GAME CHANGER

Perspectives of the Fritz-Scheffer Awardee 2022: Profile- to ecosystem-scale perspectives on soil organic matter formation as demonstrated by woody debris in forest dynamics

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Abstract

Soil organic matter (SOM) forms along a continuum from individual particles, pores, and aggregates to litter–soil profiles and larger ecosystems such as forests. However, forest management of SOM stocks and the carbon therein requires knowledge on which processes and factors at which scales determine SOM formation from forest biomass. As evident from woody debris at the profile scale, SOM forms through additions, transformations, translocations, and removals of litter by soil organisms and environmental components. Yet SOM stocks only increase if litter additions-to-removals are out of steady state or enter a new steady state that ignores older litter. Both happen through disturbance and self-selecting feedback processes in ecosystems consisting of autotrophs, heterotrophs, and their physical environment. One such positive feedback process is litter-SOM transformation by heterotrophs that releases nutrients that promote plant productivity and thus litter input. Stocks of litter-SOM, heterotrophs, nutrients, and plants thus exhibit Lotka–Volterra dynamics (i.e., predator–prey interactions) and only increase when attractor states (i.e., steady series or sets of states) change due to disturbance. Evidence of evolving feedback processes and disturbance in SOM would help identify limits, potentials, and precariousness of ecosystems in light of global change, but remains to be found.

KEYWORDS
deadwood, disturbance, evolution, LHNP model, litter, predator–prey interactions

1 | INTRODUCTION

Soil organic matter (SOM)—that is, all biologically derived organic matter residing in and on soil (Baldock & Skjemstad, 2000)—is a dynamic component of soils that influences soil functioning such as water filtration, nutrient retention, and carbon sequestration. Of particular interest are forest soils due to substantial stocks of SOM that vary between forest ecosystems. At the global scale for instance, temperate deciduous forest soils have 20% more carbon per hectare than temperate evergreen forest soils (Jobbágy & Jackson, 2000). Forest soils are also sensitive to management activities and other disturbance, which can reduce stocks of SOM through biomass removal, but also increase stocks of SOM through reforestation, fertilization, and nitrogen fixation (Mayer et al., 2020; Wambsganss et al., 2017).

However, the factors and processes by which SOM forms—that is, develops and persists—in forest ecosystems are difficult to quantitate. When investigating the effect of biodiversity, Li et al. (2019) found that tree species richness increased SOM stocks through

enhanced leaf biomass production. On the other hand, Lange et al. (2015) found that grass species richness increased SOM stocks through greater root production and microbial turnover. In addition, with increasing depth, belowground litter has greater potential to produce SOM of higher stability against mineralization (Schmidt et al, 2011), while aboveground litter is first partially mineralized in the forest floor before stabilization occurs (Stutz et al., 2019; Wambsganss et al., 2017). Yetchanges in SOM due to forest disturbance are the result of changes in aboveground litter more so than that of belowground litter (Lajtha et al., 2018). The share of microbial products in forest soils is also minor compared to the circa 70% of SOM that is residual litter (Liang et al., 2019).

Forest biomass varies in composition and contribution to litter. In annual aboveground litterfall in a temperate mixed hardwood forest, woody debris accounts for 38% of biomass, but only 22% of nitrogen (N), 22% of phosphorus (P), 31% of calcium (Ca), and 19% of magnesium (Mg) (Gosz et al., 1972); coarse woody debris is even more extreme with 15% of biomass, 1% of N, 0% of P, and 2−3% of base cations. Coarse woody debris is a unique component of forest biogeochemistry due to physical and chemical features that necessitate specialized decay pathways (Harmon, 2021; Magnússon et al., 2016). In soil, the input of wood-derived organic matter alters soil chemical and physical functioning compared to surrounding litter (Stutz, Dann, et al., 2017; Stutz et al., 2019). As such, coarse woody debris has been conceptualized as a pedogenic patch of soil formation and functioning (Stutz & Lang, 2017, 2023) as well as a specific type of forest floor (lignoform; Tatti et al., 2018). Nonetheless, soil imprints of coarse woody debris tend to be insignificant in magnitude (Krueger et al., 2017; Spears et al., 2003) and converge with their surroundings (Šamonil et al., 2020).

At the heart of this conundrum is the difference in scale between litter-profile interactions and ecosystem-wide management and disturbance. Soil organic matter cannot be understood without considering the soil profile, which in turn cannot be disentangled from its inhabitant ecosystem. Thus, it is crucial to identify which factors and processes at which scales determine SOM formation from forest biomass. This study attempts to do so by integrating profile-scale processes in SOM formation into a conceptual model of ecosystem-scale processes based on plant-heterotroph interactions via the lens of coarse woody debris, soil processes, feedback processes, and disturbance.

