

Plant species effects on nutrient cycling: revisiting litter feedbacks

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In a review published over two decades ago I asserted that, along soil fertility gradients, plant traits change in ways that reinforce patterns of soil fertility and net primary productivity (NPP). I reevaluate this assertion in light of recent research, focusing on feedbacks to NPP operating through litter decomposition. I conclude that mechanisms emerging since my previous review might weaken these positive feedbacks, such as negative effects of nitrogen on decomposition, while others might strengthen them, such as slower decomposition of roots compared to leaf litter. I further conclude that predictive understanding of plant species effects on nutrient cycling will require developing new frameworks that are broadened beyond litter decomposition to consider the full litter–soil organic matter (SOM) continuum.

Plant litter feedback paradigm

Understanding how plant species influence nutrient cycling is important in a variety of contexts, from elucidating the effects of invasive species on soil fertility, to informing land managers about the potential ecosystem consequences of species selection, to understanding the consequences of species range shifts in response to environmental change. In a review published in *Trends in Ecology and Evolution* over two decades ago [1] I asserted that, along soil fertility gradients, plant traits change in predictable ways that reinforce patterns of fertility by creating positive feedbacks to rates of ecosystem nutrient cycling, and potentially to NPP (Figure 1: Original feedback hypothesis). This assertion has a rich history in the literature, both preceding (e.g., [2,3]) and following (e.g., [4,5]) that publication. Nevertheless, since my original review research in this area has grown considerably, with some studies calling into question my original assertions. For example, while some common garden studies demonstrate that plant traits are correlated with N mineralization from surface soils [6–9], in others soil nutrient-cycling rates are not readily explained by plant traits [10,11]. Such mixed results suggest that the relationship between species traits and soil nutrient cycling deserves further attention.

I review here the evidence that suites of plant traits are arrayed predictably along fertility gradients and act to

reinforce those gradients and patterns of NPP, focusing on feedbacks operating through plant litter decomposition. Specifically, I evaluate two key assumptions underlying the plant litter feedback idea: (i) plant litter traits vary predictably along fertility gradients, and (ii) such variation reinforces soil fertility gradients through effects on decomposition and litter N release. Given the number of synthetic cross-site analyses of plant traits and their consequences for nutrient cycling over the past two decades, the time is ripe for revisiting my original assertions. Indeed, I show that my original assertion is more nuanced and complex than originally claimed. In particular, I discuss the need to consider leaf litter decomposition more carefully and move beyond consideration of leaf litter feedbacks to a more comprehensive understanding of whole-plant litter and how species affect nutrient cycling through effects on SOM dynamics.

Community-scale patterns in traits: soil fertility gradients and fertilization studies

Plant species that use limiting nutrients more efficiently should have a competitive advantage [2,12,13]. Thus, as soil fertility increases, tissue nutrient concentrations should increase because species use nutrients less efficiently and other resources become limiting. Nevertheless, several mechanisms might weaken soil fertility–trait relationships. For example, cluster roots in low-phosphorus (P) environments, arbuscular mycorrhizae in environments with low inorganic nutrient availability, ericoid mycorrhizae and ectomycorrhizae where nutrients are bound up in insoluble organic forms, and N-fixing symbioses in low-N environments all increase plant access to nutrients in low supply [14–16]. Further, increases in foliar nutrients that sometimes occur with increasing elevation [17] and latitude [18] might weaken relationships between soil nutrient availability and foliar nutrients at larger spatial scales because of negative relationships between mean annual temperature and foliar N [19] that counter the positive relationship between mean annual temperature and soil N supply [20].

Strong patterns across fertility gradients

Nevertheless, a number of studies, many published since Hobbie [1], reveal positive associations between foliar and/or litter nutrients and soil nutrients across soil fertility gradients at regional to global scales, providing evidence in support of my first assumption. For example, within regions ranging from lowland and montane tropical forests [5,21,22] to temperate forests [23–32] and grasslands [33],

