Received: 26 December 2023 | Revised: 30 May 2024 | Accepted: 11 June 2024

DOI: 10.1111/geb.13884

RESEARCH ARTICLE

Global Ecology and Biogeography A Journal of Macroecology

WILEY

Proximal microclimate: Moving beyond spatiotemporal resolution improves ecological predictions

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Funding information
Danmarks Frie Forskningsfond, Grant/Award Number: 7027-00133B; Agencia Nacional de Promoción Científica y Tecnológica, Grant/Award Number: PICT504/2020; RVO, Grant/Award Number: 67985939; Natural Environment Research Council, Grant/Award Number: NE/S01537X/1; National Science Foundation, Grant/Award Number: 1842473; Fonds Wetenschappelijk Onderzoek, Grant/Award Number: 12P1819N, 1512720N, G018919N and W001919N; European Research Council, Grant/Award Number: FORMICA-757833; Grantová Agentura České Republiky, Grant/Award Number: 23-06614S; Agence Nationale de la Recherche, Grant/Award Number: JCJC-N°ANR-19-CE32-0005-01 IMPRINT and PRC-N°ANR-21-CE32-0012-03 MaCCMic; Research Council of Finland, Grant/Award Number: 342890; Swedish research council FORMAS, Grant/Award Number: 2021-01993

Handling Editor: Fabien Leprieur

Abstract

Aim: The scale of environmental data is often defined by their extent (spatial area, temporal duration) and resolution (grain size, temporal interval). Although describing climate data scale via these terms is appropriate for most meteorological applications, for ecology and biogeography, climate data of the same spatiotemporal resolution and extent may differ in their relevance to an organism. Here, we propose that climate proximity, or how well climate data represent the actual conditions that an organism is exposed to, is more important for ecological realism than the spatiotemporal resolution of the climate data.

Location: Temperature comparison in nine countries across four continents; ecological case studies in Alberta (Canada), Sabah (Malaysia) and North Carolina/Tennessee (USA).

Time Period: 1960–2018.

Major Taxa Studied: Case studies with flies, mosquitoes and salamanders, but concepts relevant to all life on earth.

Methods: We compare the accuracy of two macroclimate data sources (ERA5 and WorldClim) and a novel microclimate model (*microclimf*) in predicting soil temperatures. We then use ERA5, WorldClim and *microclimf* to drive ecological models in three case studies: temporal (fly phenology), spatial (mosquito thermal suitability) and spatiotemporal (salamander range shifts) ecological responses.

Results: For predicting soil temperatures, *microclimf* had 24.9% and 16.4% lower absolute bias than ERA5 and WorldClim respectively. Across the case studies, we find that increasing proximity (from macroclimate to microclimate) yields a 247%

For affiliations refer to page 13.

https://doi.org/10.1111/geb.13884

improvement in performance of ecological models on average, compared to 18% and 9% improvements from increasing spatial resolution 20-fold, and temporal resolution 30-fold respectively.

Main Conclusions: We propose that increasing climate proximity, even if at the sacrifice of finer climate spatiotemporal resolution, may improve ecological predictions. We emphasize biophysically informed approaches, rather than generic formulations, when quantifying ecoclimatic relationships. Redefining the scale of climate through the lens of the organism itself helps reveal mechanisms underlying how climate shapes ecological systems.

KEYWORDS

biophysical ecology, climate change, ecophysiology, macroclimate, microclimate, nonlinearity, resolution, species distribution model

1 | INTRODUCTION

Explorations of scale are fundamental to understanding patterns and processes in the natural world (Wiens, 1989). Given that most urgent issues of global change involve phenomena that occur across spatial and temporal scales, it is crucial to understand how drivers of ecological responses shift across scales, and how a process that is shaped at one scale plays a role at another scale (Levin, 1992).

Climate is an omnipresent environmental component that is notably scale dependent. For instance, at the synoptic (or continental) spatial scale, across thousands of kilometres, climate is principally determined by latitude, elevation, distance to large bodies of water and ocean dynamics. In ecology and biogeography, climate at this scale is often referred to as macroclimate (Geiger et al., 2009). Locally (one hundred meters or less), however, climate varies substantially due to variation in vegetation, terrain, and soil conditions—climate at this scale has been referred to as microclimate (Geiger et al., 2009). Climate is also scale dependent in the temporal domain, as the processes that shape climate differ between seasonal, decadal and geological periods (Clark, 1985). Unsurprisingly, how climate drives ecological responses also differs across scales. For instance, thermal variation over the course of a day may determine periods of an organism's foraging activity or its exposure to stressful extremes, while annual fluctuations influence phenology or development (Kefford et al., 2022).

In classic macroecological studies, climate has been considered to be more important for distributions of species and communities at broad, rather than local, spatiotemporal scales (Woodward, 1987). Yet, both time-honoured and recent work have revealed the many roles of microclimate in ecology and evolution (Helmuth, 1998; Huey, 1991; Kearney & Porter, 2009; Lembrechts et al., 2019; Maclean & Early, 2023; Potter et al., 2013). Given that climate and its ecological effects are both scale dependent, the source of climate data, and the structure of such data in a modelling workflow, may critically impact the detection of ecological signals (Buckley et al., 2023a).

For much work in spatial ecology—especially related to species' distributions and diversity—researchers use macroclimate maps generated from mechanistic or statistical models (e.g. Fick & Hijmans, 2017; Hersbach et al., 2020). As with all model predictions, these climate maps are imperfect. In an effort to improve climate data for ecological applications, many studies have explored the impact of increasing either spatial or temporal resolution of climate data, and occasionally both in tandem, on the accuracy of ecological predictions (see review by Lembrechts et al., 2019). Yet, increasing spatiotemporal resolution of climate data alone does not necessarily increase the likelihood of capturing the relevant microclimates for a given organism or process, and may indeed result in lower prediction accuracy of ecological responses (Abdulwahab et al., 2022). Macroecological studies rarely measure how well climate data represent the actual exposure of an organism or system, independent of the data's spatiotemporal resolution. We call this the ‘proximity’ of climate data, which we define in further detail below (Box 1). By focusing on climate data resolution rather than proximity, many large-scale studies tend to overlook an established legacy in ecophysiology of understanding climate as experienced by organisms (Huey, 1991; Kearney & Porter, 2009). Unfortunately, this concept of climate proximity is rarely incorporated into macroecology or biogeography, and thus its importance for spatiotemporal ecological modelling has not yet been systematically explored and quantified.

Here, we investigate how climate spatial resolution, temporal resolution and proximity each influence the accuracy of temperature estimates and performance of climate-driven ecological models (Figure 1). We employ a set of temperature data sources that differ in these dimensions of scale, and perform spatial and temporal aggregation/disaggregation, to evaluate the importance of spatial resolution, temporal resolution and proximity of temperature data in each of three case studies: crop pest emergence, mosquito thermal suitability and salamander distribution changes. These case studies correspond to a spatial, temporal, and spatiotemporal ecological response, respectively, and exemplify common applications of climate data via disparate models, ecosystems and organisms. We expect to find that climate data of high proximity will predict ecological responses better than climate data that are of higher spatial or temporal resolution yet low proximity

BOX 1 The proximity of climate data

Scientists have traditionally grounded the definition of scale based upon extent (spatial area, temporal duration) and resolution (grain size, temporal interval) (Wiens, 1989). However, for climate data, resolution and extent are not comprehensive in describing their scale, as data of the same resolution and extent may differ in their ecological relevance to different organisms or processes. Here, we define 'climate proximity' as the degree to which climate data represent the actual conditions that an organism or system is exposed to, as a third dimension of scale distinct from the spatiotemporal resolution of the climate data (Figure 1). While resolution describes the quantity or frequency of data, proximity describes how well climate data capture radiation, water and heat exchange relevant to a given species for a time and location. When estimating distributions of a forest-dwelling species, a 1-km^2 temperature product that closely represents forest understory conditions is more proximal than a 100-m^2 product that represents free-air conditions as measured by weather stations and without accounting for the effects of vegetation. Similarly, mean monthly soil temperatures are more proximal for belowground organisms than daily air temperatures. We call the opposite of proximal climate, 'distal' climate, that is, only indirectly related to ecological responses (Austin, 2002; Gardner et al., 2019). Proximity is evaluated in a context-specific manner, which entails that although it can be qualified (e.g. one climate measurement is more proximal for a given species than another climate measurement) it is challenging to quantify in general terms (e.g. a 20% increase in proximity). Key to increasing climate proximity for a given organism is knowledge of the organism's microhabitats, physiology and ecology, nested within the broader habitat and landscape (Figure 1). For a gridded climate dataset, high proximity may not always involve representing the same heights or microhabitats across space or time. For ants, proximal climate might be air temperatures in forests, but soil temperatures in barren environments; for many amphibians, proximity entails aquatic conditions for tadpoles, and terrestrial conditions for adults.

