

1 **Metamicrobiome-driven homeostasis of nutrient recycling**

2

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15

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20

21 **Abstract**

22 Carbon and nutrient recycling by free-living microbial decomposers and fire - two key
23 recycling pathways - are highly sensitive to climatic variation. However, mutualistic
24 associations of microbiomes with plants and animals cause previously underestimated
25 environmental buffering effects. This close cooperation between small and large organisms
26 solves a fundamental allometric trade-off between mass-specific metabolic capacity
27 (decreasing with body size) and homeostatic capacity (environmental buffering; increasing
28 with body size), allowing the combination of the best of both worlds along the body mass
29 spectrum from microbes to elephants. A diverse metamicrobiome, where plant- and animal-
30 associated microbiomes complement the free-living microbiome, consequently increases
31 ecosystem homeostasis of recycling rates in a variable environment. We argue for better
32 integration of this fundamental ecological process in predicting the consequences of current
33 accelerated environmental change.

34 **Glossary:**

Biome	An area classified according to a characteristic group of species that lives in it, such as the tundra, savanna or tropical rainforest.
Carbon and nutrient recycling	The transformation of carbon and potentially limiting nutrients (e.g. N, P, K, Ca, Mg) from their various organic forms e.g. proteins, fats) to their biologically reactive inorganic forms (ammonium, phosphates, exchangeable bases) that can be used by plants and microbes.
Climate variation	The way aspects of climate (such as temperature and precipitation) differ from an average, due to natural and sometimes periodic changes in the circulation of the air and ocean, volcanic eruptions, and other (including anthropogenic factors at multiple temporal scales (days, seasons, years, decades).
Free-living microbiome	The set of microbes (bacteria, protists, archaea, fungi) without a close and intimate association with larger organisms together responsible for carbon and nutrient recycling in soil.
Ecosystem homeostasis	The degree to which key ecosystem processes, such as primary productivity, secondary productivity, carbon storage and nutrient recycling are kept constant by biotic interactions despite strong variations in environmental conditions imposed from larger spatial scales, such as solar radiation, air temperature and rainfall.
Homeostatic capacity of organisms	The relative ability of an organism to keep the physical and chemical conditions (e.g. temperature, moisture, osmotic potential, pH) in its internal environment (inside the organism) constant despite strong fluctuations in these factors in its external environment.

Metabolic capacity of organisms	The rate of energy turnover (J day ⁻¹) of an organism, determining its capacity for nutrient and carbon turnover from organic to inorganic reactive forms.
Metamicrobiome	The interacting set of four main microbiomes responsible for carbon and nutrient recycling in terrestrial ecosystems consisting of i) the free-living microbiome, and the mutualistic microbiomes associated with ii) plants (i.e. mycorrhizae and rhizosphere bacteria), iii) macrodetritivores (i.e. gut microbes or fungal gardens), and iv) with herbivores (gut microbes).
Mutualism/mutualistic	A symbiotic relationship between two species where both partners benefit from their interaction. Mutualistic interactions between animal or plant hosts and microbial habitués span from intracellular (e.g. endophytic fungi) to extracellular (e.g. bacteria and Archaea in gut lumen) to exosymbiotic, in which part of the microbiome is found outside of the host but is actively maintained and tended for by hosts, as in ectomycorrhizal or termite-associated fungi.
Preemption	Interaction between two species or species groups where the first species typically consumes a resource or substrate before the second species can access it.
Saprotroph	An organism that derives nourishment from detritus.
Substrate availability (equivalent term: resource availability)	The rate per unit area or soil volume at which biologically reactive forms of elements that can be directly metabolized by organisms become available. For primary producers, these include nitrate, ammonium, and phosphates while for heterotrophic organisms this is the rate of their food supply, such as sugars (bacteria), grass (herbivores), litter (decomposers).

