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

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Glossary

Stoichiometric constraints refer to the fact that living organisms needs 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).

Abstract

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

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

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

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

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

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

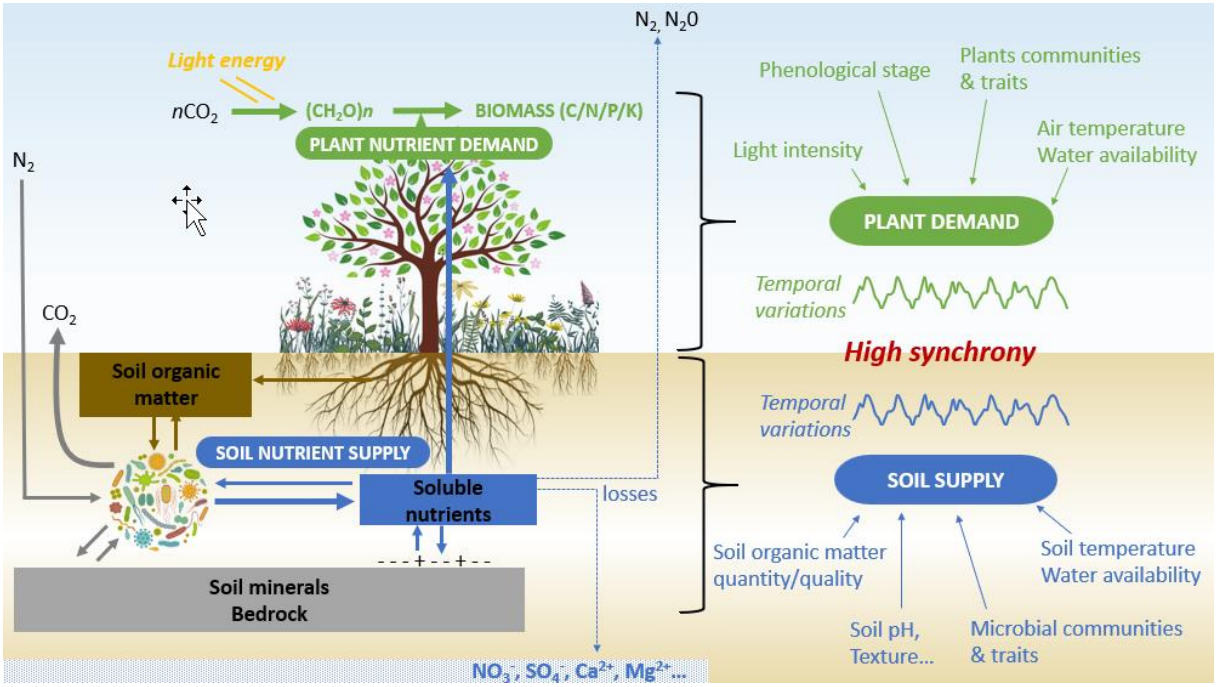

Figure 1. *The high level of synchrony between plant demand and soil supply characterizing natural ecosystems requires the coordination of numerous soil and plant functions. Plant demand corresponds to the amount of nutrients needed to convert the photosynthesis-derived carbon in biomass. It varies both over time and across species depending on multiple functions such as photosynthesis, organ formation and phenology, and factors such as the stoichiometric constraints of species and light intensity. Soil supply refers to the amount of soluble nutrients (mineral and organic), mainly released by soil biota comprising microbes and fauna. It varies over time and soil space depending on the prevalence of the various functions catalyzed by soil biota. Some functions increase soil nutrient supply (decomposition of soil organic matter -SOM-, biological N_2 fixation and nutrient release from minerals), while others decrease it (nutrient immobilization in microbial biomass and soil organic matter). A fraction of soluble nutrients can also be adsorbed as ions on the electrically charged surfaces of soil minerals but it remains available for plant uptake. The factors controlling soil supply are mostly different from those controlling plant demand, raising the issue of the plant demand-soil supply synchrony.*

