Received: 6 November 2020 | Revised: 5 February 2021 | Accepted: 14 February 2021

DOI: 10.1111/gcb.15569

RESEARCH REVIEW

Global Change Biology WILEY

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

Pieter De Frenne[1] | Jonathan Lenoir[2] | Miska Luoto[3] | Brett R. Scheffers[4] | Florian Zellweger[5] | Juha Aalto[3,6] | Michael B. Ashcroft[7] | Ditte M. Christiansen[8] | Guillaume Decocq[2] | Karen De Pauw[1] | Sanne Govaert[1] | Caroline Greiser[8] | Eva Gril[2] | Arndt Hampe[9] | Tommaso Jucker[10] | David H. Klinges[11] | Irena A. Koelemeijer[8] | Jonas J. Lembrechts[12] | Ronan Marrec[2] | Camille Meeussen[1] | Jérôme Ogée[13] | Vilna Tyystjärvi[3,6] | Pieter Vangansbeke[1] | Kristoffer Hylander[8]

[1]Forest & Nature Lab, Ghent University, Gontrode, Belgium

[2]UMR 7058 CNRS "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN), Université de Picardie Jules Verne, Amiens, France

[3]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

[4]Wildlife Ecology & Conservation, University of Florida, Gainesville, FL, USA

[5]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[6]Weather and Climate Change Impact Research, Finnish Meteorological Institute, Helsinki, Finland

[7]Centre for Sustainable Ecosystem Solutions, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, NSW, Australia

[8]Department of Ecology, Environment and Plant Sciences, and Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

[9]INRAE, Univ. Bordeaux, BIOGECO, Cestas, France

[10]School of Biological Sciences, University of Bristol, Bristol, UK

[11]School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA

[12]Plants and Ecosystems, University of Antwerp, Wilrijk, Belgium

[13]INRAE, Bordeaux Science Agro, ISPA, Villenave d'Ornon, France

Correspondence
Pieter De Frenne, Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium.
Email: Pieter.DeFrenne@UGent.be

Funding information
University of Wollongong; Natural Environment Research Council, Grant/Award Number: NE/S01537X/1; Agence National de la recherche, Grant/Award Number: ANR-19-CE32-0005-01 and ANR-10-LABX-45; National Science Foundation US; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 193645; Fonds Wetenschappelijk Onderzoek, Grant/Award Number: ASP 035-19, G0H1517N, 12P1819N and W001919N; Academy of Finland, Grant/Award Number: 337552; Bolin Centre for Climate Research, Stockholm University; H2020 European Research Council, Grant/Award Number:

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 result 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

757833; Svenska Forskningsrådet Formas, Grant/Award Number: 2014-530 and 2018- 588 2829; Oscar and Lili Lamm Memorial Foundation; EU ERA-NET BiodivERsA, Grant/Award Number: BiodivERsA3-2015-58

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

1 | 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; De Frenne et al., 2019; Geiger et al., 2009). 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 (De Frenne et al., 2019; Ewers & Banks-Leite, 2013; von Arx et al., 2013; see Figure 1 and Box 1 for the definitions of technical terms used in this paper). The

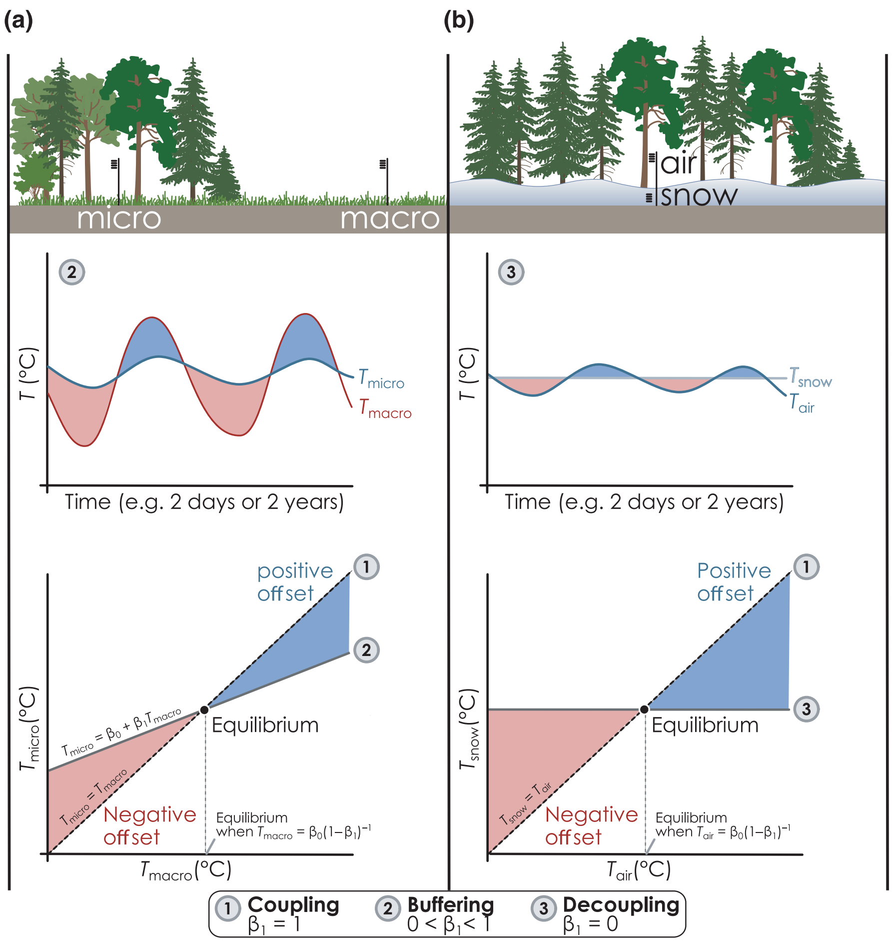

FIGURE 1 Definitions of the main processes underlying microclimate dynamics in the forest understorey (a) and due to snow cover (b): offsets; buffering; coupling; and decoupling. To be read in conjunction with Box 1

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 (Figure 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 (Figure 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 (Figure 1b).

Then, depending on the magnitude and distribution of the temperature offsets over time, it is possible to distinguish three contrasting situations (Figure 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}, that is 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 (Figure 1b).

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 (Davis et al., 2019; De Frenne et al., 2019; McLaughlin et al., 2017). 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 (Geiger et al., 2009; a book with a first edition already published in 1927; Grubb, 1977). Forests harbour 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 (Figure 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 (Barry & Blanken, 2016; De Frenne & Verheyen, 2015; Potter et al., 2013). 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 policymakers alike (IPBES, 2019; Landuyt et al., 2019; MEA, 2005).

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

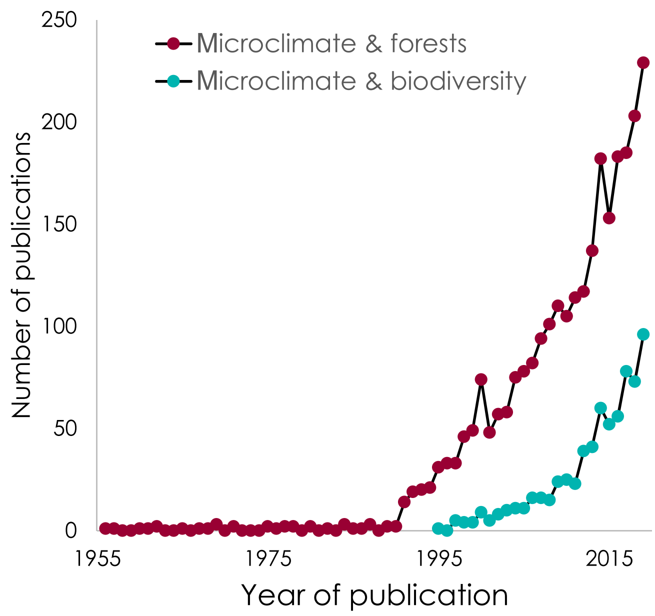

FIGURE 2 Number of publications on the topics 'microclimate & forests' (dark red) and 'microclimate & biodiversity' (blue) according to a Web of Science search on 23 October 2020 (results included till end of 2019).

available within forests (e.g. root caverns, tree holes, fallen trunks) enable organisms to avoid extreme heat and drought (Kearney et al., 2009; Scheffers, Brunner, et al., 2013; Scheffers et al., 2014). The microclimate buffering capacity of forests may provide climatic microrefugia during macroclimate warming (von Arx et al., 2013; De Frenne et al., 2019; Ewers & Banks-Leite, 2013; Lenoir et al., 2017). 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 (Ashcroft et al., 2012; Greiser et al., 2019; Hampe & Jump, 2011; Keppel et al., 2012; Lenoir et al., 2017). 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 (Lembrechts et al., 2019; Slavich et al., 2014; Zellweger, De Frenne et al., 2019). 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 coexistence, 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 (Frey, Hadley, Johnson, et al., 2016; Jucker et al., 2018; Parker, 1995; Woods et al., 2015).