Stoichiometric	The balance of biologically important elements in organisms and resources
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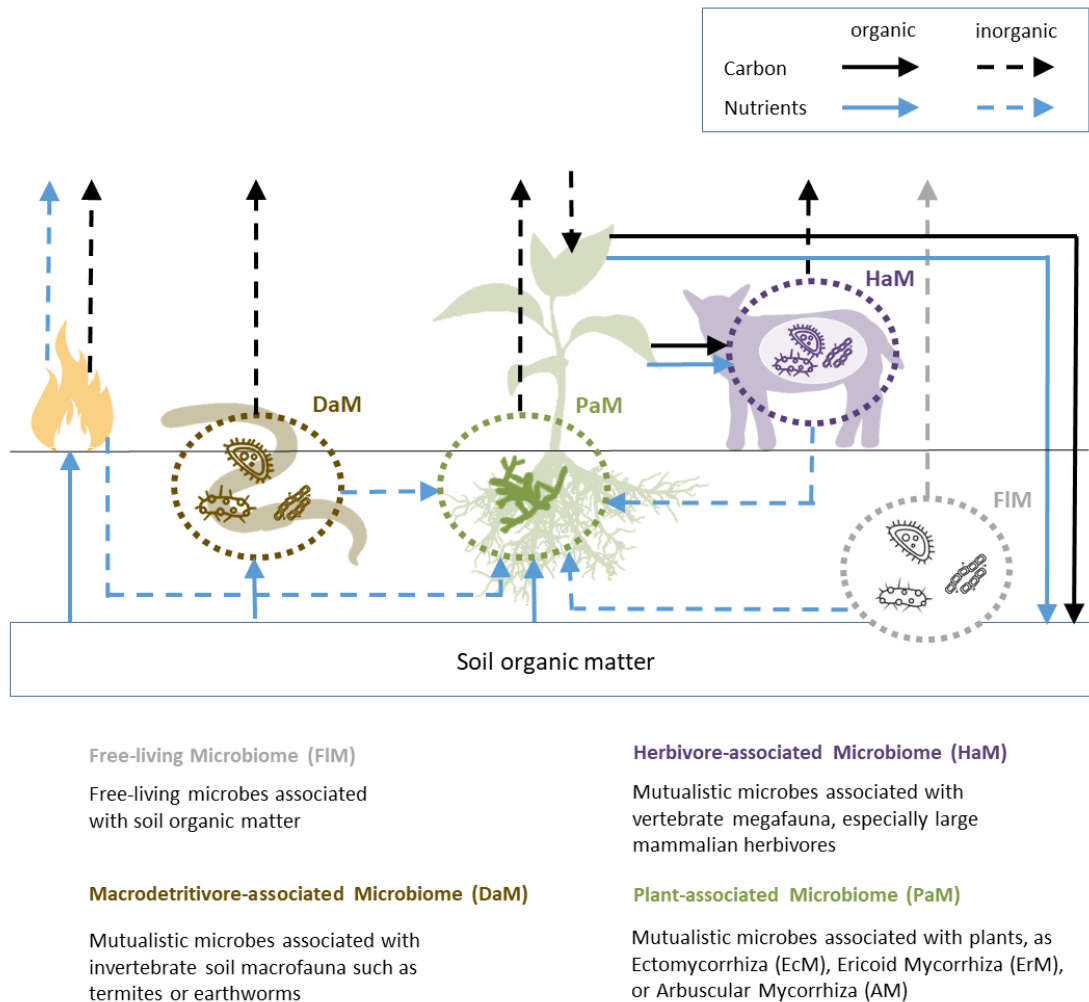
35

36 **Carbon and nutrient recycling in a changing climate**

37 **Carbon and nutrient recycling** of plant materials (here-after 'recycling') is central to ecosystem
38 functioning because it maintains primary productivity and regulates the Earth's climate [1]. However,
39 global change is strongly altering the rate and stability of recycling in many terrestrial ecosystems, with
40 consequences for ecosystem dynamics and potential feedback to global biogeochemical cycles and
41 climate [2,3]. Global carbon models generally assume that plant-assimilated carbon and nutrients are
42 predominantly returned into inorganic forms by either the **free-living soil microbiome** [4] or fire,
43 representing two major terrestrial recycling pathways [5]. Both pathways are highly sensitive to
44 forthcoming environmental change, which can induce strong climatic (e.g. extreme events) and
45 substrate limitations. For example, intensified droughts can halt litter organic matter decomposition for
46 extended periods [6]. However, **mutualistic** microbiomes associated with plants (mycorrhizal fungi),
47 macroinvertebrates (gut microbes and fungal gardens in mounts and nests), and herbivores (gut
48 microbes) are also important agents of organic matter mineralization and can dominate the recycling
49 process at local to regional scales [7-9]. Recent evidence suggests that these mutualistic microbiomes
50 increase long-term average recycling rates in most terrestrial ecosystems by reducing environmental
51 fluctuations and lifting limitations to microbial breakdown, making them less sensitive to **climate**
52 **variation**. Here, we review how the free-living soil microbiome and at least three mutualistic
53 microbiomes interact in a **metamicrobiome** (Fig. 1). To illustrate how the metamicrobiome concept is
54 key to understanding ecosystem and **biome** scale recycling (and thus to ecosystem responses to global
55 change), we have to start with the constraints on the functioning of the free-living soil microbiome.

56 **Constraints on carbon and nutrient recycling by the free-living microbiome**

57 Soil chemo-physical conditions are highly heterogeneous both in time and space. Abiotic factors that
58 determine microbial performance - i.e. soil moisture, temperature, pH and redox status - fluctuate
59 continuously, causing soil microbial activity to be highly restricted to specific microsites and periods
60 where chemo-physical limitations (or climatic limitations) are removed [10]. Because free-living soil
61 bacteria and archaea are so small, they depend primarily on substrates that move towards them
62 passively by diffusion [11]. This makes soil water essential: it prevents desiccation and acts as a solvent
63 for water-soluble organic substrates and a transport medium for microbes and their chemicals and exo-
64 enzymes [12]. Their metabolic activity therefore highly depends on temporal variation in water content
65 of the soil. In addition, soil temperature is a key factor for the metabolic activity of ectothermic
66 organisms, including microbes [13]. In regions with a long cold season such as the arctic tundra, this
67 reduces organic matter recycling and promotes carbon sequestration [14].



