

<https://helda.helsinki.fi>

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

De Frenne, Pieter

2021-06

De Frenne , P , Lenoir , J , Luoto , M , Scheffers , B R , Zellweger , F , Aalto , J , Ashcroft , M B , Christiansen , D M , Decocq , G , De Pauw , K , Govaert , S , Greiser , C , Gril , E , Hampe , A , Jucker , T , Klinges , D H , Koelemeijer , I A , Lembrechts , J J , Marrec , R , Meeussen , C , Ogee , J , Tyystjarvi , V , Vangansbeke , P & Hylander , K 2021 , ' Forest microclimates and climate change: importance, drivers and future research agenda ' , Global Change Biology , vol. 27 , no. 11 , pp. 2279-2297 . <https://doi.org/10.1111/gcb.15569> , <https://doi.org/10.1111/gcb.15569>

<http://hdl.handle.net/10138/341672>

<https://doi.org/10.1111/gcb.15569>

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

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

3
4
5 Running title: Microclimates in forests
6
7
8

9 Pieter De Frenne^{1*}, Jonathan Lenoir², Miska Luoto³, Brett R. Scheffers⁴, Florian Zellweger⁵, Juha Aalto^{3,6},
10 Michael B. Ashcroft⁷, Ditte M. Christiansen⁸, Guillaume Decocq², Karen De Pauw¹, Sanne Govaert¹,
11 Caroline Greiser⁸, Eva Gril², Arndt Hampe⁹, Tommaso Jucker¹⁰, David Klinges¹¹, Irena A. Koelemeijer⁸,
12 Jonas J. Lembrechts¹², Ronan Marrec², Camille Meeussen¹, Jérôme Ogee¹³, Vilna Tyystjärvi^{3,6}, Pieter
13 Vangansbeke¹, Kristoffer Hylander⁸

- 14
15
16 1. Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium
17 2. CNRS-UPJV, UMR CNRS 7058 "Ecologie et Dynamique des Systèmes Anthropisés", 1 Rue des
18 Louvels, F-80037 Amiens, France
19 3. University of Helsinki, Department of Geosciences and Geography, Gustaf Hällströmin katu 2,
20 00014 Helsinki, Finland
21 4. University of Florida, Wildlife Ecology & Conservation, 110 Newins-Ziegler Hall, 32611
22 Gainesville, USA
23 5. Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
24 6. Finnish Meteorological Institute, Weather and Climate Change Impact Research, Erik Palménin
25 aukio 1, 00560 Helsinki, Finland
26 7. University of Wollongong, Centre for Sustainable Ecosystem Solutions, School of Earth,
27 Atmospheric and Life Sciences, Northfields Avenue, 2522 Wollongong, Australia
28 8. Stockholm University, Department of Ecology, Environment and Plant Sciences, and Bolin
29 Centre for Climate Research, Svante Arrhenius väg 20 A, SE-106 91 Stockholm, Sweden
30 9. INRAE, Univ. Bordeaux, BIOGECO, F-33610 Cestas, France
31 10. University of Bristol, School of Biological Sciences, 24 Tyndall Avenue, BS8 1TQ Bristol, UK
32 11. University of Florida, School of Natural Resources and Environment, 103 Black Hall, Gainesville
33 FL, 32611 Gainesville, USA
34 12. University of Antwerp, Plants and Ecosystems, Universiteitsplein 1, 2610 Wilrijk, Belgium
35 13. INRAE, ISPA, 71 avenue Edouard Bourlaux, 33140 Villenave d'Ornon, France
36
37

38 *Corresponding author: Pieter.DeFrenne@UGent.be, tel.: +32 9 264 90 30
39

40 Abstract

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

61

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

64 Introduction: the importance of forest microclimates

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

76

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

89

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

110

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

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

122

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

139

140 Drivers of vertical and horizontal microclimate variation

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

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

152

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

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

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

193
194 *Vertical distribution of microclimates: from the ground to the top of the canopy*

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

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

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

217

218 Consequences of microclimates for forest biodiversity

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

227

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

236

237 *Spatial impacts of forest microclimate on biodiversity*

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

258

259 *Temporal impacts of forest microclimate on biodiversity*

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

274

275 Consequences of microclimates on forest functioning

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

295

296 How will macroclimate warming affect forest microclimates?

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

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

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

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

348 *Macroclimate warming effects on temperature offsets*

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

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

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

373 374 *Extreme event effects on temperature offsets*

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

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

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

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

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

412
413 In the tropics, the combined effects of logging, droughts and fires on canopy loss (i.e., deforestation and
414 degradation) can locally increase air dryness (Staal et al. 2020) and daily maximum temperatures more than
415 the warming associated with high emission scenarios (Senior et al. 2017). Hence, by letting in direct sunlight
416 and warm and dry air, large canopy gaps following deforestation strongly alter understorey microclimate
417 (Fig. 3 and 5), reducing the capacity to buffer macroclimatic fluctuations and thus causing many species to
418 decline in abundance, e.g. termites that are especially sensitive to desiccation (Cornelius & Osbrink, 2010;
419 see De Smedt et al. 2018 for a study from temperate forests). However, small canopy gaps (< 400 m²) in
420 tropical forests, which occur under natural forest dynamics, can quickly regain their thermal environment
421 in a few years (Mollinari et al. 2019), while secondary forests can regain their thermal environments within
422 20 – 30 years after logging (del Pliego et al 2016). These drastic changes in microclimatic conditions are not
423 only due to tree removal, but at a finer resolution also to epiphyte loss. Indeed, epiphytes represent a
424 significant functional group for microclimate dynamics in tropical forests, reducing water loss through
425 evaporative drying (Scheffers et al. 2014b) and providing buffered microhabitats for canopy-dwelling
426 organisms (Seidl et al. 2020) (Fig. 3, arrow J).

427 428 *Forest microclimate feedbacks on macroclimate warming*

429 Although we now have a better understanding of the impact of macroclimate warming on forest
430 microclimate dynamics, the potential feedback of forest microclimates on macroclimate warming itself
431 remains understudied (Barry & Blanken, 2016). Yet, the implications are important for solutions to mitigate
432 and adapt to climate change. Changes in microclimates may feed back to the macroclimate by affecting
433 localized water and carbon balances and microgradients of CO₂ within forests.