Two synchrony systems based on soil organic nutrient reserves

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

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

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

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

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

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

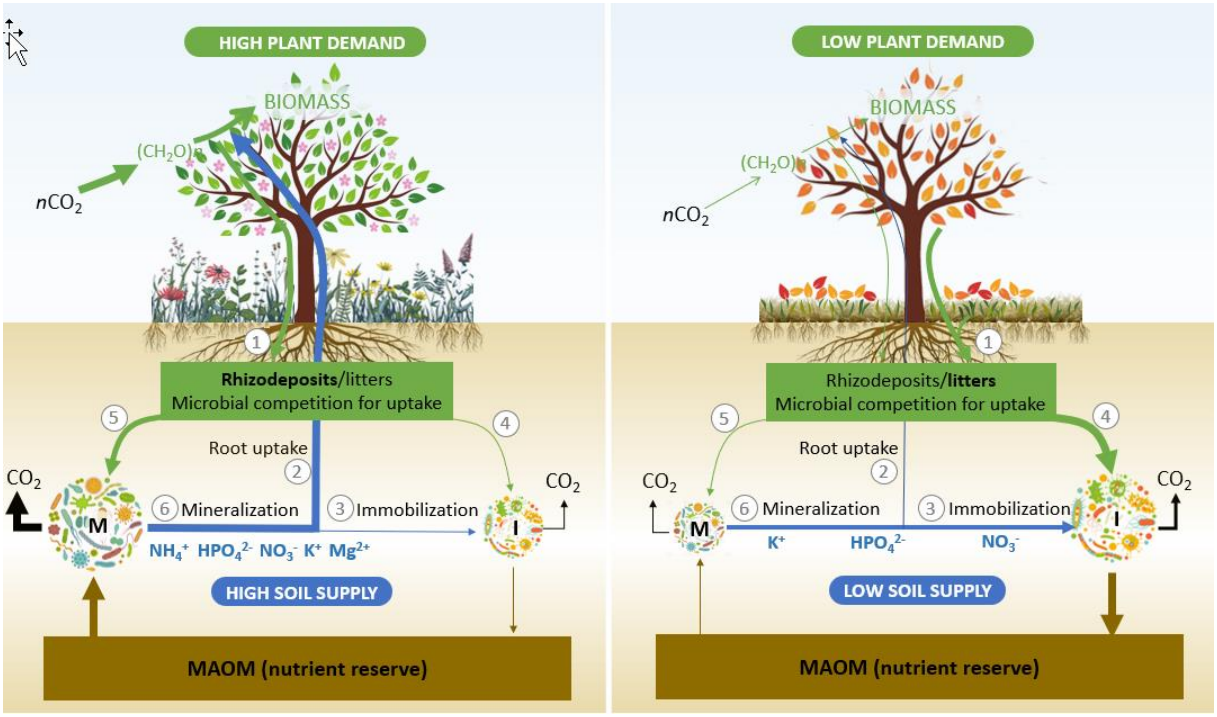

Figure 2. *Synchrony between plant nutrient demand and soil supply of mineral nutrients through mineralization of mineral-associated organic matter (Sync-MAOM). This example describes the seasonal change in plant demand and soil supply. The numbers illustrate the chronology of events in response to an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

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

Numerous studies support the existence of this synchrony system. A common garden experiment comparing 12 grassland plant species with contrasted photosynthetic activities reported that gross N mineralization (soil supply) adjusted to the demand of each of these species[44]. Recent syntheses showed that enhanced plant photosynthesis and plant demand for nutrients under elevated CO_2 induce both an increase in gross N mineralization[27] and a decrease in soil organic matter stock[69]. Moreover, a decrease in plant photosynthesis in response to plant shading/cutting induces a reduction in soil organic matter mineralization (soil supply) within 24 hours[70,71], supporting the idea of a high-speed synchrony. In many ecosystems, the mineralization to immobilization ratio changes during the season in line with changes in plant demand; immobilization dominates during the winter (low demand) whereas mineralization dominates during spring-summer (high demand)[72,73]. These functional changes have been shown to be correlated to changes in microbial community structure[72,73] supporting the idea of a synchrony driven by plant-microbes interactions.