68

69 *Fig. 1: Metamicrobiome ecology: carbon and nutrient recycling in terrestrial ecosystems is generally*
 70 *mediated by a metamicrobiome of four interacting microbiomes, i.e. the Free-living Microbiome (FIM),*
 71 *the Macrodetritivore-associated Microbiome (DaM), the Herbivore-associated Microbiome (HaM), and*
 72 *the Plant-associated Microbiome (PaM). The mutualistic microbiomes DaM, HaM, and PaM profit from*
 73 *the homeostatic conditions offered by their hosts, allowing recycling to continue when environmental*
 74 *conditions for the FIM become unfavourable. Alternatively, carbon and nutrients can be recycled by fire.*
 75 *For other nutrients such as P, K, Mg, and Ca, the same recycling principles hold, except the gaseous*
 76 *components (N₂ and NO_x) are missing.*

77

78 While soil is the largest reservoir of carbon substrates in terrestrial ecosystems, several mechanisms
 79 further limit carbon and nutrient recycling by the free-living microbiome. Physical mechanisms such as
 80 occlusion within large soil aggregates and adsorption onto mineral surfaces limit substrate accessibility
 81 [15,16]. Vegetation composition and structure determine to what extent and when organic substrates
 82 remain part of standing biomass (aerial position) or come into contact with the soil surface [17] and thus
 83 potentially limit substrate supply to free-living microbes. The mineralization rate of organic matter also
 84 depends on the C:N:P ratio of the substrate relative to the decomposers' need [18]. Because microbial

85 organisms function best at specific **stoichiometric** C:N:P ratios, nutrients in organic matter that
86 approach that ratio and thereby meet stoichiometric requirements will increase microbial activity and
87 mineralization rates [19]. In summary, substrate availability depends greatly on the microbial landscape;
88 decomposition of organic substrates can only occur when water, oxygen, (high quality) substrates, the
89 microbial organism, and their (exo-) enzymes all come together in space and time [12,20].

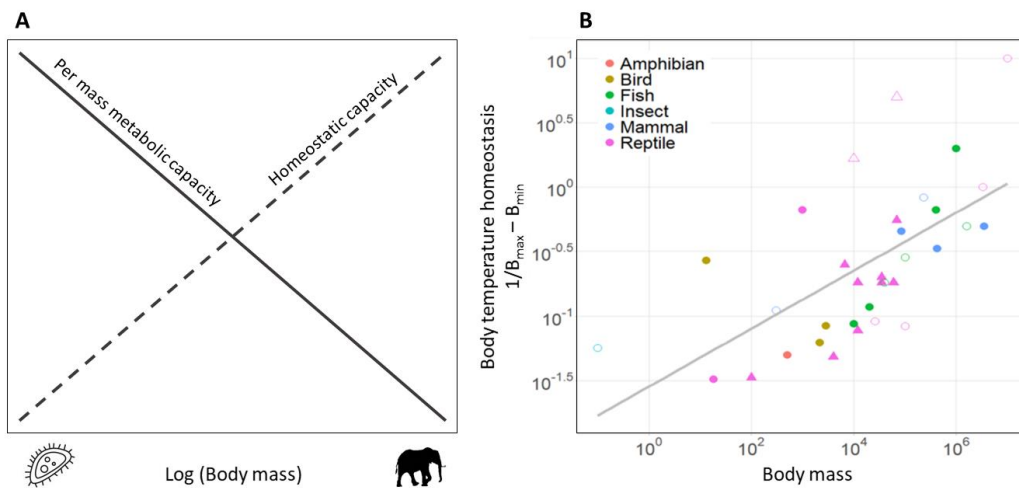
90 **Small organisms: highest metabolic capacity**

91 Organisms vary significantly in body mass, ranging by over 20 orders of magnitude from 10^{-15} g
92 microbes to $2 \cdot 10^8$ g blue whales. The size of organisms correlates with many ecological and
93 physiological traits in predictable ways [21]. A fundamental relationship underlying many of these
94 patterns is the quarter-power allometric scaling of organismal basal metabolic rate M with body mass
95 B , where $B \propto M^{3/4}$ [22]. It predicts how larger organisms have an increasingly lower rate of energy use
96 per unit of body mass, as $B/M \propto M^{-1/4}$; and holds across a wide variety of taxonomic groups [23],
97 including plants [24]. This predictably lower metabolic capacity of larger organisms, compared to
98 microbes, has been explained by constraints imposed by the architecture of their internal transport
99 network on the rates at which nutrients and oxygen can be delivered to the cells in metazoans [25,26].
100 Also, relative body area scales with body mass as $B/M \propto M^{-1/3}$, constraining the capacity for resource
101 uptake through passive diffusion in larger organisms. As a result, bacteria, archaea, protists and fungi
102 have the highest per mass capacity for energy and nutrient turnover (i.e. metabolic capacity, Fig. 2A),
103 but only if environmental conditions such as temperature and moisture are optimal as they have limited
104 capacity to control their internal conditions and direct surroundings.

