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

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4  
5 *Running title: Microclimates in forests*

6  
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34

35 **Abstract**

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

56

57 **Keywords:** biodiversity, buffering, climate change, ecosystem function, forest, future research,  
58 microclimate

59 **Introduction: the importance of forest microclimates**

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

70  
71 The physiological and ecological importance of forest microclimates has long been recognized (Grubb,  
72 1977; Geiger et al. 2009, a book with a first edition already published in 1927). Due to the increasing  
73 biodiversity loss in response to current macroclimatic warming, studies on forest microclimates are  
74 receiving much attention in global change biology (Fig. 2). However, most studies on forest biodiversity  
75 rely on gridded macroclimate data that are based on free-air temperature data from weather stations in open  
76 areas outside forests, thus neglecting forest microclimate variation in space and over time (Potter et al. 2013;  
77 Barry & Blanken, 2016; De Frenne & Verheyen, 2015). This introduces significant uncertainty into  
78 predictions of climate change impacts on forest biodiversity and functioning (Zellweger et al. 2020). Forests  
79 and their understories harbour the majority of terrestrial biodiversity, and are essential for the provision of  
80 many ecosystem services. Thus, addressing the uncertainties is a fundamental task for global change  
81 biologists, land managers, and policy makers alike (MEA, 2005; Landuyt et al. 2019; IPBES, 2020).

82  
83 Viewing forest ecology through a microclimate lens can help tease out mechanistic relationships of  
84 organisms with their environment. Buffered forest microclimates and the microhabitats within forests (e.g.,  
85 root caverns, tree holes, fallen trunks) enable organisms to avoid extreme heat and drought (Kearney et al.  
86 2009; Scheffers et al. 2013a, 2014b). The microclimate buffering capacity of forests may provide climatic  
87 microrefugia during macroclimate warming (Ewers and Banks-Leite, 2013; von Arx et al. 2013, Lenoir et  
88 al. 2017, De Frenne et al. 2019). Therefore, the pressure on individuals, populations, species and  
89 communities to respond to rapid anthropogenic climate change may be reduced, at least in the short term,  
90 by the presence of climatic microrefugia for cold-adapted organisms (Keppel et al. 2012; Ashcroft et al.  
91 2012; Hampe & Jump, 2011; Lenoir et al. 2017; Greiser et al. 2019). Through these mechanisms, forest  
92 microclimates can determine the distribution of individuals, populations, and species. Thus, incorporating  
93 microclimates into species distribution models is expected to significantly improve the accuracy of  
94 predictions (Slavich et al. 2014; Lembrechts et al. 2019; Zellweger et al. 2019b). The forest microclimate is  
95 also a driver of species interactions. Low light availability and heterogeneous moisture can enhance plant  
96 competition (Connell, 1983; Gerhardt, 1996), although microclimates can also facilitate co-existence, such  
97 as when shade offers refuge to mixed-species seedling assemblages (Holmgren et al. 1997), or when  
98 centipedes share epiphytic ferns as cool and moist nest sites (Phillips et al. 2020). In some cases, species  
99 interactions can result in a re-engineering of the microclimate environment itself, for example canopy gaps  
100 produced by leaf-cutter ant herbivory (Swanson et al. 2019). Microclimate therefore shapes – and in turn,  
101 is shaped by – the composition of forest communities (Parker, 1995; Woods et al. 2015; Frey et al. 2016a,  
102 Jucker et al. 2018).

103  
104 At the ecosystem level, microclimate is of paramount importance as a key regulator of many ecosystem  
105 functions. Rates of litter decomposition, carbon sequestration and microbial activity tend to be greater in  
106 forests than in neighbouring open habitats (Riutta et al. 2012; Wang et al. 2010; Chen et al. 2018, but see  
107 Köchy & Wilson, 1997), and also vary spatially within forests due to, among other things, gap dynamics

108 (Zhang & Zak, 1995). Tree recruitment, via seedling growth and sapling survival, is heavily contingent upon  
109 microclimatic conditions (Aussenac 2000; Campanello et al. 2007; Harper & White, 1974). Every forest tree  
110 starts as a small seedling on the floor and thus understorey conditions shaped by trees in the overstorey  
111 eventually feedback to tree recruitment and future forest structure. Therefore, threats to forest biodiversity  
112 and functioning from deforestation, forest degradation, and fragmentation are inherently linked to the loss  
113 and modification of forest microclimates by these activities (Chen et al. 1999; Jucker et al. 2020; Laurance  
114 et al. 2011).

115

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

132

### 133 **Drivers of vertical and horizontal microclimate variation**

#### 134 *Horizontal distribution of microclimates: forest vs open habitats*

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

145

146 Evaporative cooling and emitted longwave radiation both act to reduce canopy and soil surface  
147 temperatures whereas net shortwave radiation acts to warm the soil and canopy surfaces (Geiger et al. 2009;  
148 De Frenne et al. 2013). Heat exchange of surfaces with the air may contribute to warming or cooling  
149 depending on the temperature difference between the air and the surfaces (Huang et al. 2015). The  
150 efficiency of these sensible heat fluxes and of evaporative cooling (latent heat fluxes) varies with wind and  
151 turbulence conditions. Vegetation structure and composition affect these processes of heat exchange and  
152 cause a horizontal variation in buffering of ambient temperatures (Fig. 3). In particular, vegetation density  
153 (e.g., in terms of canopy cover, basal area, plant area index) via effects on albedo, evapotranspiration and  
154 radiation absorption and reflection have strong influences on understorey microclimate, especially in the  
155 warm season (Greiser et al. 2018, Zellweger et al. 2019a). The vertical and horizontal composition and  
156 distribution of forest canopies (e.g., gaps, tree age distribution, leaf clumping, distance to forest edge)

157 directly affect the amount and variability of sunlight (Sprugel et al. 2009; Valladares & Guzman, 2006). At  
158 the stand level, small-scale variations in sun-flecks cause strong gradients in near-ground temperatures and  
159 there are often strong microclimatic gradients towards forest edges, due to increased solar radiation and  
160 wind (Matlack, 1993). Microclimate gradients from forest core to edge are very large but differ strongly  
161 among microclimatic variables (e.g., light, wind, temperature), and are impacted by the edge orientation  
162 (Hylander, 2005), the cloudiness (e.g., Chen et al. 1993), the slope of the terrain or the wind direction  
163 (Davies-Colley et al. 2000).