Although proximity is distinct from spatial or temporal resolution, highly proximal climate typically varies at fine spatial and temporal scales. For instance, across horizontal space, topographic heterogeneity will determine how much local temperatures differ from macroclimate; vertically, soil temperatures can decouple considerably from air temperatures; and temporally, high-frequency wind turbulence drives thermal gradients near the ground (see Figure 2 for other mechanisms). Yet, there are also aspects of climate proximity that do not align well within the spatial or temporal dimensions, as proximity also depends upon the biotic context and how organisms 'construct' their environments through their physical properties and behaviour (Kearney & Porter, 2009; Pincebourde & Woods, 2020). Understanding the ecophysiology of tree frogs inhabiting epiphytic ferns in forest canopies requires measuring or simulating fern microclimates (Scheffers et al., 2014), which are nested within the canopy microclimate. Or for many parasites, the spatial location of climate data may matter less than accounting for host body temperatures (Thomas & Blanford, 2003). Furthermore, not all climate-forcing processes contribute to proximity for a given context; the attenuation of heat exchange by snow creates an important subnivium microclimate for small-bodied species, but less so for many large mammals or birds (Pauli et al., 2013).

Climate proximity should also be considered for understanding ecological processes for which there may be many relevant species, such as soil carbon sequestration. Given the impracticality of delineating proximal conditions for many taxa across regions, distal macroclimate may occasionally be useful as a 'mean field approximation' of climate exposure across ecological communities (Bennie et al., 2014). Yet oftentimes, this approximation is inadequate given heterogeneous microclimates and nonlinear responses to climate (Martin & Huey, 2008). Ultimately, operative conditions of organisms (body temperatures) are the broker between climate exposure and biological responses. Yet, given the challenge of estimating body conditions across space and time, generating or selecting highly proximal climate data serves as a useful surrogate for understanding bioclimatic relationships.

('distal'). Such findings would improve our understanding of the role of scale in bioclimatic relationships and would call for revision to our methods for quantifying such processes.

2 | METHODS

2.1 | Temperature data

We used three sources of global climate data that each differ for two of the three studied dimensions (spatial resolution, temporal resolution and/or proximity; Figure 2). The proximity of these climate data is gauged according to the microhabitat requirements and life-cycle processes of three case study organisms below. For these organisms (fly larvae, mosquitoes and salamanders), proximal climate is near and below the ground as well as underneath vegetation, which we represent using a microclimate model (see below).

The first climate product, ERA5, is an assimilation of numerical weather model predictions, satellite imagery and free-air weather station measurements (Hersbach et al., 2020). ERA5 data are available at several spatiotemporal resolutions and heights; here, we used hourly measurements (i.e. fine temporal resolution) at 0.25° resolution (c. 27.75×27.75 km at the equator or 770 km^2; i.e. coarse spatial resolution) at 2-m height above ground.

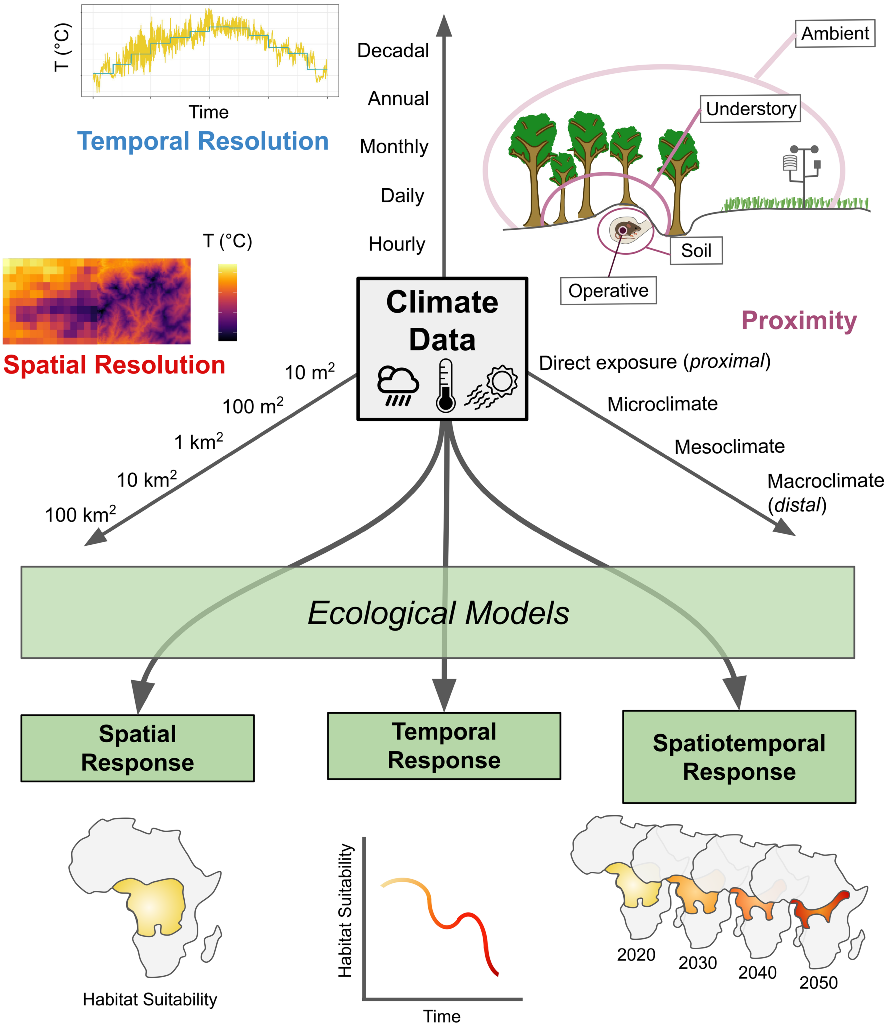


FIGURE 1 Top: the three dimensions of climate data resolution used for ecological modelling, none of which are true characteristics of climate in nature, but constructs for describing data. The proximity of climate describes its relevance to a given organism, process or system. For example, the soil temperature surrounding a fossorial mouse is more proximal (i.e. directly impacts operative body temperatures) than the forest understory microclimate, which, in turn, is more proximal than ambient free-air conditions. Bottom: the benefits of increasing each of these dimensions of climate data may then depend on the domains predicted by the ecological model: a process that is spatial, temporal or spatiotemporal.

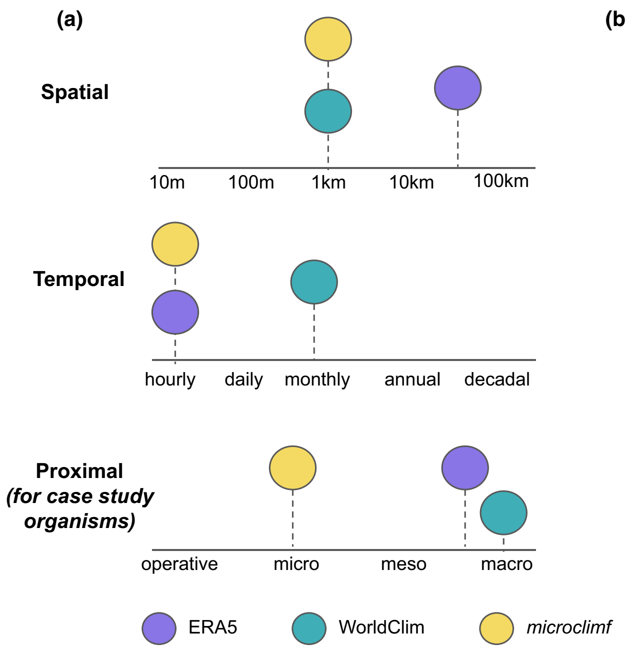
To complement ERA5's coarse spatial yet fine temporal resolution, we also included monthly (coarse temporal resolution) macroclimatic data from the WorldClim database (v2.1, Fick & Hijmans, 2017), which are global interpolations derived from weather station measurements (i.e. low proximity, or distal, for most taxa). Relative to other global gridded products, WorldClim has finer spatial resolution (30″ or c. 1 km^2 at the equator)—although we note that 1 km^2 can still contain high microclimate variability that is relevant to physiology and ecology.

