Forest microclimates and climate change: importance, drivers and future research agenda

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Running title: Microclimates in forests

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Abstract

Forest microclimates contrast strongly with the climate outside forests. To fully understand and better predict how forests' biodiversity and functions relate to climate and climate change, microclimates need to be integrated into ecological research. Despite the potentially broad impact of microclimates on the response of forest ecosystems to global change, our understanding of how microclimates within and below tree canopies modulate biotic responses to global change at the species, community and ecosystem level is still limited. Here we review how spatial and temporal variation in forest microclimates results from an interplay of forest features, local water balance, topography and landscape composition. We first stress and exemplify the importance of considering forest microclimates to understand variation in biodiversity and ecosystem functions across forest landscapes. Next, we explain how macroclimate warming (of the free atmosphere) can affect microclimates, and vice versa, via interactions with land-use changes across different biomes. Finally, we perform a priority ranking of future research avenues at the interface of microclimate ecology and global change biology, with a specific focus on three key themes: (1) disentangling the abiotic and biotic drivers and feedbacks of forest microclimates; (2) global and regional mapping and predictions of forest microclimates; and (3) the impacts of microclimate on forest biodiversity and ecosystem functioning in the face of climate change. The availability of microclimatic data will significantly increase in the coming decades, characterizing climate variability at unprecedented spatial and temporal scales relevant to biological processes in forests. This will revolutionize our understanding of the dynamics, drivers and implications of forest microclimates on biodiversity and ecological functions, and the impacts of global changes. In order to support the sustainable use of forests and to secure their biodiversity and ecosystem services for future generations, microclimates cannot be ignored.

Keywords: biodiversity, buffering, climate change, ecosystem function, forest, future research, microclimate, offset

Introduction: the importance of forest microclimates

Forest organisms living below or within tree canopies experience distinct climatic conditions that deviate considerably from the climate outside forests (Chen et al. 1999; Geiger et al. 2009; De Frenne et al. 2019). Below forest canopies, direct sunlight and wind speed are strongly reduced, leading to a dampening of temperature and humidity variations. Temperature extremes are often strongly buffered in forests compared to open habitats, with cooler below-canopy maximum temperatures, warmer minimum temperatures, and lower seasonal and interannual variability (Ewers & Banks-Leite, 2013; von Arx et al. 2013, De Frenne et al. 2019) (see Fig. 1 and Box 1 for the definitions of technical terms used in this paper). The magnitude of such positive and negative temperature differences or offsets between open lands and forest interiors can vary due to the structure of the forest, ambient temperatures and the local water balance (McLaughlin et al. 2017; Davis et al. 2019; De Frenne et al. 2019). Moreover, the structural complexity of forests creates heterogeneous microclimates at a fine spatiotemporal scale.

The physiological and ecological importance of forest microclimates has long been recognized (Grubb, 1977; Geiger et al. 2009, a book with a first edition already published in 1927). Forests harbor the majority of terrestrial biodiversity, and, due to the increasing impacts of current macroclimate warming on biodiversity, studies on forest microclimates are receiving much attention in global change biology (Fig. 2). However, most studies on forest biodiversity rely on gridded macroclimate data that are based on free-air temperature data from weather stations in open areas outside forests, thus neglecting forest microclimate variation in space and over time (Potter et al. 2013; Barry & Blanken, 2016; De Frenne & Verheyen, 2015). This discrepancy of spatiotemporal scales of forest microclimate data may bias the quantification of climate change impacts on forest biodiversity and functioning (Zellweger et al. 2020). Addressing and correcting for these biases is a fundamental task for global change biologists, land managers, and policy makers alike (MEA, 2005; Landuyt et al. 2019; IPBES, 2020).

Viewing forest ecology through a microclimate lens can help tease out mechanistic relationships of organisms with their environment. Buffered forest microclimates and the myriad of microhabitats available within forests (e.g., root caverns, tree holes, fallen trunks) enable organisms to avoid extreme heat and drought (Kearney et al. 2009; Scheffers et al. 2013a, 2014b). The microclimate buffering capacity of forests may provide climatic microrefugia during macroclimate warming (Ewers and Banks-Leite, 2013; von Arx et al. 2013, Lenoir et al. 2017, De Frenne et al. 2019). Therefore, the pressure on individuals, populations, species and communities to respond to rapid anthropogenic climate change may be reduced, at least in the short term, by the presence of climatic microrefugia for cold-adapted organisms (Keppel et al. 2012; Ashcroft et al. 2012; Hampe & Jump, 2011; Lenoir et al. 2017; Greiser et al. 2019). Through these mechanisms, forest microclimates can determine the distribution of individuals, populations, and species. Thus, incorporating microclimates into species distribution models is expected to significantly improve the accuracy of predictions (Slavich et al. 2014; Lembrechts et al. 2019; Zellweger et al. 2019b). The forest microclimate is also a driver of species interactions. Low light availability and heterogeneous moisture can enhance plant competition (Connell, 1983; Gerhardt, 1996), although microclimates can also facilitate co-existence, such as when shade offers refuge to mixed-species seedling assemblages (Holmgren et al. 1997), or when centipedes share epiphytic ferns as cool and moist nest sites (Phillips et al. 2020). In some cases, species interactions can result in a re-engineering of the microclimate environment itself, for example canopy gaps produced by leaf-cutter ant herbivory (Swanson et al. 2019). Microclimate therefore shapes – and in turn, is shaped by – the composition of forest communities (Parker, 1995; Woods et al. 2015; Frey et al. 2016a, Jucker et al. 2018).

At the ecosystem level, microclimate is of paramount importance as a key regulator of many ecosystem functions. Rates of litter decomposition, carbon sequestration and microbial activity tend to be greater in forests than in neighbouring open habitats (Riutta et al. 2012; Wang et al. 2010; Chen et al. 2018, but see

Köchy & Wilson, 1997), and also vary spatially within forests due to, among other things, gap dynamics (Zhang & Zak, 1995). Tree recruitment, via seedling growth and sapling survival, is heavily contingent upon microclimatic conditions (Aussenac 2000; Campanello et al. 2007; Harper & White, 1974). While some forest tree species regenerate best after disturbances and canopy opening, others recruit under the canopy. In such cases, understorey conditions shaped by trees in the overstorey eventually feedback to tree recruitment and future forest structure. Therefore, threats to forest biodiversity and functioning from deforestation, forest degradation, and fragmentation are inherently linked to the loss and modification of forest microclimates by these activities (Chen et al. 1999; Jucker et al. 2020; Laurance et al. 2011).

Despite the potentially broad impact of microclimates on the response of forest ecosystems to global change, our understanding of how forest microclimates modulate biotic responses to climate warming and land use change at the species, community and ecosystem level is still limited. However, ecologists are increasingly making progress in filling this major research gap. This development is expected to benefit substantially from recent advances in modelling, remote sensing and mapping of forest microclimates (Greiser et al. 2018; Jucker et al. 2018; Zellweger et al. 2019b). Here, considering the growing interest and recent advances in microclimatology, we provide a summary of where the field currently is, and where it is heading. To do so, we review the known drivers, processes and ecological importance of forest microclimates in current and future macroclimates, and layout future research directions for this emerging field of research. Our structure for this review is premised on drawing contrasts between forests vs. open habitats in tropical, temperate and boreal biomes. We discuss the physical mechanisms driving forest microclimates, present an organism's perspective on microclimates, review the effects of microclimate on biodiversity and ecosystem functioning, and discuss how and when microclimates feedback to macroclimate warming. We end with a future research agenda for forest microclimates, focused on: (1) forest microclimate feedbacks; (2) forest microclimate mapping; and (3) microclimate impacts on forest biodiversity and ecosystem functioning.

Drivers of vertical and horizontal microclimate variation

Horizontal distribution of microclimates: forest vs open habitats

The horizontal distribution of microclimates within forests and open habitats is driven by vegetation, topography, soil, the water balance, prevailing meteorological conditions, and their interactions (Geiger et al. 2009, Lembrechts et al. 2020a). Perhaps the most evident characteristic of forest microclimates is that the understorey is buffered against macroclimate temperature extremes (Fig 1). During clear and warm days, much of the incoming shortwave solar radiation is absorbed and reflected by the canopy, which, together with increased evapotranspirative cooling, leads to a cooling of the understorey maximum temperature by a global mean of 4.1°C compared to open-field conditions (De Frenne et al. 2019). On the other hand, minimum temperatures of forest understories are on average 1°C warmer, mainly as a result of understorey heat retention, for instance at night, through shielding of the outgoing longwave radiation by the canopy (Geiger et al. 2009; De Frenne et al. 2019).

