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Un(der)explored links between plant diversity and particulate and mineral-associated organic matter in soil

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Plant diversity can alter soil carbon stocks, but the effects are difficult to predict due to the multitude of mechanisms involved. We propose that these mechanisms and their outcomes can be better understood by testing how plant diversity affects particulate organic matter (POM) and mineral-associated organic matter (MAOM) depending on whether MAOM storage is "saturated" and the total soil organic matter pool is limited by plant inputs. Such context-dependency of plant-diversity effects on POM, MAOM, and total soil organic matter helps explain inconsistencies in plant-diversity–soil-carbon relationships across studies. Further illumination of this context-dependency is required to better predict consequences of biodiversity losses and gains, and manage ecosystems as carbon sinks and nutrient stores.

Recent studies have indicated that the amount of organic carbon (C) stored in soils can be sensitive to plant diversity[1–5]. Thus, widespread biodiversity losses[6,7] can be a threat to the diverse soil functions associated with soil organic C, and restoration or enhancement of plant diversity (*e.g.*, diversified crop rotation and reforestation) could increase soil C storage and help mitigate climate change[8–11]. The effectiveness of such management strategies, however, is hampered by incomplete knowledge of the processes by which plant diversity affects soil C storage. It remains especially unclear how plant diversity relates to the C that is stored in particulate organic matter (POM) and mineral-associated organic matter (MAOM), which tend to have different sources, formation pathways, residence times, and responses to land management[12–18]. We offer two explanations for the existence and persistence of this knowledge gap: (i) to the best of our knowledge, few of the hundreds of experimental studies of plant diversity gradients have measured POM and MAOM[19–21], and (ii) although conceptual frameworks of POM and MAOM have been developed and revised, none of these prior efforts have focused on the role of plant diversity.

Here, we consider how plant diversity affects the formation of POM and MAOM via the quantity of inputs of plant-derived C to soil[22–24] and transformations of organic matter in soil, as mediated by the quality of organic matter inputs and the composition and metabolic activities of bacteria, fungi, and animals in soil[25–35]. For example, effects of plant diversity on plant litter quality[36] and soil microclimate[31] could interact to determine conditions for microbial growth and utilization of the litter[37]. This, in turn, could affect the decomposition or accumulation of POM and the formation of microbial residues in MAOM. Likewise, plant diversity-related changes in rhizodeposition[28] could affect the generation of dissolved organic matter and formation of MAOM via direct sorption. Here, we briefly review and synthesize how these and various other processes link plant diversity and the two key sub-pools of soil organic matter (SOM), highlight research gaps, and provide new hypotheses and methodological recommendations for future studies.

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Plant diversity affects *particulate organic matter* directly via the production of structural plant inputs and indirectly by mediating the translocation and transformation of those inputs

Particulate organic matter represents partly decomposed plant fragments that, if not occluded within aggregates[38], have relatively short residence time in soil[39] and can be quickly decomposed under certain environmental conditions[13]. Particulate organic matter can be translocated to the mineral soil by bioturbating fauna or directly released to the soil via root mortality[40–42]. Plant diversity can both directly and indirectly affect the processes that are relevant to the accumulation of POM in organic layers or the mineral soil, including the production, decomposition, translocation, and biotic transformation of structural plant compounds (i.e., of plant litter)[43,44].