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 (Chen et al., 2018; Riutta et al., 2012; Wang et al., 2010; 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 feed back 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, De Frenne, et al., 2019). 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 lay out future research directions for this emerging field of research. Our structure for this review is premised on drawing contrasts between forests versus 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.

2 | DRIVERS OF VERTICAL AND HORIZONTAL MICROCLIMATE VARIATION

2.1 | Horizontal distribution of microclimates: Forest versus 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, Aalto, et al., 2020). Perhaps the most evident characteristic of forest microclimates is that the understorey is buffered against macroclimate temperature extremes (Figure 1). During clear and warm days, much of the incoming short-wave 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 long-wave radiation by the canopy (De Frenne et al., 2019; Geiger et al., 2009).

Evaporative cooling and emitted long-wave radiation both act to reduce canopy and soil surface temperatures, whereas net short-wave radiation acts to warm the soil and canopy surfaces (De Frenne et al., 2013; Geiger et al., 2009). 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 (von Arx et al., 2013; Dobrowski, 2011). 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; Davis et al., 2019; McLaughlin et al., 2017). Vegetation structure and composition affect heat exchange and cause horizontal variation in the buffering of ambient temperatures (Figure 3). In particular, vegetation density (e.g. in terms of canopy cover, basal

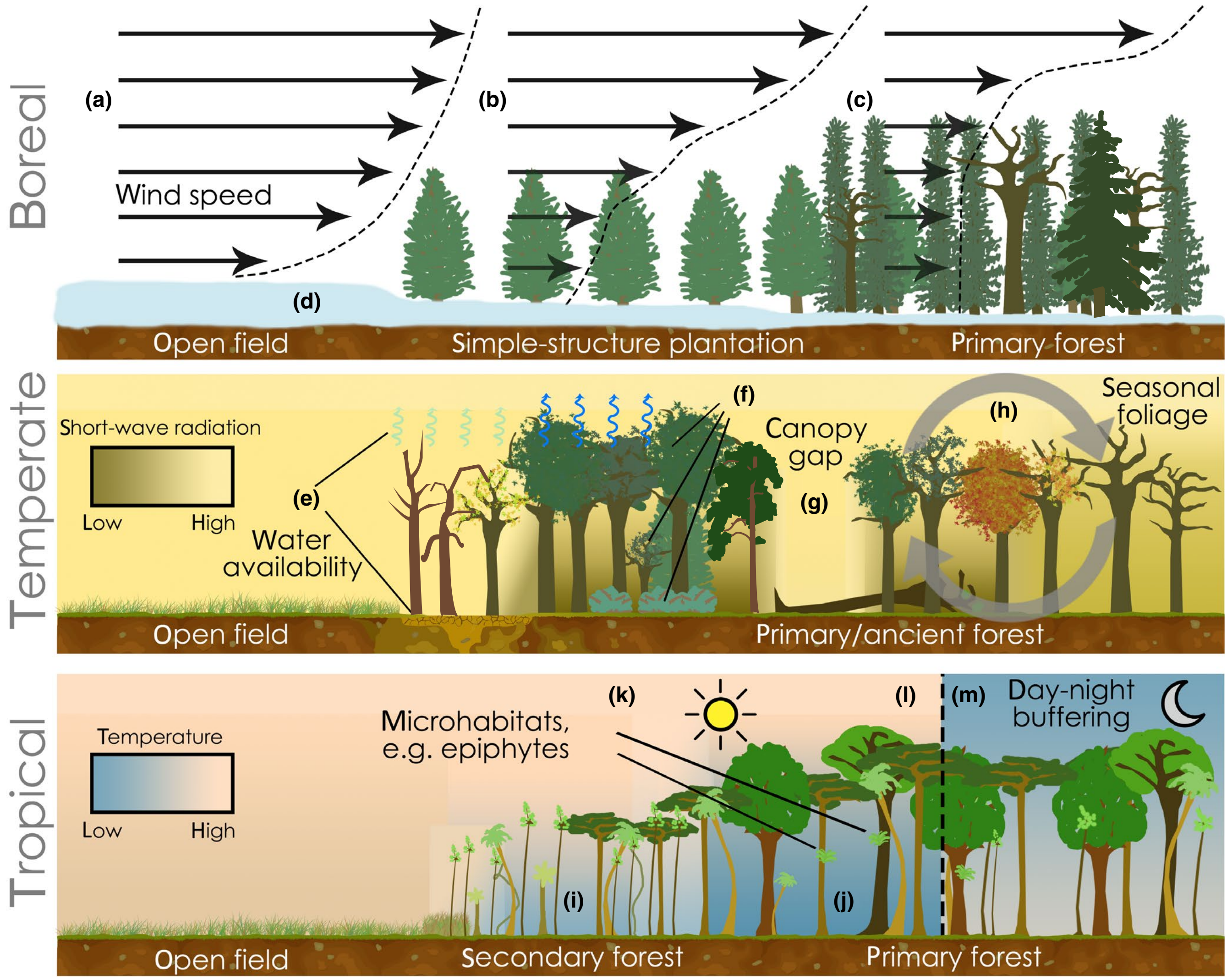

FIGURE 3 Multiple vegetation drivers of microclimate might be of different importance in forests at boreal (top), temperate (middle) and tropical (bottom) latitudes respectively. It is important to note, however, that most processes illustrated here for one biome often are also important in the other 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 short-wave radiation, outgoing long-wave 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 increase 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 (bottom panel). 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 versus open areas during the day (l) and warmer at night (m). For the sake of simplicity, we chose to depict wind, short-wave 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

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, Coomes, et al., 2019). 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 & Guzmán, 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 (Aalto et al., 2017; Ashcroft et al., 2008; Bramer et al., 2018; Davis et al., 2019; Dobrowski, 2011; Meineri & Hylander, 2017). 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, Coomes, et al., 2019). Moreover, regional precipitation patterns and the size and adjacency to water bodies influence latent and sensible heat fluxes (Meleason & Quinn, 2004; Zellweger, Coomes, et al., 2019). 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 (Figure 3).

2.2 | 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, 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 (Figure 4; Davies-Colley et al., 2000; Vanwalleghem & Meentemeyer, 2009). 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 (Bauerle et al., 2009; Hardwick & Toumi, 2015; Harley et al., 1996; Zweifel et al., 2002).

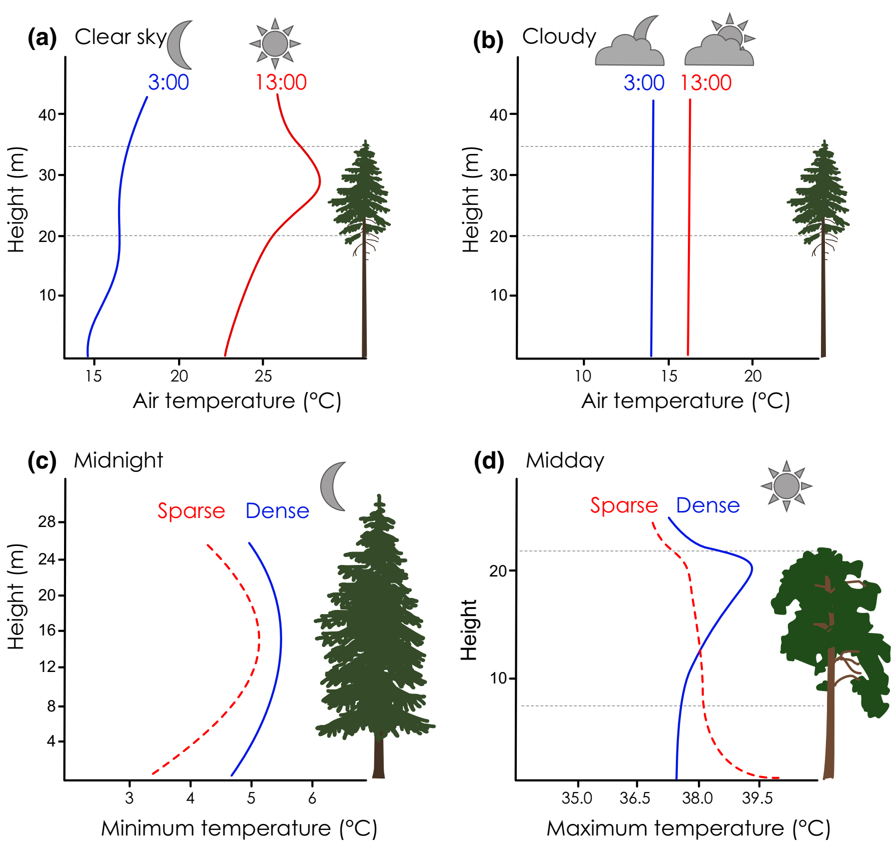

FIGURE 4 Typical vertical air temperature profiles inside forests of various canopy structure, for clear sky (a) or cloudy (b) conditions, and during the night-time (c) and daytime (d). These examples are based on, for example, Raupach (1989), Ogée et al. (2003), Brower et al. (2011) and Schilperoort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