Evaporative cooling and emitted longwave radiation both act to reduce canopy and soil surface temperatures whereas net shortwave radiation acts to warm the soil and canopy surfaces (Geiger et al. 2009; De Frenne et al. 2013). Heat exchange between surfaces and air may contribute to warming or cooling depending on their temperature difference as well as wind speed (Huang et al. 2015) and the local and regional hydroclimatic conditions (Dobrowski 2011; von Arx et al. 2013). Indeed, the short and long-term availability of soil water and atmospheric moisture shape canopy cover and control evapotranspiration, therefore influencing the buffering of maximum understorey temperatures in complex ways (e.g. von Arx et al. 2013; McLaughlin et al. 2017; Davis et al. 2019). Vegetation structure and composition affect heat exchange and cause horizontal variation in the buffering of ambient temperatures (Fig. 3). In particular, vegetation density (e.g., in terms of canopy cover, basal area, plant area index) via effects on albedo, evapotranspiration and radiation absorption have strong influences on understorey microclimate, especially during the warm season (Greiser et al. 2018, Zellweger et al. 2019a). The cooling effect by evapotranspiration will, however, diminish under cold or water-limited conditions and is a function of water vapour deficit (under near-saturated conditions of high relative air humidity, the cooling effect of evapotranspiration reduces) (Davis et al. 2019). In highly seasonal climates, the vertical and horizontal composition and distribution of forest canopies (e.g., gaps, tree age distribution, leaf clumping, distance to forest edge) directly affect the amount and variability of sunlight (Sprugel et al. 2009; Valladares & Guzman, 2006). At the stand level, small-scale variations in sun-flecks cause strong gradients in near-ground temperatures and there are often strong microclimatic gradients towards forest edges, due to increased solar radiation and wind (Matlack, 1993). Microclimate gradients from forest core to edge can be very large and penetrate deeply (up to 100 m) into the forest matrix (Schmidt et al. 2017) depending on the microclimatic variables (e.g., light, wind, temperature), the edge orientation (Hylander, 2005), the cloudiness (e.g., Chen et al. 1993), the slope of the terrain or the wind direction (Davies-Colley et al. 2000) and even the biome (e.g., tropical vs temperate forests) (Ewers & Banks-Leite 2013; Schmidt et al. 2017).

This horizontal distribution in microclimate buffering varies not only at the stand scale, but also at landscape, continental and global scales. The effects of landscape topography on near-ground temperatures can be attributed to variations in incoming solar radiation driven by slope and aspect, pooling of cold air in depressions and exposure to winds, variations in soil moisture, and the adiabatic lapse rate due to elevational gradients, all of which have been well documented (Ashcroft et al. 2008; Dobrowski, 2011; Aalto et al. 2017; Meineri & Hylander 2017; Bramer et al. 2018; Davis et al. 2019). At the continental scale, air-mixing and lateral heat transfer by wind decrease when moving further away from the coast and mountain chains, which, together with fewer cloudy days, commonly leads to larger magnitudes of the temperature offsets in continental lowland forests (Zellweger et al. 2019a). Moreover, regional precipitation patterns and the size and adjacency to water bodies influence latent and sensible heat fluxes (Meleason & Quinn, 2004; Zellweger et al. 2019a). At the global scale, the largest buffering of maximum temperatures is found in tropical forests, whereas buffering of cold extremes is largest in boreal forests (De Frenne et al. 2019), due to differences in forest structure, solar radiation, seasonality and snow cover. Therefore, drivers of forest microclimates differ across latitudes (Fig. 3).

Vertical distribution of microclimates: from the ground to the top of the canopy

In open areas, air temperature at 1-2 m above ground is mostly controlled by local topography, radiation balance and turbulent mixing of air. Inside forests, however, canopy elements interfere with these processes by influencing radiation fluxes into and out of the forest as well as decreasing turbulent mixing of air through decreased wind speeds (Chen et al. 1993; Chen et al. 1999). Vertical temperature gradients inside forests are the result of a complexity of microclimatic layers, formed and controlled in large part by the vegetation itself (Fig. 4; Vanwalleghem et al. 2009; Davies-Colley et al. 2000). Forest management can influence the vertical structure of the vegetation with implications on the vertical microclimate profile (Onaindia et al. 2004).

Air temperature differences between ground and canopy range from 0.15 to 0.25 °C m^{-1} in temperate coniferous and mixed hardwood–conifer and tropical forests (Harley et al. 1996; Zweifel et al. 2002; Hardwick et al. 2015; Bauerle et al. 2009). During the day, air temperature peaks can occur near the ground, but are most often located within the top canopy, where most of the incoming energy is absorbed (Chen et al. 1999; Didham & Ewers, 2014) (Fig. 4). The exact vertical location of air temperature maxima will depend on the density of the canopy (leaf and plant area index as a function of height) and on the intensity of turbulent air mixing (Fig. 4). However, even when understorey air is cooler than above-canopy air, leaf and litter temperatures can rise well above the local air temperature in the understorey of open forests, due to decreased wind speeds and absorption of shortwave radiation (Martin et al. 1999; Scheffers et al. 2017).

Leuzinger & Körner (2007) showed that leaf temperature regimes in canopies vary enormously over short vertical distances in several coniferous and deciduous broad-leaved tree species. Finally, snow cover in the winter will effectively decouple the near ground temperature from the temperature above the snow (Fig. 1).

Consequences of microclimates for forest biodiversity

Microclimates influence an organism's physiology, activity patterns, behaviour, and fitness. In general, by virtue of the differences in their size, mobility and lifespan, organisms respond differently to microclimate conditions with respect to their life cycle processes. In other words, the "power of resolution" of organisms is inversely proportional to their living space (Carlile et al. 1989; Decocq, 2000), so that the abundance and diversity of smaller, short-lived, and less mobile organisms often more readily reflect the small-scale variations in micro-environmental conditions. As such, the consequences of microclimates on biodiversity are scale-dependent, with the scale of operation of an organism, population, or community matching the scale of climate exposure.

Although microclimate research aims to match the scale of climate and organisms, the concept of microclimate describes a spectrum of spatiotemporal scales (from centimetres to several hundred metres, from hours to years); i.e., perception of "micro" by woodlice is different from an elephant's perception of "micro" (Weins, 1989, Lembrechts et al. 2020b). However, an interesting aspect in forests is that the trees that modify the understorey microclimate have been small in the beginning of their life cycle. This illustrates that the same individual might respond to climate at different scales across its life stages, but also how forest microclimates can be created by reinforcing feedback mechanisms. Bearing this in mind, we here describe the influence of microclimate on biodiversity across space and time.

Spatial impacts of forest microclimate on biodiversity

At the meso- to macroscale, niche partitioning occurs horizontally and vertically in ecotones, whereby plant, animal, fungal, and bacterial community turnover take place from one ecosystem to another (e.g., wet rainforests to dry woodlands) or across elevational gradients (e.g., Yuan et al. 2018). At the microscale, organisms are also distributed horizontally (e.g., from a tree fall gap to closed canopy) and vertically (e.g., from the ground up to the canopy), following their environmental preferences, or niches. Vertical stratification of animal and plant communities is a prime example of how habitat and climate interact to derive localized partitioning of niches (Nakamura et al. 2017), which includes a broad suite of organisms such as epiphytes, wasps, beetles, moths, amphibians, birds and mammals (for a vertical gradient of moths in forests, see De Smedt et al. 2019). Species have also been shown to shift their locations in response to changes in the spatial gradients of microclimates. For example, frogs of the Philippines shift their vertical niche upwards towards the canopy at higher elevations as microclimates become more favourable (Scheffers et al. 2013b) and canopy epiphytes grow much further down when trees grow sparse (Hylander & Nemomissa, 2009). Birds in western North America and moose in Finland respond to changes in microclimate by shifting their horizontal distribution (Melin et al. 2014; Frey et al. 2016b). Warm-edge populations of boreal understorey plants inhabit sites with more stable microclimates, cooler maximum temperatures and later snowmelt (Greiser et al. 2019). The performance and distribution of forest lichens and bryophytes often show clear patterns along local temperature and moisture gradients (Hylander, 2005; Stewart & Mallik, 2006; Åström et al. 2007; Gauslaa, 2014; Löbel et al. 2018). Notably, the influence of microclimates on local species diversity can be so strong that entire amphibian communities can abruptly change across a microclimate gradient spanning just a few metres (Basham & Scheffers, 2019; Basham et al. 2020).