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

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

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

459

460 A research agenda and identification of research gaps

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

467

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

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

489

490 *2) Mapping and predictions of forest microclimates*

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

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

514

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

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

530

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

549

550 *Concluding remarks*

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

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

580
581

582 Acknowledgements

583 This review resulted from extensive preparations and discussions at a scientific workshop at Ekenäs
584 Herrgård, Sweden, in February 2020, funded by “The Oscar and Lili Lamm Memorial Foundation” obtained
585 by K.H. K.H. also received funding from the Swedish Research Council Formas (grant 2014-530 and 2018-
586 2829) and the Bolin Centre for Climate Research, Stockholm University. P.D.F., P.V. and C.M. received
587 funding from the European Research Council (ERC) under the European Union’s Horizon 2020 research
588 and innovation programme (ERC Starting Grant FORMICA 757833), K.D.P. and S.G. from the Research
589 Foundation Flanders (FWO, grant number ASP 035-19 and project G0H1517N, respectively), J.L. and
590 E.G. from the French National Research Agency (ANR) within the framework of the IMPRINT project
591 “IMpacts des PRocessus mIcroclimatiques sur la redistributioN de la biodiversiTé forestière en contexte
592 de réchauffement du macroclimat” (grant number: ANR-19-CE32-0005-01), D.H.K. from the US National
593 Science Foundation Graduate Research Fellowship Program, J.J.L. from the Research Foundation Flanders
594 (FWO, grants OZ7828 and OZ7792). T.J. was supported by a NERC Independent Research Fellowship
595 (grant number: NE/S01537X/1), J.O. by the French National Research Agency (ANR) in the frame of the
596 Cluster of Excellence COTE (project HydroBeech, ANR-10-LABX-45), and A.H. by the EU ERA-NET
597 BiodivERsA (project SPONFOREST, BiodivERsA3-2015-58). MBA received a travel grant from the
598 University of Wollongong. We also thank the subject editor, and an anonymous reviewer and Dr. Solomon
599 Dobrowski for numerous helpful comments.

600 References

601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630
631
632
633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651
652
653
654
655
656
657
658

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., & Blaken, 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 CO₂ 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., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., & Franklin, J.F. (1999) Microclimate in forest ecosystem and landscape ecology - Variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*, 49, 288-297.

- 659 29. Chen, Y., Liu, Y., Zhang, J., et al. (2018). Microclimate exerts greater control over litter decomposition and enzyme
660 activity than litter quality in an alpine forest-tundra ecotone. *Scientific Reports*, 8, 1–13.
- 661 30. Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field
662 experiments. *The American Naturalist*, 122, 661–696.
- 663 31. Connon, R. et al. (2018) The influence of shallow taliks on permafrost thaw and active layer dynamics in subarctic
664 Canada. *Journal of Geophysical Research: Earth Surface*, 123, 281–297.
- 665 32. Coomes, D. A., Flores, O., Holdaway, R., Jucker, T., Lines, E.R., & Vanderwel, M. C. (2014). Wood production
666 response to climate change will depend critically on forest composition and structure. *Global Change Biology*, 20,
667 3632–3645.
- 668 33. Cornelius, M.L., & Osbrink, W.L.A. (2010). Effect of soil type and moisture availability on the foraging behavior of the
669 Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology*, 103, 799–807.
- 670 34. Cudmore, T.J. et al. (2010). Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle
671 reproduction in naïve host tree populations. *Journal of Applied Ecology*, 47, 1036-1043.
- 672 35. Davies-Colley, R. J., Payne, G. W., & Van Elswijk, M. (2000). Microclimate gradients across a forest edge. *New
673 Zealand Journal of Ecology*, 24, 111-121.
- 674 36. Davis, K.T. et al. (2019). Microclimatic buffering in forests of the future: the role of local water balance. *Ecography*,
675 42: 1-11.
- 676 37. De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., & Verheyen, K.
677 (2015). Light accelerates plant responses to warming. *Nature Plants*, 1, 15110.
- 678 38. De Frenne P., & Verheyen, K (2015). Weather stations lack forest data. *Science*, 351, 234.
- 679 39. De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., et al. 2013. Microclimate moderates plant responses to
680 macroclimate warming. *PNAS*, 110, 18561–18565.
- 681 40. De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen,
682 K. & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3, 744-
683 749.
- 684 41. De Smedt, P., Baeten, L., et al. (2018) Desiccation resistance determines distribution of woodlice along forest edge-to-
685 interior gradients. *European Journal of Soil Biology*, 85, 1-3.
- 686 42. De Smedt, P., Vangansbeke, P., Bracke, R., Schauwvlieghe, W., Willems, L., Mertens, J., & Verheyen, K. (2019). Vertical
687 stratification of moth communities in a deciduous forest in Belgium. *Insect conservation and diversity*, 12, 121-130.
- 688 43. Decocq, G. (2000). The 'masking effect' of silviculture on substrate-induced plant diversity in oak-hornbeam forests
689 from northern France. *Biodiversity and Conservation* 9, 1467–1491.
- 690 44. Decocq, G., Aubert, M., Dupont, F., Bardat, J., Watzte-Franger, A., Saguez, R., de Foucault, B., Alard, D., & Delelis-
691 Dusollier, A. (2005). Silviculture-driven vegetation change in a European temperate deciduous forest. *Annals of Forest
692 Science*, 62, 313–323.
- 693 45. del Pliego, P. G., Scheffers, B. R., Basham, E. W., Woodcock, P., Wheeler, C., Gilroy, J. J., ... & Edwards, D. P. (2016).
694 Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biological
695 Conservation*, 201, 385-395.
- 696 46. Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., & Martin, P.R. (2008).
697 Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS*, 105, 6668–6672.
- 698 47. Didham, R. K., & Ewers, R. M. (2014). Edge effects disrupt vertical stratification of microclimate in a temperate forest
699 canopy. *Pacific Science*, 68, 493-508.
- 700 48. Dobrowski, S. Z. (2011). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*,
701 17, 1022-1035.
- 702 49. Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests.
703 *PLOS one*, 8(3).
- 704 50. Ewers, R. M., Boyle, M. J., Gleave, R. et al. (2015). Logging cuts the functional importance of invertebrates in tropical
705 rainforest. *Nature Communications*, 6, 6836.
- 706 51. Frey, S.J., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016a). Spatial models reveal the
707 microclimatic buffering capacity of old-growth forests. *Science Advances*, 2(4), e1501392.
- 708 52. Frey, S.J., Hadley, A.S., Betts, M.G. (2016b). Microclimate predicts within-season distribution dynamics of montane
709 forest birds. *Diversity and Distributions*, 22, 944–959.
- 710 53. Gauslaa, Y. (2014). Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic
711 lichens. *The Lichenologist*, 1, 1–16.
- 712 54. Gauthier, S., et al. (2015) Boreal forest health and global change. *Science*, 349, 819-822.
- 713 55. Gavin, D.G., et al. (2014) Climate refugia: joint inference from fossil records, species distribution models and
714 phylogeography. *New Phytologist*, 204, 37-54.
- 715 56. Geiger, R., Aron, R. H., & Todhunter, P. (2009). *The climate near the ground*. Rowman & Littlefield.
- 716 57. Gerhardt K. (1996). Effects of root competition and canopy openness on survival and growth of tree seedlings in a
717 tropical seasonal dry forest. *Forest Ecology and Management*, 82, 33–48.

