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

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# 1 Forest microclimates and climate change: importance, 2 drivers and future research agenda

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5 Running title: Microclimates in forests  
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39

40 Abstract

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

61

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

64 Introduction: the importance of forest microclimates

65 Forest organisms living below or within tree canopies experience distinct climatic conditions that deviate  
66 considerably from the climate outside forests (Chen et al. 1999; Geiger et al. 2009; De Frenne et al. 2019).  
67 Below forest canopies, direct sunlight and wind speed are strongly reduced, leading to a dampening of  
68 temperature and humidity variations. Temperature extremes are often strongly buffered in forests  
69 compared to open habitats, with cooler below-canopy maximum temperatures, warmer minimum  
70 temperatures, and lower seasonal and inter-annual variability (Ewers & Banks-Leite, 2013; von Arx et al.  
71 2013, De Frenne et al. 2019) (see Fig. 1 and Box 1 for the definitions of technical terms used in this paper).  
72 The magnitude of such positive and negative temperature differences or offsets between open lands and  
73 forest interiors can vary due to both the structure of the forest, the ambient temperatures and the local  
74 water balance (McLaughlin et al. 2017; Davis et al. 2019; De Frenne et al. 2019). The structural complexity  
75 of forests creates heterogeneous microclimates at a fine spatiotemporal scale.

76

77 The physiological and ecological importance of forest microclimates has long been recognized (Grubb,  
78 1977; Geiger et al. 2009, a book with a first edition already published in 1927). Forests harbor the majority  
79 of terrestrial biodiversity, and, due to the increasing biodiversity loss in response to current macroclimatic  
80 warming, studies on forest microclimates are receiving much attention in global change biology (Fig. 2).  
81 However, most studies on forest biodiversity rely on gridded macroclimate data that are based on free-air  
82 temperature data from weather stations in open areas outside forests, thus neglecting forest microclimate  
83 variation in space and over time (Potter et al. 2013; Barry & Blanken, 2016; De Frenne & Verheyen, 2015).  
84 This discrepancy of spatiotemporal scales of forest microclimate data may bias the quantification of climate  
85 change impacts on forest biodiversity and functioning (Zellweger et al. 2020). Forests and their understories  
86 harbour the majority of terrestrial biodiversity, and are essential for the provision of many ecosystem  
87 services. Thus, addressing the uncertainties is a fundamental task for global change biologists, land  
88 managers, and policy makers alike (MEA, 2005; Landuyt et al. 2019; IPBES, 2020).

89

90 Viewing forest ecology through a microclimate lens can help tease out mechanistic relationships of  
91 organisms with their environment. Buffered forest microclimates and the microhabitats within forests (e.g.,  
92 root caverns, tree holes, fallen trunks) enable organisms to avoid extreme heat and drought (Kearney et al.  
93 2009; Scheffers et al. 2013a, 2014b). The microclimate buffering capacity of forests may provide climatic  
94 microrefugia during macroclimate warming (Ewers and Banks-Leite, 2013; von Arx et al. 2013, Lenoir et  
95 al. 2017, De Frenne et al. 2019). Therefore, the pressure on individuals, populations, species and  
96 communities to respond to rapid anthropogenic climate change may be reduced, at least in the short term,  
97 by the presence of climatic microrefugia for cold-adapted organisms (Keppel et al. 2012; Ashcroft et al.  
98 2012; Hampe & Jump, 2011; Lenoir et al. 2017; Greiser et al. 2019). Through these mechanisms, forest  
99 microclimates can determine the distribution of individuals, populations, and species. Thus, incorporating  
100 microclimates into species distribution models is expected to significantly improve the accuracy of  
101 predictions (Slavich et al. 2014; Lembrechts et al. 2019; Zellweger et al. 2019b). The forest microclimate is  
102 also a driver of species interactions. Low light availability and heterogeneous moisture can enhance plant  
103 competition (Connell, 1983; Gerhardt, 1996), although microclimates can also facilitate co-existence, such  
104 as when shade offers refuge to mixed-species seedling assemblages (Holmgren et al. 1997), or when  
105 centipedes share epiphytic ferns as cool and moist nest sites (Phillips et al. 2020). In some cases, species  
106 interactions can result in a re-engineering of the microclimate environment itself, for example canopy gaps  
107 produced by leaf-cutter ant herbivory (Swanson et al. 2019). Microclimate therefore shapes – and in turn,  
108 is shaped by – the composition of forest communities (Parker, 1995; Woods et al. 2015; Frey et al. 2016a,  
109 Jucker et al. 2018).

110

111 At the ecosystem level, microclimate is of paramount importance as a key regulator of many ecosystem  
112 functions. Rates of litter decomposition, carbon sequestration and microbial activity tend to be greater in

113 forests than in neighbouring open habitats (Riutta et al. 2012; Wang et al. 2010; Chen et al. 2018, but see  
114 Köchy & Wilson, 1997), and also vary spatially within forests due to, among other things, gap dynamics  
115 (Zhang & Zak, 1995). Tree recruitment, via seedling growth and sapling survival, is heavily contingent upon  
116 microclimatic conditions (Ausseinac 2000; Campanello et al. 2007; Harper & White, 1974). While some  
117 forest trees regenerate best after disturbances and canopy opening, other species recruit under the canopy  
118 and in such cases understorey conditions shaped by trees in the overstorey eventually feedback to tree  
119 recruitment and future forest structure. Therefore, threats to forest biodiversity and functioning from  
120 deforestation, forest degradation, and fragmentation are inherently linked to the loss and modification of  
121 forest microclimates by these activities (Chen et al. 1999; Jucker et al. 2020; Laurance et al. 2011).

122

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

139

140 Drivers of vertical and horizontal microclimate variation

141 *Horizontal distribution of microclimates: forest vs open habitats*

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

152

153 Evaporative cooling and emitted longwave radiation both act to reduce canopy and soil surface  
154 temperatures whereas net shortwave radiation acts to warm the soil and canopy surfaces (Geiger et al. 2009;  
155 De Frenne et al. 2013). Heat exchange of surfaces with the air may contribute to warming or cooling  
156 depending on the temperature difference between the air and the surfaces (Huang et al. 2015). The  
157 efficiency of these sensible heat fluxes and of evaporative cooling (latent heat fluxes) varies with wind and  
158 turbulence conditions. Moreover, the local and regional hydroclimate of the system is crucial as well. Both  
159 canopy cover and evapotranspiration are contingent on the short and long-term availability of water.  
160 Indeed, in non-energy limited systems, the ability of forests to produce microclimates is principally a  
161 function of water availability, its role in shaping the energy balance at a site, and its dynamics through time