2 | PROFILE SCALE

At the soil profile scale, SOM formation occurs through various additions, transformations, translocations, and removals of solid, liquid, and gaseous matter as regulated by soil-forming factors, namely ecosystem components that can vary individually (Stutz & Lang, 2023). Changes to factors alter processes and thus result in different SOM. In this sense, coarse woody debris is an organic parent material that, when retained in forest ecosystems, becomes a part of soil as do other types of litter (Stutz et al., 2019; Stutz & Lang, 2023). It thus becomes a medium
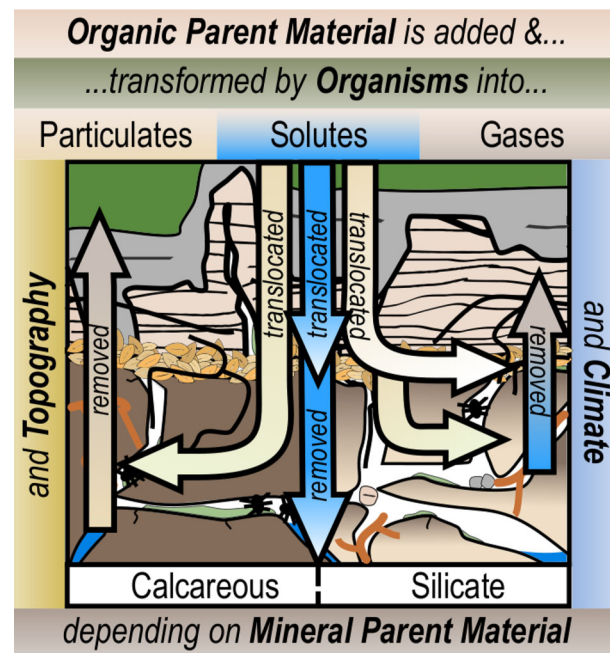
FIGURE 1 Profile-scale perspective of the formation of soil organic matter from woody debris. Additions of woody debris are transformed into and translocated and removed as particulate, dissolved, and gaseous soil organic matter in a system of the soil-forming factors parent material (organic and mineral), organisms, topography, and climate with time. Adapted from Wambsganss et al. (2017).

for diverse additions, transformations, translocations, and removals as described below and summarized in Figure 1.

2.1 | Additions

Coarse woody debris is a normal constituent of forest litter whose input depends on mortality rates. Aside from mass mortality events and other disturbances, annual input varies between forest types with maximums in boreal and tropical rain forests (Table 1). Input of coarse woody debris entails the input of wood—bark, cambium, sapwood, and heartwood—liquid and vapor water, and inhabitant epiphytes, fauna, and microorganisms. The ratio of bark and cambium to sap- and heartwood depends on the diameter of coarse woody debris, often a minimum of 10 cm, and the tree species. The latter is irrelevant to wood's elemental composition due to the high abundance of C, O, and H (Table 1).

Where tree species matter is the cellular and molecular composition of sap- and heartwood: tracheids in conifers, vessels and fibers in broadleaves, parenchyma and rays in both, calcium oxalate crystals, silica, and resin pockets in some; and various hemicelluloses, lignins, and extractives that encase cellulose microfibrils in rigid cell walls that in total constitute 90%−99% of wood's dry mass (Carlquist, 2001; Schwarze, 2007). Various combinations of cell types and wall ultrastructures result in an orthotropic structure with longitudinal

TABLE 1 Input, composition, and densities of coarse woody debris.

Property	Description	References
Annual aboveground input (Mg ha^{-1} year^{-1})	Boreal forests 0.07—9.60 Temperate conifer forests 0.17—4.54 Temperate broadleaf forests 0.12—1.18 Tropical rain forests 2.5—7.9 Tropical moist forests 1.18—2.94 Tropical dry forests 0.11—0.91	Harmon et al. (1986), Laiho and Prescott (2004), Palace et al. (2012), Meakem et al. (2018)
Wood elemental content	50% C, 43% O, 6% H, 1% N/K/Ca/Mg/P/Si	Fengel and Wegner (1984)
Pore diameters (μm)	Tracheids 14–65 Vessels 5–400 Fibers 10–40	Ilvessalo-Pfäffli (1995), Wagenführ (1999)
Specific densities (g cm^{-3})	Conifers 0.35—0.60 Broadleaf 0.45—0.75	Wagenführ (1999)
Minimum and maximum densities (g cm^{-3})	Balsa (*Ochroma pyramidale*) 0.13 African blackwood (*Dalbergia melanoxylon*) 1.33	Wagenführ (1999)

tracheids, vessels, and fibers. Vessels can be the largest in diameter, fibers the smallest, and tracheids in-between (Table 1). The dominance of tracheids in conifers compared to vessels and fibers in broadleaf means conifers tend to have lower specific densities, yet both the lightest and densest woods—balsa (*Ochroma pyramidale* [Cav. Ex Lam.] Urb.) and African blackwood (*Dalbergia melanoxylon* Guill. & Perr.), respectively—are broadleaf species (Table 1). Orthotropism and hygroscopic compounds such as tyloses in xylem result in wood's high moisture content that equilibrates slowly with ambient air humidity as a function of radius and species (Fosberg, 1970; Thybring & Fredriksson, 2021), unless in contact with soil (Levy, 1987).

