

The responsive C and N biogeochemistry of the temperate forest floor

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The existence of an active forest floor as a key ecosystem component at middle latitudes calls to mind the story of Goldilocks. At high latitudes, low temperatures limit microbial activity, greatly reducing carbon (C) and nitrogen (N) cycling in surface organic horizons. At much lower latitudes in humid tropical forest, detritus disappears too rapidly to accumulate. In temperate forest, temperatures are just right: microbial activity is high enough to drive large fluxes of C and N mineralization, yet limited enough by cool winters that a layer of detritus accumulates at the soil surface as a distinct organic layer.

The temperate forest floor differs from mineral soil organic matter (Box 1) in ways that illustrate its function as a distinct ecosystem component. Both the organic soil horizon and the underlying mineral soil contain organic matter in all stages and rates of decay. For example, wood generally decays more slowly than fine root litter in both organic and mineral horizons. However, the forest floor receives greater inputs of litter each year than the mineral soil, whereas organic C and N stocks are larger, on average, in mineral soil¹. The mean residence time of organic matter in temperate forest floors is estimated to be four years in deciduous forest and 17 years in coniferous forest¹, contrasting with an estimated residence time of 29 years in temperate forest soil overall². The large mean residence times that are sometimes reported for soil organic C, 250–175 000 years^{3,4}, refer either specifically to passive fractions of mineral horizons or to deep organic horizons in poorly drained soils.

The forest floor is a source of dissolved or colloidal organic matter that is carried downward to mineral soil,

Soil organic matter is often viewed as comprising large pools of carbon and nitrogen with long residence times. However, the organic horizon that lies on the soil surface in temperate forests is a dynamic component of ecosystem carbon and nitrogen cycling. Responses to elevated inputs of nitrogen in this organic layer are emerging as key facets of ecosystem retention or loss of dissolved nitrogen. Research along nitrogen deposition gradients in the USA and Europe reveals a link between the ratio of organic carbon:nitrogen in the forest floor and nitrogen turnover rates, nitrification and leaching losses. Characteristics and processes in the forest floor are now recognized as key indicators or determinants of ecosystem 'nitrogen status'.

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where it is largely sorbed to mineral grains⁵. Recently, Guggenberger and Zech⁶ established that these transported organics are primarily humic substances, derived from partial decomposition in the forest floor. The organics transported downward are thus less labile than forest floor litter or its fractions. Clays and organomineral complexes also offer physical protection and increase the stability of organic matter in mineral soil.

A well developed organic horizon can contain half of all the fine roots in a temperate forest⁷ and be the location of more than half of the N mineralization⁸ (Box 2). Thus, the temperate forest floor is important in supplying N for plant uptake, even though it typically contains $\leq 10\%$ of the soil N stocks bound in soil organic matter¹.

Biogeochemistry research indicates that the forest floor is a key component in the responses of forests to aspects of global change.

As the residence time for C is brief in the forest floor, and because C and N cycling are intimately linked in forest soils, one would expect the surface organic horizon in temperate forests to be responsive to changes in litter quantity or quality [resulting from carbon dioxide fertilization (CO_2)], N deposition, shifting species compositions and climate. Here, I focus primarily on elevated N deposition, where recent advances highlight the importance of the forest floor in determining ecosystem responses.

N retention in the forest floor

Over much of Europe and eastern North America, inputs of biologically reactive N compounds to forests have increased rapidly, relative to pre-industrial levels⁹. Because N was historically (and still is, in most cases)

Box 1. Soil horizon nomenclature

B horizon: a mineral soil horizon characterized by a build-up of clay, aluminum, iron, salts or organic material translocated from upper horizons, which is present in some well developed temperate soils.

Forest floor: the surface organic horizon of a temperate forest soil, dominated by organic matter in various stages of decay, including relatively stabilized compounds known as humus. The forest floor is also called the organic (O) horizon. The bottom of the forest floor can end in either an abrupt or a gradual transition to mineral soil.

Mineral soil: all soil beneath the surface organic horizon; mineral soil horizons can be rich in organic matter, but are dominated by mineral matter.

Organic subhorizons: typically broken into three layers, the upper layer of recognizable litter (L), the fragmented, mixed material below L (F) and humus, the deepest subhorizon (H). The H horizon is also rich in fine roots and fine root litter. L, F and H are also referred to as Oi, Oe and Oa, respectively.