164

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

179

#### 180 *Vertical distribution of microclimates: from the ground to the top of the canopy*

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

189

190 Air temperature differences between ground and canopy range from 0.15 to 0.25 °C m<sup>-1</sup> in temperate  
191 coniferous and mixed hardwood–conifer and tropical forests (Harley et al. 1996; Zweifel et al. 2002;  
192 Hardwick et al. 2015; Bauerle et al. 2009). During the day, air temperature peaks can occur near the ground,  
193 but are most often located within the top canopy, where most of the incoming energy is absorbed (Chen  
194 et al. 1999; Didham & Ewers, 2014) (Fig. 4). The exact vertical location of air temperature maxima will  
195 depend on the density of the canopy (leaf and plant area index as a function of height) and on the intensity  
196 of turbulent air mixing (Fig. 4). However, even when understorey air is cooler than above-canopy air, leaf  
197 and litter temperatures can rise well above the local air temperature in the understorey of open forests, due  
198 to decreased wind speeds and absorption of shortwave radiation (Martin et al. 1999; Scheffers et al. 2017).  
199 Leuzinger & Körner (2007) showed that leaf temperature regimes in canopies vary enormously over short  
200 vertical distances in several coniferous and deciduous broad-leaved tree species. Finally, snow cover in the  
201 winter will effectively decouple the near ground temperature from the temperature above the snow (Fig.  
202 1).

203

204

## 205 **Consequences of microclimates for forest biodiversity**

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

214  
215 Although microclimate research aims to match the scale of climate and organisms, the concept of  
216 microclimate describes a spectrum of spatiotemporal scales (from centimetres to several hundred metres,  
217 from hours to years); i.e., perception of "micro" by woodlice is different from an elephant's perception of  
218 "micro" (Weins, 1989, Lembrechts et al. 2020b). However, an interesting aspect in forests is that the trees  
219 that modify the understorey microclimate have been small in the beginning of their life cycle. This illustrates  
220 that the same individual might respond to climate at different scales across its life stages, but also how forest  
221 microclimates can be created by reinforcing feedback mechanisms. Bearing this in mind, we here describe  
222 the influence of microclimate on biodiversity across space and time.

223

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

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

245

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

247 Organisms also partition their niches according to microclimates in time (Jonason et al. 2014). Daily cycles  
248 of organism activity are apparent in Lepidopterans with butterflies primarily active during the day and moths  
249 active at night. However, activity can also vary within diel periods with activity peaks relative to a daytime  
250 thermal threshold (Wikström et al. 2009), a threshold that differs spatially from open habitats to closed  
251 forests (Xing et al. 2016). Similarly, leaf litter lizards will exploit sunspots or rare microclimates for  
252 thermoregulation, but only during cold morning hours (Nordberg & Schwarzkopf, 2019). Here, lizard  
253 activity varies with thermal heterogeneity driven both in time and by topographic roughness and aspect

254 (Sears et al. 2016). The dispersal mechanism of a moss is suggested to be most effective in morning hours  
255 when the moisture decreases along with increasing temperatures and wind (Johansson et al. 2016). At a  
256 weekly or monthly scale, weather patterns strongly influence small mammal habitat use and activity (Vickery  
257 & Rivest, 1992). Seasonal shifts in activity are apparent with regional and local climates. For example,  
258 arboreal frog communities shift from being highly vertically stratified in the tree canopies during the cooler,  
259 wet season to dramatically accumulating in the understorey during the hotter, dry season (Basham &  
260 Scheffers, 2019).

261

### 262 **Consequences of microclimates on forest functioning**

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

282

### 283 **How will macroclimate warming affect forest microclimates?**

284 How macroclimate warming affects forest microclimate dynamics, and vice versa, remains an open question  
285 in global change ecology (Lenoir et al. 2017; De Frenne et al. 2019). For instance, it is unclear whether the  
286 magnitude of temperature offset between macroclimate and forest microclimates (De Frenne et al. 2019)  
287 will remain stable, increase or decrease over time as macroclimate warms. As discussed previously, the  
288 magnitude of the temperature offset between forests and open habitats depends on ambient, macroclimatic  
289 conditions: forest offsets of maximum temperatures increase with ambient temperatures (De Frenne et al.  
290 2019; Su et al. 2020; Zhang et al. 2020). Assuming a space-for-time substitution, this suggests that the  
291 magnitude of the offset on maximum temperature could potentially increase under macroclimate warming  
292 (Fig. 1 and Fig. 5). This assumption only holds if: (i) the relationship between offsets and macroclimate  
293 continues to be linear; (ii) the forest canopy layer is not disturbed; (iii) we assume that the equilibrium point  
294 at which temperatures inside and outside forests are the same (cf. Fig. 1), does not shift; and (iv) other  
295 variables such as microhabitat moisture levels remain comparable (Scheffers et al. 2014b; Zellweger et al.  
296 2020). Slow, interannual climate change can, however, directly change the equilibrium point, while changes  
297 in canopy cover, moisture, etc. could directly act on the buffering and hence slope (Fig. 1). Nevertheless, if  
298 macroclimatic increases in daily maximum temperatures can be buffered, it might provide forest organisms  
299 with more time for adaptation and migration (Zellweger et al. 2020), a phenomenon that is reminiscent of  
300 the concept of microrefugia (that is, spatially-restricted habitats that sustain a favourable microclimate,  
301 which enables species to persist in an otherwise inhospitable matrix; Gavin et al. 2014). The pattern is  
302 opposite for minimum temperatures: higher ambient air temperatures decrease minimum temperature



303 offsets (De Frenne et al. 2019). Hence, still under the assumptions of a space-for-time substitution, the  
304 magnitude of the offset in minimum temperature could potentially decrease under macroclimate warming,  
305 contributing to reduce the buffering effect on minimum temperature and thus alter the microrefugial  
306 capacities of boreal forests for cold-adapted species surviving at the warmer range margin (Fig. 5). In the  
307 following subsections, we first discuss changes in forest microclimate dynamics due to macroclimate  
308 warming in different forest biomes, and then the potential impacts of macroclimate warming on future  
309 offsets.

