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PERSPECTIVE

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Microclimate, an important part of ecology and biogeography

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Abstract

Brief introduction: What are microclimates and why are they important?Microclimate science has developed into a global discipline. Microclimate science is increasingly used to understand and mitigate climate and biodiversity shifts. Here, we provide an overview of the current status of microclimate ecology and biogeography in terrestrial ecosystems, and where this field is heading next.

Microclimate investigations in ecology and biogeography: We highlight the latest research on interactions between microclimates and organisms, including how microclimates influence individuals, and through them populations, communities and entire ecosystems and their processes. We also briefly discuss recent research on how organisms shape microclimates from the tropics to the poles.

Microclimate applications in ecosystem management: Microclimates are also important in ecosystem management under climate change. We showcase new research in microclimate management with examples from biodiversity conservation, forestry and urban ecology. We discuss the importance of microrefugia in conservation and how to promote microclimate heterogeneity.

Methods for microclimate science: We showcase the recent advances in data acquisition, such as novel field sensors and remote sensing methods. We discuss microclimate modelling, mapping and data processing, including accessibility of modelling tools, advantages of mechanistic and statistical modelling and solutions for computational challenges that have pushed the state-of-the-art of the field.

What's next?We identify major knowledge gaps that need to be filled for further advancing microclimate investigations, applications and methods. These gaps include spatiotemporal scaling of microclimate data, mismatches between macroclimate and microclimate in predicting responses of organisms to climate change, and the need for more evidence on the outcomes of microclimate management.

KEYWORDS
animal ecology, biodiversity, biogeography, climate change, data acquisition, ecosystem management, microclimate, modelling, plant ecology

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1 | BRIEF INTRODUCTION: WHAT ARE MICROCLIMATES AND WHY ARE THEY IMPORTANT?

Microclimates refer to the local climate conditions that organisms and ecosystems are exposed to. In terrestrial ecosystems, microclimates often differ strongly from the macroclimate, that is, the climate representative of a large geographic region. Microclimates are chiefly mediated by topography, vegetation and soil, and they are a combination of local temperature, water (precipitation, air humidity, water availability), solar radiation, cloud, wind and evaporation conditions (Bramer et al., 2018). This fine-scale variation of microclimates is not captured by coarse-resolution macroclimatic data, because microclimates can vary over very short spatial and temporal extents. Microclimates directly influence the ecophysiology of individuals across taxa, and in turn, indirectly affect the dynamics of populations, communities and ecosystems across biomes.

Microclimates enable organisms to develop, survive and reproduce, for instance, below and near the soil surface, and in tree canopies and cavities in an otherwise unsuitable macroclimate (Bramer et al., 2018). Conversely, the same organisms can be absent in places and times where the microclimatic extremes exceed their limits. Additionally, microclimates dictate many ecosystem functions and processes, such as biogeochemical cycles. These local climatic conditions can be captured by microclimatic measurements, not by standard weather stations above short grass in the open. Thus, merging microclimate methods with ecological and biogeographic investigations and applications can provide valuable insights.

Recently, methods have become widely available for ecologists and biogeographers to inspect their study objects in relation to microclimates at high spatio-temporal resolutions and at large spatial and temporal extents (Lembrechts, Nijs, et al., 2019). Consequently, microclimate science has rapidly shown its high relevance to ecological and biogeographical investigations and applications (De Frenne et al., 2021). Now, microclimate science is recognized as an integral component of ecology and biogeography, and is used to investigate local ecological manifestations of the global climate and biodiversity patterns (Riddell et al., 2021; Zellweger et al., 2020), and to improve ecosystem management (Hylander et al., 2022).

Microclimate science has a long tradition. Already in the mid-20th century, microclimatology was identified as an important subfield of meteorology, with clear repercussions for ecology and biogeography (Geiger, 1942; Geiger et al., 1995). The physics of microclimate (Baum & Court, 1949), the appropriate spatial scale and the challenges of measuring microclimates (Geiger, 1942; Geiger et al., 1995; Shanks, 1956) have been studied for decades. Recent reviews have highlighted the importance of microclimate over macroclimate (Bramer et al., 2018), and discussed microclimate in relation to remote sensing (Zellweger et al., 2019), measurement techniques (Maclean et al., 2021), species distribution modelling (Lembrechts, Nijs, et al., 2019) and forest ecology (De Frenne et al., 2021). Following these examples, we consider that the microclimate scales and boundaries are highly dependent on the ecological context (Pincebourde & Woods, 2020; Potter et al., 2013), for example, ranging from minutes and cubic millimetres for within-leaf herbivore insects to monthly averages and hectares for understory communities in forests (Pincebourde & Woods, 2020; Zellweger et al., 2020b).

Here, our aim was to provide an overview of the current status of microclimate ecology and biogeography, and where this field is going next, from the perspective of researchers investigating diverse topics related to terrestrial microclimates (read more about the authors in Supplementary information Figures S1). In this perspective article, we focus on terrestrial ecosystems. However, we acknowledge that microclimates are crucial for aquatic ecosystems as well and that there is active microclimate research on, for example, freshwater, riparian, intertidal, coastal and marine ecosystems (e.g. Bentley et al., 2020; Enriquez-Urzelai et al., 2019; Judge et al., 2018; Nadeau et al., 2022). We discuss recent research on terrestrial ecosystems that shows when and how incorporating microclimate science into ecological and biogeographical questions can increase knowledge and predictability of fine-scale phenomena and processes that generate larger or even global patterns. Recently, microclimate science has taken major strides forward, especially at the following three frontiers: (1) investigations of microclimate ecology and biogeography, (2) microclimate applications in ecosystem management and (3) methods in microclimate science. For each of these themes, we identify a set of knowledge gaps to fill before microclimate data and concepts become a common option in ecology, biogeography and related fields, from fine scale to global scale. We herewith highlight the maturation of microclimate ecology and biogeography into a global discipline, with microclimates being investigated across taxa, ecosystems and biomes.