Synchrony based on free organic matter (Sync-FreeOM)

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

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

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

Conservative herbaceous plants have been suggested to modulate nutrient fluxes by shaping the activity of free-living decomposers through their associations with endo-mycorrhizal fungi and endophytes[86,89].

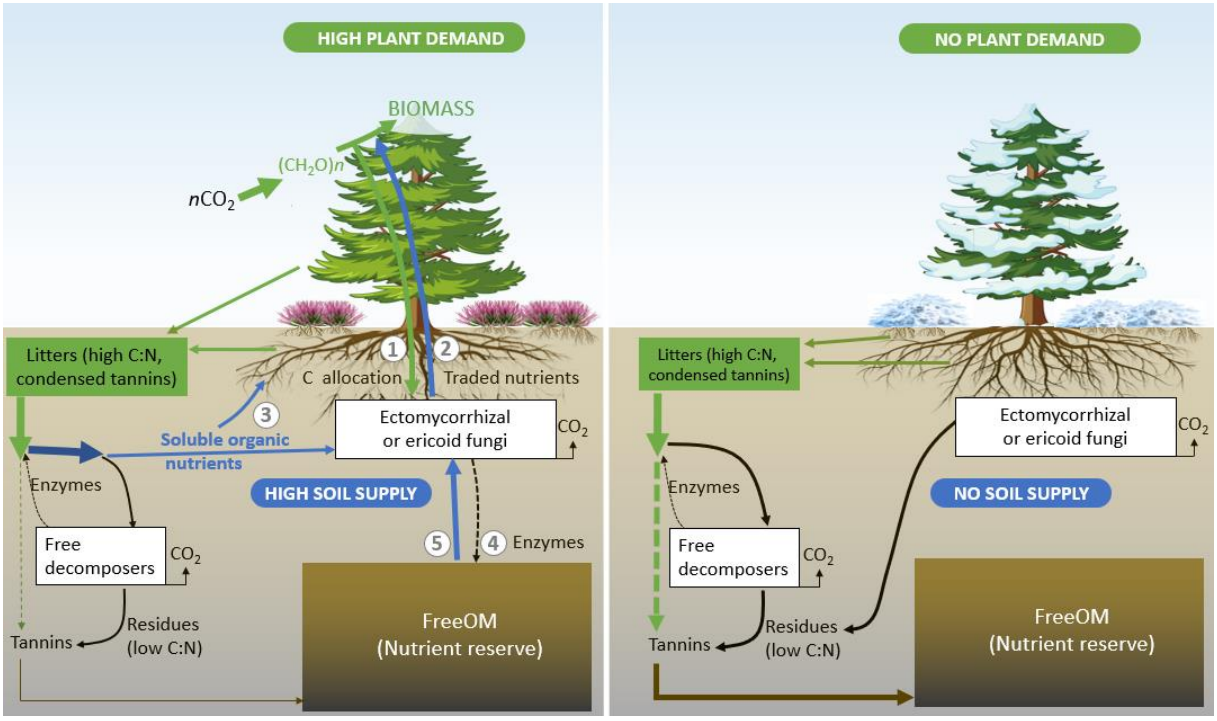

Figure 3. *Synchrony between plant nutrient demand and soil supply of dissolved organic nutrient through depolymerization of free organic matter (Sync-FreeOM). This example illustrates the case of conservative woody plants associated with ectomycorrhizal or ericoid fungi. We describe the response of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

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

Aside from soil organic reserves, plants can access several other sources of nutrients for which supply-demand regulations can occur. A classic example is N uptake from the atmosphere by legumes which depends on the rapid transfer of photosynthates to root nodules where Rhizobia carry out the costly process of N_2 fixation[90]. Given the dependency of nodules to plant C, conditions enhancing photosynthesis (plant demand) such as the increase in light intensity or atmospheric CO_2 usually lead to an increase in N_2 fixation[91]. Conversely, factors reducing photosynthesis reduce N_2 fixation[91]. Photosynthesis modulates not only nodule number and growth, but also the activity of nitrogenase[90], leading to a fast (hours) synchrony between plant demand and microbial N_2 fixation.

