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## **Plant-soil synchrony in nutrient cycles: learning from natural ecosystems to design sustainable agrosystems**

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1 *Preprint*

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3 *Plant-soil synchrony in nutrient cycles: learning from*  
4 *natural ecosystems to design sustainable agrosystems*

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## Glossary

**Stoichiometric constraints** refer to the fact that living organisms need several chemical elements (C, N, P etc.) in specific ratios for their biosynthesis (e.g., proteins).

**Plant demand** is the amount of nutrients needed to synthesize plant biomass from the carbon obtained by photosynthesis.

**Soil supply** is the amount of soluble nutrients released (from both inorganic and organic reserves) into the soil mainly by soil biota and assimilable by plant roots. Part of these soluble nutrients is also subject to losses by denitrification, volatilization and leaching.

**Plant-soil synchrony** describes the level of correspondence between plant demand and soil supply.

**Systems of synchrony** refer to the arrangements (organizations) of plants and soil biota, as well as the numerous biogeochemical functions they catalyze, contributing to increase the level of correspondence between plant demand and soil supply (high plant-soil synchrony).

**Soil biota** refers to all organisms living in soil except primary producers. It includes soil microbes and soil fauna.

**Free-living soil decomposers** correspond to soil microbes that are not attached to living plant roots and degrade soil organic matter for their energy and nutrient requirements. They can live within and outside the plant rhizosphere.

**Microbial root symbionts** correspond to microbes that are physically attached to plant roots for a close and long-term interaction. They include nitrogen-fixing bacteria present in the nodules of leguminous plants, and mycorrhizal fungi that are associated to roots of 80 % of all known terrestrial plant species.

**Rhizodeposition** is the organic matter deposited by roots in the rhizosphere including exudates (sugars, organic and amino acids, signal molecules etc), mucilage and dead root cells.

**MAOM** is the acronym of Mineral Associated Organic Matter. It corresponds to organic matter bound to soil minerals (clay, metal oxides and hydroxides) through different physicochemical interactions (electrostatic, covalent, hydrogen bridge etc).

**M-microbes** correspond to the functional type of microbes contributing to MAOM destruction and nutrient release (nutrient mineralization).

**I- microbes** correspond to the functional types of microbes contributing to MAOM formation and mineral nutrient immobilization.

**FreeOM** is the acronym of Free Organic Matter. It refers to the organic matter that is not bound to soil minerals and that accumulates either in the organic layer overlying the mineral soil or as particulate organic matter in the mineral soil.

**Soil organic matter** refers to all dead organic matter present in soil (fresh litter, rhizodepositions, MAOM and FreeOM).

83 **Abstract**

84 Redesigning agrosystems with more ecological regulations can help feed a growing population,  
85 preserve soils for future productivity and reduce environmental impacts. However, guidelines  
86 for redesigning agrosystems from natural systems are limited. Reviewing the last knowledge of  
87 ecosystem functioning, we outlined four ecological systems synchronizing the supply of soluble  
88 nutrients by soil biota to fluctuating plant nutrient demand. This synchrony limits deficiencies  
89 and excesses of soluble nutrient, which usually penalize both production and regulating services  
90 of agrosystems such as nutrient retention and soil carbon storage. We detail how ecological  
91 systems promoting synchrony can be installed in agrosystems to improve their sustainability  
92 and reduce the use of mineral fertilizers.

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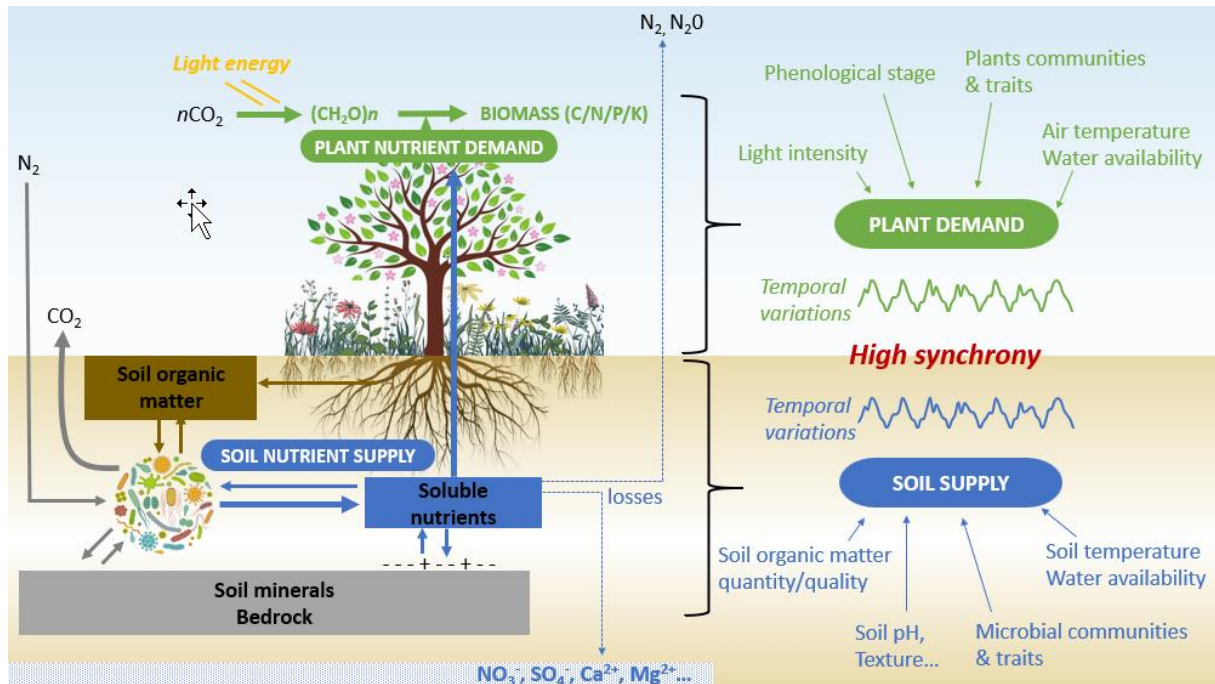
97 One of the grand challenges of humankind is to feed a growing world population while  
98 preserving soil assets for future productivity, reducing environmental impacts such as  
99 greenhouse gas emissions, eutrophication and biodiversity loss, all under more extreme climate  
100 conditions<sup>1</sup>. Researchers and actors of the agricultural sector have driven many innovations to  
101 increase the efficiency of agricultural management practices (e.g., precision fertilization)<sup>2</sup> or  
102 transforming the cropping systems themselves (reduced tillage, rotation with permanent plant  
103 cover, crop diversification) in an attempt to mitigate the ongoing degradation of soil health,  
104 biodiversity and the environment<sup>3</sup>. In the latter context, natural or semi-natural ecosystems such  
105 as grasslands and forests are increasingly being considered as benchmarks for redesigning  
106 cropping systems<sup>4-6</sup>. Indeed, these ecosystems can produce large amount of biomass,  
107 sometimes equivalent to that of high-input annual crops<sup>4,7-9</sup>, while maintaining natural assets  
108 such as soil organic matter<sup>4,10,11</sup>, high levels of biodiversity<sup>12</sup> and key regulating services such  
109 as water purification<sup>4,13</sup> and carbon (C) storage<sup>14</sup>. However, effective guidelines for redesigning  
110 cropping systems based on natural systems remain limited<sup>15,16</sup>.

111 The higher sustainability of natural ecosystems has previously been linked to  
112 characteristics such as higher plant diversity, higher root biomass, higher fungal:bacteria ratio,  
113 and the increased efficiency of particular functions, e.g. improved soil exploration and resource  
114 uptake by roots<sup>10,17</sup>. However, ecosystems also show marked differences in their characteristics  
115 such as dominant plant traits<sup>18</sup> and soil microbial diversity<sup>19</sup>, which means that the type or level  
116 of characteristics required for sustainable agricultural production cannot be easily generalized  
117 and likely vary with pedoclimatic context. Moreover, ecosystem functioning results from  
118 numerous interacting organisms and functions involved in C and nutrient cycling (Figure 1).  
119 Therefore, the higher sustainability of natural ecosystems could reflect a greater coordination  
120 between species and between biogeochemical functions (i.e., a better ecosystem organization),  
121 rather than improvements in single functions or ecosystem characteristics.

122 Here we advocate that the design of cropping systems should consider the fact that the  
123 productivity and sustainability of ecosystems are inextricably linked to the level of synchrony  
124 between the supply of soluble nutrients by soil biota and plant demand for those soluble  
125 nutrients. A low level of synchrony generates both periods of excess soluble nutrients with a  
126 risk of nutrient loss, soil impoverishment and environmental pollution, and periods of nutrient  
127 deficiency limiting plant development<sup>20,21</sup>. In contrast, high synchrony promotes the conversion  
128 of light energy to biomass by alleviating the nutrient limitation of plant growth, the closure of  
129 nutrient cycles and the conservation, or even accumulation, of soil organic nutrient<sup>20,21</sup>.  
130 Asynchrony between soil supply and plant demand is common in cropping systems, leading to  
131 increased nutrient losses and increased reliance on mineral fertilizers to maintain productivity<sup>20-</sup>  
132 <sup>22</sup>. Since plant demand and soil supply depend on a high diversity of organisms and functions  
133 characterized by different responses to environmental factors (Figure 1), it is not surprising that  
134 the temporal variation in nutrient release from soil biota rarely coincides with the time course  
135 of crop demand<sup>21</sup>. This raises the intriguing question of how multiple plant and soil functions  
136 can be coordinated to achieve a high level of synchrony in natural ecosystems, and to what  
137 extent this knowledge can be used to design sustainable agrosystems.

138 We propose here an integrated framework describing how designing sustainable  
139 agrosystems by copying the synchronized biochemical functioning of natural ecosystems. This  
140 framework is structured in two parts. By synthesizing the latest advances in ecology, we first  
141 explain how multiple plant and soil functions can be coordinated towards a synchrony between  
142 soil nutrient supply and plant demand in natural ecosystems. More specifically, we outline four  
143 systems of synchrony and discuss their relative importance in regulating nutrient cycles  
144 depending on the pedoclimatic context and the functional diversity of plants and soil microbes.  
145 The second part of the framework details how a high level of synchrony can be promoted in  
146 agrosystems. By using the knowledge from natural ecosystems, we identify the types of

147 synchrony systems to be promoted according to the pedoclimatic context, and suggest  
 148 combinations of practices that could install them in cropping systems. A review of the last  
 149 advances in agronomy shows that some of the practices suggested as promoting synchrony have  
 150 already been tested and shown to be effective in reducing nutrient losses and fertilizer use and/or  
 151 improving biomass production and soil C storage. However, our framework also highlighted  
 152 several new management strategies based on plant and microbial functional traits that should  
 153 help improve agrosystem sustainability, including in difficult pedoclimatic conditions (e.g.  
 154 coarse-textured soils).



155  
 156 **Figure 1.** The high level of synchrony between plant demand and soil supply characterizing natural ecosystems  
 157 requires the coordination of numerous soil and plant functions. Plant demand corresponds to the amount of  
 158 nutrients needed to convert the photosynthesis-derived carbon in biomass. It varies both over time and across  
 159 species depending on multiple functions such as photosynthesis, organ formation and phenology, and factors such  
 160 as the stoichiometric constraints of species and light intensity. Soil supply refers to the amount of soluble nutrients  
 161 (mineral and organic), mainly released by soil biota comprising microbes and fauna. It varies over time and soil  
 162 space depending on the prevalence of the various functions catalyzed by soil biota. Some functions increase soil  
 163 nutrient supply (decomposition of soil organic matter -SOM-, biological N<sub>2</sub> fixation and nutrient release from  
 164 minerals), while others decrease it (nutrient immobilization in microbial biomass and soil organic matter). A  
 165 fraction of soluble nutrients can also be adsorbed as ions on the electrically charged surfaces of soil minerals but  
 166 it remains available for plant uptake. The factors controlling soil supply are mostly different from those controlling  
 167 plant demand, raising the issue of the plant demand-soil supply synchrony.

168 **Two synchrony systems based on soil organic nutrient reserves**

169 A significant part of plant nutrient uptake (over 80% for nitrogen, N) is obtained through  
 170 organic matter recycling<sup>23</sup>. The traditional view of nutrient cycling was that the mineralization  
 171 of soil organic matter to mineral nutrients is the major bottleneck restricting nutrient supply to  
 172 plants (Supplementary Box 1). Over the last twenty years, however, progress in isotopic and  
 173 molecular tracing of C and N fluxes has highlighted the capacity of plants to overcome this  
 174 bottleneck<sup>24-27</sup>. Plants have been shown to exert an influence on all soil nutrient fluxes through  
 175 a combination of processes altering the accessibility of soil resources and the activity of soil  
 176 microbial communities<sup>28</sup>. These processes comprise rhizodeposition, nutrient uptake, litter  
 177 chemistry and mycorrhizal associations<sup>24,25,29</sup>  
 178

179 Nevertheless, an apparent paradox remains regarding the synchrony between soil supply  
180 and plant demand. On the one hand, root activities such as rhizodeposition stimulate the  
181 microbial decomposition of soil organic matter and the release of soluble nutrients through the  
182 so-called rhizosphere priming effect<sup>24,27,43</sup>. These root activities are primarily fueled by  
183 photosynthesis-derived C. Therefore, an increase in plant photosynthesis and nutrient demand  
184 (Figure 1) induces an increase in root activities and nutrient release from soil organic matter,  
185 suggesting a supply-demand synchrony. On the other hand, root activities are known to also  
186 accelerate microbial immobilization of mineral nutrients, and nutrient sequestration in soil  
187 organic matter<sup>24,49</sup>. This contributes to reduce soil nutrient availability when plant demand  
188 increases, suggesting a supply-demand asynchrony. This paradox can be resolved by  
189 considering two systems of synchrony where the antagonistic nutrient fluxes driving soil  
190 nutrient availability for plants (decomposition/nutrient release *versus* nutrient  
191 immobilization/sequestration) are coordinated to coincide with the time course of plant  
192 demand. These two systems are based on the two types of soil organic matter built by plant-soil  
193 systems, namely the mineral-associated organic matter -MAOM- *versus* litter-based free  
194 organic matter -FreeOM-, which are associated to two different nutrient cycles<sup>29,42</sup>.