Solum: the soil profile from the surface (including the forest floor) to the depth of significant vegetation influence, which is typically the bottom of a B horizon.

Whole soil: the forest floor and mineral soil horizons together.

a limiting nutrient in these forests¹⁰, integrated biogeochemical responses are expected to be complex. For example, not only is increased N availability expected to alter forest C cycling¹¹, but bioavailability of C in soils is expected to be a key determinant of soil N cycling¹².

For both American¹³ and European¹⁴ researchers, a defining moment came in the late 1980s with the articulation of the theory of N saturation. In an N-limited forest, increased nitrification fluxes (among other changes) and ultimately N export were predicted to occur if soil N availability rose in excess of plant and microbial demand. As this paradigm has developed, ecosystem scientists have employed several approaches to investigate shifts in forest N cycling and C-N interactions under accumulating N inputs. These include increasing the inputs of N in forest plots experimentally, introducing and recovering isotopic (¹⁵N) tracers, making use of existing regional patterns in N deposition and interpreting model results of coupled C and N cycling.

From the start, a disparity in retention and loss of experimentally elevated N inputs was observed among sites. At Bear Brook Watershed in Maine (BBWM), USA, a small forested catchment with mixed coniferous and deciduous vegetation retained little N, and export of nitrate (NO₃⁻) occurred rapidly¹⁵. In contrast, a stand of mixed oak (*Quercus* spp.) at the Harvard Forest in Massachusetts, USA, exhibited one of the greatest rates of N retention yet observed. The mixed oak stand retained 15 g N m⁻² yr⁻¹ for six years with little increase in NO₃⁻ leaching¹⁶. The entry of N into nonextractable pools in soil, which appeared to be the largest sink for the N inputs, was initially quantified by the difference between inputs, outputs and vegetation sinks. The large sizes of soil N pools, together with extreme spatial heterogeneity, make it virtually impossible to observe changes in the sizes of soil organic N pools via direct sampling. Because soil organic N pools were the last term in a difference equation, it was necessary, in this case, to lump the organic and mineral soil horizons together⁸. The importance of this large N sink in soil was widely appreciated; however, there was no means to distinguish between sinks in the forest floor versus mineral soil.

Two lines of evidence now make it possible to differentiate N sinks in the forest floor from those in mineral soil horizons. In the first, application and recovery of ¹⁵N tracers allow direct observation of soil N retention in each soil horizon. After separate applications of ¹⁵N-labelled ammonium (¹⁵NH₄⁺) and ¹⁵NO₃⁻ at N input rates elevated above background (5 g N m⁻² yr⁻¹), Nadelhoffer *et al.*¹⁷ reported that the percentage recoveries of ¹⁵N after one year was, on average, 45% in the forest floor and 27% in mineral soil in the oak stand at the Harvard Forest. As part of the European Nitrogen Experiment project (NITREX), forest floor sinks were also recently quantified using this method, although at lower percentages¹⁸; in a group of four forest manipulations in Denmark, the UK and The Netherlands, percent recoveries of ¹⁵N in the forest floors were 20–45% at relatively low rates of N inputs

Box 2. Glossary of biogeochemical terms

Assimilation of nitrogen (N): entry of N into a soil component, pool, fraction, horizon or group of horizons. More general in meaning than 'immobilization'.

Extractable N: pools of ammonium (NH₄⁺) and nitrate (NO₃⁻) in soils are typically quantified by extraction with a two molar solution of potassium chloride. Often used to estimate plant-available NH₄⁺ and NO₃⁻.

Immobilization of N: entry of inorganic N into microbial or detrital matter in soils. This is used either to denote an increase in the absolute mass of N present in a soil organic pool or any gross flux of inorganic N into a microbial or detrital fraction.

Mineralization of N: conversion of organic N to mineral forms. This is sometimes specifically defined as NH₄⁺ production, but can be quantified as the sum of increases in NH₄⁺ and NO₃⁻ appearing over an incubation, with the assumption that the new NO₃⁻ was nitrified from NH₄⁺.

Net versus gross: 'gross' indicates integration of an actual flux over a time period. 'Net' indicates the difference in an accumulated pool at the end, versus the start, of an incubation.

Nitrification: oxidation, by soil bacteria, of NH₄⁺ to NO₃⁻. This is an energy yielding process. Nitrite (NO₂⁻) is an intermediate that seldom accumulates in soils.

