New Phytologist

Review

Research review

The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests

Author for correspondence:
Richard P. Phillips
Tel: +1 812 856 0593
Email: rpp6@indiana.edu

Received: *1 December 2013*
Accepted: *9 January 2013*

Richard P. Phillips[1], Edward Brzostek[1,2] and Meghan G. Midgley[1]

[1]Department of Biology, Indiana University, 1001 E Third St, Bloomington, IN 47403, USA; [2]Department of Geography, Indiana University, Bloomington, IN 47403, USA

New Phytologist (2013) **199:** 41–51
doi: 10.1111/nph.12221

Key words: arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (ECM) fungi, mycorrhizal associations, plant–microbial feedbacks, rhizosphere.

Summary

Understanding the context dependence of ecosystem responses to global changes requires the development of new conceptual frameworks. Here we propose a framework for considering how tree species and their mycorrhizal associates differentially couple carbon (C) and nutrient cycles in temperate forests. Given that tree species predominantly associate with a single type of mycorrhizal fungi (arbuscular mycorrhizal (AM) fungi or ectomycorrhizal (ECM) fungi), and that the two types of fungi differ in their modes of nutrient acquisition, we hypothesize that the abundance of AM and ECM trees in a plot, stand, or region may provide an integrated index of biogeochemical transformations relevant to C cycling and nutrient retention. First, we describe how forest plots dominated by AM tree species have nutrient economies that differ in their C–nutrient couplings from those in plots dominated by ECM trees. Secondly, we demonstrate how the relative abundance of AM and ECM trees can be used to estimate nutrient dynamics across the landscape. Finally, we describe how our framework can be used to generate testable hypotheses about forest responses to global change factors, and how these dynamics can be used to develop better representations of plant–soil feedbacks and nutrient constraints on productivity in ecosystem and earth system models.

Introduction

A grand challenge in ecosystem science is to develop broadly applicable but mechanistically rigorous conceptual frameworks that can be used to test hypotheses about ecosystem functioning, particularly in the wake of global change (Chapin *et al.*, 2002). In forests, such frameworks have proved useful for studying ecosystem-scale responses to disturbance (Odum, 1969; Vitousek & Reiners, 1975) and nitrogen (N) deposition (Aber *et al.*, 1989). Notably absent from these frameworks is consideration of how differences in forest composition (i.e. tree species and their associated microbes) influence biogeochemical processes. Over the past several decades there has been increasing recognition that much of the biogeochemical variation that occurs within and among forests can be attributed to tree species differences in growth rates, nutrient acquisition strategies and interactions with soil microbes (Pastor *et al.*, 1984; Finzi *et al.* 1998a; Finzi *et al.*, 1998b; Lovett *et al.*, 2004; Reich *et al.*, 2005). This poses a challenge for developing a framework that considers forest composition, as it is impractical to consider species-specific impacts in highly diverse communities.

Currently the most common way to group tree species is by leaf habit and phylogeny (e.g. evergreen gymnosperms, deciduous angiosperms, etc.). Broadleaf and needleleaf trees generally differ in leaf traits such as photosynthetic rates (Reich *et al.*, 1997) and nutrient content (Reich & Oleksyn, 2004). While it is well-established that such differences contribute to variation in (C) and nutrient use in forests dominated by these species (Reich *et al.*, 1997; Wright *et al.*, 2004), trait variation among taxa within these groups can be appreciable (Hobbie *et al.*, 2007; Mueller *et al.*, 2012). Moreover, belowground traits are rarely considered in conceptual frameworks despite their importance in coupling C-nutrient cycles (Frank & Groffman, 2009) and mediating ecosystem responses to global change (Pendall *et al.*, 2004). Hence, an improved framework for considering tree species effects in ecosystems should group species by an integrated suite of aboveground and belowground traits that are functionally important and conserved across diverse ecosystems.

Here we propose a new conceptual framework to predict how tree species differences in aboveground and belowground traits influence key biogeochemical processes in temperate forests. It is well-established that differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) plants contribute to and reflect biogeochemical variation in ecosystems (Read & Perez-Moreno, 2003). However, these comparisons are often made across biomes and latitudinal gradients (Smith & Read, 2008). In temperate forests, nearly all tree species associate with either AM or ECM fungi. Given that trees from the two mycorrhizal associations differ in multiple aboveground and belowground traits and processes (Cornelissen *et al.*, 2001; Comas & Eissenstat, 2004; Phillips & Fahey, 2006; Comas & Eissenstat, 2009), we speculate that forests dominated by AM- and ECM-associated trees have unique nutrient economies and may respond to global changes in predictable ways. The objectives of this paper are (1) to describe how AM and ECM trees differ in their effects on C and nutrient couplings; (2) to propose a mycorrhizal-associated nutrient economy framework that can be used to generate testable hypotheses about biogeochemical consequences of tree species gains and losses; and (3) to identify how this framework can be used to improve our understanding of forest ecosystem responses to global change.