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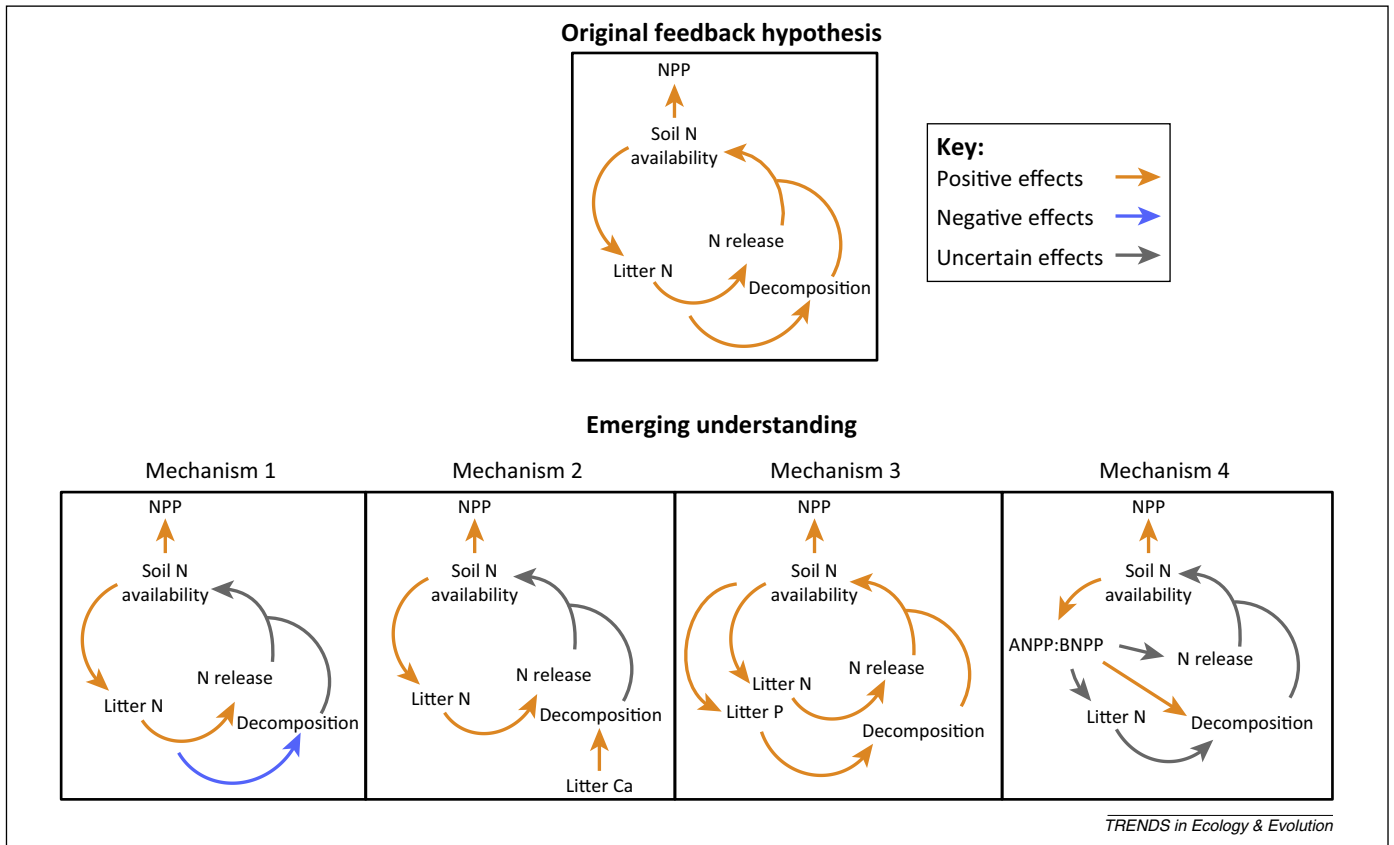


Figure 1. Mechanisms of species effects on nutrient cycling that have emerged since Hobbie [1] that might strengthen or weaken potential positive feedbacks to rates of nutrient cycling and net primary productivity (NPP). In these examples, N limits NPP. Original feedback hypothesis: The original positive feedback idea [1] posited that higher soil N availability increases NPP and the concentration of N in litter which increases decomposition rates and litter N release, creating a positive feedback loop to NPP and litter N. Mechanism 1: Negative effects of litter N on the later stages of litter decomposition could weaken the positive feedback loop. By how much is unknown because the effects of changes in decomposition and litter N release on soil N availability are uncertain and potentially offsetting. The rate of N release from litter depends on both how much N is released as litter decomposes (which should be higher for more N-rich litter) and on the decomposition rate (which in this case would be lower for more N-rich litter). Mechanism 2: If decomposition is limited by the availability of a nutrient that does not limit NPP, such as Ca, whose concentration in litter is not correlated with that of litter N, the consequences for soil N availability are uncertain. Higher litter Ca will increase decomposition rate, while higher litter N might increase how much N is released as litter decomposes, and the rate of litter N release rate will depend on both litter N and Ca, which are independent. Mechanism 3: If decomposition and litter N release are limited by the availability of a nutrient that does not limit NPP, such as P, whose concentration in litter is correlated with that of litter N (the nutrient that limits NPP in this example), then the feedback loop will operate because N and P are coupled in litter – higher litter N will lead to greater litter N release, and higher litter P will accelerate decomposition rates, increasing soil N availability. Mechanism 4: If higher soil N availability increases aboveground NPP (ANPP) relative to belowground NPP (BNPP), decomposition rates will increase because of the relatively faster decomposition of leaf litter relative to roots. Uncertainties arise because the cause of more rapid decomposition of leaf litter relative to roots is unclear, and not always predictable from N concentration. Further uncertainties arise because roots sometimes release N more rapidly despite decomposing more slowly than leaf litter, and N release is not always predictable from root N concentration.

