Title

Microclimate, an inseparable part of ecology and biogeography

Short title

Microclimate ecology and biogeography

Abstract

Brief introduction: microclimates cannot be neglected

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, and where this field is heading next.

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.

Microclimate investigations in ecology and biogeography

We highlight the latest research on interactions between microclimate and organisms, including how microclimate influences individuals, and through them populations, communities, and entire ecosystems and their processes. We also briefly discuss recent research on how organisms shape microclimate 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.

What's next?

We identify major knowledge gaps that need to be filled for further advancing microclimate methods, investigations, and applications. 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, plant ecology, microclimate, modelling

Brief introduction: microclimates cannot be neglected

Microclimate refers to the local climate conditions that organisms and ecosystems are exposed to (Bramer *et al.*, 2018). As such, microclimate influences the ecophysiology of individuals, and the dynamics of populations, communities, and ecosystems across biomes. 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 *et al.*, 2019). Consequently, microclimate science has rapidly shown its high relevance to ecological and biogeographical investigations and applications (Bramer *et al.*, 2018; De Frenne *et al.*, 2021). Now, microclimate science is recognised as an integral component of ecology and biogeography, and is used to investigate local ecological manifestations of the global climate and biodiversity patterns (Zellweger *et al.*, 2020; Riddell *et al.*, 2021), 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, 1942a, 1951). The physics of microclimate (Baum & Court, 1949), the appropriate spatial scale, and the challenges of measuring microclimates (Geiger, 1951; 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.*, 2019b), measurement techniques (Maclean *et al.*, 2021), species distribution modelling (Lembrechts *et al.*, 2019), and forest ecology (De Frenne *et al.*, 2021). Following these examples, we approach microclimate as the set of local climatic conditions (e.g., temperature, humidity, light, wind) emerging from the surrounding macroclimatic conditions and mediated by local features. We consider that the microclimate scales and boundaries are highly dependent on the ecological context (Potter *et al.*, 2013; Pincebourde & Woods, 2020), e.g., ranging from minutes and cubic millimetres for within-leaf herbivore insects to monthly averages and hectares for understory communities in forests (Lembrechts *et al.*, 2019; Pincebourde & Woods, 2020; Zellweger *et al.*, 2020; De Frenne *et al.*, 2021).

Here, we provide an overview of the current status of microclimate ecology and biogeography, and where this field is going next from the perspective of a wide range of ecologists and biogeographers investigating diverse topics related to terrestrial microclimate (read more about the authors in Supplementary information Figures S1-3). Recently, microclimate science has taken major strides forward, especially at the following three frontiers: 1) methods in microclimate science, 2) investigations of microclimate ecology and biogeography, and 3) microclimate applications in ecosystem management. 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 beyond, from fine scale to the global scale. We herewith highlight the maturation of microclimate ecology and biogeography into a global discipline.

Methods for microclimate science

Advances in data acquisition

Microclimate measurements rely to a large extent on in-situ sensors (Figure 1). In-situ sensors now form part of the toolkit of many ecological studies due to the improvements in chip devices, battery technology, cost-effectiveness, and the miniaturisation of sensors and their hardware (Mickley *et al.*, 2019; Wild *et al.*, 2019; Rebaudo *et al.*, 2023). 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 foundations for representative microclimate networks (Lembrechts *et al.*, 2021; Aalto *et al.*, 2022; Kemppinen & Niittynen, 2022), and new methods are developed to make 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). However, the accuracy of low-cost loggers can be uncertain, and the reduction in size and costs affects measurement accuracy of accompanying sensors (Terando *et al.*, 2017; Maclean *et al.*, 2021). 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 it origin in low wind speed and variation in solar radiation (Terando *et al.*, 2017; Maclean *et al.*, 2021). 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 (Faye *et al.*, 2016; Zellweger *et al.*, 2019b). 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 (Scherrer & Körner, 2009; Zhou *et al.*, 2011; De Frenne *et al.*, 2021). This limitation can be overcome by linking microclimate measurements with remote sensing data on key predictors of microclimate (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, e.g., thermal imaging or light detection and ranging (LiDAR) sensors (Båserud *et al.*, 2020; Kašpar *et al.*, 2021). For instance, high-resolution LiDAR data from aircraft surveys are openly available for some countries, such as for >15 European countries with <5 m resolution (Kakoulaki et al. 2021). UAVs enable obtaining data at even higher spatial resolution over limited spatial extents (Faye *et al.*, 2016; Duffy *et al.*, 2021; Hoffrén & García, 2023). Terrestrial and mobile remote-sensing platforms can overcome canopy occlusion by obtaining measurements from a large range of viewpoints inside the canopy (Disney, 2019; Calders *et al.*, 2020). Fusing these different types of remotely-sensed data with novel approaches of radiative transfer modelling through canopies offer interesting new avenues for microclimate ecology (Jonas *et al.*, 2020). Overall, there is great potential to exploit new modelling advances in further microclimate research.