- 718 58. Giguère-Croteau, C. et al. (2018) North America's oldest boreal trees are more efficient water users due to increased
719 [CO₂], but do not grow faster. *PNAS*, 116, 2749-2754
- 720 59. Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., & Hylander, K. (2018). Monthly microclimate models in a managed
721 boreal forest landscape. *Agricultural and Forest Meteorology*, 250, 147-158.
- 722 60. Greiser, C., Meineri, E., Ehrlén, J., & Hylander, K. (2019). Hiding from the climate: Characterizing microrefugia for
723 boreal forest understory species. *Global Change Biology*, 26, 471–483.
- 724 61. Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration
725 niche. *Biological Reviews*, 52, 107–145.
- 726 62. Hampe, A., & Jump, A. S. (2011) Climate relicts: past, present, future. *Annual Review of Ecology, Evolution and*
727 *Systematics*, 42, 313-333.
- 728 63. Hannah, L., Flint, L., Syphard, A. D., et al. (2014). Fine-grain modeling of species' response to climate change:
729 holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, 29, 390–397.
- 730 64. Hardwick, S.R., Toumi, R., et al. (2015) The relationship between leaf area index and microclimate in tropical forest
731 and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201,
732 187-195.
- 733 65. Harley, P., Guenther, A., & Zimmerman, P. (1996). Effects of light, temperature and canopy position on net
734 photosynthesis and isoprene emission from sweetgum (*Liquidambar styraciflua*) leaves. *Tree Physiology*, 16, 25-32.
- 735 66. Harper, J. L., & White, J. (1974). The demography of plants. *Annual Review of Ecology and Systematics*, 5, 419–63.
- 736 67. Heberling, M. et al. (2019). Phenological mismatch with trees reduces wildflower carbon budgets. *Ecology Letters*, 22,
737 612-623
- 738 68. Holmgren, M., Scheffer, M., & Huston, M. A. (1997). The interplay of facilitation and competition in plant
739 communities. *Ecology*, 78, 1966–1975.
- 740 69. Huang, C.W., Chu, C.R., Hsieh, C.I., Palmroth, S., & Katul, G.G. (2015). Wind-induced leaf transpiration. *Advances in*
741 *Water Resources*, 86, 240-255.
- 742 70. Hylander, K. (2005). Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of*
743 *Applied Ecology*. 42, 518-525.
- 744 71. Hylander, K., & Nemomissa, S. (2009). Complementary roles of home gardens and exotic tree plantations as
745 alternative habitats for Ethiopian montane rainforest plant biodiversity. *Conservation Biology*, 23, 400-409.
- 746 72. Hylander, K., Ehrlén, J., Luoto, M., & Meineri, E. (2015). Microrefugia: not for everyone. *Ambio*, 44, 60-68.
- 747 73. IPBES (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of
748 the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz, J. Settele, E. S.
749 Brondizio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneeth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A.
750 Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A.
751 Pfaff, S. Polasky, A. Purvis, J. Razaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis,
752 and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages.
- 753 74. Johansson, V., Lönnell, N., Rannik, Ü., Sundberg, S., & Hylander, K. (2016), Air humidity thresholds trigger active
754 moss spore release to extend dispersal in space and time. *Functional Ecology*, 30, 1196-1204.
- 755 75. Jonason, D., Franzen, M., & Ranius, T. (2014). Surveying moths using light traps: effects of weather and time of year.
756 *PLoS One*, 9(3), e92453.
- 757 76. Jucker, T., Hardwick, S. R., Both, S. et al. (2018). Canopy structure and topography jointly constrain the microclimate
758 of human-modified tropical landscapes. *Global Change Biology*, 24, 5243–5258.
- 759 77. Jucker, T., Jackson, T. D., Zellweger, F. et al. (2020). A research agenda for microclimate ecology in human-modified
760 tropical forests. *Frontiers in Forests and Global Change*, 2, 92.
- 761 78. Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-
762 blooded” animals against climate warming. *PNAS*, 106, 3835–3840.
- 763 79. Keppel, G., Niel, K. P. V., Wardell-Johnson, G. W., et al. (2012). Refugia: identifying and understanding safe havens
764 for biodiversity under climate change. *Global Ecology and Biogeography*, 21, 393–404.
- 765 80. Kerry, P., & Griffiths, S. (2000). The earth is not flat. *Global Change Biology*, 2, 214-218.
- 766 81. Kingsolver, J.G. (2009). The Well-Tempered Biologist. *The American Naturalist*, 174, 755–768.
- 767 82. Köchy, M., & Wilson, S. D. (1997). Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass
768 prairie. *Ecology*, 78, 732–739.
- 769 83. Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L., ... Verheyen, K. (2019).
770 The functional role of temperate forest understorey vegetation in a changing world. *Global Change Biology*, 2511,
771 3625-3641.
- 772 84. Lantz, T.C. et al. (2013). Recent shrub proliferation in the Mackenzie delta uplands and microclimatic implications.
773 *Ecosystems*, 16, 47-59.
- 774 85. Latimer, C. E., & Zuckerberg, B. (2017). Forest fragmentation alters winter microclimates and microrefugia in human-
775 modified landscapes. *Ecography*, 40, 158-170.

