Chapter 5

Mitigation potential of forests: challenges to carbon accrual in the ecosystem

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Introduction-main global change threats to forests

Forests are increasingly promoted as an important component in addressing the challenge of climate change and mitigating the rise in atmospheric carbon dioxide concentration (Cook-Patton et al., 2020; Griscom et al., 2017; Guo & Ren, 2014; Novick et al., 2022; United Nations, 2015). However, it is also becoming more evident that biological carbon sinks and stocks are subject to many constraints arising from the interdependencies and feedbacks between different ecosystem components, and the time and space that these processes require to achieve some level of self-stabilization. Of the different factors affecting the forest carbon sink, land-use change and forest conversion far outweigh the potential effects of environmental factors (Kondo et al., 2022; Perring et al., 2018). In addition to the harvest removals, the rate of soil carbon loss (as measured by heterotrophic soil CO₂ efflux) following a harvest is 20- to 50-fold greater than the rate of typical accrual during forest growth (Noormets et al., 2015; Schlesinger, 1997). Forest area and forest biomass have declined globally throughout human history (Erb et al., 2016; Sanderman, Hengl, Fiske, & Gregory, 2017), and in particular in the past few centuries (Watson et al., 2018) and decades (Maxwell et al., 2019; Potapov et al., 2017, 2021). About 26% of total anthropogenic CO_2 emissions since the industrial revolution are attributable to deforestation (Le Quere et al., 2016). A combination of factors, including the suitability of climate, soil fertility, and habitat, make converting forested areas particularly attractive as potential agricultural land. About 50% of the recent increase in cropland area is associated with deforestation (Gibbs et al., 2010; Potapov et al., 2021). Even though the area of formally protected forests has increased (Morales-Hidalgo, Oswalt, & Somanathan, 2015), this trend is far outpaced by deforestation and forest degradation. Today, while about 30% of the land surface is considered "forested" (as per FAO definition, forests are considered areas spanning more than 0.5 ha, with trees taller than 5 m and canopy cover of more than 10%), only about 18% of total forest area is considered "intact" (i.e., unaffected by direct human influence). However, even this small fraction is affected by obscure and diffuse factors such as hunting, air and water pollution, and altered global circulation patterns (Watson et al., 2018).

While deforestation is related to population pressure, it also brings several "obscure" risk factors that commit the forest to a path of further degradation. Maxwell et al. (2019) and Watson et al. (2018) describe eloquently how increasing fragmentation, further logging, introduction of invasive species, and hunting can lead to the loss of species that play important roles in the ecosystem as seed dispersers, links in the trophic chain, symbionts, or contributors to the structure of the ecosystem gradually lead to further decline in forest function. It is estimated that recent accelerated deforestation, fragmentation, and disruption of the interspecies interactions may have pushed the Amazon rainforest past the threshold of savannification, an irreversible transition from a forest to a savanna ecosystem (Boulton, Lenton, & Boers, 2022; Gatti et al., 2021). However, forest fragmentation is a global problem related to human habitation density and historical duration, with 50% higher fragmentation currently in the temperate than in tropical areas (Morreale, Thompson, Tang, Reinmann, & Hutyra, 2021).

Compounding the increasing direct anthropogenic pressures on forests are the indirect effects and natural ontogenetic changes in tree physiology in general. Specifically, the sink strength of two of the world's largest forest areas the Amazon and Africa—is projected to decline gradually in Africa, but rapidly in the Amazon (Hubau et al., 2020), and in both cases due to growing rates of mortality. Other projections do not predict the decline until the 22nd century and only under the high emissions climate scenario (Koven et al., 2022). The growth of temperate forests in the United States is expected to decline by 56%–91% due to high tree density and the growing frequency of drought (Evans et al., 2022). The resilience of coastal forests is expected to decline due to extended hydroperiod and salt–water intrusion associated with sea-level rise (Aguilos et al., 2021), and the increasing frequency of cyclones is projected to affect mangroves (Sippo, Lovelock, Santos, Sanders, & Maher, 2018). While the northern midlatitudinal sink has been increasing in the past (Ciais et al., 2019), it is projected to peak and begin to decline by 2030 due to a combination of age structure, climate, and management (Pilli, Alkama, Cescatti, Kurz, & Grassi, 2022), and physiological tradeoffs (Brienen et al., 2020).

Many environmental and site factors have changed over the past half-century, with combined effects on primary productivity, trophic and symbiotic interactions, and the carbon cycle more broadly. The continued anthropogenic additions of nitrogen to the global cycle (Galloway et al., 2008) have played a crucial role in increasing the productivity of both terrestrial and aquatic ecosystems (Conley et al., 2009; Greaver et al., 2016; Gundale, 2022; LeBauer & Treseder, 2008; Schulte-Uebbing, Ros, & de Vries, 2022). Increased nitrogen availability has also significantly altered the symbiotic relationships between plants and fungi, the competitive interactions between different fungal groups themselves (Carrara, Fernandez, & Brzostek, 2022; Carrara et al., 2021; Keiluweit et al., 2015; Pellitier, Zak, Argiroff, & Upchurch, 2021), carbon allocation to different plant organs, symbionts, and different metabolic C pools (Johnson, Angelard, Sanders, & Kiers, 2013; Prescott et al., 2020 and references therein). These alterations then translate to different C quality for decomposers, the rate of processing of these compounds, and the rate of mineralization of nutrients from therein. In addition, changes in temperature, precipitation dynamics, and atmospheric CO₂ affect fundamental plant physiology, including the balance between anabolic and catabolic processes, and modifying the processes associated with nutrient availability mentioned above (Bahram et al., 2020; Dai et al., 2020; Simon et al., 2020; Wallenstein & Hall, 2012). Finally, the changes in growth rate, mortality, and turnover that affect biomass pool size, also vary over a tree's life and with succession. With many of the European and North American forests recovering from widespread harvests a century ago (Clay et al., 2022) and the reforesting of previously cultivated agricultural lands, the past few decades have seen high rates of productivity (Pugh et al., 2019) attributable to the confluence of growth temperature, N deposition, increasing CO_2 , and higher water use efficiency, coinciding with the exponential growth phase of the tree's life. However, the trend of growing net productivity in recent decades is projected to run out as the current land surface carbon sink in the midlatitude forests is predicted to decrease drastically. Teasing apart the individual effects of these different factors and processes is difficult (Bellassen et al., 2011; Erb et al., 2013; Piao et al., 2015; Zhang et al., 2012), primarily due to the covariance of the driving variables and the interdependencies among different taxa and processes.