Temporal impacts of forest microclimate on biodiversity

Organisms also partition their niches according to microclimates in time (Jonason et al. 2014). Daily cycles of organism activity are apparent in Lepidopterans, with butterflies primarily active during the day and moths active at night. However, activity can also vary within the day, with activity peaks adapted to the actual temperature and dependent on species' thermal limits (Wikström et al. 2009), a threshold that differs spatially from open habitats to closed forests (Xing et al. 2016). Similarly, leaf litter lizards will exploit sunspots or rare microclimates for thermoregulation, but only during cold morning hours (Nordberg & Schwarzkopf, 2019). Here, lizard activity varies with thermal heterogeneity driven both in time and by topographic roughness and aspect (Sears et al. 2016). The dispersal mechanism of a moss is suggested to be most effective in morning hours when the moisture decreases along with increasing temperatures and wind (Johansson et al. 2016). At a weekly or monthly scale, weather patterns strongly influence small mammal habitat use and activity (Vickery & Rivest, 1992). Seasonal shifts in activity are apparent with regional and local climates. For example, arboreal frog communities shift from being highly vertically stratified in the tree canopies during the cooler, wet season to dramatically accumulating in the understorey during the hotter, dry season (Basham & Scheffers, 2019).

Consequences of microclimates on forest functioning

Microclimates strongly influence soil decomposition, primary productivity, plant communities and forest density, which further influences groundwater and carbon sequestration – via its influence on soil dynamics. For example, forest edge to interior climatic gradients are primary drivers of carbon storage and cycling (Laurance 2004; Uriarte et al. 2016; Meeussen et al. 2021). In temperate forests, carbon stocks are on average higher at the edge than in forest interiors (Meeussen et al. 2021). By contrast, in the tropics forest fragmentation generally leads to a loss of aboveground carbon stocks due to drier and warmer conditions at forest edges (Silva Junior et al. 2020). One might argue that microclimates, which dictate localized processes such as decomposition, scale up to ecosystem functioning indirectly via species interactions (Petraglia et al. 2019) or bottom-up processes to which species respond. For example, changes in understorey microclimate due to changed overstorey composition affect the herb layer composition as well as soil conditions (Decocq et al. 2005). Sometimes the ecosystem functions are maintained, despite changed microclimates. A Bornean tropical rainforest was shown to exhibit functional resilience after heavy logging, with different taxa taking over ecosystem processes such as litter decomposition and seed predation (Ewers et al. 2015). Research on the mechanisms of how changes of microscale processes scale up to ecosystems remains largely theoretical. It can be expected that the collective contribution of temperature offsets provided by forest structure simultaneously impacts many aspects of ecosystem functioning. Yet, no studies exist to our knowledge that collectively assess several ecosystem processes simultaneously, which is likely due to the enormous empirical information required for such inference to be made (see also our research agenda below).

How will macroclimate warming affect forest microclimates?

How macroclimate warming affects forest microclimate dynamics, and vice versa, remains an open question (Lenoir et al. 2017; De Frenne et al. 2019). For instance, it is unclear whether the magnitude of temperature offset between macroclimate and forest microclimates (De Frenne et al. 2019) will remain stable, increase or decrease over time as macroclimate warms. As discussed previously, the magnitude of the temperature offset between forests and open habitats depends on ambient, macroclimatic conditions: forest offsets of maximum temperatures increase with ambient temperatures as long as local water availability does not constrain evaporation and evapotranspiration (Davis et al. 2019; De Frenne et al. 2019; Su et al. 2020; Zhang et al. 2020). Assuming a space-for-time substitution, this suggests that the magnitude of the offset on maximum temperature could potentially increase under macroclimate warming (Fig. 1 and Fig. 5). This assumption only holds if: (i) the relationship between offsets and macroclimate continues to be linear; (ii) the forest canopy layer is not disturbed; (iii) we consider that the equilibrium point at which temperatures inside and outside forests are the same (cf. Fig. 1), does not shift; and (iv) other variables such as soil moisture levels remain comparable (Scheffers et al. 2014b; Zellweger et al. 2020). Slow, interannual climate change can, however, directly change the equilibrium point, while changes in canopy cover, moisture, etc. could directly act on the buffering and hence slope (Fig. 1). In particular, the future buffering capacity will be highly contingent upon changes in hydrological conditions, which not only directly influence vegetation structure, but also constrain evaporative cooling (von Arx et al. 2013; McLaughlin et al. 2017; Davis et al. 2019). Indeed, temperature offsets are larger when ambient temperature is higher because vapour pressure deficit (VPD) and evapotranspiration increase non-linearly with temperature. The differential between forested and non-forested sites is thus amplified at higher temperatures when water is non-limiting in the system (e.g., in tropical rain forests) and can continue to flow throughout trees, thus amplifying the cooling effect of the forest canopy. As a consequence, if macroclimatic increases in daily maximum temperatures can be buffered, it might provide forest organisms with more time for adaptation and migration (Zellweger et al. 2020). This phenomenon is comparable to the concept of microrefugia (that is, spatially-restricted habitats that sustain a favourable microclimate, which enables species to persist in an otherwise inhospitable matrix; Gavin et al. 2014). The pattern is opposite for minimum temperatures: higher ambient air temperatures decrease minimum temperature offsets (De Frenne et al. 2019). Hence, still under the assumptions of a space-for-time substitution, the magnitude of the offset in minimum temperature could potentially decrease under macroclimate warming, contributing to reduce the buffering effect on minimum temperature (Fig. 5). In the following subsections, we first discuss changes in forest microclimate dynamics due to macroclimate warming in different forest biomes, and then the potential impacts of macroclimate warming on future offsets before highlighting potential feedbacks on macroclimate warming.

Biome-specific effects on temperature offsets (Fig. 5)

In temperate forests, temperature buffering may happen for both maximum and minimum temperatures (De Frenne et al. 2019). Yet, during the cold season, deciduous trees shed their leaves, the primary drivers of buffering, making buffering in temperate forests likely to be more important and relevant during the growing season. Additionally, Zellweger et al. (2019a) showed that the magnitude of the thermal offset during the summer season in European temperate forests was more pronounced for daily maximum temperatures than for daily minimum temperatures. As a consequence, canopy cover density directly affects buffering capacity, with likely implications on organismal responses to climate change. For example, the thermophilisation rate – the rate of community shift towards more warm-adapted species – in understorey plant communities of temperate forests is better related to the rate at which the daily maximum temperature changes in forest interiors (i.e. the rate of microclimate warming) during the growing season than the rate of macroclimate warming (Zellweger et al. 2020). In boreal forests, buffering of minimum temperatures is most pronounced, while tropical rain forests, where water is non-limiting, have more pronounced offsets of maximum temperatures, likely due to the non-linear contribution of evapotranspiration (De Frenne et al. 2019). Although the velocity of macroclimate warming is highest at high latitudes, tropical species might also be severely impacted due to their narrow thermal niches and safety margins, particularly when high elevation refuges are not present and given the shallowness of latitudinal temperature gradients in the tropics (Tewksbury et al. 2008; Antão et al. 2020; Lenoir et al. 2020). Worryingly, daily maximum temperatures in the next decades will likely be more extreme than what tropical species have ever experienced in their recent evolutionary history (Deutsch et al. 2008; Kingsolver, 2009).

Macroclimate warming effects on temperature offsets

In their review covering the second half of the 20th century, Boisvenue & Running (2006) reported that both satellite and ground-based data support an increase in forest productivity across many temperate parts of the globe owing to climate warming. Hence, at temperate latitudes, forests with ample water and soil nutrients may become denser, thereby increasing temperate forest offsets (Zellweger et al. 2020). On the other hand, recent reports show cross-European canopy opening due to an increase in natural and anthropogenic disturbances (Senf & Seidl, 2020) and thus a potential reduction in temperature offset. And finally, as macroclimate warms, earlier timing of bud burst and leaf flush will impact the seasonal course of forest microclimates, potentially leading to phenological mismatches between trees and understorey species (Heberling et al. 2019). Earlier leaf flush might effectively shorten the growing season for understorey plants, if shade levels are enhanced earlier in the season and the temperature sensitivity of phenological advances of wildflowers is lower than trees (Heberling et al. 2019).

In the tropics, satellite-driven measures of vegetation greenness (normalized difference vegetation index, NDVI), a surrogate for photosynthetic activity and productivity, show reduced productivity in warmer years (Braswell et al. 1997; Asner et al. 2000), suggesting a reduced future buffering capacity. Conversely, in boreal forests, the impact of changes in primary productivity on the buffering capacity of forests is less clear. On the one hand, old growth boreal forests in North America showed no net increase in stem growth (Giguère-Croteau et al. 2018). On the other hand, Beck et al. (2011) have reported changes in forest productivity across Alaska that are consistent with a complete biome shift: decreased productivity at the warmer (southern) versus enhanced productivity at the colder (northern) edge of the boreal biome. If the buffering capacity of boreal forests mirrors the climatically-induced changes in primary productivity, the magnitude of the maximum temperature offsets may decrease and increase towards the warmer and colder edge of the boreal zone, respectively.