162 (e.g. McLaughlin et al. 2017; Davis et al. 2019). Vegetation structure and composition affect these processes  
163 of heat exchange and cause a horizontal variation in buffering of ambient temperatures (Fig. 3). In  
164 particular, vegetation density (e.g., in terms of canopy cover, basal area, plant area index) via effects on  
165 albedo, evapotranspiration and radiation absorption and reflection have strong influences on understory  
166 microclimate, especially in the warm season (Greiser et al. 2018, Zellweger et al. 2019a). However, the  
167 cooling effect by evapotranspiration might diminish under very dry (or cold) conditions (Davis et al. 2019).  
168 In highly seasonal climates forests The vertical and horizontal composition and distribution of forest  
169 canopies (e.g., gaps, tree age distribution, leaf clumping, distance to forest edge) directly affect the amount  
170 and variability of sunlight (Sprugel et al. 2009; Valladares & Guzman, 2006). At the stand level, small-scale  
171 variations in sun-flecks cause strong gradients in near-ground temperatures and there are often strong  
172 microclimatic gradients towards forest edges, due to increased solar radiation and wind (Matlack, 1993).  
173 Microclimate gradients from forest core to edge are very large (up to several degrees), can penetrate 50 –  
174 100 m into the forest matrix (Schmidt et al. 2017), but differ strongly among microclimatic variables (e.g.,  
175 light, wind, temperature), and are impacted by the edge orientation (Hylander, 2005), the cloudiness (e.g.,  
176 Chen et al. 1993), the slope of the terrain or the wind direction (Davies-Colley et al. 2000) and the biome  
177 (e.g. tropical vs temperate forests).

178  
179 This horizontal distribution in microclimate buffering varies not only at the stand scale, but also at  
180 landscape, continental and global scales. The effects of landscape topography on near-ground temperatures  
181 can be attributed to variations in incoming solar radiation driven by slope and aspect, pooling of cold air in  
182 depressions and exposure to winds, variations in soil moisture, and the adiabatic lapse rate due to elevational  
183 gradients, all of which have been well documented (Ashcroft et al. 2008; Dobrowski, 2011; Aalto et al. 2017;  
184 Meineri & Hylander 2017; Bramer et al. 2018; Davis et al. 2019). At the continental scale, air-mixing and  
185 lateral heat transfer by wind decrease when moving further away from the coast and mountain chains,  
186 which, together with fewer cloudy days, commonly leads to larger magnitudes of the temperature offsets in  
187 continental lowland forests (Zellweger et al. 2019a). Moreover, regional precipitation patterns and the size  
188 and adjacency to water bodies influence latent and sensible heat fluxes (Meleason & Quinn, 2004; Zellweger  
189 et al. 2019a). At the global scale, the largest buffering of maximum temperatures is found in tropical forests,  
190 whereas buffering of cold extremes is largest in boreal forests (De Frenne et al. 2019), due to differences in  
191 forest structure, sun angle, seasonality and snow cover., Therefore, drivers of forest microclimates differ  
192 across latitudes (Fig. 3).

193  
194 *Vertical distribution of microclimates: from the ground to the top of the canopy*  
195 In open areas, air temperature at 1-2 m above ground is mostly controlled by local topography, radiation  
196 balance and turbulent mixing of air. Inside forests, however, canopy elements interfere with these processes  
197 by influencing radiation fluxes into and out of the forest as well as decreasing turbulent mixing of air  
198 through decreased wind speeds (Chen et al. 1993; Chen et al. 1999). Vertical temperature gradients inside  
199 forests are the result of a complexity of microclimatic layers, formed and controlled in large part by the  
200 vegetation itself (Fig. 4; Vanwalleghem et al. 2009; Davies-Colley et al. 2000). Forest management can  
201 influence the vertical structure of the vegetation with implications on the vertical microclimate profile  
202 (Onaindia et al. 2004).

203  
204 Air temperature differences between ground and canopy range from 0.15 to 0.25 °C m<sup>-1</sup> in temperate  
205 coniferous and mixed hardwood–conifer and tropical forests (Harley et al. 1996; Zweifel et al. 2002;  
206 Hardwick et al. 2015; Bauerle et al. 2009). During the day, air temperature peaks can occur near the ground,  
207 but are most often located within the top canopy, where most of the incoming energy is absorbed (Chen  
208 et al. 1999; Didham & Ewers, 2014) (Fig. 4). The exact vertical location of air temperature maxima will  
209 depend on the density of the canopy (leaf and plant area index as a function of height) and on the intensity  
210 of turbulent air mixing (Fig. 4). However, even when understory air is cooler than above-canopy air, leaf

211 and litter temperatures can rise well above the local air temperature in the understorey of open forests, due  
212 to decreased wind speeds and absorption of shortwave radiation (Martin et al. 1999; Scheffers et al. 2017).  
213 Leuzinger & Körner (2007) showed that leaf temperature regimes in canopies vary enormously over short  
214 vertical distances in several coniferous and deciduous broad-leaved tree species. Finally, snow cover in the  
215 winter will effectively decouple the near ground temperature from the temperature above the snow (Fig.  
216 1).

217

#### 218 Consequences of microclimates for forest biodiversity

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

227

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

236

#### 237 *Spatial impacts of forest microclimate on biodiversity*

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

258

#### 259 *Temporal impacts of forest microclimate on biodiversity*

260 Organisms also partition their niches according to microclimates in time (Jonason et al. 2014). Daily cycles  
261 of organism activity are apparent in Lepidopterans with butterflies primarily active during the day and moths  
262 active at night. However, activity can also vary within the day with activity peaks adapted to the actual  
263 temperature and species' thermal limits (Wikström et al. 2009), a threshold that differs spatially from open  
264 habitats to closed forests (Xing et al. 2016). Similarly, leaf litter lizards will exploit sunspots or rare  
265 microclimates for thermoregulation, but only during cold morning hours (Nordberg & Schwarzkopf, 2019).  
266 Here, lizard activity varies with thermal heterogeneity driven both in time and by topographic roughness  
267 and aspect (Sears et al. 2016). The dispersal mechanism of a moss is suggested to be most effective in  
268 morning hours when the moisture decreases along with increasing temperatures and wind (Johansson et al.  
269 2016). At a weekly or monthly scale, weather patterns strongly influence small mammal habitat use and  
270 activity (Vickery & Rivest, 1992). Seasonal shifts in activity are apparent with regional and local climates.  
271 For example, arboreal frog communities shift from being highly vertically stratified in the tree canopies  
272 during the cooler, wet season to dramatically accumulating in the understorey during the hotter, dry season  
273 (Basham & Scheffers, 2019).