The intensifying use of ecosystems likely has negative connotations for biological carbon sequestration for two biological reasons. First, ecosystem management typically involves replacing ecosystems with high standing biomass and average productivity with low standing biomass and high productivity. As a result, human land use has doubled the carbon turnover rate compared to undisturbed natural systems (Erb et al., 2016). Second, the increasing disturbance (primarily harvest) frequency accompanying intensive land management stimulates heterotrophic activity and the mineralization of existing soil C pools (Lewis & Wheeler, 2019; Noormets et al., 2015). As soil carbon pool (including both live biomass and detritus) is a good indicator of ecosystem production potential and because its buildup is slower than its mineralization, protecting it should be the highest priority when evaluating sustainable management alternatives (Noon et al., 2022). Furthermore, as human extraction of primary production is sure to continue, and restoring high standing biomass ecosystems is unlikely, the prospects for biological carbon sequestration rely on protecting and increasing the soil carbon pool (Schlesinger & Amundson, 2019).

Recently, significant new insights have been obtained into carbon processing in the soil system, which appears much more dynamic than assumed previously and described in most carbon cycle models. New, microbially centered soil C balance models have been developed that capture the observed dynamics of the "recalcitrant" carbon pools (e.g., Robertson et al., 2019; Sulman et al., 2017), and they are being incorporated into the broader ecosystem and land surface models (Zhang et al., 2021). In addition to offering a more nuanced view and verifiable simulation of soil processes, these models also demonstrate the interdependence of plants, rhizosymbionts, and free-living saprotrophic fungi and bacteria that evolve together and complete the carbon and nutrient cycles, mutually facilitating the existence of each other (e.g., Kyaschenko, Clemmensen, Karltun, & Lindahl, 2017; Prescott et al., 2020). The rest of this chapter addresses factors that affect carbon cycling in forests, both in the vegetation and soil, and in the standing stocks and the fluxes between them. There is growing evidence that the persistence of carbon in the ecosystem is determined by a suite of factors, the physiological and chemical characteristics of the organisms and their biomass, the communities of interacting organisms, and the edaphic context and the environmental or climatic factors in which the interactions of

different biogeochemical transformations play out (Liu, García-Palacios, et al., 2022; Schmidt et al., 2011). Therefore carbon sequestration capability is difficult to accelerate and even harder to engineer with functionally incomplete (i.e., purely production-focused) ecosystems.

Carbon cycle and carbon sequestration

Carbon storage in ecosystems, at its simplest, is the cumulative difference between inputs and outputs. At times, this has been trivialized by equating carbon sequestration (change in ecosystem C storage) with productivity. It has become evident that the ideal of forest restoration for climate mitigation (Canadell & Raupach, 2008) and on-the-ground implementation (e.g., the Bonn Challenge; https://www.bonnchallenge.org/) can diverge significantly. Pursuing economically lucrative fast-growing plantations under the cover of climate friendliness compromises many of the properties that natural forests provide (Hurteau, 2021; Lewis & Wheeler, 2019) and overlooks the land cost (Doelman et al., 2020). Importantly for our current topic, there are also qualitative differences in the carbon pools that are produced in early successional fast-growing plantations and in older natural forests, with complex interactions between the producers, transformers, and decomposers that contribute to the creation of the array of chemical and physical structures that house these carbon stocks (Adamczyk, Sietiö, Biasi, & Heinonsalo, 2019; Augusto & Boča, 2022; Carrara et al., 2021; Finzi et al., 2015; Schmidt et al., 2011; Watson et al., 2018). Cebrián and Duarte (1995) showed that the detritus of fastgrowing plants also decays rapidly, as it has fewer complex secondary chemicals. The mass of standing detritus stocks in their study did not correlate with net primary production (NPP). Rather, plant turnover rate and detrital C mass were inversely related, and plant turnover and detrital turnover were positively related. Similarly, in an experimental study of moisture and nutrient availability, we showed that plant biomass accumulation and net ecosystem carbon balance can respond in a contrasting manner since heterotrophic respiration that controls the loss of carbon from an ecosystem responds to these environmental triggers differently than does plant productivity (Noormets et al., 2021). Furthermore, even plant processes of autotrophic respiration, photosynthesis, and growth all respond differently to environmental constraints (Prescott et al., 2020). Recent studies have made it clear that the assumption of proportional partitioning of carbon from photosynthesis to the growth of different organs, their respiration, and to symbiotic and free-living soil organisms is overly simplistic insofar as it does not consider the timescale of the connections and lags imposed by different pools. In the forest management context, this omission becomes most important when the effects of forest management activities on heterotrophic respiration go unaccounted. The physical disturbance of soil structure stimulates the decomposition rates of above- and below-ground detritus, which are all enhanced in the management process. Even if not harvested, the intensification of decomposition under intensive management leads to faster loss of detritus than in undisturbed forests (Mayer et al., 2020; Noormets et al., 2015; Simola, 2018). Yet, disturbances can also release nutrients and temporarily increase primary production. Biological carbon sequestration requires building the size and stability of ecosystem carbon stocks in the long term (decades to centuries, longer than the lifetime of individual organisms), factoring in inevitable disturbances that cause losses; the rate of annual accrual is only secondary (Körner, 2017). Growing the *land* C pool requires that both the live and dead (detritus) pools in both vegetation and in the soil increase with time. Growing the soil C pool requires that the inputs of new organic matter via detritus exceed the rate of mineralization by soil microbes. Currently, the terrestrial biosphere cycles about 15.7% of the atmospheric carbon each year, with roughly equal amounts being assimilated through photosynthesis and released through respiration. Here, too, there are feedback loops tying (1) the residence time and rate of turnover of C in different pools to tissue chemical composition and its processing pathway, and (2) the rates and pathways of C input to soil microbial community composition (Feng, He, Zhang, Han, & Zhu, 2022; Jacobs, Sulman, Brzostek, Feighery, & Phillips, 2018). The fraction of carbon protected from mineralization is determined by a complex interplay between tissue chemistry, processing pathway, symbiont and decomposer community, priming, competition, soil mineralogy (Von Lützow et al., 2006), climate, and disturbance. The level of mycorrhizal colonization of plant roots and the competitive interactions between the rhizosymbiont and free-living saprotrophic fungi, as affected by nutrient availability, determine the detritus processing, the stabilizing interactions available to different decomposition products, and the accumulation of C in different soil fractions (Bahram et al., 2020; Cotrufo, Haddix, Kroeger, & Stewart, 2022; Wallenstein & Hall, 2012). Furthermore, arbuscular-vesicular mycorrhizal (AM) communities are associated with consistently and significantly lower soil C stocks than ectomycorrhizal (EM) communities, a pattern that is stronger than any observed with climate or soil type (Averill, Turner, & Finzi, 2014). It appears that the mechanism for greater carbon sequestration may be through slow-growing EM plants in nutrient-limited conditions where the plants face significant carbon surplus that is passed to the EM fungal symbionts, which in turn modify the spectrum of chemicals released into the soil (Kyaschenko, Clemmensen, Karltun, & Lindahl, 2017; Prescott et al., 2020; Section "Soil carbon balance"). Unfortunately, evidence points in the opposite direction-the expansion of the AM plant communities over recent decades, driven largely by high N availability (Jo, Fei, Oswalt, Domke, & Phillips, 2019) and leading to an apparent trade-off between plant and soil carbon storage (Terrer et al., 2021).