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; Figure 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 (Figure 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 short-wave radiation (Martin et al., 1999; Scheffers et al., 2017). Leuzinger and Körner (2007) showed that leaf temperature regimes in canopies vary enormously over short vertical distances in several coniferous and deciduous broadleaved tree species. Finally, snow cover in the winter will effectively decouple the near-ground temperature from the temperature above the snow (Figure 1).

3 | 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); that is perception of 'micro' by woodlice is different from an elephant's perception of 'micro' (Lembrechts, Broeders, et al., 2020; Weins, 1989). 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.

3.1 | 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 in the Philippines shift their vertical niche upwards towards the canopy at higher elevations as microclimates become more favourable (Scheffers, Phillips, et al., 2013) 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 (Frey et al., 2016; Melin et al., 2014). 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 (Åström et al., 2007; Gauslaa, 2014; Hylander, 2005; Löbel et al., 2018; Stewart & Mallik, 2006). 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, 2020; Basham et al., 2019).

3.2 | 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, 2020).

4 | 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; Meeussen et al., 2021; Uriarte et al., 2016). 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).

5 | HOW WILL MACROCLIMATE WARMING AFFECT FOREST MICROCLIMATES?

How macroclimate warming affects forest microclimate dynamics, and vice versa, remains an open question (De Frenne et al., 2019; Lenoir et al., 2017). 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 (Figures 1 and 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. Figure 1) does not shift; and (iv) other variables such as soil moisture levels remain comparable (Scheffers, Phillips, et al., 2014; 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 (Figure 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; Davis et al., 2019; McLaughlin et al., 2017). 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 rainforests) 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 (i.e. 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 (Figure 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.

5.1 | Biome-specific effects on temperature offsets

In temperate forests, temperature buffering may happen for both maximum and minimum temperatures (De Frenne et al., 2019; Figure 5). 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, Coomes, et al. (2019) 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.

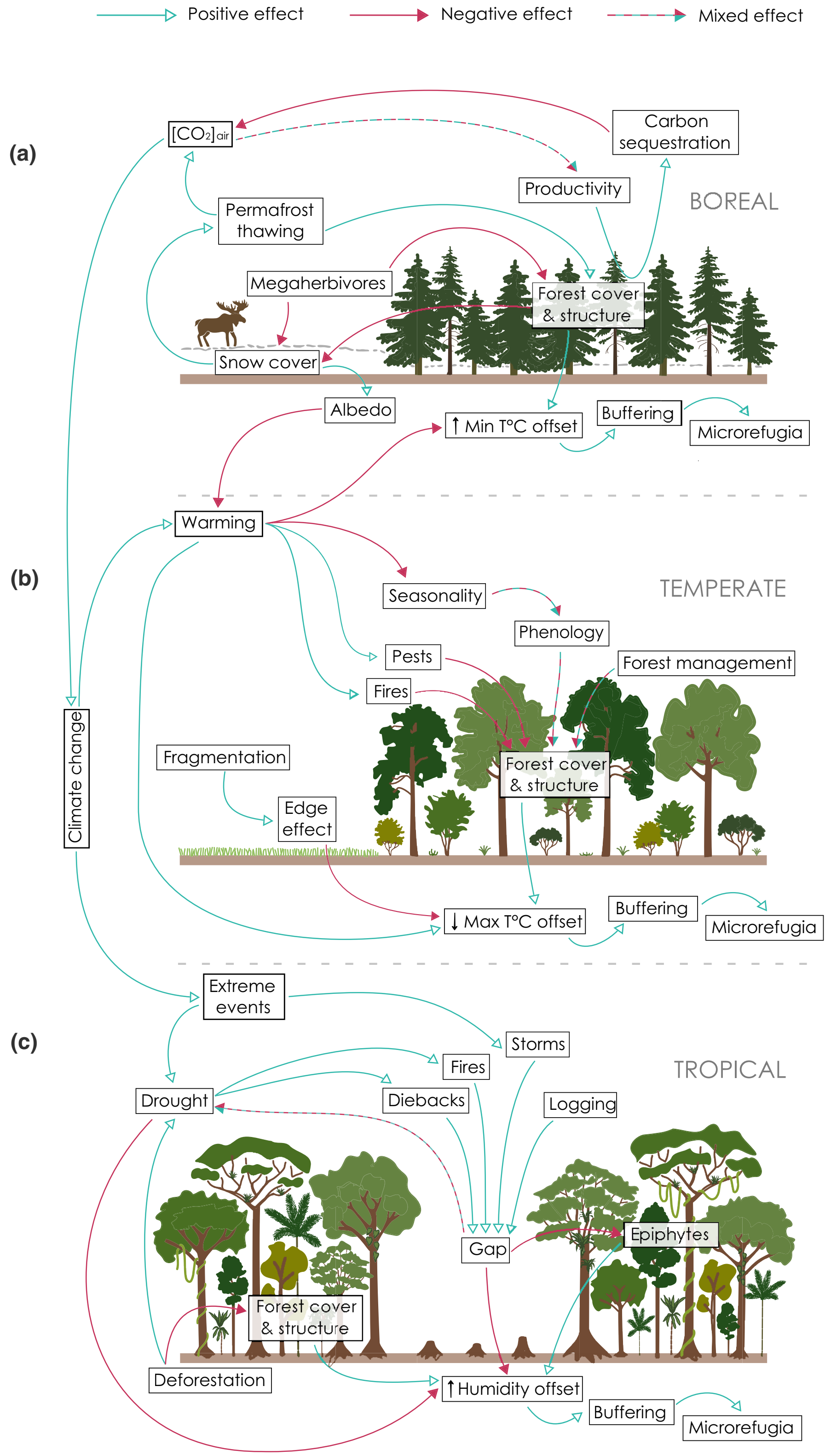

FIGURE 5 Macroclimate change effects on microclimates. Climate warming and climatic extremes affect microclimates and microrefugia by influencing forest composition and structure in boreal (a), temperate (b) and tropical forests (c). It is important to note, however, that most processes illustrated here 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

For example, the thermophilization 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 rainforests, 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 (Antão et al., 2020; Lenoir et al., 2020; Tewksbury et al., 2008). 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).

5.2 | Macroclimate warming effects on temperature offsets

In their review covering the second half of the 20th century, Boisvenue and 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), a surrogate for photosynthetic activity and productivity, show reduced productivity in warmer years (Asner et al., 2000; Braswell et al., 1997), 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 range edges of the boreal forest zone, respectively.

5.3 | 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 north-western 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, Coomes, et al., 2019). 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).

5.4 | 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, Hadley, & Betts, 2016; Frey, Hadley, Johnson, et al., 2016; 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 (Brang et al., 2014; Latimer & Zuckerberg, 2017; Vanwalleghem & Meentemeyer, 2009). 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 (Aalto et al., 2018; Lantz et al., 2013; Figures 1 and 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 (Figures 3 and 5), reducing the capacity to buffer macroclimatic fluctuations and thus causing many species to decline in abundance, for example 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, Phillips, et al., 2014) and providing buffered microhabitats for canopy-dwelling organisms (Seidl et al., 2020; Figure 3, arrow K).

5.5 | 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 feed back 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 passes 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. 5000 years 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 (Connon et al., 2018; Lantz et al., 2013). The positive feedback on macroclimate warming is derived from permafrost thaw releasing stored carbon dioxide under aerobic conditions and methane under wet, anaerobic conditions (Figure 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 (Figure 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 (Figures 1 and 5).

6 | 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 February 2020). From these voting results, we identified three key directions for future forest microclimate research as discussed below (Table S1).