- 776
777
778
779
780
781
782
783
784
785
786
787
788
789
790
791
792
793
794
795
796
797
798
799
800
801
802
803
804
805
806
807
808
809
810
811
812
813
814
815
816
817
818
819
820
821
822
823
824
825
826
827
828
829
830
831
832
833
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. McLaughlin, B.C., Ackerly, D.D., Zion Klos, P., Natali, J., Dawson, T.E. & Thompson, S.E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, 23, 2941–2961.
 102. MEA. (2005). Millennium ecosystem assessment. *Ecosystems and human well-being: Biodiversity synthesis*. Washington, DC: World Resource Institute.
 103. Meehl, G.A., & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st Century. *Science*, 305, 994–997.
 104. 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.
 105. 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.
 106. 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.
 107. 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.
 108. 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.
 109. 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.
 110. 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.
 111. 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.
 112. Ogée, J., Peylin, P., Ciais, P. et al. (2003). Partitioning net ecosystem carbon exchange into net assimilation and respiration using ^{13}C measurements: a cost-effective sampling strategy. *Global Biogeochemical Cycles*, 17, 1070.
 113. Ohler, L.-M., Lechleitner, M., Junker, R. R. (2020). Microclimatic effects on alpine plant communities and flower-visitor interactions. *Scientific Reports*, 10, 1366.
 114. Parker, G. G. (1995). Structure and microclimate of forest canopies. *Forest Canopies*. Academic Press.

- 834 115. Onaindia, M., Dominguez, I., Albizu, I., Garbisu, C., & Amezaga, I. (2004). Vegetation diversity and vertical structure
835 as indicators of forest disturbance. *Forest Ecology and Management*, 195, 341-354.
- 836 116. Pausata, F.S.R., Gaetani, M., Messori, G., Berg, A., de Souza, D.M., Sage, R.F., deMenocal, P.B. (2020). The greening of
837 the Sahara: past changes and future implications. *One Earth*, 2: 235-250.
- 838 117. Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in
839 Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3(7), 673-677.
- 840 118. Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., ... & Carbognani, M. (2019). Litter
841 decomposition: effects of temperature driven by soil moisture and vegetation type. *Plant and Soil*, 435(1-2), 187-200.
- 842 119. Phillips, J. W., Chung, A. Y. C., Edgecombe, G. D., & Ellwood, M. D.F. (2020). Bird's nest ferns promote resource
843 sharing by centipedes. *Biotropica*, 52: 335-44.
- 844 120. Potter, K. A., Arthur Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global
845 Change Biology*, 19, 2932-2939.
- 846 121. Riutta, T., Slade, E. M., Bebb, D.P., et al. (2012). Experimental evidence for the interacting effects of forest edge,
847 moisture and soil macrofauna on leaf litter decomposition. *Soil Biology and Biochemistry*, 49, 124-31.
- 848 122. Roberts, J., Cabral, O. M. R., Ferreira De Aguiar, L. (1990). Stomatal and boundary-layer conductances in an
849 Amazonian terra firme rain forest. *Journal of Applied Ecology*, 27, 336-353.
- 850 123. Rousseau, L. et al. (2019) Woody biomass removal in harvested boreal forest leads to a partial functional
851 homogenization of soil mesofaunal communities relative to unharvested forest. *Soil Biology and Biochemistry*, 133,
852 129-136
- 853 124. Russo, S. et al. (2015) Top ten European heatwaves since 1950 and their occurrence in the coming decades.
854 *Environmental Research Letters*, 10, 12
- 855 125. Scheffers, B. R., Brunner, R. M., Ramirez, S. D., et al. (2013a). Thermal buffering of microhabitats is a critical factor
856 mediating warming vulnerability of frogs in the Philippine Biodiversity Hotspot. *Biotropica*, 45, 628-35.
- 857 126. Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A., & Williams, S. E. (2013b). Increasing
858 arboreality with altitude: a novel biogeographic dimension. *Proceedings of the Royal Society B: Biological Sciences*,
859 280(1770), 20131581.
- 860 127. Scheffers, B. R., Edwards, D. P., Diesmos, A., et al. (2014a). Microhabitats reduce animal's exposure to climate
861 extremes. *Global Change Biology*, 20, 495-503.
- 862 128. Scheffers, B. R., Phillips, B. L., & Shoo, L. P. (2014b). Asplenium bird's nest ferns in rainforest canopies are climate-
863 contingent refuges for frogs. *Global Ecology and Conservation*, 2, 37-46.
- 864 129. Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R., Roslan, N., ... & Williams, S.
865 E. (2017). Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, 49, 35-44.
- 866 130. Schmidt, M., Jochhim, H., Kersebaum, K.C., Lischeid, G., Nendel, C. (2017) Gradients of microclimate, carbon and
867 nitrogen in transition zones of fragmented landscapes – a review. *Agricultural and Forest Meteorology*, 232, 659-671.
- 868 131. Sears, M. W., Angilletta, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., ... & Mitchell, W. A. (2016).
869 Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *PNAS*, 113, 10595-
870 10600.
- 871 132. Seidl, C. M., Basham, E. W., Andriamahohatra, L. R., & Scheffers, B. R. (2020). Bird's nest fern epiphytes facilitate
872 herpetofaunal arboreality and climate refuge in two paleotropical canopies. *Oecologia*, 192(2), 297-309.
- 873 133. Selva, N. N. S., Chylarecki, P., Jonsson, B. G., & Ibsch, P. L. (2020). Misguided forest action in EU Biodiversity
874 Strategy. *Science*, 368, 1438-1439.
- 875 134. Senf, C., & Seidl, R. (2020). Mapping the forest disturbance regimes of Europe. *Nature Sustainability*, in press.
- 876 135. Senior, R.A., Hill, J.K., González del Pliego, P., Goode, L.K., & Edwards, D.P. (2017). A pantropical analysis of the
877 impacts of forest degradation and conversion on local temperature. *Ecology and Evolution*, 7, 7897-7908.
- 878 136. Silva Junior, C.H.L., et al. (2020) Persistent collapse of biomass in Amazonian forest edges following deforestation
879 leads to unaccounted carbon losses. *Science Advances*, 6, eaaz8360.
- 880 137. Slavich, E., Warton, D. I., Ashcroft, M. B., et al. (2014). Topoclimate versus macroclimate: how does climate mapping
881 methodology affect species distribution models and climate change projections? *Diversity and Distributions*, 20, 952-
882 63.
- 883 138. Spracklen, D.V. et al. (2012). Observations of increased tropical rainfall preceded by air passage over forests. *Nature*,
884 489, 282-285.
- 885 139. Sprugel, D. G., Rascher, K. G., Gersonde, R., Dovčiak, M., Lutz, J. A., & Halpern, C. B. (2009). Spatially explicit
886 modeling of overstory manipulations in young forests: effects on stand structure and light. *Ecological Modelling*, 220,
887 3565-3575.
- 888 140. Staal, A., Flores, B.M., Aguiar, A. P. D., Bosmans, J. H. C., Fetzer, I., & Tuinenburg, O. A. (2020). Feedback between
889 drought and deforestation in the Amazon. *Environmental Research Letters*, 15, 044024
- 890 141. Stewart, K. J., & Mallik, A. U. (2006). Bryophyte responses to microclimatic edge effects across riparian buffers.
891 *Ecological Applications*, 16, 1474-1486.
- 892 142. Stuntz, S., Simon, U., and Zotz, G. (2002). Rainforest air-conditioning: the moderating influence of epiphytes on the
893 microclimate in tropical tree crowns. *International Journal of Biometeorology*, 46, 53-59.