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 the first microclimate models for ectotherms. 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). 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.

Microclimate varies considerably at fine spatial and 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; Greiser *et al.*, 2018; Kemppinen *et al.*, 2018), 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, vary in space and time. Thus, relationships derived at one location or time-period cannot necessarily be readily applied to others (*Kemppinen et al. Accepted*; Aalto *et al.*, 2022). This could be overcome by modelling spatiotemporally varying relationships, i.e., by using geographically weighted regression. Databases provide the large datasets that are needed for modelling the relationships accurately (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).

The fusion of statistical and mechanistic approaches to model microclimate 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 break-down 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 microclimate. 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-times comparable to Fortran or C++, and support for graphics processing unit-based programming geared at optimising parallel computing is under active development (Besard *et al.*, 2019). 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. Lembrechts *et al.*, 2020; Dietze *et al.*, 2021), such frameworks provide a robust infrastructure for collaborative model development and processing at massive scales.

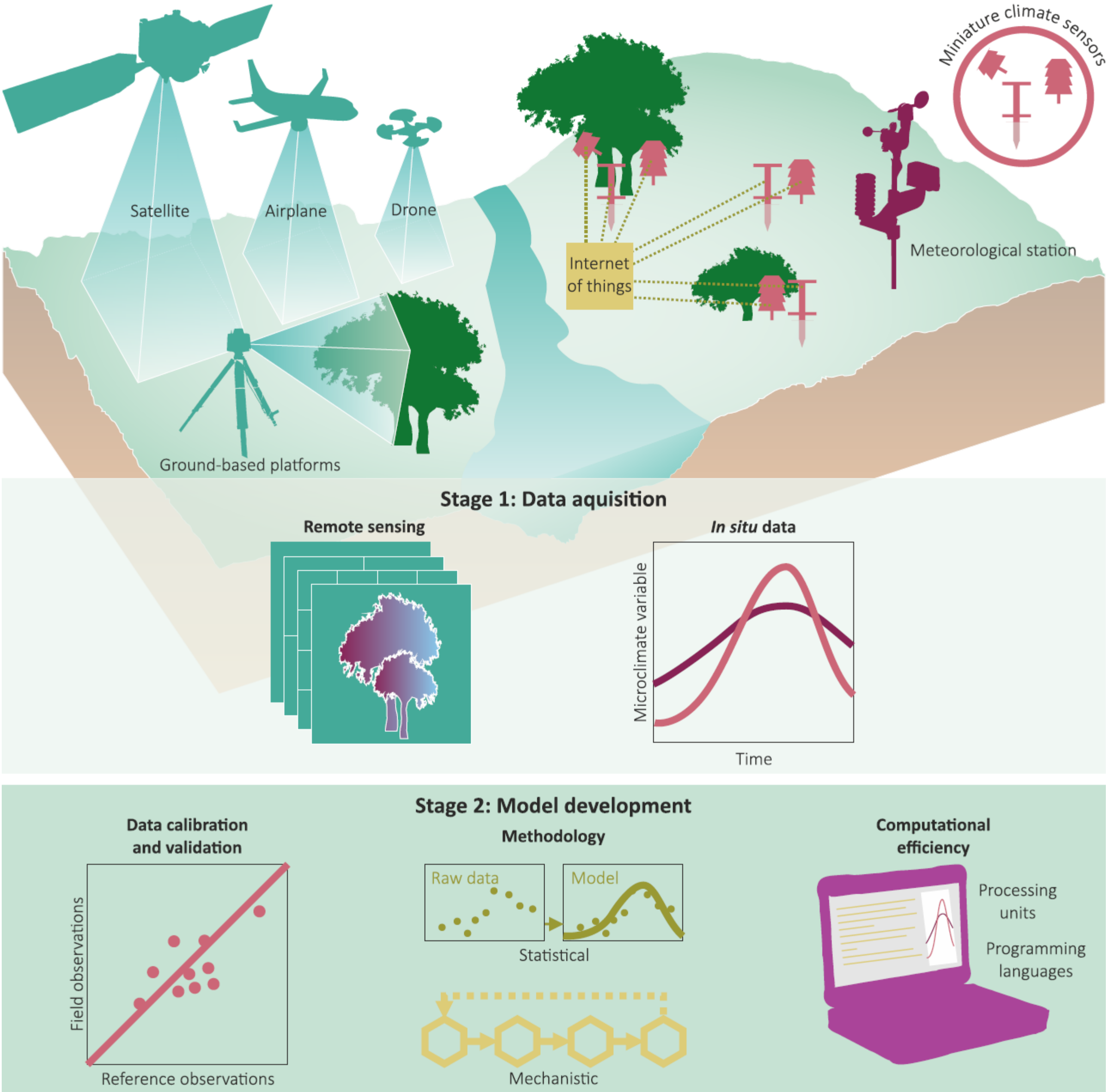

