Title

Microclimate, an important part of ecology and biogeography

Short title

Microclimate ecology and biogeography

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, plant ecology, microclimate, modelling

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 *et al.*, 2019b). 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 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.*, 2020a; 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, 1942 & 1995). The physics of microclimate (Baum & Court, 1949), the appropriate spatial scale, and the challenges of measuring microclimates (Geiger, 1942 & 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 *et al.*, 2019b), 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 (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 (Pincebourde & Woods, 2020; Zellweger *et al.*, 2020b).

Here, our aim is 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 S1-3). 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, e.g., freshwater, riparian, intertidal, coastal, and marine ecosystems (e.g., Judge et al., 2018; Enriquez-Urzelai et al., 2019; Bentley et al., 2020; 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 the 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.

Microclimate investigations in ecology and biogeography

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 (Vandvik *et al.*, 2020; De Frenne *et al.*, 2021), which generates 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 (Scheffers *et al.*, 2013; Basham *et al.*, 2023). 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 (Jones & Oldroyd, 2006; Joseph *et al.*, 2016; Gordon *et al.*, 2023). These examples highlight how diverse and active the role of organisms is in shaping microclimates.

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 is 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 showcase 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 (Sears *et al.*, 2016; Carter & Janzen, 2021; 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 (Pincebourde & Casas, 2019; von Schmalensee *et al.*, 2021; Bert *et al.*, 2022; Kim *et al.*, 2022). 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 (Sears *et al.*, 2016; Carter & Janzen, 2021; Briscoe *et al.*, 2022), 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 (Oldfather & Ackerly, 2019; Goodwin & Brown, 2023). 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).

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 (le Roux *et al.*, 2013; Checa *et al.*, 2014; Niittynen *et al.*, 2020; Momberg *et al.*, 2021; Ma *et al.*, 2022). Recent investigations on plant communities show how microclimates shape species richness, turnover, and the composition of vascular plants (Opedal *et al.*, 2015; Shen *et al.*, 2022b), bryophytes (Man *et al.*, 2022; Shen *et al.*, 2022a), 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 (Niittynen & Luoto, 2018; Massimino *et al.*, 2020; Haesen *et al.*, 2023b; 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 influences 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 colonisation 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).

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 *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.*, 2023b), 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; Suggitt *et al.*, 2018; Maclean & Early, 2023), and can have the same importance as larger ecosystem management activities for nature conservation across scales (Thorne *et al.* 2020; Ackerly *et al.* 2020).

Microclimate applications in ecosystem management

Microclimates are pivotal in ecosystem management, especially in the face of climate change (Figure 2). 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). 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; 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 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 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 (Norris *et al.*, 2011; Frey *et al.*, 2016b; Wolf *et al.*, 2021). However, as temperatures increase and water availability is more limited, forests can lose their capacity to buffer climate extremes (Davis *et al.*, 2019a). 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 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 urbanising and densely populated areas (Hartig & Kahn, 2016; Souza *et al.*, 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 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).

Methods for microclimate science

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 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), 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). 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 e.g., 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 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, 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 (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 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, e.g., thermal imaging or light detection and ranging (LiDAR) sensors (Davis et al., 2019b; Båserud *et al.*, 2020; 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 (Disney, 2019; Calders *et al.*, 2020). UAVs enable obtaining data at even higher spatial resolution over limited spatial extents (Faye *et al.*, 2016; Duffy *et al.*, 2021; Hoffrén & García, 2023). 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 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 visualisations 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 et al., 2019b), 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 (Aalto *et al.*, 2022). This could be overcome by modelling spatiotemporally varying relationships, i.e., 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.*, 2020a). 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 standardised 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 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 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 optimising 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.

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 *et al.*, 2023b; and tundra plants see Kemppinen *et al.*, 2021), yet, one approach is not necessarily transferable to other organisms (Lembrechts *et al.*, 2019a). 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.

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. Secondly, it is also important to note that in the English-written scientific literature, microclimate ecology and biogeography is largely represented by studies, researchers, and institutions of European, North American, and Australian origin. We emphasise 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).

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.*, 2020a). 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 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 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 *et al.*, 2023b; 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 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 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).