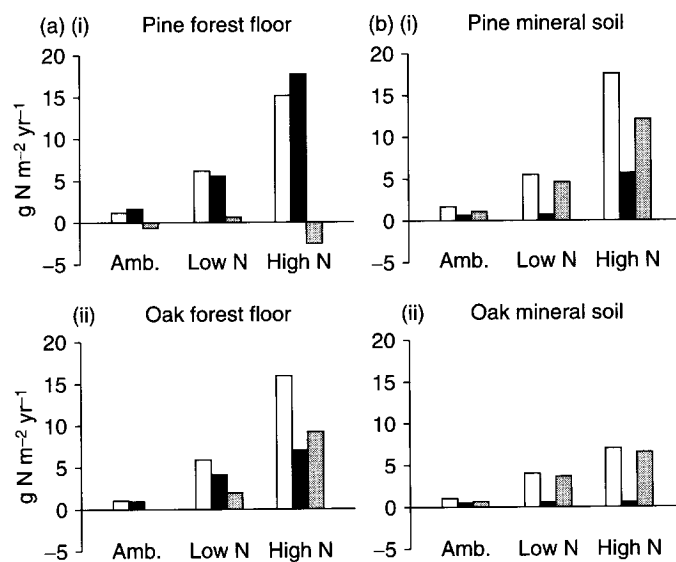
Potential (nitrification or mineralization): indicates rates measured under standardized conditions in laboratory incubations; particular methods vary.

Residence time: The mass of a biogeochemical pool divided by the summed input or output fluxes of mass. Typically, steady-state conditions are assumed for the purposes of such a calculation.

(0–3 g N m⁻² yr⁻¹) and decreased to 10–20% at higher rates of N input (3–8 g N m⁻² yr⁻¹).

The second line of evidence derives from leaching fluxes of total dissolved N (TDN). At the Harvard Forest,

Box 3. The link between forest-floor and whole-soil N retention



(Online: Fig. 1)

Inputs and leaching losses of total dissolved nitrogen [TDN, which comprises ammonium (NH₄⁺), nitrate (NO₃⁻) and dissolved organic N] are compared for (a) the forest floor and (b) mineral soil in two contrasting forest stands: (i) pine and (ii) oak at the Harvard Forest, MA, USA over a one year period. Inputs to the forest floor are calculated as annual fluxes in throughfall plus experimental N amendments. Key: Amb., ambient throughfall only; Low N, ambient plus 5 g N m⁻² yr⁻¹ as NH₄NO₃; High N, ambient plus 15 g N m⁻² yr⁻¹ as NH₄NO₃. N amendments were identical in the two forest stands.

Annual leaching losses from the forest floor are calculated as seasonal volume-weighted solute concentrations in forest-floor leachate multiplied by water flux calculated using a hydrologic model⁵. Leaching losses from mineral soil are calculated in a similar manner, using solute data from tension lysimeters in the soil B horizons (Box 1).

The forest floor showed greater retention of TDN in the oak stand compared with the pine. As a result, inputs of TDN to mineral soil were dramatically different in the two stands. In the oak stand where TDN inputs to mineral soil were lower, they were virtually all retained; the pine stand exhibited NO₃⁻ leaching. Key: white bar, TDN input; black bar, TDN leached; grey bar, TDN retained. Redrawn, with permission, from Ref. 5.

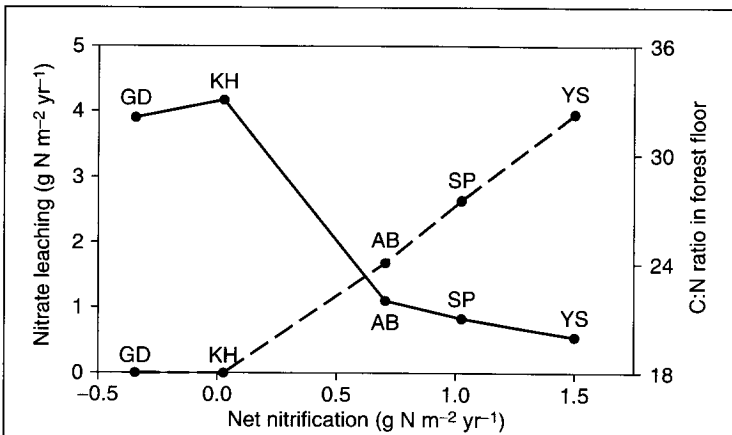


Fig. 1. Net nitrification versus nitrate leaching below the root zone (broken line) and forest floor C:N (carbon:nitrogen) mass ratio (unbroken line) in the forest floor at the five European Nitrogen Experiment project (NITREX) sites. Site labels are: AB, Aber (UK); GD, Gårdsjön (Sweden); KH, Klosterhede (Denmark); SP, Speuld (The Netherlands); YS, Ysselsteyn (The Netherlands). Adapted, with permission, from Ref. 21.