A variety of organisms also inhabit coarse woody debris. A non-exhaustive list includes amphibians, insects, arachnids, worms, bacteria, myxomycetes, fungi, mosses, lichens, and vascular plants (Chmura et al., 2016; Dittrich et al., 2014; Hardersen & Zapponi, 2018; Seibold et al., 2015; Tláskal et al., 2017; Zuo et al., 2023). The diversity of each is exemplified by the assortment of fungi: Basidiomycota, Ascomycota, Mortierellomycotina, Mucoromycotina, Chytridiomycota, Glomeromycota, Entomphthoromycota, and Kicxellomycotina that function as white rot, brown rot, saprotrophs, ectomycorrhizae, and yeasts (Baldrian et al., 2016). Legacy effects of initial communities are dependent on tree species and decisive for future community composition and transformation (Maillard et al., 2021; Purahong et al., 2018).
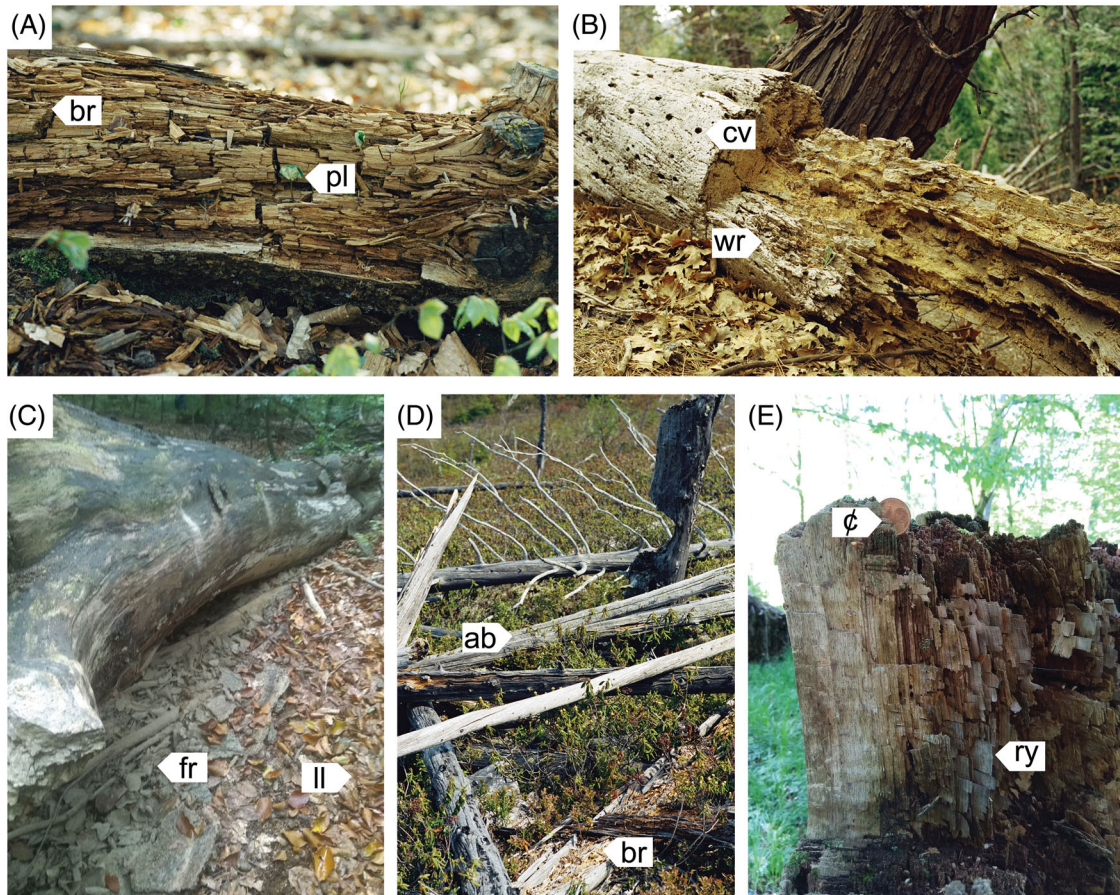
2.2 | Transformations

Before and after being added to soil, coarse woody debris undergoes biotic and abiotic transformations into fragments, solutes, liquids, and gases. It was thought that primarily brown-rot and white-rot basidiomycete fungi degrade coarse woody debris and lignocellulose therein (Eriksson et al., 1990). The former demethylate and selectively remove bonds in lignin during mineralization of cellulose and hemicellulose, which leads to brown, cubic cells rich in fragmented lignin (Figure 2A).

The latter extensively oxidize lignin in addition to mineralizing carbohydrates, which typically leaves pale, shredded fibrous cell wall material in woody debris (Figure 2B). The extensive oxidation of lignin by the latter also produces soluble, aromatic low-molecular weight compounds enriched with carboxyl groups (Kirk & Farrell, 1987).

Increasingly significant quantities of other actors and their transformation products are being found in coarse woody debris. Wood-borne bacteria are associated with specific fungal communities, become more diverse and similar to soil-borne bacteria, and utilize residual, simple degradation products as well as fix nitrogen (Odriozola et al., 2021; Tláskal et al., 2017). Resulting transformation products include bacterial cellular components, cell wall compounds, and extracellular polymeric substances (Kögel-Knabner, 2002). Additionally, insects are responsible for an estimated 29% of carbon fluxes from woody debris worldwide (Seibold et al., 2021). Such fluxes consist of in-situ feces enriched with nutrients and a microbiome, residual fragments such as frass in galleries, and various gases including volatile organic compounds (VOCs; Figure 2C). Bacteria along with fungi are also responsible for the transformation of insect-ingested wood (Geib et al., 2008). Further fragmentation occurs through foraging for insects and fungi by fauna at higher trophic levels. At each stage, metabolism of fauna, insects, bacteria, and fungi as well as extracellular enzymatic degradation produce CO_2 and H_2O.

Abiotic transformations also occur, albeit to a lesser-known extent. When applied to wood and leaf litter, light and heat decolor wood—ultraviolet light darkens and visible light bleaches—and release CO_2, CO, and CH_4 along with leachable degradation products related to lignin (Figure 2D; Bejo et al., 2019; Chang & Allan, 1971; Lee et al., 2012). Erosion, freeze-thaw cycles, and shrinking-swelling dynamics produce fragments within and between wood tissues (Figure 2E), but evidence thereof rarely has been published (Cornwell et al., 2009). Combustion of coarse woody debris by fire produces pyrogenic compounds, ash, H_2O, CO_2, and VOCs, and modifies the color and magnetism of underlying mineral soil (Cornwell et al., 2009; Goforth et al., 2005).