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.*, 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 (Roman *et al.*, 2021; Iungman *et al.*, 2023), microclimate biogeography and agriculture (Gardner *et al.*, 2021), and microclimate biogeography and health geography (Paaijmans *et al.*, 2010; 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 (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.

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., Klinges *et al.*, 2022; Haesen *et al.*, 2023a) 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.*, 2023a). 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.

Figures

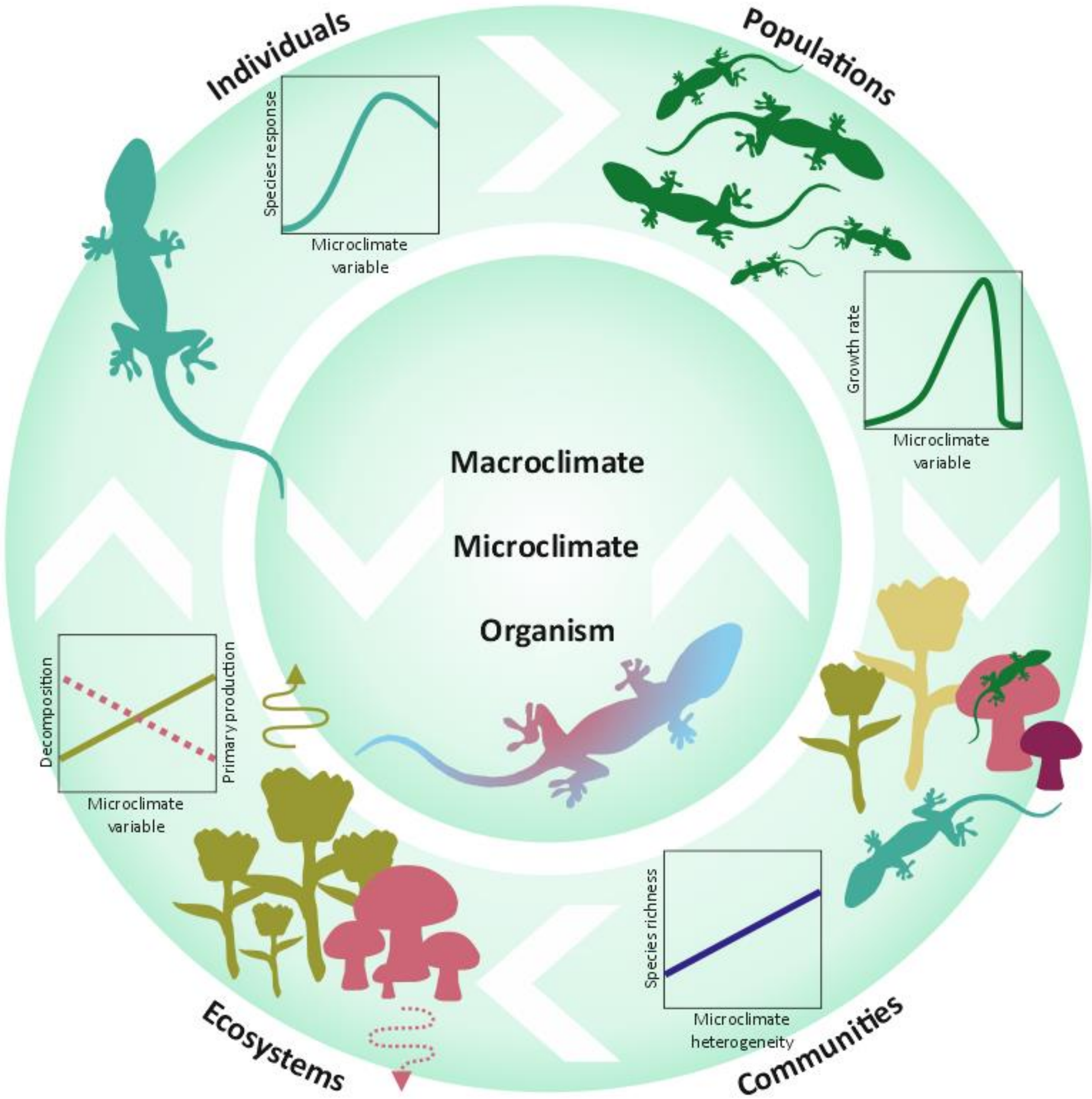


Figure 1. Microclimate investigations in ecology and biogeography. The conceptual figure highlights that microclimate is the link between macroclimate and the ecophysiology of organisms. We show examples of how microclimates influence individuals, populations, communities, and ecosystems and their processes.

