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1 Title page

2 Title:

3 **Microclimate modulation: an overlooked mechanism influencing the impact of plant**
4 **diversity on ecosystem functioning.**

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39

40 Main text

41 Abstract

42 Changes in climate and biodiversity are widely recognized as primary global change drivers
43 of ecosystem structure and functioning, also affecting ecosystem services provided to
44 human populations. Increasing plant diversity typically enhances ecosystem functioning and
45 stability. Higher plant diversity can also mitigate climate change effects and buffer extreme
46 weather conditions, but the underlying mechanisms remain largely unclear. Recent studies
47 have shown that plant diversity can mitigate climate change (e.g. reduce temperature
48 fluctuations or drought through microclimatic effects) in different compartments of the focal
49 ecosystem, which as such may contribute to the effect of plant diversity on ecosystem
50 properties and functioning. However, these potential plant diversity-induced microclimate
51 effects are not sufficiently understood. Here, we explored the consequences of climate
52 modulation through microclimate modification by plant diversity for ecosystem functioning as
53 a potential mechanism contributing to the widely documented biodiversity-ecosystem
54 functioning (BEF) relationships, using a combination of theoretical and simulation
55 approaches. We focused on a diverse set of response variables at various levels of
56 integration ranging from ecosystem-level carbon exchange to soil enzyme activity, including
57 population dynamics and activity of specific organisms. Here, we demonstrated that a
58 vegetation layer composed of many plant species has the potential to influence ecosystem
59 functioning and stability through the modification of microclimatic conditions, thus mitigating
60 the negative impacts of climate extremes on ecosystem functioning. Integrating microclimatic
61 processes (e.g. temperature, humidity, and light modulation) as a mechanism contributing to
62 the BEF relationships is a promising avenue to improve our understanding of the effects of
63 climate change on ecosystem functioning and to better predict future ecosystem structure,

64 functioning, and services. In addition, microclimate management and monitoring should be
65 seen as a potential tool by practitioners to adapt ecosystems to climate change.

66 Introduction

67 The profound impacts of changing climate and biodiversity on ecosystem functioning and
68 stability are widely acknowledged (IPBES, 2019; Pörtner et al., 2021). These threats extend
69 to the key ecosystem services that sustain human populations (IPCC, 2021; Pörtner et al.,
70 2021), particularly as climatic extremes like heatwaves, droughts, and floods become more
71 frequent, pushing ecosystems toward critical thresholds and potential collapse (Duffy et al.,
72 2021; MacDougall et al., 2013).

73 The intricate relationship between ecosystem functioning and climatic conditions holds on
74 the climate-dependency of the sum of biological processes that contribute to ecosystem
75 functioning. Net Ecosystem carbon Exchange (NEE), for instance, depends on air
76 temperature, radiation, and soil water availability (Niu et al., 2012). Similarly, organic matter
77 recycling responds to changes in temperature and water availability (Joly et al., 2023; Xiao
78 et al., 2014). With changing climatic conditions, these processes move along a climate
79 response curve that is rarely linear, and the net outcome on ecosystem properties and
80 services becomes a focal point of concern.

81 The climatic conditions experienced (i.e. temperature, light availability, concentrations of
82 greenhouse gasses, humidity) by organisms may deviate substantially from those measured
83 by using conventional meteorological standards characterizing macroclimate under highly
84 standardized conditions (Haesen et al., 2023; Lembrechts, 2023; Lembrechts et al., 2020).