310

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

312 In temperate forests, temperature buffering may happen for both maximum and minimum temperatures  
313 (De Frenne et al. 2019). Yet, during the cold season, deciduous trees shed their leaves, the primary drivers  
314 of buffering, making buffering in temperate forests likely to be more important and relevant during the  
315 growing season. Additionally, Zellweger et al. (2019a) showed that the magnitude of the thermal offset  
316 during the summer season in European temperate forests was more pronounced for daily maximum  
317 temperatures than for daily minimum temperatures. As a consequence, canopy cover density directly affects  
318 buffering capacity, with likely implications on organismal responses to climate change. For example, the  
319 thermophilisation rate – the rate of community shift towards more warm-adapted species – in understorey  
320 plant communities of temperate forests is better related to the rate at which the daily maximum temperature  
321 changes in forest interiors (i.e. the rate of microclimate warming) during the growing season than the rate  
322 of macroclimate warming (Zellweger et al. 2020). In boreal forests, buffering of minimum temperatures is  
323 most pronounced, while tropical forests have more pronounced offsets of maximum temperatures (De  
324 Frenne et al. 2019). Albeit the velocity of macroclimate warming is highest at high latitudes, tropical species  
325 will likely be more severely impacted due to their narrow thermal niches and safety margins (Tewksbury et  
326 al. 2008; Antão et al. 2020; Lenoir et al. 2020). Worryingly, daily maximum temperatures in the next decades  
327 will likely be more extreme than what tropical species have ever experienced in their recent evolutionary  
328 history (Deutsch et al. 2008; Kingsolver, 2009).

329

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

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

342

343 In the tropics, satellite-driven measures of vegetation greenness (NDVI), a surrogate for photosynthetic  
344 activity and productivity, show reduced productivity in warmer years (Braswell et al. 1997; Asner et al. 2000),  
345 suggesting a reduced future buffering capacity. Conversely, in boreal forests, the impact of changes in  
346 primary productivity on the buffering capacity of forests is less clear. On the one hand, old growth boreal  
347 forests in North America showed no net increase in stem growth (Giguère-Croteau et al. 2018). On the  
348 other hand, Beck et al. (2011) have reported changes in forest productivity across Alaska that are consistent  
349 with a complete biome shift: decreased productivity at the warmer (southern) versus enhanced productivity  
350 at the colder (northern) edge of the boreal biome. Thus, the buffering capacity of boreal forests may mirror

351 the climatically-induced changes in primary productivity with the magnitude of the offsets decreasing and  
352 increasing towards the warmer and colder edge of the boreal zone, respectively.

353

#### 354 *Extreme event effects on temperature offsets*

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

369

#### 370 *Interactions between human land-use and macroclimate warming*

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

382

383 In boreal forests, and to a lower extent in temperate and tropical forests, intensive forest management for  
384 timber and other woody biomass harvest has led to a biotic, genetic, structural and functional  
385 homogenization of forest stands across large spatial extents (Rousseau et al. 2019). The even aged single  
386 species stands typical of managed boreal forests have reduced the resilience of the whole boreal system to  
387 increasing frequency and severity of climate-induced pest outbreaks and wildfires (Cudmore et al. 2010;  
388 Gauthier et al. 2015). Although fires are part of the natural disturbance dynamics in many boreal systems,  
389 large stand-replacing wildfires have resulted in shrub proliferation and enhanced snow accumulation, with  
390 possible implications for longer decoupled ground temperatures (Lantz et al. 2013; Aalto et al. 2018) (Fig.  
391 1 and Fig. 5).

392

393 In the tropics, the combined effects of logging, droughts and fires on canopy loss (i.e., deforestation and  
394 degradation) can locally increase air dryness (Staal et al. 2020) and daily maximum temperatures more than  
395 the warming associated with high emission scenarios (Senior et al. 2017). Hence, by letting in direct sunlight  
396 and warm and dry air, large canopy gaps following deforestation strongly alter understory microclimate  
397 (Fig. 3 and 5), reducing the capacity to buffer macroclimatic fluctuations and thus causing many species to  
398 decline in abundance, e.g. termites that are especially sensitive to desiccation (Cornelius & Osbrink, 2010;  
399 see De Smedt et al. 2018 for a study from temperate forests). However, small canopy gaps (< 400 m<sup>2</sup>) in

400 tropical forests, which occur under natural forest dynamics, can quickly regain their thermal environment  
401 in a few years (Mollinari et al. 2019), while secondary forests can regain their thermal environments within  
402 20 – 30 years after logging (del Pliego et al 2016). These drastic changes in microclimatic conditions are not  
403 only due to tree removal, but at a finer resolution also to epiphyte loss. Indeed, epiphytes represent a  
404 significant functional group for microclimate dynamics in tropical forests, reducing water loss through  
405 evaporative drying (Scheffers et al. 2014b) and providing buffered microhabitats for canopy-dwelling  
406 organisms (Seidl et al. 2020) (Fig. 3, arrow J).

407

#### 408 *Forest microclimate feedbacks on macroclimate warming*

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

414

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

427

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

439

#### 440 **A research agenda and identification of research gaps**

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

447

448 *1) Drivers of forest microclimate buffering and future changes*

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

467  
468 *2) Mapping and predictions of forest microclimates*

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

492  
493 *3) Impacts on biodiversity and ecosystem functioning in forests*

494 In addition to characterizing the physiographic and biophysical processes that drive forest microclimates  
495 (Fig. 3-5) as well as developing approaches for mapping microclimate at appropriate scales (Fig. 6), careful  
496 thought is needed on how to best integrate these new data streams into biodiversity research (Jucker et al.