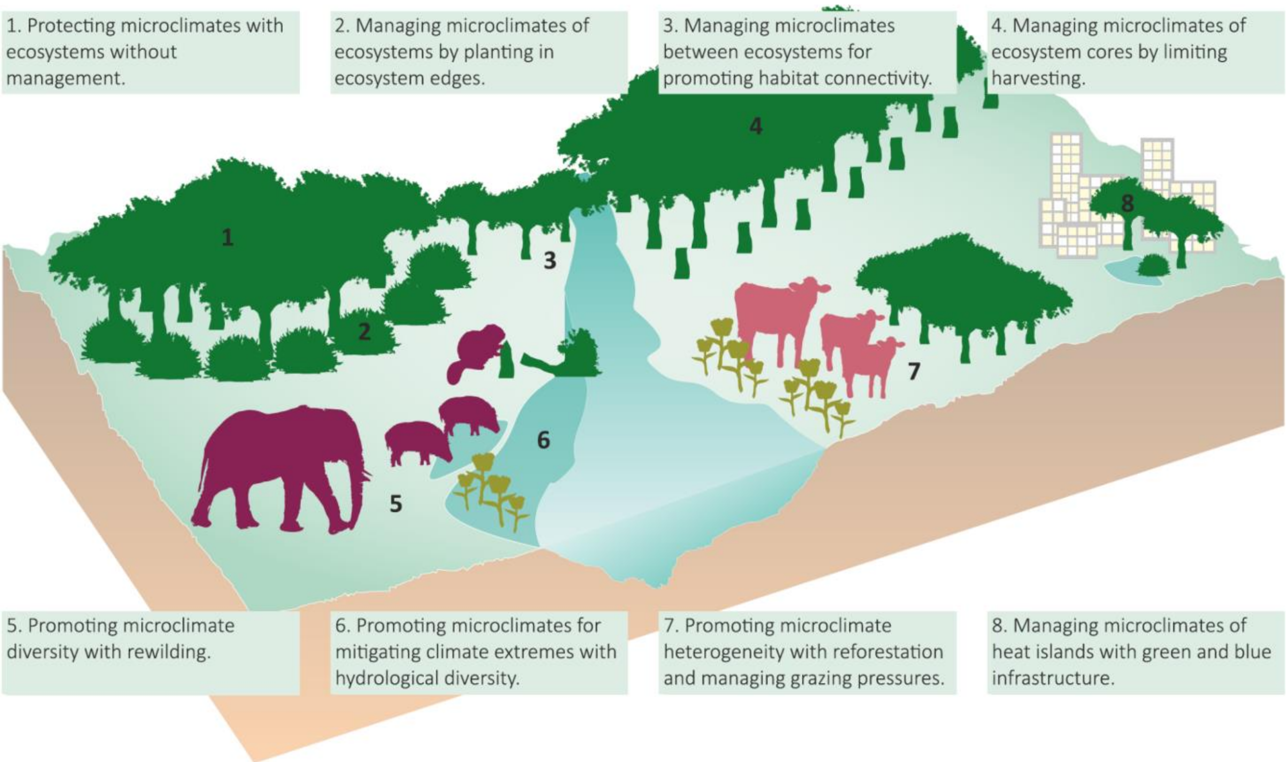


Figure 2. Microclimate applications in ecosystem management. The conceptual figure presents examples of biodiversity conservation, forestry, and urban ecology maintaining and promoting microclimate heterogeneity for the benefit of biodiversity.