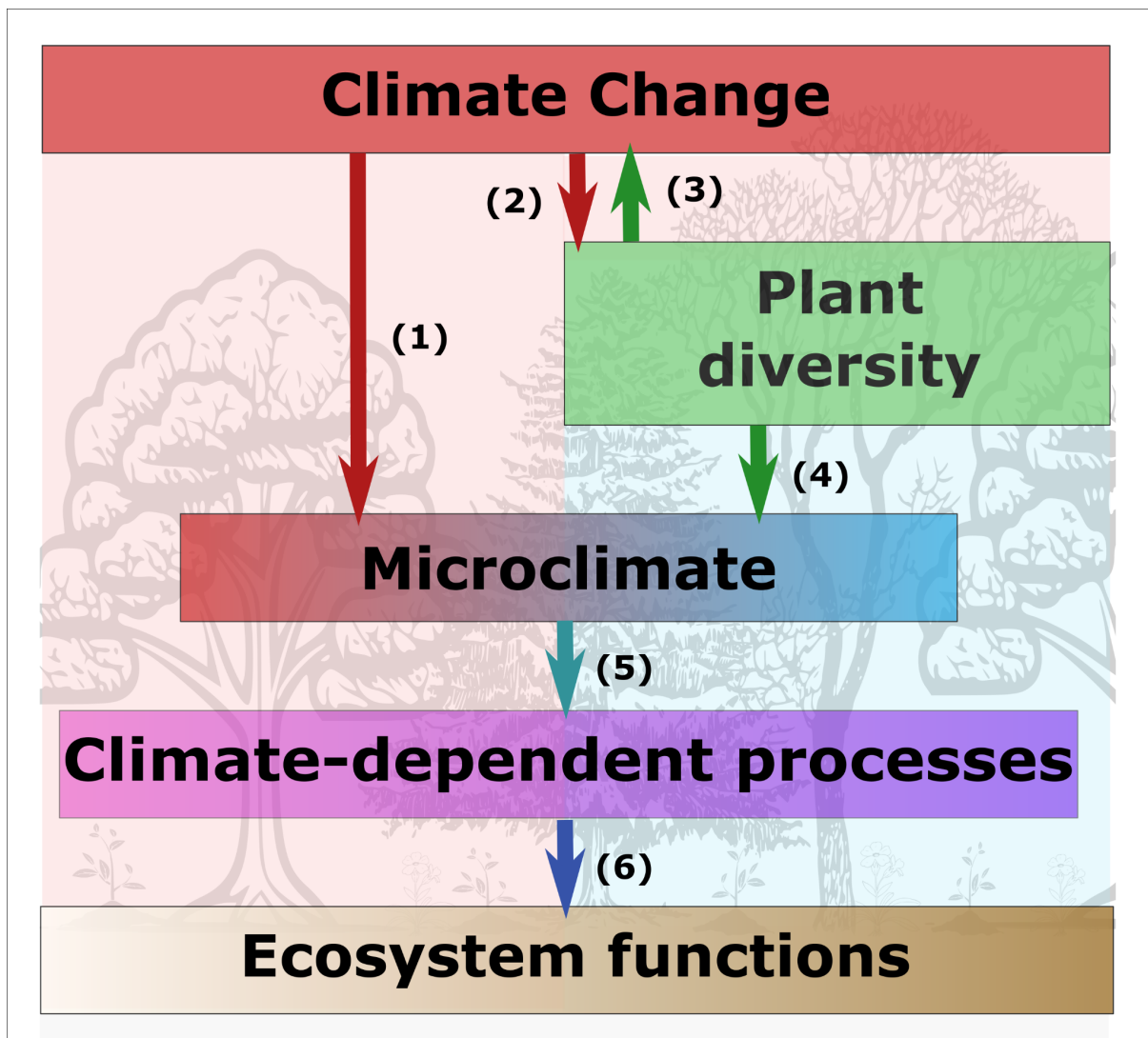
85 The climatic niche experienced by an organism is therefore defined by microclimatic
86 conditions that can differ substantially from macroclimatic conditions, potentially altering the
87 real shape of the species response curve against a given climatic parameter like
88 temperature (Haesen et al., 2023). Unsurprisingly, incorporating microclimate data, rather
89 than macroclimate data, into species distribution models (SDMs) has proven highly valuable

90 for advancing our understanding of ecosystem properties (Kemppinen et al., 2023;
91 Lembrechts, 2023; Stark & Fridley, 2022), as well as our ability to better predict the activity
92 and survival of species (Colinet et al., 2015; Dingman et al., 2013).

93 The physical structure of ecosystems and their species composition, above all that of the
94 vegetation compartment contributing to most of the biomass and controlling the key
95 ecosystem processes like the fluxes of energy and matter, play a critical role in influencing
96 differences between macro- and microclimate conditions (De Frenne et al., 2019, 2021; Gril
97 et al., 2023; Milling et al., 2018). Consequently, manipulating the species composition and
98 canopy structure of a given ecosystem offers a promising strategy to modulate microclimate,
99 and thus, the overall functioning of the focal ecosystem. Indeed, recent research highlighted
100 the potential of plant diversity, and thus ecosystem structure, to influence microclimatic
101 fluctuations (Huang et al., 2023; Ray et al., 2023; Schnabel et al., 2023; Zhang, 2022). This
102 included the further reduction of temperature extremes experienced underneath a vegetation
103 canopy that is composed of more species (Huang et al., 2023; Schnabel et al., 2023), and
104 changes in sensible heat flux and evapotranspiration resulting in higher ecosystem CO₂
105 uptake (Milcu et al., 2016). Higher plant diversity also promotes ecosystem functioning and
106 stability by increasing and securing essential functions such as productivity and carbon
107 storage (Beugnon et al., 2023; Huang et al., 2018; Liang et al., 2016; Liang et al., 2022;
108 Schnabel et al., 2019). However, the nexus between biodiversity, microclimate, and
109 ecosystem functioning remains relatively unexplored, also lacking a unified framework.