Extreme event effects on temperature offsets

The current and future increase in daily maximum temperatures during the warm season will in many areas lead to more intense, more frequent and persistent heat waves (Meehl & Tebaldi, 2004; Russo et al. 2015). Therefore, some temperate forests are becoming increasingly water-limited during the summer season, reducing evaporative cooling, generating drought stress and inducing physiological constraints in trees that make them more susceptible to pests (Trumbore et al. 2015). This combination of stressors may ultimately lead to widespread crown defoliation, tree mortality and higher risks of forest wildfires due to forest fuel accumulation (Abatzoglou & Williams, 2016; Allen et al. 2010, Trumbore et al. 2015). Davis et al. (2019) have predicted that some forests of the northwestern United States will lose their capacity to buffer extremes of maximum temperature and VPD due to changes in water balance combined with accelerating heat-induced canopy losses. A threshold in canopy cover of *c.* 75 % exists, below which buffering properties in temperate forests largely decrease (Zellweger et al. 2019a). Tree die-off causing canopy cover to drop below this threshold will thus severely reduce the degree to which forest microclimates and biodiversity will be buffered from climatic extremes. Additionally, wildfires and other disturbances such as forest management can accelerate these processes as well (Davis et al. 2019; Senf & Seidl, 2020).

Interactions between human land-use and macroclimate warming

Forest microclimates can be heavily influenced by management practices and policies that change the canopy composition and structure at the stand level and the spatial arrangement of stands across landscapes (Frey et al. 2016a,b; Greiser et al. 2018; Jucker et al. 2018). Forest management activities that have the potential to affect microclimate include the management system (such as shelterwood, single-tree selection, clear-cutting, thinning and tending), choice of tree species (and making a deliberate choice on their shade casting ability, for instance), regeneration type (natural vs artificial such as tree planting or sowing), fertilization, rotation length, presence of a shrub layer, control of large herbivores, as well as the size and distribution of management units (Vanwalleghem & Meentemeyer, 2009; Brang et al. 2014; Latimer & Zuckerberg, 2017). Thus, depending on the type of management, forest managers can influence many aspects of the below-canopy microclimate, with important consequences for biodiversity and ecosystem processes (Selva et al. 2020).

In boreal forests, but possibly also in temperate and tropical forests, intensive forest management for timber and other woody biomass harvest has led to a biotic, genetic, structural and functional homogenization of forest stands across large spatial extents (Rousseau et al. 2019). The even aged single species stands typical of intensively managed forests and plantations have reduced the resilience of the whole system to, for instance, increasing frequency and severity of climate-induced pest outbreaks and wildfires (Cudmore et al. 2010; Gauthier et al. 2015). Although fires are part of the natural disturbance dynamics in many boreal systems, large stand-replacing wildfires have resulted in shrub proliferation and enhanced snow accumulation, with possible implications for longer periods of decoupled ground temperatures (Lantz et al. 2013; Aalto et al. 2018) (Fig. 1 and Fig. 5).

In the tropics, the combined effects of logging, droughts and fires on canopy loss (i.e., deforestation and degradation) can locally reduce air humidity (Staal et al. 2020) and increase daily maximum temperatures more than the warming associated with high emission scenarios (Senior et al. 2017). Hence, by letting in direct sunlight and warm and dry air, large canopy gaps following deforestation strongly alter understorey microclimate (Fig. 3 and 5), reducing the capacity to buffer macroclimatic fluctuations and thus causing many species to decline in abundance, e.g., termites that are especially sensitive to desiccation (Cornelius & Osbrink, 2010; see De Smedt et al. 2018 for a study from temperate forests). However, small canopy gaps (< 400 m^2) in tropical forests, which occur under natural forest dynamics, can regain their thermal environment in a few years (Mollinari et al. 2019), while secondary forests can regain their thermal environments within 20 – 30 years after logging (del Pliego et al 2016). These drastic changes in microclimatic conditions are not only due to tree removal, but at a finer resolution also to epiphyte loss. Indeed, epiphytes represent a significant functional group for microclimate dynamics in tropical forests, reducing water loss through evaporative drying (Scheffers et al. 2014b) and providing buffered microhabitats for canopy-dwelling organisms (Seidl et al. 2020) (Fig. 3, arrow K).

Forest microclimate feedbacks on macroclimate warming

Although we now have a better understanding of the impact of macroclimate warming on forest microclimate dynamics, the potential feedback of forest microclimates on macroclimate warming itself remains understudied (Barry & Blanken, 2016). Yet, the implications are important in mitigating and adapting to climate change. Changes in microclimates may feedback to the macroclimate by affecting localized water and carbon balances and microgradients of CO_2 within forests.

The release of water vapour into the atmosphere by trees through transpiration affects local as well as regional precipitation patterns (Bonan, 2008; Spracklen et al. 2012). For instance, in the tropics, air that pass over extensive areas of forests produces at least twice as much rain as air that passes over short or no vegetation (Spracklen et al. 2012). Regional tropical rainfall usually decreases (in quantity and frequency) after a threshold of 30 – 50 % deforestation, especially when large forest patches are cleared, while small clearings may actually enhance rainfall via triggering processes leading to cloud formation (Lawrence & Vandecar, 2015). The importance of vegetation in land-atmosphere-ocean feedback processes is remarkably illustrated by the last Sahara desertification episode (c. 5,000 yrs ago), when precipitation-vegetation feedbacks due to deforestation by humans are considered to have played a crucial role (Pausata et al. 2020). Studies on afforestation projects in the Saharan and Sahelian zones are limited to their role in mitigating the effects of warming by carbon drawdown, while their impacts on microclimates and potentially on macroclimatic feedback currently remain understudied (Pausata et al. 2020).

Another example with feedbacks between forest cover and climate is the poleward expansion of boreal forests, which decreases the albedo and thus the ratio of incoming and outgoing radiation (Bonan, 2008; Pearson et al. 2013), and increases snow depths, as a consequence of more shrubs, thus isolating the ground from deep frost during the winter leading to permafrost thaw (Lantz et al. 2013; Connon et al. 2018). The positive feedback on macroclimate warming is derived from permafrost thaw releasing stored carbon dioxide under aerobic conditions and methane under wet, anaerobic conditions (Fig. 5). This example links to the role of snow cover in decoupling the near-ground temperature from ambient temperatures and how forest structure moderates this (Fig. 1). However, in this example, shrubs act as accumulators of snow because strong winds in the tundra remove snow from open areas, while in many other situations the snow cover and thus the buffering of near-ground temperatures is higher in open than in forested sites (Fig. 1 and Fig. 5).

A research agenda and identification of research gaps

To identify current knowledge gaps and formulate a research agenda on forest microclimates, we followed an approach adapted from Sutherland et al. (2013). First, the authors of this paper submitted questions to the group via online forms, which were summarized and grouped. These updated questions were then presented and discussed with the co-authors followed by live voting at a joint physical meeting (Ekenäs, Sweden in Feb. 2020). From these voting results, we identified three key directions for future forest microclimate research as discussed below (Supporting Information Table S1).

1) Drivers of forest microclimate buffering and future changes

Major unknowns in the quantification of the relative importance of the drivers of below-canopy microclimates are related to: (1) abiotic changes in the environment (e.g., soil nutrient and spatiotemporal water availability); (2) biotic interactions (e.g., interactions with other species such as pollinators, pests or pathogens); and (3) how the contribution of both might change in the future as a result of anthropogenic global change. Concerning the latter, forest microclimates will indeed be affected by changes in the abiotic as well as biotic part of the environment (changes in hydrology, alteration of soil characteristics, urbanization, etc.), and we need to address the key uncertainties, especially with regard to interactions of climate change (both temperature and precipitation changes) with other global-change drivers such as land-use changes, changes in forest management or enhanced atmospheric inputs of nitrogen. Given the complexity of the effects of anthropogenic global change on biotic factors, they must be a key part of the future research agenda. These factors include forest age and structure (multistorey vs. monostorey), tree species composition and forest fragmentation, all of which are linked to forest management and global environmental change (mortality due to pests and pathogens, invasive species). Future research should therefore focus on how changes in the climate system and land use interactively affect forest structures and thus the microclimate buffering, magnitude of offsets and potential level of decoupling. Besides modelling studies, there is a place for empirical work such as manipulative experiments or comparative studies on how the magnitude of forest offsets change as a means of drought, N-fertilization, changed tree species composition, introduction of exotic species, etc. Land managers and policy makers could use this information to identify management regimes that maximize temperature buffering, to aim at optimal forest functioning and guide biodiversity conservation (Greiser et al. 2019).