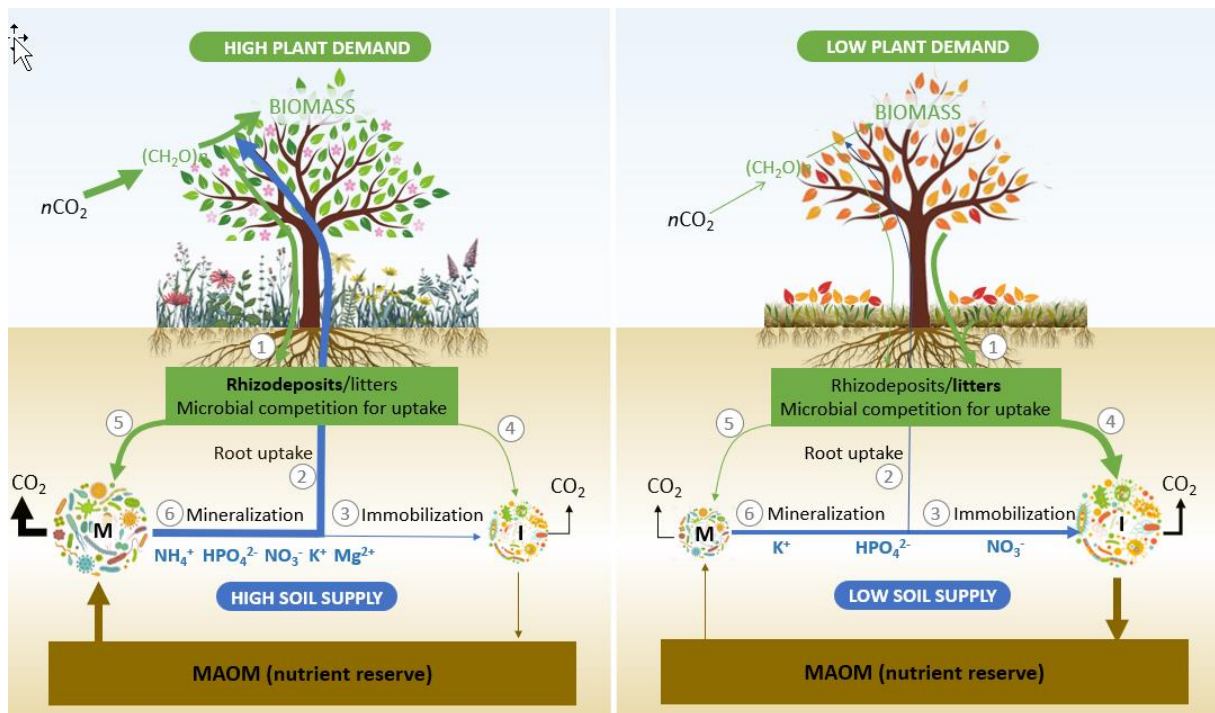
### 195 **Synchrony based on mineral-associated organic matter (Sync-MAOM)**

196 This synchrony system is promoted by resource-acquisitive<sup>50</sup> plant species characterized by  
197 rapid growth, high tissue turnover and rhizodeposition<sup>24</sup>, and litter with chemistry conducive to  
198 decomposition, e.g. low content of lignin and condensed tannins, low C:N<sup>37</sup>. Organic matter  
199 deposited by plants is rapidly decomposed by free-living soil decomposers that release smaller  
200 organic compounds characterized by lower-energy and higher-nutrient contents<sup>51,52</sup>. These  
201 compounds self-assemble, adsorb on soil minerals and also precipitate with metal cations (Fe,  
202 Al, Si), which further increases the cost to access them (secretion of exoenzymes and/or  
203 ligands)<sup>53,54</sup>. Accumulating in soils over thousands of years<sup>55,56</sup>, these compounds constitute a  
204 large reservoir of MAOM<sup>57</sup>.

205 Resource-acquisitive plants mainly absorb nutrients in mineral forms whose availability  
206 depends on the mineralization and immobilization activities<sup>29,47</sup> of two broad functional types  
207 of microbes<sup>28,58</sup>(Figure 2). It has recently been reported that these microbial types use, and  
208 compete for, plant rhizodeposits and litter as source of energy, but have different nutrient  
209 acquisition strategies<sup>28,59</sup>. The C to nutrient ratio of plant material is often too high for microbial  
210 nutrient needs, implying that microbes have to find a complementary source of nutrients<sup>32</sup>. We  
211 refer to mineralizer microbes (M-microbes) as those able to acquire nutrients by decomposing  
212 MAOM through the secretion of exoenzymes and ligands, e.g. some members from the  
213 *Tremellomycetes* class<sup>28,60</sup>. Their activities lead to net destruction of MAOM and release of  
214 mineral nutrients after excretion of excess nutrients and microbial turnover<sup>28,58</sup>. The  
215 immobilizers (I-microbes) are not able to decompose MAOM and assimilate the nutrients they  
216 need from the soil solution, e.g. some members from the *Massilia* genus<sup>28,61</sup>. Their activities  
217 lead to MAOM formation and mineral nutrient immobilization<sup>58,59</sup>.

218 These two microbial types characterized here according to their role on soil nutrient  
219 fluxes are consistent with ecological strategies, microbial traits, and microbial limitations  
220 previously described by microbiologists<sup>28,62</sup>. M-microbes refer to slow-growing microbes  
221 characterized by high investment in resource acquisition and low carbon use efficiency<sup>59</sup>. Their  
222 low carbon use efficiency, combined with the fact they have potentially unlimited access to  
223 MAOM nutrients, means that M-microbes are primarily limited by the availability of energy  
224 (rhizodeposits, litter)<sup>28,58</sup>. In contrast, I-microbes refer to fast-growing microbes characterized  
225 by low investment in resource acquisition, high carbon use efficiency and limitation by nutrient  
226 availability<sup>28,58</sup>.

227  
228



229

230 **Figure 2.** Synchrony between plant nutrient demand and soil supply of mineral nutrients through mineralization  
 231 of mineral-associated organic matter (Sync-MAOM). This example describes the seasonal change in plant demand  
 232 and soil supply. The numbers illustrate the chronology of events in response to an increased (left panel) or  
 233 decreased (right panel) plant demand. The letters M and I indicate the two functional types of microbes controlling  
 234 the availability of mineral nutrients in soils (microbial mineralizers and immobilizers, respectively). Green, blue  
 235 and brown arrows describe flows of plant material, mineral nutrients and MAOM, respectively. For clarity, the  
 236 mechanisms of MAOM decomposition such as the secretion of extracellular enzymes and ligands by microbes or  
 237 roots are not represented. The synchrony presented here contributes to maintaining very low concentrations of  
 238 soluble nutrients and hence low nutrient losses by leaching or denitrification (losses not represented).

239 We suggest that the activities of M- and I-microbes constitute a supply chain of mineral  
 240 nutrients contributing to satisfy the plant nutrient demand and conserve nutrients in ecosystem  
 241 (Figure 2). The heterogeneous distribution of roots, organic matter of contrasted quality and  
 242 communities of M- and I-microbes in soil create hotspots of nutrient immobilization and  
 243 mineralization<sup>41,63</sup>. Between these soil microsites, several hundred kilograms of mineral N per  
 244 hectare are typically diffusing each year<sup>49</sup>. These quantities exceed the yearly N requirements  
 245 of most plant species. Plants efficiently compete for mineral nutrient uptake with I-microbes  
 246 thanks to their higher lifespan and their root system that explores heterogeneous soil conditions  
 247 with the help of mycorrhizal fungi<sup>64-66</sup>. Moreover, the two nutrient fluxes of the supply chain  
 248 (mineralization & immobilization) may adjust to plant demand. Photosynthesis determines  
 249 plant demand but also plant material inputs and nutrient uptake<sup>29,44</sup>. As a result, soil resource  
 250 availability is continuously modified according to the plant demand with important  
 251 consequences for M- and I-microbes activity (Figure 2). As plant demand increases, the greater  
 252 uptake of mineral nutrients by plants reduces nutrient immobilization by I-microbes as well as  
 253 their use of plant material (Figure 2, left panel). At the same time rhizodeposition of energy-  
 254 rich substrates is increased and the ligands present in rhizodeposits desorb organic matter from  
 255 minerals making them more accessible to M-microbes<sup>67</sup>. More energy is available to M-  
 256 microbes stimulating their decomposition activities and release of mineral nutrients from  
 257 MAOM, an effect named rhizosphere priming<sup>44,58,68</sup>. Conversely, when plant demand decreases  
 258 (Figure 2 right panel), the mineral nutrients “left over” by plants induce a rapid development of  
 259 I-microbes. More I-microbes decrease the energy availability for M-microbes thus increasing  
 260 nutrient immobilization over mineralization.



261 Numerous studies support the existence of this synchrony system. A common garden  
262 experiment comparing 12 grassland plant species with contrasted photosynthetic activities  
263 reported that gross N mineralization (soil supply) adjusted to the demand of each of these  
264 species<sup>44</sup>. Recent syntheses showed that enhanced plant photosynthesis and plant demand for  
265 nutrients under elevated CO<sub>2</sub> induce both an increase in gross N mineralization<sup>27</sup> and a decrease  
266 in soil organic matter stock<sup>69</sup>. Moreover, a decrease in plant photosynthesis in response to plant  
267 shading/cutting induces a reduction in soil organic matter mineralization (soil supply) within  
268 24 hours<sup>70,71</sup>, supporting the idea of a high-speed synchrony. In many ecosystems, the  
269 mineralization to immobilization ratio changes during the season in line with changes in plant  
270 demand; immobilization dominates during the winter (low demand) whereas mineralization  
271 dominates during spring-summer (high demand)<sup>72,73</sup>. These functional changes have been  
272 shown to be correlated to changes in microbial community structure<sup>72,73</sup> supporting the idea of  
273 a synchrony driven by plant-microbes interactions.

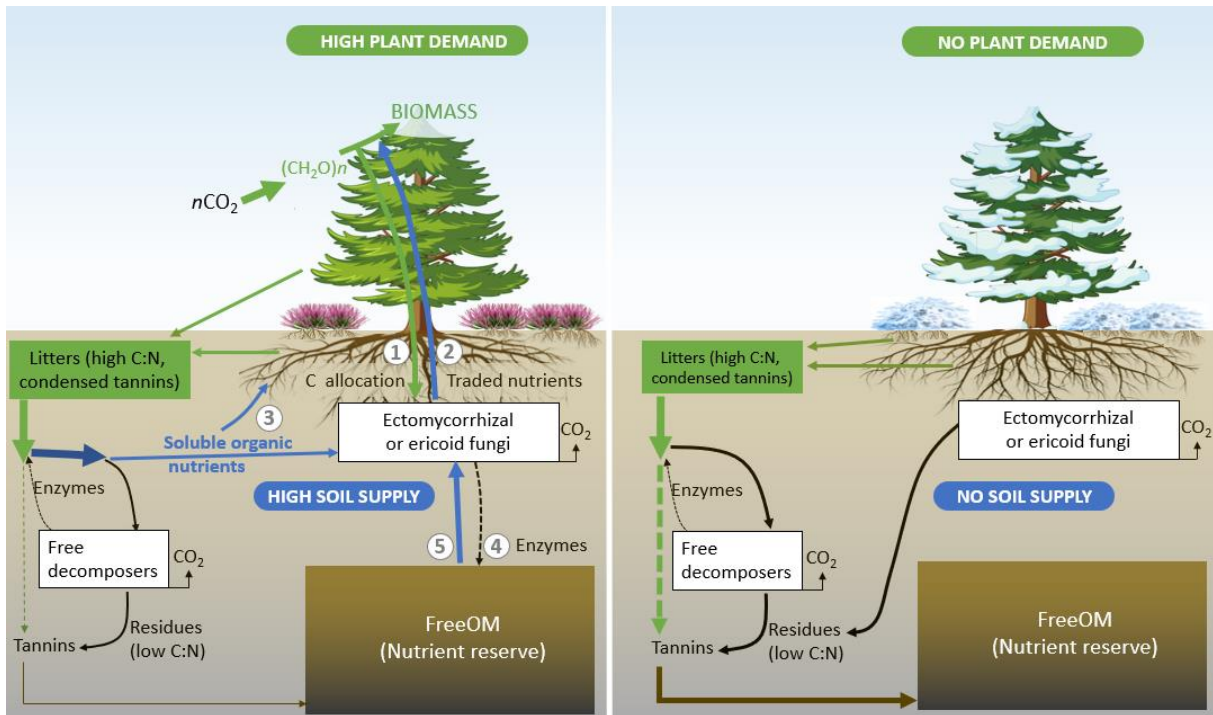
### 274 **Synchrony based on free organic matter (Sync-FreeOM)**

275 This synchrony system is promoted by resource-conservative plant species<sup>50</sup> characterized by  
276 slow growth<sup>74</sup>, low tissue turnover and rhizodeposition<sup>44,74</sup>, and litter with high C:N ratio and  
277 high content of lignin and condensed tannins<sup>37</sup>. This litter chemistry decreases the return on  
278 investment of decomposers (energy yield by decomposers once the investment in exoenzymes  
279 have been considered)<sup>59</sup> slowing down their activities and litter decomposition. Moreover,  
280 condensed tannins present in litter are able to complex small nutrient-rich organic compounds  
281 such as plant protein, exoenzymes and residues of microbial necromass<sup>75</sup> protecting them  
282 against decomposition and leaching. The accumulation of slowly-decomposing litter  
283 complexing small molecules contributes to the build-up of large reserves of organic nutrients,  
284 especially in heathland and cold ecosystems<sup>76,77</sup>. These organic matter forms are mainly free of  
285 soil minerals (FreeOM), accumulating in the organic layer and as particulate organic matter<sup>78</sup>  
286 in the mineral soil (Figure 3) for decades-centuries<sup>76,79</sup>.