Mycorrhizal associations and nutrient dynamics

Arbuscular mycorrhizal fungi are a monophyletic, species-poor group of fungi which associate obligately with *c.* 80% of all land plants – most of which are grasses (Smith & Read, 2008). While it is well-known that these fungi enhance plant phosphorus (P) acquisition by extending hyphae beyond the nutrient depletion zones around roots, their role in acquiring N – the primary limiting nutrient in most temperate ecosystems – has only recently been recognized (Fellbaum *et al.*, 2012). AM hyphae rapidly colonize soil patches rich in organic N (Hodge *et al.*, 2001; Hodge & Fitter, 2010) and take up and transport both inorganic (Govindarajulu *et al.*, 2005) and organic N forms (Whiteside *et al.*, 2012). Given that most AM fungi have limited saprotrophic abilities and inorganic N forms are relatively mobile in soils where AM plants are dominant, it is believed that these plants primarily utilize inorganic N forms (Smith & Smith, 2011).

In contrast to AM fungi, ECM fungi are a diverse group of fungi from multiple phylogenetic groups – nearly all of which associate with trees (Smith & Read, 2008). These facultative plant associates form a thick mantle around root tips from which clusters of hyphae (mycelium) extend beyond the root zone (e.g. as rhizomorphs) and turn over slowly relative to AM hyphae (e.g. months to years; Anderson & Cairney, 2007). ECM fungi are thus believed to represent a greater C cost to the plant than AM fungi (Smith & Read, 2008), a cost that is likely offset by the ability of these fungi to access nutrient pools that are inaccessible to AM fungi. ECM fungi produce hydrolytic and oxidative extracellular enzymes to degrade soil organic matter (SOM) which enable these fungi to mine soils for N-bearing compounds such as chitin, proteins and phenol–protein complexes (Chalot & Brun, 1998; Courty *et al.*, 2010) as well as P-bearing inositol phosphates (Turner, 2008). The uptake of organic N by ECM plants is consequential, as there is a reduced assimilatory cost in taking up amino acids relative to inorganic N (Allen *et al.*, 2003). Additionally, ECM fungi – but not AM fungi – can weather minerals by releasing low-molecular-weight organic chelators and hydrogen ions to increase P and calcium availability (van Breemen *et al.*, 2000; Blum *et al.*, 2002; Taylor *et al.*, 2009).

The variable nutrient acquisition strategies in AM and ECM plants reflect the different decomposition rates of AM and ECM leaf litters. AM plants – which scavenge for nutrients released by saprotrophic microbes – generally have leaf litter that decomposes rapidly whereas ECM fungi – which can mine nutrients from organic matter and are less dependent on saprotrophic microbes for nutrient release – generally have slow-decomposing litter (Read & Perez-Moreno, 2003). While such patterns have been commonly observed among plants across latitudinal gradients, only a handful of studies have investigated these dynamics for plants of the same life form that co-occur in a given ecosystem.

Several recent experiments conducted in common gardens suggest that AM and ECM trees from temperate forests follow similar patterns. Cornelissen *et al.* (2001) reported that leaf litter from AM trees ($n = 26$) decomposed twice as fast in a common plot as litter from ECM trees ($n = 11$). In a 32-yr-old common garden in Poland, AM leaf litter ($n = 2$) decomposed 51% faster in a common plot than ECM leaf litter ($n = 6$; Hobbie *et al.*, 2006), and the average decomposition rate of all litter types (i.e. both AM and ECM) was 150–190% greater in the two AM stands relative to the six ECM stands. Faster rates of AM litter decomposition may influence SOM dynamics, as soil C pools have been reported to turnover faster in AM stands ($n = 2$) relative to ECM stands ($n = 4$) in a 30-yr-old common garden in Denmark (Vesterdal *et al.*, 2012). Collectively, these studies suggest that in addition to being a good predictor of leaf litter decomposition rates, the mycorrhizal association of a given tree species may influence C and nutrient availability in temperate forests.