Figure 1. Methods for microclimate science. This conceptual figure presents examples discussed in the main text on how microclimate data and its explanatory variables are acquired from remotely-sensed products and *in situ* measurements (Stage 1). We show examples of key areas where microclimate models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

Microclimate investigations in ecology and biogeography

Organisms drive microclimate

Organisms are key drivers of microclimate. Trees and shrubs affect local light, temperature, and water conditions (Pincebourde & Casas, 2019; Zellweger *et al.*, 2019a; Kemppinen *et al.*, 2021b), and mosses and lichens regulate soil microclimate (Delgado-Baquerizo *et al.*, 2018; van Zuijlen *et al.*, 2020). Mushrooms influence temperatures and air currents for spore dispersal (Dressaire *et al.*, 2016). Animals influence microclimates; insects cool their nest by wing fanning (Jones & Oldroyd, 2006), arthropods alter leaf temperatures by feeding on them (Pincebourde & Casas, 2019), and larger herbivores such as elephants impact microclimates by grazing and trampling on vegetation (Gordon *et al.*, 2023). Organisms can create ecosystem-wide mosaics of microclimate, for instance, grass canopies create sharp vertical microclimatic gradients (Vandvik *et al.*, 2020). Also, forest canopies create these gradients from tree bases to canopy crowns (De Frenne *et al.*, 2021), and provide microclimate heterogeneity over small spatial extents (Ozanne *et al.*, 2003). This, in turn, enables arboreal species, such as frogs and epiphytes, to adjust their distributions vertically to compensate for broad-scale shifts in climate associated with elevation or latitude (Scheffers *et al.*, 2013; Basham *et al.*, 2023). These are just a few examples of how organisms engineer microclimates, but all organisms are in turn affected by microclimate, which shapes their ecology and biogeography (Figure 2).