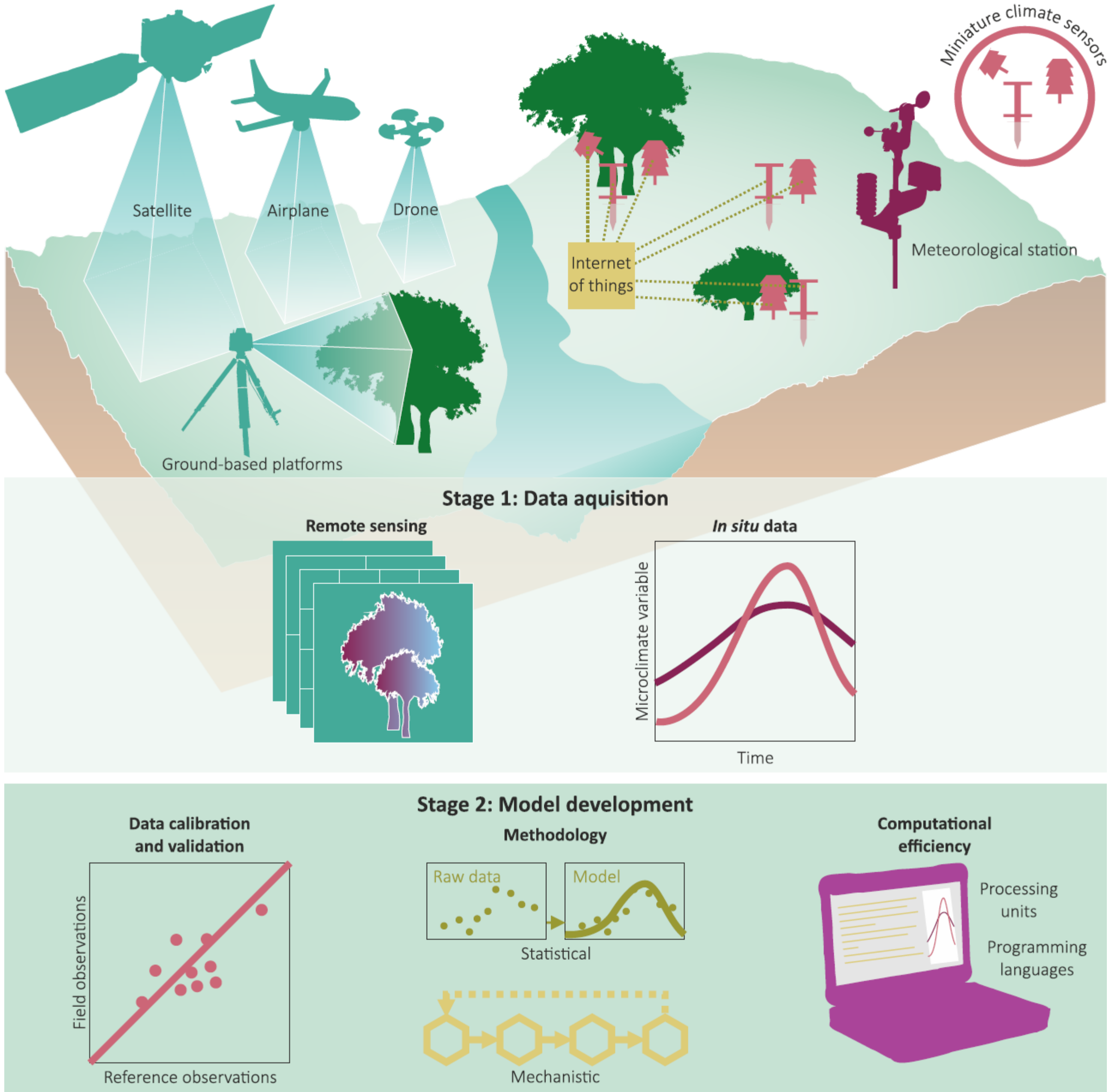