287 The activity of free-living decomposers releases little mineral N because the C/N ratios  
288 of litter and FreeOM are high relative to decomposer biomass<sup>41</sup>. To compensate for this lack of  
289 mineral nutrient, the roots of conservative plant species and their associated mycorrhizal fungi  
290 have developed the capacity to absorb soluble organic nutrients such as amino acids<sup>41,42</sup>  
291 released by the activity of microbial exoenzymes, pre-empting their uptake by decomposers.  
292 Moreover, we suggest that conservative woody species may actively control the  
293 depolymerization of FreeOM in soluble organic nutrients to satisfy their nutrient demand during  
294 the growing season (left panel Figure 3). Indeed, recent studies have shown that these plants  
295 associate with ericoid or ectomycorrhizal fungi which have large enzymatic abilities<sup>80</sup> allowing  
296 them to depolymerize the FreeOM<sup>25,81,82</sup>. Mycorrhizal fungi also have the capacity to inhibit or  
297 stimulate the activity of free-living soil decomposers and thus their release of soluble organic  
298 nutrients<sup>83</sup>. By trading photosynthate-C against nutrients with their mycorrhizal partners,  
299 conservative woody species may modulate the rate of FreeOM depolymerization and nutrient  
300 supply to their needs.

301 Conservative herbaceous plants can also lead to the accumulation of FreeOM and take up  
302 soluble organic nutrients in the tropics as well as in temperate or cold environments<sup>79,84,85</sup>.  
303 Endo-mycorrhizal fungi associated to herbaceous plants can help to satisfy plant nutrient  
304 demand by absorbing soluble organic nutrients released by the activity of free decomposers.  
305 However, contrary to ericoid and ectomycorrhizal fungi, endo-mycorrhizae have no or little  
306 degradative capability<sup>86</sup>. Therefore, it remains unclear whether these plants can control the  
307 release of nutrient from FreeOM and how they would make it. An increased mowing of  
308 conservative species has been shown to accelerate FreeOM decomposition and N cycling<sup>87,88</sup>,  
309 suggesting that roots of conservative plants have some control over soil nutrient fluxes.

310 Conservative herbaceous plants have been suggested to modulate nutrient fluxes by shaping the  
 311 activity of free-living decomposers through their associations with endo-mycorrhizal fungi and  
 312 endophytes<sup>86,89</sup>.



313  
 314 **Figure 3.** Synchrony between plant nutrient demand and soil supply of dissolved organic nutrient through  
 315 depolymerization of free organic matter (Sync-FreeOM). This example illustrates the case of conservative woody  
 316 plants associated with ectomycorrhizal or ericoid fungi. We describe the response of these ecosystems to seasonal  
 317 changes including a long period of plant inactivity (e.g., alpine ecosystems). Mycorrhizal fungi mine nutrients in  
 318 FreeOM in function to the plant demand. The activity of free-living decomposers contributes to the building of  
 319 FreeOM during period of plant inactivity, and to supply of soluble organic nutrients during period of plant growth.  
 320 The numbers show the chronology of events in response to a high plant demand (left panel). Green, blue and  
 321 brown arrows describe flows of plant material, soluble organic nutrients and FreeOM, respectively. The  
 322 synchrony presented here contributes to maintaining very low concentrations of soluble nutrients and hence low  
 323 nutrient losses by leaching or denitrification (losses not represented).

324 **Synchrony based on inorganic nutrients retrieved from the atmosphere and**  
 325 **minerals (Sync-Inorganic)**

326 Aside from soil organic reserves, plants can access several other sources of nutrients for which  
 327 supply-demand regulations can occur. A classic example is N uptake from the atmosphere by  
 328 legumes which depends on the rapid transfer of photosynthates to root nodules where Rhizobia  
 329 carry out the costly process of N<sub>2</sub> fixation<sup>90</sup>. Given the dependency of nodules to plant C,  
 330 conditions enhancing photosynthesis (plant demand) such as the increase in light intensity or  
 331 atmospheric CO<sub>2</sub> usually lead to an increase in N<sub>2</sub> fixation<sup>91</sup>. Conversely, factors reducing  
 332 photosynthesis reduce N<sub>2</sub> fixation<sup>91</sup>. Photosynthesis modulates not only nodule number and  
 333 growth, but also the activity of nitrogenase<sup>90</sup>, leading to a fast (hours) synchrony between plant  
 334 demand and microbial N<sub>2</sub> fixation.

335 Rock, soil minerals and precipitates represent a crucial source of phosphorus (P),  
 336 potassium, calcium, magnesium, and iron for plants<sup>92</sup>. These nutrients are not directly available  
 337 to plants, and first need to be solubilized (P precipitates) or released from the mineral matrix  
 338 (rock) through physical and chemical weathering before being absorbed by plants. Roots can  
 339 directly accelerate this nutrient mobilization through the secretion of protons and ligands  
 340 solubilizing and desorbing nutrients from the mineral phase. A synthesis of recent research

341 showed that rhizodeposition also supports large communities of root-associated microbes that  
342 accelerate weathering of minerals, amplifying the nutrient availability to plants by several  
343 orders of magnitude<sup>45</sup>. For example, mycorrhizal hyphae exert a mechanical pressure that  
344 provokes physical distortion of the mineral lattice structure facilitating subsequent chemical  
345 alteration<sup>45</sup>. Diverse microbes promote the dissolution of the mineral matrix<sup>45,92</sup>. All these  
346 mechanisms of nutrient supply depend on the delivery of energy by plants that trade energy  
347 against nutrients with microbes, in particular mycorrhizal fungi<sup>93</sup>. Overall, plant photosynthesis  
348 determines the amount of energy that can be allocated to microbes carrying out mineral  
349 dissolution/weathering, enabling a synchrony between plant demand and nutrient supply from  
350 minerals.

### 351 Synchrony on multiple nutrients simultaneously promoted by a common market 352 (Sync-Market)

353 In the previous sections, we summarized how the nutrient supply by soil microbes (all nutrients  
354 confounded) may adjust to overall plant nutrient demand controlled by the amount of  
355 photosynthetic C available for biosynthesis. However, plants as well as microbes need a variety  
356 of nutrients in specific ratios<sup>94</sup>. These stoichiometric constraints raise the question of a  
357 synchrony acting simultaneously on multiple nutrients. The different synchrony systems  
358 outlined above appear unable, individually, to bring nutrients in the ratios suitable for plant  
359 needs. Although research on the coupling of multiple elements in ecosystems is still in its  
360 infancy, a number of empirical results support the existence of multiple nutrient synchrony<sup>95,96</sup>.  
361 Plants can balance the macro- and micro-nutrients they receive by modulating the energy they  
362 allocate to microbial partners controlling acquisition pathways for particular nutrients<sup>96</sup>. For  
363 example, a lack of P triggers a greater allocation of C to mycorrhizal fungi and associated  
364 microbes which secrete phosphatases or protons to acquire soil P<sup>96</sup>.

365 Multiple synchrony could also occur through a common market of nutrients (Sync-  
366 Market, Figure 4). Mycorrhizal fungi form common networks that act as highways for the  
367 movement of C and nutrients, redistributing them across space and between plants of either the  
368 same or different species<sup>97,98</sup>. This redistribution suggests that mutualistic microbes not only  
369 trade their nutrients with the plant they are directly associated with, but also with other  
370 symbionts that are themselves connected to other plants that might have complementary  
371 nutrient needs (e.g., different ratios between the elements constituting plant biomass) and/or  
372 local soil supply consecutive to different plant nutrient acquisition strategies (e.g., root depth,  
373 quantity/quality of exudates, litter chemistry). This multi-partner trading creates a common  
374 carbon and nutrient market with beneficial effects for the nutrition and growth of interconnected  
375 plants and microbes<sup>97</sup>. Indeed, the capacity of mycorrhizal fungi to trade the various soil-  
376 acquired nutrients against plant-acquired energy is enhanced by this market. The nutrient  
377 redistribution between plants by the mycorrhizal network is better able to satisfy the plant  
378 demand in multiple nutrients and limit local excess of soluble nutrients. Therefore, the common  
379 market can maximize synchrony at different scales (from plant to ecosystem) and for several  
380 elements simultaneously, explaining the positive effects of common mycorrhizal networks  
381 observed on plant nutrition and growth<sup>97</sup>.

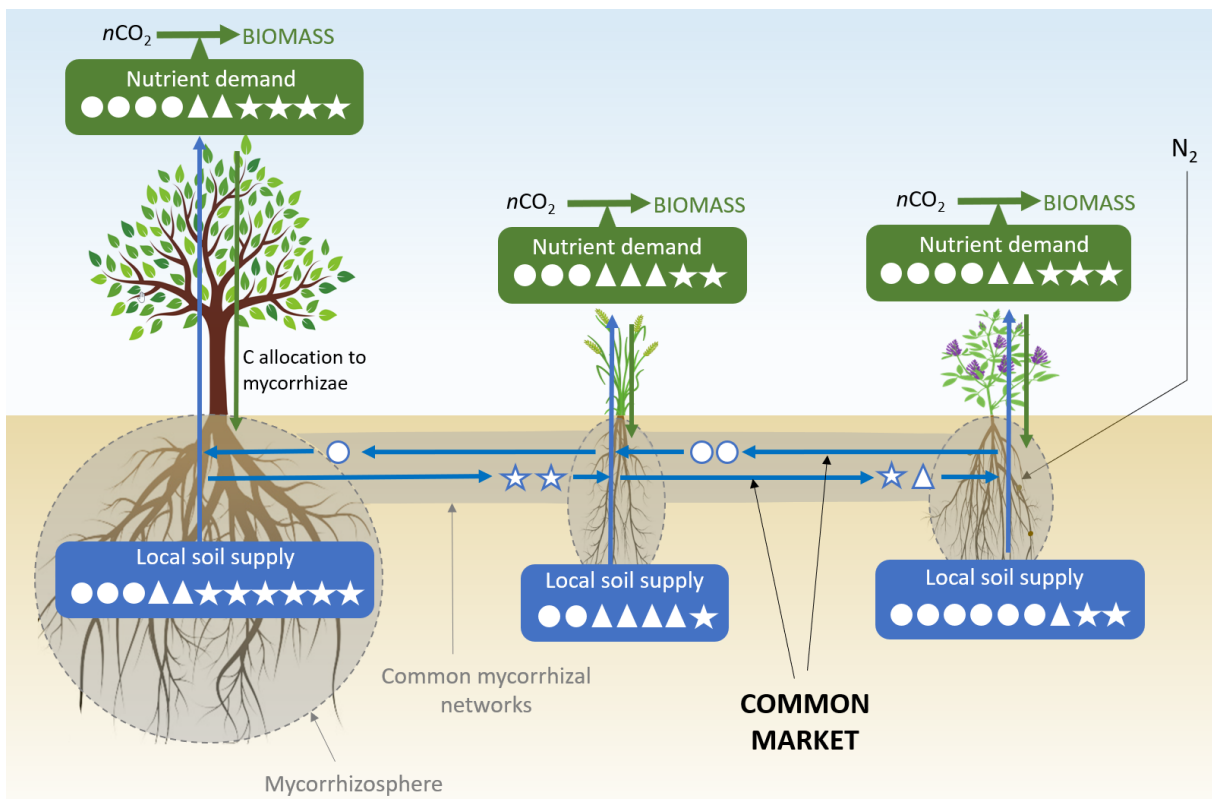
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389 **Figure 4.** Synchrony between plant demand and soil supply on multiple nutrients can be facilitated by a common  
 390 nutrient market supported by mycorrhizal networks. The symbols (triangle, circle, star) illustrate different  
 391 nutrients. The local soil supply represents the amount of soluble nutrients delivered by the soil biota (from organic  
 392 and inorganic nutrient reserves) before the nutrient redistribution between plants through the common market.  
 393 This local soil supply can vary with local soil characteristics, root depth and plant nutrient acquisition strategies.  
 394 The nutrient redistribution between plants by the mycorrhizal network is better able to satisfy the plant demand in  
 395 multiple nutrients and limit local excess of soluble nutrients.