FIGURE 2 Various transformations of coarse woody debris. (A) Brown-rot (br) degraded heartwood of silver fir (*Abies alba* Mill.) colonized by plants (pl; common ivy *Hedera helix* L.), in the Black Forest, Baden-Württemberg. (B) White-rot (wr) degraded ponderosa pine (*Pinus ponderosa* Douglas x. C. Lawson) with cavities (cv) in the San Bernardino Mountains, California. (C) Windthrown European beech (*Fagus sylvatica* L.) with substantial amounts of frass (fr) covering underlying leaf litter (ll) in the Düben Heath, Saxony-Anhalt. (D) Abiotically bleached (ab) balsam fir (*Abies balsamea* (L.) Mill.) stems with brown-rotted (br) heartwood circa 20 years after last fire in Grands-Jardins National Park, Quebec. (E) Advanced decay of a pedunculate oak (*Quercus robur* L.) stump with rays (ry) selectively preserved for unknown reasons; 5-euro cent coin (¢) is 21.25 mm in diameter. All images were photographed by the author.

Structural transformation occur as well. Loss of middle lamella during white rot separates cell walls, thus creating micron-sized pores that are new pathways for fungal mycelia and bacteria to colonize wood (Islam et al., 2017; Schwarze, 2007). Such pores would also retain water to a greater extent than tracheids and vessels. Brown rot, on the other hand, minimally degrades the middle lamella and does not change the shape or thickness of cell walls until external pressure is applied, whereupon wood cracks and ruptures due to the loss of cell wall integrity (Eriksson et al., 1990). Further openings include soft rot cavities, insect galleries, and shrinkage cracks (Figure 2b). Matric water potential of woody debris thus increases as it decays (Dix, 1985).

2.3 | Translocations

With two exceptions, only transformation products of coarse woody debris are translocated in soil. The are two exceptions: (1) the mortality of roots and stumps >10 cm in diameter (or an alternate minimum size) and (2) the burial of woody debris by vegetation and sediments (e.g., Moroni et al., 2015). Otherwise, all transformation products can be translocated within the profile if facilitated by the soil. Fragments released from coarse woody debris accumulate in the forest floor before being incorporated into mineral soil by bioturbating organisms (Stutz et al., 2019). Water with colloids and solutes—dissolved organic matter, cations, and anions—is leached from coarse woody debris into the forest floor and mineral soil typically at greater concentrations from broadleaf species in temperate forests in acidic soils (Bantle et al., 2014; Hafner et al., 2005; Spears et al., 2003; Stutz et al., 2019).

Once in mineral soil, transformation products functionalized with phenolic and carboxyl groups can complex, chelate, and exchange with other constituents of the soil solution such as Ca^{2+}, hydroxyl-Al, and phosphates (Stutz, Dann, et al., 2017). This results in the occlusion of organic matter within aggregates as decay of coarse woody debris progresses (Wambsganss et al., 2017). Further transformation of translocated woody debris may be either reduced or catalyzed due to mineral interactions, abundant metal cations, and altered microclimate

conditions (Hall & Silver, 2013; Mikutta et al., 2007; Schmidt et al., 2011). Rearrangement of aggregates and translocation of porous fragments also create soil pore volume (Stutz et al., 2019). The amelioration of acidity can lead to increased biomass, density, and richness of various microorganisms and soil fauna (Kappes et al., 2007; Minnich et al., 2020), though this is not always observed (e.g., Šamonil et al., 2020). Wood-inhabiting organisms, especially fungi, can also colonize soil directly from woody debris (Mäkipää et al., 2017).

In the other direction, soil-dwelling organisms can colonize coarse woody debris directly from the forest floor (Peršoh & Borken, 2017). Such organisms translocate nutrients, water, particles, and organic matter into woody debris. For instance, nitrogen can be fixed in woody debris from the atmosphere by bacteria, or transported into woody debris by fungi (Groß et al., 2022; Mäkipää et al., 2017; Sharp & Millbank, 1973). The latter has been reported for phosphorus too, including laterally within wood itself (Laiho & Prescott, 2004). Abiotic pathways are also possible via capillary rise and advection of soil moisture and constituent organic and mineral particles into woody debris when in direct contact with soil (Levy, 1987). After each of the above, transformation of woody debris can be accelerated due to increased resource and catalysis availability.

The presence of coarse woody debris can facilitate or attenuate an assortment of external translocation processes. For one, litter, water, and other sediments can be trapped by coarse woody debris hollows on slopes (Spielvogel et al., 2009), though any down-slope effects of entrapment remain unknown. A proxy for possible attenuation is filtering of throughfall and litterfall by woody debris to the soil directly underneath. For example, assuming no capillary rise of water from soil or production of water from mineralization, only 60%−70% of canopy throughfall is found in runoff and leachates from woody debris (Harmon & Sexton, 1995; Kuehne et al., 2008). Similarly, less heat is exchanged from soil during diurnal cycles (Spears et al., 2003). New litterfall remains aboveground and can bury woody debris if the rate of wood decay is slow or the rate of litterfall is high (Moroni et al., 2015).