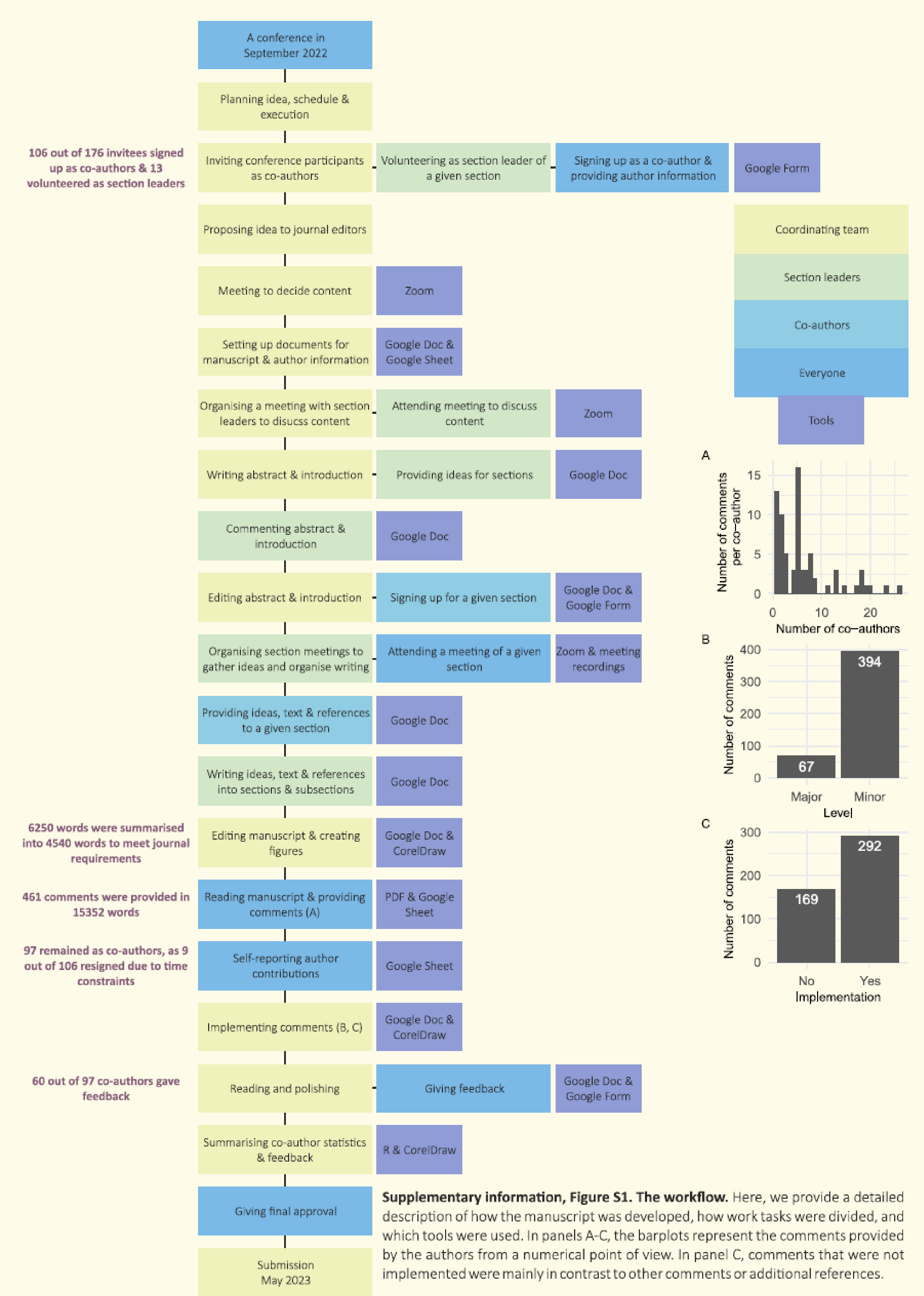