105 **Large organisms: highest homeostatic capacity**

106 In contrast, larger, multicellular species have a better capacity to stabilize their internal environment or
107 immediate surroundings through various anatomical, physiological, and behavioral adaptations that are
108 not possible in microbes [27]. This **homeostatic capacity** also scales with body mass but opposite to
109 **metabolic capacity** (Fig. 2). Lower surface-to-volume ratios in larger organisms are favourable under
110 environmental conditions where restricting water (droughts) or heat loss (cold periods) are important
111 [28]. For example, larger organisms are less likely to be seasonally disrupted in their daily activities by
112 a need to go into hibernation or torpor under cold conditions [29]. Moreover, the higher capacity (relative
113 to body mass) of larger organisms to store energy and nutrient reserves allows these organisms to
114 remain active during longer periods of resource limitation [30]. Behavioral adaptations of animals (e.g.
115 seeking shade or sun, moving long distances to find suitable food or water, or burrowing to deeper soil
116 layers to prevent climatic stress) also contribute to their homeostatic capacity. This also applies to
117 plants, e.g., through opening and closing of stomata, rolling up of graminoid leaves during drought, and
118 rooting deep to access water by dryland trees. These behavioral adaptations also scale with body size
119 [31], with larger organisms having a higher capacity to move towards essential resources. Also, larger
120 organisms have more options to improve their local environment to their benefit through ecosystem
121 engineering and extended phenotypes (e.g. beaver dams, rodent burrows, bird nests, termite mounds).

122 To summarize, larger organisms have a larger homeostatic capacity when faced with temporarily
123 unfavourable conditions (Fig. 2).



124

125 *Fig. 2: (A) The trade-off between per mass metabolic capacity (log scale) and homeostatic capacity as*
126 *a function of body mass (B). An example of the scaling relation of homeostatic capacity with body mass,*
127 *showing how the capacity to regulate body temperature changes with body mass, where body*
128 *temperature homeostasis is expressed as the difference between maximum (B_{max}) and minimum (B_{min})*
129 *body temperatures. The solid symbols represent actual data and open symbols represent simulated*
130 *data, while triangles represent data compiled by Stevenson (1985) and the circles represent additional*
131 *data listed in supplement S1.*

132

133 **The trade-off between metabolic and homeostatic capacity drives mutualisms**

134 The observed opposite relationships of body mass with metabolic and homeostatic capacity of
135 organisms suggests a fundamental trade-off: the same organism cannot excel at both (Fig. 2). Microbes
136 are best at achieving high metabolic rates under optimal conditions while large multicellular eukaryotes
137 are best at realizing such optimal conditions in their bodies and immediate surroundings. The long-term
138 outcome of this trade-off is the evolution of **mutualisms**. Multicellular eukaryotes have repeatedly
139 solved their metabolic constraints over evolutionary time by engaging in mutualisms with microbes that
140 possess complex and efficient metabolic capabilities [32], and microbes have 'accepted this request'
141 because it stabilizes their environment and resource supply. The capacity to acquire microbial partners
142 has been both a key factor in the evolution of first eukaryotes from prokaryotes [33] as well as in the
143 subsequent eukaryote diversification [34], shaping the adaptation to new habitats, lifestyles, and diets.
144 These mutualisms have therefore led to multiple synergies between metabolic and homeostatic
145 capacity (Box 1).

146

147 **Box 1: Synergies between metabolic and homeostatic capacity: different mechanisms**

148 *Stress alleviation benefits*

149 In biomes that experience seasonal or multi-annual drought, metazoans often evolve traits that promote
150 their water acquisition and conservation. They can control the water content in their body, or in their
151 direct surroundings, or by selecting constantly moist microhabitats, all of which can be beneficial for
152 their microbial mutualists. For example, fungus-growing termites, which engage in a complex three-way
153 symbiosis with their bacterial gut microbiome and a basidiomycete fungus [92,93], promote the activity
154 of the fungal symbiont by optimizing the humidity inside their mounds. They do this by 'wicking' or
155 actively transporting water to or from their nests, and regulating evaporation and respiration by
156 ventilation [94,95]. Earthworms vertically move up and down in their burrows to stabilize moisture in
157 their direct surroundings [86], supporting the continued activity of their microbiome. Stabilization of
158 chemo-physical conditions also applies to plant hosts. Ectomycorrhizas (EcM) can alleviate drought
159 stress to host trees by enhancing access to soil water [96,97]. However, when water tables fall during
160 summer, trees in Mediterranean forests and woodlands shift their primary water source to deeper soil
161 layers [98] thereby returning the water-provisioning favour to their fungal symbionts [49]. By lifting
162 moisture and temperature constraints, hosts increase the growth, survival, and resource processing
163 activity of microbes, i.e. "metabolic homeostasis" [55]. Mutualistic associations between hosts and
164 microbes, therefore, decouple microbial activity from unfavourable conditions, reducing the overall
165 control of climate on the recycling of organic matter.

166 *Complementarity benefits*

167 Hosts can also lift substrate quality limitations by facilitating complementary contributions between
168 multiple symbiotic microbial partners. The guts and rumen of mammalian herbivores and
169 macrodetritivores act as biological chemostats where hundreds of microbial species and their
170 metabolites all interact in the digestion process. Substrates that result from the metabolism of some
171 microbial species are often efficiently further metabolized by other species (metabolic cross-feeding),
172 thereby promoting fuller decomposition, from polymer degradation to sugar fermentation [99], in one
173 regulated environment. Moreover, the host continuously removes metabolic end products that are
174 released by mutualistic microbes, which favours further metabolism through reducing feedback
175 inhibition [100]. Similarly, the bacterial community inside the guts of termites, and the basidiomycete
176 fungi that they farm, contribute to the decomposition process in a complementary way [101]. The
177 termites facilitate the process by transferring the substrates and enzymes between the microbial
178 partners [93,102] and thereby speed up the recycling process.