2 | MICROCLIMATE INVESTIGATIONS IN ECOLOGY AND BIOGEOGRAPHY

2.1 | Organisms drive microclimates

Organisms play a pivotal role in shaping microclimates and have the capacity to establish mosaics of microclimates within ecosystems (Figure 1). One important example involves the creation of distinct microclimatic gradients by grass and forest canopies (De Frenne et al., 2021; Vandvik et al., 2020), which generates

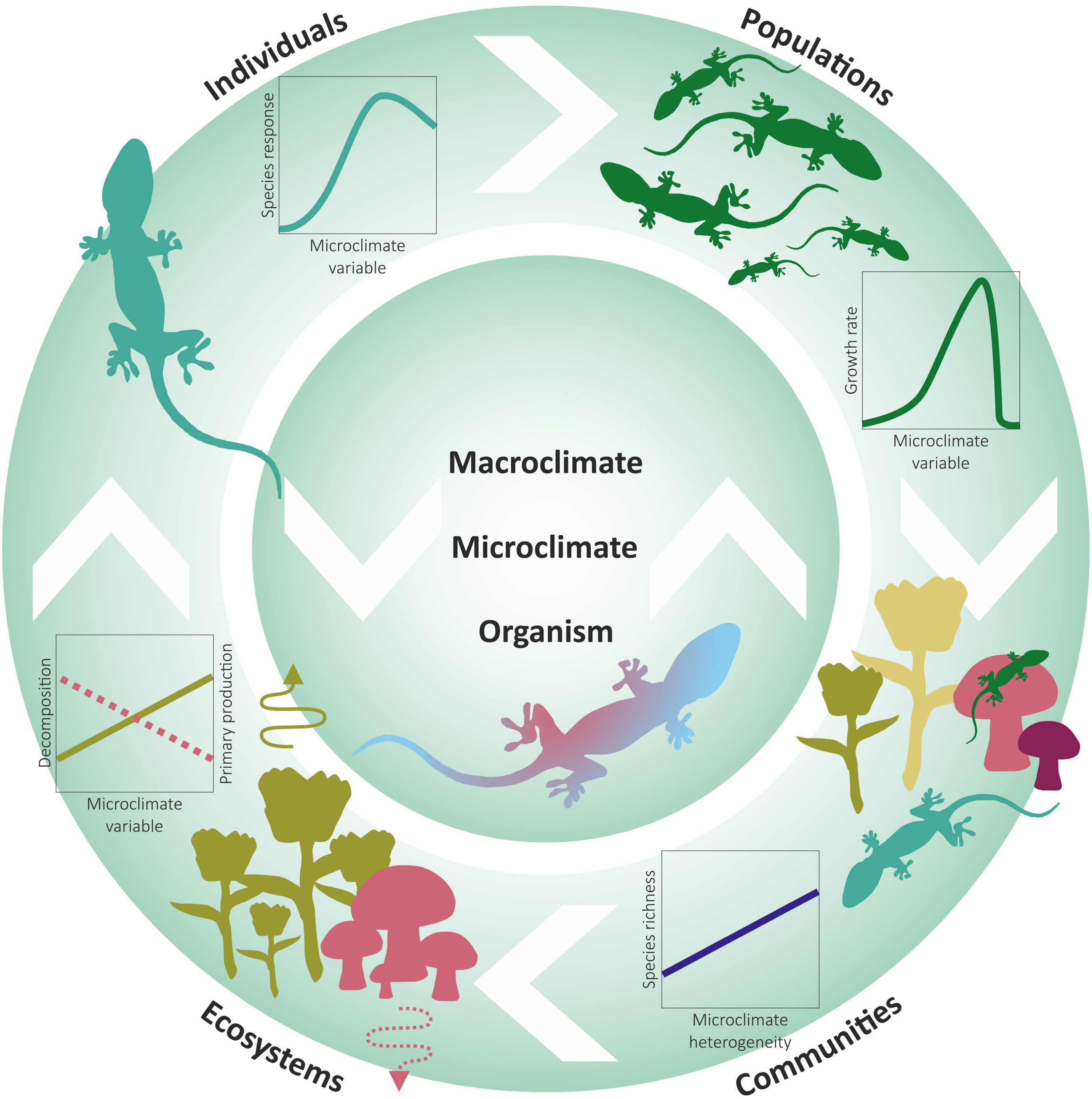

FIGURE 1 Microclimate investigations in ecology and biogeography. The conceptual figure highlights that microclimate is the link between macroclimate and the ecophysiology of organisms. We show examples of how microclimates influence individuals, populations, communities and ecosystems and their processes.

both vertical and horizontal variations within relatively confined geographic extents (Ozanne et al., 2003). These microclimatic variations become particularly crucial in mediating the impact of climate change on understory organisms (Dobrowski et al., 2015), and thus, the mosaics of microclimates offer a mechanism for adaptation to broader climatic shifts (Basham et al., 2023; Scheffers et al., 2013). Furthermore, also animals modulate microclimates, from large herbivores affecting microclimates through grazing and trampling vegetation, to insects regulating their nest temperatures through wing fanning and building temperature-modulating mounds (Gordon et al., 2023; Jones & Oldroyd, 2006; Joseph et al., 2016). These examples highlight how diverse and active the role of organisms is in shaping microclimates.

2.2 | Microclimates influence individuals and populations

Microclimates are a non-negotiable aspect of biophysical ecology across taxa, biomes and scales (Briscoe et al., 2023). The impacts of microclimates on individuals are diverse, as microclimates influence, for instance, performance (Poorter et al., 2019), structural characteristics (Kemppinen & Niittynen, 2022), organs (Opedal et al., 2015) and cellular functions (Zweifel et al., 2007). Recent research on ectotherms and insects showcases how microclimate impacts on individuals are reflected on their populations. Ectothermic organisms, in particular, experience the significant influence of microclimates through thermoregulation and temperature-dependent sex determination (Carter & Janzen, 2021; Sears et al., 2016; Stark et al., 2023). Darker ants tend to dominate tree canopies due to melanism, which provides them protection against UV radiation and reduces moisture loss (Law et al., 2020). The vertical variation in microclimates within forests has furthermore contributed to the evolution of thermal performance and desiccation resistance in ant populations (Bujan et al., 2016; Kaspari et al., 2016), which highlights the interconnectedness between biophysical adaptations and the ability to withstand thermal, hydrological and light-related stressors. Across taxa, thermal tolerance of individuals can serve as a predictor for performance, behaviour and adaptability (Bert et al., 2022; Kim et al., 2022; Pincebourde & Casas, 2019; von Schmalensee et al., 2021). The impacts of microclimates however extend beyond individuals, populations and single ecosystems, as microclimates have broader implications for global biodiversity (Trew & Maclean, 2021). Consequently, microclimate models have become invaluable tools in the field of biophysical ecology (Briscoe et al., 2022; Carter & Janzen, 2021; Sears et al., 2016), because these tools help understanding and predicting interactions between organisms and their environmental conditions.