Microclimate influences individuals and populations

Microclimate influences individuals by affecting their performance (Poorter *et al.*, 2019), structure (Kemppinen & Niittynen, 2022), organs (Opedal *et al.*, 2015), and cells (Zweifel *et al.*, 2007). For example, darker ants dominate tree canopies due to melanism that protects against UV radiation and reduces moisture loss (Law *et al.*, 2020), and size and pilosity of dung beetles mediate microclimatic temperature responses (Williamson *et al.*, 2022). These ecophysiological responses are associated with adaptations to thermal, hydrological, and light stress and tolerance. Vertical variation in forest microclimates promotes evolution of thermal performance and desiccation resistance of ants (Bujan *et al.*, 2016; Kaspari *et al.*, 2016). Thermal tolerance shapes biodiversity globally (Trew & Maclean, 2021), and it can predict species performance, behaviour, and adaptability in butterflies (Pincebourde & Casas, 2019; von Schmalensee *et al.*, 2021), ants (Baudier *et al.*, 2018), birds (Kim *et al.*, 2022), and plants (Bert *et al.*, 2022).

Microclimate shapes populations by affecting demographic rates through individual recruitment and survival (Oldfather & Ackerly, 2019; Goodwin & Brown, 2023). For instance, seed germination depends on specific temperature, humidity, and light conditions (Graae *et al.*, 2022), and plant growth and mortality rates are affected by water availability (Liu *et al.*, 2018), which also influences tree regeneration after disturbances (Lloret *et al.*, 2004; Thom *et al.*, 2022). Microclimate also shapes behavioural responses. Butterflies avoid frost by clustering at different heights in trees (Brower *et al.*, 2011), and birds consider wind characteristics in nest-site selection (Momberg *et al.*, 2023). Moreover, microclimate controls fine-scale variation in phenology as rising spring temperatures advance flowering with several days per degree (Tansey *et al.*, 2017), and in turn, such important effects on individuals affect the entire community.

Microclimate structures communities

Microclimate structures communities by shaping species distributions and species richness patterns (le Roux *et al.*, 2013; Niittynen *et al.*, 2020; Momberg *et al.*, 2021). For example, microclimate influences vascular plant species richness, species turnover, and functional community composition (Opedal *et al.*, 2015; Kemppinen *et al.*, 2021a; Shen *et al.*, 2022b), bryophyte community composition and phylogenetic structure (Man *et al.*, 2022; Shen *et al.*, 2022a), and lichen species richness and community composition (Kemppinen *et al.*, 2019). Moreover, microclimate mediates species responses to climate change (De Frenne *et al.*, 2013; Zellweger *et al.*, 2020; see also Bertrand *et al.*, 2016) and land use changes (Christiansen *et al.*, 2022). Thus, incorporating microclimate is crucial for increasing ecological realism in species distribution models (Lembrechts *et al.*, 2019; *Haesen et al. Preprint*), as has been shown in reptiles (Stickley & Fraterrigo, 2023), birds (Massimino *et al.*, 2020), and vascular plants, bryophytes, and lichens (Niittynen & Luoto, 2018).

Microclimate determines species interactions through behavioural, phenological, and ecophysiological mechanisms. For instance, microclimate influences habitat selection of insects (Carnicer *et al.*, 2019; Vives-Ingla *et al.*, 2023) and plant phenology (Kankaanpää *et al.*, 2018), and this can lead to multitrophic-level changes in community structures (Kankaanpää *et al.*, 2020). Forest microclimates modify species interactions by altering phenological responses, chemical defence phenotypes, colonisation, and competitive processes (Greiser *et al.*, 2021; Sanczuk *et al.*, 2021; Willems *et al.*, 2021). Microclimate also determines facilitation; shrubs and cushion plants facilitate seedlings by modifying microclimates (Cavieres *et al.*, 2014; Vega-Álvarez *et al.*, 2019). Overall, facilitation is an important mechanism in extreme ecosystems, especially in deserts and polar deserts, where plants facilitate other organisms by providing shade, dew, and shelter (Bruno *et al.*, 2003; Tirado & Pugnaire, 2005; Casanova-Katny & Cavieres, 2012).

Microclimate controls and creates ecosystems

Microclimate controls 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). Microclimate 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. Preprint*). Overall, microclimates are important to consider in investigating ecosystem processes, since they regulate resources for primary production and regulate many ecosystem functions.