179 *Preemption and shortcutting benefits*

180 Large hosts also bring mutualistic microbes in continuous contact with substrates through **preemption**
181 (or short-circuiting). Some fungi positioned themselves closer and closer to living plant root cells in
182 anticipation of their death, which at some point in evolutionary time likely led to the mycorrhizal habitat

183 in which substrate is colonized before death [103]. The secured and high supply of “easy” carbon
184 through plant hosts allows expansion of mycorrhiza into upper soil layers at the expense of the free-
185 living microbiome. Moreover, the supply of host photo-assimilates supports the synthesis of ‘expensive’
186 enzymes that can break down very recalcitrant organic substrates, thereby simultaneously lifting
187 substrate quality limitations. Indeed, ecto- and ericoid mycorrhizae are effective scavengers for
188 relatively recalcitrant organic N and P sources and could therefore reinforce a competitive advantage
189 over free-living **saprotrophs** by limiting the availability of these essential elements [104,105]. Fungus-
190 growing termites also preempt organic matter in the soils they occupy [106]. After a first gut passage,
191 collected litter is directly delivered as pseudo-faeces to the termite's fungal symbionts [93]. The
192 continuous directional flow of litter inside mounds explains why soils occupied by termites can be
193 depleted of soil nutrients and organic carbon [107], and why the inter-mound soil matrix may host
194 smaller populations of microbes [108]. Finally, large mammalian herbivores consume resources before
195 green plant parts turn into litter and can, therefore, be considered even better preemptors of energy-
196 rich substrates than macrodetritivores [106].

197

198 **Metamicrobiome organization along global gradients**

199 As the four microbiomes (free-living, the detritivore-associated, plant-associated and large herbivore-
200 associated) all interact in a **metamicrobiome** (Fig. 1), but each with different sets of adaptations, their
201 relative importance is expected to strongly vary between different **biomes**. Because microbial activity
202 increases with temperature and moisture availability, recycling rates are generally faster in tropical
203 regions [35,36]. Higher rainfall promotes closed-canopy systems, which excludes most of the large
204 herbivore-associated microbiome - indirectly increasing the importance of other microbiomes.
205 Permanently wet environments also limit abiotic forms of recycling, such as fire [5] and
206 photodegradation [37], making the free-living soil microbiome dominant in recycling organic matter (Fig.
207 3). This dominance under these conditions is also expected from the trade-off between metabolic and
208 homeostatic capacity: the stable environment in tropical forests allows soil microbes to remain active
209 and recycle substrates throughout the year.

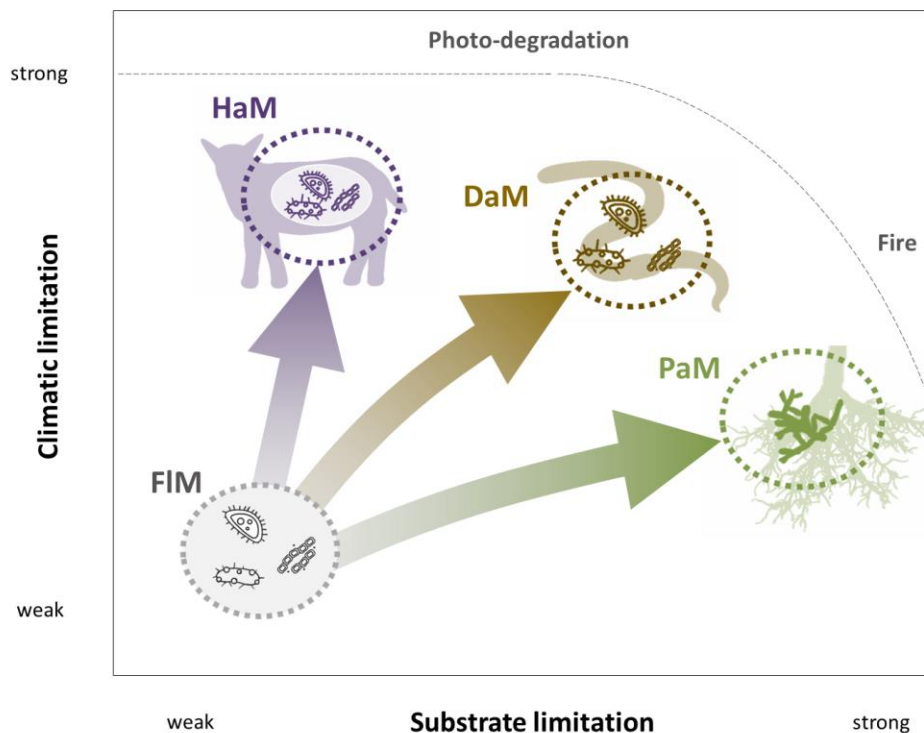
210 The herbivore-associated microbiome (HaM) is expected to dominate intermediate rainfall regions with
211 high soil fertility (Fig. 3) because high plant nutrient concentrations support high levels of herbivory
212 [38,39]. Also under cold or saline conditions, plant quality ingested by herbivores (and thus the HaM) is
213 higher due to restricted productivity, while carbohydrate accumulations can act as osmoregulation or
214 antifreeze [40], and endothermic herbivores provide warm refugia for microbial decomposition. In the
215 harshest and least productive environments (extreme drought or cold), hosts can no longer survive at
216 high densities, and photodegradation becomes increasingly important [41] (Fig. 3).