497 2020). Access to climate data that better reflect local conditions experienced by living organisms should  
498 improve our ability to model species distributions and predict how they will respond to rapid global change  
499 (Mod et al. 2016; Lenoir et al. 2017; Lembrechts et al. 2019). However, few studies have actually tested this  
500 assumption (Lembrechts et al. 2019; Ohler et al. 2020), particularly in the context of forests (Frey et al.  
501 2016a). A key question that remains to be addressed is at what spatial scale (horizontal and vertical)  
502 microclimate should be measured and modelled, and how this varies for different groups of species (e.g.,  
503 in relation to body size, dispersal and thermoregulation, Potter et al. 2013; Scheffers et al. 2014a). Similarly,  
504 we also need to determine which aspects of microclimate best predict species distributions in forests (e.g.,  
505 air temperature, humidity, soil moisture, solar radiation) and how to effectively summarize these metrics  
506 (e.g., means, extremes, fluctuations, thresholds, growing degree hours/days; Hylander et al. 2015; Bramer  
507 et al. 2018).

508  
509 Empirical and modelling approaches that allow different facets of microclimate to be manipulated  
510 independently are crucial to addressing these questions (for an example to separate light and temperature  
511 effects, see De Frenne et al. 2015). Beyond the immediate need to better characterize how microclimate  
512 shapes current-day ecological processes in forests, a major challenge is to determine how long different  
513 types of forests can continue to act as microrefugia (also referred to as hold-outs in this context) for species  
514 in a warming world (Hannah et al. 2014). As global mean temperatures continue to rise, so too will those  
515 in forest understoreys (albeit slower if buffering is at play). But perhaps more importantly, long-term climate  
516 change in interaction with forest management will eventually lead to changes in the species composition  
517 and structure of forests (e.g., the number and size of trees, as well as canopy height and density) (Coomes  
518 et al. 2014; Albrich et al. 2020) – with clear cascading effects for understorey microclimate (Jucker et al.  
519 2018). Very few studies have effectively evaluated ecosystem multifunctionality, and translated this to  
520 services, let alone relate it to microclimates (e.g., of the type suggested by Byrnes et al. 2014). Although  
521 policy documents abound with statements about climate change mitigation and adaptation, there is a lack  
522 of understanding about forest (micro)climate and biodiversity, which might lead to misguided actions (Selva  
523 et al. 2020). There are thus large knowledge gaps in biodiversity – ecosystem functioning – microclimate  
524 research. While these longer-term effects of climate change on forest microrefugia have been largely  
525 overlooked, a promising avenue for exploring them would be to integrate microclimate projections into  
526 forest dynamics models used to simulate forests under future conditions (Albrich et al. 2020).

## 527 528 **Concluding remarks**

529 In sum, we have outlined the contemporary research interests and gaps linking microclimatic variation to  
530 biodiversity and the functioning of forest ecosystems worldwide. The urgency is clear; compelling evidence  
531 is accumulating to suggest that distinct below-canopy microclimatic conditions in forests arising from  
532 vertical and horizontal processes can mediate the amount of macroclimate warming in forests all around  
533 the globe. However, even though the microclimatic changes in forests due to macroclimate warming may  
534 be smaller than those in other ecosystems, the ecological impact may be just as large if forest species have  
535 narrower niches and thus are more sensitive. Moreover, other global changes such as forest disturbance  
536 and widespread canopy opening (Senf & Seidl, 2020) might accelerate the effects of climate change in  
537 forests through their impact on microclimates. Our priority voting of important questions suggested that  
538 future forest microclimate research should focus on three overarching themes (drivers & global change,  
539 mapping & predictions, and biodiversity & ecosystem functioning). These themes reflect the wealth of  
540 fundamental research gaps that still exist in forest microclimate research. Recent studies highlighting the  
541 role of microclimate in helping to sustain local biodiversity and ecosystem functions have paved a way  
542 towards “microclimate forest restoration”, or in other words, restoring forest ecosystems with the explicit  
543 purpose to increase their capacity to buffer the local microclimates from macroclimatic change. Such  
544 arguments are to date hardly considered in the pros and cons of the global tree restoration debate (e.g.,  
545 Bastin et al. 2019). In tandem with the steadily increasing number of microclimate monitoring sites

546 (Lembrechts et al. 2020a), novel microclimate modelling approaches have been developed. These crucial  
547 methodological advances are likely to encourage the use of microclimate data instead of settling for coarse-  
548 scale climate data of long-term average conditions. Once the global variation in forest microclimates is  
549 properly documented and analysed, more efforts should be placed in order to implement this information  
550 into further analyses of ecosystem functioning. Doing so is expected to greatly increase our understanding  
551 of the impacts of climate change on forest ecosystems. Although the importance of microclimate in  
552 regulating many biophysical processes has been acknowledged by ecologists and biologists for nearly a  
553 century, we are finally stepping into an era where we have a solid conceptual and methodological foundation  
554 for testing many fundamental research questions related to forest functioning. This is important as a better  
555 understanding of the magnitude, drivers and implications of forest microclimate on biodiversity is urgently  
556 required in order to better manage forests, support their sustainable use and secure viable ecosystem  
557 services for future generations in a warmer climate.