6.1 | 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 in 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 policymakers 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).

6.2 | 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 (Lembrechts, Aalto, et al., 2020; Zellweger, De Frenne, et al., 2019). 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; Figure 6). Further increases in the spatial resolution of such microclimate maps are possible thanks to the recent emergence of both large-scale global databases of in situ measured (forest) microclimate (De Frenne et al., 2019; Lembrechts, Aalto, et al., 2020) 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) is further complicated by the interactions between climate change and land-use changes, as discussed in the previous paragraph (Lembrechts & Nijs, 2020; Zellweger et al., 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).

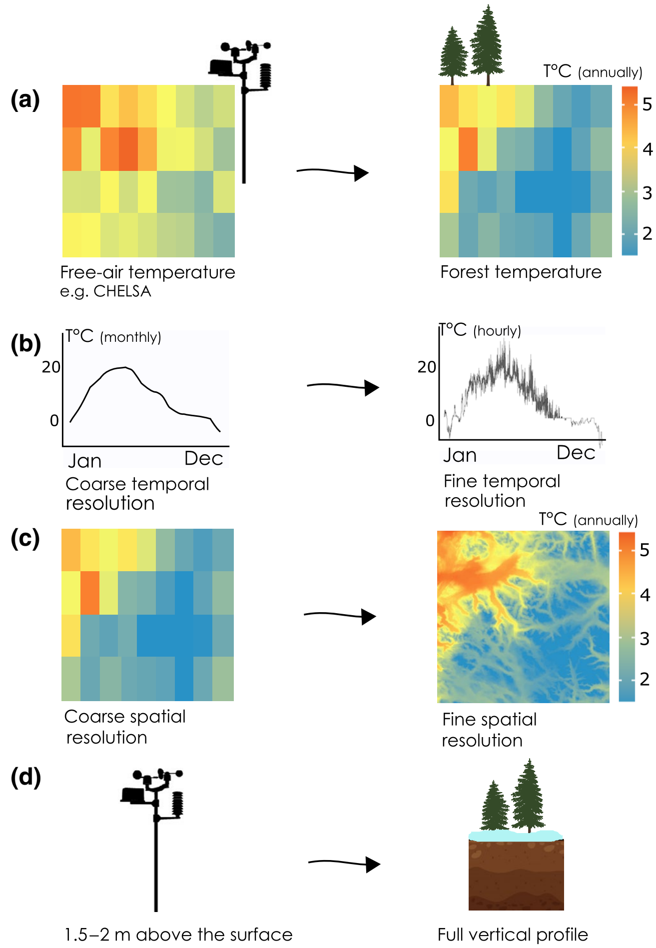

FIGURE 6 The four dimensions of improving gridded microclimate products for forests. First, (a) one can turn coarse-grained free-air temperature grids (products such as CHELSA and WorldClim) into coarse-grained forest temperature maps using the offset between weather station and forest temperatures. 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

6.3 | 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; Figures 3–5) as well as developing approaches for mapping microclimate at appropriate scales (Figure 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 (Lembrechts et al., 2019; Lenoir et al., 2017; Mod et al., 2016).

However, few studies have actually tested this assumption (Lembrechts et al., 2019; Ohler et al., 2020), particularly in the context of forests (Frey, Hadley, Johnson, et al., 2016). 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., 2014). 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; Bramer et al., 2018; Hylander et al., 2015).

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; Albrich et al., 2020; Coomes et al., 2014;)—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).

7 | 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 of increasing 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, Aalto, et al., 2020), 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.

ACKNOWLEDGEMENTS

This review resulted from extensive preparations and discussions at a scientific workshop at Ekenäs Herrgård, Sweden, in February 2020, funded by the Oscar and Lili Lamm Memorial Foundation to K.H. K.H. also received funding from the Swedish Research Council Formas (grants 2014-530 and 2018-2829) and the Bolin Centre for Climate Research, Stockholm University. P.D.F., P.V. and C.M. received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833), K.D.P. and S.G. from the Research Foundation Flanders (FWO, grant number ASP 035-19 and project G0H1517N respectively), J.L. and E.G. from the French National

Research Agency (ANR) within the framework of the IMPRINT project 'IMpacts des PRocessus mIcroclimatiques sur la redistributioN de la biodiversiTé forestière en contexte de réchauffement du macroclimat' (grant number ANR-19-CE32-0005-01), D.H.K. from the US National Science Foundation Graduate Research Fellowship Program, and J.J.L. from the Research Foundation Flanders (FWO, grants 12P1819N and W001919N). T.J. was supported by an NERC Independent Research Fellowship (grant number NE/S01537X/1), J.O. by the French National Research Agency (ANR) in the frame of the Cluster of Excellence COTE (project HydroBeech, ANR-10-LABX-45), F.Z. by the Swiss National Science Foundation (grant number 193645), and A.H. by the EU ERA-NET BiodivERsA (project SPONFOREST, BiodivERsA3-2015-58). M.B.A. received a travel grant from the University of Wollongong. J.A. was supported by the Academy of Finland Flagship funding (grant no. 337552). We also thank the subject editor and the two reviewers (Solomon Dobrowski and a second anonymous reviewer) for numerous helpful comments.

DATA AVAILABILITY STATEMENT

This is a review, so no data available.

ORCID

Pieter De Frenne https://orcid.org/0000-0002-8613-0943
Jonathan Lenoir https://orcid.org/0000-0003-0638-9582
Brett R. Scheffers https://orcid.org/0000-0003-2423-3821
Michael B. Ashcroft https://orcid.org/0000-0003-2157-5965
Ditte M. Christiansen https://orcid.org/0000-0002-7020-5082
Sanne Govaert https://orcid.org/0000-0002-8939-1305
Eva Gril https://orcid.org/0000-0002-7340-8264
Jonas J. Lembrechts https://orcid.org/0000-0002-1933-0750
Ronan Marrec https://orcid.org/0000-0003-1607-4939
Camille Meeussen https://orcid.org/0000-0002-5869-4936
Jérôme Ogée https://orcid.org/0000-0002-3365-8584

REFERENCES

Aalto, J., Riihimäki, H., Meineri, E., Hylander, K., & Luoto, M. (2017). Revealing topoclimatic heterogeneity using meteorological station data. *International Journal of Climatology*, *37*, 544–556. https://doi.org/10.1002/joc.5020

Aalto, J., Scherrer, D., Lenoir, J., Guisan, A., & Luoto, M. (2018). Biogeophysical controls on soil-atmosphere thermal differences: Implications on warming Arctic ecosystems. *Environmental Research Letters*, *13*, 074003. https://doi.org/10.1088/1748-9326/aac83e

Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 11770–11775. https://doi.org/10.1073/pnas.1607171113

Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, *26*, 4013–4027. https://doi.org/10.1111/gcb.15118

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (T.)., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Antão, L. H., Bates, A. E., Blowes, S. A., Waldock, C., Supp, S. R., Magurran, A. E., Dornelas, M., & Schipper, A. M. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology & Evolution*, *4*, 927–933. https://doi.org/10.1038/s41559-020-1185-7

Ashcroft, M. B., Chisholm, L. A., & French, K. O. (2008). The effect of exposure on landscape scale soil surface temperatures and species distribution models. *Landscape Ecology*, *23*, 211–225. https://doi.org/10.1007/s10980-007-9181-8

Ashcroft, M. B., Gollan, J. R., Warton, D. I., & Ramp, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, *18*, 1866–1879. https://doi.org/10.1111/j.1365-2486.2012.02661.x

Asner, G. P., Townsend, A. R., & Braswell, B. H. (2000). Satellite observation of El Niño effects on Amazon forest phenology and productivity. *Geophysical Research Letters*, *27*, 981–984. https://doi.org/10.1029/1999GL011113

Åström, M., Dynesius, M., Hylander, K., & Nilsson, C. (2007). Slope aspect modifies community responses to clear-cutting in boreal forests. *Ecology*, *88*, 749–758. https://doi.org/10.1890/06-0613

Aussenac, G. (2000). Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, *57*, 287–301. https://doi.org/10.1051/forest:2000119

Barry, R. G., & Blanken, P. D. (2016). *Microclimate and local climate*. Cambridge University Press.