## 396 Influence of abiotic and biotic factors on synchrony

### 397 Pedoclimatic context and plant functional types

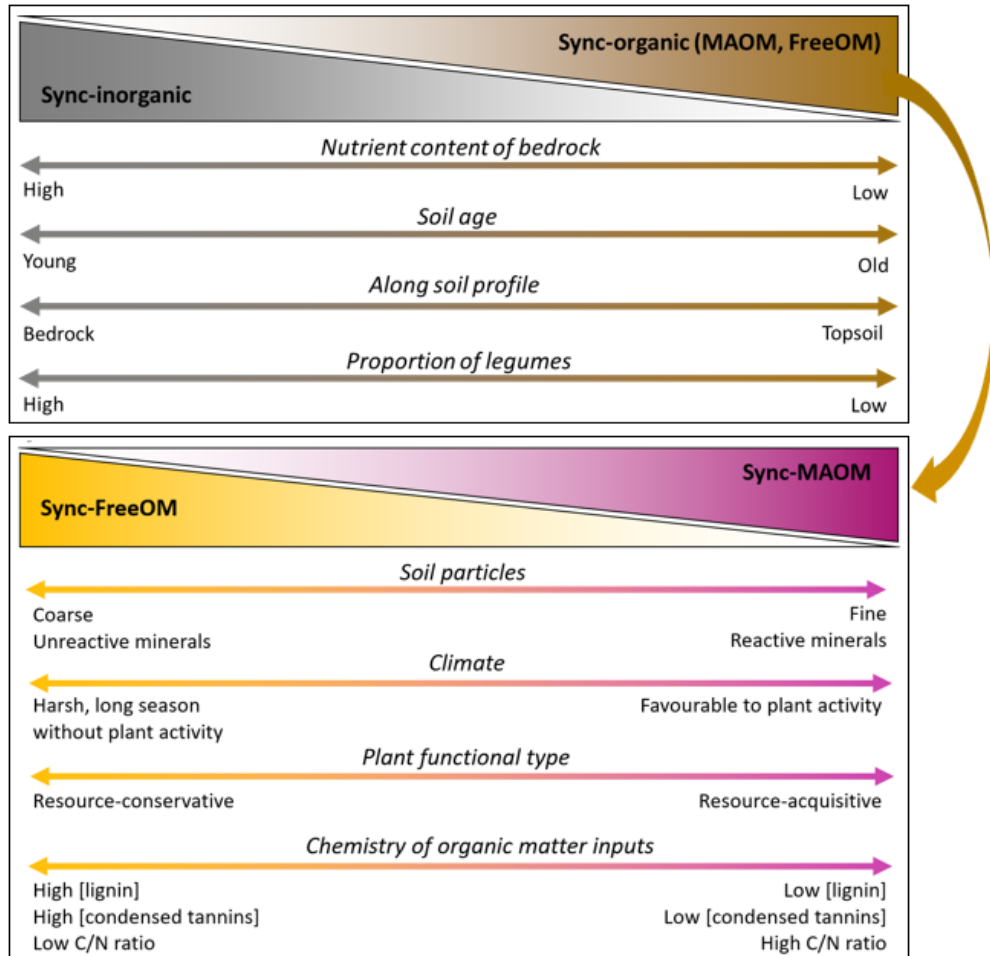
398 Building on the recent scientific advances, we propose a framework with four systems capable  
 399 of synchronizing the soil nutrient supply to plant demand at a range of time scales (from hours  
 400 to seasons). Two systems (Sync-FreeOM, Sync-Inorganic) are based on plant-products such as  
 401 litter or nodule-supporting tissues of legumes, and microbial symbionts that tightly interact with  
 402 plant roots such that they can be considered as the extended phenotype of certain plants<sup>99</sup>. For  
 403 the remaining systems (Sync-MAOM, Sync-Market), synchrony emerges from diffuse  
 404 interactions between distinct functional types of microbes and plants and therefore can be  
 405 considered as ecosystemic regulations. These four synchrony systems co-occur in most  
 406 ecosystems, their relative importance in regulating nutrient cycles depending on pedoclimatic  
 407 context, plant functional type and biodiversity level (Figure 5 & 6).

408 Sync-inorganic plays a key role in young soils where organic nutrient reserves are  
 409 limited and soil inorganic nutrient reserves dominate (Figure 5). Sync-inorganic is also  
 410 determined by the ability of the plant community to retrieve nutrients from atmosphere and soil  
 411 minerals, which depends, for example, on the proportion of legumes. The contribution of  
 412 synchrony systems based on soil organic reserves (Sync-MAOM, Sync-FreeOM) increases  
 413 with soil age as organic matter accumulates and inorganic reserves are depleted.

414 Sync-MAOM is promoted by resource-acquisitive plant species producing litter with a  
 415 chemistry conducive to rapid decomposition by microbes that release the organic compounds

416 leading to MAOM formation. This formation depends on interactions with minerals, and the  
 417 contribution of Sync-MAOM increases as soil particle size decreases and mineral reactivity  
 418 increases<sup>100</sup>. Moreover, Sync-MAOM requires a regular plant supply of energy-rich substrates  
 419 to M- and I-microbes. Thus, Sync-MAOM may dominate where climatic conditions are  
 420 favorable to plant activity most of the year.

421 Sync-FreeOM is promoted by resource-conservative species producing litters with a  
 422 chemistry unfavorable to decomposition. When rich in condensed tannins, this litter  
 423 complexes the small organic compounds released by microbes building large reserves of  
 424 FreeOM. This contributes to nutrient conservation even under context of low MAOM formation  
 425 potential and periods of plant inactivity. Thus, Sync-FreeOM is expected to dominate in coarse-  
 426 textured soils and/or under climates with long season(s) without plant activity<sup>76,77</sup>.



427 **Figure 5.** Relative importance for ecosystem functioning of the synchrony systems based on nutrients retrieved  
 428 from atmosphere and soil minerals (Sync-Inorganic) and from soil organic nutrient (Sync-Organic) in relation to  
 429 pedoclimatic contexts and plant functional type. The Sync-Organic is composed of two distinct synchrony systems  
 430 mobilizing different types of soil organic matter, namely the mineral-associated organic matter (Sync—MAOM)  
 431 and the free organic matter (Sync-FreeOM). The change of the dominant organic nutrient reserve (MAOM versus  
 432 FreeOM) can be paralleled to the change in humus forms (Mull, Moder and Mor) described by soil scientists  
 433 along environmental gradients.  
 434

435 Sync-Market is induced when different plants connected by common mycorrhizal  
 436 networks have complementary nutrient needs and/or local soil nutrient supply (Supplementary  
 437 material 2). Thus, the contribution of Sync market is expected to increase with spatial  
 438 heterogeneity (from nanoscale to soil profile) of soil nutrient reserves (organic and inorganic)  
 439 and their elemental composition (e.g., N/P/S ratio). Plant functional diversity (e.g. plant with  
 440 different C/N ratio in biomass, root depth and root architecture, quantity/quality of exudates)

441 within the canopy promotes Sync-Market by increasing the complementary effects between  
442 plants in terms of nutrient needs and local soil nutrient supply. The contribution of Sync-Market  
443 to ecosystem functioning is also determined by the capacity of plants to form common  
444 mycorrhizal networks.

#### 445 **Biodiversity: a key asset promoting synchrony**

446 Higher plant and microbial diversity improve multiple ecosystem functions such as primary  
447 production, nutrient retention and soil C storage<sup>101-104</sup> that are related to synchrony. Recent  
448 evidence also indicates that the higher primary production promoted by plant diversity is  
449 associated with an improved soil nutrient supply<sup>105,106</sup>. We propose that biodiversity could  
450 promote synchrony across scales ranging from individual plants to whole ecosystems, through  
451 three non-exhaustive pathways.

452 *Biodiversity promotes synchrony through the functional complementarity of organisms.*  
453 Synchrony systems clearly show an ecological division of labor<sup>103</sup> that may emerge from  
454 evolutionary processes<sup>81,107</sup>: each function of the system is carried out by specific groups of  
455 biota such as organic nutrient reserve formation (I-microbes, conservative plants) and  
456 decomposition (M-microbes, ectomycorrhizal & ericoid fungi), N<sub>2</sub> fixation (Rhizobium,  
457 legumes) etc. The maintenance of these functional groups is fundamental for the synchrony  
458 generated by each of these systems. Moreover, co-occurrence of plant species with different  
459 nutrient strategies<sup>108</sup> (e.g., legumes/non-legumes, acquisitive/conservative, P-mobilizing-  
460 plants) is also expected to induce different synchrony systems. The proximity of roots of  
461 neighboring plants with different strategies facilitates nutrient transfer from plant to plant for  
462 their mutual benefit in terms of nutrition and growth<sup>109</sup>. This nutrient transfer takes place at  
463 different time scales (hours to years) according to the processes involved<sup>109</sup>, including nutrient  
464 exchanges across mycorrhizal networks (Sync-Market), direct transfer of root exudates and  
465 decomposition of plant materials. The exchange of N and P between legumes and P-mobilizing  
466 plants is a classic example of plant-plant interactions which improve overall plant-soil  
467 synchrony. More broadly, a high functional diversity of microbes and plants promotes both the  
468 existence of - and the interaction between - synchrony systems with complementary roles in  
469 ecosystems. Sync-Inorganic brings nutrients from atmosphere and bedrock to the ecosystem  
470 while sync-MAOM and sync-FreeOM accumulate these nutrients in organic reserves, limiting  
471 nutrient loss and allowing nutrient recycling when needed by plants. These synchrony systems  
472 create major nutrient sources for plants while Sync-Market helps to balance the proportion of  
473 different nutrients supplied in relation to the multiple element requirement of plants.

474 *Biodiversity facilitates synchrony by ensuring the temporal and spatial stability of plant-soil*  
475 *interactions.* Synchrony requires that the connection between plants and microbes is maintained  
476 in space and time. Given that species can occupy different niches, this space-to-time occupation  
477 by plants and microbes often depends on species diversity. For example, soil occupation at  
478 various soil depths but also across coarse and fine spatial scales requires multiple plant species  
479 with contrasted root architecture and traits<sup>110</sup>. Succession of plant species with different  
480 phenology contributes to maintaining a permanent plant cover in diversified ecosystems<sup>111</sup> and  
481 a continuous energy supply to microbes, which is particularly important for sync-MAOM  
482 (Figure 2). Importantly, increased diversity will also promote temporal and spatial stability by  
483 promoting functional redundancy among species conferring greater resistance to environmental  
484 fluctuation and disturbance overtime<sup>112</sup>.

485 *Biodiversity stabilizes resource-exchange mutualisms.* We detailed several systems of  
486 synchrony based on mutualism between plants and their microbial symbionts, and the  
487 subsequent resource exchanges (e.g., Sync-Market). The maintenance of such mutualisms is  
488 not obvious from an evolutionary point of view : any partner that invests less in the resource  
489 exchange would have an immediate benefit, while the cost (lower partner abundance or activity)  
490 would be shared by all, creating a classical tragedy of the commons<sup>113</sup>. We suggest that

491 diversity on both sides (plants and microbes) facilitates the maintenance of the resource  
492 exchange. Indeed, the diversity of partners allows the possibility of partner choice and  
493 reward/sanction, known to stabilize this type of mutualistic interaction<sup>113–115</sup>.

#### 494 **Plant plasticity and adaptations to unbalanced soil supply**

495 Despite existing mechanisms that facilitate supply-demand synchrony, strong spatial and  
496 temporal variations in soil nutrient availability or plant demand generated by exogenous factors  
497 such as animal excretion or extreme climatic events can induce transient periods of asynchrony  
498 (excess or deficiency)<sup>116,117</sup>. Insufficient soil supply in relation to the demand of a given plant  
499 may also arise due to limiting nutrient reserves in soil and to localized plant-plant competition  
500 for nutrients<sup>118</sup>. Plants can respond in two ways to unbalanced soil supply:

501 *Changes in physiology and morphology to enhance acquisition of limiting resources.* Plants are  
502 able to adapt their physiology and morphology over short-time scales (hours-weeks) in response  
503 to nutrient availability<sup>119</sup>. Under high nutrient supply, plant allocation of C and nutrients shifts  
504 towards greater investment in shoots and photosynthetic proteins enhancing C acquisition<sup>120</sup>.  
505 In contrast, under low nutrient supply, plants promote nutrient acquisition and nutrient supply  
506 from microbes by increasing root-to-shoot ratios, up-regulating root membrane transporters,  
507 and changing root architecture and exudation<sup>121,122</sup>.

508 *Nutrient storage.* When supply exceeds plant demand, many plant species adopt a luxury  
509 nutrient uptake<sup>123</sup>. These excess nutrients are stored in vacuoles in the short-term (days), or in  
510 large storage organs such as rhizomes for remobilization several months-years later during  
511 periods of insufficient soil supply<sup>124</sup>. Reserves play a central role in the nutrition of perennial  
512 plants, with remobilized N from previous year storage often representing more than 50% of N  
513 recovered in new shoots<sup>124</sup>. At the ecosystem scale, plant nutrient storage presents the same  
514 advantages as synchrony since it promotes i) biomass production by alleviating the nutrient  
515 limitation of plants and ii) nutrient retention by preventing accumulation of soluble nutrients in  
516 soil. Plant reserves can also support the rapid recovery of photosynthesis and root activities  
517 following disturbances<sup>124</sup> helping to maintain synchrony in these disturbed ecosystems.

#### 518 **Implications for agrosystems**

##### 519 **Fertility: an emerging property of plant-soil interactions**

520 Most definitions of soil fertility refer to the inherent capacity of a soil to sustain plant growth  
521 and production by providing nutrients in adequate amounts and in suitable proportions<sup>125</sup>. We  
522 argue that recent work on plant-soil synchrony calls for an in-depth revision of this concept  
523 because 1) plants can influence the quantity and proportion of soluble nutrients they receive  
524 from soil *via* at least four systems of synchrony, and 2) soil nutrient supply should be considered  
525 in relation to the fluctuating plant demand. Hence, nutrient supply from soil is not an inherent  
526 property of soil but an emerging property of plant-soil interactions, even if soil characteristics  
527 influence the nature and efficiency of these interactions (Figure 5). This has a practical  
528 consequence: depending on the plant species and microbial taxa present and their ability to  
529 influence soil nutrient supply, the same soil can support different levels of biomass production  
530 as underlined in several experiments<sup>24,42</sup>. It may also explain why soils defined as infertile can  
531 support similar levels of biomass production as soils defined as fertile in some cases<sup>126,127</sup>.  
532 Identifying plant species capable of stimulating soil nutrient supply *via* synchrony systems  
533 opens avenues towards ecological intensification of plant production.