274

#### 275 Consequences of microclimates on forest functioning

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

295

#### 296 How will macroclimate warming affect forest microclimates?

297 How macroclimate warming affects forest microclimate dynamics, and vice versa, remains an open question  
298 in global change ecology (Lenoir et al. 2017; De Frenne et al. 2019). For instance, it is unclear whether the  
299 magnitude of temperature offset between macroclimate and forest microclimates (De Frenne et al. 2019)  
300 will remain stable, increase or decrease over time as macroclimate warms. As discussed previously, the  
301 magnitude of the temperature offset between forests and open habitats depends on ambient, macroclimatic  
302 conditions: forest offsets of maximum temperatures increase with ambient temperatures as long as the local  
303 water availability does not constrain evaporation and evapotranspiration (Davis et al. 2019; De Frenne et  
304 al. 2019; Su et al. 2020; Zhang et al. 2020). Assuming a space-for-time substitution, this suggests that the  
305 magnitude of the offset on maximum temperature could potentially increase under macroclimate warming  
306 (Fig. 1 and Fig. 5). This assumption only holds if: (i) the relationship between offsets and macroclimate  
307 continues to be linear; (ii) the forest canopy layer is not disturbed; (iii) we assume that the equilibrium point  
308 at which temperatures inside and outside forests are the same (cf. Fig. 1), does not shift; and (iv) other



309 variables such as soil moisture levels remain comparable (Scheffers et al. 2014b; Zellweger et al. 2020). Slow,  
310 interannual climate change can, however, directly change the equilibrium point, while changes in canopy  
311 cover, moisture, etc. could directly act on the buffering and hence slope (Fig. 1). The future buffering  
312 capacity will be also highly contingent upon the changes in the hydrological conditions, which both directly  
313 shape the vegetation and indirectly the possibility for evaporative cooling (McLaughlin et al. 2017; Davis et  
314 al. 2019). Indeed, temperature offsets are larger with increased temperature because the vapour pressure  
315 deficit (VPD) and evapotranspiration increase non-linearly with temperature and thus the differential  
316 between forested and non-forested sites is amplified at higher temperatures, as long as water is available for  
317 evapotranspiration. Nevertheless, if macroclimatic increases in daily maximum temperatures can be  
318 buffered, it might provide forest organisms with more time for adaptation and migration (Zellweger et al.  
319 2020), a phenomenon that is comparable to the concept of microrefugia (that is, spatially-restricted habitats  
320 that sustain a favourable microclimate, which enables species to persist in an otherwise inhospitable matrix;  
321 Gavin et al. 2014). The pattern is opposite for minimum temperatures: higher ambient air temperatures  
322 decrease minimum temperature offsets (De Frenne et al. 2019). Hence, still under the assumptions of a  
323 space-for-time substitution, the magnitude of the offset in minimum temperature could potentially decrease  
324 under macroclimate warming, contributing to reduce the buffering effect on minimum temperature and  
325 thus alter the microrefugial capacities of boreal forests for cold-adapted species surviving at the warmer  
326 range margin (Fig. 5). In the following subsections, we first discuss changes in forest microclimate dynamics  
327 due to macroclimate warming in different forest biomes, and then the potential impacts of macroclimate  
328 warming on future offsets.

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

330 In temperate forests, temperature buffering may happen for both maximum and minimum temperatures  
331 (De Frenne et al. 2019). Yet, during the cold season, deciduous trees shed their leaves, the primary drivers  
332 of buffering, making buffering in temperate forests likely to be more important and relevant during the  
333 growing season. Additionally, Zellweger et al. (2019a) showed that the magnitude of the thermal offset  
334 during the summer season in European temperate forests was more pronounced for daily maximum  
335 temperatures than for daily minimum temperatures. As a consequence, canopy cover density directly affects  
336 buffering capacity, with likely implications on organismal responses to climate change. For example, the  
337 thermophilisation rate – the rate of community shift towards more warm-adapted species – in understorey  
338 plant communities of temperate forests is better related to the rate at which the daily maximum temperature  
339 changes in forest interiors (i.e. the rate of microclimate warming) during the growing season than the rate  
340 of macroclimate warming (Zellweger et al. 2020). In boreal forests, buffering of minimum temperatures is  
341 most pronounced, while tropical forests have more pronounced offsets of maximum temperatures (De  
342 Frenne et al. 2019). Albeit the velocity of macroclimate warming is highest at high latitudes, tropical species  
343 might also be severely impacted due to their narrow thermal niches and safety margins, particularly when  
344 far removed from higher elevation habitat and given the shallowness of latitudinal temperature gradients in  
345 the tropics (Tewksbury et al. 2008; Antão et al. 2020; Lenoir et al. 2020). Worryingly, daily maximum  
346 temperatures in the next decades will likely be more extreme than what tropical species have ever  
347 experienced in their recent evolutionary history (Deutsch et al. 2008; Kingsolver, 2009).

#### 348 *Macroclimate warming effects on temperature offsets*

349 In their review covering the second half of the 20th century, Boisvenue & Running (2006) reported that  
350 both satellite and ground-based data support an increase in forest productivity across many temperate parts  
351 of the globe owing to climate warming. Hence, at temperate latitudes, forests with ample water and soil  
352 nutrients may become denser, thereby increasing temperate forest offsets (Zellweger et al. 2020). On the  
353 other hand, recent reports show cross-European canopy opening due to an increase in natural and  
354 anthropogenic disturbances (Senf & Seidl, 2020) and thus a potential reduction in temperature offset. And  
355 finally, as macroclimate warms, earlier timing of bud burst and leaf flush will impact the seasonal course of  
356  
357

358 forest microclimates, potentially leading to phenological mismatches between trees and understorey species  
359 (Heberling et al. 2019). Earlier leaf flush might effectively shorten the growing season for understorey  
360 plants, if shade levels are enhanced earlier in the season and the temperature sensitivity of phenological  
361 advances of wildflowers is lower than trees (Heberling et al. 2019).

362  
363 In the tropics, satellite-driven measures of vegetation greenness (NDVI), a surrogate for photosynthetic  
364 activity and productivity, show reduced productivity in warmer years (Braswell et al. 1997; Asner et al. 2000),  
365 suggesting a reduced future buffering capacity. Conversely, in boreal forests, the impact of changes in  
366 primary productivity on the buffering capacity of forests is less clear. On the one hand, old growth boreal  
367 forests in North America showed no net increase in stem growth (Giguère-Croteau et al. 2018). On the  
368 other hand, Beck et al. (2011) have reported changes in forest productivity across Alaska that are consistent  
369 with a complete biome shift: decreased productivity at the warmer (southern) versus enhanced productivity  
370 at the colder (northern) edge of the boreal biome. Thus, the buffering capacity of boreal forests may mirror  
371 the climatically-induced changes in primary productivity with the magnitude of the offsets decreasing and  
372 increasing towards the warmer and colder edge of the boreal zone, respectively.