110 The aim of this study is to better understand the biodiversity - microclimate - ecosystem
111 functioning relationships by exploring the cascading effects of biodiversity-induced changes
112 on microclimatic processes and ecosystem functioning. While climate encompasses various
113 environmental factors, such as temperature, air pressure, humidity, precipitation, solar
114 radiation, cloudiness, and wind, in this study, we specifically concentrate on the effects of
115 temperature. To address this, we take a four-fold approach (Fig. 1). First, we emphasize the
116 climate-dependency of ecosystem functions across organizational levels. Second, we
117 examine the evidence supporting the effect of plant diversity on microclimate. Third, through

118 the implementation of a common simulation framework, we quantify the potential
119 consequences of increased plant diversity for temperature-dependent ecosystem functions.
120 Finally, we discuss the implications of our findings for the general understanding of the BEF
121 relationship and their practical applications.
122



123
124 **Figure 1: Conceptual framework linking the nexus between plant diversity,**
125 **microclimate, and ecosystem functions.** Examples of pairwise relationships from the
126 scientific literature: (1) Bertrand et al., 2011; Lembrechts, 2023, (2) Pörtner et al., 2021, (3)
127 Beugnon et al., 2021; Messier et al., 2021, (4) Huang et al., 2023; Schnabel et al., 2023;
128 Zhang, 2022, (5-6) Gottschall et al., 2019; Huang et al., 2019; Joly et al., 2017.

129 Climate context dependencies of process rates across 130 organizational levels

131 Formulated by Brown and colleagues (2004), “the metabolic theory of ecology” proposes a
132 temperature dependency of biological processes across organizational levels, from specific
133 processes at the molecular scale to integrated processes at the ecosystem scale. Beyond its
134 primary emphasis on temperature, this theory proposes that similar causal relationships exist
135 for other climatic parameters, such as humidity and light, all influencing the performance of
136 organisms and ultimately their contribution to ecosystem functioning (Brown et al., 2004).

137 At the molecular level, temperature acts as a strong driver of enzymatic activity due to the
138 strong dependence of the reaction rate on temperature. The temperature dependence of
139 enzyme catalytic reactions shows a reaction-specific optimum and an upper-temperature
140 limit that is ultimately reached when thermal inactivation of enzymes occurs (Alster et al.,
141 2016; Peterson et al., 2007). This temperature-enzyme activity relationship has historically
142 been modeled with the Arrhenius law, although recently proposed models better represent
143 the experimentally observed bell-shaped response curve (Alster et al., 2020). Concurrently,
144 other climatic variables also impact enzyme functioning, for instance, changes in soil
145 moisture alter substrate diffusion and the likelihood of substrate-enzyme encounters and the
146 production of microbial extracellular enzymes, ultimately leading to changes in enzyme
147 activity, as observed for the extracellular beta-glucosidase enzyme, a key player in soil
148 organic carbon decomposition (Puissant et al., 2015, 2018; Wallenstein & Weintraub, 2008;
149 Zhang et al., 2011). Changes in microclimate can also affect substrate concentration, such
150 as an increase in CO₂ concentrations that enhance the activity of the photosynthetic enzyme
151 Rubisco (Galmés et al., 2019).

152 The climate, or more generally the environmental control of enzymatic kinetics, affects
153 individual performance and the functions the organisms have in the ecological context via
154 the organisms’ metabolic activities. This holds particular significance for species unable to