Through individuals, microclimates have a significant impact on the growth and survival of populations. The microclimatic control of the biophysical processes of individuals influences their recruitment and survival, and in turn, microclimates indirectly influence demographic rates (Goodwin & Brown, 2023; Oldfather & Ackerly, 2019). Plant populations are a great example of this, as recent discoveries show that crucial processes like seed germination and seedling establishment depend on specific temperature, humidity and light conditions (Davis et al., 2016; Graae et al., 2022). Water availability is another factor that has been shown to affect the growth and mortality of plants (Liu et al., 2018), and water availability also controls the regeneration of trees after disturbances (Lloret et al., 2004; Thom et al., 2022). Besides affecting many physiological processes, microclimates also influence behavioural responses across taxa. For instance, butterflies employ strategies such as clustering at different heights in trees to avoid frost (Brower et al., 2011), birds take into account wind characteristics when selecting nest sites (Momberg et al., 2023) and stomatal responses in plants are regulated by microclimate conditions (Zweifel et al., 2007).

2.3 | Microclimates structure communities

The individual-level effects of microclimates ultimately shape the composition and dynamics of communities. Microclimates serve as an important determinant in structuring communities, by influencing both species distributions and patterns of species richness (Checa et al., 2014; le Roux et al., 2013; Ma et al., 2022; Momberg et al., 2021; Niittynen et al., 2020). Recent investigations on plant communities show how microclimates shape species richness, turnover and the composition of vascular plants (Opedal et al., 2015; Shen, Song, et al., 2022), bryophytes (Man et al., 2022; Shen, Corlett, et al., 2022) and lichens (Kemppinen et al., 2019). Knowledge on how microclimates structure communities and their dynamics is increasingly more important in the light of ongoing rapid environmental changes. Ultimately, this means that the heterogeneity of microclimates can mediate how species respond to climate change (Zellweger et al., 2020a), see also (Bertrand et al., 2016), and this heterogeneity can also play a critical role in the context of land use changes (Christiansen et al., 2022). Consequently, the incorporation of microclimate data is crucial for increasing ecological realism of species distribution models across taxa and ecosystems, particularly when investigating environmental changes (Haesen, Lenoir, et al., 2023; Massimino et al., 2020; Niittynen & Luoto, 2018; Stickley & Fraterrigo, 2023).

Species interactions are influenced by microclimate conditions through a variety of mechanisms, encompassing behavioural, phenological and ecophysiological processes. The influence of microclimates on species interactions has been well illustrated by recent evidence on how microclimates significantly shape the habitat preferences of insects (Carnicer et al., 2019; Vives-Ingla et al., 2023) and influence the timing of plant phenological events (Kankaanpää et al., 2018), and how all this ultimately leads to cascading effects on community structures across multiple trophic levels (Kankaanpää et al., 2020). Microclimates can significantly modify species interactions by altering phenological responses, and also by influencing the development of chemical defence traits, impacting colonization patterns and competitive processes (Greiser et al., 2021; Sanczuk et al., 2021; Willems et al., 2021). Furthermore, microclimates play a critical role in determining facilitation. For instance, shrubs and cushion plants modify their below-canopy microclimates which facilitate the growth of seedlings (Cavieres et al., 2014; Vega-Álvarez et al., 2019).

2.4 | Microclimates control and create ecosystems

Microclimates control ecosystem processes, the most essential of these being the cycles of energy, water and matter, such as the carbon cycle (Cahoon et al., 2012; Gora et al., 2019; Meeussen et al., 2021). Microclimates can regulate litter decomposition (Chen et al., 2018), heterotrophic and autotrophic soil respiration (Fernández-Alonso et al., 2018), and photosynthesis (Poorter et al., 2019). Hence, microclimatic temperatures drive biogeochemical cycles, such as greenhouse gas fluxes, and fine-scale moisture conditions determine local methane sinks and sources (Virkkala et al., 2024). Overall, microclimates are important to consider in investigating ecosystem processes, since they regulate resources for primary production and regulate many ecosystem functions.

Through the many impacts on plant and animal individuals, populations and communities, microclimates support microrefugia, small ecosystems buffered from climate change. In microrefugia, temporal changes in local temperature, water and light conditions are smaller than in the surrounding areas (Ashcroft, 2010; Keppel et al., 2012; McLaughlin et al., 2017). Thus, microrefugia can buffer climate change impacts (Morelli et al., 2020), and preserve biodiversity and ecosystem functions (Ashcroft, 2010; Ellis & Eaton, 2021). Microrefugia affect seed survival and plant growth and can create opportunities for animals to hide, feed and reproduce (Checa et al., 2014; Frey, Hadley, & Betts, 2016; Lucid et al., 2021). Microrefugia can be identified using thermal imaging (Hoffrén & García, 2023), high-resolution gridded microclimate products (Haesen, Lenoir, et al., 2023), topographic data (Ashcroft et al., 2012; Meineri & Hylander, 2017), or exploring disjunct populations (Finocchiaro et al., 2023). Overall, microrefugia can shape species redistributions under climate change (Lenoir et al., 2017; Stark et al., 2022). Thus, microrefugia are important for maintaining biodiversity (Dobrowski, 2011; Maclean & Early, 2023; Suggitt et al., 2018), and can have the same importance as larger ecosystem management activities for nature conservation across scales (Ackerly et al., 2020; Thorne et al., 2020).