#### 373 374 *Extreme event effects on temperature offsets*

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

#### 389 390 *Interactions between human land-use and macroclimate warming*

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

402  
403 In boreal forests, but possibly also in temperate and tropical forests, intensive forest management for timber  
404 and other woody biomass harvest has led to a biotic, genetic, structural and functional homogenization of  
405 forest stands across large spatial extents (Rousseau et al. 2019). The even aged single species stands typical  
406 of intensively managed forests and plantations have reduced the resilience of the whole system to, for

407 instance, increasing frequency and severity of climate-induced pest outbreaks and wildfires (Cudmore et al.  
408 2010; Gauthier et al. 2015). Although fires are part of the natural disturbance dynamics in many boreal  
409 systems, large stand-replacing wildfires have resulted in shrub proliferation and enhanced snow  
410 accumulation, with possible implications for longer decoupled ground temperatures (Lantz et al. 2013;  
411 Aalto et al. 2018) (Fig. 1 and Fig. 5).

412  
413 In the tropics, the combined effects of logging, droughts and fires on canopy loss (i.e., deforestation and  
414 degradation) can locally increase air dryness (Staal et al. 2020) and daily maximum temperatures more than  
415 the warming associated with high emission scenarios (Senior et al. 2017). Hence, by letting in direct sunlight  
416 and warm and dry air, large canopy gaps following deforestation strongly alter understory microclimate  
417 (Fig. 3 and 5), reducing the capacity to buffer macroclimatic fluctuations and thus causing many species to  
418 decline in abundance, e.g. termites that are especially sensitive to desiccation (Cornelius & Osbrink, 2010;  
419 see De Smedt et al. 2018 for a study from temperate forests). However, small canopy gaps (< 400 m<sup>2</sup>) in  
420 tropical forests, which occur under natural forest dynamics, can quickly regain their thermal environment  
421 in a few years (Mollinari et al. 2019), while secondary forests can regain their thermal environments within  
422 20 – 30 years after logging (del Pliego et al 2016). These drastic changes in microclimatic conditions are not  
423 only due to tree removal, but at a finer resolution also to epiphyte loss. Indeed, epiphytes represent a  
424 significant functional group for microclimate dynamics in tropical forests, reducing water loss through  
425 evaporative drying (Scheffers et al. 2014b) and providing buffered microhabitats for canopy-dwelling  
426 organisms (Seidl et al. 2020) (Fig. 3, arrow J).

#### 427 428 *Forest microclimate feedbacks on macroclimate warming*

429 Although we now have a better understanding of the impact of macroclimate warming on forest  
430 microclimate dynamics, the potential feedback of forest microclimates on macroclimate warming itself  
431 remains understudied (Barry & Blanken, 2016). Yet, the implications are important for solutions to mitigate  
432 and adapt to climate change. Changes in microclimates may feed back to the macroclimate by affecting  
433 localized water and carbon balances and microgradients of CO<sub>2</sub> within forests.

434  
435 The release of water vapor into the atmosphere by trees through transpiration affects local as well as  
436 regional precipitation patterns (Bonan, 2008; Spracklen et al. 2012). For instance, in the tropics, air that  
437 passed over extensive areas of forests produced at least twice as much rain as air that has passed over short  
438 or no vegetation (Spracklen et al. 2012). Regional tropical rainfall usually decreases (in quantity and  
439 frequency) after a threshold of 30 – 50 % deforestation, especially when large forest patches are cleared,  
440 while small clearings may actually enhance rainfall via convective processes leading to cloud formation  
441 (Lawrence & Vandecar, 2015). The importance of vegetation in land-atmosphere-ocean feedback processes  
442 is remarkably illustrated by the last Sahara desertification episode (c. 5000 yrs ago), when precipitation-  
443 vegetation feedbacks due to deforestation by humans are considered to have played a crucial role (Pausata  
444 et al. 2020). Studies on afforestation projects in the Saharan and Sahelian zones are limited to their role in  
445 mitigating the effects of warming by carbon drawdown, while their impacts on microclimates currently  
446 remain understudied (Pausata et al. 2020).

447  
448 Another example with feedbacks between forest cover and climate is the poleward expansion of boreal  
449 forests, which decreases the albedo and thus the ratio of incoming and outgoing radiation (Bonan, 2008;  
450 Pearson et al. 2013), and increases snow depths, as a consequence of more shrubs, thus isolating the ground  
451 from deep frost during the winter leading to permafrost thaw (Lantz et al. 2013; Connon et al. 2018). The  
452 positive feedback on macroclimate warming is derived from permafrost thaw releasing stored carbon  
453 dioxide under aerobic conditions and methane under wet, anaerobic conditions (Fig. 5). This example links  
454 to the role of snow cover in decoupling the near-ground temperature from ambient temperatures and how  
455 forest structure moderates this (Fig. 1). However, in this example, shrubs act as accumulators of snow

456 because strong winds in the tundra remove snow from open areas, while in many other situations the snow  
457 cover and thus the buffering of near-ground temperatures is higher in open than in forested sites (Fig. 1  
458 and Fig. 5).

459  
460 A research agenda and identification of research gaps

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

467

#### 468 *1) Drivers of forest microclimate buffering and future changes*

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

489

#### 490 *2) Mapping and predictions of forest microclimates*

491 While the mechanisms driving the buffering between forest microclimate and macroclimate, and other  
492 global-change drivers get disentangled, focus should also go towards the creation of (1) open-access, free-  
493 to-use, global gridded products of forest microclimate and (2) automated protocols for past and future  
494 microscale geospatial data (Zellweger et al. 2019b; Lembrechts et al. 2020a). This can, for example, be  
495 achieved by applying correction factors based on the offset between micro- and macroclimate to existing  
496 macroclimate maps (e.g., WorldClim and CHELSA) (Fig. 6). Further increases in the spatial resolution of  
497 such microclimate maps is possible thanks to the recent emergence of both large-scale global databases of  
498 in-situ measured (forest) microclimate (De Frenne et al. 2019; Lembrechts et al. 2020a) as well as ever-  
499 higher resolution remotely-sensed global forest cover products (down to 30 m resolution, and better). More  
500 methodological development is, however, needed to incorporate the vertical and temporal components of  
501 forest microclimate in these mapping efforts, as reliable and repeated info about 3D forest structure (e.g.,  
502 using laser scanning) is only now becoming available, for instance via GEDI LiDAR data. Obtaining  
503 accurate microclimate time series for forest understories (for the past, present and future) are further  
504 complicated by the interactions between climate change and land use changes, as discussed in the previous