2.4 | Removals

Removals occur when matter from coarse woody debris is translocated out of the soil profile. These are translocations to the atmosphere, migrant organisms, and outflows via erosion, runoff, or leaching. Belowground, some woody debris must be removed as total SOM does not increase to the same extent as the amount of translocated woody debris (Kahl et al., 2012). The extent of removal depends on the level of biological activity in the soil as labile SOM decreases in calcareous soils but increases in silicate soils (Wambsganss et al., 2017). Such removals likely occur through the atmosphere and organisms—fungi as well as soil-dwelling ants and termites—instead of seepage as no increase in dissolved organic C (DOC) has been observed in subsoil under woody debris (Evans et al., 2020). Nutrients and water may suffer a similar fate especially through mycorrhizae and roots, but evidence so far suggests that nutrients are as likely to accumulate in woody debris itself (Herrmann & Bauhus, 2018). In addition, the soil itself is not immune: Pore

volume can be lost if bioturbation induces turnover of aggregates or if translocated acidity disperses clay particles (Stutz et al., 2019).

As such, most coarse woody debris—specifically C—is thought to be lost via CO_2 emissions following respiration (Russell et al., 2015) with estimates ranging from 65% to 95% of woody debris C (Chambers et al., 2001; Spears et al., 2003). Yet, different methods yield different results: First-order decay rates based on respiration can be twice as large as those based on mass loss (Herrmann & Bauhus, 2013), while density losses have been observed to be negative (Kahl et al., 2017). The reality is each method captures more pools than desired. Displacement for respiration measurements releases entrapped wood air-CO_2, which can be as high as 20% in concentration (Chambers et al., 2001; Jensen, 1969; Thacker & Good, 1952), and disrupts fungal bodies that are quickly mineralized. In-situ respiration measurements without displacement indicate similar CO_2 respiration rates to soil (Warner et al., 2017), but they include autotrophic and heterotrophic respiration of carbon not from woody debris (e.g., mosses, roots, mycorrhizal fungi, and fungivores). Mass balances account for fragmentation and foraging, and density balances are easy to measure, but as with other forest litter, transformation and translocation of matter by organisms entail lower apparent mass and density losses than that of the wood itself (Laiho & Prescott, 2004; Prescott & Vesterdal, 2021).

Not to be forgotten is the removal of coarse woody debris by forest management both before and after tree mortality. Fuelwood collection varies both historically and regionally depending on the level of development, availability of other fuel sources, and socioeconomic support for wood-based climate mitigation measures. Timber harvesting removes standing woody biomass that would have become woody debris. More intense harvesting—that is, whole-tree harvesting systems instead of stem-only systems—increasingly removes nutrients and habitat in addition to carbon (Achat et al., 2015; Rousseau et al., 2018). Yet, unlike fuelwood collection, timber harvesting adds a pulse of woody debris in the form of aboveground and belowground residues. The former are branches, treetops, and bark that can be equivalent in quantity to stocks of woody debris in mature forest stands (Harmon et al., 1986) and are often concentrated on skid trails (Stutz et al., 2015; Stutz, Schack-Kirchner et al., 2017). The latter are residual stumps and roots, the quantity of which is uncertain even when trees are still standing.

2.5 | Spatiotemporal rates and steady states

Changes to coarse woody debris and SOM are the result of net intensities of each process within a unit of time. For woody debris, net decomposition differs up to several orders of magnitude and is closely associated with species identity followed by environment (Harmon et al., 2020; Herrmann et al., 2015; Kahl et al., 2017). For soil profiles, net changes to SOM—and nutrients and pore volume—vary just as much and occur within patches (Kruerger et al., 2017; Laiho & Prescott, 2004; Wambsganss et al., 2017; Stutz et al., 2019). This is because woody debris can be pedogenic patches when process rates differ spatially or temporally to surroundings (Stutz & Lang, 2023).

Numerous processes related to SOM have different rates near and underneath coarse woody debris compared to leaf litter. Seepage from coarse woody debris ranges from 20% to 50% of throughfall, yet fluxes of DOC can be 100% larger than under leaf litter (Bantle et al., 2014; Harmon & Sexton, 1995; Kuehne et al., 2008). When degraded by white-rot fungi, more functionalized organic matter enters mineral soil in DOC fluxes that lead to greater amelioration of soil acidity and thus nutrient availability than the surroundings (Bantle et al., 2014; Spears & Lajtha, 2004; Stutz, Dann, et al., 2017). Organisms such as earthworms congregate underneath woody debris in response to altered moisture, temperature, and organic input regimes, which in turn lead to larger rates of bioturbation and incorporation of fragments than neighboring soils (Scheu & Schulz, 1996; Stutz et al., 2019). Input of woody debris also frequently entails pit and mound structures formed through tree uprooting, which bury various soil materials and can persist for half a millennium (Harrison-Day & Kirkpatrick, 2019; Schaetzl et al., 1989).

More often than not though, forest stands with more woody debris do not have higher SOM stocks despite persistence of organic matter from woody debris as indicated by δ^{13}C signatures and lignin biomarkers (Kahl et al., 2012; Krzyszowska-Waitkus et al., 2006; Lajtha et al., 2018; Spears et al., 2003; Stutz et al., 2019). Thus, process rates in woody debris-soil profiles either do not differ from rates in surrounding leaf litter-soil profiles, or *first diverge and then converge*. The former happens when heterotrophic activity increases to match organic matter transfers to soil, but this is unlikely as respiration rates from woody debris are similar to surrounding litter (Warner et al., 2017). The latter is more likely given the persistence of wood-derived OM and dendrochronological studies that find patterns of convergence (e.g., Šamonil et al., 2020).

Convergence suggests that SOM stocks and thus SOM formation have (open) steady states that are reached faster than the frequency a soil profile experiences coarse woody debris. This reaffirms that the input of woody debris is a pulse and patch of litter that persists when woody debris additions-to-removals is out of steady state in favor of the former. When pulses and patches of woody debris establish new steady states of SOM formation through feedback processes that are self-selecting, wood-derived organic matter may persist longer.