budgets of TDN entering and leaving the forest floor showed a clear link to ecosystem N losses in two stands responding differently to experimental N amendments. The forest floor of the mixed oak stand showed much greater retention of TDN than the forest floor of a *Pinus resinosa* (red pine) stand on similar soil (Box 3). The high rate of N retention in the oak ecosystem as a whole, relative to the pine, can be attributed partly to the much stronger N sink in the oak forest floor.

The C:N ratio as an indicator

In the 1980s, a link between soil C:N ratios and NO₃⁻ leaching was observed following comparison of N cycling patterns across 17 sites in the Integrated Forest Study (IFS)¹⁹. Generally, a lower mass ratio of whole-soil organic C:whole-soil organic N corresponded with greater leaching losses of NO₃⁻ in this dataset¹⁹. In theory, the progression of a forest through the stages of N saturation requires an increase in net nitrification, which transforms N into the highly mobile NO₃⁻ ion and is usually considered to precede the onset of NO₃⁻ leaching¹³. A link between forest floor N concentration and nitrification was observed in another dataset at about the time the IFS study ended²⁰. Potential nitrification, determined in laboratory incubations, was assessed in forest floors of high-elevation spruce-fir communities along a regional gradient in N deposition across New York and New England, USA. Nitrification increased

with greater forest floor N content, which in turn increased along the N deposition gradient. Perhaps equally significant was the observation of an apparent threshold at a forest floor N content of 1.4%. Thus, in the early 1990s some pieces of the puzzle were in place, relating organic C and N in whole soil, potential nitrification and ecosystem NO₃⁻ losses.

This link is now clearly established in one dataset, which at the same time highlights the C:N ratio in the forest floor as opposed to whole soil. Across a regional gradient in N deposition in Europe, a strong relationship between forest floor C:N ratio, net nitrification in field incubations and ecosystem exports of NO₃⁻ was observed in the NITREX study²¹ (Fig. 1). In a principal components analysis, observations of dozens of environmental variables and parameters of ecosystem C and N cycling were analysed across five sites. The first principal component (PC1) correlated well with nitrification flux and forest floor C:N ratio (Table 1), and is considered to indicate the 'N status' of the system (i.e. the location along the spectrum from N limitation to N saturation). In addition, PC1 correlated with N-input rates along a regional gradient, foliar N concentration and N-mineralization, which are variables important in the theory of the onset of N saturation¹³.

The responsive forest floor

N retention

In the context of changes in forest N cycling fluxes, the forest floor can exhibit a tremendous biogeochemical response in its presaturation retention of N. Retention (or net assimilation) of N is a difference between fluxes, and thus has the units of a flux (g N m⁻² yr⁻¹). In a forest manipulation at Gårdsjön, Sweden, inorganic N input fluxes were elevated sixfold over ambient (0.9 g N m⁻² yr⁻¹) input fluxes, with the result that net assimilation fluxes in soils also increased sixfold over ambient fluxes²² (Fig. 2). By comparison, N uptake by vegetation increased by only 40%, and N flux in litter increased by 51%. Tracer ¹⁵N data were not available, but Kjønaas *et al.*²² calculated N sinks in the soil horizon based on the measurement of N leaching fluxes. The upper 5 cm of the forest floor ('L' and part of the 'F' subhorizon; Box 1) retained or transformed 92% of the NH₄⁺ inputs, whereas the upper 10 cm of the forest floor ('L' and 'F'; Box 1) retained 52% of the NO₃⁻ inputs.

