **18**, 20210551 (2022).
115. Lenoir, J. & Comte, L. Rapid range shifters show unexpected population dynamics. *Nat Ecol Evol* **8**, 850–851 (2024).
116. Hampe, A. & Petit, R. J. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* **8**, 461–467 (2005).
117. Comte, L. *et al.* BioShifts: a global geodatabase of climate-induced species redistribution over land and sea. figshare https://doi.org/10.6084/m9.figshare.7413365.v1 (2020).
118. Brodie, J. F., Freeman, B. G., Mannion, P. D. & Hargreaves, A. L. Shifting, expanding, or contracting? Range movement consequences for biodiversity. *Trends in Ecology & Evolution* **40**, 439–448 (2025).
119. Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* **333**, 1024–1026 (2011).
120. Maclean, I. M. D. & Wilson, R. J. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences* **108**, 12337–12342 (2011).
121. Stickley, S. F. & Fraterrigo, J. M. Microclimate species distribution models estimate lower levels of climate-related habitat loss for salamanders. *Journal for Nature Conservation* **72**, 126333 (2023).

122. Maclean, I. M. D. & Early, R. Macroclimate data overestimate range shifts of plants in response to climate change. *Nat. Clim. Chang.* **13**, 484–490 (2023).
123. Foden, W. B. *et al.* Climate change vulnerability assessment of species. *WIREs Climate Change* **10**, e551 (2019).
124. Watts, M. E. *et al.* Marxan with Zones: Software for optimal conservation based land- and sea-use zoning. *Environmental Modelling & Software* **24**, 1513–1521 (2009).
125. Alves, W. de F. *et al.* Connectivity and climate influence diversity–stability relationships across spatial scales in European butterfly metacommunities. *Global Ecology and Biogeography* **33**, e13896 (2024).
126. Thomas, J. Why Did the Large Blue Become Extinct in Britain? *Oryx* **15**, 243–247 (1980).
127. Munguira, M. L. & Martín, J. *Action Plan for Maculinea Butterflies in Europe*. (Council of Europe, 1999).
128. Ausden, M. Climate Change Adaptation: Putting Principles into Practice. *Environmental Management* **54**, 685–698 (2014).
129. Słowińska, S., Słowiński, M., Marcisz, K. & Lamentowicz, M. Long-term microclimate study of a peatland in Central Europe to understand microrefugia. *Int J Biometeorol* **66**, 817–832 (2022).
130. Prober, S. M., Doerr, V. A. J., Broadhurst, L. M., Williams, K. J. & Dickson, F. Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecological Monographs* **89**, e01333 (2019).
131. Ebersole, J. L., Liss, W. J. & Frissell, C. A. Cold Water Patches in Warm Streams: Physicochemical Characteristics and the Influence of Shading. *JAWRA Journal of the American Water Resources Association* **39**, 355–368 (2003).
132. Mejia, F. H. *et al.* Closing the gap between science and management of cold-water refuges in rivers and streams. *Global Change Biology* **29**, 5482–5508 (2023).