To represent proximal climate data, we employed *microclimf* (Maclean, 2023), a recently developed grid version of a previously published mechanistic microclimate model (Maclean & Klinges, 2021). In brief, *microclimf* estimates near-ground air and soil temperatures principally based upon the net energy flux density absorbed by surfaces (vegetation/soils) by emulating a Lagrangian localized near-field model (see Table S1 and Supporting Information for details). Using *microclimf*, we generated spatiotemporal predictions of below-canopy topsoil temperature (5-cm depth), which is proximal for the case study organisms as detailed below, at 1 km^2 and hourly resolution. While estimating microclimate can be better achieved at the meter scale (Briscoe et al., 2023), here we matched *microclimf* predictions to the 1 km^2 spatial resolution of WorldClim and hourly resolution of ERA5 to compare climate data of the same resolution yet different proximity.

We assessed how closely ERA5, WorldClim and *microclimf* temperature predictions matched 371 time series of in situ soil temperature measurements (proximal microclimate for our case study organisms) from across four continents (Lembrechts et al., 2020; see Figure S1 and Supporting Information for details).

2.2 | Case study 1: Temporal crop pest emergence

Temporal models with climate as input are commonly employed for modelling population dynamics, tracking phenology and ecological forecasting. To illustrate a biological process using a temporally explicit model, we predicted the emergence rates of fossorial larvae for two fly species: the cabbage maggot (*Delia radicum*; Linnaeus, 1758) and the seedcorn maggot (*Delia platura*; Meigen, 1826). As two prominent pests that feed on crop roots, these flies cause massive damage, such as up to a $73 million annual loss in Canada (Broatch et al., 2006). Accurate predictions of fly phenology are useful for informing management practices, such as the timing of planting new crops or of pesticide treatments



(b)

Proximal Mechanisms				
Solar	Latitude (solar radiation angle)	●	●	●
Solar	Season (axial tilt)	●	●	●
Solar	Earth's rotation	●	●	●
Air	Sensible heat flux (convective exchange)	●	●	●
Air	Vapour pressure gradient (latent heat exchange)	●	●	●
Air	Cloud cover (radiation scattering/interception)	●	●	●
Water	Coastal effects (latent heat exchange)	●	●	●
Terrain	Altitudinal lapse rate	●	●	●
Terrain	Radiation interception	●		●
Terrain	Heat storage and conductance	●		●
Terrain	Longwave radiation	●		●
Terrain	Albedo	●		●
Terrain	Topographic shading			●
Terrain	Cold air drainage			●
Terrain	Topographic wetness			●
Vegetation	Stomatal conductance	●		●
Vegetation	Woody conductance			●
Vegetation	Radiation interception			●
Vegetation	Albedo			●

FIGURE 2 Climate data can be described in spatial, temporal and proximal domains, as illustrated by the contrasting scales of the data products employed in this study: ERA5, WorldClim and *microclimf* (a). The proximity of climate describes its relevance to the actual exposure of a given organism, process or system. To categorize the proximity of climate data, one must consider the meteorological and geographical mechanisms that such data adequately represent, which drive how radiation, moisture and heat exchange (latent and sensible) determine the temperature of a time and location. In (b), we present a nonexhaustive ordered list of temperature-forcing mechanisms and categorize which are represented by each climate data product, either explicitly (for the process-based ERA5 and *microclimf*) or implicitly (through covariates used in the statistical interpolation employed by WorldClim).

(Dent, 2000). Given that larval survival and growth of both species is suspected to be more sensitive to soil temperatures than air temperatures (Lepage et al., 2012), phenological predictions may diverge when calculated from temperature sources of different proximity (e.g. ERA5 or WorldClim macroclimate vs. *microclimf* soil microclimate).

We derived rates of insect emergence from topsoil as predicted by ERA5, WorldClim and *microclimf*, during 2002 averaged across five locations in Alberta, Canada, matching locations and days of observations of these two species by Broatch et al. (2006), who reported the proportion of a larval population that emerged as a winged adult per day. We extracted hourly temperature predictions from ERA5 and *microclimf* for the year 2002, while for WorldClim we extracted the average monthly means, minima and maxima for the corresponding decade (2000–2009), as 1-km^2 WorldClim does not include hourly data, nor data for just 2002. We also temporally aggregated/disaggregated each climate data source (hourly to monthly) to isolate the effects of spatial resolution, temporal resolution and proximity (see Supporting Information for details). We then converted temperature data into growing degree days (GDDs). GDDs are indices for the accumulation of heat units above a minimum (base) temperature for organismal development, and are frequently used for predicting insect and plant phenology (Arnold, 1960). Per Arnold (1960), we calculated GDDs as the cumulative sum of the deviations of the average of daily minima and maxima above species-specific base temperature thresholds: 4.0°C for *D. radicum* (Collier & Finch, 1985), 3.9°C for *D. platura* (Sanborn et al., 1982). We then used GDDs from ERA5, WorldClim and *microclimf* to drive a simple mathematical model for emergence rates of each fly species. We used the model originally developed by Pearl and Reed (1920) and parameterized by Broatch et al. (2006), which estimates the proportion of insect emergence per day using a logistic function driven by GDDs (see Supporting Information for model specification). Given that this model was developed to inform the timing of pesticide application, it does not necessitate, nor provide, absolute values of adult abundance, only proportions of adults emerging over time for identifying the timing of peak emergence. To validate predictions from each temperature-driven emergence model, we measured the absolute error of species-specific predictions from the observed emergence rates (error measured as the number of days between predicted timing of an emergence threshold, e.g. 50% emergence by day of year 180, and the observed day of year when that threshold was actually crossed).

2.3 | Case study 2: Spatial bioclimate and mosquito thermal performance

To examine whether the spatial, temporal and proximal dimensions of climate data may differentially change estimates of bioclimate and organismal thermal performance, we generated maps of (1) mean temperature, (2) extreme temperature and (3) temperature-dependent fecundity for the mosquito *Aedes aegypti* (Linnaeus, 1762) in Sabah within Malaysian Borneo (45,785 km^2). *Aedes aegypti* is a prominent vector of several human diseases, including dengue and yellow fever, which causes millions of infections and deaths per year (Bhatt et al., 2013). We chose this tropical region given its widespread land use change from primary forest to plantation forest (e.g. oil palm), which may facilitate mosquito establishment (Saager et al., 2023). *Aedes aegypti* rests under vegetation or in urban microhabitats, where it deposits eggs in water (Cheong et al., 2014). Therefore, microclimate predictions that represent vegetative shading (e.g. *microclimf*) are more proximal than free-air macroclimate for adult mosquitoes. Across Sabah, we extracted hourly temperature predictions from ERA5 and *microclimf* for the year 2018, while for WorldClim we extracted the monthly means, minima and maxima estimated at 1 km^2 for the corresponding decade (2010–2019). From each temperature product, we then calculated spatial layers of mean annual temperature (BIO1), maximum temperature of the warmest month (BIO5), and average fecundity of *A. aegypti* using a thermal reaction norm (see Supporting Information for details). This reaction norm was developed by Mordecai et al. (2017) using air temperatures, rather than water temperatures, although the latter more proximally represents exposure of larval mosquitoes (Paaijmans et al., 2013). To validate fecundity predictions, we averaged *A. aegypti* fecundity measurements across temperature from several laboratory studies (Braks et al., 2006; Day et al., 1994) to generate a normally-distributed range of fecundity values. We then measured the area of integration (overlap) between lab-derived fecundity observations with ERA5, WorldClim and *microclimf* fecundity predictions (see Klinges & Scheffers, 2021 and Supporting Information for details).