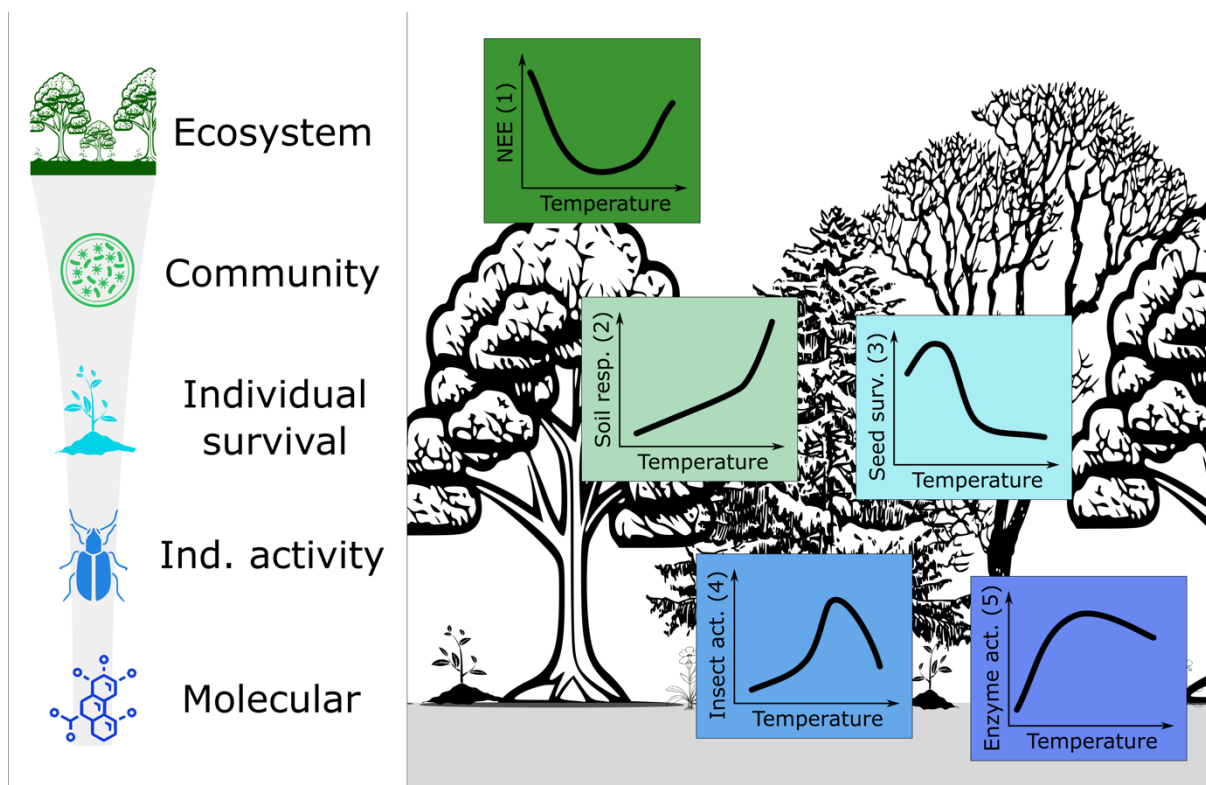
155 regulate their body temperature, such as ectotherms. For instance, insects, being
156 ectotherms, demonstrate an increase in activity with rising temperatures, reaching an
157 optimal point before experiencing a drastic decline (Colinet et al., 2015; Sinclair et al., 2016;
158 Terlau et al., 2023). Although primarily assessed at the microbial community scale, the
159 temperature response of microbes plays a critical role in nutrient recycling and ecosystem
160 functioning (Bradford et al., 2019; Dacal et al., 2019). The temperature dependency of
161 microbes is a subject of intense debate, representing a major uncertainty in the projections
162 of carbon cycle models in response to climate warming (García-Palacios et al., 2021; Duffy
163 et al., 2021). Consequently, microclimate buffering could emerge as a critical factor in
164 regulating the rate of soil carbon decomposition. Such control over specific activities of
165 organisms is also exerted by other environmental factors such as light availability. When
166 light penetrates a plant canopy, it is increasingly absorbed following the Beer-Lambert law
167 (Larcher, 2003) affecting, for example, leaf functional traits and microclimatic conditions
168 along the vertical profile (Govaert et al., 2023; Messier et al., 2017; Niinemets & Valladares,
169 2004), growth of understorey plants, as well as their composition and cover in the
170 understorey (Messier et al., 1998; Tinya & Ódor, 2016).

171 Climate responses of individual organisms ultimately transition to the community level by
172 impacting their survival (Allen et al., 2010; Dingman et al., 2013; McDowell et al., 2022),
173 phenology (Cleland et al., 2007; Møller et al., 2023), and productivity (Huang et al., 2019),
174 which all determine competitive interactions and community composition. Through its
175 influence on individuals, biotic interactions and communities, climate effects also transcend
176 trophic levels and food-web structure and dynamics (Sentis et al., 2014).

177 Collectively, these responses to climate variables across various organizational levels from
178 single biochemical reactions to organisms, communities, and food web structure may have
179 cascading effects on ecosystem-level processes such as photosynthesis (Crous et al., 2022;
180 Kirschbaum, 2004), evapotranspiration (Kirschbaum, 2004), organic matter recycling
181 (Bradford et al., 2017; Xiao et al., 2014), and soil respiration (Jones et al., 2006). A notable
182 example is the temperature dependence of the Net Ecosystem CO₂ Exchange (NEE) that

183 can vary between net C-influx at average temperatures to net C-efflux at extreme
184 temperatures (Fig. 2, Niu et al., 2012; Yuan et al., 2011). Other climate-related variables
185 such as atmospheric CO₂ concentrations and water availability additionally or interactively
186 affect NEE (Milcu et al., 2014). Similarly, net ecosystem nitrous oxide (N₂O) emissions are
187 contingent upon soil moisture and temperature (Schindlbacher et al., 2004). It is particularly
188 important to better understand all these ecosystem-level responses to climate variables with
189 ongoing climate change (IPBES, 2019; IPCC, 2021; Pörtner et al., 2021), especially since
190 the responses across organizational levels span different time scales, ranging from
191 immediate reactions to long-lasting effects.

192



193

194 **Fig. 2: Climate dependencies of various processes across different levels of**
195 **organization**, here using temperature dependency as an example: (1) Net Ecosystem CO₂
196 Exchange (NEE, Niu et al 2012), (2) soil respiration (Jones et al 2006), (3) tree seedlings
197 survival (Dingman et al., 2013), (4) insect activity (Colinet et al., 2015), and (5) Rubisco
198 activity (Galmés et al., 2019).