558

559

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577 **References**578  
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1. 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.
2. Aalto et al. (2018) Biogeophysical controls on soil-atmosphere thermal differences: implications on warming Arctic ecosystems. *Environmental Research Letters*, 13, 074003
3. Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *PNAS*, 113, 11770–11775.
4. Albrich K., Rammer, W., & Seidl, R. (2020) Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, 26, 4013-4027.
5. Allen, C.D. et al. (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
6. 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.
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.
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, 1866–79.
9. Asner, G. P., Townsend, A. R., Braswell, B. H. et al. (2000) Satellite observation of El Niño effects on Amazon forest phenology and productivity. *Geophysical Research Letters*, 27, 981– 984.
10. Åström, M., Dynesius, M., Hylander, K., & Nilsson, C. (2007). Slope aspect modifies community responses to clear-cutting in boreal forests. *Ecology*, 88, 749-758.
11. Aussenac, G. (2000). Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, 57: 287–301.
12. Barry, R. G., & Blanken, P. D. (2016). *Microclimate and local climate*. New York: Cambridge University Press.
13. 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.
14. Basham, E. W., & Scheffers, B. R. (2020). Vertical stratification collapses under seasonal shifts in climate. *Journal of Biogeography*, 47, 1888-1898.
15. Bastin, J.F., et al. (2019) The global tree restoration potential. *Science*, 365, 76-79.
16. 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.
17. Beck, P.S.A., et al. (2011) Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*, 14, 373-379.
18. 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.
19. Bonan, G.B. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, 320, 1444-1449.
20. Bramer, I., Anderson, B. J., Bennie, J. et al. (2018) Advances in monitoring and modelling climate at ecologically relevant scales. *Advances in Ecological Research*, 58, 101-161.
21. 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.
22. Braswell, B. H., Schimel, D. S., Linder, E. et al. (1997) The response of global terrestrial ecosystems to interannual temperature variability. *Science*, 278, 870– 872.
23. Byrnes, J.E.K., et al. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions.
24. Campanello, P. I., Genoveva Gatti, M., Ares, A., et al. (2007). Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *Forest Ecology and Management*, 252, 108–117.
25. Carlile, D. W., Skalski, J. R., Batker, J. E., et al. (1989). Determination of ecological scale. *Landscape Ecology*, 2, 203–213.
26. Carney, K. M., Hungate, B. A., Drake, B. G., & Megonigal, J. P. (2007). Altered soil microbial community at elevated CO<sub>2</sub> leads to loss of soil carbon. *PNAS*, 104, 4990–4995.
27. 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.
28. Chen, J.Q., Saunders, S.C., Crow, T.R., Naiman, R.J., Brososke, 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.

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694
29. Chen, Y., Liu, Y., Zhang, J., et al. (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.
  30. Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist*, 122, 661–696.
  31. Connon, R. et al. (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.
  32. 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.
  33. 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.
  34. Cudmore, T.J. et al. (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.
  35. 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.
  36. Davis, K.T. et al. (2019). Microclimatic buffering in forests of the future: the role of local water balance. *Ecography*, 42: 1–11.
  37. 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.
  38. De Frenne P., & Verheyen, K (2015). Weather stations lack forest data. *Science*, 351, 234.
  39. De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., et al. 2013. Microclimate moderates plant responses to macroclimate warming. *PNAS*, 110, 18561–18565.
  40. De Frenne, P., Zellweger, F., Rodríguez-Sánchez, 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.
  41. De Smedt, P., Baeten, L., et al. (2018) Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. *European Journal of Soil Biology*, 85, 1–3.
  42. De Smedt, P., Vangansbeke, P., Bracke, R., Schauwvlieghe, 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.
  43. 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.
  44. 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.
  45. del Pliego, P. G., Scheffers, B. R., Basham, E. W., Woodcock, P., Wheeler, C., Gilroy, J. J., ... & Edwards, D. P. (2016). Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biological Conservation*, 201, 385–395.
  46. 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. *PNAS*, 105, 6668–6672.
  47. Didham, R. K., & Ewers, R. M. (2014). Edge effects disrupt vertical stratification of microclimate in a temperate forest canopy. *Pacific Science*, 68, 493–508.
  48. Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, 17, 1022–1035.
  49. Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLOS one*, 8(3).
  50. Ewers, R. M., Boyle, M. J., Gleave, R. et al. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications*, 6, 6836.
  51. Frey, S.J., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016a). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, 2(4), e1501392.
  52. Frey, S.J., Hadley, A.S., Betts, M.G. (2016b). Microclimate predicts within-season distribution dynamics of montane forest birds. *Diversity and Distributions*, 22, 944–959.
  53. Gauslaa, Y. (2014). Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *The Lichenologist*, 1, 1–16.
  54. Gauthier, S., et al. (2015) Boreal forest health and global change. *Science*, 349, 819–822.
  55. Gavin, D.G., et al. (2014) Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytologist*, 204, 37–54.
  56. Geiger, R., Aron, R. H., & Todhunter, P. (2009). *The climate near the ground*. Rowman & Littlefield.
  57. 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.