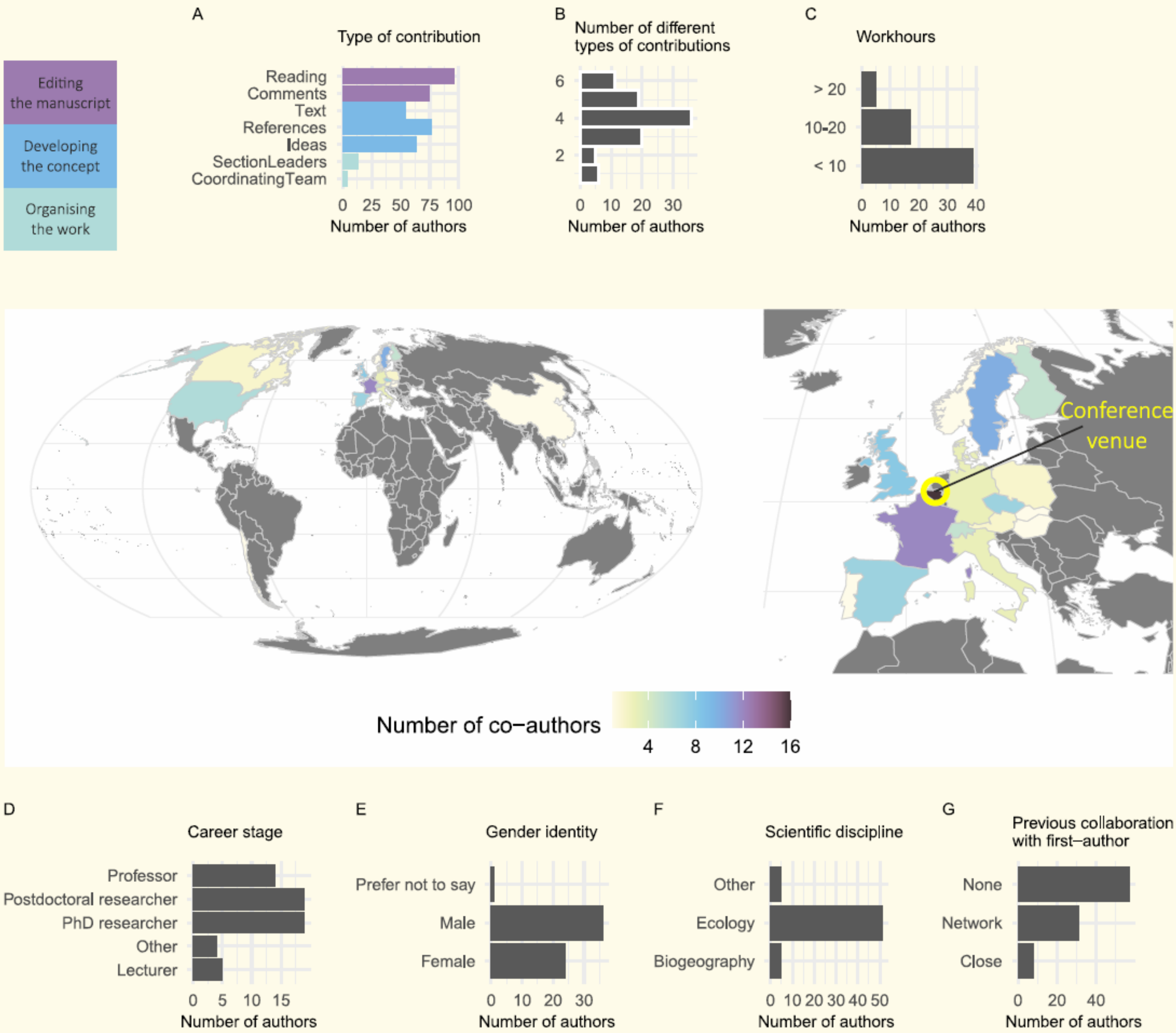