505 paragraph (Zellweger et al. 2020; Lembrecht & Nijs, 2020). Other important challenges are the dynamic  
506 nature of managed forest landscapes, how to incorporate wind effects in models of complex fragmented  
507 landscapes and, for global applications, the current computer power. Obtaining high-resolution long-term  
508 microclimate time series for the whole world requires effective assimilation of in-situ measurements, and  
509 mechanistic and statistical models. While existing mechanistic models of microclimate currently largely  
510 focus on open terrain (e.g., Maclean, 2020), this is a rapidly expanding field where workable solutions for  
511 forest microclimates can be expected in the near future. Complementing these models with in-situ  
512 measurements for calibration, and statistical models for global extrapolations, should be able to deliver the  
513 gridded projects we need (Lembrechts & Lenoir, 2020).

514

### 515 *3) Impacts on biodiversity and ecosystem functioning in forests*

516 In addition to characterizing the physiographic and biophysical processes that drive forest microclimates  
517 (Fig. 3-5) as well as developing approaches for mapping microclimate at appropriate scales (Fig. 6), careful  
518 thought is needed on how to best integrate these new data streams into biodiversity research (Jucker et al.  
519 2020). Access to climate data that better reflect local conditions experienced by living organisms should  
520 improve our ability to model species distributions and predict how they will respond to rapid global change  
521 (Mod et al. 2016; Lenoir et al. 2017; Lembrechts et al. 2019). However, few studies have actually tested this  
522 assumption (Lembrechts et al. 2019; Ohler et al. 2020), particularly in the context of forests (Frey et al.  
523 2016a). A key question that remains to be addressed is at what spatial (horizontal and vertical) and temporal  
524 scale microclimate should be measured and modelled, and how this varies for different groups of species  
525 (e.g., in relation to body size, dispersal and thermoregulation, Potter et al. 2013; Scheffers et al. 2014a).  
526 Similarly, we also need to determine which aspects of microclimate best predict species distributions in  
527 forests (e.g., air temperature, humidity, soil moisture, solar radiation) and how to effectively summarize  
528 these metrics (e.g., means, extremes, fluctuations, thresholds, growing degree hours/days; Hylander et al.  
529 2015; Bramer et al. 2018).

530

531 Empirical and modelling approaches that allow different facets of microclimate to be manipulated  
532 independently are crucial to addressing these questions (for an example to separate light and temperature  
533 effects, see De Frenne et al. 2015). Beyond the immediate need to better characterize how microclimate  
534 shapes current-day ecological processes in forests, a major challenge is to determine how long different  
535 types of forests can continue to act as microrefugia (also referred to as hold-outs in this context) for species  
536 in a warming world (Hannah et al. 2014). As global mean temperatures continue to rise, so too will those  
537 in forest understoreys (albeit slower if buffering is at play). But perhaps more importantly, long-term climate  
538 change in interaction with forest management will eventually lead to changes in the species composition  
539 and structure of forests (e.g., the number and size of trees, as well as canopy height and density) (Coomes  
540 et al. 2014; Albrich et al. 2020) – with clear cascading effects for understorey microclimate (Jucker et al.  
541 2018). Very few studies have effectively evaluated ecosystem multifunctionality, and translated this to  
542 services, let alone relate it to microclimates (e.g., of the type suggested by Byrnes et al. 2014). Although  
543 policy documents abound with statements about climate change mitigation and adaptation, there is a lack  
544 of understanding about forest (micro)climate and biodiversity, which might lead to misguided actions (Selva  
545 et al. 2020). There are thus large knowledge gaps in biodiversity – ecosystem functioning – microclimate  
546 research. While these longer-term effects of climate change on forest microrefugia have been largely  
547 overlooked, a promising avenue for exploring them would be to integrate microclimate projections into  
548 forest dynamics models used to simulate forests under future conditions (Albrich et al. 2020).

549

### 550 *Concluding remarks*

551 In sum, we have outlined the contemporary research interests and gaps linking microclimatic variation to  
552 biodiversity and the functioning of forest ecosystems worldwide. The urgency is clear; compelling evidence  
553 is accumulating to suggest that distinct below-canopy microclimatic conditions in forests arising from

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

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581

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939 Figure captions

940 Fig. 1. Definitions of the main processes underlying microclimate dynamics: offsets, buffering, coupling  
941 and decoupling. To be read in conjunction with Box 1.

942

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

945

946 Fig. 3. Multiple vegetation drivers of microclimate might be of different importance in forest at boreal  
947 (top), temperate (middle), and tropical (bottom) latitudes, respectively. It is important to note, however,  
948 that, most processes illustrated here for one biome often are also important in the other biomes. Increasing  
949 tree density from open non-forest habitats (A), to plantations with a simple canopy structure (B), to (semi-  
950 )natural forest with complex structure (C) reduces below-canopy wind speeds above ground. Forest  
951 canopies can reduce ground snow cover and thus decrease the insulating effect of snow cover on cool soil  
952 temperatures during the cold season (D). Vertical layering of vegetation (E) influences the amount and  
953 quality of incoming shortwave radiation, outgoing longwave radiation and moisture exchange. Disturbances  
954 can create canopy gaps (F), providing a local shift in microclimate. Seasonal reductions in canopy cover  
955 (tree phenology, G) during the cool and/or dry season increases the exposure of the internal forest to  
956 ambient conditions. Soil moisture is a driver of evaporation and evapotranspiration, thus being a key driver  
957 of the temperature buffering. During very dry conditions, the forest temperature offset might decrease.  
958 Forests also buffer the temporal (i.e. diurnal, seasonal and interannual) variability in temperature conditions  
959 relative to adjacent non-forest systems (bottom panel). This buffering effect varies with vegetation height  
960 and structure, with reduced buffering in secondary, post-agricultural forests (H) relative to primary or  
961 ancient, (semi-)natural forests (I). Microhabitats within a forest, such as those created by epiphytic plants  
962 (J) can offer an even more buffered microclimate, critical for the ecology and physiology of many forest  
963 species. nally, the temperature offset in forests can change throughout the diel cycle, with cooler forest  
964 interiors vs. open areas during the day (K) and warmer at night (L). For the sake of simplicity, we chose to  
965 depict wind, shortwave radiation, and temperature in the boreal, temperate, and tropical panel, respectively.  
966 However, of course all of these microclimate variables can be relevant to systems across latitudes.