- 695 58. Giguère-Croteau, C. et al. (2018) North America's oldest boreal trees are more efficient water users due to increased  
696 [CO<sub>2</sub>], but do not grow faster. *PNAS*, 116, 2749-2754
- 697 59. Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., & Hylander, K. (2018). Monthly microclimate models in a managed  
698 boreal forest landscape. *Agricultural and Forest Meteorology*, 250, 147-158.
- 699 60. Greiser, C., Meineri, E., Ehrlén, J., & Hylander, K. (2019). Hiding from the climate: Characterizing microrefugia for  
700 boreal forest understory species. *Global Change Biology*, 26, 471–483.
- 701 61. Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration  
702 niche. *Biological Reviews*, 52, 107–145.
- 703 62. Hampe, A., & Jump, A. S. (2011) Climate relicts: past, present, future. *Annual Review of Ecology, Evolution and*  
704 *Systematics*, 42, 313-333.
- 705 63. Hannah, L., Flint, L., Syphard, A. D., et al. (2014). Fine-grain modeling of species' response to climate change:  
706 holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, 29, 390–397.
- 707 64. Hardwick, S.R., Toumi, R., et al. (2015) The relationship between leaf area index and microclimate in tropical forest  
708 and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201,  
709 187-195.
- 710 65. Harley, P., Guenther, A., & Zimmerman, P. (1996). Effects of light, temperature and canopy position on net  
711 photosynthesis and isoprene emission from sweetgum (*Liquidambar styraciflua*) leaves. *Tree Physiology*, 16, 25-32.
- 712 66. Harper, J. L., & White, J. (1974). The demography of plants. *Annual Review of Ecology and Systematics*, 5, 419–63.
- 713 67. Heberling, M. et al. (2019). Phenological mismatch with trees reduces wildflower carbon budgets. *Ecology Letters*, 22,  
714 612-623
- 715 68. Holmgren, M., Scheffer, M., & Huston, M. A. (1997). The interplay of facilitation and competition in plant  
716 communities. *Ecology*, 78, 1966–1975.
- 717 69. Huang, C.W., Chu, C.R., Hsieh, C.I., Palmroth, S., & Katul, G.G. (2015). Wind-induced leaf transpiration. *Advances in*  
718 *Water Resources*, 86, 240-255.
- 719 70. Hylander, K. (2005). Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of*  
720 *Applied Ecology*. 42, 518-525.
- 721 71. Hylander, K., & Nemomissa, S. (2009). Complementary roles of home gardens and exotic tree plantations as  
722 alternative habitats for Ethiopian montane rainforest plant biodiversity. *Conservation Biology*, 23, 400-409.
- 723 72. Hylander, K., Ehrlén, J., Luoto, M., & Meineri, E. (2015). Microrefugia: not for everyone. *Ambio*, 44, 60-68.
- 724 73. IPBES (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of  
725 the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz, J. Settele, E. S.  
726 Brondizio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A.  
727 Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A.  
728 Pfaff, S. Polasky, A. Purvis, J. Razaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis,  
729 and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages.
- 730 74. Johansson, V., Lönnell, N., Rannik, Ü., Sundberg, S., & Hylander, K. (2016), Air humidity thresholds trigger active  
731 moss spore release to extend dispersal in space and time. *Functional Ecology*, 30, 1196-1204.
- 732 75. Jonason, D., Franzen, M., & Ranius, T. (2014). Surveying moths using light traps: effects of weather and time of year.  
733 *PLoS One*, 9(3), e92453.
- 734 76. Jucker, T., Hardwick, S. R., Both, S. et al. (2018). Canopy structure and topography jointly constrain the microclimate  
735 of human-modified tropical landscapes. *Global Change Biology*, 24, 5243–5258.
- 736 77. Jucker, T., Jackson, T. D., Zellweger, F. et al. (2020). A research agenda for microclimate ecology in human-modified  
737 tropical forests. *Frontiers in Forests and Global Change*, 2, 92.
- 738 78. Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-  
739 blooded” animals against climate warming. *PNAS*, 106, 3835–3840.
- 740 79. Keppel, G., Niel, K. P. V., Wardell-Johnson, G. W., et al. (2012). Refugia: identifying and understanding safe havens  
741 for biodiversity under climate change. *Global Ecology and Biogeography*, 21, 393–404.
- 742 80. Kerry, P., & Griffiths, S. (2000). The earth is not flat. *Global Change Biology*, 2, 214-218.
- 743 81. Kingsolver, J.G. (2009). The Well-Tempered Biologist. *The American Naturalist*, 174, 755–768.
- 744 82. Köchy, M., & Wilson, S. D. (1997). Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass  
745 prairie. *Ecology*, 78, 732–739.
- 746 83. Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L., ... Verheyen, K. (2019).  
747 The functional role of temperate forest understorey vegetation in a changing world. *Global Change Biology*, 2511,  
748 3625-3641.
- 749 84. Lantz, T.C. et al. (2013). Recent shrub proliferation in the Mackenzie delta uplands and microclimatic implications.  
750 *Ecosystems*, 16, 47-59.
- 751 85. Latimer, C. E., & Zuckerberg, B. (2017). Forest fragmentation alters winter microclimates and microrefugia in human-  
752 modified landscapes. *Ecography*, 40, 158-170.

- 753  
754  
755  
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806  
807  
808  
809  
810
86. Laurance, W. F. (2004). Forest-climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 359, 345–52.
  87. Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C., et al. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, 144, 56–67.
  88. Lawrence, D., & Vandecar, K. (2015). Effects of tropical deforestation on climate and agriculture. *Nature Climate Change*, 5, 27–36.
  89. Lembrechts, J. J., Nijs, I., & Lenoir, J. (2019). Incorporating microclimate into species distribution models. *Ecography*, 42, 1267–79.
  90. Lembrechts, J. J., & Lenoir, J. (2020). Microclimatic conditions anywhere at any time! *Global Change Biology*, 26(2), 337-339.
  91. Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., ... & García, R. A. (2020a). SoilTemp: a global database of near-surface temperature. *Global Change Biology*, 26, 6616-6629.
  92. Lembrechts, J. J., Broeders, L., De Gruyter, J., Radujković, D., Ramirez-Rojas, I., Lenoir, J., & Verbruggen, E. (2020b). A framework to bridge scales in distribution modeling of soil microbiota. *FEMS Microbiology Ecology*, 96(5), fiae051.
  93. Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography*, 40, 253–266.
  94. Lenoir, J., Bertrand, R., Ciomte, 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.
  95. Leuzinger, S., & Körner, C. (2007). Tree species diversity affects canopy leaf temperatures in a mature temperate forest. *Agricultural and Forest Meteorology*, 146, 29-37.
  96. Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462, 1052-1055.
  97. 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.
  98. Maclean, I.M.D. (2020) Predicting future climate at high spatial and temporal resolution. *Global Change Biology*, 26, 1003-1011
  99. 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.
  100. Matlack, G.R. (1993) Microenvironment variation within and among forest edge sites in the eastern United-States. *Biological Conservation*, 66, 185-194.
  101. MEA. (2005). Millennium ecosystem assessment. Ecosystems and human well-being: Biodiversity synthesis. Washington, DC: World Resource Institute.
  102. Meehl, G.A., & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st Century. *Science*, 305, 994-997.
  103. Meeussen, C., Govaert, S., Vanneste, T., Haesen, S., Van Meerbeek, K., Bollmann, K., et al. (2021) Drivers of carbon stocks in forest edges across Europe. *Science of the Total Environment*, in press.
  104. 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.
  105. 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.
  106. Melin, M., et al. (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.
  107. 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.
  108. 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.
  109. Nakamura, A., Kitching, R. L., Cao, M., Creedy, T. J., Fayle, T. M., Freiberg, M., ... & Malhi, Y. (2017). Forests and their canopies: achievements and horizons in canopy science. *Trends in Ecology & Evolution*, 32(6), 438-451.
  110. 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.
  111. Ogée, J., Peylin, P., Ciais, P. et al. (2003). Partitioning net ecosystem carbon exchange into net assimilation and respiration using  $^{13}\text{C}$  measurements: a cost-effective sampling strategy. *Global Biogeochemical Cycles*, 17, 1070.
  112. Ohler, L.-M., Lechleitner, M., Junker, R. R. (2020). Microclimatic effects on alpine plant communities and flower-visitor interactions. *Scientific Reports*, 10, 1366.
  113. Parker, G. G. (1995). Structure and microclimate of forest canopies. *Forest Canopies*. Academic Press.
  114. 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.