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). For instance, microrefugia affect seed survival and plant growth, and can create opportunities for animals to hide, feed, and reproduce

(Frey *et al.*, 2016a; Lucid *et al.*, 2021). Microrefugia can be identified using thermal imaging (Hoffrén & García, 2023), high-resolution gridded microclimate products *(Haesen et al. Preprint)*, topographic data (Ashcroft *et al.*, 2012; Meineri & Hylander, 2017), or exploring disjunct populations (Finocchiaro *et al.*, 2023). Overall, microrefugia are extremely important for maintaining biodiversity under climate change (Suggitt *et al.*, 2018; Maclean & Early, 2023), and consequently, for nature conservation (Ackerly *et al.*, 2020; Lembrechts, 2023), and can have the same importance as larger ecosystem management activities (Thorne *et al.*, 2020).

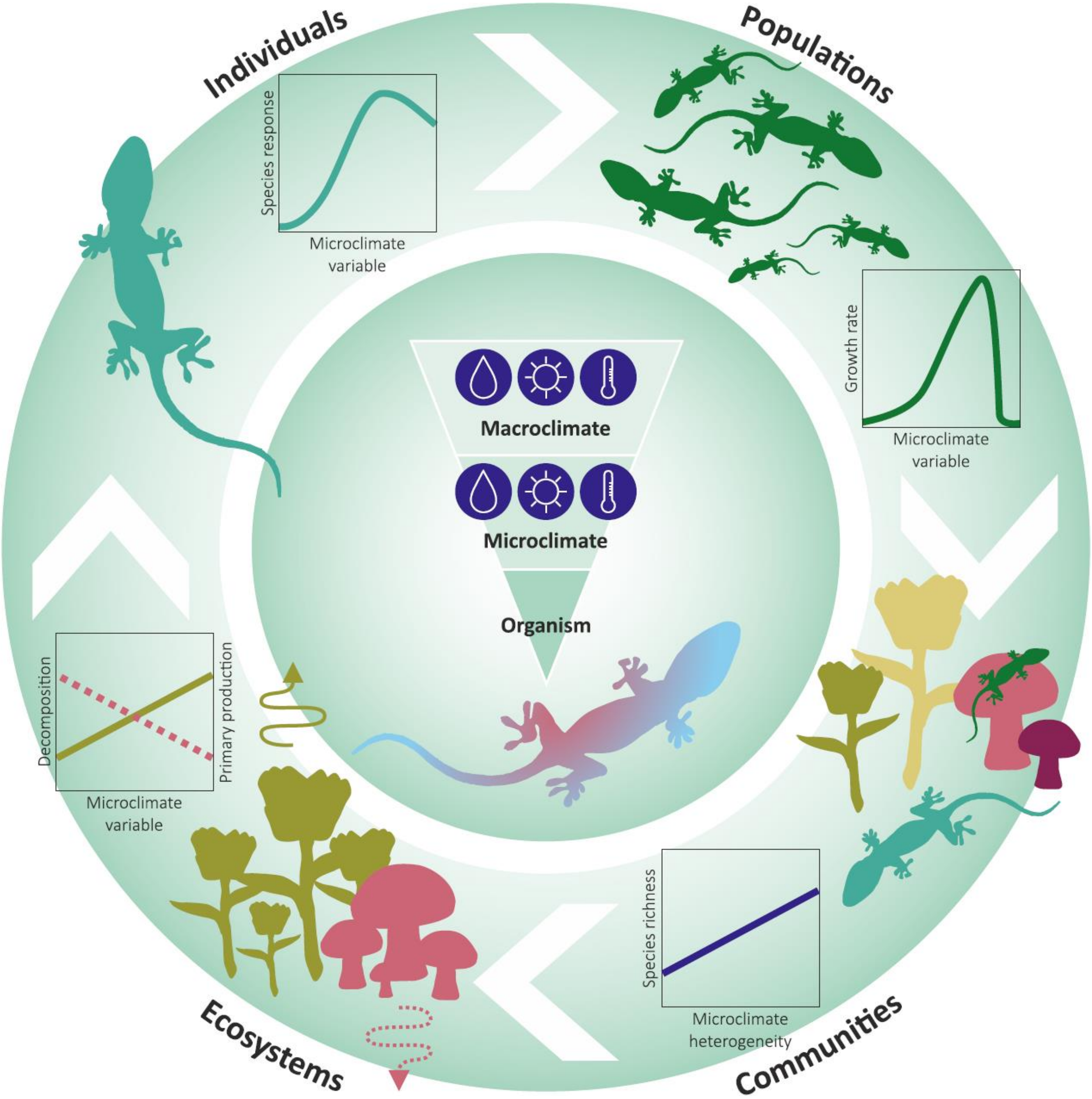

Figure 2. Microclimate investigations in ecology and biogeography. The conceptual figure highlights that microclimate is the link between macroclimate and the ecophysiology of organisms. We show examples of how microclimate influences individuals, populations, communities, and ecosystems and their processes.

Microclimate applications in ecosystem management

Microclimate is pivotal in ecosystem management, especially in the face of climate change (Figure 3). The question of how management practices affect microclimates has been discussed for decades (Kraus, 1911; Geiger, 1942b). 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 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.

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), as it can slow down the perception of the rate of climate change by organisms (Lembrechts, 2023). 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 (Thers *et al.*, 2019; Malhi *et al.*, 2022). For example, beaver constructions buffer microclimates from extreme fluctuations by increasing hydrological connectivity and creating floodplains (Weber *et al.