The mechanisms by which soils effect such dramatic increases in N retention under elevated N inputs are the subject of ongoing research and debate. When sinks in the horizon are calculated from solution fluxes, plant uptake through roots in each horizon is included. However, over-all retention in these horizons can be much greater than plant uptake^{16,17,22}. Could unexpectedly rapid uptake into, and turnover of, fine roots explain the retention? To aid in interpreting ¹⁵N tracer recoveries, a biogeochemical process model of ecosystem C and N cycling was recently constructed with the ability to simulate ¹⁴N and ¹⁵N redistributions among soil pools and vegetation tissues using principles of mass balance and pool dilution (the TRACE model)²³. At the Harvard Forest, this model showed that litter inputs (including fine root turnover) of ¹⁵N were too low to account for quantities of ¹⁵N recovered in forest floor detritus, even when the model over-predicted ¹⁵N recovery in fine roots relative to field data²³. Some means of direct entry of both ¹⁵NH₄⁺ and ¹⁵NO₃⁻ into detrital or microbial pools must provide the major sinks at the Harvard Forest²⁴. The TRACE model can reproduce the rapid forest floor ¹⁵N sinks in both the pine and oak stands if ratios of gross:net N mineralization over the whole solums (Box 1) are between 4:1 and 6:1 and driven largely by a ratio of 12:1

Table 1. Results from a principal components analysis of ecosystem N-cycling variables across the five NITREX^a sites^b

Variable	Correlation coefficient ^c (n=55)
N flux in needle litterfall	0.93
N concentration in current needles	0.95
Net mineralization/(g organic matter)	0.96
Net nitrification flux	0.99
Forest floor C:N ratio	-0.94
Percentage of total variance explained by PC1	77.70

^aNITREX: European Nitrogen Experiment project.

^bResults from Ref. 21.

^cPearson correlation coefficients for each variable with the first principal component (PC1).

in humus. These high ratios of gross:net N mineralization at the Harvard Forest are speculative, although ratios of 30:1 and higher have been observed in 'F' and 'H' material (Box 1) elsewhere in a coniferous forest floor²⁵. Ratios of gross:net N mineralization, measured in forest floors across the five NITREX sites, range from about 2:1 to 4:1. However, Tietema and colleagues¹⁸ working at the two Dutch NITREX sites, concur with the basic conclusion of the ¹⁵N modeling analysis at Harvard Forest: because the bulk (85%) of ¹⁵N tracer recovered in the forest floor was found in 'older, N-rich litter', it was concluded that rapid turnover takes place in this material through 'simultaneous immobilization and mineralization of inorganic N'.

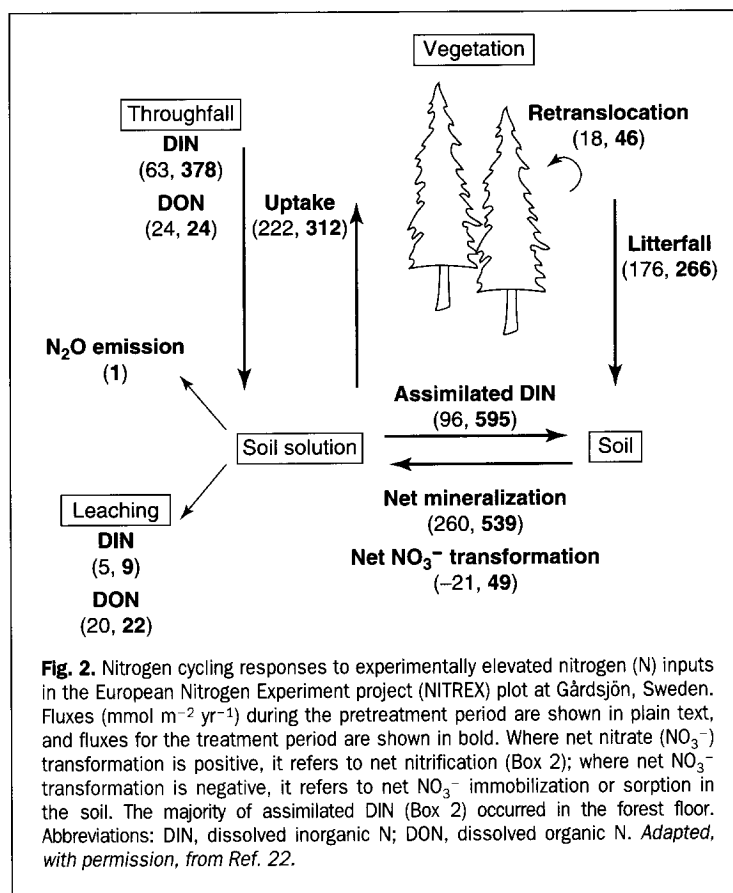
Detailed mechanisms of soil N turnover that allow the presaturation retention of N in the forest floor, together with the sources of C or energy that might be required to drive these responses, constitute a major gap in our knowledge. The hypothesis that dissolved organic C (DOC) might offer a source of reserve C to drive soil microbial immobilization of N was recently discarded because concentrations of DOC did not decrease under chronic N amendments and N retention²⁶. Furthermore, Aber *et al.*²⁷ now calculate that the soil N sinks and observed fluxes of CO₂ from soils at the Harvard Forest are inconsistent with growth of new microbial biomass at traditional values of C-use efficiency and microbial C:N ratios.