199 The climate-modulating impact of plant diversity

200 The dominating contribution of primary producers in terms of biomass in terrestrial
201 ecosystems confers to plants a particularly important role in structuring and engineering their
202 proximal environment. The soil development during successional dynamics with a
203 continuous modification of soil properties resulting from plant colonization in early
204 successional stages and the accumulation of organic matter and nitrogen (through symbiotic
205 N-fixation) with ongoing succession is a well-documented example of how plants reshape
206 environmental properties (Northup et al., 1995; Rahmonov et al., 2021; Wardle & Ghani,
207 1995). Specific plant species can alter environmental conditions for associated species
208 through Facilitation by “nursing” can indirectly modify biodiversity, then making it less
209 exposed to climate extremes (Bulleri et al., 2016) and sometimes improving access to limited
210 resources such as water (hydraulic lift, Caldwell et al., 1998) or nitrogen for N-fixing plants.
211 Due to their large size, trees often have a particularly strong influence on both their proximal
212 and distal environments by modifying biogeochemical cycles and providing food and shelter
213 for many other species in their environment. Coniferous trees, for example, typically reduce
214 litter and soil pH in forests where they dominate with far-ranging consequences for soil
215 microbial and fauna communities, nutrient availability, and associated plant species in the
216 understorey (Burgess-Conforti et al., 2019; Phillips et al., 2013; Wardle & Ghani, 1995). The
217 tree canopies of forests as a whole have been shown to substantially alter microclimatic
218 conditions underneath (De Frenne et al., 2019), generally providing climatically more
219 favorable conditions to understorey plants by alleviating climate extremes (Bertrand et al.,
220 2011; De Frenne et al., 2021). Forest tree canopies affect microclimate via different
221 mechanisms, such as shading, reducing air movement that diminishes mixing between air
222 layers, and active cooling by alive foliage through transpiration (Geiger et al., 1995;
223 Zellweger et al., 2020). Increasing canopy thickness and structural complexity consequently
224 enhance the strength of the buffering capacity of the upper canopy layer (Ehbrecht et al.,
225 2019; Gril et al., 2023).

226 Plant diversity was found to foster canopy thickness and complexity (Peng et al., 2017;
227 Perles–Garcia et al., 2021; Williams et al., 2017), potentially also enhancing the buffering
228 capacity of vegetation cover on microclimatic processes in the understorey. Results from
229 experiments manipulating plant diversity in the field (BEF experiments) indicate that
230 microclimatic conditions are even more stable with increasing plant species richness (Huang
231 et al., 2023; Schnabel et al., 2023; Zhang, 2022) and that microclimate interacts with stand
232 complexity in promoting forest productivity (Ray et al., 2023). Similar effects by more diverse
233 plant communities on microclimatic conditions via thicker canopies were also observed in
234 grasslands (Huang et al., 2023), yet empirical evidence in grassland ecosystems remains
235 limited, particularly regarding comprehensive global quantification across various
236 ecoregions. Further, *in-situ* measurements are necessary to fully understand the scope of
237 this relationship on a global scale, especially, long-term measurements are essential to
238 quantify the potential mitigation of climatic extremes within the context of climate change.
239 Such diversity-driven canopy feedbacks may be particularly important in mitigating effects on
240 soil temperature that have recently been shown to be more frequently affected by
241 temperature extremes than air temperature (García-García et al., 2023) at a global extent.
242 The present, still limited, evidence suggests that higher plant diversity potentially modifies
243 ecosystem functioning through climate-dependent ecosystem properties. Among the
244 possible (and non-exclusive) mechanistic hypotheses proposed to explain the effect of plant
245 diversity on ecosystem properties (e.g. hydraulic lift, architecture complementarity leading to
246 canopy packing), microclimatic processes appear as a promising explanation allowing a
247 direct link with physiology-based mechanisms. However, the effects of plant diversity on
248 microclimate dynamics depend on seasons (Huang et al., 2023; Schnabel et al., 2023;
249 Zhang, 2022), owing to structural mediation in winter (e.g. branch structure in forests) and
250 leaf mediation in summer (Schnabel et al., 2023). Consequently, the impact of plant diversity
251 on climate-dependent ecosystem functions is anticipated to be dynamic over time. It still
252 could accumulate over larger time scales, because increase in productivity with species-rich

253 communities is expected to increase with time (Dietrich et al., 2023; Huang et al., 2018;
254 Perles–Garcia et al., 2021, Weisser et al. 2017).