Basham, E. W., & Scheffers, B. R. (2020). Vertical stratification collapses under seasonal shifts in climate. *Journal of Biogeography*, *47*, 1888–1898. https://doi.org/10.1111/jbi.13857

Basham, E. W., Seidl, C. M., Andriamahohatra, L. R., Oliveira, B. F., & Scheffers, B. R. (2019). Distance–decay differs among vertical strata in a tropical rainforest. *Journal of Animal Ecology*, *88*, 114–124. https://doi.org/10.1111/1365-2656.12902

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., & Crowther, T. W. (2019). The global tree restoration potential. *Science*, *365*, 76–79. https://doi.org/10.1126/science.aax0848

Bauerle, W. L., Bowden, J. D., Wang, G. G., & Shahba, M. A. (2009). Exploring the importance of within-canopy spatial temperature variation on transpiration predictions. *Journal of Experimental Botany*, *60*, 3665–3676. https://doi.org/10.1093/jxb/erp206

Beck, P. S. A., Juday, G. P., Alix, C., Barber, V. A., Winslow, S. E., Sousa, E. E., Heiser, P., Herriges, J. D., & Goetz, S. J. (2011). Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*, *14*, 373–379. https://doi.org/10.1111/j.1461-0248.2011.01598.x

Boisvenue, C. E. L., & Running, S. W. (2006). Impacts of climate change on natural forest productivity – Evidence since the middle of the 20th century. *Global Change Biology*, *12*, 862–882. https://doi.org/10.1111/j.1365-2486.2006.01134.x

Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, *320*, 1444–1449. https://doi.org/10.1126/science.1155121

Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., Frenne, P., Hemming, D., Hill, R., Kearney, M., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I., Marsh, C., Morecroft, M., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F., & Gillingham, P. K. (2018). Advances in monitoring and modelling climate at ecologically relevant scales. *Advances in Ecological Research*, *58*, 101–161. https://doi.org/10.1016/bs.aecr.2017.12.005

Brang, P., Spathelf, P., Larsen, J. B., Bauhus, J., Boncina, A., Chauvin, C., Drossler, L., Garcia-Guemes, C., Heiri, C., Kerr, G., Lexer, M. J., Mason, B., Mohren, F., Muhlethaler, U., Nocentini, S., & Svoboda, M. (2014). Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry*, *87*, 492–503. https://doi.org/10.1093/forestry/cpu018

Braswell, B. H., Schimel, D. S., Linder, E., Moore, B. (1997). The response of global terrestrial ecosystems to interannual temperature variability. *Science*, *278*, 870–872. https://doi.org/10.1126/science.278.5339.870

Brower, L. P., Williams, E. H., Fink, L. S., Slayback, D., Isabel Ramírez, M., Ván Limón García, M., Zubieta, R. R., Weiss, S. B., Calvert, W. H., & Zuchowski, W. (2011). Overwintering clusters of the monarch butterfly coincide with the least hazardous vertical temperatures in the oyamel forest. *Journal of the Lepidopterists' Society*, *65*, 27–46.

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E., & Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, *5*(2), 111–124. https://doi.org/10.1111/2041-210X.12143

Campanello, P. I., Genoveva Gatti, M., Ares, A., Montti, L., & Goldstein, G. (2007). Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *Forest Ecology and Management*, *252*, 108–117. https://doi.org/10.1016/j.foreco.2007.06.032

Carlile, D. W., Skalski, J. R., Batker, J. E., Thomas, J. M., & Cullinan, V. I. (1989). Determination of ecological scale. *Landscape Ecology*, *2*, 203–213. https://doi.org/10.1007/BF00125091

Chen, J. Q., Franklin, J. F., & Spies, T. A. (1993). Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, *63*, 219–237. https://doi.org/10.1016/0168-1923(93)90061-L

Chen, J. Q., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., Brookshire, B. L., & Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology – Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, *49*, 288–297. https://doi.org/10.2307/1313612

Chen, Y., Liu, Y., Zhang, J., Yang, W., He, R., & Deng, C. (2018). Microclimate exerts greater control over litter decomposition and enzyme activity than litter quality in an alpine forest-tundra ecotone. *Scientific Reports*, *8*, 1–13. https://doi.org/10.1038/s41598-018-33186-4

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *The American Naturalist*, *122*, 661–696. https://doi.org/10.1086/284165

Connon, R., Devoie, É., Hayashi, M., Veness, T., & Quinton, W. (2018). The influence of shallow taliks on permafrost thaw and active layer dynamics in subarctic Canada. *Journal of Geophysical Research: Earth Surface*, *123*, 281–297. https://doi.org/10.1002/2017JF004469

Coomes, D. A., Flores, O., Holdaway, R., Jucker, T., Lines, E. R., & Vanderwel, M. C. (2014). Wood production response to climate change will depend critically on forest composition and structure. *Global Change Biology*, *20*, 3632–3645. https://doi.org/10.1111/gcb.12622

Cornelius, M. L., & Osbrink, W. L. A. (2010). Effect of soil type and moisture availability on the foraging behavior of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology*, *103*, 799–807. https://doi.org/10.1603/EC09250

Cudmore, T. J., Björklund, N., Carroll, A. L., & Staffan Lindgren, B. (2010). Climate change and range expansion of an aggressive bark beetle: Evidence of higher beetle reproduction in naïve host tree populations. *Journal of Applied Ecology*, *47*, 1036–1043. https://doi.org/10.1111/j.1365-2664.2010.01848.x

Davies-Colley, R. J., Payne, G. W., & Van Elswijk, M. (2000). Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*, *24*, 111–121.

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., & Abatzoglou, J. T. (2019). Microclimatic buffering in forests of the future: The role of local water balance. *Ecography*, *42*, 1–11.

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Romermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hedl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 18561–18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., & Verheyen, K. (2015). Light accelerates plant responses to warming. *Nature Plants*, *1*, 15110. https://doi.org/10.1038/nplants.2015.110

De Frenne, P., & Verheyen, K. (2015). Weather stations lack forest data. *Science*, *351*, 234. https://doi.org/10.1126/science.351.6270.234-a

De Frenne, P., Zellweger, F., Rodriguez-Sanchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*, 744–749. https://doi.org/10.1038/s41559-019-0842-1

De Smedt, P., Baeten, L., Berg, M. P., Gallet-Moron, E., Brunet, J., Cousins, S. A. O., Decocq, G., Diekmann, M., Giffard, B., De Frenne, P., Hermy, M., Bonte, D., & Verheyen, K. (2018). Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. *European Journal of Soil Biology*, *85*, 1–3. https://doi.org/10.1016/j.ejsobi.2017.12.002

De Smedt, P., Vangansbeke, P., Bracke, R., Schauwvliege, W., Willems, L., Mertens, J., & Verheyen, K. (2019). Vertical stratification of moth communities in a deciduous forest in Belgium. *Insect Conservation and Diversity*, *12*, 121–130. https://doi.org/10.1111/icad.12320

Decocq, G. (2000). The 'masking effect' of silviculture on substrate-induced plant diversity in oak-hornbeam forests from northern France. *Biodiversity and Conservation*, *9*, 1467–1491.

Decocq, G., Aubert, M., Dupont, F., Bardat, J., Wattez-Franger, A., Saguez, R., de Foucault, B., Alard, D., & Delelis-Dusollier, A. (2005). Silviculture-driven vegetation change in a European temperate deciduous forest. *Annals of Forest Science*, *62*, 313–323. https://doi.org/10.1051/forest:2005026

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 6668–6672. https://doi.org/10.1073/pnas.0709472105

Didham, R. K., & Ewers, R. M. (2014). Edge effects disrupt vertical stratification of microclimate in a temperate forest canopy. *Pacific Science*, *68*, 493–508. https://doi.org/10.2984/68.4.4

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS One*, *8*(3), e58093. https://doi.org/10.1371/journal.pone.0058093

Ewers, R. M., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T. R., Bakhtiar, E. Y., Chey, V. K., Chung, A. Y. C., Davies, R. G., Edwards, D. P., Eggleton, P., Fayle, T. M., Hardwick, S. R., Homathevi, R., Kitching, R. L., Khoo, M. S., Luke, S. H., … Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications*, *6*, 6836. https://doi.org/10.1038/ncomms7836

Frey, S. J., Hadley, A. S., & Betts, M. G. (2016). Microclimate predicts within-season distribution dynamics of montane forest birds. *Diversity and Distributions*, *22*, 944–959. https://doi.org/10.1111/ddi.12456

Frey, S. J., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Gauslaa, Y. (2014). Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *The Lichenologist*, *46*, 1–16. https://doi.org/10.1017/S0024282913000753

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, *349*, 819–822. https://doi.org/10.1126/science.aaa9092

Gavin, D. G., Fitzpatrick, M. C., Gugger, P. F., Heath, K. D., Rodríguez-Sánchez, F., Dobrowski, S. Z., Hampe, A., Hu, F. S., Ashcroft, M. B., Bartlein, P. J., Blois, J. L., Carstens, B. C., Davis, E. B., de Lafontaine, G., Edwards, M. E., Fernandez, M., Henne, P. D., Herring, E. M., Holden, Z. A., … Williams, J. W. (2014). Climate refugia: Joint inference from fossil records, species distribution models and phylogeography. *New Phytologist*, *204*, 37–54. https://doi.org/10.1111/nph.12929

Geiger, R., Aron, R. H., & Todhunter, P. (2009). *The climate near the ground*. Rowman & Littlefield.