3 | MICROCLIMATE APPLICATIONS IN ECOSYSTEM MANAGEMENT

Microclimates are pivotal in ecosystem management, especially in the face of climate change (Figure 2). The question of how

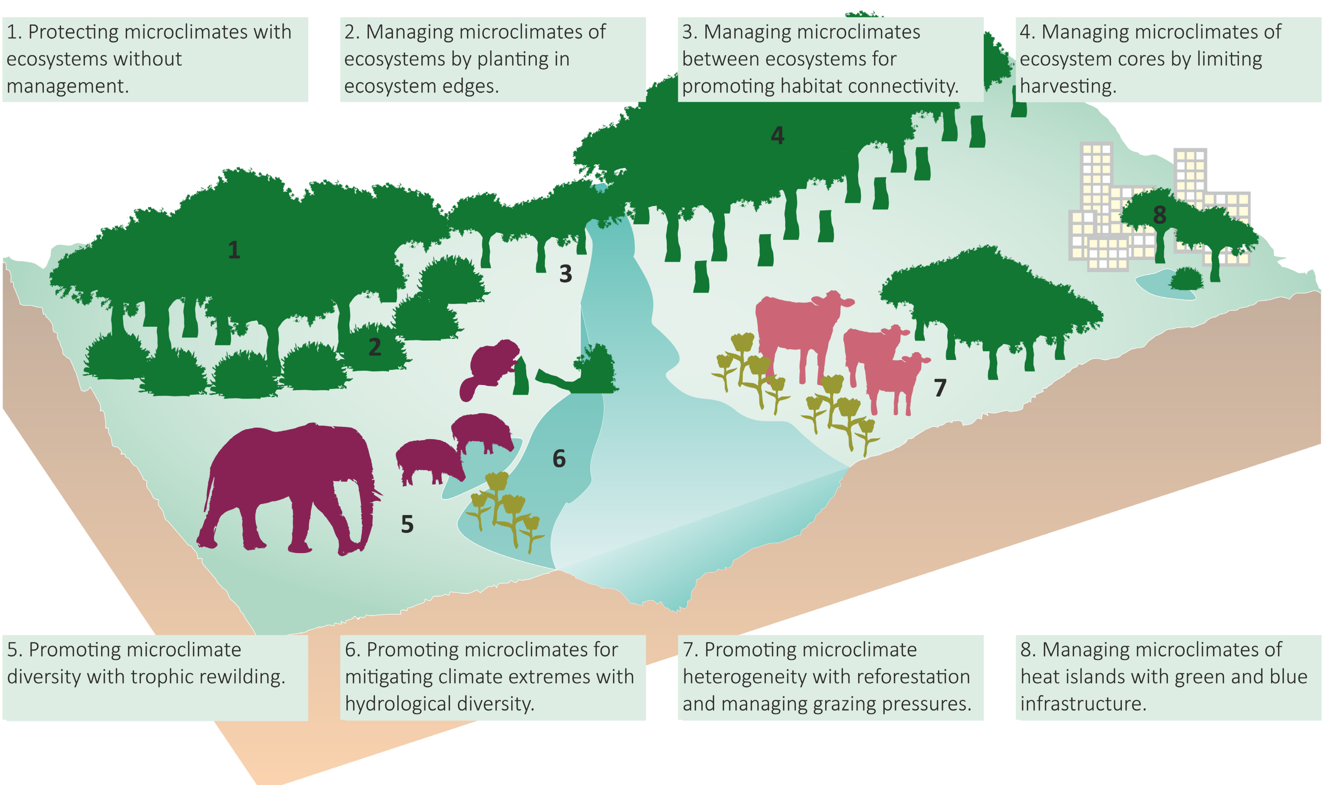

FIGURE 2 Microclimate applications in ecosystem management. The conceptual figure presents examples of biodiversity conservation, forestry and urban ecology maintaining and promoting microclimate heterogeneity for the benefit of biodiversity.

management practices affect microclimates has been discussed for decades (Geiger, 1942; Kraus, 1911). Similarly, managing microclimates has long been part of land-use practices, especially in agriculture. In agriculture, microclimates can be managed, for example, by planting shade trees for enhancing the growing conditions of crops, such as coffee and vanilla (Beer et al., 1998; Lin et al., 2008). Microclimate management can help pest management by creating microclimates beneficial for retaining natural enemies (Begg et al., 2017), and planting trees or small forest patches can also benefit agrobiodiversity (Wurz et al., 2022). Overall, more focus has recently been drawn to managing microclimates for mitigating climate change and for promoting and protecting biodiversity.

3.1 | Microclimate management in biodiversity conservation

Microclimate management is crucial for protecting biodiversity under climate change (Greenwood et al., 2016) and land use change (Williamson et al., 2021). Microclimate heterogeneity is an indicator of microrefugia (Keppel et al., 2015), and can reduce extinction risks (Moritz & Agudo, 2013; Suggitt et al., 2018). Microclimate heterogeneity can be increased by altering vegetation structure (Curtis & Isaac, 2015; Hylander et al., 2022). Vegetation structure can be modified using silvicultural practices, managing grazing pressure by livestock and trophic rewilding with wild megafauna (Malhi et al., 2022; Thers et al., 2019). For example, beaver constructions buffer microclimates from extreme fluctuations by increasing hydrological connectivity and creating floodplains (Larsen et al., 2021; Weber et al., 2017). Also, elephants, wild boars, horses and donkeys engineer microclimates by grazing and trampling on vegetation, and modifying topography and water availability (Gordon et al., 2023; Lundgren et al., 2021; Sandom et al., 2013). Maintaining and creating microclimate heterogeneity and habitat connectivity is an effective basis for future-proofing ecosystems which increases resilience to climate change (Hylander et al., 2022; Maclean & Early, 2023; Stark et al., 2023). Moreover, knowledge and data on microclimate heterogeneity can help identify organisms and ecosystems most vulnerable to climate change (McCullough et al., 2016), and when combined with biophysical ecology, this knowledge can improve and create new management practices to promote biodiversity (Briscoe et al., 2022; Ononye et al., 2023; Welman & Pichegru, 2023).

Microclimate management is used for buffering against gradual environmental change and short-term climate extremes, such as heat waves or droughts, and this increases resistance and enables the proactive transformation of managed ecosystems (Brang et al., 2014; Hylander et al., 2022). Proactive transformation considers the protection of cool microclimates which promotes microrefugia (Hylander et al., 2022; Schmalholz & Hylander, 2011). Microclimate management is constantly evolving (Kermavnar et al., 2020; Thom et al., 2020), and is increasingly applied to principles of close-to-nature management (Brang et al., 2014; Hylander et al., 2022). For example, in selective logging, the post-logging recovery of forest microclimates can be rapid (Senior et al., 2018; Mollinari et al., 2019). This suggests that, in contrast to clear-cutting, selective-logging can provide timber while maintaining microclimate heterogeneity, if logging rotations allow sufficient space and time for regeneration of understorey vegetation (Menge et al., 2023).