255 Consequences for ecosystem functioning and services

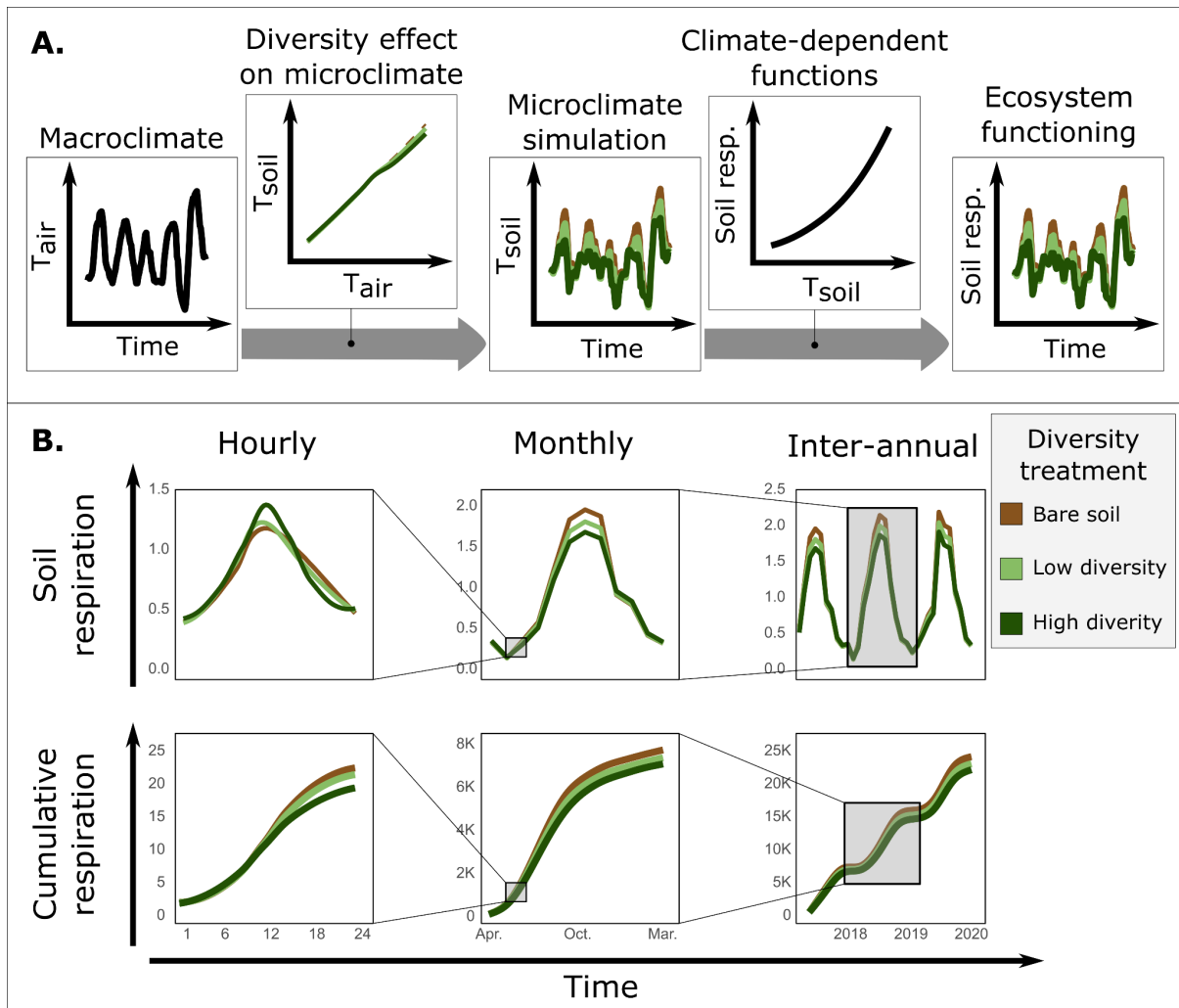
256 Plant diversity effects on microclimate have the potential to influence ecosystem functioning
257 and services through climate-dependent processes across various levels of organization
258 (Fig. 2). However, the extent of these effects remains largely unexplored, partly because
259 they are not easy to experimentally tease apart microclimatic processes from other
260 mechanisms of diversity effects. Therefore, it is unclear how diversity-driven climate
261 modulation cascades through different levels of organization and how large the resulting
262 consequences on ecosystem functioning may be. For instance, some studies on litter
263 decomposition indicate a positive influence of tree species richness on leaf litter
264 decomposition through microclimate modulation (Gottschall et al., 2019; Joly et al., 2017;
265 Makkonen et al., 2013). However, the quantification of these causal relationships remains
266 limited and the resulting consequences on ecosystem carbon and nutrient cycling are
267 untested.