Gerhardt, K. (1996). Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, *82*, 33–48. https://doi.org/10.1016/0378-1127(95)03700-4

Giguère-Croteau, C., Boucher, É., Bergeron, Y., Girardin, M. P., Drobyshev, I., Silva, L. C., Hélie, J. F., & Garneau, M. (2018). North America's oldest boreal trees are more efficient water users due to increased [CO_2], but do not grow faster. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 2749–2754. https://doi.org/10.1073/pnas.1816686116

González del Pliego, P., Scheffers, B. R., Basham, E. W., Woodcock, P., Wheeler, C., Gilroy, J. J., Medina Uribe, C. A., Haugaasen, T., Freckleton, R. P., & Edwards, D. P. (2016). Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biological Conservation*, *201*, 385–395. https://doi.org/10.1016/j.biocon.2016.07.038

Greiser, C., Meineri, E., Ehrlén, J., & Hylander, K. (2019). Hiding from the climate: Characterizing microrefugia for boreal forest understory species. *Global Change Biology*, *26*, 471–483. https://doi.org/10.1111/gcb.14874

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., & Hylander, K. (2018). Monthly microclimate models in a managed boreal forest landscape. *Agricultural and Forest Meteorology*, *250*, 147–158. https://doi.org/10.1016/j.agrformet.2017.12.252

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, *52*, 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Hampe, A., & Jump, A. S. (2011). Climate relicts: Past, present, future. *Annual Review of Ecology, Evolution and Systematics*, *42*, 313–333. https://doi.org/10.1146/annurev-ecolsys-102710-145015

Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, *29*, 390–397. https://doi.org/10.1016/j.tree.2014.04.006

Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., & Ewers, R. M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, *201*, 187–195. https://doi.org/10.1016/j.agrformet.2014.11.010

Harley, P., Guenther, A., & Zimmerman, P. (1996). Effects of light, temperature and canopy position on net photosynthesis and isoprene emission from sweetgum (*Liquidambar styraciflua*) leaves. *Tree Physiology*, *16*, 25–32. https://doi.org/10.1093/treephys/16.1-2.25

Harper, J. L., & White, J. (1974). The demography of plants. *Annual Review of Ecology and Systematics*, *5*, 419–463. https://doi.org/10.1146/annurev.es.05.110174.002223

Heberling, J. M., McDonough MacKenzie, C., Fridley, J. D., Kalisz, S., & Primack, R. B. (2019). Phenological mismatch with trees reduces wildflower carbon budgets. *Ecology Letters*, *22*, 612–623. https://doi.org/10.1111/ele.13224

Holmgren, M., Scheffer, M., & Huston, M. A. (1997). The interplay of facilitation and competition in plant communities. *Ecology*, *78*, 1966–1975. https://doi.org/10.1890/0012-9658(1997)078%5B1966:TIOFAC%5D2.0.CO;2

Huang, C. W., Chu, C. R., Hsieh, C. I., Palmroth, S., & Katul, G. G. (2015). Wind-induced leaf transpiration. *Advances in Water Resources*, *86*, 240–255. https://doi.org/10.1016/j.advwatres.2015.10.009

Hylander, K. (2005). Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology*, *42*, 518–525. https://doi.org/10.1111/j.1365-2664.2005.01033.x

Hylander, K., Ehrlén, J., Luoto, M., & Meineri, E. (2015). Microrefugia: Not for everyone. *Ambio*, *44*, 60–68. https://doi.org/10.1007/s13280-014-0599-3

Hylander, K., & Nemomissa, S. (2009). Complementary roles of home gardens and exotic tree plantations as alternative habitats for Ethiopian montane rainforest plant biodiversity. *Conservation Biology*, *23*, 400–409. https://doi.org/10.1111/j.1523-1739.2008.01097.x

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, & C. N. Zayas (Eds.). IPBES Secretariat. 56 pp.

Johansson, V., Lönnell, N., Rannik, Ü., Sundberg, S., & Hylander, K. (2016). Air humidity thresholds trigger active moss spore release to extend dispersal in space and time. *Functional Ecology*, *30*, 1196–1204. https://doi.org/10.1111/1365-2435.12606

Jonason, D., Franzen, M., & Ranius, T. (2014). Surveying moths using light traps: Effects of weather and time of year. *PLoS One*, *9*(3), e92453. https://doi.org/10.1371/journal.pone.0092453

Jucker, T., Hardwick, S. R., Both, S., Elias, D. M. O., Ewers, R. M., Milodowski, D. T., Swinfield, T., & Coomes, D. A. (2018). Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global Change Biology*, *24*, 5243–5258. https://doi.org/10.1111/gcb.14415

Jucker, T., Jackson, T. D., Zellweger, F., Swinfield, T., Gregory, N., Williamson, J., Slade, E. M., Phillips, J. W., Bittencourt, P. R. L., Blonder, B., Boyle, M. J. W., Ellwood, M. D. F., Hemprich-Bennett, D., Lewis, O. T., Matula, R., Senior, R. A., Shenkin, A., Svátek, M., & Coomes, D. A. (2020). A research agenda for microclimate ecology in human-modified tropical forests. *Frontiers in Forests and Global Change*, *2*, 92. https://doi.org/10.3389/ffgc.2019.00092

Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3835–3840. https://doi.org/10.1073/pnas.0808913106

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*, 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kingsolver, J. G. (2009). The well-temperatured biologist. *The American Naturalist*, *174*, 755–768. https://doi.org/10.1086/648310

Köchy, M., & Wilson, S. D. (1997). Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology*, *78*, 732–739. https://doi.org/10.1890/0012-9658(1997)078%5B0732:LDANDI%5D2.0.CO;2

Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B. K., Wang, B., Wasof, S., & Verheyen, K. (2019). The functional role of temperate forest understorey vegetation in a changing world. *Global Change Biology*, *2511*, 3625–3641. https://doi.org/10.1111/gcb.14756

Lantz, T. C., Marsh, P., & Kokelj, S. V. (2013). Recent shrub proliferation in the Mackenzie delta uplands and microclimatic implications. *Ecosystems*, *16*, 47–59. https://doi.org/10.1007/s10021-012-9595-2

Latimer, C. E., & Zuckerberg, B. (2017). Forest fragmentation alters winter microclimates and microrefugia in human-modified landscapes. *Ecography*, *40*, 158–170. https://doi.org/10.1111/ecog.02551

Laurance, W. F. (2004). Forest-climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *359*, 345–352. https://doi.org/10.1098/rstb.2003.1430

Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., Stouffer, P. C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H. L., Van Houtan, K. S., Zartman, C. E., Boyle, S. A., Didham, R. K., Andrade, A., & Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, *144*, 56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Lawrence, D., & Vandecar, K. (2015). Effects of tropical deforestation on climate and agriculture. *Nature Climate Change*, *5*, 27–36. https://doi.org/10.1038/nclimate2430

Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., Luoto, M., Maclean, I. M., Roupsard, O., Fuentes-Lillo, E., & García, R. A. (2020). SoilTemp: A global database of near-surface temperature. *Global Change Biology*, *26*, 6616–6629.