3.2 | Microclimate management in forestry

Forestry is an excellent example of how ecosystem management affects microclimate heterogeneity (Menge et al., 2023; Scheffers et al., 2017). In forestry, microclimates are managed to reduce insect outbreaks (Kautz et al., 2013), support tree regeneration (Thom et al., 2022) and reduce frost damage (Örlander, 1993). Forest microclimates are affected by the diversity in tree species, forest structures, management practices (e.g. thinning) and distance to forest edge (Chen et al., 1993; Geiger, 1942; Meeussen et al., 2021). For example, cool and wet microclimates are lost when humid tropical forests are degraded (Senior et al., 2017), even where tree cover remains, such as within tree plantations (Luskin & Potts, 2011) and selectively logged forests (Blonder et al., 2018). This loss is consequential because it decreases the capacity of the forest to buffer climate change impacts and maintain biodiversity (Scheffers et al., 2014). Old-growth forests with diverse microclimatic conditions are especially important for climate change mitigation and biodiversity conservation (Frey, Hadley, Johnson, et al., 2016; Norris et al., 2011; Wolf et al., 2021). However, as temperatures increase and water availability is more limited, forests can lose their capacity to buffer climate extremes (Davis, Dobrowski, et al., 2019). Knowledge and practices found in forestry can be further applied also in other anthropogenically modified environments.

3.3 | Microclimate management in urban ecology

Increasing recognition of the importance of microclimates has led to a proactive approach also in urban ecology to achieve desired microclimate outcomes (Lai et al., 2019). Microclimate heterogeneity is particularly important to consider in rapidly urbanizing and densely populated areas (de Souza et al., 2016; Hartig & Kahn, 2016; Xue et al., 2017). In urban ecosystems, microclimatic anomalies are driven by the lack of vegetation and abundance of impervious, dark surfaces, which create heat islands (Schwaab et al., 2021; Iungman et al., 2023). Recent discoveries show that urban heat islands affect organisms, including altering spider behaviour (de Tranaltes et al., 2022), and changing diversity in plant, bird and insect species

(Aronson et al., 2014; McGlynn et al., 2019). Management practices can optimize microclimate conditions of urban heat islands by using green and blue infrastructure (Bowler et al., 2010; Lin et al., 2020), which consists of water bodies, green roofs and facades, street trees and urban forests (Zölch et al., 2016; Taleghani, 2018; Lai et al., 2019). Responses to green infrastructure are taxa-specific, but overall, green infrastructure can significantly benefit urban biodiversity (Filazzola et al., 2019), and also improve human thermal comfort and decrease human heat mortality in cities (Gillerot et al., 2022; Iungman et al., 2023).

4 | METHODS FOR MICROCLIMATE SCIENCE

4.1 | Advances in data acquisition

Microclimate measurements rely to a large extent on in situ sensors for obtaining data on local temperature, water, solar radiation, cloud, wind and evaporation conditions (Figure 3). In-situ sensors now form part of the toolkit of many ecological studies due to the improvements in chip devices, battery