- 894 143. Su, Y. et al. (2020). Phenology acts as a primary control of urban vegetation cooling and warming: A synthetic analysis
895 of global site observations. *Agricultural and Forest Meteorology*, 280, 107765.
896 144. Sutherland, W.J., et al. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101, 58-67.
897 145. Swanson, A. C., Schwendenmann, L., Allen, M. F., Aronson, E. L., Artavia-León, A., Dierick, D., ... Zelikova, T. J.
898 (2019). Welcome to the Atta world: A framework for understanding the effects of leaf-cutter ants on ecosystem
899 functions. *Functional Ecology*, 33, 1386-1399.
900 146. Tewksbury, J.J. et al. (2008). Putting the heat on tropical animals. *Science*, 320, 1296-1297.
901 147. Trumbore, S. et al. (2015). Forest health and global change. *Science*, 349, 814-818.
902 148. Uriarte, M., Schwartz, N., Powers, J. S., et al. (2016). Impacts of climate variability on tree demography in second
903 growth tropical forests: the importance of regional context for predicting successional trajectories. *Biotropica*, 48, 780–
904 97.
905 149. Valladares, F., & Guzmán, B. (2006). Canopy structure and spatial heterogeneity of understory light in an abandoned
906 Holm oak woodland. *Annals of Forest Science*, 63, 749-761.
907 150. Vickery, W. L., & Rivest, D. (1992). The influence of weather on habitat use by small mammals. *Ecography*, 15(2),
908 205-211.
909 151. Vanwallegem, T., & Meentemeyer, R. K. (2009). Predicting forest microclimate in heterogeneous landscapes.
910 *Ecosystems*, 12, 1158-1172.
911 152. von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., & Gilliam, F. (2013). Microclimate in forests with varying
912 leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *Journal of*
913 *Ecology*, 101(5), 1201–1213.
914 153. Wang, S., Ruan, H., & Han, Y. (2010). Effects of microclimate, litter type, and mesh size on leaf litter decomposition
915 along an elevation gradient in the Wuyi Mountains, China. *Ecological Research*, 25, 1113–20.
916 154. Wiens, J. A. (1989) Spatial scaling in ecology. *Functional ecology*, 3(4), 385-397.
917 155. Wikström, L., Milberg, P., & Bergman, K. O. (2009) Monitoring of butterflies in semi-natural grasslands: diurnal
918 variation and weather effects. *Journal of Insect Conservation*, 13(2), 203.
919 156. Woods, C. L., Cardelus, C. L., & DeWalt, S.J. (2015) Microhabitat associations of vascular epiphytes in a wet tropical
920 forest canopy. *Journal of Ecology*, 103, 421–30.
921 157. Xing, S., Bonebrake, T. C., Tang, C. C., Pickett, E. J., Cheng, W., Greenspan, S. E., ... & Scheffers, B. R. (2016). Cool
922 habitats support darker and bigger butterflies in Australian tropical forests. *Ecology and Evolution*, 6, 8062-8074.
923 158. Yuan, F. L., Freedman, A. H., Chirio, L., LeBreton, M., & Bonebrake, T. C. (2018) Ecophysiological variation across a
924 forest-ecotone gradient produces divergent climate change vulnerability within species. *Ecography*, 41(10), 1627-1637.
925 159. Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S.L., Wulf, M., Kirby, K.J., Brunet, J., Kopecky, M., Malis, F.,
926 Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K. & De Frenne, P.
927 (2019a) Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global*
928 *Ecology and Biogeography*, 28, 1774-1786.
929 160. Zellweger F., De Frenne P., Lenoir J., Rocchini D., & Coomes D. (2019b) Advances in microclimate ecology arising
930 from remote sensing. *Trends in Ecology & Evolution*, 34, 327-341.
931 161. Zellweger, F., De Frenne, P., et al. (2020) Forest microclimate dynamics drive plant responses to warming. *Science*,
932 368, 772-775.
933 162. Zhang, Q., & Zak, J. C. (1995) Effects of gap size on litter decomposition and microbial activity in a subtropical forest.
934 *Ecology*, 76, 2196–204.
935 163. Zhang, Q., et al. (2020) Reforestation and surface cooling in temperate zones: mechanisms and implications. *Global*
936 *Change Biology*, in press.
937 164. Zweifel, R., Böhm, J.P., & Häsler, R. (2002) Midday stomatal closure in Norway spruce—reactions in the upper and
938 lower crown. *Tree Physiology*, 22, 1125-1136.