217 Nutrient-poor environments generally promote plant species with low-quality tissues, which produce
218 poor-quality litter (i.e. substrates) via so-called traits after-life effects [42]. Due to the small size and,

219 therefore, high nutrient requirements of microbes, the activity of the soil microbiome is negatively
220 impacted by recalcitrant compounds and the low concentrations of nutrients in these substrates, which
221 slows recycling and reinforces the low nutrient availability in poor sites. The proportion of mycorrhiza
222 relative to saprotrophs (part of the FIM) increases with decreasing soil fertility in boreal forests [43].
223 From a metamicrobiome perspective, preemption makes a mycorrhizal association increasingly
224 beneficial compared to living alone in an energy-depleted environment, giving the plant-associated
225 microbiome an outsized role in recycling in poor ecosystems (Fig. 3). Abiotic forms of recycling may
226 also increase in importance when aboveground standing biomass accumulates in poor environments
227 due to low herbivore abundance. Especially in climatically seasonal environments (but with high enough
228 productivity for fuel production), this may lead to increased recycling by fire [44] (Fig. 3) as both the
229 free-living and plant-associated microbiome predominantly act on substrates within soils.

230 Lastly, there are various examples of nest or mound-building macrodetritivores that can lift both climatic
231 and substrate limitations, which may give the macrodetritivore-associated microbiome a dominant role
232 in relatively nutrient-poor environments that are either periodically cold or dry (Fig. 3). Many temperate
233 and boreal zone ant species build above-ground nest-mounds and keep them free from plants to obtain
234 heat from solar radiation. The nests of yellow meadow ants (*Lasius flavus* and *L. umbratus*) significantly
235 increase in temperature in the summer, creating favourable conditions for their own gut microbiome and
236 other soil biota and serving as 'hot spots' for recycling [45,46]. Because the burrows of desert isopods
237 provide more stable temperature and higher moisture, the recycling of plant litter is controlled by macro-
238 detritivores in desert ecosystems [47].

239 In summary, the contribution of the different mutualistic microbiomes to recycling should increase with
240 climatic and substrate limitations (Fig. 3). The improved homeostatic and pre-emptive capacity
241 contributed by hosts allows mutualistic microbiomes to maintain recycling even throughout
242 unfavourable periods. However, homeostasis and preemption require investments and only work when
243 costs are balanced by sufficient benefit in exploiting energy-rich substrates, increasing the importance
244 of abiotic forms of recycling in the most limiting environments.



245

246 *Fig. 3: The relative importance of the free-living soil microbiome (FIM, grey) and mutualistic Herbivore-*
 247 *associated Microbiome (HaM, purple) of vertebrate megafauna, invertebrate Macrodetritive-associated*
 248 *Microbiomemacrofauna (MaM, green), and the Plant-associated Microbiome (PaM, brown) for recycling*
 249 *of plant organic matter along gradients of climatic and substrate limitation. Large arrows represent the*
 250 *dominant switches in relative importance. See fig. 1 for further explanation of the different microbiomes.*

251

252 Homeostasis in variable environments

253 The organization of the metamicrobiome is not only expected to vary with average environmental
 254 conditions but also interacts with their temporal variability. Microbial activity is expected to be highest
 255 when the environment is not too dry and not too wet (leading to soil anoxia) [48], not too cold and not
 256 too hot, leading to a restricted set of conditions for nutrient recycling (green area in Fig. 4A). Soil organic
 257 matter thus is subject to temporal variation in both moisture and temperature on multiple time scales
 258 (Fig. 4A). In seasonally variable habitats, soil moisture and temperature will frequently move in and out
 259 of the optimal range of free-living microbes. Consequently, the rate of recycling by the free-living
 260 microbiome is expected to be tightly linked to seasonal changes in rainfall (Fig. 4B) and to vary much
 261 more than mutualistic microbiomes, which experience less variation in chemo-physical conditions (Fig.
 262 4B).