2.4 | Case study 3: Spatiotemporal salamander prevalence shifts

Given the widespread interest in climate change-induced range shifts (Lenoir et al., 2020), we tested how the spatial resolution, temporal resolution and proximity of climate data affect predictions of spatiotemporal changes in prevalence of Jordan's red-cheeked salamander (*Plethodon jordani*; Blatchley, 1901) across its range. *Plethodon jordani* is a fossorial salamander, endemic to the Great Smoky Mountains National Park (GSMNP, 2090 km^2) in the eastern United States, and relies upon cool, moist subsurface microhabitats (i.e. under rocks, logs or in burrows). Given that such microclimates are better represented by soil temperatures than free-air temperatures, *microclimf* is more proximal than either ERA5 or WorldClim for *P. jordani*. Across GSMNP's wide elevation range (267–2025 masl), *P. jordani* is climatically constrained to above 600 m (Gifford & Kozak, 2012). With climate change, this mountain-dwelling species may either shift towards higher elevations and/or experience abundance changes (Feeley et al., 2012).

To explore the impact of climate data resolution and proximity on spatiotemporal salamander prevalence change predictions, we conducted two steps, as detailed below. First, we fitted species distribution models (SDMs) separately for the 1960s and 1990s but without using any climate covariates (i.e. only using observer bias and topographic variables). Then, we compared how generalized additive models (GAMs) with climate covariates built from ERA5, WorldClim or *microclimf* were able to predict changes in SDM prevalence estimates over time.

For SDMs, we collated georeferenced occurrence (presence-only) data from two primary survey periods: 1961–1970 ('1960s', 975 surveys) and 1991–2000 ('1990s', 704 surveys) (IRMA, 2021). Separately for the 1960s and 1990s, we fitted inhomogeneous Poisson point process models (IPPMs, Renner et al., 2015) to estimate relative prevalence of *P. jordani* on a 0–1 scale. The topographic predictors used in each of these models included elevation, slope and aspect (measured in radians) at 1-km^2 resolution (obtained from the Amazon Web Services Terrain Tiles). An additional spatial predictor, distance from the closest trail on which salamander surveys were conducted, was also included in each model to control for observer bias. The quality of fit was determined through five-fold cross validation and model performance was assessed using CBI, AUC and TSS criteria (Allouche et al., 2006). CBI results, which are most appropriate for presence-only data paired with pseudo-absences (Boyce et al., 2002), are presented in the main text. Salamander prevalence changes were then considered as the differences in SDM-derived prevalence from the 1960s to the 1990s (see Supporting Information for details on model calibration, tuning, pseudo-absence point selection, and validation).

Next, we aimed to understand how prevalence shifts over time, as predicted by our SDMs, were explained by climatic changes expressed by different temperature products. For this, we fitted a set of GAMs using bioclimatic layers from one of either ERA5, WorldClim or *microclimf* as predictors, and changes in salamander prevalence as the response variable assuming a Gaussian distribution. For bioclimatic variables, we used the only two variables with historic decadal WorldClim data at 1 km^2—annual thermal maximum (BIO5) and minimum (BIO6)—which have been shown to correlate with distributions of salamanders in this region (Baken et al., 2021). For each climate source, we calculated the per-pixel change in each bioclimatic variable between the 1960s and 1990s, and used these climate change estimates as GAM predictors. To further explore how the spatial resolution of climate data influences predictions independent of the temperature product used, we spatially aggregated (averaged across cells) and disaggregated (bilinear interpolation) temperatures from *microclimf*, WorldClim and ERA5—each at 1-km, 3-km, 10-km and 27.75-km resolution. We then fitted GAMs for each temperature product at each of these spatial resolutions, corresponding to 12 models in total (see Supporting Information for more details on climate data processing, fitting GAMs and measures taken to control for survey effort and initial prevalence).

2.5 | Software

All analyses were conducted in R v4.2 (R Core Team, 2022); all packages used for data access, processing and analysis are provided in the Supporting Information.

3 | RESULTS

Across 371 time series of in situ soil temperature data globally, *microclimf* had 8.2% and 25.2% lower root mean square error (RMSE) than ERA5 and WorldClim, respectively, and 24.9% and 16.4% lower absolute bias than ERA5 and WorldClim respectively (Figure 3, Table S2, Figure S2).

In case study 1, temperature predictions by ERA5, WorldClim and *microclimf* in Alberta, Canada were similar (Figure 4a). Yet, marginal differences among the three temperature products yielded disparate calculations of growing degree days (Figure 4b), thereby resulting in divergent estimates of insect emergence (Figure 4c, Table S3). Emergence models driven by *microclimf* (proximal climate) at hourly resolution were most accurate, with an average error of 6.57 days, followed by ERA5 at hourly resolution (17.0 days) and all other models descending with temporal resolution except monthly *microclimf* (17.6 days), which performed better than daily WorldClim (20.42 days; Figure S3). Average error reported here is the mean error across all proportion emergence thresholds for both species.

In case study 2, *microclimf* predictions of *A. aegypti* mosquito fecundity were the most accurate, with 6.22-fold and 7.76-fold increases in overlap with the empirical fecundity distribution as compared to those of ERA5 and WorldClim respectively (Table S4). *microclimf* fecundity predictions were also higher ($\bar{x} = 6.96$ eggs laid / day) than fecundity derived from ERA5 or WorldClim ($\bar{x} = 5.30$ and $\bar{x} = 4.92$ respectively; Figure 5, Table S5). Contrasting with fecundity predictions, BIO1 calculated from ERA5, WorldClim and *microclimf* all had similar distributions that overlapped considerably (mean overlap = 70.1%), while BIO5 distributions diverged between temperature products (mean overlap = 16.9%, Table S4).

In case study 3, the three temperature products yielded different predictions of changes in the prevalence of *P. jordani* salamanders between the 1960s and the 1990s (Figure 6b,c). The *microclimf*-driven GAM performed best, explaining 58.1% of all deviance compared to only 39.1% and 17.2% for GAMs using WorldClim and ERA5 respectively (Tables S6 and S7). Furthermore, the predicted rate of historic warming differed considerably across climate data products (Figure 6a). For instance, the increase in BIO5 computed from WorldClim was 0.597°C per decade, which was 84% and 88% faster than the rate at which BIO5 was warming based on ERA5 and *microclimf* respectively. Such warming corroborates upslope shifts of salamanders as predicted by species distribution models (SDMs): the elevations of pixels with at least 80% salamander prevalence on average shifted up by 136 m. SDMs had good fit to hold out validation data as indicated by their CBI (CBI: 0.963 for 1960s model, 0.988 for 1990s model; see Supporting Information for further validation).

4 | DISCUSSION

Measuring the role of scale in biological and environmental processes requires proper definition of scale itself. In our study, we defined climate proximity (Box 1) and explored its importance as an ecologically relevant component of climate scale. We incorporated several temperature data products into a suite of ecological models to evaluate the benefits of increasing spatial resolution, temporal resolution or proximity of climate data relative to the focal species. We found via our case studies that the predictive power of climate-driven ecological models is maximized when temporal resolution, spatial resolution and proximity are all high. Yet, increasing climate proximity (i.e. from macroclimate to microclimate while the spatiotemporal resolution remained constant) resulted in a 247% mean improvement in ecological models across case studies, relative to only an 18% improvement from a mean 20-fold increase in spatial resolution, and a 9% improvement from a mean 30-fold increase in temporal resolution. This entails that when selecting or processing climate data, prioritizing higher proximity, yet coarser spatiotemporal resolution, may increase data quality (for ecological prediction) and also decrease quantity (i.e. data density in space and time), and therefore, possibly entail less computational demand or storage space. Here, we discuss how treating proximity separately from spatiotemporal scale is not just a change of semantics, but it advances theory by helping to identify the mechanisms of organismal responses to climate. By considering climate proximity, one emphasizes biophysically informed approaches rather than generic formulations when matching climate data to an ecological system.