133. Edwards, C. B. *et al.* Rapid butterfly declines across the United States during the 21st century. *Science* **387**, 1090–1094 (2025).
134. McCain, C. M. & Garfinkel, C. F. Climate change and elevational range shifts in insects. *Current Opinion in Insect Science* **47**, 111–118 (2021).
135. Garcia-Rosello, E., Gonzalez-Dacosta, J., Guisande, C. & Lobo, J. M. GBIF falls short of providing a representative picture of the global distribution of insects. *Systematic Entomology* **48**, 489–497 (2023).
136. Urban, M. C. Climate change extinctions. *Science* **386**, 1123–1128 (2024).
137. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315 (2017).
138. GBIF: The Global Biodiversity Information Facility. GBIF Occurrence Download. GBIF https://doi.org/10.15468/dl.hjmu6m (2025).
139. Turlure, C., Choutt, J., Baguette, M. & Van Dyck, H. Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change. *Global Change Biology* **16**, 1883–1893 (2010).
140. Pateman, R. M., Thomas, C. D., Hayward, S. A. L. & Hill, J. K. Macro- and microclimatic interactions can drive variation in species' habitat associations. *Global Change Biology* **22**, 556–566 (2016).
141. Carlson, C. J., Bannon, E., Mendenhall, E., Newfield, T. & Bansal, S. Rapid range shifts in African Anopheles mosquitoes over the last century. *Biology Letters* **19**, 20220365 (2023).
142. Patterson, T. A., Grundel, R., Dzurisin, J. D. K., Knutson, R. L. & Hellmann, J. J. Evidence of an extreme weather-induced phenological mismatch and a local extirpation of the endangered Karner blue butterfly. *Conservation Science and Practice* **2**, e147 (2020).
143. Packer, L. The extirpation of Karner Blue butterfly in Ontario. in *Karner Blue butterfly: a symbol of vanishing landscape* 143–151 (University of Minnesota, St. Paul, Minnesota, 1994).

144. Velu, R. M. *et al.* Ecological Niche Modeling of Aedes and Culex Mosquitoes: A Risk Map for Chikungunya and West Nile Viruses in Zambia. *Viruses* **15**, 1900 (2023).
145. Christidis, N., Jones, G. S. & Stott, P. A. Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. *Nature Clim Change* **5**, 46–50 (2015).
146. Harris, R. M. B. *et al.* Biological responses to the press and pulse of climate trends and extreme events. *Nature Clim Change* **8**, 579–587 (2018).
147. Chan, S.-F., Shih, W.-K., Chang, A.-Y., Shen, S.-F. & Chen, I.-C. Contrasting forms of competition set elevational range limits of species. *Ecology Letters* **22**, 1668–1679 (2019).
148. Chan, S.-F. *et al.* Higher temperature variability in deforested mountain regions impacts the competitive advantage of nocturnal species. *Proceedings of the Royal Society B: Biological Sciences* **290**, 20230529 (2023).
149. Tsai, H.-Y. *et al.* Antagonistic effects of intraspecific cooperation and interspecific competition on thermal performance. *eLife* **9**, e57022 (2020).
150. Sun, S.-J. *et al.* Climate-mediated cooperation promotes niche expansion in burying beetles. *eLife* **3**, e02440 (2014).
151. Chan, S.-F. *et al.* Land-use changes influence climate resilience through altered population demography in a social insect. *Ecological Monographs* **95**, e1638 (2025).
152. Colwell, R. K. & Rangel, T. F. Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences* **106**, 19651–19658 (2009).
153. Angilletta, M. J., Niewiarowski, P. H. & Navas, C. A. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* **27**, 249–268 (2002).
154. Sinclair, B. J. *et al.* Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters* **19**, 1372–1385 (2016).
155. Chen, I.-C., Shen, S.-F. & Chan, S.-F. Niche Theory and Species Range Limits Along Elevational Gradients: Perspectives and Future Directions. *Annual Review of Ecology, Evolution, and Systematics* **55**, 449–469 (2024).

Acknowledgements

Jeremy T. Kerr is grateful to the Natural Sciences and Engineering Research Council of Canada (NSERC) for Discovery Grant and Discovery Accelerator Supplement support. Jeremy T. Kerr holds the University Research Chair in Macroecology and Conservation, and associated funding from University of Ottawa supported this work.

Author contributions

JTK and SCCG planned and led the collaborative effort on this article. All authors wrote, reviewed, and edited the article.

Competing interests

The authors declare no competing interests.

Peer review information

Nature Reviews Biodiversity thanks Nicole Miller-Struttmann and the other, anonymous, reviewers for their contribution to the peer review of this work.