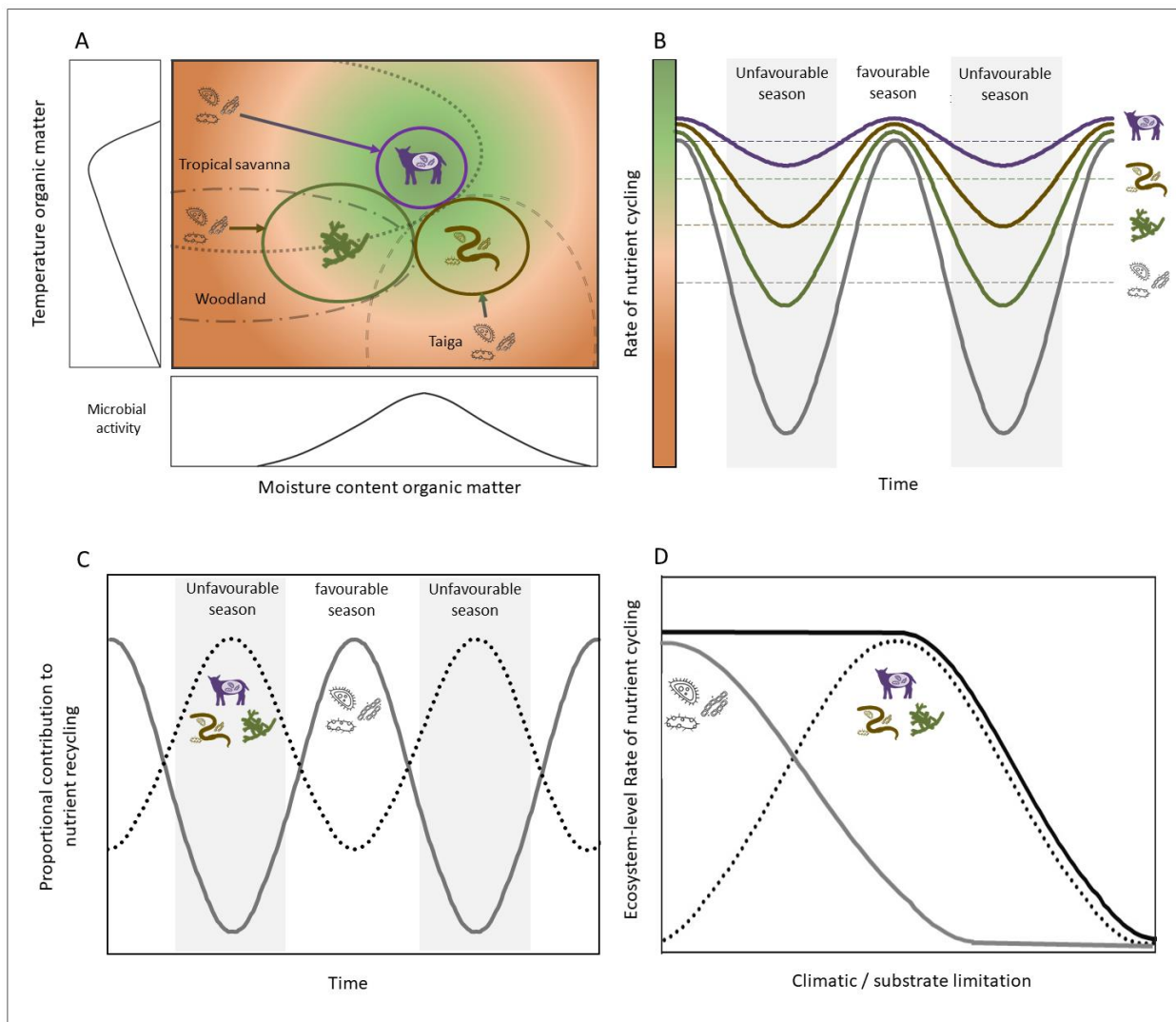
263 Microbiomes can also alternate over time in their dominance of the recycling process, which stabilizes
 264 its overall rate. For instance, in temperate woodlands, mycorrhizal fungi are most important during the

265 summer, likely due to increased water supply by plants [49], while free-living fungi reach their maximum
266 abundance in autumn [50] associated with peak litter production [51]. Similar alterations are found for
267 other microbiomes. Foraging activity by termites (*Macrotermes* sp.) and desert isopods (*Hemilepistus*
268 *reaumuri*) peaks during the hot and dry season [52,53], which can lead to a proportional increase in
269 macrodetritivore-driven recycling during drier periods relative to the free-living microbiome [54,55] (Fig.
270 4D). Finally, many populations of large herbivores migrate seasonally to overcome periodic limitations
271 associated with food quality or quantity [56,57], which can amplify the contribution of grazing to recycling
272 during unfavourable climatic conditions. A diverse metamicrobiome - where different host-associated
273 microbiomes complement the free-living microbiome - therefore leads to **ecosystem homeostasis** of
274 carbon and nutrient recycling rates in variable environments (Fig. 4C).

275 **Global change relevance**

276 Climate change, especially extreme events (increase in frequency, duration and amplitude of heat
277 waves and extreme droughts) can bring soil environmental conditions more frequently outside the
278 optimal conditions for the free-living soil microbiome. Drought-induced changes in community
279 composition can cause long-term effects, reducing recycling rates for up to one year, even when water
280 becomes available again [6]. More climatic variation also increasingly exposes the free-living
281 microbiome to repeated dry-rewetting or freeze-thaw cycles, which damage the microbial community
282 [58]. Such cycles may cause nutrient losses through leaching to ground and surface waters [59,60]
283 because soil microbes are important dynamic sinks for carbon and nutrients [61]. Warming furthermore
284 loosens microbial association networks in colder biomes [62], which can lead to a loss of cooperative
285 interactions (e.g. syntrophy) between microbes [63,64]. Also, droughts and intense rainfall events can
286 cause more pulses in microbial recycling [65], leading to more mismatches with plant uptake needs,
287 impairing primary productivity [65,66]. All these factors make recycling by the free-living microbiome
288 highly sensitive to climate change.