Soil carbon balance

Maximizing net primary production versus biomass/carbon stocks

Humankind uses about 38% of the total land surface (Foley et al., 2011; Riggio et al., 2020) and appropriates more than 25% of NPP (Haberl, Erb, & Krausmann, 2014), 41% in some areas (Abdi, Seaquist, Tenenbaum, Eklundh, & Ardö, 2014). Conversion of natural vegetation to crops maintains comparable primary production, but the turnover time is reduced several-fold (Erb et al., 2016), and the associated physical disturbance accelerates heterotrophic respiration, the loss of soil carbon and nutrients, and the degradation of its structure. It is estimated that agricultural cultivation throughout human history has caused the release of about 110 billion tons of soil organic carbon (SOC) (Sanderman, 2021). With a growing global population and ever-expanding and intensifying land use, management-related disturbance is expected to affect a growing fraction of global land, shifting the global carbon dynamics (Bond-Lamberty, Bailey, Chen, Gough, & Vargas, 2018). The comparison of actively managed forests to unmanaged ones shows that they have about 50% lower carbon stocks in all pools—live biomass both above and below ground, as well as detritus and mineral soil carbon (Noormets et al., 2015). Soil carbon stocks are also further from the soil carbon holding capacity in managed than natural ecosystems (Slocum, Nguyen, Solomon, Lehmann, & Plante, 2021).

Throughout history, humankind has applied selective pressure to achieve greater primary production (much of which is edible) at the cost of lower standing biomass (which is not) (Cebrián & Duarte, 1995; Erb et al., 2016). Thus, maximizing carbon sequestration in the form of greater C stocks represents a 180-degree departure from the traditional management approaches that have been used to maximize productivity. The latter can be achieved by selectively cultivating the faster-growing and greater-yielding genotypes, improving their growth conditions, and minimizing stresses. In contrast, maximum carbon stocks are seen in ecosystems that have been allowed to reach advanced structural and functional complexity (Lehmann et al., 2020), with a multilayered canopy, diverse ecological niches, where specialist species utilize resources in a different manner or at a different time than their competitors (Messier et al., 2022; Perry, Oren, & Hart, 2008). In fact, competition, resource scarcity, and complex alternative interactions are key to achieving the structural and functional relationships that create and hold on to the biological matter in live biomass, detritus, and mineral-associated pools. The recently formulated "surplus carbon" hypothesis (Prescott et al., 2020) convincingly demonstrates that the interaction of carbon, nutrient, and water dynamics determine plant carbon sink strength, the processing of the "surplus carbon" not used by plants either in secondary chemistry pathways, export to mycorrhizae, or exudation, with the net effect of more chemically complex secondary compounds being produced under stressful growth-limiting conditions. These compounds are energetically expensive, but also chemically recalcitrant, and tend to accumulate over time. Fast-growing plants, in contrast, tend to have low concentrations of complex secondary chemicals, which upon death are also fast to decompose (Cebrián & Duarte, 1995; Craig et al., 2022). Thus, rapid productivity and the production of persistent chemical structures appear to be mutually exclusive (Terrer et al., 2021).

All organic soil carbon originates from primary production that reaches the soil directly or through an intermediate trophic level. The pathways of carbon input to soil-whether as aboveground or belowground, plant or fungal, nutrientrich or -poor, chemically simple or complex-are associated with a distinct chemical composition and exposure to different decomposer communities and environmental conditions that then determine the persistence of that material in the soil (Cotrufo et al., 2022; Drigo et al., 2010). For example, systematic differences between forest types have been observed in the level of carbon allocation to mycorrhizal fungi (Averill & Hawkes, 2016; Ouimette et al., 2020), which may be related to soil characteristics and its C and nutrient dynamics (Hobbie, 2006). In addition to direct mycorrhizal fungal production that can consume 1%-30% of total ecosystem NPP (Allen & Kitajima, 2014; Frey, 2019; Ryan, Hubbard, Pongracic, Raison, & McMurtrie, 1996; Zhang et al., 2019), there are also the costs of fungal respiration and exudation of low-molecular-weight compounds by both plant roots and fungi (2%-17% of NPP; Nguyen, 2003; Yin, Wheeler, & Phillips, 2014), and that also exhibit systematic relationships with plant taxonomic and life strategy characteristics (Colombi, Chakrawal, & Herrmann, 2021; Sun et al., 2021). The chemical composition of the exuded compounds differs both between plant roots and fungi (Dietz et al., 2020; Ding, Ye, Liu, Shi, & Liang, 2021; Kaiser et al., 2015) and between different fungal taxa (Frey, 2019; Huang et al., 2022), which can have both stimulating and inhibitory effects on free-living soil microbes. Furthermore, the coevolutionary history of plants and different symbiotic fungi has led to the deactivation or even complete loss of different enzymes, that affects their access to different carbon and nutrient sources (Carrara et al., 2022; Keller, Brzostek, Craig, Fisher, & Phillips, 2021) and the different pathways to