Table 1. Common methods of measure microclimates

Method	Spatial resolution	Temporal resolution	Variable(s) inferred or measured	Incorporates vertical thermal profile?	Available models or databases	Reference for database or method
Model predictions	commonly 1m or less	~Hourly (dependent on data availability)	Model estimates of aboveground (air) and belowground (soil) temperature and moisture availability	Yes	*microclima*, *NicheMapR*, *Microclimc*	47, 49, 50, 51
In situ measurements	~1cm; customizable	Continuous throughout an insects' life cycle	Direct measurement of air temperature and moisture	Yes	SoilTemp	55
Aerial imagery	~1cm; customizable	Customizable, within constraints of battery endurance	Direct observation of ground surface temperature and land cover characteristics (sensor dependent)	No	Imagery may be available from country-specific programs, such as the Canadian Aerial Imagery Database; thermal imagery infrequently available	63, 64
Satellite imagery	Currently moderate resolution (~15m or more) for publicly available imagery	Subject to constraints on revisit frequency; provides only snapshots across the insect lifecycle	Direct measures of ground surface temperature, soil moisture, and landscape heterogeneity	No	Public thermal infrared satellites include ASTER, ECOSTRESS, Landsat 8/9	60

Figures

Figure 1: Insects experience climatic variation at broad and local spatial scales. Thermal position index[57] is a measure of thermal tolerance, calculated using the extreme hot and cold temperatures experienced by species within their range as their thermal limits; thermal position index values near 0 represent temperatures close to a species' lower thermal (cool) limits, values near 1 represent temperatures close to a species' upper thermal (hot) limits. Negative values, or those exceeding 1, indicate conditions are beyond the species cold or warm thermal

tolerance limits, respectively, as derived from field-based observations. The thermal position index can be applied to temperature measurements across a species' range – at any spatial resolutions – to calculate variation in temperature (or other environmental) suitability. **a|** Mean thermal position index for the months June, July, and August for the years 2020-2023 throughout the range of the clouded sulphur butterfly *Colias philodice*, at coarse ~1km resolution (data from [137,138]). **b|** Mean thermal position index for June 2nd 2020 at Burnt Lands Provincial Park near Ottawa, Canada, within the range of *C. philodice*. Aerial image in **b** was captured by G. Ednie at 1cm resolution (data from [57]).

Figure 2: Thermal and hydric microclimates can provide refugia and facilitate range expansion opportunities. **a|** Range expansion of the silver-spotted skipper (*Hesperia comma*) is facilitated by warm microclimates on south-facing slopes[104]. **b|** Colonization of new sites by the speckled wood butterfly (*Pararge aegerie*) is facilitated by moist microclimates that prevent drying of the host grasses[140]. **c|** The host plant of adonis blue (*Lysandra bellargus*), horseshoe vetch, requires warm, sheltered microclimates[77]. **d|** Host plants of the cranberry fritillary (*Boloria aquilonaris*) require moist sphagnum moss microclimates[139].

Figure 3: Favorable microclimates for insects in natural, agricultural, and urban areas. Forests with high structural complexity should be preserved, as their topography and plant biodiversity creates useful microclimate variation compared to forest with lower complexity. In agricultural settings, hedgerows benefit insects by providing shade and increasing moisture, relative to heavily grazed or planted areas. In urban environments, leaving leaf litter in yards provides beneficial microclimate variation; urban green spaces provide shade, but relatively little structural complexity.

Box 2: Press and Pulse Events

Press and pulse events refer to distinct types of environmental changes. Press events are long-term, continuous, and relatively gradual climatic changes impacting species and ecosystems. For example, the rate of elevational range shifts of species such as the African malaria mosquito (*Anopheles* spp.) mirrors the velocity of ongoing local climate change[141]. Conversely, pulse events are short-term and can have immediate consequences. Heatwaves and droughts, for example, are implicated in the local extinctions of many Karner blue butterfly populations in North America[142,143]. For mosquitoes, extreme precipitation can benefit these

insects by creating pools of standing water for breeding, or can harm their populations by scouring those same standing pools[144]. Whether in the form of extreme heat or precipitation, pulse events are becoming more frequent and severe[145].