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

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

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

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

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

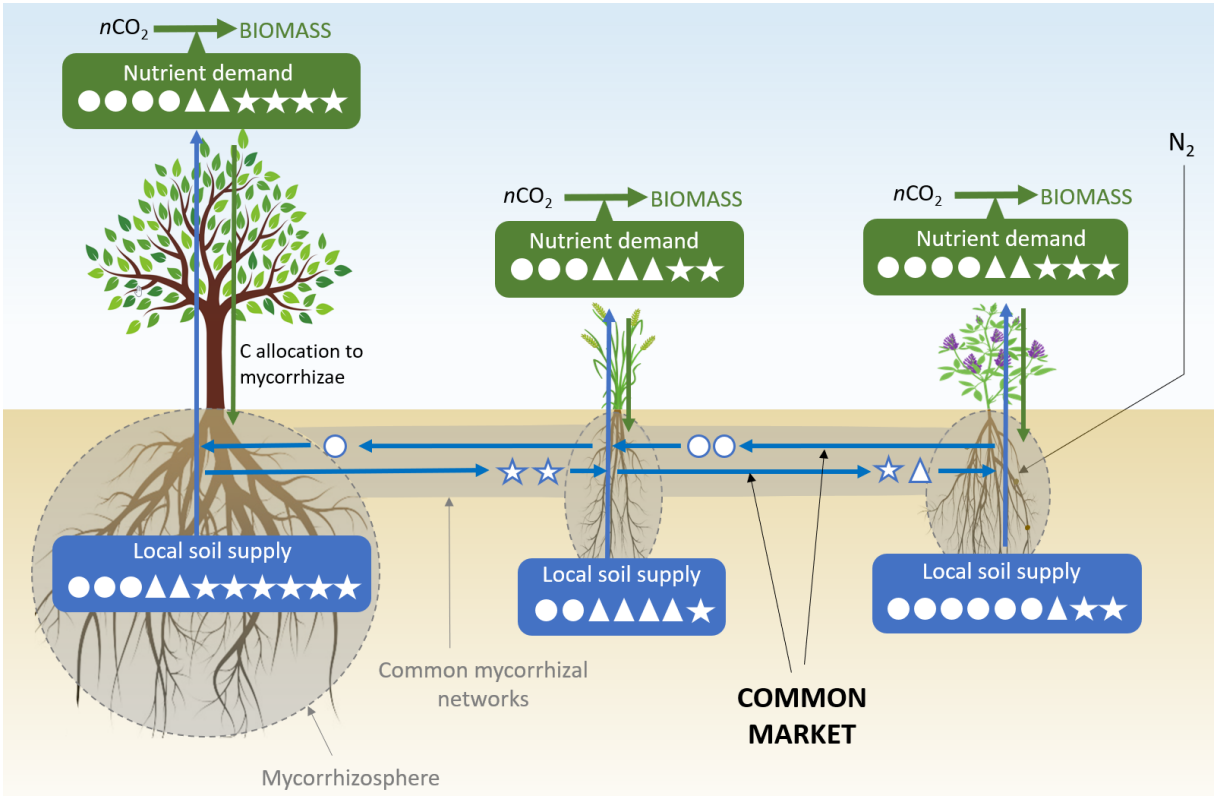

Figure 4. *Synchrony between plant demand and soil supply on multiple nutrients can be facilitated by a common nutrient market supported by mycorrhizal networks. The symbols (triangle, circle, star) illustrate different nutrients. The local soil supply represents the amount of soluble nutrients delivered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