2) Mapping and predictions of forest microclimates

While the mechanisms driving the buffering between forest microclimate and macroclimate, and other global-change drivers get disentangled, focus should also go towards the creation of (1) open-access, free-to-use, global gridded products of forest microclimate and (2) automated protocols for past and future microscale geospatial data (Zellweger et al. 2019b; Lembrechts et al. 2020a). This can, for example, be achieved by applying correction factors based on the offset between micro- and macroclimate to existing macroclimate maps (e.g., WorldClim and CHELSA) (Fig. 6). Further increases in the spatial resolution of such microclimate maps is possible thanks to the recent emergence of both large-scale global databases of in-situ measured (forest) microclimate (De Frenne et al. 2019; Lembrechts et al. 2020a) as well as ever-higher resolution remotely-sensed global forest cover products (down to 30 m resolution, and better). More methodological development is, however, needed to incorporate the vertical and temporal components of forest microclimate in these mapping efforts, as reliable and repeated info about 3D forest structure (e.g., using laser scanning) is only now becoming available, for instance via GEDI LiDAR data (https://gedi.umd.edu/). Obtaining accurate microclimate time series for forest understories (for the past, present and future) are further complicated by the interactions between climate change and land use changes, as discussed in the previous paragraph (Zellweger et al. 2020; Lembrecht & Nijs, 2020). Other important challenges are the dynamic nature of managed forest landscapes, how to incorporate wind effects in models of complex fragmented landscapes and, for global applications, the current computer power. Obtaining high-resolution long-term microclimate time series for the whole world requires effective assimilation of in-situ measurements, and mechanistic and statistical models. While existing mechanistic models of microclimate currently largely focus on open terrain (e.g., Maclean, 2020), this is a rapidly expanding field where workable solutions for forest microclimates can be expected in the near future. Complementing these models with in-situ measurements for calibration, and statistical models for global extrapolations, should be able to deliver the gridded projects we need (Lembrechts & Lenoir, 2020).

3) Impacts on biodiversity and ecosystem functioning in forests

In addition to characterizing the physiographic and biophysical processes that drive forest microclimates (Lenoir et al. 2017) (Figs. 3-5) as well as developing approaches for mapping microclimate at appropriate scales (Fig. 6), careful thought is needed on how to best integrate these new data streams into biodiversity research (Jucker et al. 2020). Access to climate data that better reflect local conditions experienced by living organisms should improve our ability to model species distributions and predict how they will respond to rapid global change (Mod et al. 2016; Lenoir et al. 2017; Lembrechts et al. 2019). However, few studies have actually tested this assumption (Lembrechts et al. 2019; Ohler et al. 2020), particularly in the context of forests (Frey et al. 2016a). A key question that remains to be addressed is at what spatial (horizontal and vertical) and temporal scale microclimate should be measured and modelled, and how this varies for different groups of species (e.g., in relation to body size, dispersal and thermoregulation, Potter et al. 2013; Scheffers et al. 2014a). Similarly, we also need to determine which aspects of microclimate best predict species distributions in forests (e.g., air temperature, humidity, soil moisture, solar radiation) and how to effectively summarize these metrics (e.g., means, extremes, fluctuations, thresholds, growing degree hours/days; Hylander et al. 2015; Bramer et al. 2018).

Empirical and modelling approaches that allow different facets of microclimate to be manipulated independently are crucial to addressing these questions (for an example to separate light and temperature effects, see De Frenne et al. 2015). Beyond the immediate need to better characterize how microclimate shapes current-day ecological processes in forests, a major challenge is to determine how long different types of forests can continue to act as microrefugia (also referred to as hold-outs in this context) for species in a warming world (Hannah et al. 2014). As global mean temperatures continue to rise, so too will those in forest understoreys (albeit slower if buffering is at play). But perhaps more importantly, long-term climate change in interaction with forest management will eventually lead to changes in the species composition and structure of forests (e.g., the number and size of trees, as well as canopy height and density) (Coomes et al. 2014; Albrich et al. 2020) – with clear cascading effects for understorey microclimate (Jucker et al. 2018). Very few studies have effectively evaluated ecosystem multifunctionality, and translated this to services, let alone relate it to microclimates (e.g., of the type suggested by Byrnes et al. 2014). Although policy documents abound with statements about climate change mitigation and adaptation, there is a lack of understanding about forest (micro)climate and biodiversity, which might lead to misguided actions (Selva et al. 2020). There are thus large knowledge gaps in biodiversity – ecosystem functioning – microclimate research. While these longer-term effects of climate change on forest microrefugia have been largely overlooked, a promising avenue for exploring them would be to integrate microclimate projections into forest dynamics models used to simulate forests under future conditions (Albrich et al. 2020).

Concluding remarks

In sum, we have outlined the contemporary research interests and gaps linking microclimatic variation to biodiversity and the functioning of forest ecosystems worldwide. The urgency is clear; compelling evidence is accumulating to suggest that, as long as the upper canopy layer remains unaffected, distinct below-canopy microclimatic conditions in forests arising from vertical and horizontal processes can mediate how organisms in the understorey experience macroclimate warming. However, even though the microclimatic changes in forests due to macroclimate warming may be smaller than those in other ecosystems, the ecological impact may be just as large if forest species have narrower niches and thus are more sensitive. Moreover, other global changes such as forest disturbance and widespread canopy opening (Senf & Seidl, 2020) might accelerate the effects of climate change in forests through their impact on microclimates. Our priority voting of important questions suggested that future forest microclimate research should focus on three overarching themes (drivers & global change, mapping & predictions, and biodiversity & ecosystem functioning). These themes reflect the wealth of fundamental research gaps that still exist in forest microclimate research. Recent studies highlighting the role of microclimate in helping to sustain local biodiversity and ecosystem functions have paved a way towards "microclimate forest restoration", or in other words, restoring forest ecosystems with the explicit purpose to increase their capacity to buffer the local microclimates from macroclimatic change. Such arguments are to date hardly considered in the pros and cons of the global tree restoration debate (e.g., Bastin et al. 2019). In tandem with the steadily increasing number of microclimate monitoring sites (Lembrechts et al. 2020a), novel microclimate modelling approaches have been developed (Maclean 2020). These crucial methodological advances are likely to encourage the use of microclimate data instead of settling for coarse-scale climate data of long-term average conditions. Once the global variation in forest microclimates is properly documented and analysed, more efforts should be placed in order to implement this information into further analyses of ecosystem functioning. Doing so is expected to greatly increase our understanding of the impacts of climate change on forest ecosystems. Although the importance of microclimate in regulating many biophysical processes has been acknowledged by ecologists and biologists for nearly a century, we are finally stepping into an era where we have a solid conceptual and methodological foundation for testing many fundamental research questions related to forest functioning. This is important, as a better understanding of the magnitude, drivers and implications of forest microclimate on biodiversity is urgently required in order to better manage forests, support their sustainable use and secure viable ecosystem services for future generations in a warmer climate. Microclimates should be considered as an ecosystem service in itself.