4.1 | Modelling temporal ecological processes

In our first case study, we found that temperature data with both fine temporal resolution and high climate proximity yielded the most accurate predictions of the emergence rates of two fossorial insect species, *D. platura* and *D. radicum* (Figure 4). Prediction errors varied across temperature products from 6.57 days (hourly topsoil temperatures from *microclimf*) to 33.25 days (ERA5 macroclimate aggregated to monthly, Table S3). Given that 75% of all individual *D. platura* and *D. radicum* emerged within windows of just 22.8 and 15.3 days, respectively, predictions from temperature data with low proximity and coarse temporal resolution (e.g. monthly WorldClim and monthly ERA5) almost entirely missed the emergence event. Noteworthy is that even when *microclimf* predictions were aggregated to monthly resolution, they yielded more accurate emergence predictions than WorldClim disaggregated to daily, and were comparable in performance to hourly ERA5. These findings suggest that,

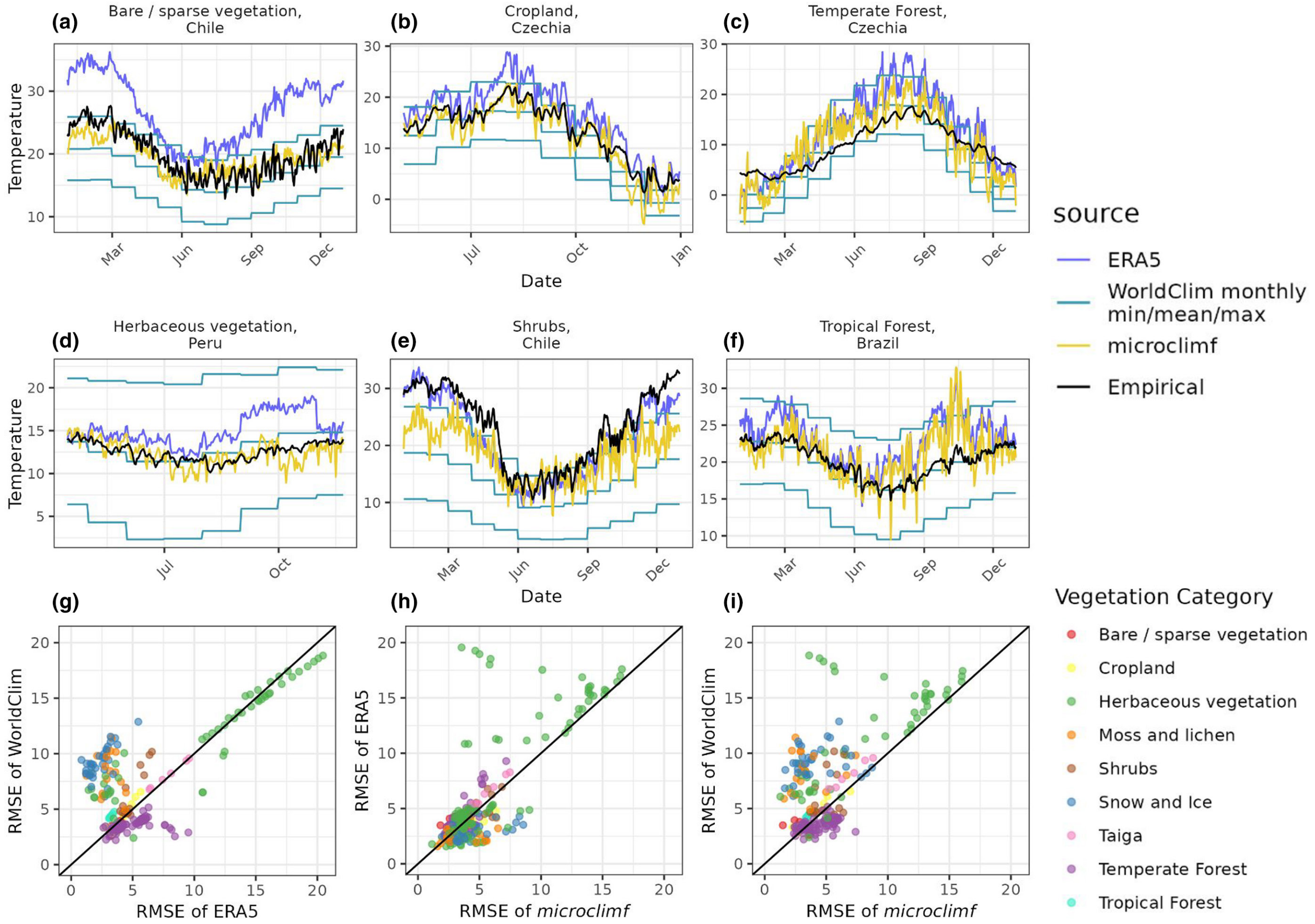


FIGURE 3 Comparison of temperature predictions from ERA5, WorldClim and *microclimf* using empirical temperature measurements from in situ loggers. (a–f) panels display time series from six example locations (from 371 in total) representing different vegetation categories from four continents (see Figure S1 for all locations). Vegetation categories are 2015 estimates from the Copernicus Global Land Service Land Cover product. Black lines indicate empirical observations of soil temperature, coloured lines indicate temperature predictions from each temperature product. (g–i) scatter plots of the root mean square error (RMSE) between predictions from each temperature product and empirical temperature data (RMSE calculated from monthly resolution predictions for comparisons against WorldClim, and hourly resolution predictions for the ERA5-*microclimf* comparison). Each point corresponds to RMSE from measurements of one logger during 1 year, and black lines represent the lines of equality (equal error between the two temperature products). The *microclimf* model performed best (lowest RMSE), followed by ERA5 and then WorldClim (also see Table S2).

for this system, the proximity of climate data may be more important than their temporal resolution.

Several mechanisms might explain why climate data of both high temporal resolution and high proximity accurately predict ecological time series. First, given that many ecological responses to temperature are nonlinear, the *mean ecological response* to thermal variation over time (what is typically of interest) does not necessarily equal the ecological response to the *mean temperature* (Martin & Huey, 2008). This mathematical principle, known as Jensen's inequality, explains why the predicted emergence rates in response to coarse temporal data (e.g. monthly WorldClim and ERA5) differed considerably from average true emergence rates, which are likely sensitive to short-term fluctuations in temperature (e.g. across hours; Denny, 2019).

Second, individual organisms are exposed not only to instantaneous temperature but also to cumulative thermal variation at the scale of hours to months and beyond (Kefford et al., 2022). Even if differences between climate products are minimal at any given timestep (Figure 4a), small thermal deviations accumulate over time (e.g. divergence in GDDs, Figure 4b), rendering distal macroclimate unsuitable for capturing the collective climate exposure of organisms and their phenological responses (Figure 4c). Only proximal climate data of fine temporal resolution will adequately capture the cumulative effect of such intraseasonal variability. Yet, temporal variation can be irrelevant when the climate data are not proximal to the ecological responses of interest. Therefore, distal, yet fine temporal resolution, climate data may have a low 'signal-to-noise' ratio. Increasing proximity entails representing ecologically relevant climate variation (i.e. signal), while increasing resolution of distal climate data can introduce irrelevant climate variation (i.e. noise; for instance, the hot extreme air temperature of hourly free-air macroclimate that is not relevant to