Influence of abiotic and biotic factors on synchrony

Pedoclimatic context and plant functional types

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

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

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

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

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

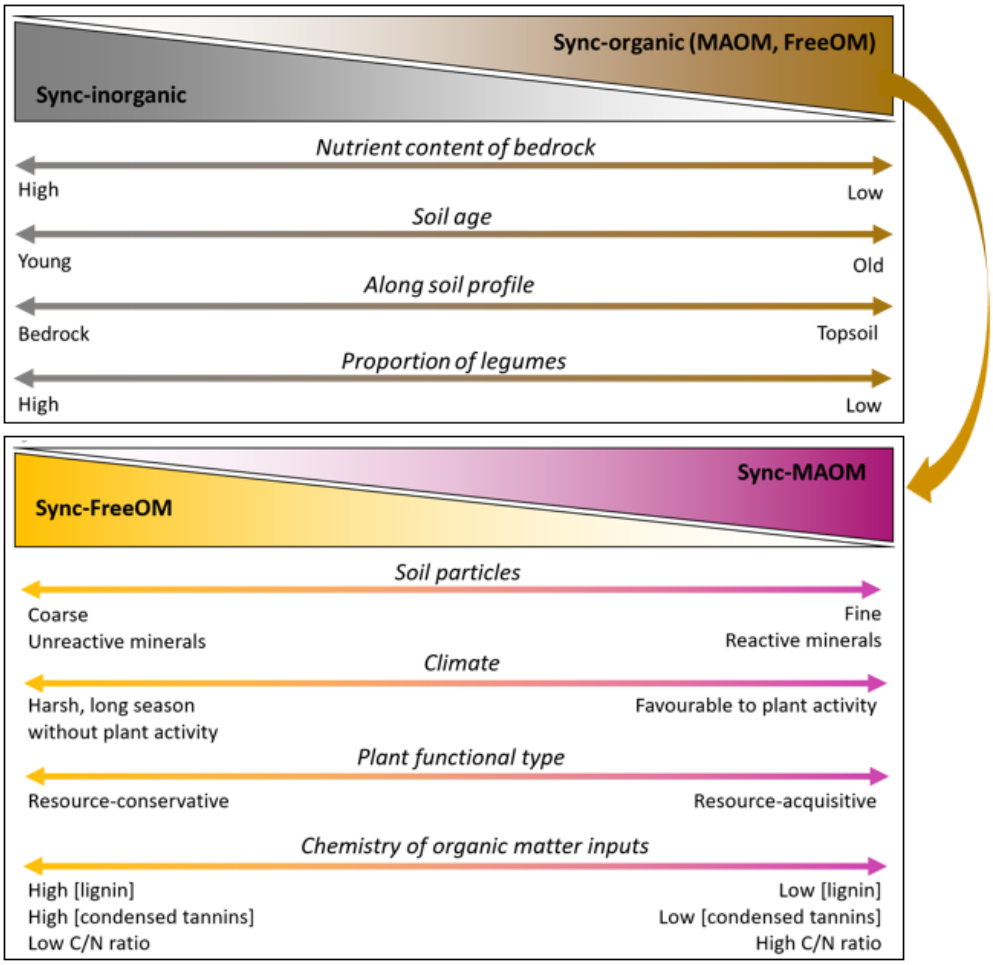

Figure 5. *Relative importance for ecosystem functioning of the synchrony systems based on nutrients retrieved from atmosphere and soil minerals (Sync-Inorganic) and from soil organic nutrient (Sync-Organic) in relation to pedoclimatic contexts and plant functional type. The Sync-Organic is composed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