Greater plant diversity often enhances above- and/or belowground productivity across land uses[3,43,45–52], which likely results in higher inputs of aboveground and belowground litter to the soil[53–56]. Belowground inputs could directly replenish POM pools as these inputs are released into the mineral soil[57]. In contrast, aboveground litter commonly decomposes prior to incorporation into the mineral soil. Mixtures of aboveground litter under diverse plant communities could decompose more slowly than the individual litters these mixtures are composed of, if: (i) phenolics are transported between litters and form resistant complexes with proteins[58], which hinder biotic decomposition, (ii) decomposer communities that are adapted to decompose specific components of litter are impaired by the heterogeneity of litter mixtures[59], or (iii) resource competition among fungi hinders decomposition of part of the litter[60,61]. Increased aboveground litter production and decelerated decomposition of that litter could result in the accumulation of POM in organic layers (e.g., in coniferous forests)[62]. POM may also accumulate more in diverse forest and grassland communities with higher abundance of bioturbators such as earthworms[63–66] due to enhanced transfer of structural compounds to the mineral soil. However, aboveground litter mixtures can also decompose more quickly[67] due to improved microclimatic conditions[68], greater habitat diversity, substrate diversity, enzymatic capabilities[36,60], and nutrient transfer via leaching or fungi[58,69–71] among litters. Such increases in litter decomposition in more diverse plant communities may be more likely if litters with sufficiently different biochemical qualities (pertaining to C/N or lignin/N ratios) co-occur[72]. Likewise, experimental communities with more plant species have sometimes been reported to have higher community-weighted N contents (N content weighted according to the abundance of individual species in a community) in plant biomass, which could alleviate potential microbial N limitations and accelerate the decomposition of that biomass once senescent[73–75]. Such accelerated decomposition could, in turn, reduce the retention of structural litter compounds in soil and thus POM. Notably, whether litter mixtures decompose more quickly, including belowground mixtures[54], or whether community-weighted N contents in plant biomass are higher in diverse communities, may vary with time and may strongly depend on the environmental context, such as soil texture, fertility, or moisture[68,76,77], and the presence of certain plant functional groups, such as legumes[66,78,79]. There is persistent uncertainty about the relevance of litter decomposition studies (i.e., litter mass loss studies) for the formation and dynamics of SOM[80–82], and biodiversity-mediated effects on litter composition (e.g., N content) may have opposing effects on the persistence of litter-derived organic matter over short and long time scales[21,83,84]. An understanding of the effects of plant diversity on POM dynamics thus requires more research on the links between rates of litter mass loss and retention of POM in organic and mineral soil layers (sensu Mueller et al.[82]).

Whether POM accumulates in the mineral soil does not only depend on the amount of structural plant inputs, but also on the capacity of the microbial community to further transform those inputs, which is reflected in individual or combined microbial traits such as C use efficiency or diversity[25,26,85]. Studies in grassland biodiversity experiments, forests, and diversified crop rotations reported positive effects of plant diversity on microbial biomass C[28,63,86–92], microbial diversity[1,90,93] (but see Prober et al. and Dasser et al.[94,95]), and microbial C use efficiency[96,97] (but see Prommer et al.[98]) across climates and soil types, which indicates that the microbial community may often have higher capacity to degrade litter and POM under more vs. less diverse plant communities. This capacity could further be altered by plant-mediated differences in the abundance of saprophagous soil fauna[29]. Such animals can transform POM into feces, which are often more easily decomposable than the material the feces originate from[99]. However, the fact that many studies investigate plant diversity and productivity, litter decomposition, and SOM dynamics separately complicates predictions of how plant diversity affects the formation of POM. This is complicated further by the fact that plant diversity has not always been found to be related to productivity[100].

Plant diversity affects *mineral-associated organic matter* directly via the production of dissolved organic matter and indirectly by altering soil microbial traits and processes

Mineral-associated organic matter is bound to minerals or occluded within small microaggregates (<50 μm[18]) and can persist in soil for centuries to millennia[101]. However, recent studies indicate that at least part of that pool can also cycle on shorter time scales[102,103]. Mineral-associated organic matter forms via interaction of reactive mineral surfaces with microbial residues[12] and dissolved organic matter (e.g., root exudates or dissolved organic matter produced via depolymerization of plant biomolecules in organic layers or the mineral soil). Thus, plant diversity-mediated changes in the production and quality of root exudates and other dissolved organic matter, and alteration of factors influencing the formation of microbial residues (e.g., microbial traits as affected by faunal abundance, nutrient contents, and microclimatic conditions) have high potential to affect the formation of MAOM[28,31,104].