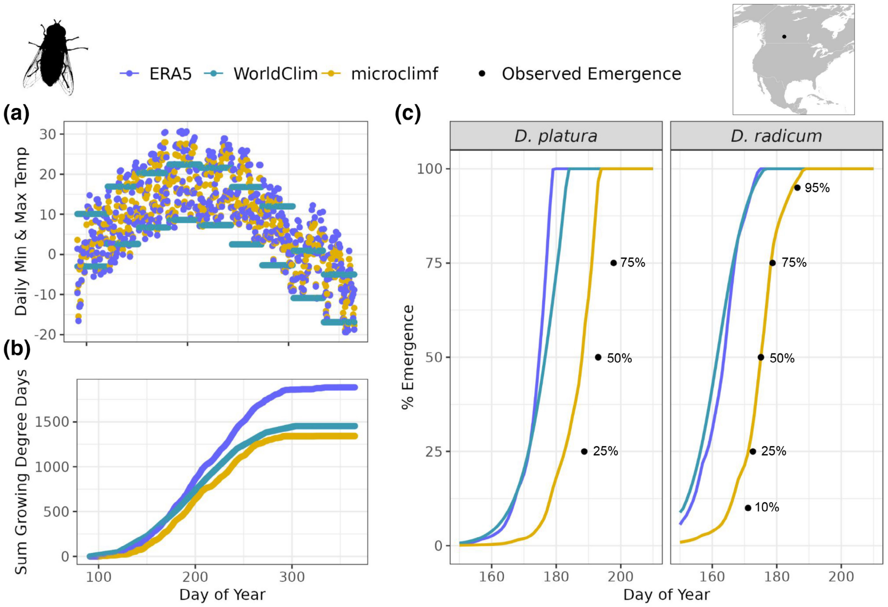


FIGURE 4 Case study 1: temperature predictions (a), growing degree days (GDDs, b) and emergence rate predictions (c) for the soil-dwelling larvae of two crop pest insects in Alberta, Canada, all calculated separately from ERA5, WorldClim and *microclimf*. GDDs are indices for the cumulative sum of temperatures above a minimum (base) temperature for organismal development, and we predicted emergence rates using a logistic model driven by GDDs. Black points in panel (c) indicate empirical observations for the two species (no empirical data for 10% and 95% emergence for *Delia platura*). Although all three temperature products had similar temporal patterns in temperature (a; average difference in daily means across climate sources = 0.49°C) and growing degree days (b; average difference across climate sources = 200.0 GDDs; displayed here are GDDs just for *Delia radicum*), even such small differences yielded divergent predictions of nonlinear biological responses (c; Table S3). High proximity (*microclimf*) yielded the most accurate biological predictions. See Figure S3 for results with temporally aggregated/disaggregated climate data.

a fossorial organism; see also Dillon et al., 2016). This may explain why WorldClim disaggregated to daily intervals performed worse than monthly *microclimf* predictions.

4.2 | Modelling spatial ecological processes

In our second case study, we illustrated that the method by which climate data are summarized from a time series and mapped into a single spatial index may either enhance or mitigate the variability and utility, of fine-resolution proximal data. For the tropical region of Sabah in Malaysian Borneo, microclimate and macroclimate products yielded similar spatial distributions of mean annual temperatures (BIO1, Figure 5a), which may lead the modeller to conclude that microclimates reflect macroclimate in this region. However, when we calculated the maximum temperature of the warmest month (BIO5, Figure 5b) from each temperature product, there were larger differences in spatial profiles than for BIO1. Furthermore, when we calculated temperature-sensitive fecundity rates of *A. aegypti*, microclimate-derived estimates diverged considerably from macroclimate-derived estimates, and were more accurate (Figure 5c). Of note is that even microclimate still underpredicted mosquito fecundity, perhaps because *microclimf* predictions were imperfect at representing conditions of both airborne adult mosquitoes and waterborne larvae. Given that *Aedes* mosquitoes are sensitive to microclimatic gradients across land uses (Saager et al., 2023) and respond to temperature in a nonlinear fashion (Kearney et al., 2009), spatial and temporal patterns of thermal suitability for this species are likely more complex than what a simple annual mean (BIO1) can capture (see also Jensen's inequality as described above). Our results, therefore, showcase the importance of carefully selecting bioclimatic variables deemed most relevant to the ecological response in question.

Many species distribution models (SDMs) use climate data that have been aggregated into a set of particular bioclimatic variables (BIO1–BIO19), first established by Nix (1986) and adopted in many commendable climate databases (Fick & Hijmans, 2017; Haesen et al., 2023; Karger et al., 2017). These sets of bioclimatic variables are convenient as (1) they are sometimes useful indices for representing climate suitability, (2) they can match the temporal resolution of some ecological observations, such as seasonal or annual occurrence records and (3) their generality enables standardization of methods across species, studies and systems. Yet, the popularity of standard bioclimatic variables may also be at their peril, as many modellers default to using these same simple approaches rather than seek to identify the biophysically relevant exposure that bioclimatic variables attempt to represent (Gardner et al., 2019). Comparing average temperatures (e.g. BIO1) across systems may mask ecologically important differences (Körner & Hiltbrunner, 2018); for instance, mean annual temperatures may not deviate substantially between degraded and unmodified forests, even though thermal buffering across the same vegetation gradient is clear when measured via other indices (De Frenne et al., 2019). Using maps of the

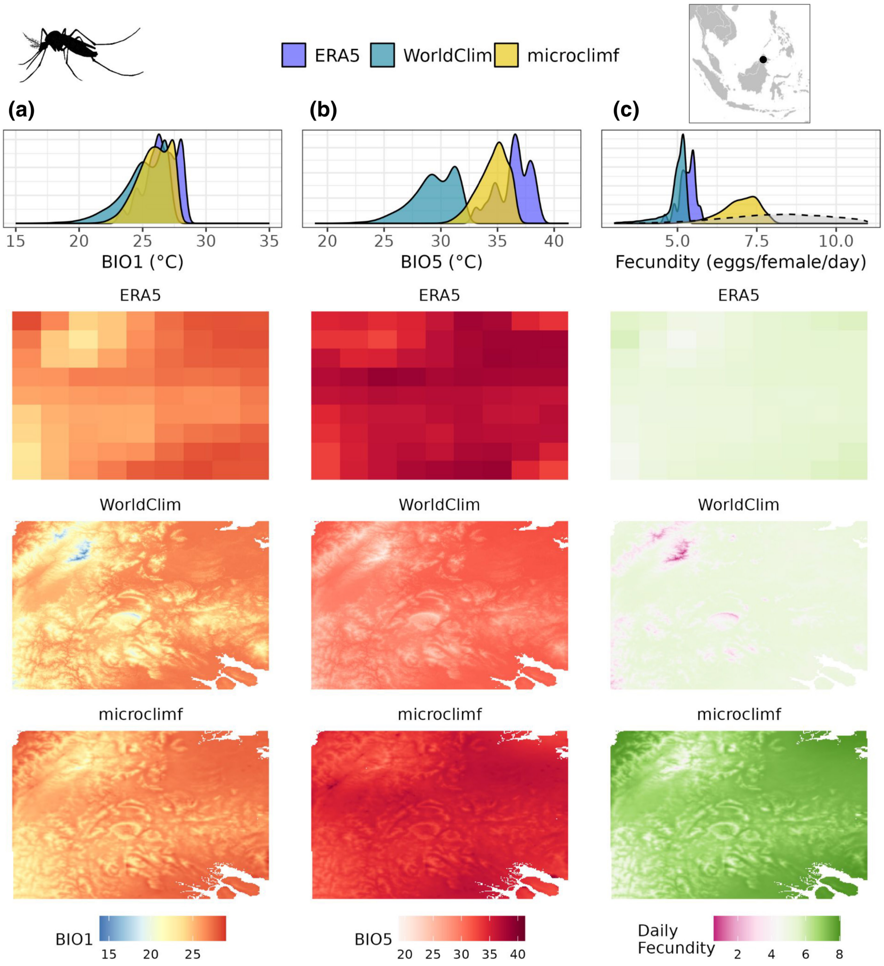


FIGURE 5 Case study 2: estimates of mean annual temperature (BIO1, column a), maximum temperature of the warmest month (BIO5, column b) and average fecundity as a metric of thermal performance for *Aedes aegypti* mosquitoes (column c), derived from ERA5, WorldClim and *microclimf* predictions across Sabah in Malaysian Borneo. Differences in spatial resolution, temporal resolution and proximity can result in shifts in thermal profiles (density plots at top), depending on what bioclimatic variable is calculated. Column (a) as an annual average, BIO1 was not sensitive to differences in temporal variability between microclimate and macroclimate, and therefore, thermal distributions across temperature products were similar (mean overlap = 70.1%). Column (b) maximum temperatures of the warmest month (BIO5) diverge more among the three temperature products (mean overlap = 16.9%), with hourly resolution products (ERA5 and *microclimf*) yielding higher warmest extremes than the monthly resolution WorldClim. Column (c) estimates of fecundity rates from a temperature-driven reaction norm empirically parameterized for *A. aegypti* were fairly similar between the two macroclimate products (overlap = 47.2%), but higher and more accurate when derived from *microclimf* microclimate predictions. Dashed grey density plot indicates a distribution generated from empirical fecundity measurements, which overlapped more with *microclimf* predictions (37.8%) than ERA5 (6.1%) or WorldClim (4.9%). Averaging climate (e.g. to BIO1) suppresses the variability that characterizes high-resolution or proximal climate data, while biophysically informed summaries (e.g. average fecundity from a thermal reaction norm) are more sensitive to such variability, and therefore, result in greater divergence between macroclimate and microclimate.