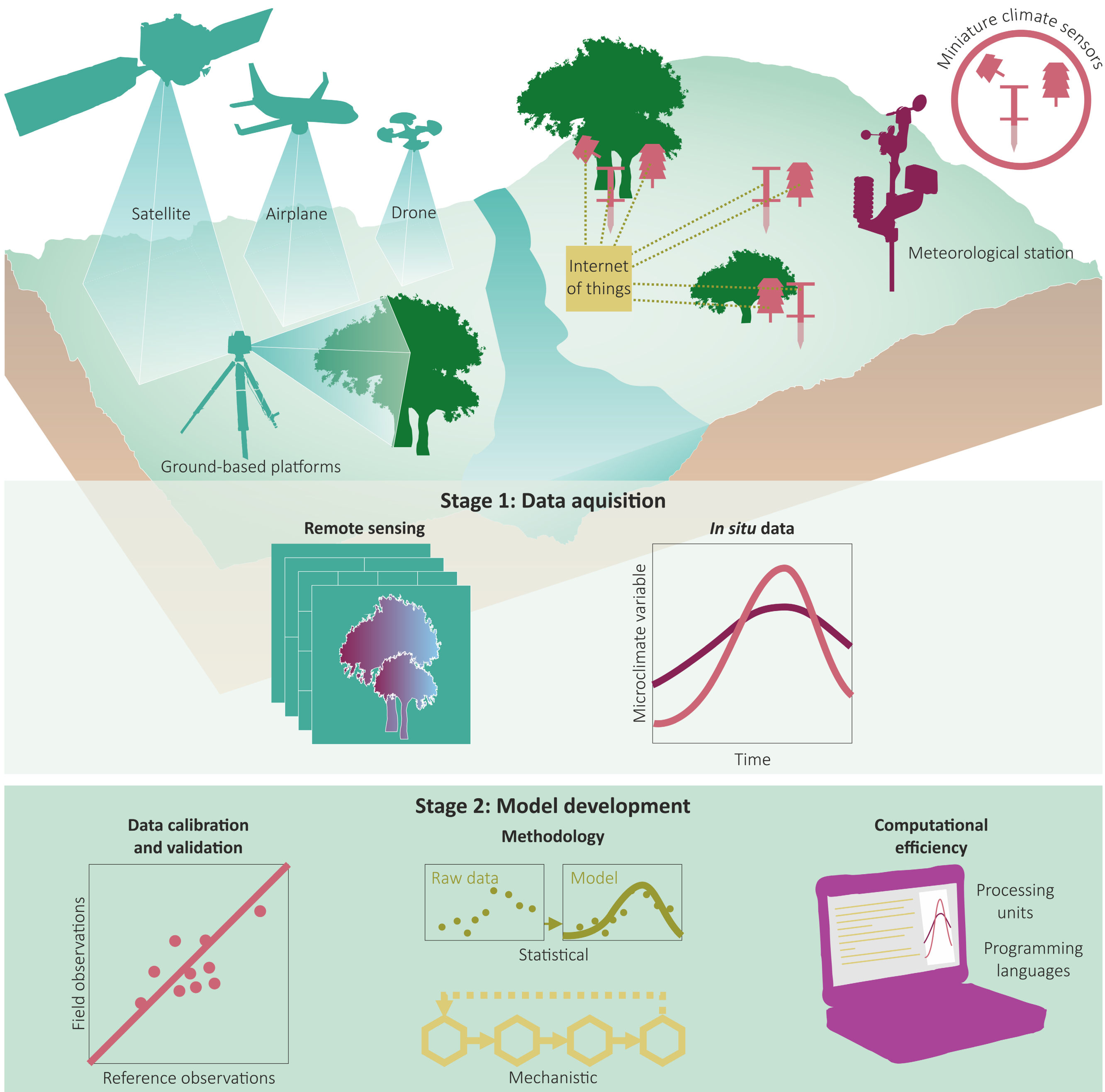

FIGURE 3 Methods for microclimate science. This conceptual figure presents examples discussed in the main text on how microclimate data and its explanatory variables are acquired from remotely sensed products and in situ measurements (Stage 1). We show examples of key areas where microclimate models have recently improved, from calibration to modelling methods and computational efficiency (Stage 2).

technology, cost-effectiveness and the miniaturization of sensors and their hardware (Mickley et al., 2019; Rebaudo et al., 2023; Wild et al., 2019). Moreover, advancements in wireless communications, such as the 'Internet of things' (Li et al., 2015), and data transmission using cellular technology or potentially via satellite, increasingly allow the deployment of these devices in ad hoc mesh networks across a landscape (Keitt & Abelson, 2021). Here, strategically planned study designs lay the foundations for representative microclimate networks (Lembrechts et al., 2021), and new methods are developed to make then most of sparse microclimate ground data, such as signal processing theory, which leverages cyclic microclimate patterns and temporally downscales sparse time-series (von Schmalensee, 2023). Also, animal-borne microclimate sensor networks can provide a biological lens to obtaining microclimate data from land and air (Ellis-Soto et al., 2023), and as a by-product, wildlife camera imagery can provide micrometeorological data on, for example, sunshine, snow and hail (Alison et al., 2023). However, the accuracy of low-cost loggers can be uncertain, and the reduction in size and costs affects the measurement accuracy of accompanying sensors (Maclean et al., 2021; Terando et al., 2017). Therefore, it is often advisable to calibrate sensors against laboratory measurements (e.g. climatic chambers for temperature sensors), to validate sensors by comparing them to a reference, and also to inter-calibrate sensors by comparing them to each other (Heinonen et al., 2014; Playà-Montmany & Tattersall, 2021). In the case of temperature measurements, standard weather station protocols including shading and ventilating thermometers often do not apply as measured microclimatic temperature variation mainly has its origin in low wind speed and variation in solar radiation (Maclean et al., 2021; Terando et al., 2017). Therefore, ultra-fine-wire thermocouples remain recommended for specific purposes, especially when sensors are subjected to direct sunlight (Maclean et al., 2021). Hydric microclimate data can also be challenging to calibrate and validate, both for air and soil humidity measurements. For instance, measurements of soil moisture are influenced by soil heterogeneity and stoniness that affect sensor-soil contact (Robinson et al., 2008; Wild et al., 2019).

Remote sensing allows researchers to capture leaf- to landscape-scale microclimate data with spatio-temporal representativeness, for instance on local temperature conditions (Faye et al., 2016; Zellweger et al., 2019). In structurally complex areas, such as forests, mountains or cities, measurements from a small number of sensors over a short time period will fail to adequately capture the range of microclimate conditions present (De Frenne et al., 2021; Scherrer & Körner, 2009; Zhou et al., 2011). This limitation can be overcome by linking microclimate measurements with remote sensing data on key predictors of microclimates (e.g. Haesen et al., 2021): vegetation and topographic features, and also snow in seasonally snow-covered areas. These data can be used for modelling microclimates across landscapes by filling the gaps between the microclimatic ground data. Spatially continuous structural or spectral data on vegetation and terrain structures can be obtained from satellites, aeroplanes and unoccupied aerial vehicles (UAVs) mounted with, for example, thermal imaging or light detection and ranging (LiDAR) sensors (Båserud et al., 2020; Davis, Synes, et al., 2019; Kašpar et al., 2021). For instance, high-resolution LiDAR data are openly available for some countries, such as for >15 European countries (<5 m resolution) (Kakoulaki et al., 2021). Terrestrial and mobile remote-sensing platforms can overcome canopy occlusion by obtaining measurements from a large range of viewpoints inside the canopy (Calders et al., 2020; Disney, 2019). UAVs enable obtaining data at even higher spatial resolution over limited spatial extents (Duffy et al., 2021; Faye et al., 2016; Hoffrén & García, 2023). Fusing these different types of remotely sensed data with novel approaches of radiative transfer modelling through canopies offers interesting new avenues for microclimate ecology (Jonas et al., 2020). Overall, there is great potential to exploit new modelling advances in further microclimate research.

4.2 | Advances in microclimate modelling and data processing

Microclimate models tend to be based on mechanistic understanding of the physical processes governing the energy balance. These models owe their origins to the pioneering work on weather forecasting by Richardson (1922), who demonstrated the application of energy balance equations for modelling the turbulent mixing of the atmosphere-biosphere boundary, and microclimate modelling by Porter et al. (1973), who developed a general microclimate model for solving the heat and water budgets of organisms. Thus, the most recent developments are not in the modelling of microclimate itself, but rather in making complex models more accessible to a wider audience. Recently, a series of microclimate models have been written using the R programming environment (R Core Team, 2022), enabling easy application by ecologists (Kearney et al., 2020; Maclean & Klinges, 2021). There are also guides with interactive visualizations for selecting and accessing microclimate data (Meyer et al., 2023). In parallel, the climate modelling community has been including multi-layered canopy representations in multiple land surface models (CLM-ml, ORCHIDEE-CAN, CLM-FATES) (Lawrence et al., 2019) allowing for point site evaluation of coarse microclimate data (Bonan et al., 2021). Such models have the advantage to be directly embedded in earth system model frameworks, therefore opening avenues to study coupled vegetation-microclimate feedbacks from small to large spatial extents.