the concentrations of leaf and/or litter nutrients, including N, P, and calcium (Ca), relate positively to various measures of soil nutrient availability both because of sorting of species along fertility gradients and because of plasticity within widespread species [31]. Positive associations between green leaf and soil nutrients (e.g., [22]) should translate into steeper positive associations between leaf litter and soil nutrients because leaves with higher nutrient concentrations resorb less nutrients than do those with lower nutrient concentrations [34,35], although most studies of retranslocation efficiency have found little variation across soil fertility gradients (e.g., [32]). The few studies that have examined tissue carbon chemistry across soil fertility gradients suggest that plants have higher concentrations of carbon-based structural and defense compounds in infertile sites [22,27,36,37].

Weaker patterns in fertilization studies

Such correlations cannot distinguish the influence of soil fertility on plant traits (via sorting in response to variation in nutrient supply) from that of plant traits on soil fertility

(e.g., via effects of plant species on soil biotic processes). Demonstrating the former requires fertilization studies at spatial and temporal scales appropriate to examining community responses and associated trait changes. Gradients in atmospheric deposition arising from human activities provide unintended ‘experiments’ in which to examine soil fertility–trait relationships. Multi-decadal changes in herbaceous vegetation in regions with chronic N deposition show increased abundance of species with higher foliar N concentrations [38]. Deliberate fertilization studies reveal that, in forests, added nutrients increase litterfall and its nutrient concentration [39–41], although forest experiments generally are too short to examine how species turnover might influence ecosystem response to nutrient addition. In short-statured ecosystems, added N and/or P increased plant nutrient concentrations in alpine [42] and arctic [43] tundra, as well as in temperate grasslands [44]. A meta-analysis of fertilization studies showed higher root N concentrations with N addition [45]. While these examples are compelling, most studies of plant response to nutrient enrichment have focused on individual

species; a better understanding of soil fertility-trait relationships requires long-term studies of the relative importance of intra-specific phenotypic plasticity, genotypic sorting, and shifts in species composition in mediating community-level trait responses to long-term nutrient addition (e.g., [46]), including traits other than foliar nutrient concentrations, such as foliar carbon chemistry and traits of other plant organs.

In summary, evidence to support my first assertion, that plant traits relevant to litter-mediated nutrient-cycling feedbacks vary predictably across soil fertility gradients, has become stronger since Hobbie [1], particularly for leaf N and P across soil N and P gradients, although understanding could be enhanced by more long-term fertilization studies. In the following I revisit my second assumption, that such patterns in plant litter traits reinforce soil fertility gradients through effects on decomposition and litter N release.

Leaf litter N effects on decomposition

Contrasting N effects on different litter fractions

Many studies have demonstrated that higher leaf litter N concentrations are associated with faster litter decomposition rates, although most of these studies lasted 1 year or less ([47] and many others). A growing number of longer studies have found evidence that litter with higher initial N concentrations ends up with a larger fraction decomposing at near-zero rates, such that overall decomposition rates can be slowed by higher N concentrations [48,49]. This phenomenon should weaken positive feedbacks between litter N and rates of soil N cycling and NPP (Figure 1: Mechanism 1). However, litter with higher initial N concentrations immobilizes less N and releases N earlier in the decomposition process [50], such that net effects on the rate of litter N release and litter-driven feedbacks to soil N availability are uncertain.