annual warmest and coldest temperatures (e.g. BIO5 and BIO6) for habitat suitability modelling may also have its caveats: BIO5 and BIO6 maps can be sensitive to just the most extreme values, which may be anomalous or physiologically inconsequential. If an ecological process is sensitive to a particular threshold (e.g. freezing of water at 0°C), the extremity of values is trivial if well beyond the threshold value (Buckley, Carrington, et al., 2023). When annual averages, extremes or others in the BIO1–BIO19 set do not covary with more relevant climatic variables (e.g. hours below freezing), as they often do not, relying on such averages or extremes can lead to poor habitat suitability prediction and result in misguided conclusions.

4.3 | Modelling spatiotemporal ecological processes

Most processes in nature vary in space and time and are best modelled as such (Levin, 1992). In our spatiotemporal case study, using the highly proximal *microclimf* microclimate predictions instead of ERA5 or WorldClim dramatically improved the explanatory power of our models of prevalence shifts of a fossorial salamander species, *P. jordani* (Figure 6). The *microclimf*-driven statistical model of prevalence shifts explained 1.5× more variation than the WorldClim-driven model, and 3.5× more variation than the ERA5-driven

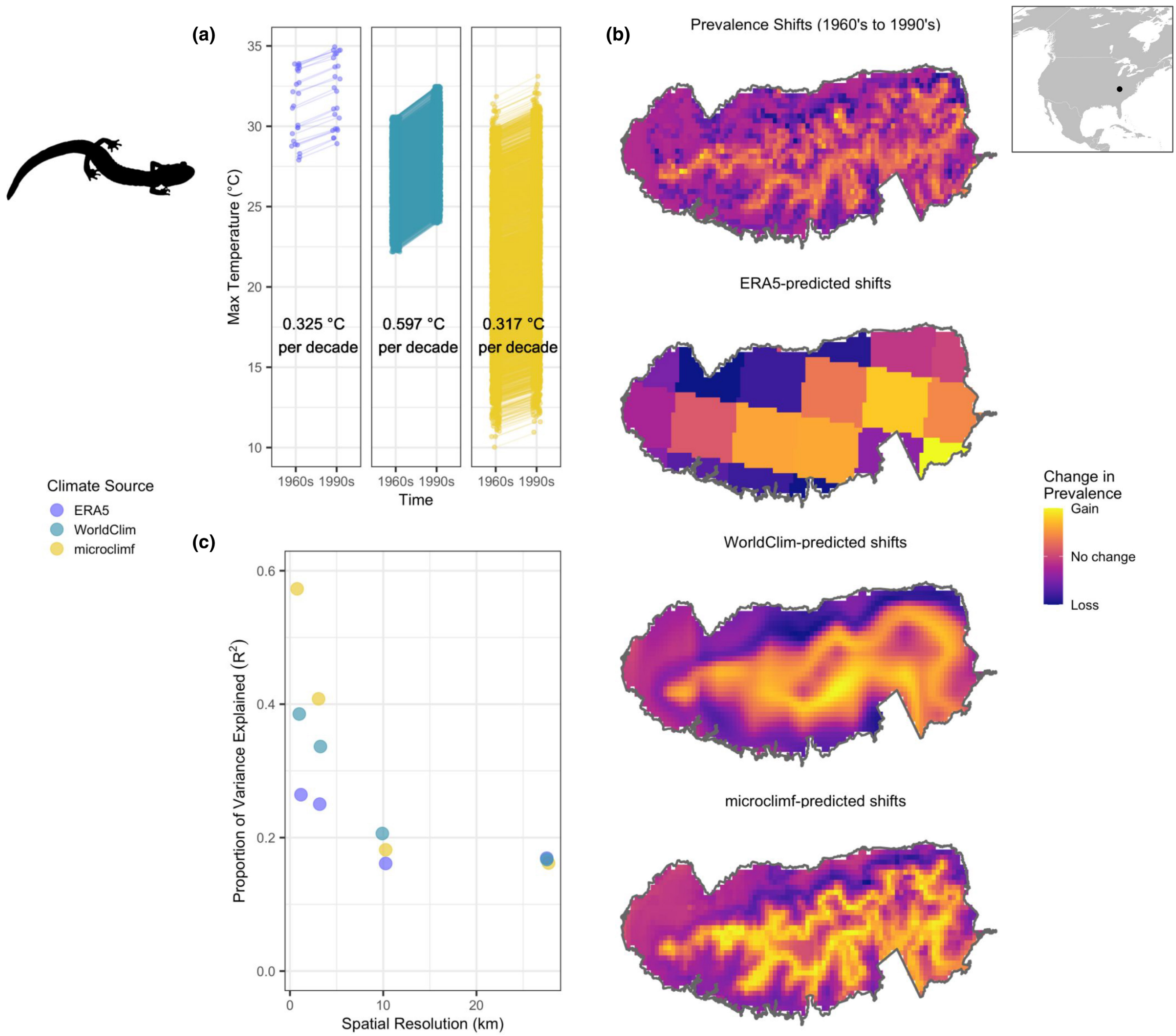


FIGURE 6 Case study 3: incorporating microclimate results in improved prediction accuracy of spatiotemporal prevalence shifts, as indicated by predicted changes in salamander prevalence in Great Smoky Mountains National Park. (a) Estimates of warming (slopes of lines) between the 1960s and 1990s were higher for WorldClim (0.597°C per decade) than either ERA5 or *microclimf*. Furthermore, *microclimf*—which predicted topsoil temperatures both below canopies and exposed to full sun, as opposed to just free-air temperatures from ERA5 and WorldClim—expressed greater spatial variability in maximum temperature than the macroclimate products. (b) During the same four-decade timespan, areas of high salamander prevalence shifted towards higher elevations in the centre of the park (top map). Predictions of changes in salamander prevalence from generalized additive models (GAMs) driven by the three temperature products had vastly different patterns, with *microclimf*-driven predictions (bottom map) visually and quantitatively capturing the spatial signal of empirical prevalence shifts (top map). (c) The GAM driven by 1-km resolution *microclimf* predictions performed best as indicated by the proportion of variance explained (R^2), and this advantage was held by *microclimf* until spatially aggregated to 10-km resolution.

model. Furthermore, *microclimf* still outperformed WorldClim and ERA5 even when at coarser spatial resolution than them (Figure 6c, Table S6). Warming rates predicted by the highly proximal *microclimf* model were also slower than those of either ERA5 or WorldClim. These results, in tandem, suggest that climate proximity may influence findings of climate change velocity or its ecological implications: coarse-resolution, distal climate data commonly used in macroecology may exaggerate predictions of climate change-induced species' extinctions and range shifts (Colwell, 2021; Maclean & Early, 2023).