Press and pulse events interact with insect tolerances to determine whether populations and species will benefit from, or be harmed by, emerging conditions[146]. Species are expected to respond to these changes based on their environmental tolerances. For example, *Bombus impatiens* has an activity thermal maximum of 45.65 ºCelsius, and population declines are expected when temperatures exceed this limit[41] (Box Figure); declines might occur in response to press events (panel A), or a combination of press and pulse events (panel B).

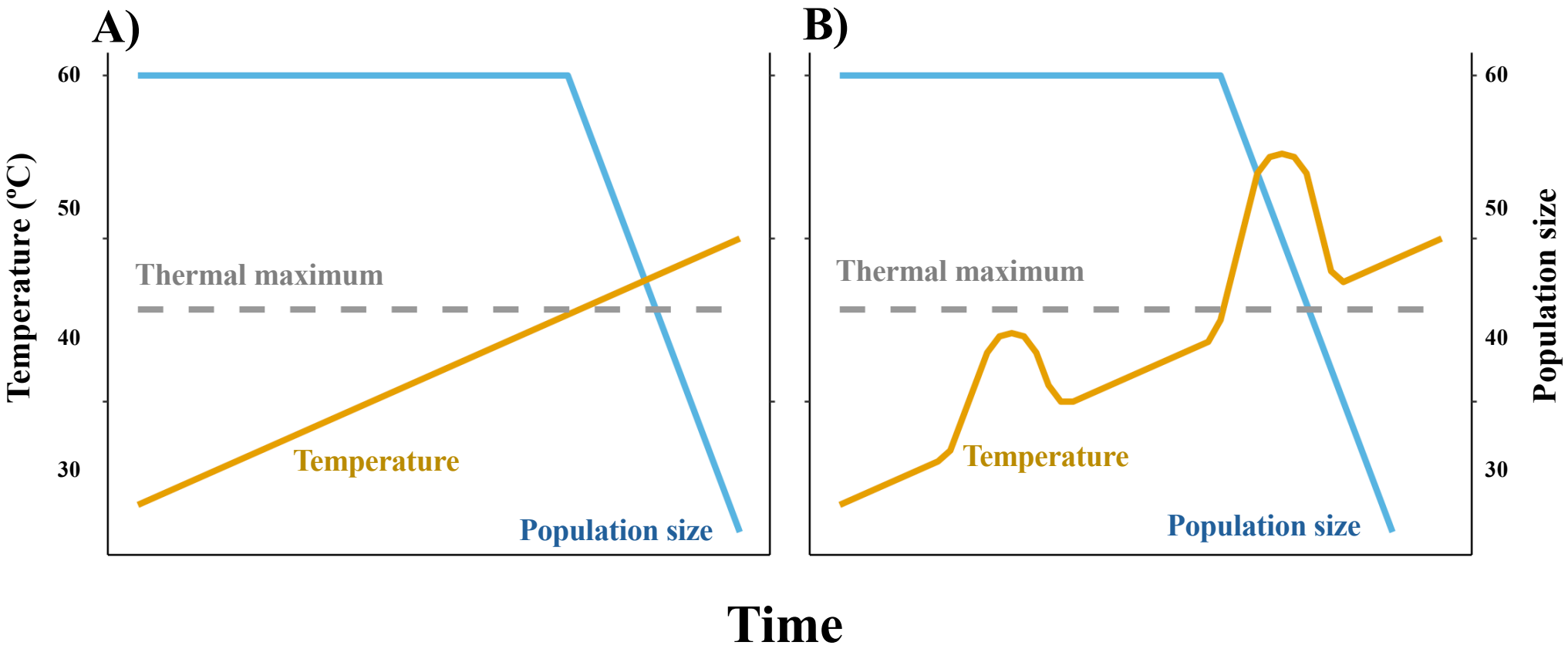
Box 1: Case study of the burying beetle

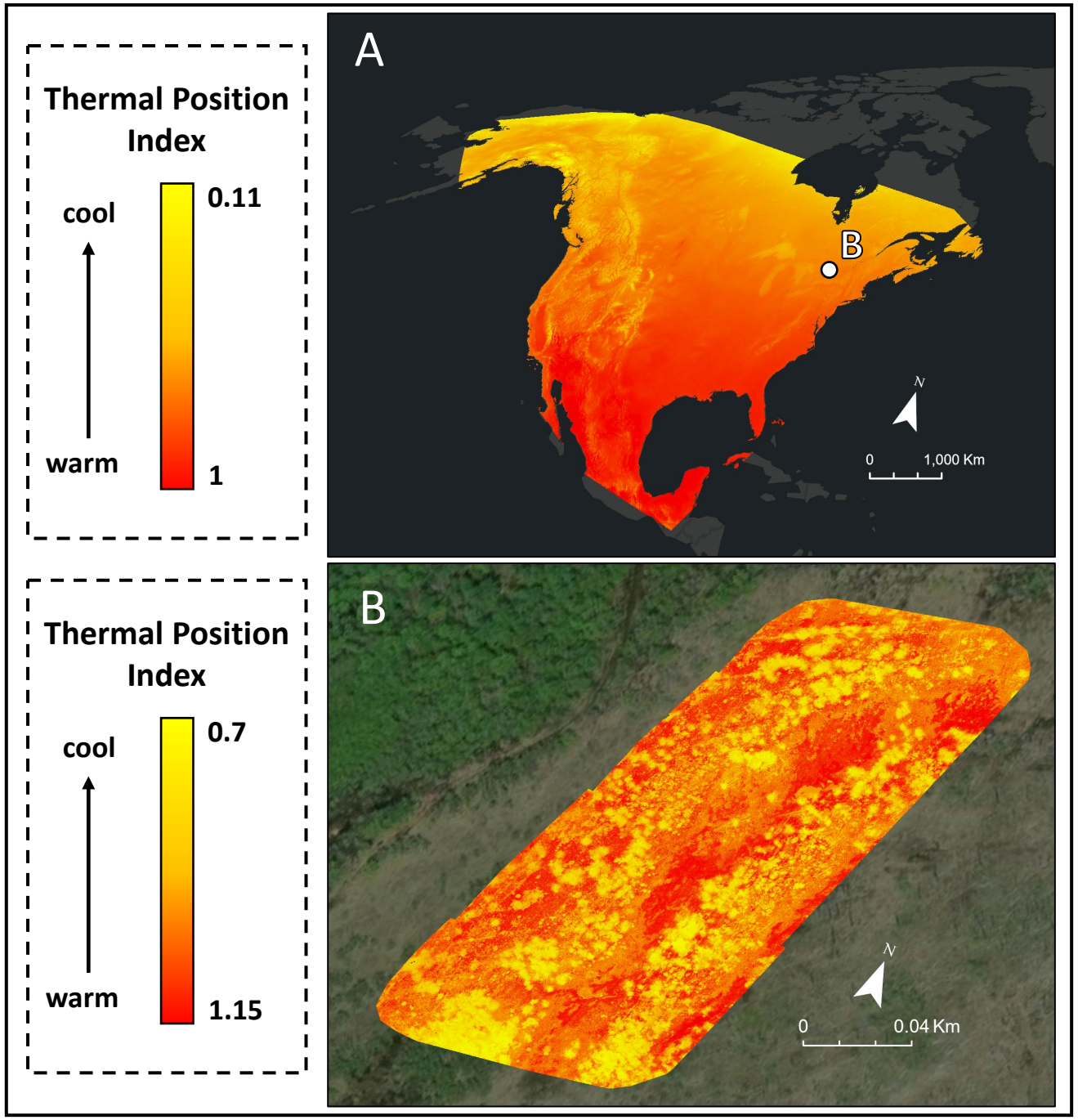
Detailed investigations into species' thermal requirements in the context of other ecological factors, such as species interactions and landcover change, provide insight into the potential complexity of microclimate impacts on species performance.