268 Here, we chose a different approach to experimental testing in an attempt to move forward
269 with this critically important question. We employed a simple simulation approach to assess
270 the effects of species diversity on ecosystem functioning via microclimate, using temperature
271 as an example for a microclimate variable and soil respiration as a temperature-dependent
272 ecosystem process (Fig. 3.A, for details on the workflow see Suppl. S1). Initially, we
273 simulated soil temperature for grasslands with various plant species richness scenarios
274 (bare soil, monoculture, sixty-species mixtures), using air temperature records from central
275 Germany (2017-2019, ERA5 hourly data, Copernicus Climate Change Service, 2019) and
276 the soil temperature-grassland species richness relationship from Huang et al. (2023).
277 Subsequently, based on the soil respiration-temperature relationship from Jones et al.
278 (2006), we predicted soil respiration for each scenario and calculated cumulative soil

279 respiration (Fig. 3.B). Our simulation illustrated the potential of plant species diversity to
280 modulate soil respiration by modifying microclimate. We demonstrated that diversity primarily
281 affects soil respiration during warm hours, days, and months, rapidly increasing the
282 divergence between scenarios during these periods. Despite the fact that the magnitude of
283 this climate-mediated effect of diversity on soil respiration varied among different time
284 periods, it accumulated over time with an increasing difference in total respiration between
285 the low and high plant diversity scenarios (Fig. 3.B). The simulations that illustrate how soil
286 respiration depends on microclimate highlight the possible effects of climate modulation on
287 ecosystem functioning. However, these simulations oversimplify the relationship by
288 considering only temperature as the factor affecting soil respiration's dependence on
289 microclimate. In reality, the relationship between soil respiration and microclimate is
290 multifaceted and is modulated by additional factors such as soil humidity (Wood et al., 2013),
291 nutrient availability and CO₂ diffusivity (Davidson et al., 2012; Skopp et al., 1990). To
292 accurately predict long-term trends in soil respiration, it is imperative to consider these
293 various aspects, their interactions, and the direct effects of plant diversity on soil quality
294 (Weisser et al., 2017).

295 These simulations underscore the potential of plant diversity to influence ecosystem
296 processes through microclimate modulation, particularly when considering cumulative
297 processes such as carbon fluxes that occur not only during soil respiration but also during
298 organic matter decomposition or through biomass production, which can greatly accentuate
299 overall effects beyond the slight differences measured at specific points in time. Given that
300 numerous ecosystem functions across various organizational levels are contingent on
301 climatic conditions, the vegetation-microclimate-ecosystem functioning nexus may play a
302 pivotal role in overall ecosystem functioning. This simulation exercise emphasizes the
303 necessity for empirically measuring the vegetation-microclimate-ecosystem functioning
304 nexus to better understand the consequences at the ecosystem level. A way forward to
305 tackle the issue of confounding mechanisms influencing ecosystem functions at a yearly

306 extent could then be to increase the temporal resolution of sampling allowing to identify
 307 potential mechanisms and their temporality.
 308



309
 310 **Figure 3: Climate-mediated biodiversity-ecosystem functioning (BEF) relationships:**
 311 **(A) simulation framework and (B) outputs.** A. Simulation framework tested on soil
 312 temperature mediation: microclimate simulations using air temperature records and plant
 313 species diversity effects on soil temperature from Huang et al. (2023), and prediction of soil
 314 respiration using Jones et al. (2006) soil respiration temperature dependency (holding all
 315 other parameters to a constant value). B. Simulation outputs: soil respiration and cumulative
 316 respiration over time (Suppl. S1).

317 Perspective for research and management

318 Microclimate is an ecologically important environmental parameter that regulates ecosystem
319 functioning to an important degree (e.g. Gottschall et al., 2019; Joly et al., 2017; Kemppinen
320 et al., 2023), which can be co-determined by plant diversity and canopy structure (Huang et
321 al., 2023; Schnabel et al., 2023; Zhang, 2022). Thus, integrating microclimate into the BEF
322 relationship seems critically important and promises an enhanced understanding of the
323 mechanisms underlying BEF relationships, particularly given the multitude of climate-
324 dependent processes at different organizational levels ultimately determining ecosystem
325 functions. The mediation of microclimate in the relationship between biodiversity and
326 ecosystem functioning, coupled with its direct correlation to macroclimate fluctuations, could
327 offer an explanation for the observed climate and context dependency in the strength of the
328 biodiversity-ecosystem functioning relationship (Liu et al., 2022; Spohn et al., 2023; Cesarz
329 et al., 2022). Incorporating microclimate mediation into the biodiversity-ecosystem
330 functioning framework may advance our understanding of ecosystem functioning by
331 providing mechanistic insights.