In 1992, Johnson²⁸ raised a possibility that has appeared and reappeared in the literature for decades: chemical reactions might incorporate inorganic N into soil organic pools. However, the lack of evidence that the proposed reactions occur under field conditions is a problem. Compounding this problem is the fact that randomized structures of lignin and humic molecules have impeded characterization of the bulk of soil organic N bonds for the whole of the 20th century. Current research is making strides with new spectroscopic methods such as ¹⁵N-nuclear magnetic resonance (NMR). In the meantime, Aber and colleagues²⁷ estimate that this class of reactions probably accounts for <15% of inorganic N retention in soil at the Harvard Forest. These authors instead propose that dramatic responses in soil N retention might be a result of increased uptake by soil mycorrhizae, producing N-rich exoenzymes instead of new microbial biomass, and possibly also tapping into the supply of photosynthetically derived plant C (Ref. 27).

N saturation

N saturation is viewed as a whole-system phenomenon. However, it is tempting to view the data in Box 3 as exhibiting saturation of sinks in the forest floor, causing increased N fluxes to mineral soil, followed by saturation of N sinks in mineral soil. A forest floor might initially respond to elevated N inputs with high rates of N retention. Over time, potentially decades, this would narrow the C:N ratio in the forest floor. Narrower C:N ratios would shift the N cycling in the forest floor to increased rates of nitrification, followed by NO₃⁻ leaching from the organic horizon. Kjønaas *et al.*²² suggest a three-phase response of coniferous ecosystems to accumulating N inputs, with assimilation in 'L' and 'F' horizons in the first phase and NO₃⁻ leaching in the last phase.

When NO₃⁻ from the forest floor enters mineral soil, should we expect a high level of retention because mineral soil contains large organic stocks of C and N? In an early paper, Ågren and Bosatta¹⁴ emphasized that N saturation should be a kinetic phenomenon, related to the dynamics of a system rather than its static attributes. Gundersen and



colleagues²¹ recently concluded that although mineral soil might ultimately have a large capacity to retain N, changes in the forest floor and vegetation can be sufficient to shift ecosystem N cycling and result in NO₃⁻ leaching from solums. Across the five NITREX sites, the PC1 (representing N status) is closely aligned with the forest floor C:N ratio, but does not correlate with characteristics of mineral soil organic matter.

Future research

Global change comprises many factors that one expects to interact with ecosystem nutrient and C cycling. Future research will continue to focus on biogeochemical processes and on the synthesis of these processes with ecological understanding. A detailed understanding of mechanisms of C and N turnover in the forest floor is lacking, and thus the reasons why a gross-scale attribute such as C:N ratio relates to N retention and nitrification remains unclear. The NITREX relationship between C:N ratio and NO₃⁻ export is not apparent in the data from individual sites, but only in the combined analysis across a regional gradient in N deposition²⁹. Does the C:N ratio integrate differences in land-use history, past disturbances and deposition history? If so, what is the required timescale? What role is played by forest succession, plant competition and plant-soil feedbacks in C and N cycling? Many processes must be better understood or synthesized with our current understanding. In addition, new developments continue to surprise: a current area of research concerns the availability and plant uptake of organic N compounds such as amino acids.

Ideally, mechanisms in the explanation of ecosystem function will link across scales and levels of organization. The C:N ratio in the temperate forest floor is such a link. This ratio has long been associated with net N dynamics in fine-scale detritus. Now it is also associated with retention

of N in the aggregated detritus that comprises the forest floor and, in turn, with shifts in N status and N losses at the ecosystem level.

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