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Figure captions

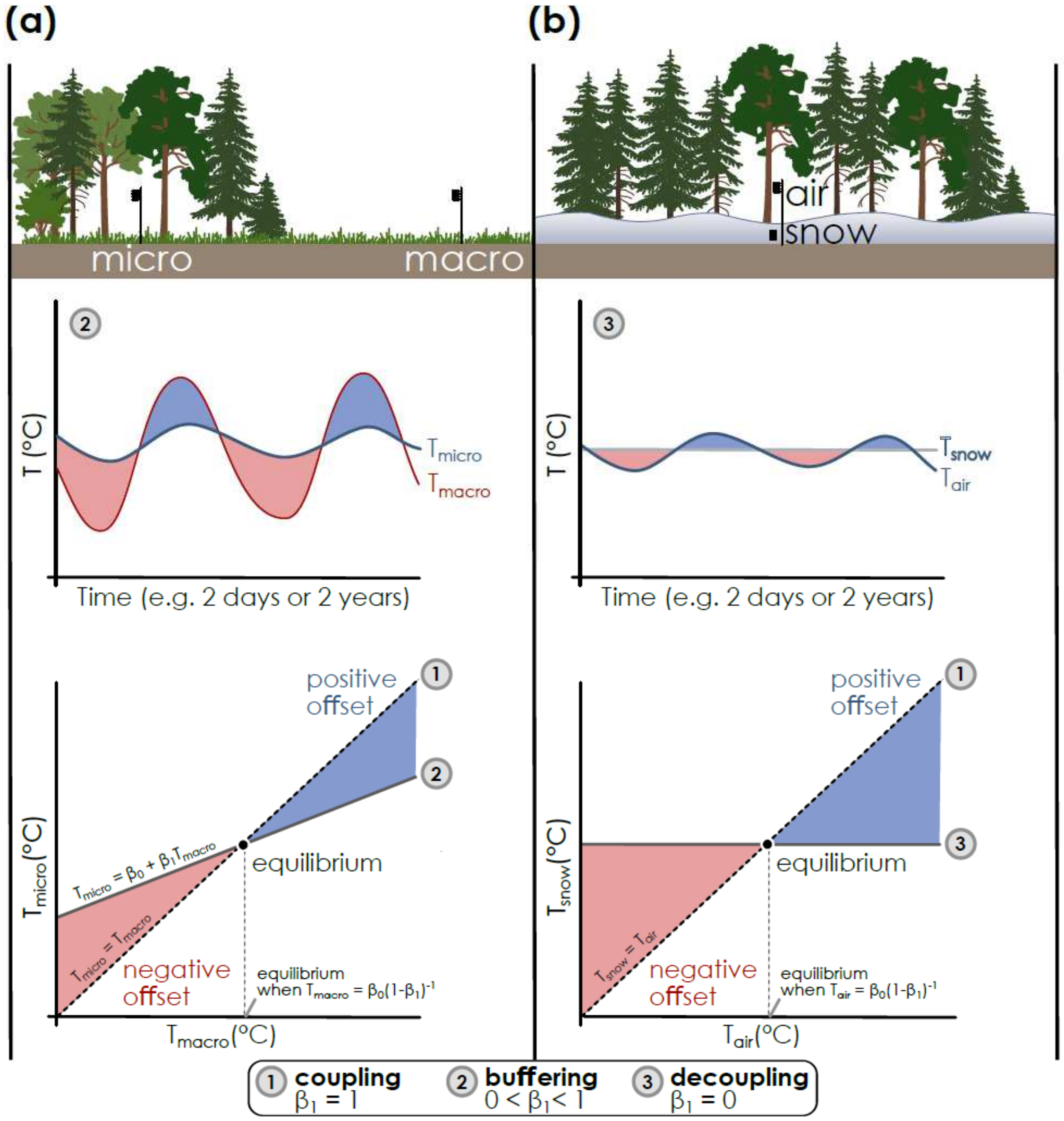

Fig. 1. Definitions of the main processes underlying microclimate dynamics in the forest understorey (a) and due to snow cover (b): offsets, buffering, coupling, and decoupling. To be read in conjunction with Box 1.

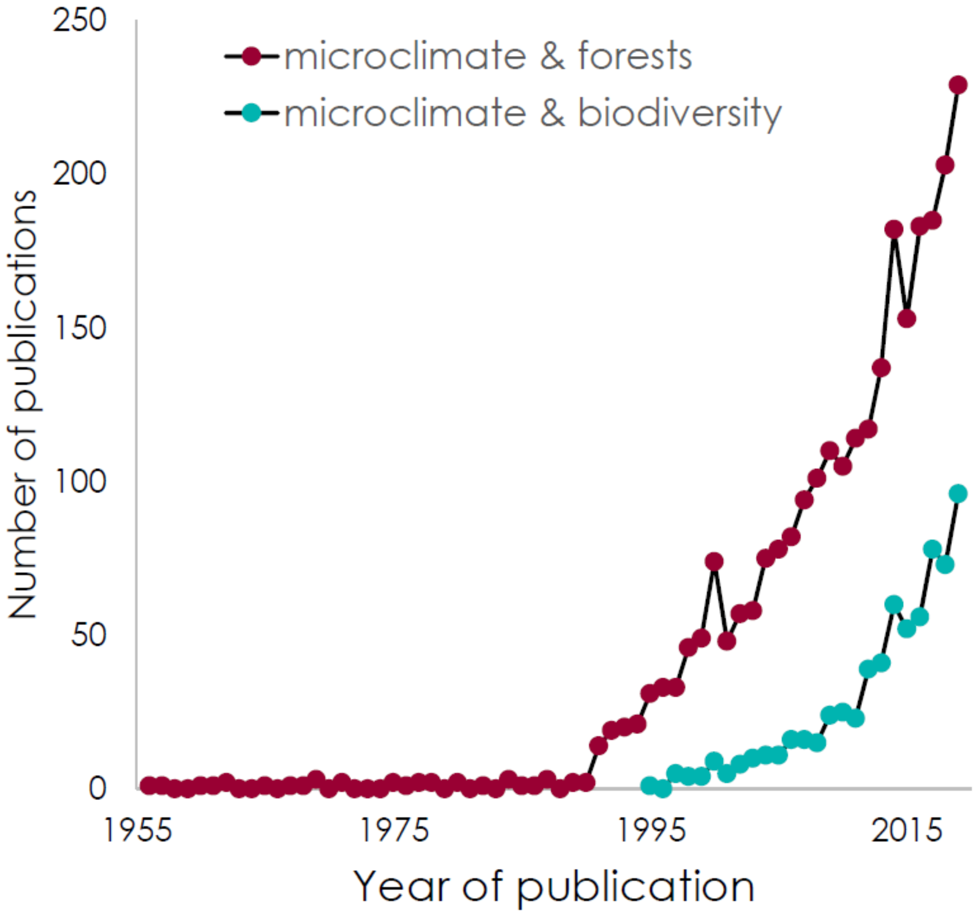

Fig. 2. Number of publications on the topics "microclimate & forests" (dark red) and "microclimate & biodiversity" (blue) according to a Web of Science search on 23 Oct. 2020 (results included till 2019).