##### 534 **Managing synchrony to ensure both productivity and sustainability**

535 There is a great diversity of management approaches currently being explored to reinforce the  
536 sustainability of agriculture (no or reduced tillage, organic farming, crop rotation, conservation  
537 agriculture, permaculture...), yet finding efficient combinations of agroecosystem features for  
538 a given pedoclimatic and socio-economic context remains difficult. The adoption of  
539 “sustainable” practices does not always solve asynchrony issues. For instance, the incorporation

540 of legumes as green manure in rotation can lead to N losses as high as mineral fertilizers<sup>20</sup>,  
541 though this practice has the advantage of reducing the use of mineral N fertilizers whose  
542 production generates greenhouse gases. Moreover, management practices often appear to  
543 involve trade-offs or offsets between expected outcomes, for instance between yield and  
544 greenhouse gas emissions, between soil C storage and emission of N<sub>2</sub>O<sup>128</sup>. Focusing on plant-  
545 soil synchrony can help address these difficulties by guiding the changes to be made in  
546 agrosystems to make them sustainably productive; understanding when and how synchrony is  
547 enhanced is needed for management decisions. Analyzing the four synchrony systems, we have  
548 identified the types of synchrony systems to be promoted according to the pedoclimatic context  
549 (Figure 5 & supplementary material 2), and suggest combinations of practices that could install  
550 them in cropping systems (Figure 6).

551 In young soils (e.g., Andosols), where inorganic reserves are high and organic reserves  
552 can be low (Figure 5), management options should give greater importance to Sync-inorganic,  
553 for example, by incorporating a high proportion of legumes and plant species mobilizing  
554 nutrients from soil minerals through their rhizodeposition and association with mycorrhizae.  
555 With organic nutrient accumulation and depletion of inorganic nutrient reserves as soils evolve,  
556 agricultural practices should promote Sync-organic, for example by introducing species with  
557 high rhizodeposition of energy-rich C for microbes (MAOM-sync; Figure 6). In the longer-  
558 term, the inorganic and organic reserves of some rock-originated nutrients (e.g., P) can limit  
559 synchrony in the topsoil of highly-weathered soils (e.g., Ferralsols). In these soils, synchrony  
560 can be enhanced by including deep-rooting species capable of mobilizing the nutrients from  
561 bedrock and redistribute them to the topsoil (Figure 6). Recent studies have shown the  
562 possibility of stimulating different nutrient acquisition pathways (organic-P mineralization,  
563 inorganic-P dissolution, N<sub>2</sub> fixation) through the selection of specific plant traits (N<sub>2</sub>-fixation  
564 efficiency, but also types of exudates)<sup>129,130</sup>. It has also been reported that the level of soil  
565 weathering determines the type of diversification and nutrient acquisition strategies able to  
566 enhance ecosystem productivity and sustainability<sup>130</sup>. In this study, legumes increased biomass  
567 production (+18%) in Andosols but not in Ferralsols, while soil-P-mobilizing tree species  
568 increased biomass production(+39%) and soil C stock(+26%) in Ferralsols but not in  
569 Andosols<sup>130</sup>.

570 Current industrial grain production systems are mostly based on fast-growing  
571 acquisitive plant species<sup>131</sup> generating MAOM-type soil organic matter. Given that the sync-  
572 MAOM system requires a continuous C input from plants to microbes (Figure 2 & 5), practices  
573 promoting a permanent plant cover in annual cropping systems could enhance synchrony.  
574 Along a gradient of increasing novelty, these practices include lengthening of crop rotations,  
575 cover/relay cropping and introduction of perennial grain crops (Figure 6). In agreement with  
576 this idea, meta-analyses have shown that cover cropping reduces nitrate leaching by 70% on  
577 average<sup>132</sup> and increase soil organic C by 15.5%<sup>133</sup>, provided the cover crop is not a pure legume  
578 stand. Indeed, plant materials must have a carbon to nutrient ratio high enough to stimulate  
579 nutrient immobilization by I-microbes (Figure 2).

580 In view of the involvement of soil minerals in MAOM formation, the synchrony system  
581 that most crop species may generate (Sync-MAOM) is inadequate for coarse-textured soils with  
582 low mineral reactivity. This explains why ecosystem conversion to cropping induces faster and  
583 higher losses of C and N in sandy than in clay soils<sup>134</sup>. Traditional management practices such  
584 as extensive heathland grazing show that sandy soils can support sustainable production when  
585 conservative plants are present (Sync-FreeOM, Figure 6)<sup>135</sup>. We suggest that the sustainability  
586 of many agrosystems or forestry systems established on coarse-textured soils may be improved  
587 by introducing conservative species. These conservative species can be grown alone or in  
588 association with acquisitive species such as annual crops (e.g., intercropping). In these  
589 associations, the litter of conservative species will compensate the lack of reactive soil minerals



590 by chemically binding small organic nutrients released by microbes, preventing their leaching  
591 (Figure 3). Rhizodeposition from acquisitive crop species will induce higher mineralization-  
592 immobilization fluxes (Figure 2) allowing them to feed on mineral nutrients. The feasibility of  
593 such intercropping is supported by the co-existence of resource-acquisitive and resource-  
594 conservative species within many different ecosystems, including in coarse-textured soils<sup>136</sup>.  
595 However, research is needed to quantify the effect of such associations in an agricultural context  
596 involving disturbances and species with particular traits<sup>131</sup>. The other strength of conservative  
597 species is to maintain a high level of synchrony even when the ecosystem faces long period of  
598 plant inactivity (*Sync-FreeOM versus Sync-MAOM*, Figure 5). Therefore, the use of  
599 conservative species could be a way to promote agrosystem sustainability in situations where  
600 maintaining an active plant cover throughout the year (condition for *Sync-MAOM*) is not  
601 possible due to climatic, economic or technical constraints.

602 By coupling complementary synchrony systems, the association of plant species with  
603 different nutrient economies (legumes/non-legumes; acquisitive/conservative; organic-P-  
604 mobilizing-plants...) could increase the overall level of synchrony in agrosystems. Plant  
605 associations can be implemented over time (crop rotation) and space (intercropping)(Figure 6).  
606 The complementary effects between plant species can be facilitated by mycorrhizal networks  
607 and the resulting common nutrient market (Figure 4), which depends on a combination of  
608 practices (Figure 6). Although current plant associations are made with limited knowledge on  
609 the nutrient economy of plants, recent meta-analyses confirm the strong positive impact of crop  
610 associations on agrosystem productivity and sustainability<sup>137-139</sup>. For example, grain yields in  
611 annual intercropping systems have been shown to be on average 22% higher than in  
612 corresponding monocultures and have greater year-to-year stability<sup>137,140</sup>. This over yielding  
613 can be ascribed to a soil nutrient supply better synchronized with plant demand, with plant  
614 uptake of P and N increased by 24% and 15-29% under intercropping relative to  
615 monocultures<sup>138,141</sup>. Studies have estimated that, for the same yields, current intercropping  
616 systems can reduce the fertilizer requirement by 12% for P<sup>138</sup> and up to 44% for N<sup>139</sup>. Another  
617 example is the simultaneous insertion of grain legumes and cover crops in long rotations that  
618 can reduce N requirements by 49-61% (according to species) with no detrimental effect on  
619 wheat yield and grain quality<sup>142</sup>. Until now, most of the associations tested were limited to two  
620 species, but some farmers mix more than ten species (Figure 6). These crops are harvested as  
621 fodder or consumed on site by animals, promoting nutrient recycling and preservation of soil  
622 organic nutrient reserves over time.

623 Significant amounts of nutrients leave croplands in harvested products and losses  
624 through leaching and denitrification (e.g., export of on average 120 kg N and 30 kg P per hectare  
625 for a wheat grain harvest)<sup>143</sup>. These exports often lead to either a rapid decrease of available  
626 nutrients and production in soils of developing countries, or the application of mineral fertilizer  
627 to maintain a high level of production such as in intensive cropping systems. It has also been  
628 reported that approximately 50% of the applied N fertilizer is lost in the environment<sup>20,144</sup>.  
629 Several regions of the world have adopted policies to reduce mineral fertilizer applications as  
630 such applications seriously harm climate and ecosystem health, and rely on depleting mineral  
631 deposits<sup>145,146</sup>. Our review suggests that practices promoting synchrony can help to decrease  
632 mineral fertilizer amounts while maintaining, or even increasing, production. This may result  
633 from 1) a reduction of nutrient losses (70% for N) enhancing nutrient use efficiency<sup>132</sup>, 2) a  
634 better use of water and light resources (+22%<sup>137</sup>) by reducing the nutrient limitation of plant  
635 growth and periods of bare soil, and 3) the mobilization of nutrients from natural reserves  
636 (atmospheric N<sub>2</sub> and soil minerals), which can represent several hundred kilograms per hectare  
637 and per year for N<sup>147</sup>. Managing synchrony may therefore have important implications for the  
638 economic and environmental outcomes of modern agriculture. Nevertheless, it is important to  
639 keep in mind that the reservoir of rock-derived nutrients has limits, especially in old highly-

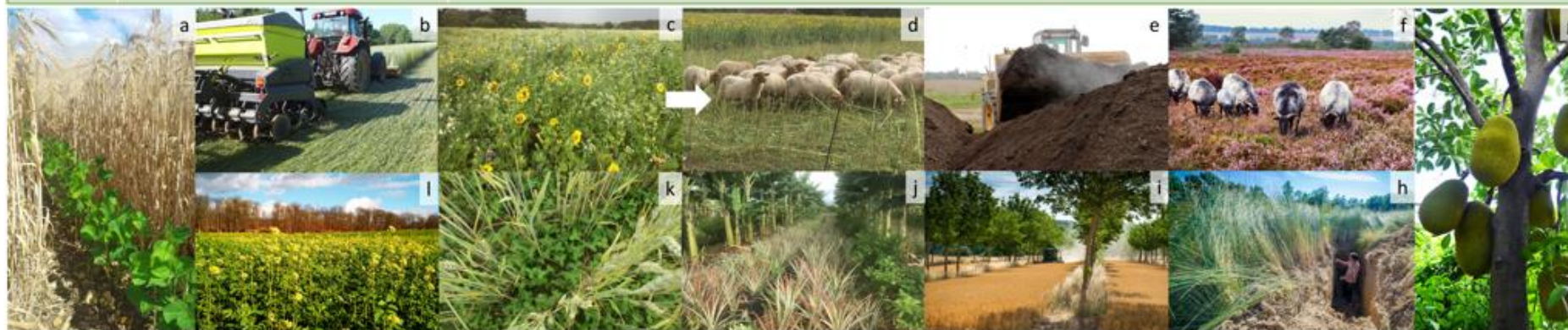
640 weathered soils, and the long-term sustainability (decades-centuries) of agrosystems relies on a  
641 balance between nutrient inputs and outputs at field scale, in particular through practices  
642 promoting organic nutrient recycling (Figure 6).

643 We have focused our discussion on plant functional diversity as the simplest, and most  
644 informed (in terms of impacts), way to manage synchrony in agrosystems. However, our  
645 framework points to other key components of synchrony such as soil diversity, plant/microbial  
646 phenotypes and quantity/quality of organic matter inputs. Considering these components  
647 suggests other synchrony-promoting practices that are ready-to-use such as field inoculation  
648 with microbes<sup>148,149</sup>, or deserve long-term research such as the breeding of new crop  
649 varieties/species<sup>150,151</sup> (Figure 6). Managing synchrony will systematically require a systemic  
650 approach and a combination of practices.

651 In conclusion, some of the management practices identified as promoting synchrony  
652 have already been tested and shown to be effective in reducing nutrient losses and fertilizer use  
653 and/or improving biomass production and soil C storage under specific conditions. The recent  
654 insights synthesized here draw out the conditions of success of these practices in terms of  
655 pedoclimatic context and combination with other practices (Figure 6). This synthesis also  
656 suggests new management options based on plant traits (e.g., amount and type of  
657 rhizodeposition, content of condensed tannins in litter) that should help improve agrosystem  
658 sustainability, including in the most difficult pedoclimatic conditions (e.g., sandy soils, long  
659 season without plant activity). Future priorities are to (1) integrate this scientific knowledge  
660 into tools used by practitioners for redesigning agrosystems, (2) develop methods/proxies to  
661 quantify the level of synchrony and (3) continue efforts to fill knowledge gaps on the synchrony  
662 in various natural ecosystems. In particular, additional research is needed to better understand  
663 i) the mechanisms of FreeOM synchrony under conservative herbaceous plants, ii) quantities  
664 of nutrients that can be released from rocks *via* the Sync-Inorganic each year to compensate  
665 nutrient outputs, iii) the synergies and trade-offs between synchrony systems and iv) the  
666 resistance and resilience of the different synchrony systems to disturbances (e.g., climate, plant  
667 cutting and harvest). These advances will allow future cropping systems to better benefit from  
668 nature-based solutions.