The burying beetle (*Nicrophorus nepalensis*) is a nocturnal scavenger that competes with blowflies for vertebrate carcasses, which the beetles bury and use to feed their larvae[147]. Across an elevational gradient on He-Huan Mountain in Taiwan, deforestation increased maximum and minimum daily temperatures in microclimates inhabited by the beetles, as measured using *in-situ* temperature sensors (iButtons). Under constant temperature conditions in a lab setting, beetles performed best at lower temperatures (16.7C) than their blowfly competitors (range of 29-37 °C). With small diurnal temperature fluctuations characteristic of intact forests, beetle's optimal performance temperature dropped to 14.2°C, consistent with temperatures present at higher

927 elevations. Conversely, with large diurnal temperature variations typical of deforested habitats,
928 their optimal performance temperature increased to 18.6°C, consistent with temperatures at
929 lower elevations[148]. This counterintuitive result is because the more extreme temperature
930 fluctuations caused by deforestation negatively impact burying beetles while benefiting their
931 competitors, ultimately shifting optimal performance to lower elevations. However, when
932 competitors were excluded, beetles were able to bury carcasses for their larvae across a broad
933 temperature gradient, suggesting that without competitors present, beetles would still be able to
934 maintain populations at those cooler, high-elevation deforested sites.
935 These dynamics are incredibly complex, as habitat modification and fragmentation also
936 reduces beetle population density, triggering Allee effects that slow carcass detection[147]. This
937 reduces the beetles' ability to compete with blowflies for resources, causing their realized
938 thermal niche to contract[149,150], and ultimately reducing reproductive success[151]. This research
939 demonstrates how integrating niche theory[152] with thermal performance curves[153,154] for
940 quantifying temperature-dependent fitness has expanded understanding of realized thermal
941 niches. This framework extends beyond simply considering temperature ranges (niche breadth)
942 for survival and reproduction to encompass how climate indirectly affects fitness through species
943 interactions like competition[149,155], a more comprehensive exploration of the complex
944 mechanisms through which microclimates influence organisms.
945
946 **Table of Contents**
947 The ecological importance of microclimate variation is increasingly recognized. This Perspective
948 discusses the extent to which favorable microclimates (in other words, areas with temperature

949 and precipitation within a species' niche) can facilitate adaptation, plasticity, colonization of new
950 patches, and ultimately persistence under global change.


A)
B)
60
50
40
30
Temperature (°C)
Population size
Thermal maximum
Temperature
Population size
Time

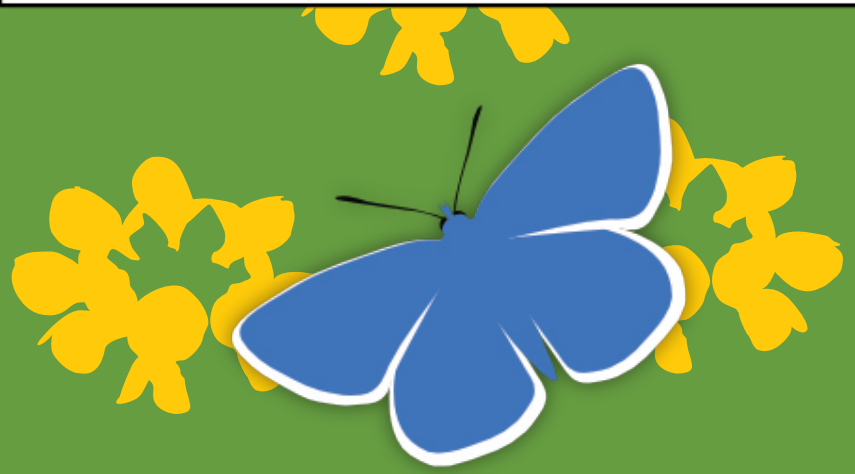

Thermal Position Index
cool
warm
0.11
1
A
B
N
0
1,000 Km
Thermal Position Index
cool
warm
0.7
1.15
B
N
0
0.04 Km