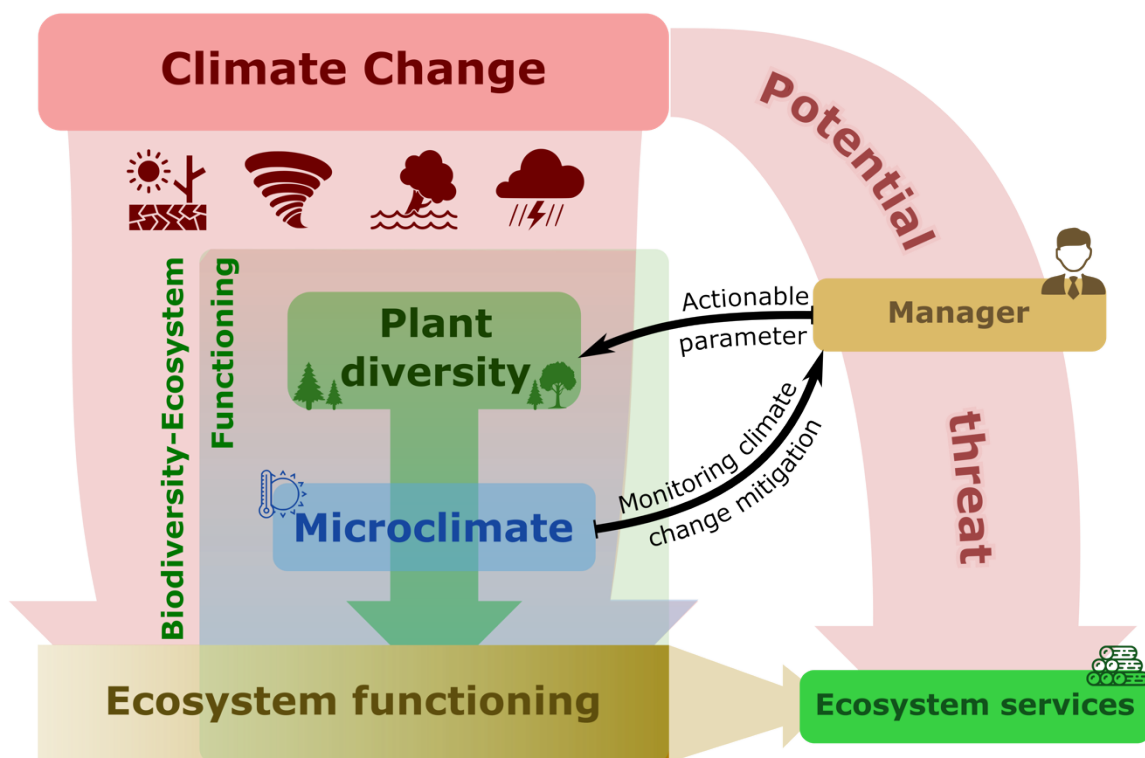
332 Microclimate spans a continuum from the top of the canopy to the soil layers, with specific
333 microclimates affecting distinct processes. For example, the soil microbial community will
334 respond to variations in the topsoil microclimate rather than to variations in the microclimate
335 within the plant canopy (Kemppinen et al., 2023). Consequently, microclimate variations will
336 have to be quantified in space and time simultaneously with the assessment of how plant
337 diversity affects microclimate dynamics in space and time. Additionally, there is a growing
338 need to quantify the climate responses of ecosystem functions over time, particularly when
339 considering functions that integrate temporal dynamics in microclimate effects.

340 The impact of plant diversity on microclimate acts primarily through modifications of canopy
341 parameters such as thickness and structural complexity (Ehbrecht et al., 2019; Gril et al.,
342 2023). It is therefore critical to include stand age and structure beyond the diversity of

343 species composing the canopy for a detailed understanding of plant diversity control over
 344 microclimate (Au et al., 2022).

345 Recognizing the importance of plant diversity in promoting ecosystem functioning and
 346 services, as well as their stability, has been emphasized to ecosystem managers (Messier et
 347 al., 2021), particularly in the context of climate change (Beugnon et al., 2021; Pires et al.,
 348 2018). Understanding the biodiversity-microclimate-ecosystem functioning nexus offers new
 349 perspectives. Microclimate monitoring becomes a valuable non-invasive tool for assessing
 350 climate change mitigation, allowing stakeholders to quantify the effects of plant diversity,
 351 both taxonomic and structural diversity, on ecosystem functioning (Fig. 4). Microclimate
 352 monitoring, being low-cost, effortless, and non-invasive (Kempainen et al., 2023), emerges
 353 as an important approach for tracking ecosystem functioning, given its influence on
 354 numerous functions across all organizational levels.

355



356

357 **Figure 4: Perspectives and consequences for Biodiversity-Ecosystem Functioning**
358 **(BEF) research and ecosystem management.**

359 Conclusions

360 We showed that the influence of plant diversity on microclimate is promising for advancing
361 our understanding of the relationship between biodiversity and ecosystem functioning,
362 especially considering the climate-dependency of ecosystem functions and services.
363 Therefore, future research should strengthen our understanding of biodiversity-microclimate-
364 ecosystem functioning by developing and testing these connections theoretically as much as
365 experimentally. Consequently, the manipulation of microclimate, through plant diversity, both
366 in terms of taxonomic and structural diversity, presents an opportunity to effectively manage
367 ecosystems functioning in the face of climate change.

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745

746 Conflict of Interest

747 The authors declare no conflict of interest.

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749 Data and code availability

750 All datasets and codes used for the simulations are available in the supplementary material

751 S1.