- 811 115. Pausata, F.S.R., Gaetani, M., Messori, G., Berg, A., de Souza, D.M., Sage, R.F., deMenocal, P.B. (2020). The greening of  
812 the Sahara: past changes and future implications. *One Earth*, 2: 235-250.
- 813 116. Pearson, R. G., Phillips, S. J., Lorant, M. M., Beck, P. S., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in  
814 Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3(7), 673-677.
- 815 117. Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., ... & Carbognani, M. (2019). Litter  
816 decomposition: effects of temperature driven by soil moisture and vegetation type. *Plant and Soil*, 435(1-2), 187-200.
- 817 118. Phillips, J. W., Chung, A. Y. C., Edgecombe, G. D., & Ellwood, M. D.F. (2020). Bird's nest ferns promote resource  
818 sharing by centipedes. *Biotropica*, 52: 335-44.
- 819 119. Potter, K. A., Arthur Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global  
820 Change Biology*, 19, 2932-2939.
- 821 120. Riutta, T., Slade, E. M., Bebb, D.P., et al. (2012). Experimental evidence for the interacting effects of forest edge,  
822 moisture and soil macrofauna on leaf litter decomposition. *Soil Biology and Biochemistry*, 49, 124-31.
- 823 121. Roberts, J., Cabral, O. M. R., Ferreira De Aguiar, L. (1990). Stomatal and boundary-layer conductances in an  
824 Amazonian terra firme rain forest. *Journal of Applied Ecology*, 27, 336-353.
- 825 122. Rousseau, L. et al. (2019) Woody biomass removal in harvested boreal forest leads to a partial functional  
826 homogenization of soil mesofaunal communities relative to unharvested forest. *Soil Biology and Biochemistry*, 133,  
827 129-136
- 828 123. Russo, S. et al. (2015) Top ten European heatwaves since 1950 and their occurrence in the coming decades.  
829 *Environmental Research Letters*, 10, 12
- 830 124. Scheffers, B. R., Brunner, R. M., Ramirez, S. D., et al. (2013a). Thermal buffering of microhabitats is a critical factor  
831 mediating warming vulnerability of frogs in the Philippine Biodiversity Hotspot. *Biotropica*, 45, 628-35.
- 832 125. Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A., & Williams, S. E. (2013b). Increasing  
833 arboreality with altitude: a novel biogeographic dimension. *Proceedings of the Royal Society B: Biological Sciences*,  
834 280(1770), 20131581.
- 835 126. Scheffers, B. R., Edwards, D. P., Diesmos, A., et al. (2014a). Microhabitats reduce animal's exposure to climate  
836 extremes. *Global Change Biology*, 20, 495-503.
- 837 127. Scheffers, B. R., Phillips, B. L., & Shoo, L. P. (2014b). *Asplenium* bird's nest ferns in rainforest canopies are climate-  
838 contingent refuges for frogs. *Global Ecology and Conservation*, 2, 37-46.
- 839 128. Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R., Roslan, N., ... & Williams, S.  
840 E. (2017). Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, 49(1), 35-44.
- 841 129. Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., ... & Mitchell, W. A. (2016).  
842 Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *PNAS*, 113(38),  
843 10595-10600.
- 844 130. Seidl, C. M., Basham, E. W., Andriamahohatra, L. R., & Scheffers, B. R. (2020). Bird's nest fern epiphytes facilitate  
845 herpetofaunal arboreality and climate refuge in two paleotropical canopies. *Oecologia*, 192(2), 297-309.
- 846 131. Selva, N. N. S., Chylarecki, P., Jonsson, B. G., & Ibsch, P. L. (2020). Misguided forest action in EU Biodiversity  
847 Strategy. *Science*, 368, 1438-1439.
- 848 132. Senf, C., & Seidl, R. (2020). Mapping the forest disturbance regimes of Europe. *Nature Sustainability*, in press.
- 849 133. Senior, R.A., Hill, J.K., González del Pliego, P., Goode, L.K., & Edwards, D.P. (2017). A pantropical analysis of the  
850 impacts of forest degradation and conversion on local temperature. *Ecology and Evolution*, 7, 7897-7908.
- 851 134. Silva Junior, C.H.L., et al. (2020) Persistent collapse of biomass in Amazonian forest edges following deforestation  
852 leads to unaccounted carbon losses. *Science Advances*, 6, eaaz8360.
- 853 135. Slavich, E., Warton, D. I., Ashcroft, M. B., et al. (2014). Topoclimate versus macroclimate: how does climate mapping  
854 methodology affect species distribution models and climate change projections? *Diversity and Distributions*, 20, 952-  
855 63.
- 856 136. Spracklen, D.V. et al. (2012). Observations of increased tropical rainfall preceded by air passage over forests. *Nature*,  
857 489, 282-285.
- 858 137. Sprugel, D. G., Rascher, K. G., Gersonde, R., Dovčiak, M., Lutz, J. A., & Halpern, C. B. (2009). Spatially explicit  
859 modeling of overstory manipulations in young forests: effects on stand structure and light. *Ecological Modelling*, 220,  
860 3565-3575.
- 861 138. Staal, A., Flores, B M., Aguiar, A. P. D., Bosmans, J. H. C., Fetzer, I., & Tuinenburg, O. A. (2020). Feedback between  
862 drought and deforestation in the Amazon. *Environmental Research Letters*, 15, 044024
- 863 139. Stewart, K. J., & Mallik, A. U. (2006). Bryophyte responses to microclimatic edge effects across riparian buffers.  
864 *Ecological Applications*, 16, 1474-1486.
- 865 140. Stuntz, S., Simon, U., and Zotz, G. (2002). Rainforest air-conditioning: the moderating influence of epiphytes on the  
866 microclimate in tropical tree crowns. *International Journal of Biometeorology*, 46, 53-59.
- 867 141. Su, Y. et al. (2020). Phenology acts as a primary control of urban vegetation cooling and warming: A synthetic analysis  
868 of global site observations. *Agricultural and Forest Meteorology*, 280, 107765.
- 869 142. Sutherland, W.J., et al. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101, 58-67.