Various mechanisms have been proposed to explain why and where N might slow the rate of decomposition in its later stages [48]. Nitrogen might induce abiotic formation of compounds that resist microbial attack [51–54], inhibit oxidative enzymes involved in lignin degradation [55,56], stimulate microbial biomass production early in decomposition, leading to the accumulation of microbial residues that are resistant to decay [57], or increase microbial carbon-use efficiency [58,59]. Empirical evaluations of these various mechanisms are sparse.

Complicating matters is that higher litter N increases the fraction of slowly-cycling litter in some instances but not others, for reasons that are unclear but that could be elucidated by cross-site studies in ecosystems with contrasting decomposer and plant communities. For example, inhibition of oxidative enzyme activity might not cause negative effects of litter N on decomposition in ecosystems where oxidative enzyme activity is not a bottleneck to decomposition, such as in grasslands with low plant lignin concentrations [60]. Future studies need to be coupled with measurements that allow investigators to identify and distinguish among possible mechanisms giving rise to negative effects of N on decomposition. For example, measures of enzyme activity [55,56,61], characterization of abiotic chemical incorporation of N into potentially

recalcitrant organic matter [53], and measurements of microbial biomass and necromass [62] as well as carbon-use efficiency might elucidate the underlying mechanisms.

Incomplete representation in ecosystem models

The treatment of interactions between N and decomposition in ecosystem models requires revisiting. Some models partition litter into fast- and slow-cycling pools according to the litter N concentration in a manner opposite to what empirical studies show [48]. For example, in the Century model, less litter is partitioned into the slow-cycling pool as litter N increases [63]. Other models include inhibitory effects of increases in external supply of N on decomposition, by increasing the amount of detritus that enters more stable organic matter pools with added N [64,65], but do not include effects of changes in litter N concentrations on decomposition. Because the mechanisms underlying these effects of N and how they vary among ecosystems are poorly understood, and thus not explicit, the models are limited in their predictive capacity.

Moving beyond leaf litter N and lignin

Other traits are important

Studies of plant species effects on nutrient cycling have logically focused on plant traits known to affect decomposition of leaf litter, notably foliar and litter nutrient (especially N) and lignin concentrations [66]. However, leaf litter N and lignin might not cause expected variation in nutrient cycling if other litter characteristics are more important drivers of decomposition and litter nutrient release, in other words because the dominant or keystone decomposers in a system have unique nutritional requirements [67] (Figure 1: Mechanism 2). For example, the high Ca requirement of lumbricid earthworms leads to positive relationships between litter Ca and decomposition rates [8,68]. A similar relationship could arise for sodium (Na) because of the Na requirement of some detritus consumers [69]. Yet, these kinds of relationships are unlikely to emerge from regional and synthetic studies of litter decomposition using litter bags, which largely exclude macro-invertebrates [8]. On the microbial side of things, the requirement for manganese (Mn) by fungi that use Mn peroxidase to break down lignin presumably underlies the positive relationship between litter Mn and decomposition rates [48,70]. Notably, Na and Mn, and to lesser degree Ca, are not commonly measured in litter decomposition studies.

In these examples, the nutrients that limit NPP differ from those that influence decomposition and nutrient release from litter (Figure 1: Mechanism 2). Thus, any sorting of plant species on the landscape in response to underlying nutrient availability gradients will create positive nutrient-driven feedbacks to NPP only insofar as concentrations of the nutrient that limits NPP and those of nutrients or carbon fractions that influence decomposition covary in litter (Figure 1: Mechanism 3). While litter N and P often exhibit such correlations, litter concentrations of other elements, such as Ca or Mn, are inconsistently related to those of N and P, the elements that most commonly limit NPP ([71], but see [70]).

Other organs contribute significantly to ecosystem detritus production

Although leaf traits influence leaf litter decomposition and nutrient release, whether they influence ecosystem-scale nutrient cycling beyond the process of leaf litter decomposition is less clear, particularly because nutrients released during leaf litter decomposition might not directly support substantial plant nutrient uptake [72]. Variation in leaf litter traits will only predict ecosystem-scale variation in carbon and nutrient dynamics of detritus insofar as (i) leaf litter dominates detrital inputs to soils, or (ii) the characteristics of leaf litter are correlated with decomposition and nutrient release from other, dominant components of detritus. The former is unlikely in most ecosystems because other components of plant production besides leaves (root biomass, stem biomass, root exudates, mycorrhizae) are often significant fractions of total detritus production. For example, in non-agricultural ecosystems, belowground NPP (BNPP) is at least 40% of aboveground NPP (ANPP), and exceeds ANPP in many ecosystems [73]. In some ecosystems, substantial ANPP is removed via burning, mowing, or herbivory, further increasing the relative importance of belowground inputs to soils.