967

968 Fig. 4. Typical vertical air temperature profiles inside forests of various canopy depth and density, during  
969 nighttime and daytime and for cloudy or clear sky conditions. These typical examples are mainly based on  
970 e.g. Roberts et al. (1990), Chen et al. (1999), Ogée et al. (2003), Geiger et al. (2009), and Brower et al. (2011).

971

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

977

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

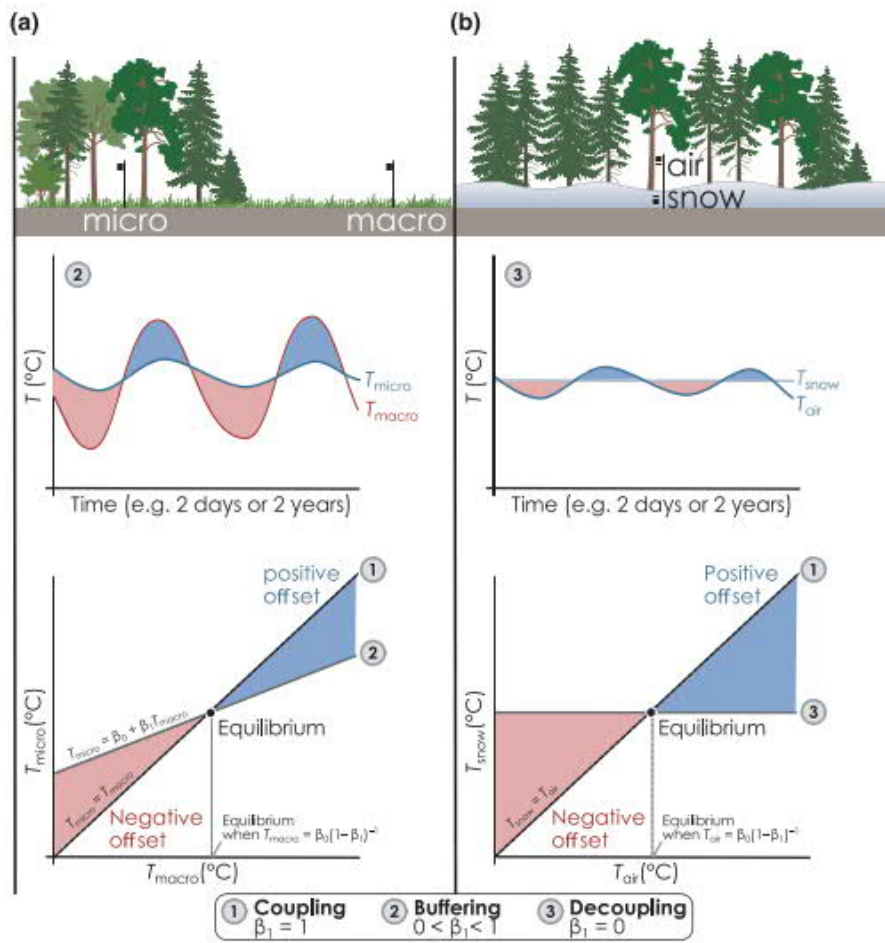
984 Box 1 Definitions of offsets, buffering, coupling and decoupling

985 Many terms related to microclimate dynamics have been used in the scientific literature, such as 'buffering',  
986 'coupling', 'decoupling' and 'offset' to imply divergence from macroclimatic fluctuations over time.  
987 However, no uniform definition of these terms exists yet. For this reason, we here suggest a uniform  
988 terminology including all terms by illustrating the processes behind each of them (Fig. 1).  
989

990 First of all, we define the temperature offset as the instantaneous difference between a reference  
991 temperature at a given time  $t_0$  and the focal temperature under study at the same time  $t_0$ . For instance, the  
992 horizontal temperature offset due to the presence of a forest canopy is the instantaneous difference between  
993 the free-air temperature in open conditions (i.e., macroclimate) and the sub-canopy temperature at the same  
994 height (i.e., microclimate), with positive and negative offset values meaning colder and warmer conditions  
995 in the forest understorey, respectively (Fig. 1, left panel). Similarly, the vertical temperature offset due to  
996 snow cover is the instantaneous temperature difference between the air above the snow and inside the snow  
997 layer, with positive and negative offset values meaning colder and warmer conditions inside the snow layer,  
998 respectively (Fig. 1, right panel).  
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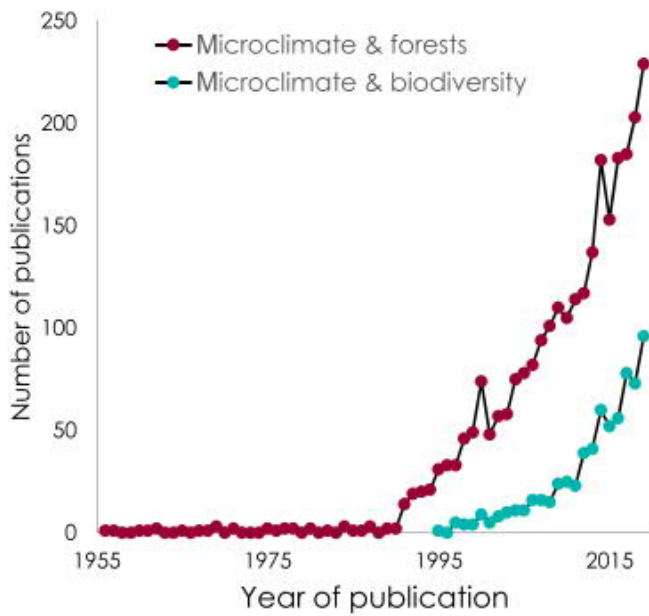
1000 Then, depending on the magnitude and distribution of the temperature offsets over time, it is possible to  
1001 distinguish three contrasting situations (Fig. 1): (1) perfect coupling; (2) buffering; and (3) perfect  
1002 decoupling:

- 1003 (1) Perfect coupling occurs when microclimatic temperatures ( $T_{\text{micro}}$ ) equal macroclimatic  
1004 temperatures ( $T_{\text{macro}}$ ). In other words, the slope ( $\beta_1$ ) of the linear relationship between  $T_{\text{macro}}$  and  
1005  $T_{\text{micro}}$  ( $T_{\text{micro}} = \beta_0 + \beta_1 \times T_{\text{macro}}$ ) is equal to one (identity) and the offset is zero and constant over  
1006 time.
- 1007 (2) Buffering means a dampening of  $T_{\text{macro}}$  fluctuations over time such that temporal fluctuations in  
1008  $T_{\text{micro}}$  still exist but are much less pronounced than for  $T_{\text{macro}}$ . This generates a cycle of positive and  
1009 negative offset values which tend to diminish the positive correlation between  $T_{\text{macro}}$  and  $T_{\text{micro}}$ ,  
1010 such that  $\beta_1$  is lower than 1 but greater than 0. The closer  $\beta_1$  is to zero, the more pronounced the  
1011 magnitude of buffering.
- 1012 (3) Perfect decoupling occurs when  $T_{\text{micro}}$  behaves independently from  $T_{\text{macro}}$ , i.e. when the slope ( $\beta_1$ )  
1013 is zero and the buffering is so strong that the positive correlation between  $T_{\text{micro}}$  and  $T_{\text{macro}}$  is totally  
1014 lost. For instance, temperatures inside the snow layer during winter are completely decoupled from  
1015 temperatures above the snow layer (Fig. 1, right panel).  
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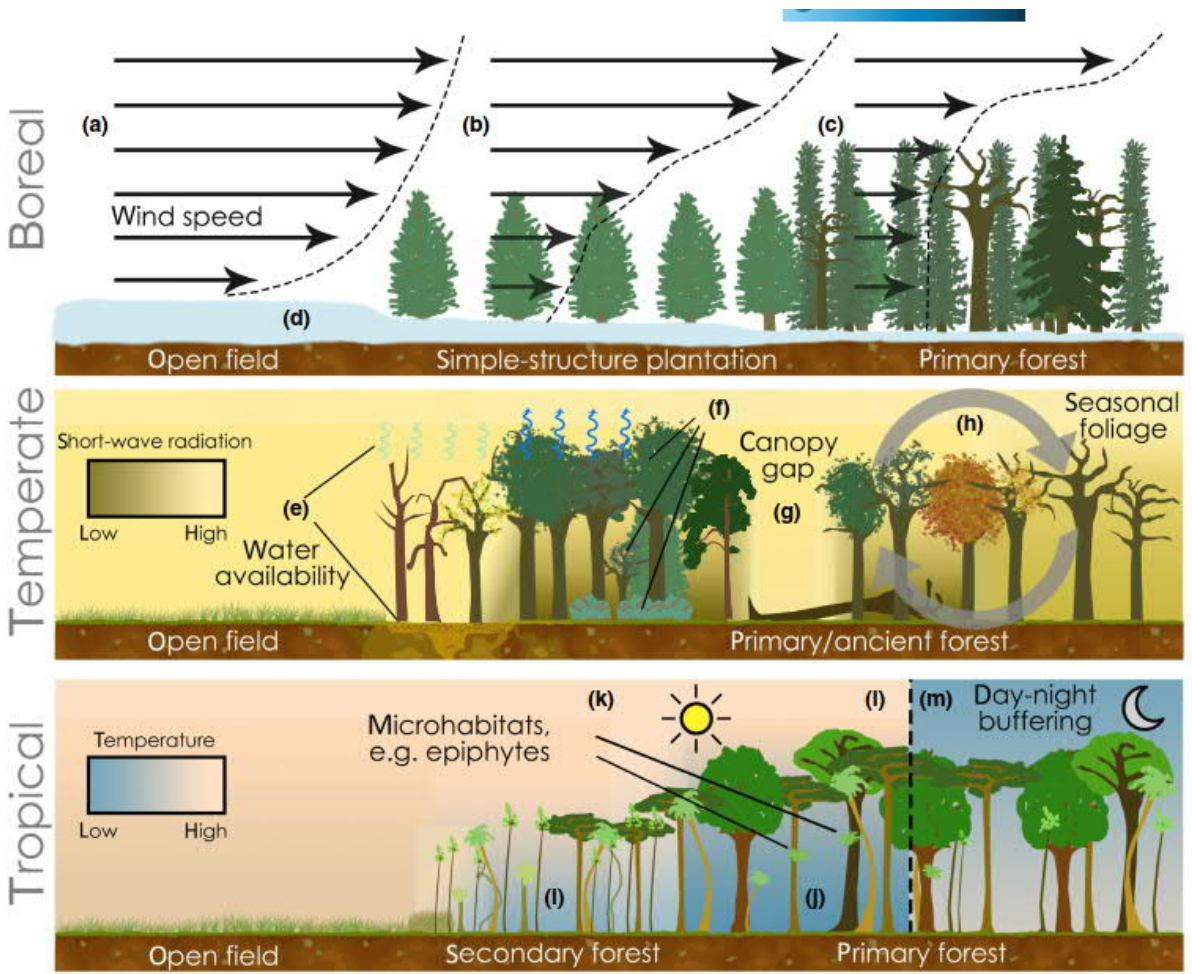
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Fig. 1.



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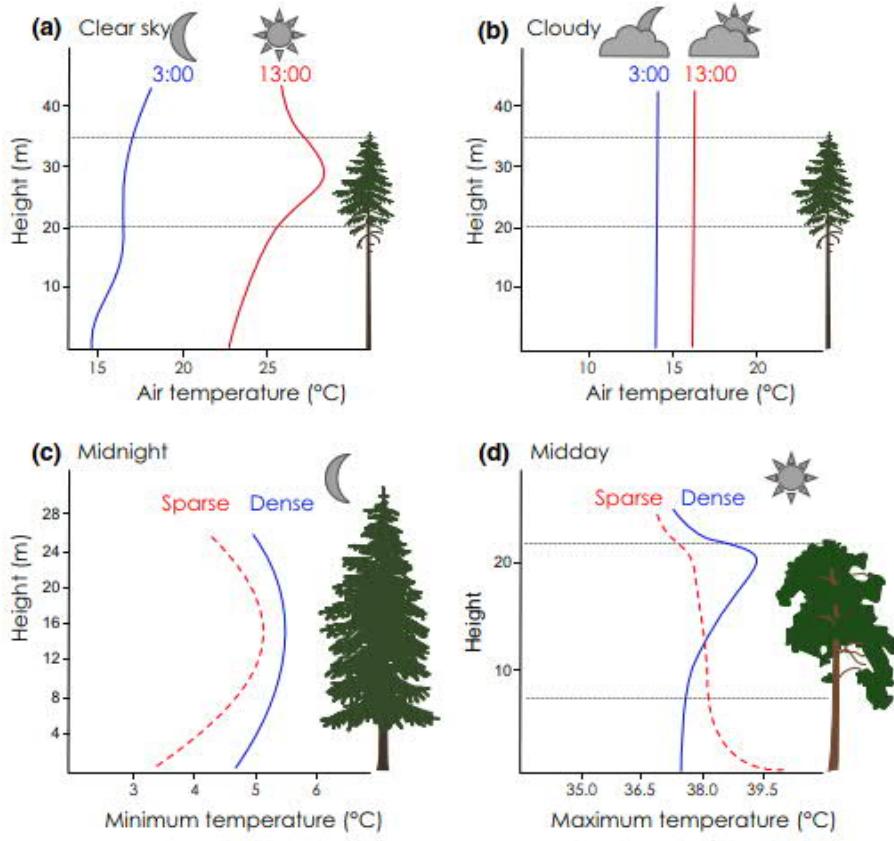
Fig. 2.