and rates of soil carbon input (Cotrufo et al., 2022), stabilization (Cotrufo et al., 2022; Kallenbach, Frey, & Grandy, 2016), and destabilization (Bailey, Pries, & Lajtha, 2019). AM fungi, in particular, have become very dependent on their plant hosts for carbohydrates as the energy source and have a very limited set of genes for producing both Cmining and N-mining enzymes (Frey, 2019). At the same time, AM fungi also appear to be drawing more carbohydrates from their host plants than EM symbionts, and also exuding more of those assimilates to the soil medium (Keller et al., 2021). However, whether this represents an additional metabolic burden or simply an inevitable by-product of "surplus carbon" in plants (Prescott et al., 2020), where plant productivity is limited by other nutrients and accumulated assimilates need to be discharged to minimize product-mediated suppression of photosynthesis, remains to be determined. Curiously, it is the EM-dominated ecosystems that tend to have higher soil C stocks than AM ecosystems, suggesting that the EM plant and fungal detritus are harder to metabolize (Cornelissen, Aerts, Cerabolini, Werger, & van der Heijden, 2001; Sulman et al., 2017), EM-derived exudates trigger less priming (Kuzyakov, 2010) than AM exudates (Sun et al., 2018; but see Augusto & Boča, 2022) or that the environments dominated by EM ecosystems are less conducive for soil organic matter decomposition overall. It is also possible that EM fungi use a greater fraction of the plant-derived carbohydrates for their own metabolism, producing N-mining enzymes, and consequently exude less (Fig. 5.1). The widespread pattern of contrasting SOC accumulation in ecosystems with a different mycorrhizal type (Averill et al., 2014) correlates well with the mycorrhizal ability to produce enzymes that mine nutrients from soil organic matter (SOM) (Terrer et al., 2018) and is likely a key factor behind the variability of priming across biomes, climate conditions, and soil properties (Ren et al., 2022). Bacteria that further decompose fungal tissue and partial decomposition products make up only 1%-3% of SOM, contribute to the stabilization of soil C through aggregate formation (Frey, 2019), partly attributable to their high turnover, partly to their chemical composition (Bailey et al., 2019; Cotrufo et al., 2022; Kallenbach et al., 2016; Keiluweit et al., 2015). It may at first appear counter-intuitive, but greater carbon stabilization requires a more structurally and functionally complex decomposer pathway, as summarized by Cotrufo et al. (2022). Fungal and bacterial decomposition products appear to be some of the most stable and longestlived compounds, contributing disproportionately to soil C (Kallenbach et al., 2016; Strukeli et al., 2013; Strukeli, Brais, Quideau, & Oh, 2012). Some studies implicate fungal melanin as the primary contributor to soil C (Fernandez & Kennedy, 2016, 2018; Fernandez, Langley, Chapman, McCormack, & Koide, 2016; Frey, 2019). In contrast, some have found that fungal chitin individually (Godbold et al., 2006 and references therein) or partly decomposed and crosslinked with root tannins persist the longest (Adamczyk et al., 2019), and yet others that bacterial cell walls and other



FIGURE 5.1 Hypothetical schematic of carbon allocation to the mycorrhiza's own metabolism versus exudation, the effect of the latter on priming, and the overall observed soil C stock. Please also see Sections "Nutrient availability" and "Global change factors: carbon dioxide, temperature, and precipitation", and Terrer et al. (2018). The width of the arrows indicates the size of the flux. The mycorrhizal types differ in their relative contribution to priming versus respiration, and in the use of soil C in priming.

residues do (Geyer, Schnecker, Grandy, Richter, & Frey, 2020; Yang et al., 2022). In all cases, the accumulation of any material has to do with the low abundance or activity of enzymes capable of metabolizing that material and may be limited by the availability of energy source for producing these enzymes.

Plant-microbe integrated system

Plants and mycorrhizal fungi are often obligate symbionts—each depends on the other to access necessary resources (Kohout et al., 2018; Mushinski, Gentry, & Boutton, 2018, 2019; Mushinski, Zhou, Gentry, & Boutton, 2018). Even though their complementarity and exchange of nutrients for carbon has been seen through the lens of the economic trading model for a long time, the recent review of evidence by Prescott et al. (2020) suggests that the connections run deeper, that the exchange is not optional or actively controlled by plants (Prescott et al., 2021). Rather, the coordinated functioning of these organisms suggests coevolution, where the partner is both a living organism, but also simply a part of the environmental context for the other. The concept of "surplus carbon" presented by (Prescott et al., 2020) explains how and why resource sharing could have become reinforced. It is noteworthy that while up to two-thirds of new root C inputs may wind up in mycorrhizae (Meier, Pritchard, Brzostek, McCormack, & Phillips, 2015; Zhang et al., 2019), it could also decrease to near zero in situations where strong plant C sinks remain present. Thus, the sharing or exchange of resources between plants and mycorrhizal symbionts is dynamic and manifests in a wide range of carbon allocation to different tissues (See et al., 2022), with corresponding changes in chemical composition (Averill et al., 2014), and implications for biological and chemical C processing pathways (Drigo et al., 2010; Wang et al., 2021) and soil physical structure (Lehmann, Kinyangi, & Solomon, 2007).

The direct access of mycorrhizal fungi to plant carbohydrate supply puts them at a tremendous metabolic advantage compared to free-living saprotrophic fungi, which has further contributed to the selective activation and inactivation of different C- and N-mining genes (Weemstra et al., 2020). EM fungi, in particular, exhibit distinct profiles of N-mining enzymes (Nicolás et al., 2019), whereas the C-mining pathways found in their saprotrophic ancestors are missing (Pellitier et al., 2021). Notably, this adaptation appears to have evolved independently in different fungal lineages and resulted in different suites of active enzymes that achieved the same end-outcompeting free-living saprotrophic fungi in access to nitrogen by using plant-derived new assimilates as the energy source. In contrast, the saprotrophs must mine for both carbon and nitrogen from dead organic matter. Furthermore, it has been observed that EM-litter tends to be richer in aromatic compounds than AM-litter (Terrer et al., 2018), leading to different levels of specialization in N extraction (Weemstra et al., 2020). Arbuscular mycorrhizae have a more limited arsenal of enzymes, and their primary contribution to plant nutrient acquisition appears to be through an increased surface area (Terrer et al., 2018 and references therein). Given the greater N extraction efficiency of EM fungi (Pellitier et al., 2021), which have more specialized enzymes for extracting N from complex organic molecules, the N cycle tends to be more closed in EM-associated communities, limited to the few taxa that possess the metabolic capacity. In contrast, in AM-associated communities, the exudates of simple carbohydrates and organic acids provide a ready energy source for a broader range of microbes and make the mineable resources available to a broader group of decomposers (Lin, Guo, Li, Ma, & Zeng, 2018). Whether that means that EM symbiosis is more Cexpensive for plants is not immediately obvious, nor does it have to be causal. The surplus carbon hypothesis (Prescott et al., 2020) allows for the photosynthetic surplus of carbohydrates that needs to be dissipated. Both secondary compounds and belowground allocation could be mechanisms allowing the plant to reduce product accumulation-driven suppression of photosynthesis. If plant sinks are limited by other resources (e.g., nutrients), the process of carbon dissipation through symbionts and exudation may be energetically more favorable than the accumulation of non-structural storage carbohydrates.