Microclimate data provide several benefits for spatiotemporal analyses, with one benefit concerning drivers of climate, and a second concerning how organisms respond to climate. First, the relative importance of microclimate-forcing variables changes across the same spatial and temporal scales at which most organisms live. For instance, across space, atmospheric turbulence and wind speeds drive near-surface temperature in barren environments but can have a negligible effect on understory temperatures within nearby forests. Across time, soil surface temperatures are largely a function of solar radiation during the day, yet are more dependent on cold air drainage and soil composition at night (Geiger et al., 2009). Such heterogeneous microclimate forcing makes it difficult to compress a microclimatic dataset—of sufficient extent and duration to be ecologically relevant—into static spatial layers or single time series that adequately represent the climate history across an area. Conversely, the forcing of macroclimate, although complex, primarily operates at scales broader than any single organism is normally exposed to. This results in spatiotemporally smoother distributions of macroclimate that can be summarized to two- or one-dimensional data across kilometres and months. Second, organisms directly respond to proximal conditions (microclimates) rather than distal conditions but realized exposure to microclimates can change in both space and time. For instance, mobile species can move between microclimates to behaviourally thermoregulate (Kearney & Porter, 2009). *In concreto*, when the structures of both climate data and ecological models are such to allow variability in both space and time, then climate data of high proximity will become dramatically more useful for accurate ecological predictions.

4.4 | Leveraging climate data for ecological predictions

When generating, accessing or processing climate data, researchers should consider not just spatiotemporal resolution, but also climate proximity: how well such data represent the conditions that organisms actually experience within their habitats. In our case studies, we found that increasing proximity can yield far greater improvements in ecological predictions than increasing either spatial or temporal resolution. Accordingly, a unified definition of 'microclimate' should be couched in terms of proximity for a given organism or process, rather than just the spatial and temporal resolution of climate observation or prediction.

Re-evaluating climate scale in this manner questions the use of some generic formulations of the relationship between climate and ecology as often employed in large-scale biogeographical studies. For any individual organism, actual exposure is best represented with physiologically informed predictors (Gardner et al., 2019). Such predictors can range from simple sums of the cumulative time beyond a threshold (e.g. the critical thermal maximum), to calculating average performance based upon a thermal reaction norm (Figure 5c), or fully embracing a biophysical model to link energy exchange between an organism and its environment to the corresponding physiological impacts (Briscoe et al., 2023). When possible, employing spatiotemporally explicit data and models will also better capture the diverse processes that shape climate and its roles in ecology and biogeography, and will best leverage high-resolution proximal climate data.

Microclimate datasets and models make different trade-offs to represent proximal microclimates that may serve certain applications better than others. The *microclimf* model employed here spatially predicts subcanopy and soil microclimate in a computationally efficient manner by simplifying treatment of some physical processes; *NicheMapR* (Kearney & Porter, 2017) trades computational speed for greater fidelity to physical processes; *microclimc* (Maclean & Klinges, 2021) includes more detail on canopy effects and *TrenchR* (Buckley et al., 2023b) trades complexity for accessibility. Gridded microclimate datasets are also becoming increasingly available across broad expanses (Haesen et al., 2023; Kearney et al., 2014; Lembrechts et al., 2022). When selecting between models and datasets to represent proximal microclimate, we advise ecologists to especially consider the home range size (for animals), phenology and activity windows, and an organism's morphology, all of which determine climate exposure (Kearney & Porter, 2009; Potter et al., 2013). Body size, in particular, can be used to quantitatively define microclimates for a given organism (Kearney et al., 2021; Pincebourde & Woods, 2020). Using several tools in tandem may also represent multi-scale microclimates relevant to a species, such as variable tree bark surface temperatures nested within forest understories (Pincebourde & Woods, 2020).

Our case studies are inherently limited in scope (e.g. all are ectothermic animals with restricted mobility), as they serve only as illustrative examples of several ecoclimatic relationships worth exploring (phenology, thermal suitability and range shifts). Similar to much of the climate change ecology literature, we focused primarily on temperature, yet climate consists of many other relevant variables (Stocker et al., 2014). Furthermore, the spatial resolution of climate data explored here matches that of many studies of species' distributions, but is coarser than that of data collected in most field-based ecological studies (Estes et al., 2018). Yet, while increasing climate proximity is useful across scales, even down to operative or body conditions (including leaf surface or phyllospheric temperatures; Pincebourde & Casas, 2019), finer resolution data can sometimes decrease prediction accuracy due to overfitting or bias from a scale mismatch (also see Box 1). We recommend modellers to perform scale-of-effect analyses (e.g. van de Pol et al., 2016), which identify the temporal periods and/or spatial extents that are most correlated to a chosen ecological response, and therefore do not assume that finer resolution entails higher accuracy. By doing so, one may find that the spatiotemporal density of climate measurements and estimates may matter less than how those data were collected or derived, and how they are integrated into models.

Both climate and its ecological responses are multifaceted and scale dependent. Here, we have highlighted some of the inadequacies of coarse or even fine-resolution climate data, and demonstrate the importance of proximity for spatial, temporal and spatiotemporal processes. By redefining climate scale with an emphasis on proximity to a target application, we not only better distinguish the language used to express climate's impact on ecology and improve modelling practices, but also advance theory. Considering climate proximity uncovers important mechanisms by exploring how climate drives biology through the lens of the organism itself. Rather than relying on analytical shortcuts that may be easily generalizable (e.g. standard bioclimatic variables derived from distal data), it is every ecologist's duty to identify what conditions are most proximal for their study system and species. Using available data and tools that measure and model biologically relevant climate, ecologists can gain a more refined and process-focused understanding of global change.

AUTHOR CONTRIBUTIONS

DHK initiated the project and conceived the core concepts, with early input from BRS, IMDM, MRK and JL. JJL collated co-author data for the climate data comparison. DHK performed all microclimate modelling, and analyses for the temperature product comparison and case studies 1 and 2. JAB collated data and performed initial model fitting for case study 3, with subsequent analyses by DHK. DHK wrote the first draft of the manuscript, with early contributions by JAB, JJL, IMDM, LJE, MRK and BRS. BRS supervised DHK. IB, PDF, JG, MK, MM, JU, LvdB, JvO, JW, JB, RC, MN, AR and JSB all contributed data for the temperature data comparison. All authors contributed substantially to manuscript editing.

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ACKNOWLEDGEMENTS

We thank the following funding sources: NSF-GRFP N°DGE-1842473 (DK); FWO-G018919N, FWO-12P1819N, FWO-1512720N and FWO-W001919N and BiodivERsA+ projects ASICS and Forest-Web-3.0 (JJL, IN); ANR JCJC-N°ANR-19-CE32-0005-01 IMPRINT (JL); ANR PRC-N°ANR-21-CE32-0012-03 MaCCMic (JL); Swedish research council FORMAS 2021-01993 (CG); NERC-NE/S01537X/1 (TJ); Czech Science Foundation project 23-06614S and Academy of Sciences of the Czech Republic project RVO 67985939 (MK, MM, JW); Academy of Finland 342890 (ML); Academy of Finland 337552 (JA); GACR-21-11487S (JU); DFG TI 338/14-1 and -2, ANID PIA/ACT 210038 (LvdB); European Research Council ERC Starting Grant FORMICA-757833 (PDF and PV); Danmarks Frie Forskningsfond 7027-00133B (JvO); and PIP-363/2020 and Agencia Nacional de Promoción Científica y Tecnológica PICT504/2020 (MN). We thank T. Michael Keesey, Sean McCann, Benjamin Monod-Droca and PhyloPic for providing animal silhouettes for free modification under CC licences.

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

All data and code for ecological case studies and figures are available via Zenodo at 10.5281/zenodo.8110832. Code for the *microclimf* model is available at https://github.com/ilyamaclean/microclimf. Empirical temperature data used for the temperature product comparison will be made available as part of the SoilTemp database Version 1.0 (*in preparation*).

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BIOSKETCHES

We are a collective of researchers focusing on the impact of global change on animal and plant communities and ecological functions, with a shared interest in exploring the importance of climate scale and microclimate.

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How to cite this article: Klinges, D. H., Baecher, J. A., Lembrechts, J. J., Maclean, I. M. D., Lenoir, J., Greiser, C., Ashcroft, M., Evans, L. J., Kearney, M. R., Aalto, J., Barrio, I. C., De Frenne, P., Guillemot, J., Hylander, K., Jucker, T., Kopecký, M., Luoto, M., Macek, M., Nijs, I., … Scheffers, B. R. (2024). Proximal microclimate: Moving beyond spatiotemporal resolution improves ecological predictions. *Global Ecology and Biogeography*, *00*, e13884. https://doi.org/10.1111/geb.13884