289 In contrast, mutualistic microbiomes can provide important buffering effects in a changing climate. Large
290 mammalian herbivores can accelerate recycling through the modification of growing conditions (e.g.
291 sunlight) and the direct return of nutrients to soils through urination and defecation [67-69]. Higher rates
292 of recycling boost plant productivity, even in climatically harsh environments. The arctic region was
293 much colder and drier during the last glacial maximum but was much more productive, a discrepancy
294 that has been termed the "productivity paradox" [70]. The paradox can be explained by the much higher
295 mean body size of the animal hosts that were present at the time [71]. A large body enabled mammoths
296 to efficiently exploit and preempt substrates, giving rise to the highly productive grasslands of the
297 Pleistocene: the mammoth steppe [71]. The loss of megaherbivores during the Pleistocene



298

299 *Fig. 4. A) Phase space of temperature and moisture content of organic matter. The colour gradient*
 300 *visualizes the optimal conditions (green) for microbial activity. Mutualistic microbiomes experience less*
 301 *variation in chemo-physical conditions, as represented by the smaller circles, compared to free-living*
 302 *microbes in different biomes. B) The rate of recycling by the free-living microbiome should be intimately*
 303 *linked to fluctuations in soil temperature and moisture, while recycling by mutualistic microbiomes is*
 304 *more stable over time. C) Temporal alternation in the relative contribution of the FIM (grey solid line)*
 305 *and mutualistic microbiomes (dotted line) to recycling, leading to D) higher rates of recycling at the*
 306 *ecosystem level even at high climatic and substrate limitations.*

307

308 megafaunal extinctions slowed recycling, made recycling more seasonally limited, and consequently
 309 may have turned the highly productive steppes into tundra ecosystems [72]. Currently, the (sub)arctic
 310 is the strongest atmospheric carbon source due to a positive feedback between a warming climate and

311 the thaw of carbon-rich permafrost layers [73]. Reverting the moss and shrub-dominated tundra back
312 to a productive grassy steppe ecosystem by the reintroduction of large herbivores could potentially slow
313 down carbon emission because the increased recycling and productivity would improve carbon capture
314 [74]. Moreover, grazing can prevent fuel accumulation and therefore limit fire frequencies in seasonally
315 dry ecosystems, reducing nutrient and carbon losses [75,76]. This adds evidence to findings that large
316 herbivores are important in mitigating the negative impacts of climate change [77].

317 Plant-associated microbiomes also buffer against the currently observed acceleration of carbon
318 release. Warming promotes higher rates of recycling by the soil microbiome, stimulating a net loss of
319 soil carbon that may further accelerate global warming [78]. Higher atmospheric CO₂ concentration and
320 temperatures generally result in higher net primary productivity (NPP) which means that (everything
321 else being equal), nutrients can become more limiting [79]. A higher fraction of NPP would therefore
322 have to go to nutrient acquisition, reducing the buffering effect that increased productivity has on rising
323 CO₂ levels. The plant-associated microbiome can delay this so-called 'progressive nutrient limitation'
324 because EcM mines the soil organic matter for nutrients, promoting carbon sequestration also in
325 nutrient-limited areas [80].

326 **Concluding remarks**

327 The relative contributions of the different mutualistic microbiomes as outlined in Fig. 1 are currently
328 undergoing rapid change in ecosystems worldwide. Among animal hosts, larger herbivores seem to be
329 more sensitive to ongoing land-use change and climate change [81], as was the case during the
330 Pleistocene defaunation. Large animals have vulnerable life-history strategies [82], need more space
331 because of larger home ranges [31,83], and have only a limited capacity to adapt to hotter daytime
332 temperatures [84]. Intensive land use reduces soil insect nest and mound densities [85] and dries out
333 topsoils to unfavourable levels for earthworms [86], and so forms a significant challenge to the
334 macrodetritivore-associated microbiome. The plant-associated microbiome is also vulnerable:
335 ectomycorrhiza-dependent vegetation is declining on all continents and is being replaced by non-
336 mycorrhizal vegetation due to forest logging and agricultural intensification [87].

337 Such challenges to mutualistic microbiomes will reduce the rate and stability of recycling, with cascading
338 effects on the biodiversity and productivity of terrestrial ecosystems that will eventually impact the whole
339 system Earth. Better protection of (semi-)natural ecosystems that support a diverse metamicrobiome
340 preserves their resilience to climate change. For example, ecological restoration through rewilding can
341 stop further defaunation by re-introducing missing wildlife and can thereby restore multiple important
342 ecosystem functions [88]. Different studies indeed show that restoration of megaherbivores can lead to
343 a more productive plant community and the moderation of fire regimes [89,90]. Similarly, restoring
344 native (forest) vegetation in abandoned agricultural fields supports the recovery of the plant-associated
345 microbiome [87,91].

346 By mapping the connections between the fields of microbial ecology, community ecology, and
347 ecosystem ecology, we have provided an integrated framework that accounts for the prominent role of

348 host-mediated microbiomes in the recycling of plant matter. Especially for biomes where the activity of
349 the free-living microbiome is chronically or periodically limited, inclusion of mutualistic microbiomes may
350 radically modify predictions on the sensitivity of ecosystems to increased variability and soil carbon
351 sequestration under current and future climate and land-use. To test the general ideas outlined in this
352 paper and advance this line of research, there is now a need for more empirical data on the importance
353 of different microbiomes across biomes and soil types (see outstanding questions). We recommend the
354 simultaneous measurement of the activity of mutualistic microbes in comparison to free-living microbes
355 in controlled field experiments and across main environmental gradients. Finally, we underscore the
356 need for common linguistic and conceptual currencies between microbiologists and ecologists to merge
357 our understanding of the factors that control the activity of the metamicrobiome.

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