939 Figure captions

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

942

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

945

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

967

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

971

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

977

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

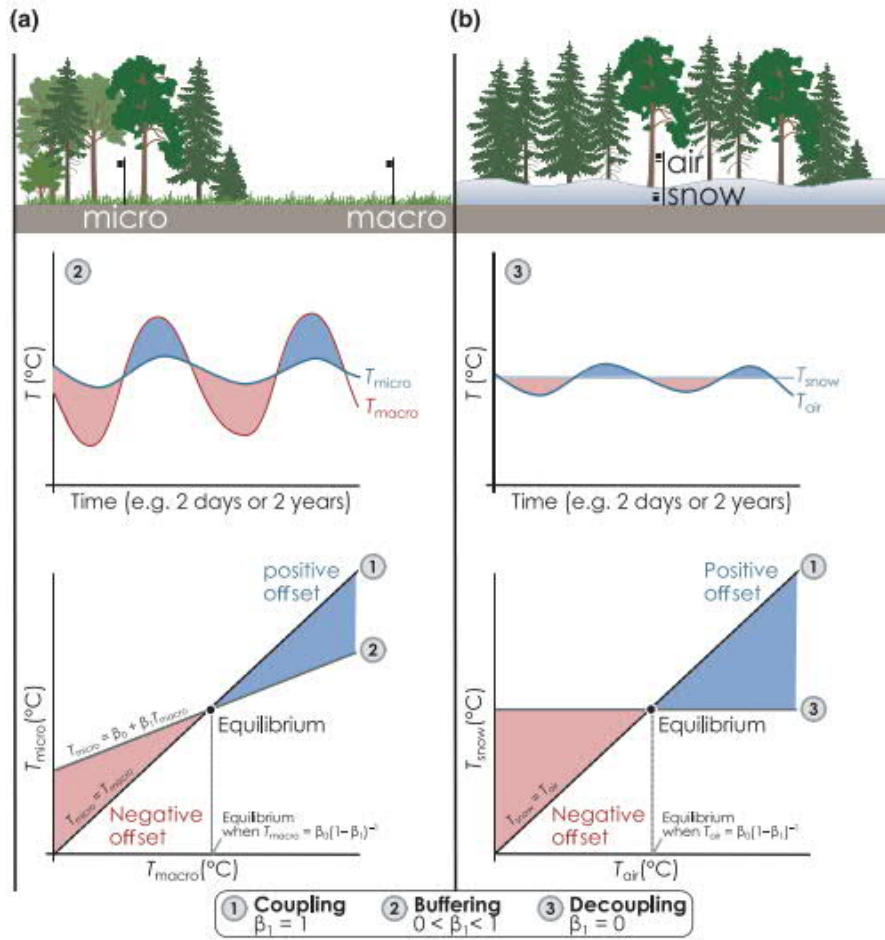
984 Box 1 Definitions of offsets, buffering, coupling and decoupling

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

990 First of all, we define the temperature offset as the instantaneous difference between a reference
991 temperature at a given time t_0 and the focal temperature under study at the same time t_0 . For instance, the
992 horizontal temperature offset due to the presence of a forest canopy is the instantaneous difference between
993 the free-air temperature in open conditions (i.e., macroclimate) and the sub-canopy temperature at the same
994 height (i.e., microclimate), with positive and negative offset values meaning colder and warmer conditions
995 in the forest understorey, respectively (Fig. 1, left panel). Similarly, the vertical temperature offset due to
996 snow cover is the instantaneous temperature difference between the air above the snow and inside the snow
997 layer, with positive and negative offset values meaning colder and warmer conditions inside the snow layer,
998 respectively (Fig. 1, right panel).
999

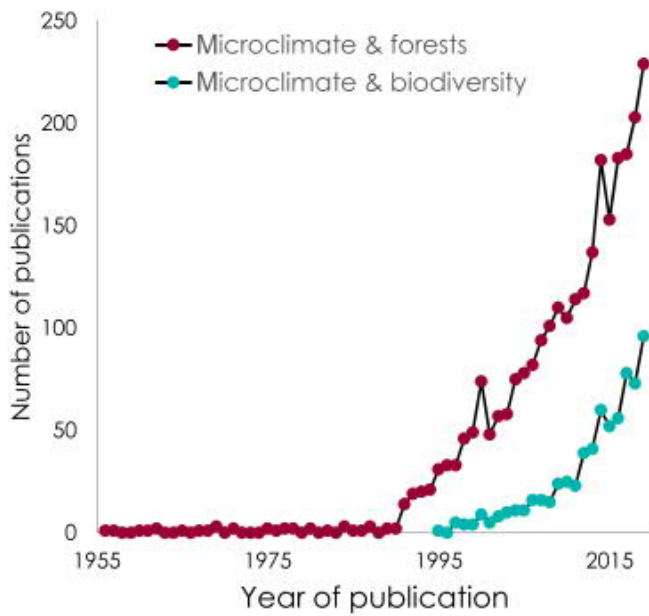
1000 Then, depending on the magnitude and distribution of the temperature offsets over time, it is possible to
1001 distinguish three contrasting situations (Fig. 1): (1) perfect coupling; (2) buffering; and (3) perfect
1002 decoupling:

- 1003 (1) Perfect coupling occurs when microclimatic temperatures (T_{micro}) equal macroclimatic
1004 temperatures (T_{macro}). In other words, the slope (β_1) of the linear relationship between T_{macro} and
1005 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
1006 time.
- 1007 (2) Buffering means a dampening of T_{macro} fluctuations over time such that temporal fluctuations in
1008 T_{micro} still exist but are much less pronounced than for T_{macro} . This generates a cycle of positive and
1009 negative offset values which tend to diminish the positive correlation between T_{macro} and T_{micro} ,
1010 such that β_1 is lower than 1 but greater than 0. The closer β_1 is to zero, the more pronounced the
1011 magnitude of buffering.
- 1012 (3) Perfect decoupling occurs when T_{micro} behaves independently from T_{macro} , i.e. when the slope (β_1)
1013 is zero and the buffering is so strong that the positive correlation between T_{micro} and T_{macro} is totally
1014 lost. For instance, temperatures inside the snow layer during winter are completely decoupled from
1015 temperatures above the snow layer (Fig. 1, right panel).
1016
1017
1018
1019
1020
1021
1022
1023
1024
1025
1026
1027
1028
1029
1030
1031
1032