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

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

Biodiversity: a key asset promoting synchrony

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

Biodiversity promotes synchrony through the functional complementarity of organisms. Synchrony systems clearly show an ecological division of labor[103] that may emerge from evolutionary processes[81,107]: each function of the system is carried out by specific groups of biota such as organic nutrient reserve formation (I-microbes, conservative plants) and decomposition (M-microbes, ectomycorrhizal & ericoid fungi), N_2 fixation (Rhizobium, legumes) etc. The maintenance of these functional groups is fundamental for the synchrony generated by each of these systems. Moreover, co-occurrence of plant species with different nutrient strategies[108] (e.g., legumes/non-legumes, acquisitive/conservative, P-mobilizing-plants) is also expected to induce different synchrony systems. The proximity of roots of neighboring plants with different strategies facilitates nutrient transfer from plant to plant for their mutual benefit in terms of nutrition and growth[109]. This nutrient transfer takes place at different time scales (hours to years) according to the processes involved[109], including nutrient exchanges across mycorrhizal networks (Sync-Market), direct transfer of root exudates and decomposition of plant materials. The exchange of N and P between legumes and P-mobilizing plants is a classic example of plant-plant interactions which improve overall plant-soil synchrony. More broadly, a high functional diversity of microbes and plants promotes both the existence of - and the interaction between - synchrony systems with complementary roles in ecosystems. Sync-Inorganic brings nutrients from atmosphere and bedrock to the ecosystem while sync-MAOM and sync-FreeOM accumulate these nutrients in organic reserves, limiting nutrient loss and allowing nutrient recycling when needed by plants. These synchrony systems create major nutrient sources for plants while Sync-Market helps to balance the proportion of different nutrients supplied in relation to the multiple element requirement of plants.

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

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

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

Plant plasticity and adaptations to unbalanced soil supply

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

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

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

Implications for agrosystems

Fertility: an emerging property of plant-soil interactions

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

Managing synchrony to ensure both productivity and sustainability

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

of legumes as green manure in rotation can lead to N losses as high as mineral fertilizers[20], though this practice has the advantage of reducing the use of mineral N fertilizers whose production generates greenhouse gases. Moreover, management practices often appear to involve trade-offs or offsets between expected outcomes, for instance between yield and greenhouse gas emissions, between soil C storage and emission of N_2O[128]. Focusing on plant-soil synchrony can help address these difficulties by guiding the changes to be made in agrosystems to make them sustainably productive; understanding when and how synchrony is enhanced is needed for management decisions. Analyzing the four synchrony systems, we have identified the types of synchrony systems to be promoted according to the pedoclimatic context (Figure 5 & supplementary material 2), and suggest combinations of practices that could install them in cropping systems (Figure 6).

In young soils (e.g., Andosols), where inorganic reserves are high and organic reserves can be low (Figure 5), management options should give greater importance to Sync-inorganic, for example, by incorporating a high proportion of legumes and plant species mobilizing nutrients from soil minerals through their rhizodeposition and association with mycorrhizae. With organic nutrient accumulation and depletion of inorganic nutrient reserves as soils evolve, agricultural practices should promote Sync-organic, for example by introducing species with high rhizodeposition of energy-rich C for microbes (MAOM-sync; Figure 6). In the longer-term, the inorganic and organic reserves of some rock-originated nutrients (e.g., P) can limit synchrony in the topsoil of highly-weathered soils (e.g., Ferralsols). In these soils, synchrony can be enhanced by including deep-rooting species capable of mobilizing the nutrients from bedrock and redistribute them to the topsoil (Figure 6). Recent studies have shown the possibility of stimulating different nutrient acquisition pathways (organic-P mineralization, inorganic-P dissolution, N_2 fixation) through the selection of specific plant traits (N_2-fixation efficiency, but also types of exudates)[129,130]. It has also been reported that the level of soil weathering determines the type of diversification and nutrient acquisition strategies able to enhance ecosystem productivity and sustainability[130]. In this study, legumes increased biomass production (+18%) in Andosols but not in Ferralsols, while soil-P-mobilizing tree species increased biomass production(+39%) and soil C stock(+26%) in Ferralsols but not in Andosols[130].