Figure 3. Methods for microclimate science. This conceptual figure presents examples discussed in the main text on how microclimate data and its explanatory variables are acquired from remotely-sensed products and *in situ* measurements (Stage 1). We show examples of key areas where microclimate models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

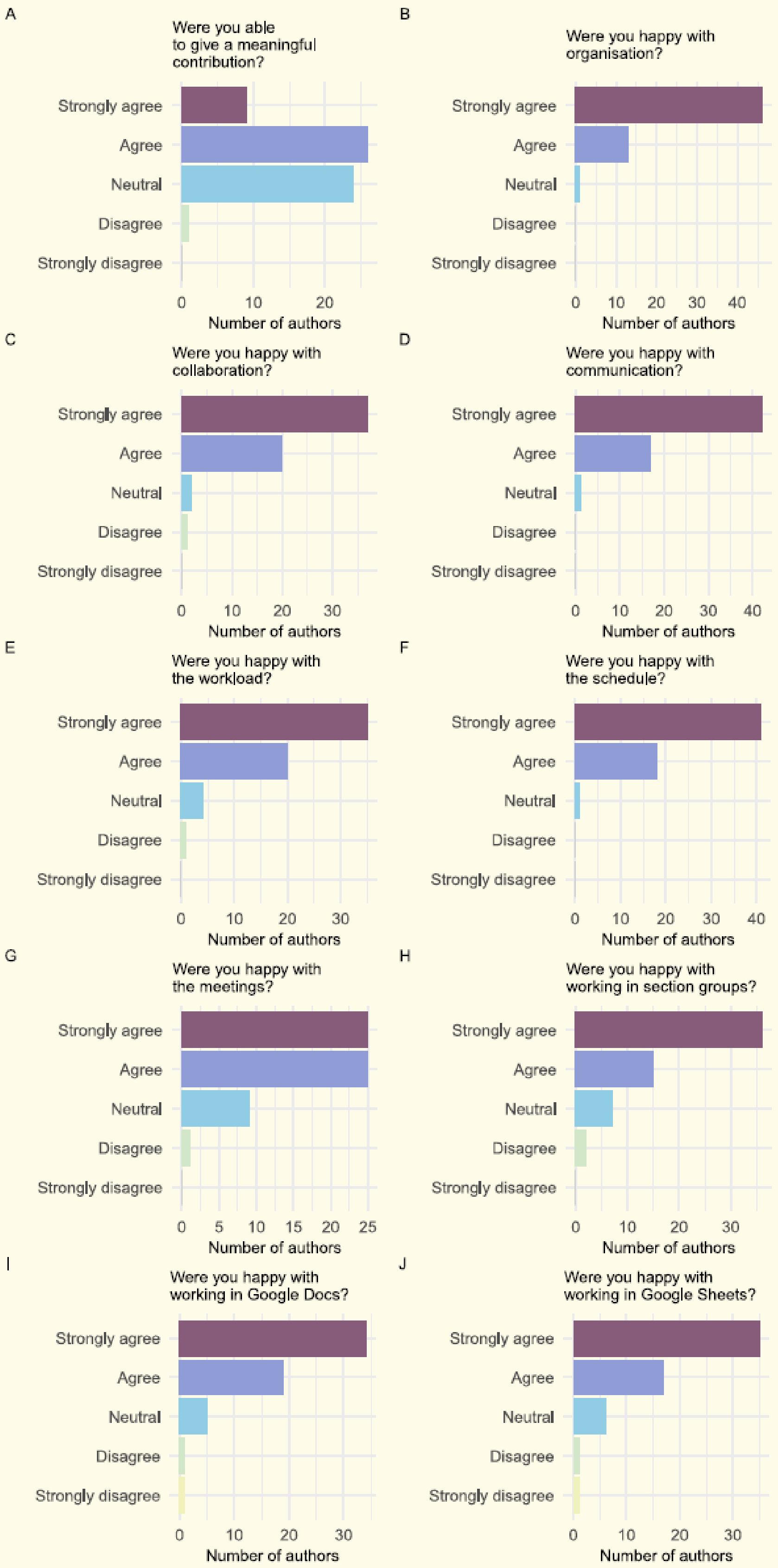
Supporting information



Supplementary information, Figure S1. The workflow. Here, we provide a detailed description of how the manuscript was developed, how work tasks were divided, and which tools were used. In panels A-C, the barplots represent the comments provided by the authors from a numerical point of view. In panel C, comments that were not implemented were mainly in contrast to other comments or additional references.



Supplementary information, Figure S2. The author demographics. Here, we provide background information on the authors of the manuscript. In panels A-B, the barplots represent how contributions were distributed among authors. The maps present the geographical distribution of the authors' institutions. Here, the yellow circle represents the location of the conference that initiated the manuscript. In panel G, the barplot represents collaborations with the first-author prior to the manuscript. Here, "Network" refers to collaboration via network publications, and "Close" refers to collaboration via other publications and projects. Note that 61 out of 97 authors gave information presented in panels C-F.



Supplementary information, Figure S3. Anonymous feedback from authors. Here, we provide a summary of the anonymously given feedback from the authors. In panels A-J, the barplots represent answers to the given questions. Note that 60 out of 97 authors gave feedback.

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