669  
670

Synchrony	Conditions of synchrony	Combination of practices to set up for promoting the targeted synchrony
Sync-MAOM	-Acquisitive plant species -Continuous activity of microbes M & I -Reserve of MAOM in soil	- Use/breeding of acquisitive species with strong capacity of stimulating nutrient mineralization/immobilization, e.g. high C rhizodeposition - The carbon:nutrient ratio of plant species or organic residues must be high enough to induce nutrient immobilization. Ideally, the different plant species have contrasting carbon:nutrient ratios (a, c, l, j, k) - Maintaining a continuous cover of active plants fueling microbes in energy-rich C (all pictures but e) - Recycling organic nutrients at local scale (farm-watershed) to preserve soil organic reserve on the long-term (d, e, f)
Sync-FreeOM	-Conservative plant species -Mycorrhizal fungi -Reserve of FreeOM in soil	- Use/breeding of conservative species producing recalcitrant litter with reactive compounds fixing organic nutrients (e, f)* - Or/and amendment of recalcitrant organic residues harboring reactive compounds more or less charged in organic nutrients (e) - Recycling organic nutrients at local scale (farm-watershed) to preserve soil organic reserve on the long-term (d, e, f)
Sync-Inorganic	-Plant symbiosis with mycorrhizal fungi & N <sub>2</sub> fixing bacteria -Nutrients stored in bedrock, soil minerals and/or precipitates	- Use/breeding of species with strong capacity of mobilizing nutrients from rock and soil minerals, e.g. mycorrhized roots exerting strong mechanic pressure on minerals, secreting high amount of organic acids & ligands - Use of plant with deep roots colonizing bedrock (g, h, i) - Use of legumes (a, c, k) - Inoculation with mixed mycorrhizal fungi & N <sub>2</sub> fixing bacteria in highly degraded soils
Sync-Market	-Plant species with complementary nutritional needs -Common mycorrhizal networks	- Mixing plant species with different nutrient acquisition strategies and carbon:nutrient ratios (a, c, l, j, k) - Promoting perennial plants (f, g, h, l, k) and/or permanent plant cover (all pictures but e) to fuel mycorrhizae in energy-rich carbon - No or limited use of soil tillage (b) and pesticides to preserve mycorrhizae networks - Inoculation with mixed mycorrhizal fungi in highly degraded soils
Increasing overall synchrony	-Synchrony systems adapted to pedoclimatic context -Complementary synchrony systems -Plant plasticity & reserve	- Analyzing the soil profile and climate, defining the most adapted synchrony systems - Mixing plant species with different nutrient acquisition strategies (a, c, l, j, k) - Breeding crops species for their suitability to association - Promoting perennial plants with high reserve and organ plasticity (f, g, h, l, j, k)



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674 **Figure 6.** Combinations of agricultural practices promoting synchrony between soil nutrient supply and plant nutrient demand through the four major systems of coordination  
675 of plant-soil functions synthesized in this framework (Sync-MAOM, Sync-FreeOM, Sync-Inorganic, Sync-Market). Some practices can enhance the overall synchrony in  
676 agrosystems by improving the efficiency of each system of coordination and by combining several systems of coordination. Photographs illustrate examples of practices  
677 promoting synchrony. Some of them have ancestral origins (f, g, j), others have been developed and tested in the last decades (a, b) or are still under development in agricultural  
678 research centres and/or farmers' networks. (c, d, h, k). (a) relay cropping with soybeans sown during barley growth (©ARVALIS/GENDRE Sophie); (b) direct drill on a rolled  
679 barley cover (©ISARA/VINCENT-CABOUD Laura); (c) mixture of twelve species of annual crops that (d) was consumed as a standing crop by sheep (©A2C/THOMAS  
680 Frédéric); (e) production of compost used as a substrate in market gardening or as an amendment in agriculture. Once stabilized, the compost is composed of recalcitrant plant  
681 residues enriched with microbial compounds (©INRAE/MAITRE Christophe); (f) extensive grazing of heathlands (©SHUTTERSTOCK); (g) the “bread-tree” *Artocarpus altilis*  
682 (©SHUTTERSTOCK) and (h) the cereal *Thinopyrum intermedium* (©ISARA/DUCHENE Olivier) are two examples of perennial plants that can be used as source of  
683 carbohydrates and proteins; (i) agroforestry associating a barley crop with a walnut tree plantation (©INRAE/NICOLAS Bertrand); (j) association of banana, pineapple and  
684 pepper plantations (©A2C/THOMAS Frédéric); (k) wheat cultivation on a living clover cover (©ISARA/DUCHENE Olivier); (l) cover cropping with mustard (©INRAE/WEBER  
685 Jean).

686 Literature

687

688 1. *The future of food and agriculture: trends and challenges*. (Food and Agriculture  
689 Organization of the United Nations, 2017).

690 2. Ju, X.-T. *et al.* Reducing environmental risk by improving N management in intensive  
691 Chinese agricultural systems. *Proc. Natl. Acad. Sci.* **106**, 3041–3046 (2009).

692 3. Wezel, A. *et al.* Agroecological practices for sustainable agriculture. A review. *Agron.*  
693 *Sustain. Dev.* **34**, 1–20 (2014).

694 4. Glover, J. D. *et al.* Harvested perennial grasslands provide ecological benchmarks for  
695 agricultural sustainability. *Agric. Ecosyst. Environ.* **137**, 3–12 (2010).

696 5. Bardgett, R. D. & Gibson, D. J. Plant ecological solutions to global food security. *J. Ecol.*  
697 **105**, 859–864 (2017).

698 6. Bender, S. F., Wagg, C. & van der Heijden, M. G. A. An underground revolution:  
699 Biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol.*  
700 *Evol.* **31**, 440–452 (2016).

701 7. Loges, R. *et al.* Forage production in rotational systems generates similar yields compared  
702 to maize monocultures but improves soil carbon stocks. *Eur. J. Agron.* **97**, 11–19 (2018).

703 8. Gilmanov, T. G. *et al.* Gross primary production and light response parameters of four  
704 Southern Plains ecosystems estimated using long-term CO<sub>2</sub>-flux tower measurements:  
705 GPP OF SOUTHERN PLAINS ECOSYSTEMS. *Glob. Biogeochem. Cycles* **17**, n/a-n/a  
706 (2003).

707 9. Tilman, D., Hill, J. & Lehman, C. Carbon-Negative Biofuels from Low-Input High-  
708 Diversity Grassland Biomass. *Science* **314**, 1598–1600 (2006).

709 10. Yang, Y., Tilman, D., Lehman, C. & Trost, J. J. Sustainable intensification of high-  
710 diversity biomass production for optimal biofuel benefits. *Nat. Sustain.* **1**, 686–692 (2018).

- 711 11. Jenkinson, D., Poulton, P., Johnston, A. & Powlson, D. Turnover of nitrogen-15-labeled  
712 fertilizer in old grassland. *Soil Sci. Soc. Am. J.* **68**, 865–875 (2004).
- 713 12. Habel, J. C. *et al.* European grassland ecosystems: threatened hotspots of biodiversity.  
714 *Biodivers. Conserv.* **10**, 2131–2138 (2013).
- 715 13. Laurent, F. & Ruelland, D. Assessing impacts of alternative land use and agricultural  
716 practices on nitrate pollution at the catchment scale. *J. Hydrol.* **409**, 440–450 (2011).
- 717 14. Bai, Y. & Cotrufo, M. F. Grassland soil carbon sequestration: Current understanding,  
718 challenges, and solutions. *Science* **377**, 603–608 (2022).
- 719 15. Malézieux, E. Designing cropping systems from nature. *Agron. Sustain. Dev.* **32**, 15–29  
720 (2012).
- 721 16. Pulleman, M. M., de Boer, W., Giller, K. E. & Kuiper, T. W. Soil biodiversity and nature-  
722 mimicry in agriculture; the power of metaphor? *Outlook Agric.* **51**, 75–90 (2022).
- 723 17. DuPont, S. T. *et al.* Root traits and soil properties in harvested perennial grassland, annual  
724 wheat, and never-tilled annual wheat. *Plant Soil* **381**, 405–420 (2014).
- 725 18. Joswig, J. S. *et al.* Climatic and soil factors explain the two-dimensional spectrum of  
726 global plant trait variation. *Nat. Ecol. Evol.* **6**, 36–50 (2022).
- 727 19. Delgado-Baquerizo, M. *et al.* A global atlas of the dominant bacteria found in soil. *Science*  
728 **359**, 320–325 (2018).
- 729 20. Crews, T. E. & Peoples, M. B. Can the synchrony of nitrogen supply and crop demand be  
730 improved in legume and fertilizer-based agroecosystems? A Review. *Nutr. Cycl.*  
731 *Agroecosystems* **72**, 101–120 (2005).
- 732 21. Myers, R. J. K., Palm, C. A., Cuevas, E., Gunatilleke, I. U. N. & Brossard, M. The  
733 synchronisation of nutrient mineralisation and plant nutrient demand. in *The biological*  
734 *management of tropical soil fertility* 81–116 (John Wiley & Sons, 1994).

- 735 22. Fowler, D. *et al.* The global nitrogen cycle in the twenty-first century. *Philos. Trans. R.*  
736 *Soc. B Biol. Sci.* **368**, 20130164–20130164 (2013).
- 737 23. Cleveland, C. C. *et al.* Patterns of new versus recycled primary production in the terrestrial  
738 biosphere. *Proc. Natl. Acad. Sci.* **110**, 12733–12737 (2013).
- 739 24. Henneron, L., Kardol, P., Wardle, D. A., Cros, C. & Fontaine, S. Rhizosphere control of  
740 soil nitrogen cycling: a key component of plant economic strategies. *New Phytol.* **228**,  
741 1269–1282 (2020).
- 742 25. Trap, J. *et al.* Slow decomposition of leaf litter from mature *Fagus sylvatica* trees promotes  
743 offspring nitrogen acquisition by interacting with ectomycorrhizal fungi. *J. Ecol.* **105**,  
744 528–539 (2017).
- 745 26. Lama, S. *et al.* Plant diversity influenced gross nitrogen mineralization, microbial  
746 ammonium consumption and gross inorganic N immobilization in a grassland experiment.  
747 *Oecologia* **193**, 731–748 (2020).
- 748 27. Kuzyakov, Y. Review and synthesis of the effects of elevated atmospheric CO<sub>2</sub> on soil  
749 processes: No changes in pools, but increased fluxes and accelerated cycles. *Soil Biol.*  
750 *Biochem.* **128**, 66–78 (2019).
- 751 28. Bernard, L. *et al.* Advancing the mechanistic understanding of the priming effect on soil  
752 organic matter mineralisation. *Funct. Ecol.* **36**, 1355–1377 (2022).
- 753 29. Sulman, B. N. *et al.* Feedbacks between plant N demand and rhizosphere priming depend  
754 on type of mycorrhizal association. *Ecol. Lett.* **20**, 1043–1053 (2017).
- 755 30. Knops, J. M. H., Bradley, K. L. & Wedin, D. A. Mechanisms of plant species impacts on  
756 ecosystem nitrogen cycling. *Ecol. Lett.* **5**, 454–466 (2002).
- 757 31. Balesdent, J., Wagner, G. H. & Mariotti, A. Soil organic matter turnover in long-term field  
758 experiments as revealed by carbon-13 natural abundance. *Soil Sci. Soc. Am. J.* **52**, 118–  
759 124 (1988).

- 760 32. Mooshammer, M. *et al.* Adjustment of microbial nitrogen use efficiency to  
761 carbon:nitrogen imbalances regulates soil nitrogen cycling. *Nat. Commun.* **5**, (2014).
- 762 33. Parton, W. *et al.* Global-scale similarities in nitrogen release patterns during long-term  
763 decomposition. *Science* **315**, 361–364 (2007).
- 764 34. McGill, W. B. Review and classification of ten soil organic matter (SOM) models. in  
765 *Evaluation of Soil Organic Matter Models* 111–132 (Powlson, D.S., Smith, P., Smith,  
766 J.U., 1996).
- 767 35. Berardi, D. *et al.* 21st-century biogeochemical modeling: Challenges for Century-based  
768 models and where do we go from here? *GCB Bioenergy* **12**, 774–788 (2020).
- 769 36. Vitousek, P. & Howarth, R. Nitrogen limitation on land and in the sea - How can it occur.  
770 *Biogeochemistry* **13**, 87–115 (1991).
- 771 37. Hobbie, S. E. Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends*  
772 *Ecol. Evol.* **30**, 357–363 (2015).
- 773 38. Jager, M. M., Richardson, S. J., Bellingham, P. J., Clearwater, M. J. & Laughlin, D. C.  
774 Soil fertility induces coordinated responses of multiple independent functional traits. *J.*  
775 *Ecol.* **103**, 374–385 (2015).
- 776 39. Perring, M. P., Hedin, L. O., Levin, S. A., McGroddy, M. & de Mazancourt, C. Increased  
777 plant growth from nitrogen addition should conserve phosphorus in terrestrial ecosystems.  
778 *Proc. Natl. Acad. Sci.* **6**, 1971–1976 (2008).
- 779 40. Daufresne, T. & Hedin, L. O. Plant coexistence depends on ecosystem nutrient cycles:  
780 extension of the resource-ratio theory. *Proc. Natl. Acad. Sci.* **102**, 9212–9217 (2005).
- 781 41. Schimel, J. P. & Bennett, J. Nitrogen mineralization: challenges of a changing paradigm.  
782 *Ecology* **85**, 591–602 (2004).
- 783 42. Chapman, S. K., Langley, J. A., Hart, S. C. & Koch, G. W. Plants actively control nitrogen  
784 cycling: uncorking the microbial bottleneck. *New Phytol.* **169**, 27–34 (2006).