This holds true for all litter, not solely woody debris. Only systems indefinitely out of steady state or with a new steady state that ignores past litter inputs can increase SOM stocks. Both are achieved through disturbance and self-selecting feedback processes that are regulated by the soil's constituent ecosystem of autotrophs, heterotrophs, and their physical environment. Therefore, any model of SOM formation must consider feedback processes between populations and their environment at the scale of ecosystems.

3 | ECOSYSTEM SCALE

At the ecosystem scale, litter additions, transformations, translocations, and removals that underpin SOM formation occur through the exchange of matter and energy in a structure of interacting organisms and their incorporated environment. The system in "ecosystem" entails a scale-specific hierarchy with dynamics that are jointly based on populations and processes, not solely one or the other (O'Neill et al., 1986). It also entails a set of feedback processes between populations, resources, and their environment. Therefore, any model of SOM formation needs scale and system dynamics, namely feedback processes, to be set accordingly.

3.1 | Assumptions and system formulation

The resolution necessary to interpret ecosystem-scale SOM formation is that of the ecosystem and the soil therein. In other words, SOM formation in an ecosystem summates the granularity of particle interactions, individual organisms, diurnal cycles, and seasonal fluctuations into the decades and centuries that constitute grassland and forest ecosystems. For instance, along a soil chronosequence of volcanic mudflows and vegetation cover at Mt. Shasta, California, total SOM accumulates even though individual SOM fractions diverge in their response to mudflow depth, rockiness, and tree proximity (Dickson & Crocker, 1953b; Sollins et al., 1983). Soil properties matter: The mudflows are relatively young (exact age is still disputed) with allophane-majority mineral surface area increasing with age, which increases the capacity of soils to store persistent SOM (Lilienfein et al., 2003). But vegetation cover and ecosystem development appear to matter more: Tree basal area and root production increase along the mudflow chronosequence (Dickson & Crocker, 1953a; Uselman et al., 2007), while new litter transforms at similar rates, thus implying additional SOM is due to additional litter inputs rather than protection of SOM by allophane in older soils (Qualls & Bridgham, 2005).

At decadal and centennial time scales, SOM begins to mirror population dynamics. More precisely, the commonly accepted definition of SOM as being all biologically derived organic matter in and on soil entails that SOM is originally litter x_L produced by a population of autotrophs, namely plants x_p. Litter-SOM x_L is understood to be biological matter that has undergone mortality and translocated to soil. Plant litter can be foliage, woody debris, bark, bud scales, fruiting bodies, roots, exudates, and volatiles. A portion of x_L is transformed by heterotrophs x_h—herbivores, detritivores, and other saprotrophic organisms—into residues, gases, and biomass, which may in turn be consumed by higher trophic levels. Yet as long as all trophic levels remain in the ecosystem, x_h ultimately undergoes mortality and is translocated to soil as x_L. Thus, more mortality as well as more productivity of x_p results in more x_L all other things being equal. Janzen et al. (2022) proposed a model of SOM stocks that goes one step in this direction by linking SOM to photosynthesis. Similarly, Augusto and Boča (2022) found global correlations for forest soil C stocks with leaf photosynethic capacity and forest biomass.

There is also a feedback process not commonly modeled due to a difference in temporal scales between plant population dynamics and decomposition processes (e.g., Manzoni & Porporato, 2009; Sierra & Müller, 2015; Zheng et al., 1997): Nutrients x_n made available by the transformation of x_L by x_h are taken up by x_p (Figure 3). When
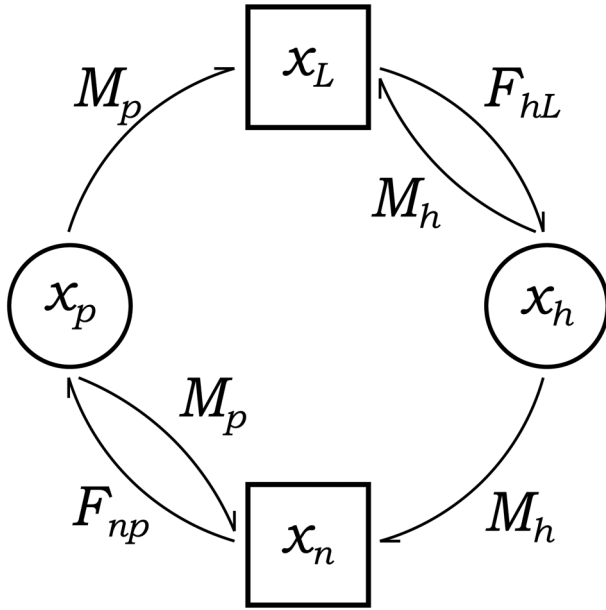
FIGURE 3 Ecosystem-scale perspective of soil organic matter formation per the Litter-Heterotroph-Nutrient-Plant (LHNP) model. Trophic interactions F_{ij} and mortality M_j of plants x_p and heterotrophs x_h result in litter-SOM x_L and available nutrients x_n.

newly available nutrients cause x_p to increase, especially when ecosystem nutrient stocks become depleted (Vitousek, 1982; Lang et al., 2016), inputs to x_L also increase. Such positive feedback mechanisms are avoided when modeling ecosystems, but they exist and contribute to evolutionary processes and population dynamics (DeAngelis et al., 1986), including SOM formation. They also do not continue in perpetuity as resources can become limiting (e.g., geological sources of phosphorus; Walker & Syers, 1976).