Plant diversity could affect the quantity of dissolved organic matter indirectly, if dissolved organic matter is simply proportional to plant litter or biomass, but also directly, because some plant species release more dissolved organic matter (e.g., lignin monomers) from their decomposing litter or exude more C from their roots[105–107]. Plant diversity in temperate grasslands has also been shown to alter community-weighted root traits that are related to exudation rates, such as root length, density, or diameter[105,108]. Some studies harboring more diverse plant communities have indeed found higher quantities of dissolved organic matter in general[109], and root exudates in particular, mostly in temperate grasslands[1,28,92,110,111] but also in subtropical forests[112]. These root exudates, and dissolved organic matter in general, could extend to deeper soil layers likely due to increased rooting depth and density[109,111] and/or increased number of preferential flow paths created through roots or macrofauna such as earthworms[113]. Such increased concentrations of dissolved organic matter can boost MAOM formation via direct sorption on mineral surfaces[114]. However, dissolved organic matter can also desorb existing organic matter from mineral surfaces[115,116] and thus decrease MAOM-C or accelerate its turnover.

Higher inputs of dissolved vs. structural organic matter, e.g., via more complete litter decomposition[117], and higher amounts of bioavailable compounds in dissolved organic matter[109] under more diverse plant communities could also indirectly boost the formation of MAOM via microbial residues. That is, microorganisms can produce biomass, dissolved organic matter, and eventually residues more efficiently when growing on easily decomposable substrates, which is reflected in emergent microbial traits such as diversity or C use efficiency[25,26,118]. These traits can further be influenced by plant-diversity effects on nutrients, the microenvironment, and soil fauna. Lower leaching losses of nitrogen and higher contents of total and available phosphorus under diverse plant communities across climates and ecosystems[119,120] could alleviate potential microbial nutrient limitations and enhance C use efficiency[121]. Plant diversity can also stabilize microenvironmental conditions: higher levels of shade by plant cover may result in a more uniform water distribution in the topsoil[86,122], increased soil porosity may improve drainage[33], or soil temperatures may be more constant due to elevated canopy shade and/or reduced soil thermal diffusivity with increased SOM[31,123]. Combined, these conditions could directly influence microbial growth, activity, or C use efficiency[123,124] and alter the formation of microbial residues in MAOM[16]. These conditions could also indirectly affect microbial growth and activity via positive effects on the species richness and abundance of soil fauna such as arthropods[29,125–130], protists[129,131], and bacterial-feeding and omnivorous nematodes[132–134]. For example, selective feeding of soil fauna such as nematodes and protists on certain microbial groups can alter microbial community structure, increase microbial activity[135], and may affect traits such as C use efficiency[42]. However, negative or neutral effects of plant diversity on the abundance and richness of soil fauna have been reported as well[136–140], and multiple studies indicate higher relevance of plant identity or functional group than plant diversity in affecting the composition of soil fauna, at least in short-term studies[141–148]. The lack of quantitative linkages between plant diversity and MAOM in general, and between dissolved organic matter inputs and the direct sorption and microbial pathways of MAOM formation in particular, render sound statements on how plant diversity affects the formation of MAOM difficult. Long-term biodiversity experiments are scarce but urgently needed to test such relationships on adequate time scales.

Context specificity of plant-diversity effects on C storage in soil via POM and MAOM

The varied and complex interactions of processes by which plant diversity can influence POM and MAOM, as highlighted above, and the scarcity of empirical studies that mechanistically link POM and MAOM dynamics to plant diversity, make it difficult to generalize about the direction and magnitude of plant-diversity effects on these SOM pools and total SOM. There is some evidence, however, that certain plant diversity-mediated processes are more relevant and predictable in certain environmental contexts, and that progress in this field can be made by investigating plant diversity and SOM dynamics in light of these contexts. We specifically hypothesize that (i) net effects of plant diversity on C contents are the most positive, and result in accrual of both POM and MAOM, for soils whose C storage is limited primarily by plant inputs, that (ii) net effects of plant diversity on C contents are positive, but weaker and mediated largely through effects on POM, for soils closer to their capacity for MAOM formation, and that (iii) some links between plant diversity and SOM dynamics can weaken or offset positive effects on C contents. These hypotheses provide a basis for future research and help explain why the observed effects of plant diversity on soil C are not consistently positive and vary in strength across sites[3].