Lembrechts, J. J., Broeders, L., De Gruyter, J., Radujković, D., Ramirez-Rojas, I., Lenoir, J., & Verbruggen, E. (2020). A framework to bridge scales in distribution modeling of soil microbiota. *FEMS Microbiology Ecology*, *96*(5), fiaa051. https://doi.org/10.1093/femsec/fiaa051

Lembrechts, J. J., & Lenoir, J. (2020). Microclimatic conditions anywhere at any time! *Global Change Biology*, *26*(2), 337–339. https://doi.org/10.1111/gcb.14942

Lembrechts, J. J., & Nijs, I. (2020). Microclimate shifts in a dynamic world. *Science*, *368*, 711–712. https://doi.org/10.1126/science.abc1245

Lembrechts, J. J., Nijs, I., & Lenoir, J. (2019). Incorporating microclimate into species distribution models. *Ecography*, *42*, 1267–1279. https://doi.org/10.1111/ecog.03947

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*, 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, *40*, 253–266. https://doi.org/10.1111/ecog.02788

Leuzinger, S., & Körner, C. (2007). Tree species diversity affects canopy leaf temperatures in a mature temperate forest. *Agricultural and Forest Meteorology*, *146*, 29–37. https://doi.org/10.1016/j.agrformet.2007.05.007

Löbel, S., Mair, L., Lönnell, N., Schröder, B., & Snäll, T. (2018). Biological traits explain bryophyte species distributions and responses to forest fragmentation and climatic variation. *Journal of Ecology*, *106*(4), 1700–1713. https://doi.org/10.1111/1365-2745.12930

Maclean, I. M. D. (2020). Predicting future climate at high spatial and temporal resolution. *Global Change Biology*, *26*, 1003–1011. https://doi.org/10.1111/gcb.14876

Martin, T. A., Hinckley, T. M., Meinzer, F. C., & Sprugel, D. G. (1999). Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. *Tree Physiology*, *19*, 435–443. https://doi.org/10.1093/treephys/19.7.435

Matlack, G. R. (1993). Microenvironment variation within and among forest edge sites in the eastern United-States. *Biological Conservation*, *66*, 185–194. https://doi.org/10.1016/0006-3207(93)90004-K

McLaughlin, B. C., Ackerly, D. D., Zion Klos, P., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, *23*, 2941–2961. https://doi.org/10.1111/gcb.13629

MEA. (2005). *Millennium ecosystem assessment. Ecosystems and human well-being: Biodiversity synthesis*. World Resource Institute.

Meehl, G. A., & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st Century. *Science*, *305*, 994–997. https://doi.org/10.1126/science.1098704

Meeussen, C., Govaert, S., Vanneste, T., Haesen, S., Van Meerbeek, K., Bollmann, K., Brunet, J., Calders, K., Cousins, S. A., Diekmann, M., & Graae, B. J. (2021). Drivers of carbon stocks in forest edges across Europe. *Science of the Total Environment*, *759*, 143497.

Meineri, E., & Hylander, K. (2017). Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography*, *40*, 1003–1013. https://doi.org/10.1111/ecog.02494

Meleason, M. A., & Quinn, J. M. (2004). Influence of riparian buffer width on air temperature at Whangapoua Forest, Coromandel Peninsula, New Zealand. *Forest Ecology and Management*, *191*, 365–371. https://doi.org/10.1016/j.foreco.2004.01.016

Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O. P., Maltamo, M., Pusenius, J., & Packalen, P. (2014). Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests – An analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biology*, *20*, 1115–1125. https://doi.org/10.1111/gcb.12405

Mod, H. K., Scherrer, D., Luoto, M., & Guisan, A. (2016). What we use is not what we know: Environmental predictors in plant distribution models. *Journal of Vegetation Science*, *27*, 1308–1322. https://doi.org/10.1111/jvs.12444

Mollinari, M. M., Peres, C. A., & Edwards, D. P. (2019). Rapid recovery of thermal environment after selective logging in the Amazon. *Agricultural and Forest Meteorology*, *278*, 107637. https://doi.org/10.1016/j.agrformet.2019.107637

Nakamura, A., Kitching, R. L., Cao, M., Creedy, T. J., Fayle, T. M., Freiberg, M., Hewitt, C. N., Itioka, T., Koh, L. P., & Ma, K. & Malhi, Y. (2017). Forests and their canopies: Achievements and horizons in canopy science. *Trends in Ecology & Evolution*, *32*(6), 438–451. https://doi.org/10.1016/j.tree.2017.02.020

Nordberg, E. J., & Schwarzkopf, L. (2019). Heat seekers: A tropical nocturnal lizard uses behavioral thermoregulation to exploit rare microclimates at night. *Journal of Thermal Biology*, *82*, 107–114. https://doi.org/10.1016/j.jtherbio.2019.03.018

Ogée, J., Brunet, Y., Loustau, D., Berbigier, P., & Delzon, S. (2003). MuSICA, a CO_2, water and energy multilayer, multileaf pine forest model: Evaluation from hourly to yearly time scales and sensitivity analysis. *Global Change Biology*, *9*, 697–717. https://doi.org/10.1046/j.1365-2486.2003.00628.x

Ohler, L.-M., Lechleitner, M., & Junker, R. R. (2020). Microclimatic effects on alpine plant communities and flower-visitor interactions. *Scientific Reports*, *10*, 1366. https://doi.org/10.1038/s41598-020-58388-7

Onaindia, M., Dominguez, I., Albizu, I., Garbisu, C., & Amezaga, I. (2004). Vegetation diversity and vertical structure as indicators of forest disturbance. *Forest Ecology and Management*, *195*, 341–354. https://doi.org/10.1016/j.foreco.2004.02.059

Parker, G. G. (1995). Structure and microclimate of forest canopies. In M. D. Lowman & N. M. Nadkarni (Eds.), *Forest canopies* (pp. 73–106). Academic Press.

Pausata, F. S. R., Gaetani, M., Messori, G., Berg, A., de Souza, D. M., Sage, R. F., & deMenocal, P. B. (2020). The greening of the Sahara: Past changes and future implications. *One Earth*, *2*, 235–250.

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*(7), 673–677. https://doi.org/10.1038/nclimate1858

Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., Abeli, T., Orsenigo, S., & Carbognani, M. (2019). Litter decomposition: Effects of temperature driven by soil moisture and vegetation type. *Plant and Soil*, *435*(1–2), 187–200. https://doi.org/10.1007/s11104-018-3889-x

Phillips, J. W., Chung, A. Y. C., Edgecombe, G. D., & Ellwood, M. D. F. (2020). Bird's nest ferns promote resource sharing by centipedes. *Biotropica*, *52*, 335–344. https://doi.org/10.1111/btp.12713

Potter, K. A., Arthur Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, *19*, 2932–2939. https://doi.org/10.1111/gcb.12257

Raupach, M. R. (1989). A practical Lagrangian method for relating scalar concentrations to source distributions in vegetation canopies. *Quarterly Journal of the Royal Meteorological Society*, *115*, 609–632. https://doi.org/10.1002/qj.49711548710

Riutta, T., Slade, E. M., Bebber, D. P., Taylor, M. E., Malhi, Y., Riordan, P., Macdonald, D. W., & Morecroft, M. D. (2012). Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. *Soil Biology and Biochemistry*, *49*, 124–131. https://doi.org/10.1016/j.soilbio.2012.02.028

Rousseau, L., Venier, L., Aubin, I., Gendreau-Berthiaume, B., Moretti, M., Salmon, S., & Handa, I. T. (2019). Woody biomass removal in harvested boreal forest leads to a partial functional homogenization of soil mesofaunal communities relative to unharvested forest. *Soil Biology and Biochemistry*, *133*, 129–136. https://doi.org/10.1016/j.soilbio.2019.02.021

Russo, S., Sillmann, J., & Fischer, E. M. (2015). Top ten European heatwaves since 1950 and their occurrence in the coming decades. *Environmental Research Letters*, *10*, 12.

Scheffers, B. R., Brunner, R. M., Ramirez, S. D., Shoo, L. P., Diesmos, A., & Williams, S. E. (2013). Thermal buffering of microhabitats is a critical factor mediating warming vulnerability of frogs in the Philippine Biodiversity Hotspot. *Biotropica*, *45*, 628–635. https://doi.org/10.1111/btp.12042

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, *20*, 495–503. https://doi.org/10.1111/gcb.12439

Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R., Roslan, N., Rogers, A. M., Haugaasen, T., Wright, P., & Williams, S. E. (2017). Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, *49*, 35–44. https://doi.org/10.1111/btp.12355

Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A., & Williams, S. E. (2013). Increasing arboreality with altitude: A novel biogeographic dimension. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1770), 20131581.