3.2 | LHNP model of soil organic matter formation

The following differential equations are rates of change for x_L, x_h, x_n, and x_p in terms of biomass at hectare and decadal scales [kg ha^{-1} 10 year^{-1}] similar to Zheng et al. (1997). Populations x_h and x_p are heterotrophs and plants, and resources x_L and x_n are litter-SOM and available nutrients. Translocations from populations j to resources i and vice versa—transformations of resources i into populations j—respectively involve non-predation mortality functions M_j and trophic interactions F_{ij}. Conversion factors c_{jL} and c_{jn} account for efficiency of converting population necromass into litter-SOM x_L or available nutrients x_n. Per population x_j, these factors are <1, which account for removals from the system (e.g., respiration, leaching) as well as any direct interactions between populations x_h and x_p (e.g., herbivory and parasitism). Efficiency factors e_h and e_p account for production of biomass per consumption of litter or available nutrients; these factors are likewise <1.

Thus, inputs to litter-SOM x_L are proportions c_{jL} of populations x_p and x_h that undergo mortality M_j and translocation to soil (Figure 3). Litter-SOM is transformed into heterotrophs x_h by consumption, which

is expressed by the trophic interaction F_{Lh}. To account for respiration losses, the production of x_h is proportion e_h of F_{Lh}. To complete the feedback process, inputs to available nutrients x_n are proportions c_{jn} of organisms x_h and x_p that undergo mortality M_j and translocation into plant-available forms. Similarly, available nutrients are transformed into plants x_p via the trophic interaction F_{np}. To account for respiration, the production of x_p likewise is proportion e_p of F_{np}. The only new additions to the system are dx_p.

$$\frac{dx_L}{dt} = c_{pL}M_p - F_{Lh} + c_{hL}M_h \tag{1}$$

$$\frac{dx_h}{dt} = e_h F_{Lh} - M_h \tag{2}$$

$$\frac{dx_n}{dt} = c_{hn}M_h - F_{np} + c_{pn}M_p \tag{3}$$

$$\frac{dx_p}{dt} = e_p F_{np} - M_p \tag{4}$$

M_j and F_{ij} functions remain to be explicitly defined depending on the soil and ecosystem in question. Nonetheless, a recommendation can be made on whether the functions are density dependent or independent. When litter or nutrients are transformed into biomass by heterotrophs or plants, respectively, an organism successfully found and competed for the resource in a defined span of space and time. If litter or nutrients are more abundant in the defined environment, the chances of organisms successfully finding and competing for resources increase. Likewise, when an organism undergoes mortality, the organism unsuccessfully competed with other organisms for resources in a defined span of space and time. If organisms are more abundant in the defined environment, the chances of organisms unsuccessfully finding and competing for resources increase. Both interactions are akin to density dependent Lotka–Volterra dynamics, specifically predator populations that track prey populations with a time delay due to cycles of unregulated exponential reproduction followed by excess predation and subsequent resource collapse. Therefore, both functions are assumed to be density dependent given the ubiquity of intra- and interspecific competition in populations.

The trophic interaction F_{ij} could be defined as a Lotka–Volterra feeding rate $F_{ij} = f x_i x_j$. Yet, there are situations where a change in resource or consumer density does not affect the other, for example, when so much resources are available that consumption and accompanying transformation becomes insensitive to additional resources. A suitable alternative is the trophic function F_{ij} proposed by DeAngelis et al. (1975), which captures unlimited resource conditions as well as Lotka–Volterra interactions (e.g., Zheng et al., 1997): $F_{ij} = f_{ij}x_i x_j/(b_j + x_j + w_{ij}x_i)$ for resource density x_i, consumer density x_j, specific feeding rate f_{ij} for x_j in kg^{-1} ha 10 year^{-1}, consumer population density b_j, and consumer-to-resource density ratio w_{ij}.

Less is known about the non-predation mortality function M_j, especially as most mortality of organisms is the result of predation. In soil, however, it is feasible that organisms that cannot sustain themselves undergo non-predation mortality or the functional equivalent

(e.g., dormancy). Plants also undergo non-predation mortality or the functional equivalent that is litter production. A possibility is the density-dependent mortality function M_j proposed by Zheng et al. (1997) so that trophic and mortality rates have the same dimensions: $M_j = \mu_j x_j^2$ for population density x_j and specific mortality rate μ_j in kg^{-1} ha 10 year^{-1}.

3.3 | Model validation, parameters, and stability

The LHNP model of SOM formation has several limits, foremost of which is the difficulty of validating M_p and M_h. Ideally M_p expresses *total* plant mortality and translocation to soil, but that requires both net primary productivity and all (functional) litter to be quantified *before* being removed or transformed; validation for M_h faces the same difficulty. Past efforts for plants rely on allometric modeling and upscaling from individual observations (e.g., Brunn et al., 2022), or laboratory-scale pulse experiments with isotope-labeled CO_2 (e.g., Kuzyakov et al., 1999). Even less is known about microorganisms: (functionally) dead microorganisms can be identified, but mortality rates are often assumed or fitted to models (e.g., Blagodatskaya & Kuzyakov, 2013; Pansu et al., 2010). Possible methods to trace total mortality as well as growth rates are those that use multiple isotope labels as per quantitative stable isotope probing (qSIP, Hungate et al., 2015), or explicitly follow the fate of root exudates such as reverse microdialysis (König et al., 2022). In practice, though, M_j expresses *net* mortality at the time scale of observation. Other models face similar difficulties to validate total rather than net fluxes, especially when patch-like or pulse-like, or belowground (Stutz & Lang, 2023; Tierney & Fahey, 2007).