The saprotroph activity, lacking direct access to plant-derived carbohydrates, receives some energy from root and fungal exudates (Canarini, Kaiser, Merchant, Richter, & Wanek, 2019; Keller et al., 2021) or must mine it from different organically complex decomposition products, which is energetically very expensive. Therefore, when mycorrhizal fungi thrive, saprotrophs are suppressed. Such suppression of free-living saprotrophs by symbiotic fungi is called the Gadgil effect (Gadgil & Gadgil, 1971). It is frequent but not universal (Malik, 2019; Peršoh, Stolle, Brachmann, Begerow, & Rambold, 2018), depending on the fungal taxa involved, the soil type, nutrient availability, and the level of carbohydrate subsidy available to the symbiotic fungi from their plant hosts (Beidler, Oh, Pritchard, & Phillips, 2021). The balance of carbon-advantaged mycorrhizal fungi and free-living saprotrophs could change quickly if plant sink strength were to change in response to nutrient, light, or water availability (Kyaschenko, Clemmensen, Karltun, & Lindahl, 2017). For example, fertilization would increase plant sink strength (Prescott et al., 2020), leading to the retention of a greater fraction of assimilates in the plant and consequently starve the mycorrhizae, which, in turn, would increase resource availability to free-living saprotrophs. Similarly, there can be competition between fungi from different taxa that form mycorrhizae on the same plant's roots (Heklau et al., 2021; Teste, Jones, & Dickie, 2020). Furthermore, priming and Gadgil effects may be taking place at the same time and in the same soil volume. Thus, even though mycorrhizal fungi themselves cannot survive as saprotrophs (i.e., get their energy and nutrient needs met solely with dead organic matter), their presence and activity strongly influence saprotroph activity and soil carbon decomposition (Moore et al., 2015; Read & Perez-Moreno, 2003).

Combined, the obligate codependence of plants and symbionts (Kohout et al., 2018; Mushinski, Gentry, & Boutton, 2018, 2019; Mushinski, Zhou, et al., 2018), competition between different fungal groups (Brzostek, Dragoni, Brown, & Phillips, 2015; Keiluweit et al., 2015; Peršoh et al., 2018), species-specific allelopathic interactions (Pizano, Kitajima, Graham, & Mangan, 2019), and tight relationships between community composition and productivity (Carteron, Vellend, & Laliberté, 2021; Laliberte, Lambers, Burgess, & Wright, 2015; Van der Heijden et al., 1998; Van der Heijden, Martin, Selosse, and Sanders, 2015), it begins to emerge that soil carbon processing is the result of the complex interaction of plants, their symbionts, and free-living soil microbes rather than the sum of their individual activities (Brzostek et al., 2015; Craig et al., 2022; Keiluweit et al., 2015; Zhu, Riley, Tang, & Koven, 2016). Or, as Schmidt et al. (2011) put it, soil organic matter's persistence is an emergent ecosystem property. Plant-microbe interactions affect both the C input side of soil carbon balance (via surplus carbon dissipation, carbon transformations, novel katabolic enzymes, and the broader spectrum of exudates and detritus, to name some) and the C loss side (via priming, liberating C from the minerally bound pool, surplus carbon dissipation, and broader spectrum of exudates and detritus, to name some; Fig. 5.2). We postulate that the complex pathways of interdependence, the coupling of carbon, nutrient, and water economies, and the cooccurrence of symbiotic and competitive relationships contribute to the greater carbon sequestration potential of natural than plantation forests (Lewis & Wheeler, 2019). The amount of marketable timber may be lower, but the total biomass is greater in multispecies than in monospecific plantations (Feng, Schmid, et al., 2022).

Nutrient availability

The primary determinant of the extent of mycorrhizal colonization of roots is soil nutrient availability. Therefore the widespread and growing use of supplementary fertilization has an immediate and powerful impact on not only plant productivity (Fox, Allen, Albaugh, Rubilar, & Carlson, 2007), but also on plant–mycorrhizae interactions (Carrara et al., 2022; Gilliam et al., 2019 and references therein, Pellitier & Zak, 2021). Broadly, it leads to greater aboveground and lower belowground carbon allocation (Chen, Yang, & Robinson, 2013, 2014), lower root colonization by fungi, lower exudation rates (Keller et al., 2021; Sun et al., 2021), and reduced mycorrhizal growth (Högberg, Högberg, Wallander, & Nilsson, 2021). However, as mycorrhizal taxa differ in nutrient acquisition efficiency (ectomycorrhizae being more efficient than arbuscular mycorrhizae; Pellitier et al., 2021), changing nutrient availability can have contrasting effects on their interaction with plants (Carrara et al., 2022). The changing plant needs and fungal efficiencies



FIGURE 5.2 Conceptual model of the mediation of long-term carbon sequestration (the surplus of assimilated carbon compared to respired carbon) of plant-derived assimilates by symbiotic and saprotrophic fungi and the mineral soil. The flow of carbon between organisms and soil pools is shown with brown arrows, the flow of nutrients in orange, and the flow of water in blue. The competing interactions for both carbon and nutrients occur between symbionts, saprotrophs and soil mineral surfaces, except the latter is finite and passive, whereas the former two are more dynamic and affected by nutrient and water availability. Priming of old organic matter decomposition can be triggered by new carbohydrate input from either plant roots, symbionts, saprotrophs, old exudates, or release from minerally exchanged compounds. Sequestration is the net difference between the necessary assimilatory and mineralization processes.

may also be behind the changes in the predominant fungal communities with the degree of nutrient limitation within the successional stage of the ecosystem (Sulman et al., 2017) and even the lifetime of an individual plant (Hagenbo, Kyaschenko, Clemmensen, Lindahl, & Fransson, 2018; Kyaschenko, Clemmensen, Hagenbo, Karltun, & Lindahl, 2017). The changing intensity of resource mining by mycorrhizal fungi relieves competition on free-living saprotrophic fungi, and should their access to exudates improve their energy supply, this may lead to increased priming (Ning et al., 2021; Fig. 5.2). The changes in the competitive balance between fungal functional groups have direct impacts on both plant and microbial productivity, detritus production pathways, litter chemistry, the energetics of carbon dissipation pathways within plants (Prescott et al., 2020), and the competitive relationships among the plant hosts (Clark, Morefield, Gilliam, & Pardo, 2013; DeForest & Snell, 2020).