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

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

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

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

Significant amounts of nutrients leave croplands in harvested products and losses through leaching and denitrification (e.g., export of on average 120 kg N and 30 kg P per hectare for a wheat grain harvest)[143]. These exports often lead to either a rapid decrease of available nutrients and production in soils of developing countries, or the application of mineral fertilizer to maintain a high level of production such as in intensive cropping systems. It has also been reported that approximately 50% of the applied N fertilizer is lost in the environment[20,144]. Several regions of the world have adopted policies to reduce mineral fertilizer applications as such applications seriously harm climate and ecosystem health, and rely on depleting mineral deposits[145,146]. Our review suggests that practices promoting synchrony can help to decrease mineral fertilizer amounts while maintaining, or even increasing, production. This may result from 1) a reduction of nutrient losses (70% for N) enhancing nutrient use efficiency[132], 2) a better use of water and light resources (+22% [137]) by reducing the nutrient limitation of plant growth and periods of bare soil, and 3) the mobilization of nutrients from natural reserves (atmospheric N_2 and soil minerals), which can represent several hundred kilograms per hectare and per year for N[147]. Managing synchrony may therefore have important implications for the economic and environmental outcomes of modern agriculture. Nevertheless, it is important to keep in mind that the reservoir of rock-derived nutrients has limits, especially in old highly-

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

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

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

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_2 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_2 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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Figure 6. *Combinations of agricultural practices promoting synchrony between soil nutrient supply and plant nutrient demand through the four major systems of coordination of plant-soil functions synthetized in this framework (Sync-MAOM, Sync-FreeOM, Sync-Inorganic, Sync-Market). Some practices can enhance the overall synchrony in agrosystems by improving the efficiency of each system of coordination and by combining several systems of coordination. Photographs illustrate examples of practices 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 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 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 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 residues enriched with microbial compounds (©INRAE/MAITRE Christophe); (f) extensive grazing of heathlands (©SHUTTERSTOCK); (g) the "bread-tree" Artocarpus altilis (©SHUTTERSTOCK) and (h) the cereal Thinopyrum intermedium (©ISARA/DUCHENE Olivier) are two examples of perennial plants that can be used as source of carbohydrates and proteins; (i) agroforestry associating a barley crop with a walnut tree plantation (©INRAE/NICOLAS Bertrand); (j) association of banana, pineapple and pepper plantations (©A2C/THOMAS Frédéric); (k) wheat cultivation on a living clover cover (©ISARA/DUCHENE Olivier): (l) cover cropping with mustard (©INRAE/WEBER Jean).*

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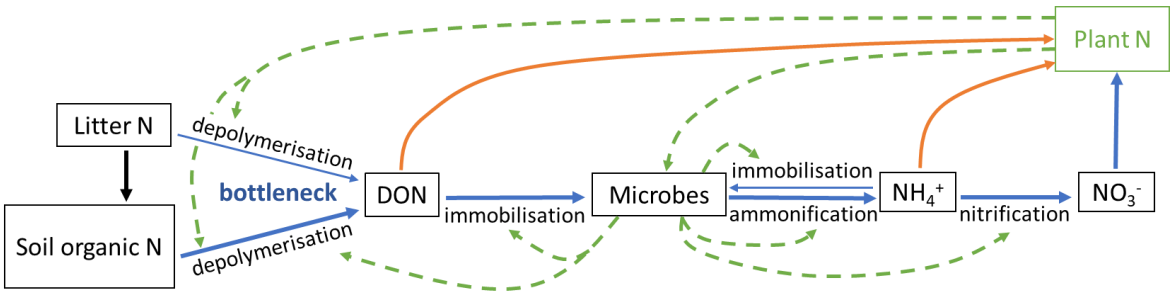
Supplementary 1. The dominant paradigm of nutrient (N taken as a model here) cycling, up the end of the 2000's.

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[30–33]. 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[34,35]. 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 << plant demand)[36]. 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)[24,37,38]. This view largely influences the representation of the nutrient cycle in models in ecology and biogeochemistry[35,39,40].



Although some support for these ideas can be found in cultivated soils[41], 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[41,42] – 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 [43–46] – represented by green dashed arrows in the figure. This calls for an overhaul of our vision of nutrient cycles[47,48].

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.