- 785 43. Trap, J. *et al.* Slow decomposition of leaf litter from mature *Fagus sylvatica* trees promotes  
786 offspring nitrogen acquisition by interacting with ectomycorrhizal fungi. *J. Ecol.* **105**,  
787 528–539 (2017).
- 788 44. Henneron, L., Cros, C., Picon-Cochard, C., Rahimian, V. & Fontaine, S. Plant economic  
789 strategies of grassland species control soil carbon dynamics through rhizodeposition. *J.*  
790 *Ecol.* **108**, 528–545 (2020).
- 791 45. Finlay, R. D. *et al.* Reviews and syntheses: Biological weathering and its consequences at  
792 different spatial levels – from nanoscale to global scale. *Biogeosciences* **17**, 1507–1533  
793 (2020).
- 794 46. Subbarao, G. V. *et al.* Suppression of soil nitrification by plants. *Plant Sci.* **233**, 155–164  
795 (2015).
- 796 47. Daly, A. B. *et al.* A holistic framework integrating plant-microbe-mineral regulation of  
797 soil bioavailable nitrogen. *Biogeochemistry* **154**, 211–229 (2021).
- 798 48. Grandy, A. S. *et al.* The nitrogen gap in soil health concepts and fertility measurements.  
799 *Soil Biol. Biochem.* **175**, 108856 (2022).
- 800 49. Booth, M. S., Stark, J. M. & Rastetter, E. Controls on nitrogen cycling in terrestrial  
801 ecosystems: a synthetic analysis of literature data. *Ecol. Monogr.* **75**, 139–157 (2005).
- 802 50. Grime, J. *Plant strategies, vegetation processes, and ecosystem properties.* (John Wiley  
803 & Sons, 2001).
- 804 51. Barré, P. *et al.* The energetic and chemical signatures of persistent soil organic matter.  
805 *Biogeochemistry* **130**, 1–12 (2016).
- 806 52. Kallenbach, C. M., Frey, S. D. & Grandy, A. S. Direct evidence for microbial-derived soil  
807 organic matter formation and its ecophysiological controls. *Nat. Commun.* **7**, 13630  
808 (2016).

- 809 53. Sutton, R. & Sposito, G. Molecular structure in soil humic substances: the new view.  
810 *Environ. Sci. Technol.* **39**, 9009–9015 (2005).
- 811 54. Basile-Doelsch, I., Balesdent, J. & Pellerin, S. Reviews and syntheses: The mechanisms  
812 underlying carbon storage in soil. *Biogeosciences* **17**, 5223–5242 (2020).
- 813 55. Syers, J. K., Adams, J. A. & Walker, T. W. Accumulation of organic matter in a  
814 chronosequence of soils developed on wind-blown sand in New Zealand. *J. Soil Sci.* **21**,  
815 146–153 (1970).
- 816 56. Balesdent, J. *et al.* Atmosphere–soil carbon transfer as a function of soil depth. *Nature*  
817 **559**, 599–602 (2018).
- 818 57. Lavalley, J. M., Soong, J. L. & Cotrufo, M. F. Conceptualizing soil organic matter into  
819 particulate and mineral-associated forms to address global change in the 21st century.  
820 *Glob. Change Biol.* **26**, 261–273 (2020).
- 821 58. Perveen, N. *et al.* Priming effect and microbial diversity in ecosystem functioning and  
822 response to global change: a modeling approach using the SYMPHONY model. *Glob.*  
823 *Change Biol.* **20**, 1174–1190 (2014).
- 824 59. Malik, A. A., Puissant, J., Goodall, T., Allison, S. D. & Griffiths, R. I. Soil microbial  
825 communities with greater investment in resource acquisition have lower growth yield. *Soil*  
826 *Biol. Biochem.* **132**, 36–39 (2019).
- 827 60. Yu, Z. *et al.* Feedstock determines biochar-induced soil priming effects by stimulating the  
828 activity of specific microorganisms. *Eur. J. Soil Sci.* **69**, 521–534 (2018).
- 829 61. Liu, B. *et al.* Microbial metabolic efficiency and community stability in high and low  
830 fertility soils following wheat residue addition. *Appl. Soil Ecol.* **159**, 103848 (2021).
- 831 62. Sokol, N. W. *et al.* Life and death in the soil microbiome: how ecological processes  
832 influence biogeochemistry. *Nat. Rev. Microbiol.* **20**, 415–430 (2022).

- 833 63. Schimel, J. P. & Hättenschwiler, S. Nitrogen transfer between decomposing leaves of  
834 different N status. *Soil Biol. Biochem.* **39**, 1428–1436 (2007).
- 835 64. Bergmann, J. *et al.* The fungal collaboration gradient dominates the root economics space  
836 in plants. *Sci. Adv.* **6**, eaba3756 (2020).
- 837 65. Korsaeath, A., Molstad, L. & Bakken, L. R. Modelling the competition for nitrogen  
838 between plants and microfora as a function of soil heterogeneity. *Soil Biol.* **12** (2001).
- 839 66. Kuzyakov, Y. & Xu, X. Competition between roots and microorganisms for nitrogen:  
840 mechanisms and ecological relevance. *New Phytol.* **198**, 656–669 (2013).
- 841 67. Jilling, A. *et al.* Minerals in the rhizosphere: overlooked mediators of soil nitrogen  
842 availability to plants and microbes. *Biogeochemistry* **139**, 103–122 (2018).
- 843 68. Fontaine, S. *et al.* Fungi mediate long term sequestration of carbon and nitrogen in soil  
844 through their priming effect. *Soil Biol. Biochem.* **43**, 86–96 (2011).
- 845 69. Terrer, C. *et al.* A trade-off between plant and soil carbon storage under elevated CO<sub>2</sub>.  
846 *Nature* **591**, 599–603 (2021).
- 847 70. Shahzad, T. *et al.* Plant clipping decelerates the mineralization of recalcitrant soil organic  
848 matter under multiple grassland species. *Soil Biol. Biochem.* **51**, 73–80 (2012).
- 849 71. Tang, M., Cheng, W., Zeng, H. & Zhu, B. Light intensity controls rhizosphere respiration  
850 rate and rhizosphere priming effect of soybean and sunflower. *Rhizosphere* **9**, 97–105  
851 (2019).
- 852 72. Yokobe, T., Hyodo, F. & Tokuchi, N. Seasonal effects on microbial community structure  
853 and nitrogen dynamics in temperate forest soil. *Forests* **9**, 153 (2018).
- 854 73. Schmidt, S. K. *et al.* Biogeochemical consequences of rapid microbial turnover and  
855 seasonal succession in soil. *Ecology* **88**, 1379–1385 (2007).

- 856 74. Lambers, H. & Poorter, H. Inherent variation in growth rate between higher plants: a  
857 search for physiological causes and ecological consequences. in *Advances in ecological*  
858 *research* 187–261 (Academic Press, 1992).
- 859 75. Kraus, T. E. C., Dahlgren, R. A. & Zasoski, R. J. Tannins in nutrient dynamics of forest  
860 ecosystems - a review. *Plant Soil* **256**, 41–66 (2003).
- 861 76. Clemmensen, K. E. *et al.* Roots and associated fungi drive long-term carbon sequestration  
862 in boreal forest. *Science* **339**, 1615–1618 (2013).
- 863 77. Adamczyk, B. *et al.* Plant roots increase both decomposition and stable organic matter  
864 formation in boreal forest soil. *Nat. Commun.* **10**, 3982 (2019).
- 865 78. Cotrufo, M. F., Ranalli, M. G., Haddix, M. L., Six, J. & Lugato, E. Soil carbon storage  
866 informed by particulate and mineral-associated organic matter. *Nat. Geosci.* **12**, 989–994  
867 (2019).
- 868 79. Leifeld, J., Zimmermann, M., Fuhrer, J. & Conen, F. Storage and turnover of carbon in  
869 grassland soils along an elevation gradient in the Swiss Alps. *Glob. Change Biol.* **15**, 668–  
870 679 (2009).
- 871 80. Miyauchi, S. *et al.* Large-scale genome sequencing of mycorrhizal fungi provides insights  
872 into the early evolution of symbiotic traits. *Nat. Commun.* **11**, 5125 (2020).
- 873 81. Lu, M. & Hedin, L. O. Global plant–symbiont organization and emergence of  
874 biogeochemical cycles resolved by evolution-based trait modelling. *Nat. Ecol. Evol.* **3**,  
875 239–250 (2019).
- 876 82. Phillips, R. P., Brzostek, E. & Midgley, M. G. The mycorrhizal-associated nutrient  
877 economy: a new framework for predicting carbon-nutrient couplings in temperate forests.  
878 *New Phytol.* **199**, 41–51 (2013).
- 879 83. Smith, G. R. & Wan, J. Resource-ratio theory predicts mycorrhizal control of litter  
880 decomposition. *New Phytol.* **223**, 1595–1606 (2019).

- 881 84. Näsholm, T., Kielland, K. & Ganeteg, U. Uptake of organic nitrogen by plants. *New*  
882 *Phytol.* **182**, 31–48 (2009).
- 883 85. Abbadie, L., Mariotti, A. & Menaut, J. Independence of savanna grasses from soil organic  
884 matter for their nitrogen supply. *Ecology* **73**, 608–613 (1992).
- 885 86. Frey, S. D. Mycorrhizal Fungi as Mediators of Soil Organic Matter Dynamics. *Annu. Rev.*  
886 *Ecol. Evol. Syst.* **50**, 237–259 (2019).
- 887 87. Klumpp, K. *et al.* Grazing triggers soil carbon loss by altering plant roots and their control  
888 on soil microbial community. *J. Ecol.* **97**, 876–885 (2009).
- 889 88. Robson, T. M., Baptist, F., Clément, J.-C. & Lavorel, S. Land use in subalpine grasslands  
890 affects nitrogen cycling via changes in plant community and soil microbial uptake  
891 dynamics: Land-use gradients affect N cycle via plants and microbes. *J. Ecol.* **98**, 62–73  
892 (2010).
- 893 89. Binet, M. N. *et al.* Effects of mowing on fungal endophytes and arbuscular mycorrhizal  
894 fungi in subalpine grasslands. *Fungal Ecol.* **6**, 248–255 (2013).
- 895 90. Udvardi, M. & Poole, P. S. Transport and Metabolism in Legume-Rhizobia Symbioses.  
896 *Annu. Rev. Plant Biol.* **64**, 781–805 (2013).
- 897 91. Lawn, R. J. & Brun, W. A. Symbiotic nitrogen fixation in soybeans. I. Effect of  
898 photosynthetic source-sink manipulations. *Crop Sci.* **14**, 11–16 (1974).
- 899 92. Landeweert, R., Hoffland, E., Finlay, R. D., Kuyper, T. W. & van Breemen, N. Linking  
900 plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. *Trends Ecol.*  
901 *Evol.* **16**, 248–254 (2001).
- 902 93. Selosse, M.-A. & Rousset, F. The Plant-Fungal Marketplace. *Science* **333**, 828–829  
903 (2011).
- 904 94. Elser, J., Dobberfuhl, D. R., MacKay, N. A. & Schampel, J. H. Organism size, life history,  
905 and N:P stoichiometry. *BioScience* **46**, 674–684 (1996).

- 906 95. Nasto, M. K., Winter, K., Turner, B. L. & Cleveland, C. C. Nutrient acquisition strategies  
907 augment growth in tropical N<sub>2</sub>-fixing trees in nutrient-poor soil and under elevated CO<sub>2</sub>.  
908 *Ecology* **100**, e02646 (2019).
- 909 96. Treseder, K. K. & Vitousek, P. M. Effects of Soil Nutrient Availability on Investment in  
910 Acquisition of N and P in Hawaiian Rain Forests. *Ecology* **82**, 946–954 (2001).
- 911 97. Wipf, D., Krajinski, F., Tuinen, D. van, Recorbet, G. & Courty, P.-E. Trading on the  
912 arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks. *New*  
913 *Phytol.* **223**, 1127–1142 (2019).
- 914 98. Beiler, K. J., Durall, D. M., Simard, S. W., Maxwell, S. A. & Kretzer, A. M. Architecture  
915 of the wood-wide web: Rhizopogon spp. genets link multiple Douglas-fir cohorts. *New*  
916 *Phytol.* **185**, 543–553 (2010).
- 917 99. Fernandez, M. *et al.* Plant N economics and the extended phenotype: Integrating the  
918 functional traits of plants and associated soil biota into plant–plant interactions. *J. Ecol.*  
919 **110**, 2015–2032 (2022).
- 920 100. Kögel-Knabner, I. & Amelung, W. Soil organic matter in major pedogenic soil groups.  
921 *Geoderma* **384**, 114785 (2021).
- 922 101. Lange, M. *et al.* Plant diversity increases soil microbial activity and soil carbon storage.  
923 *Nat. Commun.* **6**, 6707 (2015).
- 924 102. Scherer-Lorenzen, M., Palmborg, C., Prinz, A. & Schulze, E.-D. The role of plant diversity  
925 and composition for nitrate leaching in grasslands. *Ecology* **84**, 1539–1552 (2003).
- 926 103. Hector, A. Diversity favours productivity. *Nature* **472**, 45–46 (2011).
- 927 104. Wagg, C., Bender, S. F., Widmer, F. & van der Heijden, M. G. A. Soil biodiversity and  
928 soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad.*  
929 *Sci.* **111**, 5266–5270 (2014).