Temperature

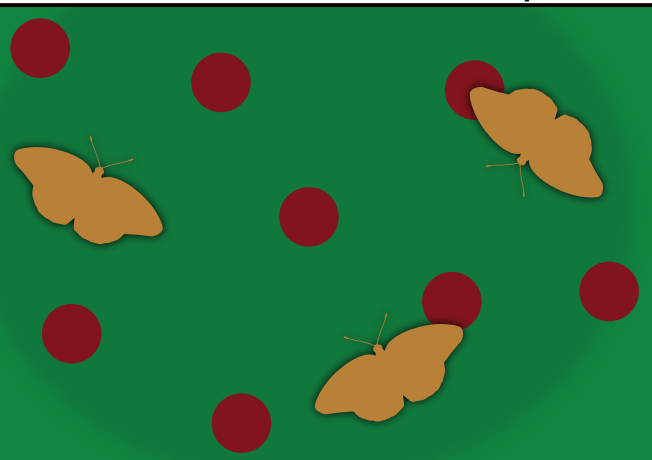
Moisture

Refugia

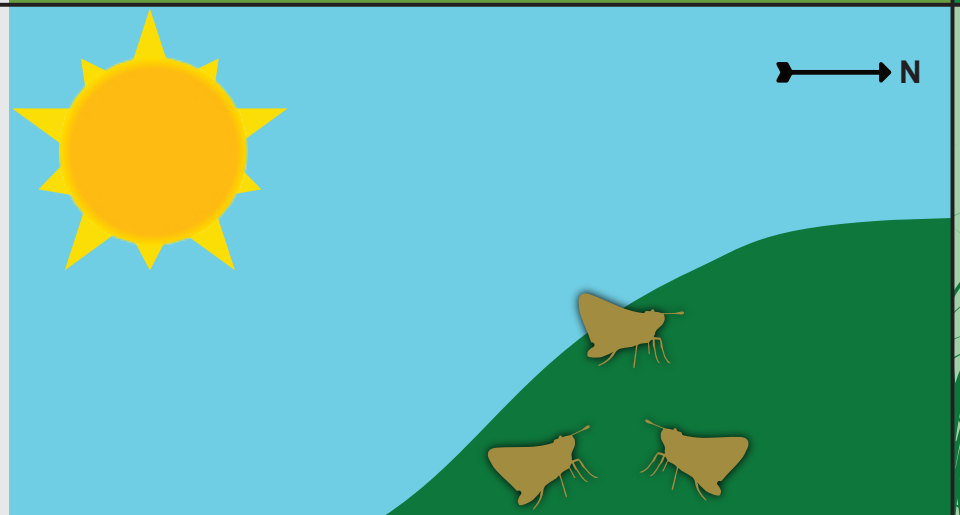
Warm, sheltered microclimates support horseshoe vetch, the host plant for *Lysandra bellargus*.



Moist sphagnum moss microclimates support host plants of *Boloria aquilonaris*, such as cranberry.