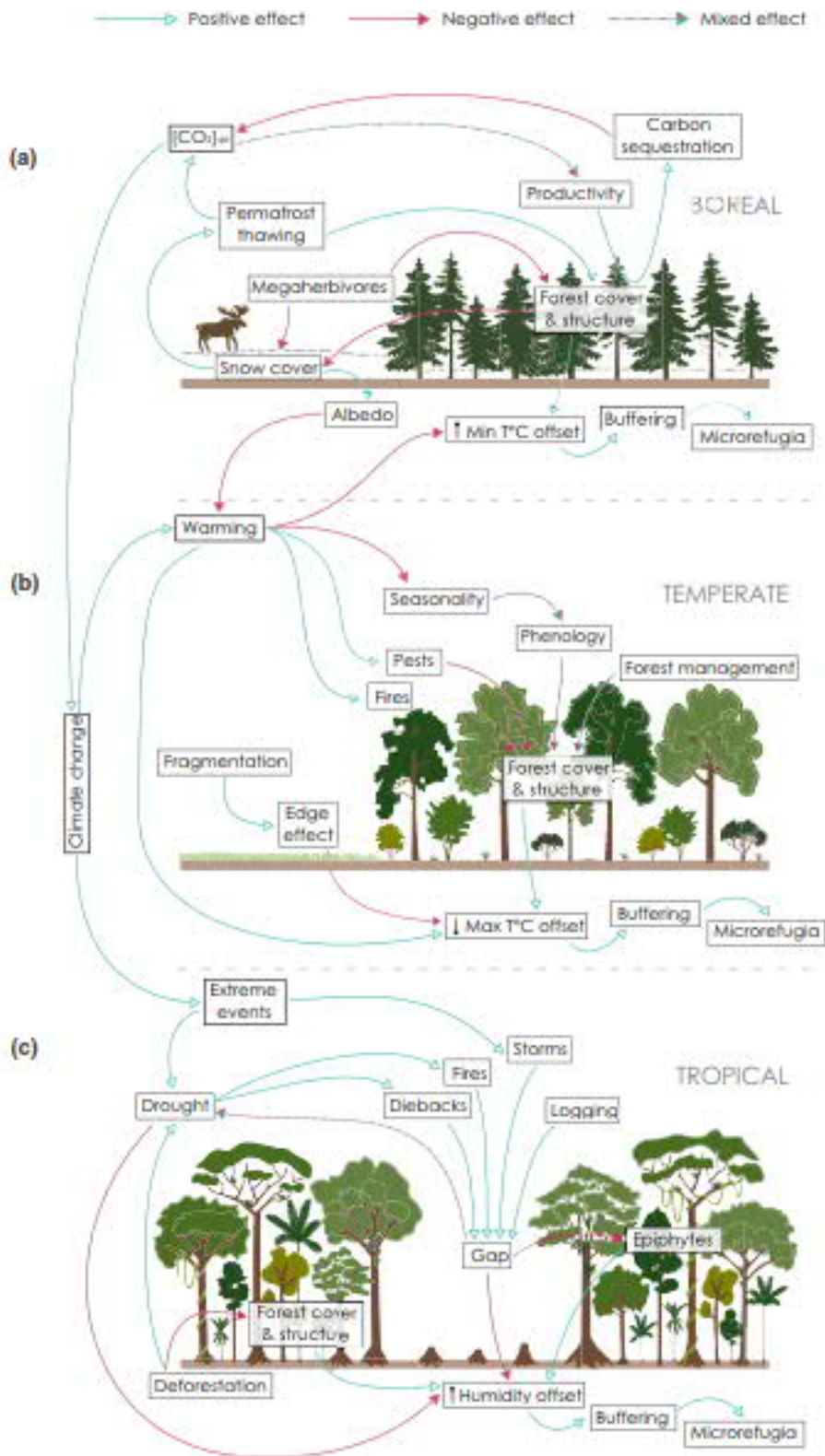
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Fig. 3.

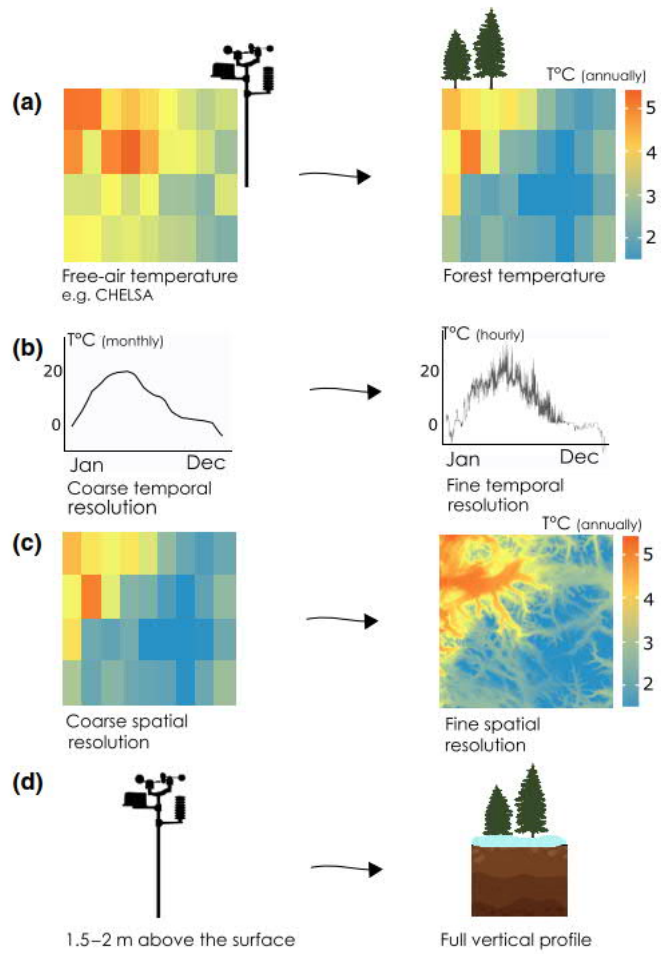




1043  
 1044 Fig. 4.  
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1046  
 1047 Fig. 5.  
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Fig. 6.