That other components of production in addition to leaves, in other words roots and stems, can be as or more important to detrital carbon and nutrient cycling raises questions about the predictability of litter feedbacks to fertility and NPP based on knowledge of leaf litter traits alone. Are rates of leaf litter decomposition and nutrient release related to those of roots and stems across species? Do root and stem traits vary predictably across fertility gradients in ways that affect decomposition? On a global scale, root, stem, and leaf N and P concentrations are correlated across species [74], but these relationships are not always apparent within sites [75]. Nevertheless, there is evidence that root and leaf N can change in concert across gradients in soil resources: across an aridity gradient [76], a temperate fire frequency gradient [77], and a temperate rain forest soil chronosequence [30] leaf and root N and/or P were positively related. Although stem and leaf N are related among species [74], I was unable to find studies that characterized stem traits across fertility gradients. Further, although traits of leaf, stem, and root may be correlated across fertility gradients, whether those traits similarly affect decomposition rates across such gradients has rarely been evaluated (but see [78]).

In a meta-analysis of decomposition studies of root, stem, and leaf litter of multiple species, decomposition rates of roots and leaf litter were strongly positively related [79], as were those of leaf litter and fine stems. These relationships were less consistent within sites, where some sites showed weak or no relationships between decomposition rates of different plant organs (e.g., [75]). Roots and stems decomposed on average 1.5- and 2.8-fold more slowly, respectively, than did leaf litter. Furthermore, root traits associated with slower decomposition could promote fungal over bacterial biomass, further slowing decomposition via production of fungal necromass with relatively poor carbon quality [80]. Thus, patterns of allocation among plant organs across fertility gradients might be

as or more important in driving feedbacks to nutrient cycling than the patterns of traits within any single plant organ [79]. For example, higher BNPP:ANPP in infertile sites [81] combined with slow decomposition of roots relative to leaf litter should reinforce low soil fertility (Figure 1: Mechanism 4).

N dynamics of decomposing roots

Complicating this prediction is the need to understand not only the decomposition rates of root and stem detritus but also their nutrient dynamics during decomposition. In studies comparing nutrient dynamics of decomposing roots and leaf litter within species, some showed that decomposing roots immobilized nutrients at lower or similar rates compared with leaf litter of the same species [82–86]. By contrast, other studies found that roots immobilized more nutrients than did leaf litter of the same species [8,75,78,87]. More N-rich roots sometimes immobilized less N than roots with lower initial N concentrations [75,84]. However, roots sometimes immobilized less [84] or more [87] N than leaf litter with similar initial N concentrations. More comprehensive analyses of nutrient dynamics during root decomposition are necessary to elucidate general patterns – a higher root fraction of NPP in low-fertility systems combined with their relatively slow decomposition rate [79] would reinforce low fertility only if slower decomposition is not accompanied by more rapid nutrient release from decomposing roots (Figure 1: Mechanism 4).

Moving beyond litter altogether: species effects on SOM nutrient dynamics

Both litter and SOM contribute to nutrient supply

Given that SOM in mineral soil horizons can contribute as much to ecosystem-scale nutrient supply as litter-dominated horizons, the emphasis on litter decomposition should be broadened to consider the litter–SOM continuum [88]; even in organic horizons, fresh litter can be but a small fraction of the organic matter. For example, on an area basis, gross rates of N mineralization in the mineral soil can exceed those in the O horizon [89]. Averaged across monocultures of 14 tree species, potential rates of net N mineralization were fourfold higher in the uppermost A horizon compared to the O horizon, and, on an area basis, ranged from less than 5% of O horizon rates for species with substantial O horizon accumulation to ~400% for species with rapidly decomposing litter, high earthworm activity, and sparse O horizons (unpublished data).

Plant litter traits might not predict SOM feedbacks

Therefore, understanding how plant species influence SOM dynamics might be as important to understanding ecosystem fertility as understanding species effects on litter dynamics [90]. Nevertheless, paradigms regarding species effects developed for litter might not predict how plant species affect SOM dynamics because plant traits that contribute biochemical recalcitrance to fresh litter might not confer long-term (>decadal scale) stability to SOM [88,91,92]. For example, plant species with relatively rapid litter decomposition do not always cause rapid decomposition of SOM [93], and in fact can be associated with

relatively greater accumulation of SOM in mineral horizons [6,57]. This can occur because more efficient microbial degradation of high-quality litter in the O horizon leads to accumulation of microbial necromass that promotes the aggregation and chemical stabilization of SOM in association with clay minerals in deeper horizons [57]; or because of processes (leaching, earthworm activity) that transport organic matter into deeper horizons where it can be stabilized onto mineral surfaces [94].