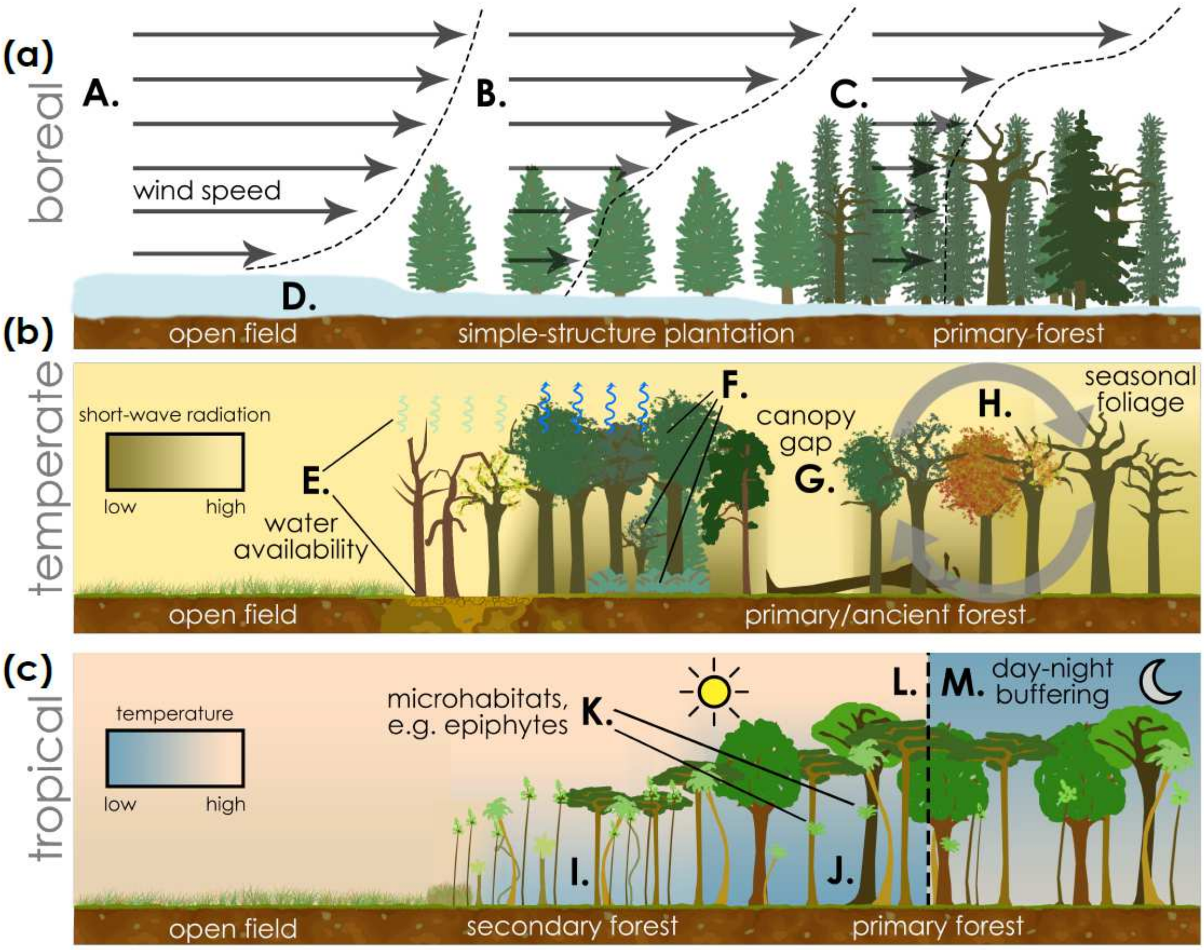

Fig. 3. Multiple vegetation drivers of microclimate might be of different importance in forest at boreal (a), temperate (b), and tropical (c) latitudes, respectively. It is important to note, however, that most processes illustrated here for one biome often are also important in the other biomes. Increasing tree density from open non-forest habitats (A), to plantations with a simple canopy structure (B), to (semi-)natural forest with complex structure (C) reduces below-canopy wind speeds above ground. Forest canopies can reduce ground snow cover and thus decrease the insulating effect of snow cover on cool soil temperatures during the cold season (D). Microclimate is also in part a function of water availability; for instance during drought, lower soil moisture reduces the rate of evapotranspiration (E), thereby decreasing temperature buffering as plants defoliate and die. Vertical layering of vegetation (F) influences the amount and quality of incoming shortwave radiation, outgoing longwave radiation and moisture exchange. Disturbances such as tree mortality can create canopy gaps (G), providing a local shift in microclimate. Seasonal reductions in canopy cover (tree phenology, H) during the cool and/or dry season increases the exposure of the internal forest to ambient conditions. Forests also buffer the temporal (i.e., diurnal, seasonal and interannual) variability in temperature conditions relative to adjacent non-forest systems (c). This buffering effect varies with vegetation height and structure, with reduced buffering in secondary, post-agricultural forests (I) relative to primary or ancient, (semi-)natural forests (J). Microhabitats within a forest, such as those created by epiphytic plants (K) can offer an even more buffered microclimate, critical for the ecology and physiology of many forest species. Finally, the temperature offset in forests can change throughout the diel cycle, with cooler forest interiors vs. open areas during the day (L) and warmer at night (M). For the sake of simplicity, we chose to depict wind, shortwave radiation, and temperature in the boreal, temperate, and tropical panel, respectively. However, of course all of these microclimate variables can be relevant to systems across latitudes.

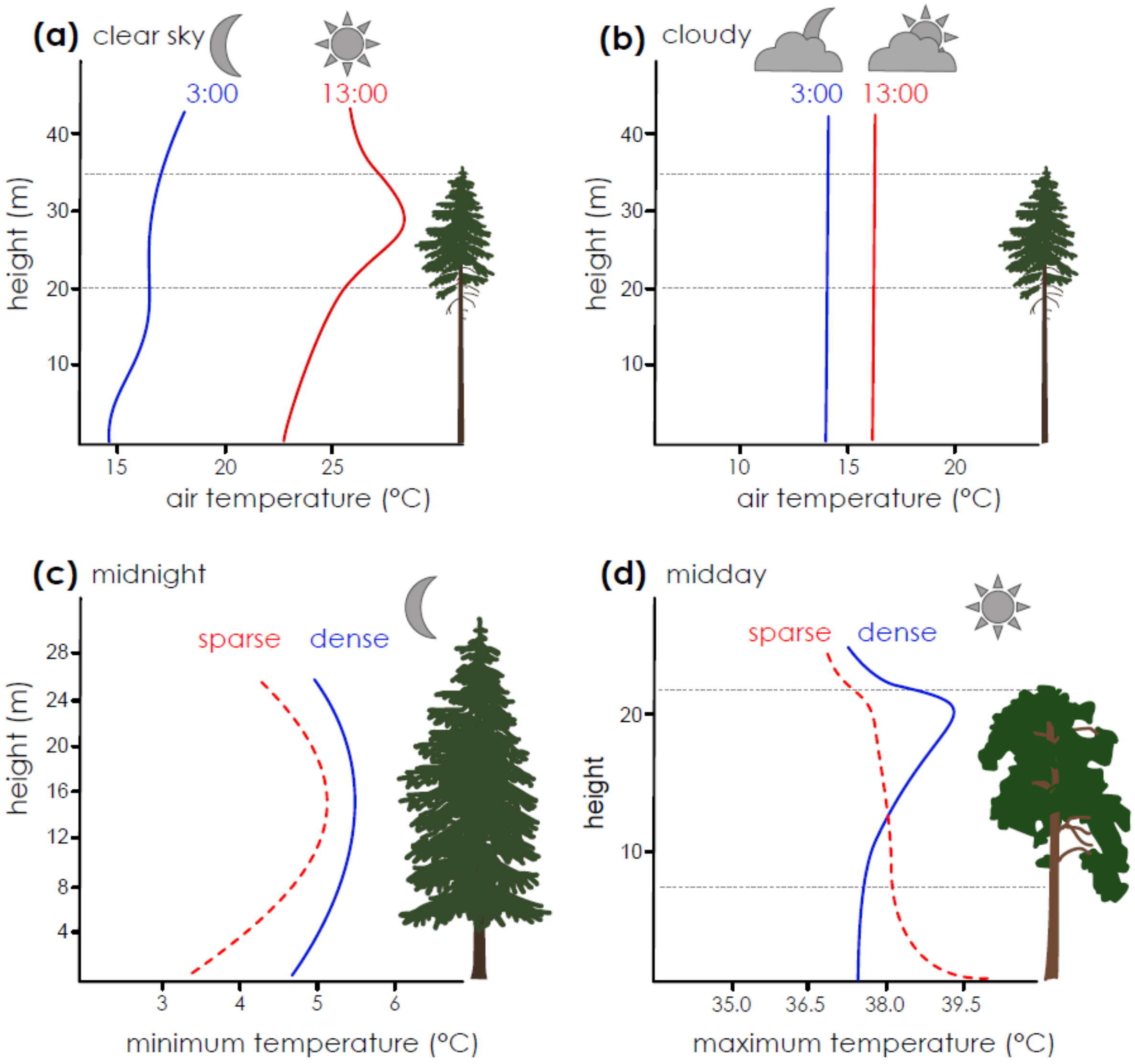

Fig. 4. Typical vertical air temperature profiles inside forests of various canopy structure, for clear sky (a) or cloudy (b) conditions, and during the nighttime (c) and daytime (d). These examples are based on e.g. Raupach (1989), Ogée et al. (2003), Brower et al. (2011), and Schilperoot et al. (2020).