- 930 105. Oelmann, Y. *et al.* Above- and belowground biodiversity jointly tighten the P cycle in  
931 agricultural grasslands. *Nat. Commun.* **12**, 4431 (2021).
- 932 106. Maestre, F. T. *et al.* Plant species richness and ecosystem multifunctionality in global  
933 drylands. *Science* **335**, 214–218 (2012).
- 934 107. Williams, H. T. P. & Lenton, T. M. The Flask model: emergence of nutrient-recycling  
935 microbial ecosystems and their disruption by environment-altering ‘rebel’ organisms.  
936 *Oikos* **116**, 1087–1105 (2007).
- 937 108. Gross, N., Suding, K. N., Lavorel, S. & Roumet, C. Complementarity as a mechanism of  
938 coexistence between functional groups of grasses. *J. Ecol.* **95**, 1296–1305 (2007).
- 939 109. Homulle, Z., George, T. S. & Karley, A. J. Root traits with team benefits: understanding  
940 belowground interactions in intercropping systems. *Plant Soil* **471**, 1–26 (2022).
- 941 110. Roscher, C. *et al.* Using Plant Functional Traits to Explain Diversity–Productivity  
942 Relationships. *PLoS ONE* **7**, e36760 (2012).
- 943 111. Valencia, E. *et al.* Synchrony matters more than species richness in plant community  
944 stability at a global scale. *Proc. Natl. Acad. Sci.* **117**, 24345–24351 (2020).
- 945 112. García-Palacios, P., Gross, N., Gaitán, J. & Maestre, F. T. Climate mediates the  
946 biodiversity–ecosystem stability relationship globally. *Proc. Natl. Acad. Sci.* **115**, 8400–  
947 8405 (2018).
- 948 113. Foster, K. R. & Kokko, H. Cheating can stabilize cooperation in mutualisms. *Proc. R. Soc.*  
949 *B Biol. Sci.* **273**, 2233–2239 (2006).
- 950 114. Bull, J. J., Molineux, I. J. & Rice, W. R. Selection of Benevolence in a Host–Parasite  
951 System. *Evolution* **45**, 875–882 (1991).
- 952 115. Kiers, E. T. & Denison, R. F. Sanctions, cooperation, and the stability of plant–rhizosphere  
953 mutualisms. *Annu. Rev. Ecol. Evol. Syst.* **39**, 215–236 (2008).

- 954 116. Augustine, D. J. & McNaughton, S. J. Temporal asynchrony in soil nutrient dynamics and  
955 plant production in a semiarid ecosystem. *Ecosystems* **7**, (2004).
- 956 117. Xi, N., Carrère, P. & Bloor, J. M. G. Nitrogen form and spatial pattern promote asynchrony  
957 in plant and soil responses to nitrogen inputs in a temperate grassland. *Soil Biol. Biochem.*  
958 **71**, 40–47 (2014).
- 959 118. Lekberg, Y. *et al.* Relative importance of competition and plant–soil feedback, their  
960 synergy, context dependency and implications for coexistence. *Ecol. Lett.* **21**, 1268–1281  
961 (2018).
- 962 119. Hermans, C., Hammond, J. P., White, P. J. & Verbruggen, N. How do plants respond to  
963 nutrient shortage by biomass allocation? *Trends Plant Sci.* **11**, 610–617 (2006).
- 964 120. Maier, C. A., Palmroth, S. & Ward, E. Short-term effects of fertilization on photosynthesis  
965 and leaf morphology of field-grown loblolly pine following long-term exposure to  
966 elevated CO<sub>2</sub> concentration. *Tree Physiol.* **28**, 597–606 (2008).
- 967 121. Meier, I. C. *et al.* Root exudation of mature beech forests across a nutrient availability  
968 gradient: the role of root morphology and fungal activity. *New Phytol.* **226**, 583–594  
969 (2020).
- 970 122. Nacry, P., Bouguyon, E. & Gojon, A. Nitrogen acquisition by roots: physiological and  
971 developmental mechanisms ensuring plant adaptation to a fluctuating resource. *Plant Soil*  
972 **370**, 1–29 (2013).
- 973 123. Tripler, C., Canham, C., Inouye, R. & Schnurr, J. Soil nitrogen availability, plant luxury  
974 consumption, and herbivory by white-tailed deer. *Oecologia* **133**, 517–524 (2002).
- 975 124. Millard, P. & Grelet, G. -a. Nitrogen storage and remobilization by trees: ecophysiological  
976 relevance in a changing world. *Tree Physiol.* **30**, 1083–1095 (2010).
- 977 125. FAO - Global Soil Partnership. Soil fertility.



- 978 126. Hansson, K. *et al.* Chemical fertility of forest ecosystems. Part 1: Common soil chemical  
979 analyses were poor predictors of stand productivity across a wide range of acidic forest  
980 soils. *For. Ecol. Manag.* **461**, 117843 (2020).
- 981 127. Legout, A. *et al.* Chemical fertility of forest ecosystems. Part 2: Towards redefining the  
982 concept by untangling the role of the different components of biogeochemical cycling.  
983 *For. Ecol. Manag.* **461**, 117844 (2020).
- 984 128. Gregorich, E., Rochette, P., Vandenbygaart, A. & Angers, D. Greenhouse gas  
985 contributions of agricultural soils and potential mitigation practices in Eastern Canada.  
986 *Soil Tillage Res.* **83**, 53–72 (2005).
- 987 129. Sauvadet, M. *et al.* Agroecosystem diversification with legumes or non-legumes improves  
988 differently soil fertility according to soil type. *Sci. Total Environ.* **795**, 148934 (2021).
- 989 130. Waithaisong, K. *et al.* Introducing N<sub>2</sub>-fixing trees (*Acacia mangium*) in eucalypt  
990 plantations rapidly modifies the pools of organic P and low molecular weight organic acids  
991 in tropical soils. *Sci. Total Environ.* **742**, 140535 (2020).
- 992 131. Milla, R., Osborne, C. P., Turcotte, M. M. & Violle, C. Plant domestication through an  
993 ecological lens. *Trends Ecol. Evol.* **30**, 463–469 (2015).
- 994 132. Tonitto, C., David, M. B. & Drinkwater, L. E. Replacing bare fallows with cover crops in  
995 fertilizer-intensive cropping systems: A meta-analysis of crop yield and N dynamics.  
996 *Agric. Ecosyst. Environ.* **112**, 58–72 (2006).
- 997 133. Jian, J., Du, X., Reiter, M. S. & Stewart, R. D. A meta-analysis of global cropland soil  
998 carbon changes due to cover cropping. *Soil Biol. Biochem.* **143**, 107735 (2020).
- 999 134. Burke, I. C. *et al.* Texture, Climate, and Cultivation Effects on Soil Organic Matter  
1000 Content in U.S. Grassland Soils. *Soil Sci. Soc. Am. J.* **53**, 800–805 (1989).
- 1001 135. Rosa García, R. *et al.* Grazing land management and biodiversity in the Atlantic European  
1002 heathlands: a review. *Agrofor. Syst.* **87**, 19–43 (2013).

- 1003 136. Gross, N. *et al.* Functional trait diversity maximizes ecosystem multifunctionality. *Nat.*  
1004 *Ecol. Amp Evol.* **1**, 0132 (2017).
- 1005 137. Yu, Y., Stomph, T.-J., Makowski, D. & van der Werf, W. Temporal niche differentiation  
1006 increases the land equivalent ratio of annual intercrops: A meta-analysis. *Field Crops Res.*  
1007 **184**, 133–144 (2015).
- 1008 138. Tang, X. *et al.* Intercropping legumes and cereals increases phosphorus use efficiency; a  
1009 meta-analysis. *Plant Soil* **460**, 89–104 (2021).
- 1010 139. Xu, Z. *et al.* Intercropping maize and soybean increases efficiency of land and fertilizer  
1011 nitrogen use; A meta-analysis. *Field Crops Res.* **246**, 107661 (2020).
- 1012 140. Li, X.-F. *et al.* Long-term increased grain yield and soil fertility from intercropping. *Nat.*  
1013 *Sustain.* **4**, 943–950 (2021).
- 1014 141. Fan, Z. *et al.* Synchrony of nitrogen supply and crop demand are driven via high maize  
1015 density in maize/pea strip intercropping. *Sci. Rep.* **9**, 10954 (2019).
- 1016 142. Plaza-Bonilla, D., Nolot, J.-M., Raffaillac, D. & Justes, E. Innovative cropping systems to  
1017 reduce N inputs and maintain wheat yields by inserting grain legumes and cover crops in  
1018 southwestern France. *Eur. J. Agron.* **82**, 331–341 (2017).
- 1019 143. Debaeke, Ph. *et al.* Grain nitrogen content of winter bread wheat (*Triticum aestivum* L.)  
1020 as related to crop management and to the previous crop. *Eur. J. Agron.* **5**, 273–286 (1996).
- 1021 144. Zhang, X. *et al.* Quantification of global and national nitrogen budgets for crop  
1022 production. *Nat. Food* **2**, 529–540 (2021).
- 1023 145. Farm to Fork Strategy. For a fair, healthy and environmentally-friendly food system.  
1024 (2020).
- 1025 146. Stokstad, E. Can farmers fight climate change? New U.S. law gives them billions to try.  
1026 (2022) doi:10.1126/science.ade4432.

- 1027 147. Carlsson, G. & Huss-Danell, K. Nitrogen fixation in perennial forage legumes in the field.  
1028 **253**, 353–372 (2003).
- 1029 148. Rillig, M. C. *et al.* Why farmers should manage the arbuscular mycorrhizal symbiosis.  
1030 *New Phytol.* **222**, 1171–1175 (2019).
- 1031 149. Ryan, M. H. & Graham, J. H. Little evidence that farmers should consider abundance or  
1032 diversity of arbuscular mycorrhizal fungi when managing crops. *New Phytol.* **220**, 1092–  
1033 1107 (2018).
- 1034 150. Barot, S. *et al.* Designing mixtures of varieties for multifunctional agriculture with the  
1035 help of ecology. A review. *Agron. Sustain. Dev.* **37**, (2017).
- 1036 151. Litrico, I. & Violle, C. Diversity in Plant Breeding: A New Conceptual Framework.  
1037 *Trends Plant Sci.* **20**, 604–613 (2015).

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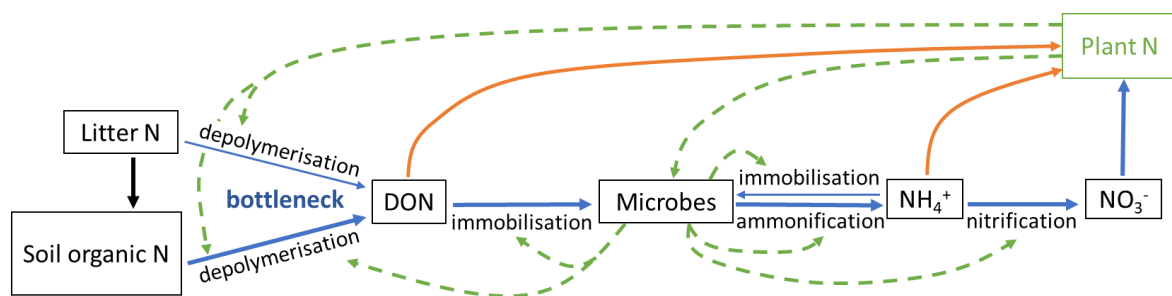
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**Supplementary 1.** The dominant paradigm of nutrient (N taken as a model here) cycling, up the end of the 2000's.

The mineralization of soil organic N has long been considered as the major bottleneck restricting supply of N to plants (blue arrows in the Figure below, depolymerization being considered the limiting step in the mineralization process). Indeed, a large part of N present within plant litter is not released as mineral N during decomposition but incorporated and maintained into soil organic N for several decades to centuries<sup>30-33</sup>. Moreover, microbial mineralization of soil organic N was conventionally viewed and modelled as a process whose velocity is controlled by soil N content and environmental factors ( $d/dt N = -k.N$ ), and not by the plant<sup>34,35</sup>. According to this paradigm, the soil supply of mineral N is decoupled from the plant demand and is the limiting process for plant growth in most ecosystems (soil supply  $\ll$  plant demand)<sup>36</sup>. This view was so pervasive that it continues to shape current-day vocabulary, with the concept of soil fertility still used to explain differences in plant communities and primary production between environments (e.g. plants from nutrient-rich versus nutrient-poor soils)<sup>24,37,38</sup>. This view largely influences the representation of the nutrient cycle in models in ecology and biogeochemistry<sup>35,39,40</sup>.

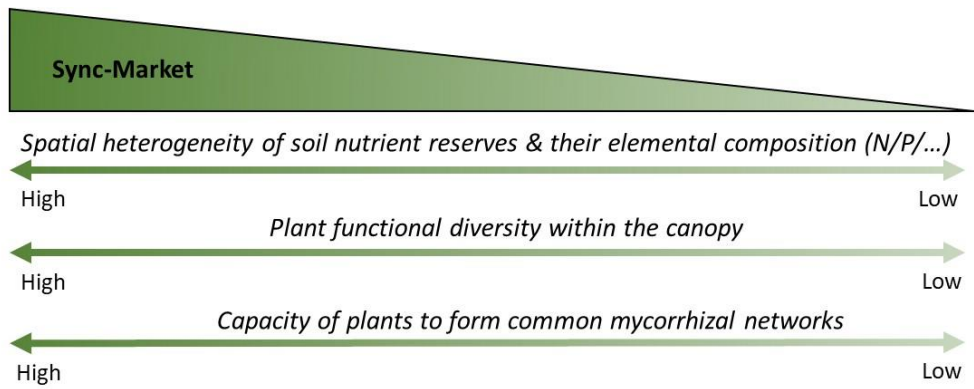


Although some support for these ideas can be found in cultivated soils<sup>41</sup>, research over these last two decades has deeply modified our knowledge on nutrient cycling, especially in natural ecosystems. A first revision of the classical paradigm was made in 2000's to include the ability of some plants and their mycorrhizal associates to uptake dissolved organic N and to compete for mineral N with microbes<sup>41,42</sup> – represented by orange arrows in the figure. There is now a growing body of studies demonstrating the ability of plants to control most soil N fluxes<sup>43-46</sup> – represented by green dashed arrows in the figure. This calls for an overhaul of our vision of nutrient cycles<sup>47,48</sup>.

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**Supplementary 2.** Expected contribution to ecosystem functioning of the synchrony system based on a common nutrient market (Sync-Market) in relation to pedoclimatic contexts and plant functional diversity.



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