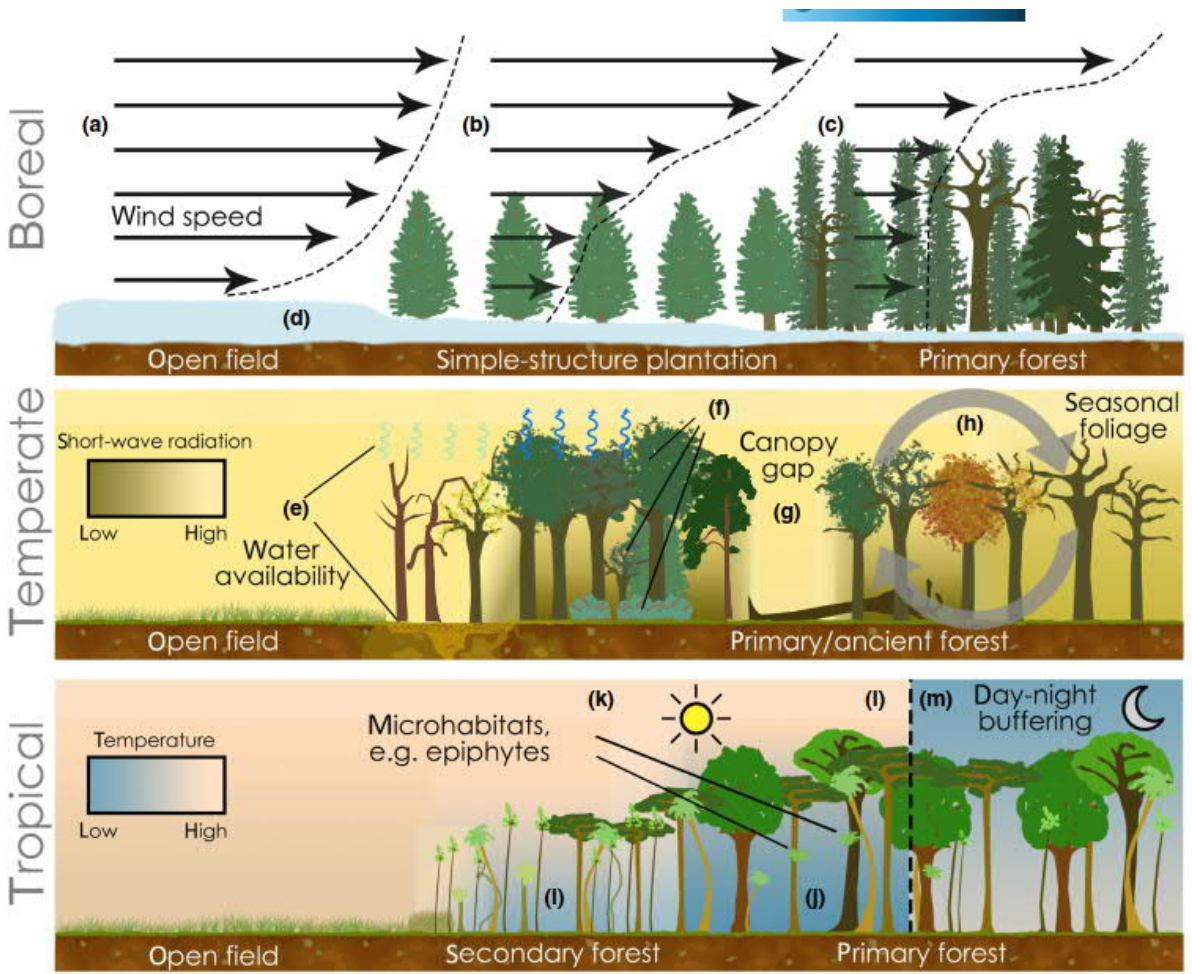
1034
1035
1036

Fig. 1.



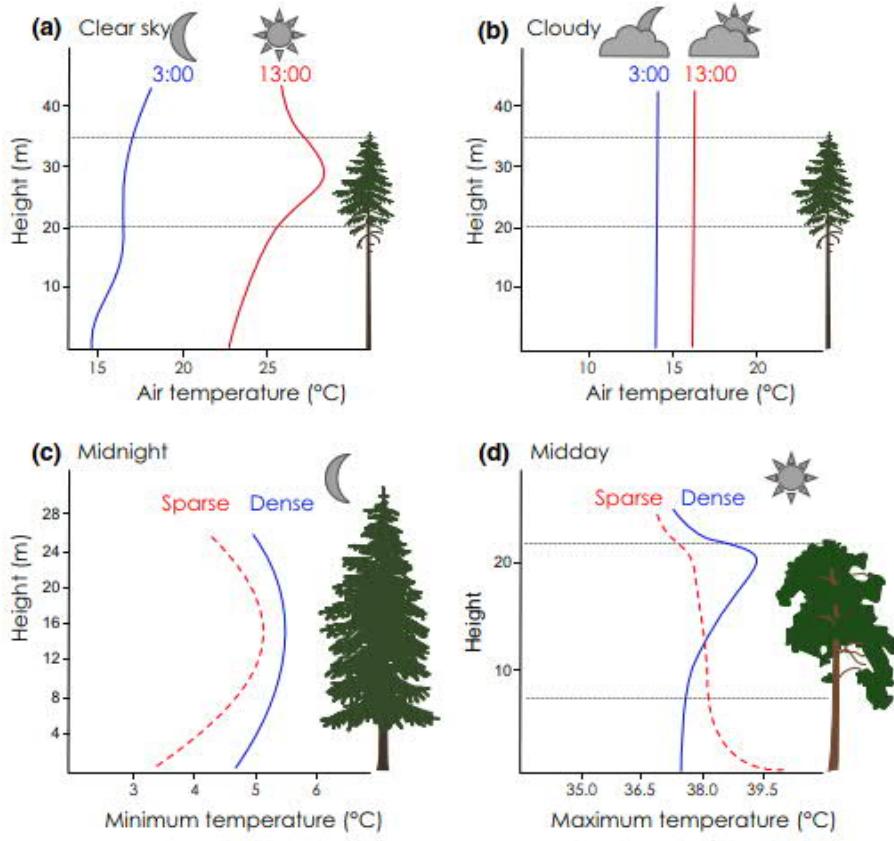
1037
1038
1039

Fig. 2.