*, 2017; Larsen *et al.*, 2021). Also, elephants, wild boars, horses, and donkeys engineer microclimates by grazing and trampling on vegetation, and modifying topography and water availability (Sandom *et al.*, 2013; Lundgren *et al.*, 2021; Gordon *et al.*, 2023). 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).

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 proactive transformation of managed ecosystems (Brang *et al.*, 2014; Hylander *et al.*, 2022). Proactive transformation considers protection of cool microclimates which promote microrefugia (Schmalholz & Hylander, 2011; Hylander *et al.*, 2022). Microclimate management is constantly evolving (Kermavnar *et al.*, 2020; Thom *et al.*, 2020), and increasingly applied within 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).

Microclimate management in forestry

Forestry is an excellent example of how ecosystem management affects microclimate heterogeneity (Scheffers *et al.*, 2017; Menge *et al.*, 2023). 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 (Geiger, 1942b; Chen *et al.*, 1993; 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 is severe 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 (Norris *et al.*, 2011; Frey *et al.*, 2016b; Wolf *et al.*, 2021). Knowledge and practices found in forestry can be further applied also in other anthropogenically modified environments.

Microclimate management in urban ecology

Increasing recognition of the importance of microclimate has led to a proactive approach also in urban ecology to achieve desired microclimate outcomes (Lai *et al.*, 2019). 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). Urban heat islands have been shown to alter spider behaviour (de Tranaltes *et al.*, 2022), and result in diversity changes in plant, bird, and insect species (Aronson *et al.*, 2014; McGlynn *et al.*, 2019). Management practices can optimise 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).