In principle, the nutrient availability-mediated effects on soil microbial community can be readily reversible (Carrara et al., 2022), except if the ecosystem has large amounts of N in long turnover pools or if the microbial community has already changed and lost N-sensitive species (Morrison et al., 2016; Mushinski, Gentry, & Boutton, 2018, 2019), in which case the recovery may take decades (Gilliam et al., 2019). Different nutrient loading can also affect the predominance of AM versus EM plant species and communities. Jo et al. (2019) reported a shift toward greater AM predominance in eastern US forest communities over the past three decades, attributed largely to growing N deposition, with decreasing fire frequency and rising temperatures also playing a role. The net effect of such a transition is the acceleration and further opening of both the carbon and nutrient cycles. Finally, nutrient availability also alters live tissue chemistry and associated trophic relationships. At low surplus nutrient levels, plants gain the ability to produce extra secondary defense chemicals (Mur, Simpson, Kumari, Gupta, & Gupta, 2017), whereas at excess nutrient levels, pathogens may flourish due to both greater nutritional value and lower concentration of secondary defense compounds in plants (Blakeslee et al., 1999). Both excess and insufficient nutrients can lead to increased carbon accumulationmediated by limited microbial access to carbohydrate energy sources in the first case, and by increased chemical recalcitrance and competitive limitation to carbohydrate energy sources in the latter. However, in the longer term, as the microbial communities and litter chemistry adjust, the persistence of carbon in the soil is expected to be greater in the nutrient-limited and functionally complex ecosystem than in the one with excess nutrients, functionally simpler structure, and lower mycorrhizal colonization (Wilkins, Clark, & Aherne, 2022).

Management, forest structure, and disturbance

Human land management aims to increase the productivity of a particular crop tissue per unit of time and is achieved by maximizing resource delivery to those tissues. The side effects of managing for productivity include reduced pools of other non-target tissues and functions. The shorter disturbance interval of managed forests has resulted in about twofold lower C stocks compared to unmanaged forests (Noormets et al., 2015), observable both in live biomass (aboveand belowground), detritus, and soil C stock, and is attributable to increased heterotrophic activity by soil disturbance and mixing. As shown by Law et al. (2018), landscape-level carbon retention responds strongly to reduced harvest intensity and extended harvest cycles. The loss of organic matter from the soil is as universal in a managed forest as in agricultural lands (Baker, Ochsner, Venterea, & Griffis, 2007), except occurring slower in forests, owing to the lower frequency of disturbance. Throughout human agricultural history (for practical purposes, roughly 10,000 years), it is estimated that we have reduced carbon turnover time in terrestrial ecosystems by about twofold (threefold in intensive agricultural systems; Erb et al., 2016; Sanderman et al., 2017), facilitated by deliberate changing of ecosystem structure and composition, and supported by modifying supporting processes of competition, trophic interactions, and nutrient availability. In pursuit of ever greater productivity, the planting of fast-growing non-native tree species is widespread globally (e.g., poplar in China, eucalypt in the US south, loblolly pine in South America and Europe, lodgepole pine in Scandinavia). While the full ecosystem implications of this practice are unknown, some evidence is emerging that the dominant canopy species may significantly change the habitat it is planted into. Not only is novel plant species establishment dependent on the microbes available locally (Pizano et al., 2019), but the plant species can also affect the interactions among the microbial community, as well as other species in the ecosystem. For example, Löfroth, Andersson, Roberge, and Sjögren (2022) found that the introduction of lodgepole pine to Sweden in the 1970s has led to reduced ant activity in lodgepole pine compared to the native Scots pine forests. Declines were seen in ant foraging and the number of species.

Even though the increasing relaxation of the definition of what constitutes a "forest" (Chazdon et al., 2016) partly masks the trend, the reality is that natural forests remain under intense logging and land conversion pressure (Maxwell et al., 2019; Potapov et al., 2017; Potapov et al., 2021). Furthermore, land converted from prior agricultural use to forested is nearly universally intended for intensive production forestry (with rotation cycles only a fraction of the typical

lifetime of the native species), with all the differences and limitations compared to natural forests that were described above. Even forests that have been allowed to develop for a relatively long (200 years) following intensive management show legacies of past management. For example, Perring et al. (2018) observed that forests that had been unmanaged in the 1800s have responded to increased nitrogen deposition with greater species diversity and tree height, whereas forests that were managed intensively 200 years ago have responded to the same environmental change with reduced species diversity and tree height. Although forests were not actively fertilized 200 years ago, the elevated disturbance frequency, greater canopy openness and altered species composition may have altered soil microbial communities, carbon allocation, and soil nutrient pools. As noted above, plant and fungal species composition and diversity are interdependent (Liu, García-Palacios, et al., 2022), and the metabolic capacity of microbial populations to mine nutrients and their competitive interactions with other soil microbes determine the carbon and nutrient accumulation in the soil (Augusto & Boča, 2022). Modern intensive management approaches that disrupt plant mycorrhizal relationships by supplying abundant inorganic nitrogen and other minerals disrupt several of the carbon stabilization mechanisms described above-the competitive suppression of saprotrophic microbes by mycorrhizal fungi (Keiluweit et al., 2015; Pellitier et al., 2021), competitive binding of nutrients and carbon compounds to mineral surfaces (Craig et al., 2022; Zhu et al., 2016), chemical modification of mycorrhizal-exuded compared to root-exuded carbon (Frey, 2019; Kaiser et al., 2015; Zhang et al., 2019), the cross-linking of root and fungal decomposition products (Adamczyk et al., 2019), and limiting physical occlusion by degrading soil aggregates (Lehmann et al., 2007). While purely hypothetical, it is possible that the observed increase of heterotrophic respiration in recent decades (Bond-Lamberty et al., 2018; Noormets et al., 2015) is related to soil nutrient dynamics (stimulating the saprotroph activity) as much as to the rising temperature (Bond-Lamberty & Thomson, 2010). Even though high nutrient availability is often associated with reduced organic matter decomposition, in managed ecosystems fertilization often co-occurs with physical disturbance, and the net result is accelerated loss of organic matter (Clarke et al., 2021; Mayer et al., 2020; Noormets et al., 2015; Simola, 2018). Given the intensification of disturbances (Bowman et al., 2020) and the multipronged and positive feedback-enhanced effects of disturbances on forest carbon (Seidl, Schelhaas, Rammer, & Verkerk, 2014), it is more important than ever to consider all dimensions of the ecosystem and soil resilience to disturbance (Yi & Jackson, 2021) and ensure their vigor and sustainability (Nabuurs et al., 2019; Nagel et al., 2017). Therefore, the widespread substitution of fossil fuels or even building materials with biomass may be unsustainable (Leturcq, 2020) once the costs on soil health and long-term ecosystem function are factored in. A growing number of studies find that whole-tree harvesting is detrimental to soil health and C content (Clarke et al., 2021), particularly if the forest floor is affected (James et al., 2021). As human extraction of primary production is certain to continue, and restoring high standing biomass ecosystems is unlikely, the prospects for biological carbon sequestration must rely on protecting and increasing the soil carbon pool (Schlesinger & Amundson, 2019). Three ways to increase forest live carbon stocks (but not necessarily timber yield), soil C stocks, microbial taxonomic and functional diversity, and the resilience of these elements to disturbance are (1) reduce the intensity of each disturbance (Law et al., 2022); (2) extend the harvest interval (Noormets et al., 2015); and (3) ensure the continued biodiversity of both plant and microbial components, including increasing tree species diversity of plantation forests (Feng, Schmid, et al., 2022; Gurevitch, 2022; Messier et al., 2022) (Fig. 5.3).