- 870  
871  
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874  
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880  
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898  
899  
900  
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904  
905  
906  
907  
908  
909  
910  
911
143. 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.
  144. Tewksbury, J.J. et al. (2008). Putting the heat on tropical animals. *Science*, 320, 1296-1297.
  145. Trumbore, S. et al. (2015). Forest health and global change. *Science*, 349, 814-818.
  146. Uriarte, M., Schwartz, N., Powers, J. S., et al. (2016). Impacts of climate variability on tree demography in second growth tropical forests: the importance of regional context for predicting successional trajectories. *Biotropica*, 48, 780–97.
  147. 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.
  148. Vickery, W. L., & Rivest, D. (1992). The influence of weather on habitat use by small mammals. *Ecography*, 15(2), 205-211.
  149. Vanwallegem, T., & Meentemeyer, R. K. (2009). Predicting forest microclimate in heterogeneous landscapes. *Ecosystems*, 12, 1158-1172.
  150. 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.
  151. 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, 1113–20.
  152. Wiens, J. A. (1989) Spatial scaling in ecology. *Functional ecology*, 3(4), 385-397.
  153. 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.
  154. 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, 421–30.
  155. Xing, S., Bonebrake, T. C., Tang, C. C., Pickett, E. J., Cheng, W., Greenspan, S. E., ... & Scheffers, B. R. (2016). Cool habitats support darker and bigger butterflies in Australian tropical forests. *Ecology and Evolution*, 6, 8062-8074.
  156. 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.
  157. 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. (2019a) Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, 28, 1774-1786.
  158. Zellweger F., De Frenne P., Lenoir J., Rocchini D., & Coomes D. (2019b) Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution*, 34, 327-341.
  159. Zellweger, F., De Frenne, P., et al. (2020) Forest microclimate dynamics drive plant responses to warming. *Science*, 368, 772-775.
  160. Zhang, Q., & Zak, J. C. (1995) Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology*, 76, 2196–204.
  161. Zhang, Q., et al. (2020) Reforestation and surface cooling in temperate zones: mechanisms and implications. *Global Change Biology*, in press.
  162. Zweifel, R., Böhm, J.P., & Häslner, R. (2002) Midday stomatal closure in Norway spruce—reactions in the upper and lower crown. *Tree Physiology*, 22, 1125-1136.

912 **Figure captions**

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

915

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

918

919 **Fig. 3.** Multiple vegetation drivers of microclimate might be of different importance in forest at boreal  
920 (top), temperate (middle), and tropical (bottom) latitudes, respectively, even if most processes are general.  
921 Increasing tree density from open non-forest habitats (A), to plantations with a simple canopy structure  
922 (B), to (semi-)natural forest with complex structure (C) reduces below-canopy wind speeds above ground.  
923 Forest canopies can reduce ground snow cover and thus decrease the insulating effect of snow cover on  
924 cool soil temperatures during the cold season (D). Vertical layering of vegetation (E) influences the amount  
925 and quality of incoming shortwave radiation, outgoing longwave radiation and moisture exchange.  
926 Disturbances can create canopy gaps (F), providing a local shift in microclimate. Seasonal reductions in  
927 canopy cover (tree phenology, G) during the cool and/or dry season increases the exposure of the internal  
928 forest to ambient conditions. Forests also buffer the temporal (i.e. diurnal, seasonal and interannual)  
929 variability in temperature conditions relative to adjacent non-forest systems (bottom panel). This buffering  
930 effect varies with vegetation height and structure, with reduced buffering in secondary, post-agricultural  
931 forests (H) relative to primary or ancient, (semi-)natural forests (I). Microhabitats within a forest, such as  
932 those created by epiphytic plants (J) can offer an even more buffered microclimate, critical for the ecology  
933 and physiology of many forest species. Finally, the temperature offset in forests can change throughout the  
934 diel cycle, with cooler forest interiors vs. open areas during the day (K) and warmer at night (L). For the  
935 sake of simplicity, we chose to depict wind, shortwave radiation, and temperature in the boreal, temperate,  
936 and tropical panel, respectively. However, of course all of these microclimate variables can be relevant to  
937 systems across latitudes.

938

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

942

943 **Fig. 5.** Macroclimate change effects on microclimates. Climate warming and climatic extremes affect  
944 microclimates and microrefugia by influencing forest composition and structure in boreal (top panel),  
945 temperate (middle) and tropical forests (lower panel). We here highlight the processes influencing  
946 microclimatic offsets that are most relevant for each biome, although most processes are important in all  
947 the biomes. Complex, indirect effects of climate change on microrefugia involve feedback with natural and  
948 anthropogenic factors.

949

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

956 **Box 1 Definitions of offsets, buffering, coupling and decoupling**

957 Many terms related to microclimate dynamics have been used in the scientific literature, such as ‘buffering’,  
958 ‘coupling’, ‘decoupling’ and ‘offset’ to imply divergence from macroclimatic fluctuations over time.  
959 However, no uniform definition of these terms exists yet. For this reason, we here suggest a uniform  
960 terminology including all terms by illustrating the processes behind each of them (Fig. 1).  
961

962 First of all, we define the temperature offset as the instantaneous difference between a reference  
963 temperature at a given time  $t_0$  and the focal temperature under study at the same time  $t_0$ . For instance, the  
964 horizontal temperature offset due to the presence of a forest canopy is the instantaneous difference between  
965 the free-air temperature in open conditions (i.e., macroclimate) and the sub-canopy temperature at the same  
966 height (i.e., microclimate), with positive and negative offset values meaning colder and warmer conditions  
967 in the forest understorey, respectively (Fig. 1, left panel). Similarly, the vertical temperature offset due to  
968 snow cover is the instantaneous temperature difference between the air above the snow and inside the snow  
969 layer, with positive and negative offset values meaning colder and warmer conditions inside the snow layer,  
970 respectively (Fig. 1, right panel).  
971

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

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

988 **Supplementary Information**

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