The importance of SOM in influencing nutrient availability, together with the evolving view of the factors that influence SOM dynamics [95], suggest the need for integrated thinking about how plant species influence decomposition and nutrient dynamics of both SOM and litter, and whether such combined influences will reinforce versus weaken gradients of soil fertility. Although developing such a framework is beyond the scope of this review, I provide some examples of how plant traits might be expected to influence SOM decomposition and nutrient dynamics in ways that could feed back either positively or negatively to NPP and plant traits.

As one example, plant allocation to roots and mycorrhizae, likely higher in infertile systems [81], will have myriad effects on SOM decomposition and soil nutrient dynamics [80]. Roots, mycorrhizae, and associated exudates promote soil aggregation and can increase the mean residence time (MRT) of SOM [80,96]. Stabilization of SOM into large macroaggregates (MRT <5 years [97]) could promote soil fertility by reducing nutrient losses and supplying nutrients to plants as aggregates destabilize (negative feedback). By contrast, stabilization of SOM and associated nutrients into smaller macroaggregates and microaggregates, with longer MRT, could depress soil fertility (positive feedback). Root exudates could either accelerate or decelerate SOM decomposition and nutrient mineralization via priming or promotion of aggregate formation, respectively (positive or negative feedback [80,98]).

As a second example, concentrations of nutrients in plant tissues, that track soil nutrient supply as outlined above, influence SOM decomposition and nutrient dynamics in ways that could feed back either positively or negatively to NPP and plant traits. By promoting nitrification, high tissue N can increase soil acidity and solubilize aluminum (Al) and iron (Fe) [99]. High concentrations of plant tissue Ca generally promote Ca-rich soils [100]. High concentrations of polyvalent cations in soil (Al, Fe, Ca) facilitate the stabilization of SOM onto mineral surfaces [99], likely reducing its turnover and release of nutrients on a per unit soil mass basis (negative feedback), although a larger SOM pool might release more N on a per unit ground area basis (positive feedback).

Predicting the effects of plant species on soil nutrient dynamics is further complicated because different plant traits likely influence the simultaneous mineralization versus immobilization of nutrients by different SOM and/or litter pools. For example, even in soils where the majority of gross nutrient mineralization is derived from turnover of SOM, and potentially is not directly influenced by plant litter traits, leaf litter and root traits of fresh detritus might influence net nutrient mineralization via their effects on nutrient immobilization, perhaps

explaining the correlations between litter or root traits and N mineralization in surface soils [6–9].

Conclusions and recommendations for future research

Does my original assertion that plant species reinforce patterns of soil fertility through litter feedbacks hold up? In reviewing the evidence I conclude that plant species can indeed create positive feedbacks to rates of nutrient cycling because of predictable variation in plant traits across soil fertility gradients. However, these feedbacks are likely to be strongest when plant traits are tightly related to underlying gradients in soil nutrient supply, the same nutrients limit NPP and decomposition, low soil fertility leads to relatively greater allocation to roots that decompose and release nutrients relatively slowly, and gross mineralization and/or immobilization occurs predominantly from detritus rather than from SOM. By contrast, several conditions might weaken such potential feedbacks (Figure 1), including negative effects of N on decomposition, limitation of NPP and decomposition by different nutrients, and rapid nutrient release from decomposing roots.

Through evaluating the evidence amassed since Hobbie [1], several research needs have emerged. A more comprehensive understanding of the patterns and mechanisms of litter nutrient effects on decomposition and nutrient release is needed, including of the mechanisms and generality of negative effects of N on decomposition, and of where different nutrients limit decomposition and litter nutrient release versus NPP. Such understanding will require decomposition studies that last long enough to elucidate the dynamics of the later stages of decomposition, assessment of a full suite of plant traits and organs that potentially influence those dynamics at the ecosystem scale, and approaches to measuring decomposition that allow access to a broader suite of decomposing organisms than soil microbes. Finally, frameworks are needed for predicting plant species effects on nutrient cycling that are broadened beyond litter decomposition to consider the full litter–SOM continuum.

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