FIGURE 5.3 Modern monospecific forests can remain structurally and functionally impoverished even well into maturity. In this shortleaf pine and loblolly pine forest in Davy Crockett National Forest, the biannual prescribed fires maintain the understory in the early successional stage, favorable for the federally endangered red-cockaded woodpecker, but keeping the forest as an ecosystem from recruiting late-successional hardwood species and reaching greater structural and functional diversity. The regular disturbances affect both vegetation as well as soil microbial composition, with the symbionts of late successional species disappearing, making their reestablishment that much more challenging. *Photo by Asko Noormets, lead author.*

Global change factors: CO₂, temperature, and precipitation

The global change factors affecting productivity, allocation, auto- and heterotrophic respiration, and soil carbon processing pathways are atmospheric CO_2 , temperature, and the amount and temporal distribution of precipitation. Conceptually, their effect on soil carbon balance is depicted on Fig. 5.4.

CO_2

The rise in atmospheric CO₂ since preindustrial times is estimated to have increased forest productivity by 21% (Chen, Riley, Prentice, & Keenan, 2022; De Graaff et al., 2006) and 12% in the past 40 years alone (Keenan et al., 2021). The stimulation of belowground growth can be greater or lower than the aboveground stimulation, depending on nutrient availability (Terrer et al., 2021). With an increased demand for nutrients, elevated CO₂ can promote mycorrhizal colonization of roots, increase belowground carbon allocation and exudation, intensifying soil carbon and nutrient cycles (Frew & Price, 2019; Meier et al., 2015). While the processes involved are not fully understood, the evidence suggests that the cumulative effects of priming and community shift lead to lower soil C stocks in forest soils under elevated CO₂ (Terrer et al., 2018, 2021; Van Groenigen, Qi, Osenberg, Luo, & Hungate, 2014). This is associated with "nutrient mining" as mediated by fungal enzymes and both root and fungal carbon exudates that supply free-living saprotrophic microbes with an energy source, as well as liberate mineral-bound carbon compounds (Meier et al., 2015; Section "Plant-microbe integrated system") and may also be due to greater C surplus and fewer secondary compounds (Prescott et al., 2020). The magnitude of soil C change correlates with the mycorrhizal type (AM vs EM) and photosynthetic pathway (C_3 vs C_4), predominant vegetation (grasslands and tropical forests typically host AM, whereas EM predominate in temperate and boreal trees, even though they occur in the tropics, too), soil mineralogy, and climate. Despite the apparent divergence in the response of soil C dynamics to rising CO₂ between AM and EM species (Terrer et al., 2021), earlier analyses show that, by and large, decomposition tends to accelerate under elevated CO_2 (Van Groenigen et al., 2014), perhaps due (1) to lower tissue quality and fewer secondary compounds (Cebrián & Duarte, 1995; Erb et al., 2016); and (2) improved carbohydrate supply to saprotrophs from increased exudation (Jin, Wood, Franks, Armstrong, & Tang, 2020). The mycorrhizal types differ, though, in that a greater response was seen in plants associating with AM than EM. In contrast, among the fungi, the increase in biomass and nutrient content was greater in the EM than AM (Dong, Wang, Sun, Yang, & Xu, 2018). At high nutrient availability, the allocation may also shift toward more aboveground (rather than belowground) production, which has a faster turnover rate and is exposed to a



FIGURE 5.4 Conceptual diagram of soil-centered ecosystem carbon sequestration as the balance of carbon inputs and outputs. Significant uncertainties exist about the interactions between the plant and microbial processes as set in the climatic, competitive, and resource availability context. Shaded boxes indicate processes sensitive to climate factors (CO₂, temperature, precipitation), bold arrows indicate two-way effects, and light arrows one-way effects.

more diverse group of detritivores. For example, accelerated turnover of modern-day tropical forests was detected already 30 years ago (Phillips & Gentry, 1994) and is projected to continue, driven by active management and rising atmospheric CO_2 (Cebrián & Duarte, 1995).

On the other hand, it has been found that the greater productivity afforded by rising CO₂ has increased N demand to the point that many natural ecosystems may operate under nitrogen deficiency (Mason et al., 2022). This may seem counter-intuitive at a time when nitrogen deposition continues to increase (Galloway et al., 2008) and, in many areas, exceed ecosystems' ability to retain it (Galloway et al., 2004; Lovett & Goodale, 2011). On the other hand, such nutrient stress likely helps maintain the mycorrhizal status of plants and greater soil microbial diversity that facilitates carbon retention, as described above. It may counteract the otherwise growing decomposability of plant detritus under elevated CO₂. Finally, the combination of CO₂ and N availability determine the nutritional value of plant biomass to herbivores as well as the level of secondary defense compounds and the rate of herbivory (Frew & Price, 2019). Reviews on this topic indicate that under elevated CO₂, plant nutrient concentrations tend to drop even though mycorrhizal nutrient concentrations increase (Dong et al., 2018; reflecting perhaps a transient phase), resulting in lower foliar herbivory (Frew & Price, 2019).

Temperature

The effect of temperature is expected to be greatest in the high latitudes, where both photosynthesis and respiration are temperature-limited (Tao et al., 2020; Yamaguchi et al., 2019). In lower latitudes and drier climates, higher temperature effects are expected to be felt primarily through altered water availability (Pilli et al., 2022). Temperature-mediated changes in nutrient and water availability have been found to affect photosynthesis, plant carbon allocation (Liu, Wang, et al., 2022), leaf and root morphology, nutrient acquisition and retention (Freschet et al., 2017) as well as maintenance respiration, which suggests potential connections to root and mycorrhizal function. For example, Parts et al. (2019) identified a critical threshold for Norway spruce between $+4^{\circ}C$ and $+6^{\circ}C$ above ambient, at which point fine root biomass collapsed. Feng, Zhang, et al. (2022) reported that among saprotrophic fungi, there is a specific temperature threshold of 9° C, at which the community composition changes abruptly, with a similarly abrupt change in the C processing pathways and soil C content. Similarly, AM fungal community composition has been found to respond to increased N and P availability with reduced species diversity, with a few specific specialist species gaining dominance (Xu et al., 2022). In contrast, the EM community in spruce forests became more diverse with warming, although the emergence of a novel thermophilic species was also detected (Parts et al., 2019). Higher temperature may also favor AM plant species and communities in the US Midwest, with consistent transitions playing out over the past three decades (Jo et al., 2019). While the opposite trend for the greater predominance of EM plants and communities has also been observed in New England and the Southeast Atlantic and Gulf Coastal Plains, it is occurring in a smaller area. The observed changes in soil C stocks and soil C transformations associated with these changes have been consistent with those described above. Frey, Lee, Melillo, and Six (2013) reported a decline in microbial efficiency and an increased total soil C loss under long-term warming, presumably mediated by shifts in both community composition and exudation profiles. The authors argued that higher temperature sensitivity of microbial efficiency indicates the predominance of specialized enzymes that degrade more complex substrates (Frey et al., 2013).