Microclimate varies considerably at fine temporal resolutions (Bramer et al., 2018). Therefore, mechanistic models are run in sub-daily time increments. It is, in turn, computationally challenging to model microclimate mechanistically over large areas, even with the ongoing rapid advances in computing power. Also, lack of data can hinder the use of mechanistic models that require a comprehensive set of predictors. In part for these reasons, ecologists and biogeographers have tended to seek statistical relationships between microclimates and their drivers, such as topography and vegetation features (Ashcroft et al., 2009; Davis, Synes, et al., 2019), or have sought to establish these relationships through machine learning (Haesen et al., 2021; Lembrechts et al., 2022). The advantage of statistical and machine learning approaches is that bioclimatic variables of interest are not always needed at high temporal resolution (Hijmans et al., 2005), which can reduce the computational demands of the models. A significant drawback of statistical approaches is that the influence of variables used as predictors in statistical models, such as terrain and vegetation, varies in space and time. Thus, relationships derived at one location or time-period cannot necessarily be readily applied to others (Aalto et al., 2022). This could be overcome by modelling spatiotemporally varying relationships, that is, by using geographically weighted regression. Databases have emerged to provide the large precalculated microclimate datasets that are needed for modelling the relationships accurately across a range of spatial extents up to global coverage, including, for instance, projections of past and future microclimates (Levy et al., 2016), hourly estimates of historical microclimates (Kearney, 2019) and global soil temperatures (Lembrechts et al., 2020). However, the data can originate from different sources and require preprocessing. Also, microclimate data processing has advanced, for instance, with the advent of automated R packages that are suited for gap filling, flagging erroneous measurements, calculation of summary statistics and analysing thermal images (Senior et al., 2019), and for microclimate data handling and standardized analyses (Man et al., 2023).

The fusion of statistical and mechanistic approaches to model microclimates shows promise for developing mechanistically informed and computationally efficient methods. The application of statistical model emulation techniques that reproduce the behaviour of more complex models using techniques routinely adopted in other areas of climate modelling could significantly reduce computational run times (Baker et al., 2022). Further implementation requires a breakdown of traditional barriers between disciplines as far apart as ecology, meteorology and computer science (Briscoe et al., 2023). Also, recent developments in hardware and software provide potential solutions to the computational challenge of modelling microclimates. First is the modern computationally efficient programming language, Julia (Bezanson et al., 2018). Julia is similar to dynamic languages like Python and R, yet it compiles packages and user scripts down to machine code at run-time, thereby achieving speed comparable to Fortran or C++, and support for graphics processing unit-based programming geared at optimizing parallel computing is under active development (Besard et al., 2019; Schouten et al., 2022). Second is the burgeoning computational infrastructure for model processing, development and testing. Central to this infrastructure is the growing availability of affordable cloud-based computing and storage for back-end processing. Coupled with databases for model testing and comparisons (see e.g. Dietze et al., 2021), such frameworks provide a robust infrastructure for collaborative model development and processing at massive scales. These advancements in data collection, modelling and processing collectively enable us to attain microclimatic data at increasingly finer spatio-temporal resolutions and increasingly larger spatio-temporal extents, aligning more and more closely with the scales at which organisms operate.

4.3 | Finer resolution is not necessarily the better solution

Despite the importance of microclimates across many aspects of ecology and biogeography, we stress that a finer spatio-temporal resolution is not always necessary. Indeed, some organisms and ecosystem functions operate at spatial or temporal extents at which macroclimate data are more appropriate, thus, research questions do not automatically require a microclimate approach. In some cases, microclimate data did improve ecological models (forest plants, see Haesen, Lenoir, et al., 2023; and tundra plants see Kemppinen et al., 2021), yet, one approach is not necessarily transferable to other organisms (Lembrechts, Lenoir, et al., 2019). For instance, decade-long gridded air temperature data did outperform short-term soil temperature data in distribution models of bacterial membrane lipids with long-term stability in the soil (Halffman et al., 2022), as patterns that form over decades or centuries do not relate to short-term microclimatic fluctuations. These examples highlight that methods, including microclimate data and tools, should always be hypothesis-driven and justified by ecological and biogeographical theory. In many cases, the use of macroclimate data can be sufficient, or macroclimate data could simply be downscaled using, for example, fine-scaled topographic proxies (Kusch & Davy, 2022). Therefore, the microclimate approach is not a default answer to all ecological and biogeographical questions.

5 | WHAT'S NEXT?

In this perspective paper, we showcased that microclimate ecology and biogeography have evolved into a distinct, global discipline that is relevant across taxa, ecosystems and biomes. We highlighted the most substantial recent microclimate advances at the core of ecology and biogeography. Microclimate science is rooted in environmental biophysics and has recently experienced a surge of methodological progress, such as in logger autonomy, measurement accuracy and computing power allowing advancements in microclimate investigations and applications. This recent unlocking of microclimatic data and knowledge is welcomed, as microclimates are inseparable from the physiological constraints of individuals, populations, communities and ecosystems. Consequently, microclimates are also critical for understanding the influence of global change drivers, such as climate and land-use change on ecology and biogeography. As a result, microclimate science stands at the core of multiple important applications in ecosystem management, such as biodiversity conservation, forestry and urban ecology. Nevertheless, major steps are also ahead for this emerging field to have it reach its full potential.

First of all, global microclimate research should be conscious of its biases. For instance, forest and tundra biomes are well represented in the microclimate literature, while microclimates matter to many terrestrial organisms across all terrestrial biomes. Second, it is also important to note that in the English-written scientific literature, microclimate ecology and biogeography are largely represented by studies, researchers and institutions of European, North American and Australian origin. We emphasize that these knowledge gaps and biases are important to consider in all future research that aims for a genuinely global coverage in microclimate investigations. This is key for making ecology and biogeography a more global endeavour (Nuñez et al., 2021).