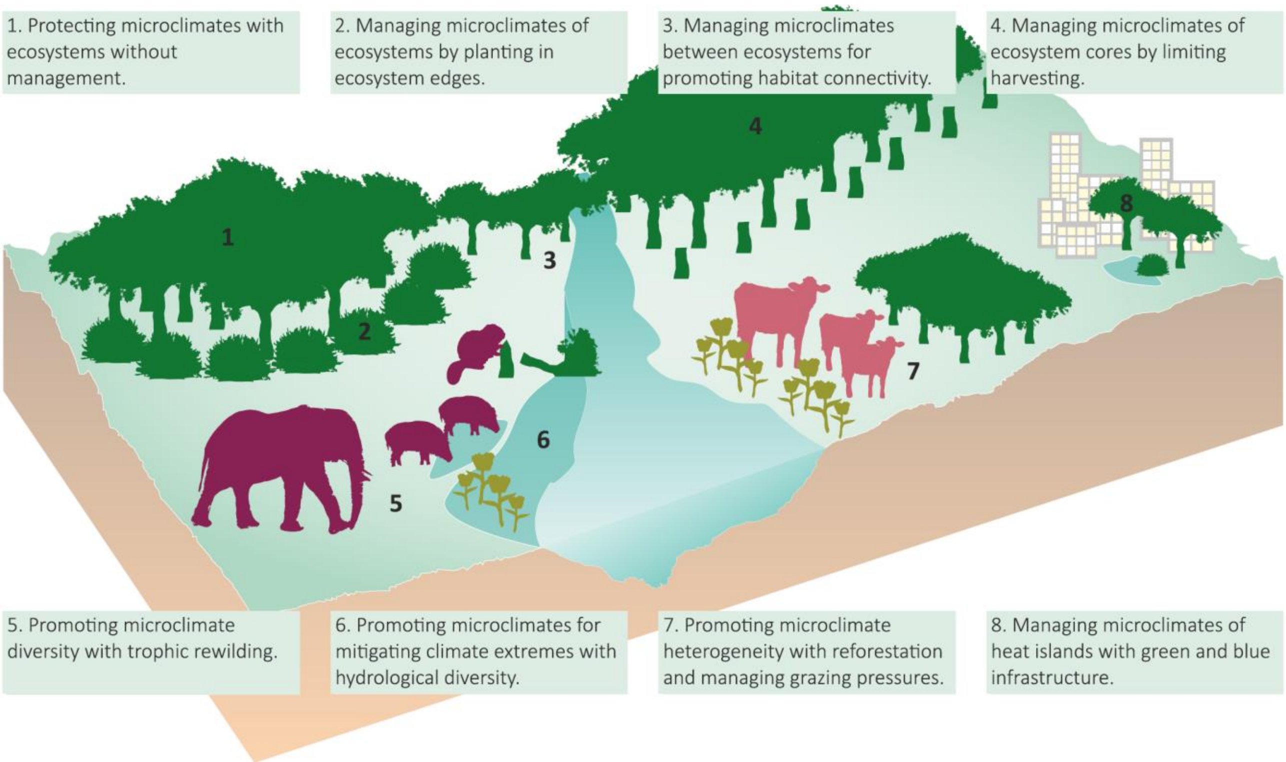

Figure 3. Microclimate applications in ecosystem management. The conceptual figure presents examples of biodiversity conservation, forestry, and urban ecology maintaining and promoting microclimate heterogeneity for the benefit of biodiversity.

What's next?

In this perspective paper, we showcased that microclimate ecology and biogeography have evolved into a distinct, global discipline. 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 microclimate is inseparable from the physiological constraints of individuals, populations, communities, and ecosystems. Consequently, microclimate is 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.

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.*, 2020), gridded microclimate products generated for example through fusion with remote sensing and macroclimate products, such as CHELSA or WorldClim (Haesen *et al.*, 2023), 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 is largely lacking, since the currently available microclimate datasets with a broad spatial extent only provide bioclimatic variables for the present (Lembrechts *et al.*, 2022; Haesen *et al.*, 2023). Ideally, datasets would also capture microclimate in all three dimensions of space. Ultimately, predictors used for modelling microclimate 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.

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 microclimate 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 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 *et al.*, 2016a; Kim *et al.*, 2022), however, more investigation is needed to understand which organisms exploit microrefugia under climate change and why.

Microclimate 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., Risch *et al.*, 2023; *Haesen et al. Preprint*). 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 harmonisation of measurement methods and increased monitoring of remote, undersampled areas and ecosystems, such as tropics, deserts and tundra. The first is partly hindered by 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 models of soil and near-surface temperatures, have recently become openly available at continental and global extents (Haesen *et al.*, 2021; Lembrechts *et al.*, 2022).

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). Moreover, microclimate ecology and biogeography is currently focused on terrestrial ecosystems, and therefore, more efforts should be directed towards compiling data to study microclimates of aquatic ecosystems, such as freshwater, riparian, coastal, and marine ecosystems.

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

We have demonstrated that endeavours in microclimate ecology and biogeography are worthwhile, and will 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 microclimate and its importance in our fields and beyond.

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