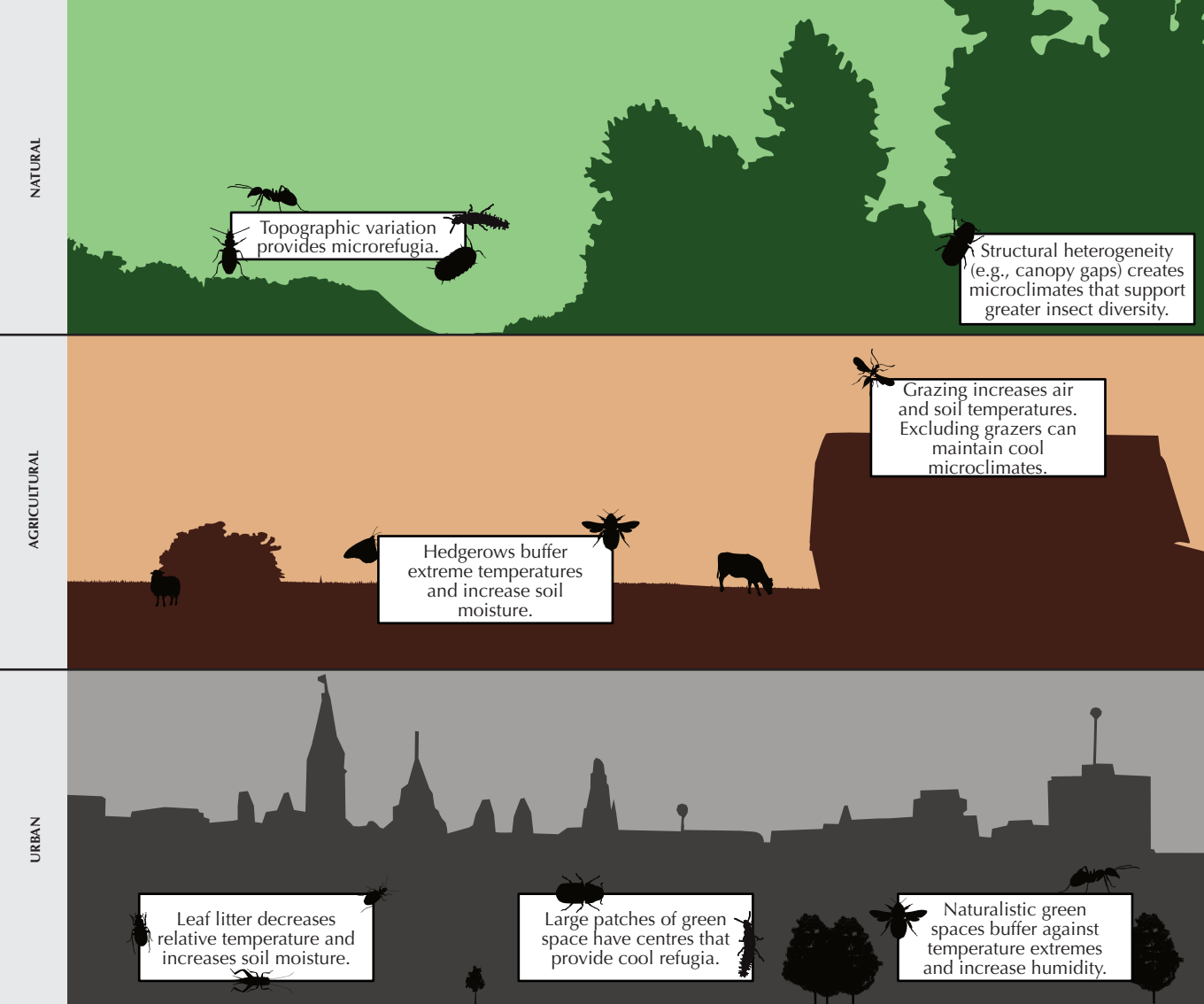


Range Expansion



South-facing slopes provide warm microclimates for *Hesperia comma*

Moist microclimates prevent drying of host grasses and allow colonization of new sites by *Pararge aegeria*


NATURAL
Topographic variation provides microrefugia.
Structural heterogeneity (e.g., canopy gaps) creates microclimates that support greater insect diversity.
AGRICULTURAL
Grazing increases air and soil temperatures. Excluding grazers can maintain cool microclimates.
Hedgerows buffer extreme temperatures and increase soil moisture.
URBAN
Leaf litter decreases relative temperature and increases soil moisture.
Large patches of green space have centres that provide cool refugia.
Naturalistic green spaces buffer against temperature extremes and increase humidity.