5.1 | Knowledge gaps in microclimate investigations in ecology and biogeography

The mismatches between macroclimate and microclimate should be considered when predicting responses of organisms to climate change (Liancourt et al., 2020; Zellweger et al., 2020). It is crucial to understand the influence of microclimates on organisms under climate change, but there are many remaining unknowns. This would require measuring and modelling the effects of all different microclimatic conditions that influence a given organism and its functions (Kemppinen & Niittynen, 2022). This could, for example, be achieved by coupling observational approaches with experiments, which would allow understanding of the climatic optima and tolerance levels of the organism (Ripley et al., 2020; Vandvik et al., 2020). Also, mobile organisms can move between microclimates in search of more suitable conditions (Frey, Hadley, & Betts, 2016; Kim et al., 2022), however, more investigation is needed to understand which organisms exploit microrefugia under climate change and why.

Microclimate science is increasingly incorporated into ecological and biogeographical questions at local to regional extents (De Frenne et al., 2021), but questions of continental or global extents are rare (but see e.g. Haesen, Lenoir, et al., 2023; Risch et al., 2023). Incorporating the principles and approaches of microclimate science into studies beyond local extents would call for improved global data integration. This would also require the harmonization of measurement methods and increased monitoring of remote, undersampled areas and ecosystems, such as tropics, deserts and tundra. The first is partly hindered by the lack of standard guidelines that would increase comparability of microclimate data (Maclean et al., 2021), and the latter by the cost of microclimate sensors which is not globally accessible (Nuñez et al., 2021). However, some microclimate products, such as databases of modelled soil and near-surface temperatures, have recently become openly available at continental and global extents (Haesen et al., 2021; Lembrechts et al., 2022).

Lastly, microclimate investigations on larger organisms and above-ground systems are plentiful, whereas, more research is needed on microclimate relationships of microorganisms and below-ground organisms and ecosystem processes. However, investigations in soil ecology are partly hindered due to a lack of high-resolution data on belowground microclimates (Eisenhauer et al., 2022).

5.2 | Knowledge gaps in microclimate applications in ecosystem management

More evidence is needed on the outcomes of microclimate management. This evidence should show when and where microclimate management is required for promoting and protecting biodiversity (Ellis, 2020; Tinya et al., 2021). Currently, the evidence for microclimate management to build climate-resilient ecosystems is often theoretical (Hylander et al., 2022; Morelli et al., 2020), and therefore, additional data could strengthen these links.

There is a need for identifying general patterns of microclimate-organism relationships across and within ecosystems (Kemppinen et al., 2021). For example, what makes microclimates act as microrefugia varies by site, by species and potentially by life stage, each depending on different spatiotemporal factors and scales (Caron et al., 2021; Greiser et al., 2022). Thus, not all microrefugia are equally valuable for protecting biodiversity (Hylander et al., 2015).

Microclimate science can be used beyond ecology and biogeography. This could lead to new knowledge and applications in microclimate ecology and urban ecology (Iungman et al., 2023; Roman et al., 2021), microclimate biogeography and agriculture (Gardner et al., 2021) and microclimate biogeography and health geography (Paaijmans et al., 2010; Wimberly et al., 2020; Wong & Jim, 2017). Microclimate science can be used to address major societal challenges, such as health and well-being (Gillerot et al., 2022; Jenerette et al., 2016), green energy efficiency (Shafique et al., 2020) and socioeconomic injustice (Ghosh et al., 2022; Yin et al., 2023). By embracing interdisciplinarity, microclimate science can be exploited in solving these crucial issues for an ecologically and socioeconomically sustainable future.

5.3 | Knowledge gaps in methods for microclimate science

Methods for microclimate science should aim to achieve a more flexible spatio-temporal scaling of microclimate data. This entails developing a comprehensive library of gridded microclimate products that match the scale and extent required in specific research questions. However, pursuing higher resolutions is not valuable in itself in ecological and biogeographical investigations, as the inclusion of microclimate mechanisms, especially those non-linearly related to macroclimate, takes precedence over spatiotemporal resolution (Bennie et al., 2014; Bütikofer et al., 2020). Nonetheless, most existing products lack in at least one dimension, whether it be in spatial or temporal resolution, and/or mechanistic proximity. Enhancing these dimensions can be accomplished by integrating open access data platforms for in situ data, such as the SoilTemp database (Lembrechts et al., 2020b), gridded microclimate products (e.g. Haesen, Lembrechts, et al., 2023; Klinges et al., 2022) and increased efficiency and scalability of mechanistic microclimate models (Maclean & Klinges, 2021).

Importantly, microclimate data should evolve from stationary to dynamic products (Kearney et al., 2020). For instance, future microclimatic data are largely lacking, since the currently available microclimate datasets with a broad spatial extent only provide bioclimatic variables for the present (Haesen, Lembrechts, et al., 2023; Lembrechts et al., 2022). Ideally, datasets would also capture microclimates in all three dimensions of space. Ultimately, predictors used for modelling microclimates should be advanced to accommodate this progress (e.g. land-use change scenarios).

Integrating microclimate-vegetation feedback into global change biology is an important avenue (Bonan et al., 2021). This could be further developed by coupling airborne laser scanning-based single tree-delineation methods with radiative transfer and microclimate models (Webster et al., 2020). This would allow for spatially extensive and explicit simulations of microclimate dynamics under, for instance, different management regimes, natural disturbance dynamics or climate scenarios.

We have demonstrated that endeavours in microclimate ecology and biogeography are worthwhile and can provide many new avenues for future research. The constantly evolving methods for microclimate science open new possibilities in the investigations of microclimate-organism relationships that can be further applied into ecosystem management, such as biodiversity conservation. We hope to have inspired fellow ecologists and biogeographers to find more ways to increase the awareness of microclimates and their importance in our fields and beyond.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Not applicable.

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BIOSKETCH

The authors are participants of the Microclimate Ecology and Biogeography conference held in Antwerp, Belgium in 2022. Together they collaboratively wrote this perspective paper that brings together 97 experts and their views on the recent advancements and knowledge gaps in terrestrial microclimates. The paper was coordinated by Julia Kemppinen, Jonas J. Lembrechts, Koenraad Van Meerbeek, and Pieter De Frenne, and writing different sections was led by Jofre Carnicer, Nathalie Isabelle Chardon, Paul Kardol, Jonathan Lenoir, Daijun Liu, Ilya Maclean, Jan Pergl, Patrick Saccone, Rebecca A. Senior, Ting Shen, Sandra Słowińska, Vigdis Vandvik, and Jonathan von Oppen. For more details on authors statistics and how the work was organised, please see Supplementary information Figures S1.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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