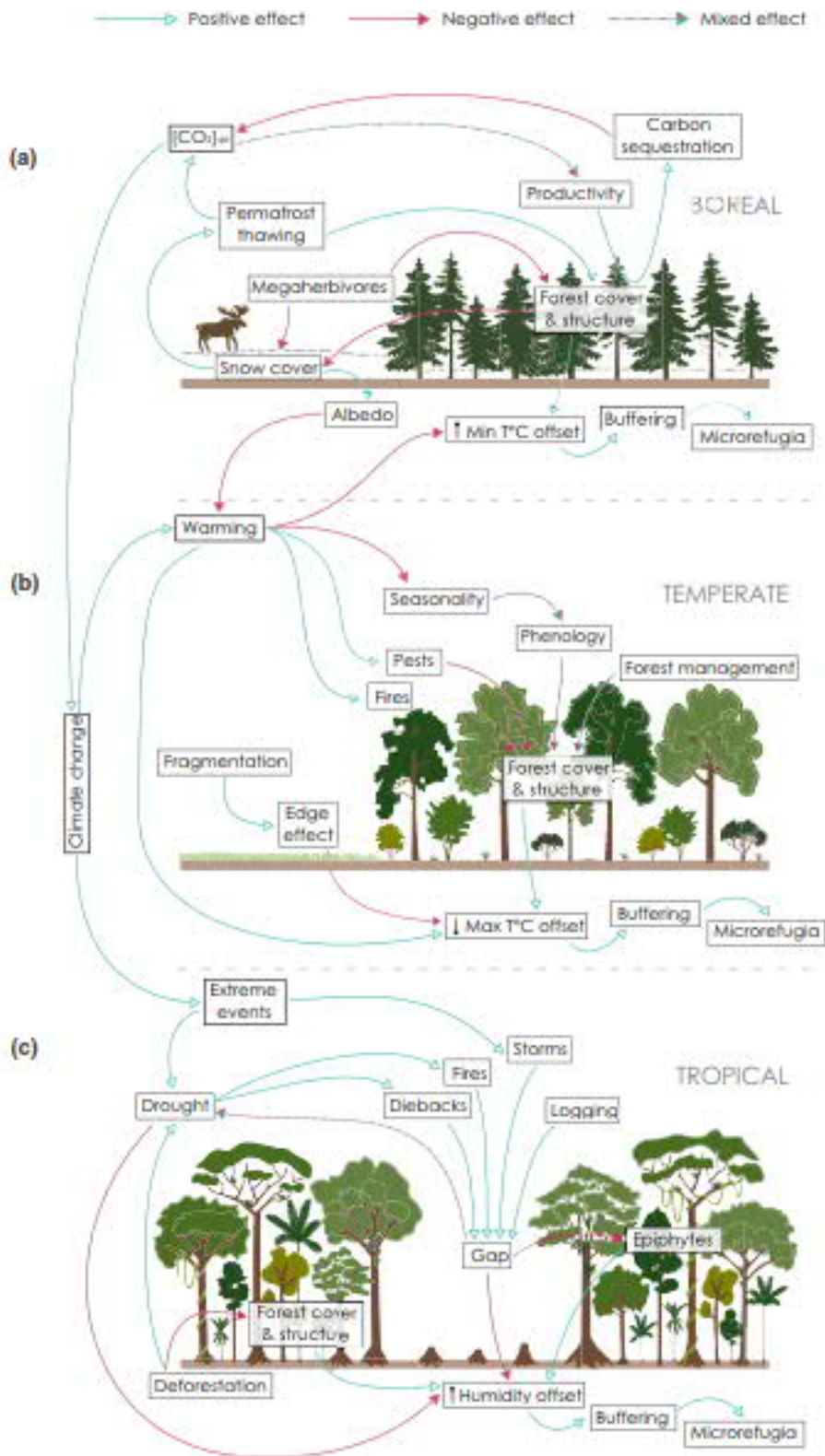


1040
1041
1042

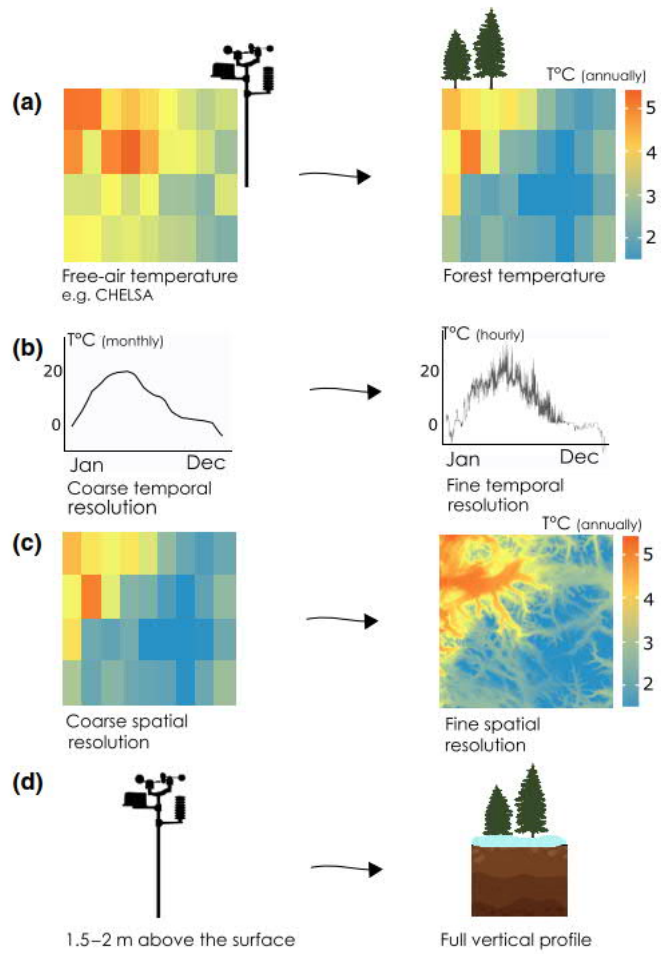
Fig. 3.



1043
 1044 Fig. 4.
 1045



1046
 1047 Fig. 5.
 1048



1049
 1050
 1051
 1052

Fig. 6.