Plant-diversity effects on soil C are the most positive in soils whose C storage is limited by plant inputs

Soils that have low C contents and/or abundant reactive mineral surfaces have the potential to store large additional amounts of C, perhaps most persistently in MAOM, but also in POM[13]. However, this potential often remains untapped due to insufficient inputs of organic matter. Such soils include those newly developing, e.g., after glacier retreat[149]; soils under agricultural use[150], where plant residues are often removed and nutrient retention is low; soils after disturbances, such as mining[151,152]; grasslands and forests recovering from intensive grazing and timber harvest[153,154], respectively; or deeper soil layers[150]. Although C-saturation, which assumes a finite capacity of soils for C storage, is an evolving and debated concept[155–158], global-scale studies suggest that the majority of soils may currently exist in a state characterized by SOM pools that are smaller than their potential and constrained by plant inputs[150,159]. More diverse plant communities in such environmental contexts could alleviate this deficiency of plant inputs by boosting plant productivity[160], enhanced rooting depths[111], and increased abundance of bioturbators. These factors would foster the processes involved in both POM (e.g., production of plant litter and transfer of this litter to the mineral soil) and MAOM formation (e.g., root exudation) and result in a net increase of C stored in these pools and overall soil C storage (Fig. 1).

Plant-diversity effects on soil C are positive but weaker in soils closer to their capacity for MAOM formation

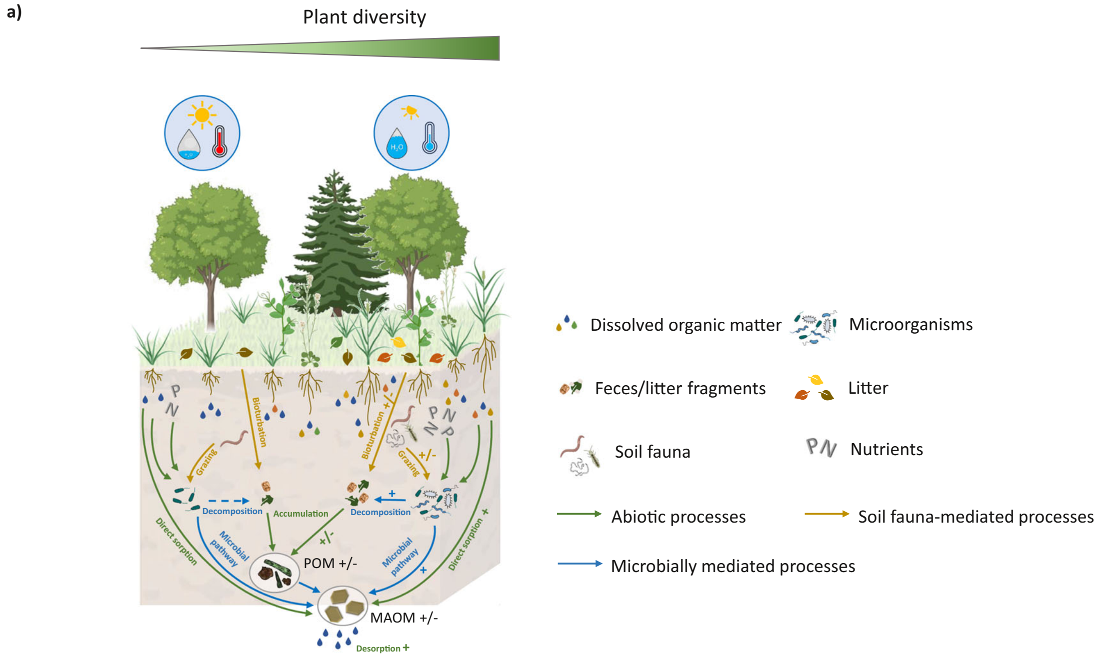
Soils with higher C contents and a mineral phase closer to their theoretical C saturation threshold likely have lower capacity to store additional amounts of C in MAOM[150]. Such soils include those under many "natural," older forests and, to a lesser extent, grasslands[150]. Plant diversity-mediated processes that foster MAOM formation (such as favorable conditions for microbial growth or increased quantity and quality of dissolved organic matter/root exudates) will thus be less relevant in such contexts, but plant-diversity effects on soil C can still be positive, albeit weaker, when retention of C in POM is fostered due to (i) increased plant productivity and plant litter production and/or (ii) reduced decomposition and mineralization of that litter or POM in mineral soil (e.g., due to antagonistic effects of litter mixtures on decomposition or conditions that hamper microbial activity in the mineral soil, such as low oxygen availability or pH). Losses in plant diversity and reduced plant inputs could have more profound effects on soil C in such ecosystems than gains in plant diversity. This may specifically be true in soils that are more reliant on POM, such as many coniferous forests in both mineral soil and organic horizons[161], as POM in these soils can be more quickly lost upon disturbance than MAOM[161].