Precipitation and drought

As described in detail in Chapters 2 and 3 in this volume (Liu, Goodrick, Williams, & Zhang, 2023; Steel, Hinckley, Richards, & D'Amore, 2022), water stress and prolonged droughts are projected to become more common and frequent, fueling a cascade from warming, drought stress, insect outbreaks, forest mortality, and wildfires (Anderegg et al., 2022). The instantaneous effects of droughts are likely to be greater on young than old stands due to their shallower rooting depth and earlier onset of water limitation (Domec, Warren, Meinzer, Brooks, & Coulombe, 2004; Irvine et al., 2004). Furthermore, the growing demand for land for agricultural use may push forests to increasingly water-limited areas (Suweis, Rinaldo, Maritan, & D'Odorico, 2013), with associated declines in productivity. On one hand, water-expensive species like poplars, pines, and eucalypts that provide much of today's pulp and fiber will be harder to justify and find land for. On the other hand, the growth of drought-tolerant species in water-limited marginal areas may produce more chemically complex and recalcitrant biomass with long-term sequestration potential. It has also been projected that many of today's marginal forest lands may convert to shrub- or grasslands, particularly under the more extreme climate warming scenarios (Overpeck, Bartlein, & Webb, 1991). Furthermore, given the stochastic nature of severe droughts and the associated mortality that has been observed (Allen et al., 2010; Allen, Breshears, & McDowell,

2015), it has been hypothesized that the future hotter and more water-limited world may see reduced tree lifetimes (Searle & Chen, 2018; Yi, Hendrey, Niu, McDowell, & Allen, 2022). Water stress will also restrict carbon transport and belowground allocation in plants (Prescott et al., 2020), leading to substrate limitation, altered competitive interactions, and ultimately a transition in the composition of the soil microbial community (Hopkins et al., 2018). As ecosystem resilience to stresses has been related to its functional diversity (Anderegg et al., 2018; Mau et al., 2015; Oliver, Heard, et al., 2015; Oliver, Isaac, et al., 2015; Van der Heijden et al., 1998), it may come as a surprise that of soil biota, it is the free-living saprotroph community diversity rather than mycorrhizal symbiont diversity that correlates with forest resilience under drought (Liu, García-Palacios, et al., 2022). Finally, while the net effect of wildfires on forest carbon stocks is negative, the effect of prescribed burns and mechanical fuel management treatments is even more so, at least in the US Pacific Northwest (Law & Waring, 2015).

On the other end of the spectrum, increasing atmospheric humidity, as is projected for boreal and hemiboreal zones (IPCC, 2007), may or may not affect the productivity and ecosystem carbon sequestration potential (Lõhmus et al., 2019; Rosenvald et al., 2021). Both field and chamber studies suggest that increased humidity triggers initial shifts in belowground carbon allocation, root respiration, and exudation (Lõhmus et al., 2019; Sell et al., 2021), but these may be transient (Rosenvald et al., 2021). The consistent changes in response to elevated air humidity were decreased root density, increased specific root length and exudation (Sell et al., 2021), and a shift toward more hydrophilic mycorrhizal taxa (Parts et al., 2013) that tend to decompose faster and thus reduce soil C sequestration (Almeida, Rosenstock, Woche, Guggenberger, & Wallander, 2022).

Conclusion

Carbon sequestration is an ecosystem-level property (Schmidt et al., 2011), representing the balance of assimilatory carbon input, carbon allocation, transformations, and mineralization, controlled by the interactions of plants, their symbionts, free-living soil microbes, soil mineralogy, climate, and time. While the path to carbon sequestration begins with assimilation, long-term sequestration depends more on carbon retention and stabilization, protection of existing live and dead biomass pools from decomposition. In particular, it appears that carbon retention in the ecosystem is positively related to the nature of the decomposer community in the soil. Attempts to engineer ecosystems to sequester carbon may be ineffective if they forget the forest behind the trees—the dual role of microbes in sustaining both productivity and decomposition, the role of nutrients in both productivity and chemical recalcitrance, the role of resource scarcity in both slowed productivity as well as resource retention in biological pools and improved stress tolerance, and the diversity of the decomposer community in carbon loss as well as in nutrient recirculation and increased chemical recalcitrance of the residues. Therefore, for "climate-smart forestry" (Bowditch et al., 2020) and other "natural climate solutions" (Novick et al., 2022) to be effective, they must not focus solely on productivity but on the full biogeochemical cycling over a relevant timeframe (exceeding the lifetime of the predominant species and encompassing a spectrum a natural disturbance events). Greater C sequestration in the soil appears to require nothing less than slowing of the soil C cycle in the longer term and increasing the taxonomic, structural and functional diversity of C processing pathways.

The unprecedented recent investments of \$1 billion, approved by the US Senate in 2021 with the "Growing Climate Solutions Act," will spur nationwide monitoring of soil carbon and other soil health metrics, and bring these indicators more acutely to the awareness of agricultural producers and land managers. While the current state-of-the-science tools (Natural Resources Conservation Service's Soil Health Assessment) still lack the necessary nuance and predictive power, there have been significant recent developments in our understanding of soil microbial processing that may be well poised to answer the challenge of growing ecosystem carbon pools and stabilizing them in the long term. Given that current evidence strongly points to the importance of protecting the integrity of complex interconnected ecosystems to protect the carbon reserves (Maxwell et al., 2019; Noon et al., 2022), this should be the highest priority moving forward. Initiatives like the "30 by 30" plan-to protect 30% of the natural environment, both land and sea, by the year 2030 (IPCC, 2022), or more (Allan et al., 2022; Law et al., 2022)—may seem draconian. However, this may be the cheapest option, given the near impossibility of restoring the full complexity of stabilizing interactions in a natural forest by ecological engineering. Secondarily, reducing the soil health costs of land management, preserving and enhancing soil and whole ecosystem diversity will open the door to gradual reconstruction of these ecosystems. Focusing solely on maximizing primary productivity will continue on the path of land management over the past 200 years, where the productivity was pursued for commodity value. The side effect of intensive forest management—soil degradation-has become acutely apparent and needs to be urgently addressed.

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