Scheffers, B. R., Phillips, B. L., & Shoo, L. P. (2014). Asplenium bird's nest ferns in rainforest canopies are climate-contingent refuges for frogs. *Global Ecology and Conservation*, *2*, 37–46. https://doi.org/10.1016/j.gecco.2014.06.004

Schilperoort, B., Coenders-gerrits, M., Rodríguez, C. J., Van Der Tol, C., Van De Wiel, B., & Savenije, H. (2020). Decoupling of a Douglas fir canopy: A look into the subcanopy with continuous vertical temperature profiles. *Biogeosciences*, *17*, 6423–6439. https://doi.org/10.5194/bg-17-6423-2020

Schmidt, M., Jochhim, H., Kersebaum, K. C., Lischeid, G., & Nendel, C. (2017). Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes – A review. *Agricultural and Forest Meteorology*, *232*, 659–671. https://doi.org/10.1016/j.agrformet.2016.10.022

Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., & Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 10595–10600. https://doi.org/10.1073/pnas.1604824113

Seidl, C. M., Basham, E. W., Andriamahohatra, L. R., & Scheffers, B. R. (2020). Bird's nest fern epiphytes facilitate herpetofaunal arboreality and climate refuge in two paleotropic canopies. *Oecologia*, *192*(2), 297–309. https://doi.org/10.1007/s00442-019-04570-2

Selva, N. N. S., Chylarecki, P., Jonsson, B. G., & Ibisch, P. L. (2020). Misguided forest action in EU Biodiversity Strategy. *Science*, *368*, 1438–1439. https://doi.org/10.1126/science.abc9892

Senf, C., & Seidl, R. (2020). Mapping the forest disturbance regimes of Europe. *Nature Sustainability*, *4*(1), 63–70.

Senior, R. A., Hill, J. K., González del Pliego, P., Goode, L. K., & Edwards, D. P. (2017). A pantropical analysis of the impacts of forest degradation and conversion on local temperature. *Ecology and Evolution*, *7*, 7897–7908. https://doi.org/10.1002/ece3.3262

Silva Junior, C. H. L., Aragao, L. E., Anderson, L. O., Fonseca, M. G., Shimabukuro, Y. E., Vancutsem, C., Achard, F., Beuchle, R., Numata, I., Silva, C. A., & Maeda, E. E. (2020). Persistent collapse of biomass in Amazonian forest edges following deforestation leads to unaccounted carbon losses. *Science Advances*, *6*, eaaz8360. https://doi.org/10.1126/sciadv.aaz8360

Slavich, E., Warton, D. I., Ashcroft, M. B., Gollan, J. R., & Ramp, D. (2014). Topoclimate versus macroclimate: How does climate mapping methodology affect species distribution models and climate change projections? *Diversity and Distributions*, *20*, 952–963. https://doi.org/10.1111/ddi.12216

Spracklen, D. V., Arnold, S. R., & Taylor, C. M. (2012). Observations of increased tropical rainfall preceded by air passage over forests. *Nature*, *489*, 282–285. https://doi.org/10.1038/nature11390

Sprugel, D. G., Rascher, K. G., Gersonde, R., Dovčiak, M., Lutz, J. A., & Halpern, C. B. (2009). Spatially explicit modeling of overstory manipulations in young forests: Effects on stand structure and light. *Ecological Modelling*, *220*, 3565–3575. https://doi.org/10.1016/j.ecolmodel.2009.07.029

Staal, A., Flores, B. M., Aguiar, A. P. D., Bosmans, J. H. C., Fetzer, I., & Tuinenburg, O. A. (2020). Feedback between drought and deforestation in the Amazon. *Environmental Research Letters*, *15*, 044024. https://doi.org/10.1088/1748-9326/ab738e

Stewart, K. J., & Mallik, A. U. (2006). Bryophyte responses to microclimatic edge effects across riparian buffers. *Ecological Applications*, *16*, 1474–1486. https://doi.org/10.1890/1051-0761(2006)016%5B1474:BRTMEE%5D2.0.CO;2

Su, Y., Liu, L., Liao, J., Wu, J., Ciais, P., Liao, J., He, X., Liu, X., Chen, X., Yuan, W., Zhou, G., & Lafortezza, R. (2020). Phenology acts as a primary control of urban vegetation cooling and warming: A synthetic analysis of global site observations. *Agricultural and Forest Meteorology*, *280*, 107765. https://doi.org/10.1016/j.agrformet.2019.107765

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., … Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*, 58–67. https://doi.org/10.1111/1365-2745.12025

Swanson, A. C., Schwendenmann, L., Allen, M. F., Aronson, E. L., Artavia-León, A., Dierick, D., & Zelikova, T. J. (2019). Welcome to the Atta world: A framework for understanding the effects of leaf-cutter ants on ecosystem functions. *Functional Ecology*, *33*, 1386–1399. https://doi.org/10.1111/1365-2435.13319

Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Putting the heat on tropical animals. *Science*, *320*, 1296–1297. https://doi.org/10.1126/science.1159328

Trumbore, S., Brando, P., & Hartmann, H. (2015). Forest health and global change. *Science*, *349*, 814–818. https://doi.org/10.1126/science.aac6759

Uriarte, M., Schwartz, N., Powers, J. S., Marín-Spiotta, E., Liao, W., & Werden, L. K. (2016). Impacts of climate variability on tree demography in second growth tropical forests: The importance of regional context for predicting successional trajectories. *Biotropica*, *48*, 780–797. https://doi.org/10.1111/btp.12380

Valladares, F., & Guzmán, B. (2006). Canopy structure and spatial heterogeneity of understory light in an abandoned Holm oak woodland. *Annals of Forest Science*, *63*, 749–761. https://doi.org/10.1051/forest:2006056

Vanwalleghem, T., & Meentemeyer, R. K. (2009). Predicting forest microclimate in heterogeneous landscapes. *Ecosystems*, *12*, 1158–1172. https://doi.org/10.1007/s10021-009-9281-1

Vickery, W. L., & Rivest, D. (1992). The influence of weather on habitat use by small mammals. *Ecography*, *15*(2), 205–211. https://doi.org/10.1111/j.1600-0587.1992.tb00026.x

von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., & Gilliam, F. (2013). Microclimate in forests with varying leaf area index and soil moisture: Potential implications for seedling establishment in a changing climate. *Journal of Ecology*, *101*(5), 1201–1213. https://doi.org/10.1111/1365-2745.12121

Wang, S., Ruan, H., & Han, Y. (2010). Effects of microclimate, litter type, and mesh size on leaf litter decomposition along an elevation gradient in the Wuyi Mountains, China. *Ecological Research*, *25*, 1113–1120. https://doi.org/10.1007/s11284-010-0736-9

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*(4), 385–397. https://doi.org/10.2307/2389612

Wikström, L., Milberg, P., & Bergman, K. O. (2009). Monitoring of butterflies in semi-natural grasslands: Diurnal variation and weather effects. *Journal of Insect Conservation*, *13*(2), 203–211. https://doi.org/10.1007/s10841-008-9144-7

Woods, C. L., Cardelús, C. L., & DeWalt, S. J. (2015). Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. *Journal of Ecology*, *103*, 421–430. https://doi.org/10.1111/1365-2745.12357

Xing, S., Bonebrake, T. C., Tang, C. C., Pickett, E. J., Cheng, W., Greenspan, S. E., Williams, S. E., & Scheffers, B. R. (2016). Cool habitats support darker and bigger butterflies in Australian tropical forests. *Ecology and Evolution*, *6*, 8062–8074. https://doi.org/10.1002/ece3.2464

Yuan, F. L., Freedman, A. H., Chirio, L., LeBreton, M., & Bonebrake, T. C. (2018). Ecophysiological variation across a forest-ecotone gradient produces divergent climate change vulnerability within species. *Ecography*, *41*(10), 1627–1637. https://doi.org/10.1111/ecog.03427

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecky, M., Malis, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., & De Frenne, P. (2019). Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, *28*, 1774–1786. https://doi.org/10.1111/geb.12991

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., & Coomes, D. (2019). Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution*, *34*, 327–341. https://doi.org/10.1016/j.tree.2018.12.012

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*, 772–775. https://doi.org/10.1126/science.aba6880

Zhang, Q., Barnes, M., Benson, M., Burakowski, E., Oishi, A. C., Ouimette, A., Sanders-DeMott, R., Stoy, P. C., Wenzel, M., Xiong, L., Yi, K., & Novick, K. A. (2020). Reforestation and surface cooling in temperate zones: Mechanisms and implications. *Global Change Biology*, *26*(6), 3384–3401. https://doi.org/10.1111/gcb.15069

Zhang, Q., & Zak, J. C. (1995). Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology*, *76*, 2196–2204. https://doi.org/10.2307/1941693

Zweifel, R., Böhm, J. P., & Häsler, R. (2002). Midday stomatal closure in Norway spruce – Reactions in the upper and lower crown. *Tree Physiology*, *22*, 1125–1136. https://doi.org/10.1093/treephys/22.15-16.1125

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: De Frenne P, Lenoir J, Luoto M, et al. Forest microclimates and climate change: Importance, drivers and future research agenda. *Glob Change Biol*. 2021;00:1–19. https://doi.org/10.1111/gcb.15569