Some links between plant diversity and SOM dynamics can weaken or offset positive effects on C contents

Net positive effects of plant diversity in the ecosystem contexts highlighted above could be weakened (or even offset) by potential negative links between plant diversity and POM and MAOM. For example, plant-diversity effects that stabilize microenvironmental conditions and render them more favorable for microbial activity may increase C mineralization and offset some of the positive effects that are mediated by increased C inputs. This negative link may be the most relevant in soils with a mineral phase closer to its C saturation threshold [hypothesis ii)], where potential gains in C due to increased structural plant inputs can be offset by accelerated decomposition of POM, or in ecosystems in which climate is a strong limiting factor for microbial processes and in which SOM contains high amounts of POM, such as in colder climates and/or permafrost soils[162,163]. Likewise, increased inputs of dissolved organic matter do not necessarily lead to net formation of MAOM if desorbing existing SOM from mineral surfaces[116]. This has potentially high relevance in soils with a mineral phase closer to its theoretical C saturation threshold [hypothesis ii)]. Finally, interactions among different litter types that result in synergistic effects on litter decomposition could increase C mineralization and result in smaller positive or neutral to negative net effects of plant diversity on POM (and/or MAOM) stocks, which may specifically be relevant in ecosystems that store large amounts of C in organic layers, such as coniferous forests[161].

Synergy and outlook

Plant diversity can be a potent regulator of the dynamics of POM and MAOM via various interrelated pathways (Fig. 1) and thus has a sustained impact on C storage in soil. However, the mechanistic links between these pathways and the quantity and dynamics of POM and MAOM have hardly been explored. We thus emphasize the need to



b)

	MAOM	POM	Total SOM	Most relevant for	Research pathways
Soils in which C storage is limited by plant inputs *(hypothesis i)*	++	++	++	• Newly developing soils • Agricultural soils • Disturbed soils • Deeper soil layers	Quantify POM and MAOM in plant-diversity gradients
Soils closer to their theoretical C saturation threshold *(hypothesis ii)*	o/-	++	+	• Organic horizons • Plant-diversity losses in more mature forests and grasslands	Quantify POM and MAOM in plant-diversity and soil C saturation gradients, and upon losses in plant diversity
Links that can reduce/offset positive effects of plant diversity on soil C *(hypothesis iii)*					
Environmental conditions favorable for microbial activity	+/o	-	+/o/-	• Soils closer to C saturation; Cold climates/ permafrost soils	Monitor microclimate, microbial composition/traits, and POM/MAOM in plant-diversity and soil C saturation gradients over time
Synergistic effects of litter mixtures on decomposition	+/o	-	+/o/-	• Soils closer to C saturation	Link decomposition of litter mixtures to POM and MAOM in soil C saturation gradients using stable isotopes, monitor soil fauna
Increased amounts of dissolved organic matter	+/o/-	o	+/o/-	• Soils closer to C saturation	Quantify dissolved organic matter and MAOM in plant-diversity and soil C saturation gradients over time upon exclusion/inclusion of aboveground inputs