Another limit is the difficulty of parameterizing F_{np} and F_{Lh}. Mycorrhizal associations, root architecture, internal storage, and the form of nutrient availability regulate F_{np} (D. W. Johnson & Turner, 2019; Rennenberg & Herschbach, 2013). Parameterization of F_{np} ranges from the production ecology equation based on nutrient supply, nutrient capture, and nutrient use efficiency (Binkley et al., 2004; Monteith, 1977) to ecosystem nutrition indicators based on nutrient distribution in soils, nutrient speciation, turnover rates, and root distributions (Lang et al., 2017; Prietzel et al., 2022). More challenging is parameterizing F_{Lh}, which is regulated by mineral and aggregate interactions, litter and community composition, and environmental boundary conditions (Schmidt et al., 2011; Kästner et al., 2021). Despite being feasible, parameterizing all factors for F_{Lh} is impractical. Recommendations range from focusing on the diversity of soil surfaces, litter inputs, and microorganisms (Lehmann et al., 2020) to relying on stochastic processes to disentangle age and residence times (Sierra et al., 2018).

Stochastic approaches may be especially promising given that soils, soil evolution, and SOM are patchy as evident from woody debris (Stutz & Lang, 2023). Soils and SOM do not change continuously from state to state (Sollins et al., 1983), rather they experience various phases of progressive and regressive changes (D. L. Johnson & Watson-Stegner, 1987; Phillips, 1993). Soils and SOM are therefore the remains of pulses and patches that persist, and thus repositories of historical contingency and disturbance (Stutz & Lang, 2023).

Yet, discovering the effects of disturbance as well as feedback processes on SOM require attractor states—that is, steady series or sets of states—of the LHNP model to be found. That is, if the LHNP model is perturbed (or the ecosystem is disturbed), the model may shift to a new steady state depending on the perturbation intensity and the model's thresholds between points of attraction. This can be done through mathematical analysis via phase planes akin to the analysis of the general trophic function F_{ij} in DeAngelis et al. (1975) and analysis of ecosystem stability in Ludwig et al. (1997).

Take coarse woody debris as an example: When disturbance creates downed woody debris—that is, a perturbation to plant biomass and thus translocation of litter to soil—dx_L increases by several factors. If dx_h increases due to heterotrophic consumption of woody debris, litter-SOM x_L reverts back to the attractor state. If dx_h does not increase due to an inability of the community to digest wood, either physically or biochemically, then x_L remains elevated (most often in the forest floor) unless the community adapts into a new system or another disturbance occurs. If dx_h increases beyond dx_L due to unrestricted consumption, then x_L decreases due to priming (e.g., Wambsganss et al., 2017) until dx_L increases again. Such attractor states are likely the norm as the input of coarse woody debris may not reach equilibrium within a millennium, but instead remains primarily dependent on forest disturbance (Spies et al., 1988).

4 | CONCLUSION AND OUTLOOK

Soil organic matter is the product of litter, soils, and their ecosystems, forests or otherwise. Formation of SOM occurs through additions, transformations, translocations, and removals of litter in disturbed and self-selecting (i.e., evolving) systems of autotrophic and heterotrophic organisms in their environment. Changes to either soil or the wider ecosystem affect the other and thus change SOM. As such, SOM is an indicator for disturbance and evolution of both soil and ecosystems, not only one or the other.

That is, SOM can record self-selective feedback processes—for example, community succession, ecosystem strategies, evolutionary pathways (Lang et al., 2016; Odum, 1969; Phillips, 2019)—of soils and ecosystems. For instance, Henry and Swan (1974) determined from coarse woody debris (and standing trees) that forest structure in a temperate mixed hardwood forest was more driven by disturbance than autogenic succession. Development of nutrient limitations of microorganisms (e.g., Camenzind et al., 2018, Kidinda et al., 2023) can also be determined through nutrient and carbon responses of plants and litter-SOM. Differing SOM responses to additional resources such as CO_2 in grasslands and forests (Terrer et al., 2021) and temperature in peatlands (Zeh et al., 2022) similarly can be clarified through plant resource economies, be it competition, growth form, litter production, or a combination thereof. And potential SOM saturation points can be simulated with the LHNP model under different starting conditions and deterministic parameters or stochastic probabilities. When saturation points are known, only then can SOM deficits be estimated and attributed to specific ecosystem disturbances (e.g., Sanderman et al., 2017).

When reversed, the same self-selecting feedback processes drive SOM degradation, especially in precarious ecosystems. Windthrown stands in alpine forests retain SOM when regeneration establishes, but when hindered by harsh microclimatic changes, loss of organic topsoil through decomposition and erosion reduces SOM and soil depth, thus excluding more regeneration and thus accelerating SOM and soil loss (Mayer et al., 2023). Fires in tropical forests create sandy soil savannas within 40 years when loss of litter, clay, and nutrients through seepage and erosion hinders regrowth and facilitates topsoil erosion (Flores & Holmgren, 2021). Yet, in other ecosystems, the direction of feedback processes may be changed quickly if timing, intensity, and composition of litter additions favor plant productivity over degradation processes. In other words, SOM losses can be reversed faster than previously thought with the right litter and disturbance regime (e.g., ruminants and adaptive multi-paddock grazing; Teague et al., 2016). Identifying such precarious and prospective ecosystems and their tipping points is crucial in light of global change.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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