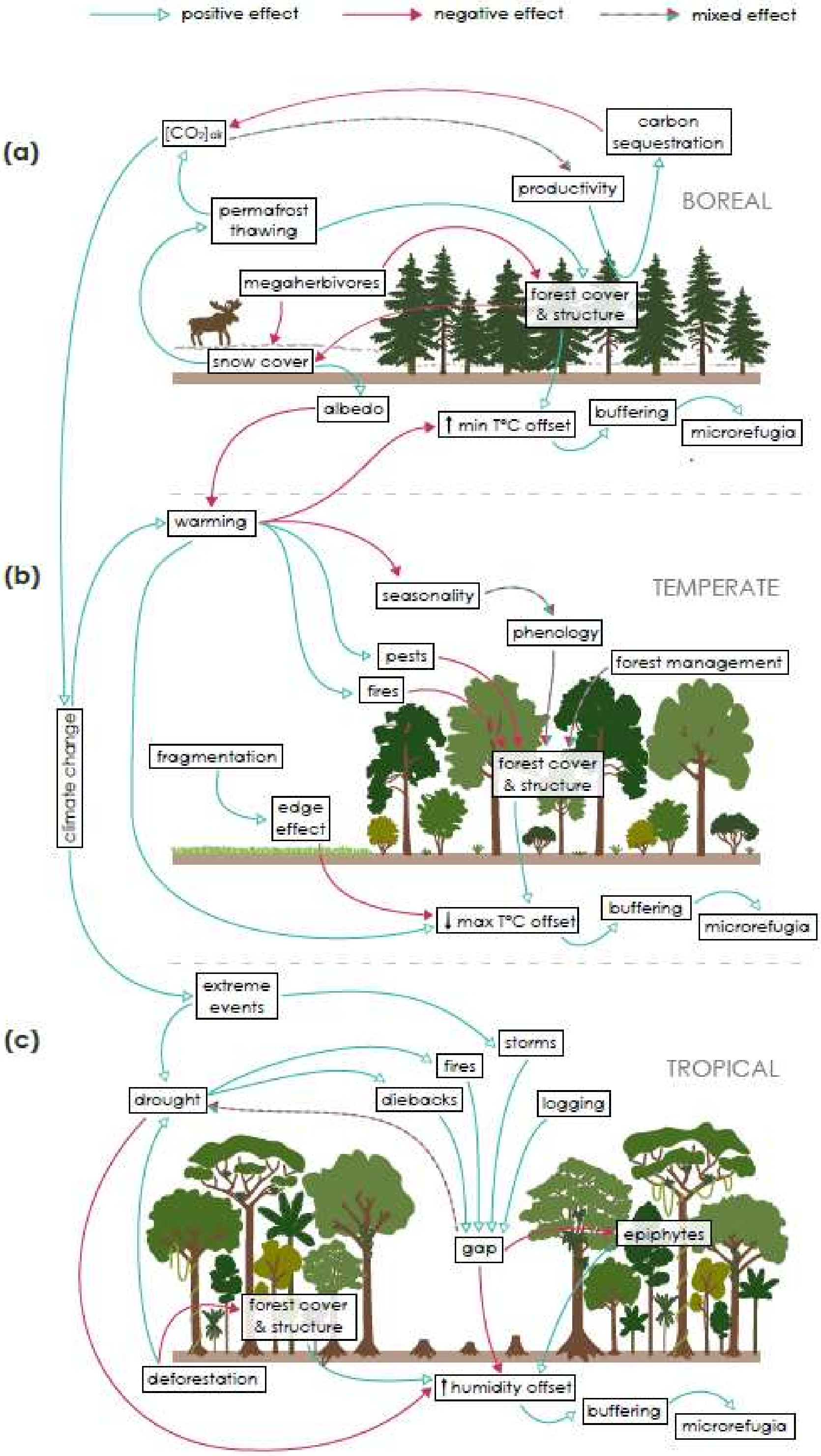

Fig. 5. Macroclimate change effects on microclimates. Climate warming and climatic extremes affect microclimates and microrefugia by influencing forest composition and structure in boreal (a), temperate (b) and tropical forests (c). It is important to note, however, that, most processes illustrated here for one biome often are also important drivers in the other biomes. Complex, indirect effects of climate change on microrefugia involve feedback with natural and anthropogenic factors.

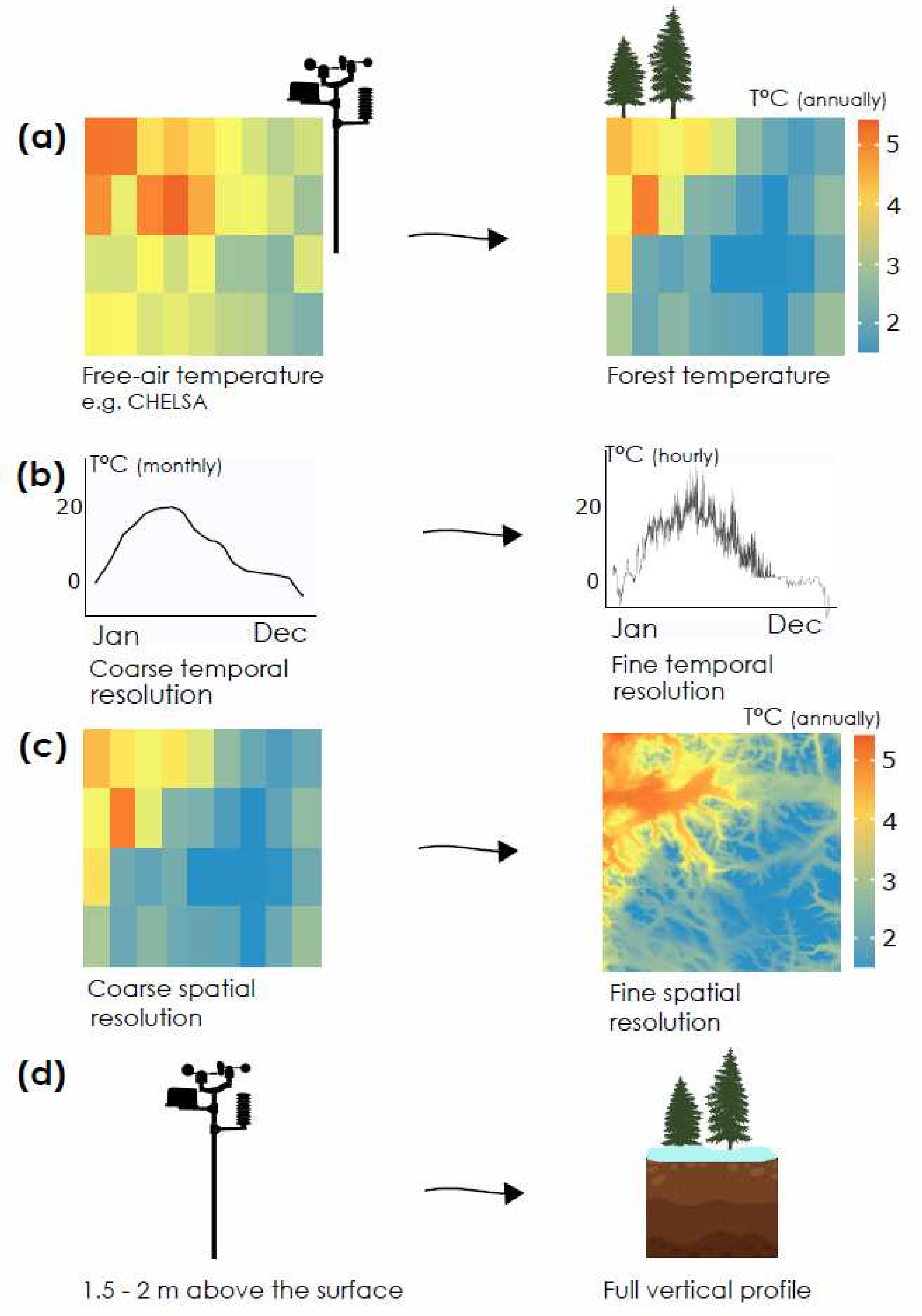

Fig. 6. The four dimensions of improving gridded microclimate products for forests. First, (a) one can turn coarse-grained free-air temperature grids (products such as CHELSA and WorldClim) into coarse-grained forest temperature maps using the offset between weather station and forest temperatures. Next, to increase the temporal (b) and spatial (c) resolution of forest microclimate maps, and to create the full vertical temperature profile (d), one should aim for the integration of in-situ measurements, and mechanistic and statistical models.

Box 1 Definitions of offsets, buffering, coupling and decoupling

Many terms related to microclimate dynamics have been used in the scientific literature, such as 'buffering', 'coupling', 'decoupling' and 'offset' to imply divergence from macroclimatic fluctuations over time. However, no uniform definition of these terms exists yet. For this reason, we here suggest a uniform terminology including all terms by illustrating the processes behind each of them (Fig. 1).

First of all, we define the temperature offset as the instantaneous difference between a reference temperature at a given time t_0 and the focal temperature under study at the same time t_0. For instance, the horizontal temperature offset due to the presence of a forest canopy is the instantaneous difference between the free-air temperature in open conditions (i.e., macroclimate) and the sub-canopy temperature at the same height (i.e., microclimate), with positive and negative offset values meaning colder and warmer conditions in the forest understorey, respectively (Fig. 1a). Similarly, the vertical temperature offset due to snow cover is the instantaneous temperature difference between the air above the snow and inside the snow layer, with positive and negative offset values meaning colder and warmer conditions inside the snow layer, respectively (Fig. 1b).

Then, depending on the magnitude and distribution of the temperature offsets over time, it is possible to distinguish three contrasting situations (Fig. 1): (1) perfect coupling; (2) buffering; and (3) decoupling:

(1) Perfect coupling occurs when microclimatic temperatures (T_{micro}) equal macroclimatic temperatures (T_{macro}). In other words, the slope (β_1) of the linear relationship between T_{macro} and T_{micro} ($T_{micro} = \beta_0 + \beta_1 \times T_{macro}$) is equal to one (identity) and the offset is zero and constant over time.

(2) Buffering means a dampening of T_{macro} fluctuations over time such that temporal fluctuations in T_{micro} still exist but are much less pronounced than for T_{macro}. This generates a cycle of positive and negative offset values which tend to diminish the positive correlation between T_{macro} and T_{micro}, such that β_1 is lower than 1 but greater than 0. The closer β_1 is to zero, the more pronounced the magnitude of buffering.

(3) Decoupling occurs when T_{micro} behaves independently from T_{macro}, i.e. when the slope (β_1) is zero and the buffering is so strong that the positive correlation between T_{micro} and T_{macro} is totally lost. For instance, temperatures inside the snow layer during winter are completely decoupled from temperatures above the snow layer (Fig. 1b).

Supplementary Information

Table S1. Ranked submitted research questions on microclimates, grouped separately for 'forests' and 'soil temperatures' (more generally, also including other ecosystems), from high to low voting results (scores). Each participant (18 participants in total) of the workshop had to score their top 3 questions, both in the forests and in the soil category. Each participant's number 1 question received 3 points, the second ranked question received 2 points, and the third ranked question received one point. After this voting procedure, all points across all participants were summed per question. With 18 participants, and assuming each participant would vote for the same question as their top question, the maximum score was 54.