Fig. 1 | Context-specific links between plant diversity and particulate organic matter (POM) and mineral-associated organic matter (MAOM). a Overview of mechanistic links between plant diversity and POM and MAOM. Increases in plant diversity (from left to right) also increase: plant productivity (indicated by more leaves and deeper roots), diversity of litter species and dissolved organic matter/root exudates (indicated by the various colors of leaves and drops), and abundance and diversity of soil fauna and microorganisms. In turn, these changes could increase bioturbation rates and production of feces, grazing of soil fauna on microorganisms, direct sorption (or desorption) of dissolved organic matter on (from) mineral surfaces, and microbial C use efficiency (or other microbial traits), all of which can influence both accumulation and/or decomposition of POM and MAOM. High plant diversity can also affect the microclimate, such as via increased shading, maintenance of soil temperature and moisture (indicated in circles aboveground), or elevated nutrient abundance and availability, which can favor microbial activity/biomass production and the microbial pathway of MAOM formation and decomposition of POM. Arrows indicate processes; "+" and "−" indicate expected intensification/weakening of processes. Nutrients are indicated by capital "N" and "P." "+/−" after POM and MAOM indicates that increases in plant diversity can have both positive and negative effects on these pools, and we hypothesize that the direction of plant-diversity effects is context-dependent, as highlighted in panel **b. b** Relevance of links between increased plant diversity and POM, MAOM, and total SOM in different environmental contexts, including recommendations on how to test these hypotheses; ++, +, o, and − indicate strong and moderate increases, no change, and decreases, respectively. Created in BioRender. Eisenhauer, N. (2025) https://BioRender.com/1hwb0e8.

directly link plant diversity and the processes highlighted here to POM and MAOM dynamics. This includes: (i) disentangling the effects of above- and belowground inputs in diversity-induced gradients of plant productivity, e.g., by excluding aboveground inputs in one set of plots[164–166]; (ii) testing the role of decomposition of aboveground and belowground litter in diverse litter mixtures with different qualities in the formation of POM and MAOM (perhaps using isotopically labeled litter[167]), which is often studied separately[77]; (iii) determining net effects of increased quantities of dissolved organic matter and root exudates, including their molecular composition, on MAOM formation under plant-diversity gradients, e.g., using ^{13}C pulse labeling[168]; and (iv) establishing soil fauna inventories and exploring changes in microbial community composition and traits, such as C use efficiency, as affected by plant diversity[97,169]. Individual and combined effects of two or more mechanisms could be systematically investigated in mesocosm or Ecotron experiments[170,171] and cross-institutional field experiments[100,172], respectively, employing standardized soil fractionation schemes[12,173], microbial methods such as phospholipid fatty-acid and DNA extractions, multi omics[174], and isotopic and spectroscopic techniques such as ^{13}C/^{15}N labeling and Fourier-transform infrared or nuclear magnetic resonance spectroscopy.

We believe that mechanistically studying the links between plant diversity and POM and MAOM will help better predict the consequences of gains and losses in plant diversity on C and nutrient storage in different ecosystems and eventually inform related soil management strategies. However, it will be important to study these links in different environmental contexts [as per our hypotheses (i)–(iii) highlighted above; Fig. 1], which likely determine whether plant diversity has positive, neutral, or negative effects on POM and MAOM, and overall C storage. To optimally test this context-dependency of plant diversity effects requires multi-site, distributed field experiments[175], or mesocosm experiments that span climates or soil types (e.g., with low and high organic matter contents). We specifically call for studies (i) along C-saturation gradients, including gradients in soil texture, mineralogy, and depth, (ii) along gradients of soil parameters that affect microbial traits, such as pH or oxygen availability[176], and (iii) in the presence and absence of certain key plant functional groups, such as N-fixing plants and trees with divergent leaf or mycorrhizal traits (e.g., needle-leaves vs. broadleaves; associations with arbuscular vs ectomycorrhizal fungi). This also necessitates that such experiments have to be performed over longer periods of time, e.g., for several years, with repeated samplings or isotopic tracers.

We believe that further research along the lines of our hypotheses above [(i)–(iii); Fig. 1] is essential in gaining knowledge necessary to effectively guide biodiversity restoration efforts and management practices that aim at establishing or maintaining soils as C sinks and nutrient stores. Only if we close the remaining knowledge gaps can we comprehend the consequences of biodiversity loss for SOM dynamics and the related ecosystem functions and implement appropriate countermeasures (e.g., restoration).

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Author contributions

Š.A. and G.A. conceived of the idea and designed the conceptual framework of the review. Š.A. and G.A. performed the literature review and wrote the first manuscript draft. K.E.M., M.L., and N.E. critically commented on the paper and added and/or revised content.

Competing interests

The authors declare no competing interests.

Additional information

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