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► To cite this version:

Pieter de Frenne, Jonathan Roger Michel Henri Lenoir, Miska Luoto, Brett Scheffers, Florian Zellweger, et al.. Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 2021, 27 (11), pp.2279-2297. 10.1111/gcb.15569 . hal-03293490

HAL Id: hal-03293490

<https://hal.science/hal-03293490>

Submitted on 23 Jul 2021

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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*
6

7 Pieter De Frenne^{1*}, Jonathan Lenoir², Miska Luoto³, Brett R. Scheffers⁴, Florian Zellweger⁵, Juha Aalto^{3,6},
8 Michael B. Ashcroft⁷, Ditte M. Christiansen⁸, Guillaume Decocq², Karen De Pauw¹, Sanne Govaert¹,
9 Caroline Greiser⁸, Eva Gril², Arndt Hampe⁹, Tommaso Jucker¹⁰, David Klings¹¹, Irena A. Koelemeijer⁸,
10 Jonas J. Lembrechts¹², Ronan Marrec², Camille Meeussen¹, Jérôme Ogee¹³, Vilna Tyystjärvi^{3,6}, Pieter
11 Vangansbeke¹, Kristoffer Hylander⁸

- 12 1. Ghent University, Forest & Nature Lab, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium
13 2. CNRS-UPJV, UMR CNRS 7058 "Ecologie et Dynamique des Systèmes Anthropisés", 1 Rue des
14 Louvels, F-80037 Amiens, France
15 3. University of Helsinki, Department of Geosciences and Geography, Gustaf Hällströmin katu 2,
16 00014 Helsinki, Finland
17 4. University of Florida, Wildlife Ecology & Conservation, 110 Newins-Ziegler Hall, 32611
18 Gainesville, USA
19 5. Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
20 6. Finnish Meteorological Institute, Weather and Climate Change Impact Research, Erik Palménin
21 aukio 1, 00560 Helsinki, Finland
22 7. University of Wollongong, Centre for Sustainable Ecosystem Solutions, School of Earth,
23 Atmospheric and Life Sciences, Northfields Avenue, 2522 Wollongong, Australia
24 8. Stockholm University, Department of Ecology, Environment and Plant Sciences, and Bolin
25 Centre for Climate Research, Svante Arrhenius väg 20 A, SE-106 91 Stockholm, Sweden
26 9. INRAE, Univ. Bordeaux, BIOGECO, F-33610 Cestas, France
27 10. University of Bristol, School of Biological Sciences, 24 Tyndall Avenue, BS8 1TQ Bristol, UK
28 11. University of Florida, School of Natural Resources and Environment, 103 Black Hall, Gainesville
29 FL, 32611 Gainesville, USA
30 12. University of Antwerp, Plants and Ecosystems, Universiteitsplein 1, 2610 Wilrijk, Belgium
31 13. INRAE, ISPA, 71 avenue Edouard Bourlaux, 33140 Villenave d'Ornon, France

32
33 *Corresponding author: Pieter.DeFrenne@UGent.be, tel.: +32 9 264 90 30
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⁻¹ 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 m²) 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 CO₂ 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

560 **Acknowledgements**

561 This review resulted from extensive preparations and discussions at a scientific workshop at Ekenäs
562 Herrgård, Sweden, in February 2020, funded by "The Oscar and Lili Lamm Memorial Foundation" obtained
563 by K.H. K.H. also received funding from the Swedish Research Council Formas (grant 2014-530 and 2018-
564 2829) and the Bolin Centre for Climate Research, Stockholm University. P.D.F., P.V. and C.M. received
565 funding from the European Research Council (ERC) under the European Union's Horizon 2020 research
566 and innovation programme (ERC Starting Grant FORMICA 757833), K.D.P. and S.G. from the Research
567 Foundation Flanders (FWO, grant number ASP 035-19 and project G0H1517N, respectively), J.L. and
568 E.G. from the French National Research Agency (ANR) within the framework of the IMPRINT project
569 "IMpacts des PRocessus mIcroclimatiques sur la redistributioN de la biodiversiTé forestière en contexte
570 de réchauffement du macroclimat" (grant number: ANR-19-CE32-0005-01), D.H.K. from the US National
571 Science Foundation Graduate Research Fellowship Program, J.J.L. from the Research Foundation Flanders
572 (FWO, grants OZ7828 and OZ7792). T.J. was supported by a NERC Independent Research Fellowship
573 (grant number: NE/S01537X/1), J.O. by the French National Research Agency (ANR) in the frame of the
574 Cluster of Excellence COTE (project HydroBeech, ANR-10-LABX-45), and A.H. by the EU ERA-NET
575 BiodivERsA (project SPONFOREST, BiodivERsA3-2015-58). MBA received a travel grant from the
576 University of Wollongong.

577 **References**578
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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.

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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).

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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_{micro}) equal macroclimatic
976 temperatures (T_{macro}). In other words, the slope (β_1) of the linear relationship between T_{macro} and
977 T_{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_{macro} fluctuations over time such that temporal fluctuations in
980 T_{micro} still exist but are much less pronounced than for T_{macro} . This generates a cycle of positive and
981 negative offset values which tend to diminish the positive correlation between T_{macro} and T_{micro} ,
982 such that β_1 is lower than 1 but greater than 0. The closer β_1 is to zero, the more pronounced the
983 magnitude of buffering.
- 984 (3) Perfect decoupling occurs when T_{micro} behaves independently from T_{macro} , i.e. when the slope (β_1)
985 is zero and the buffering is so strong that the positive correlation between T_{micro} and T_{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.