The degree to which litter decomposition differences contribute to biogeochemical differences in AM- and ECM-dominated forests is currently unknown. One reason for this knowledge gap is that AM tree species are often reported to be largely restricted to the forest understory or early stages of succession (Langley & Hungate, 2003; Read & Perez-Moreno, 2003; Chapman *et al.*, 2006). However, this assumption is not supported by known AM tree species distributions. Sugar maple (*Acer saccharum* Marsh) is a shade-tolerant canopy dominant tree in mature hardwood and mixed mesophytic forests (Burns & Honkala, 1990). Co-dominant trees in these forests include other AM trees such as red maple (*Acer rubrum* L.), American elm (*Ulmus Americana* L.) and white ash (*Fraxinus Americana* L.). Tulip poplar (*Liriondedron tulipifera*), black cherry (*Prunus serotina*), sycamore (*Platanus occidentalis* L.) and black walnut (*Juglans nigra* L.) – although less shade-tolerant than maples and ashes – are some of the most abundant trees (in terms of basal area) in forests across the USA (Burns & Honkala, 1990).

We used the spatially extensive forest inventory analysis (FIA) data (maintained by the US Forest Service) and previously described mycorrhizal designations (Table S1; Brundrett *et al.*, 1990; Wang & Qiu, 2006) to examine the relative abundance of AM and ECM trees across the eastern and midwestern US. We calculated the relative basal area of AM and ECM trees for 21 000 individual plots consisting of over 100 000 trees, excluding plots that were planted or only partially forested (< 37% of the total; see Methods S1). For the few taxa reported to associate with both AM or ECM fungi, we assigned an equal percentage of the species basal area to each mycorrhizal group. In northeastern forests (e.g. Maine, Massachusetts, New York, New Jersey and Vermont), AM and ECM trees comprise 41% and 59% of the basal area respectively, with angiosperms comprising under half of the ECM trees but the vast majority of AM trees (Fig. 1). In Midwestern forests (e.g. Kentucky, Illinois, Indiana, Ohio and Wisconsin), AM and ECM trees are evenly distributed across the region and are mostly angiosperms. In Southeastern forests (e.g. Georgia, North Carolina, South Carolina and Virginia), AM and ECM trees comprise 37% and 63% of the basal area respectively, and just over half the ECM trees (and nearly all of the AM trees) are angiosperms. Collectively, our analysis shows a remarkably even distribution of AM and ECM trees across broad regions of the US and challenges previous assumptions about the abundance of AM trees in temperate forests. To the extent that plots dominated by AM and ECM trees differ in their biogeochemical attributes, a framework based on mycorrhizal associations may lead to improved predictions of nutrient dynamics across the temperate region.

The mycorrhizal-associated nutrient economy (MANE) framework

We sought to test the hypothesis that AM and ECM-domainted plots have unique biogeochemical syndromes in mature forests in the central hardwood region of the U.S. We established 20 m × 20 m plots in Indiana University's Moores Creek Research and Teaching Preserve – a *c.* 80-yr-old forest in south-central Indiana. In all plots, trees from the dominant mycorrhizal type (AM vs ECM) contained > 75% of the basal area of the plot ($n = 7$ replicates for each mycorrhizal group; Supporting Information Methods S1). AM plots contained a mixture of sugar maple, tulip poplar and sassafras (*Sassafras albidum*) while ECM plots contained white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), American beech (*Fagus grandifolia* Ehrh.), pignut hickory (*Carya glabra* P. Mill.) and black oak (*Quercus velutina* Lam.). All plots were located in similar landscape positions and soils derived from the same parent material (silty-loams derived from sandstone and shale), and contained more than one species from each mycorrhizal group (Methods S1).

We found clear differences in rates of C, N and P cycling between AM-dominated and ECM-dominated plots (Table 1). Across all plots, leaf litter from AM species decomposed 80% faster than litter from ECM species ($P = 0.0002$), consistent with the results of the previously described common garden experiments. The slower rates of litter turnover in the ECM plots likely contributed to the development of a thick organic horizon and greater soil acidity at the surface ($P = 0.003$; Table 1). Further, the concentration of dissolved organic C and the ratio of organic N to inorganic N were both greater in ECM-dominated plots than in AM-dominated plots (Table 1), likely reflecting the presence of an organic horizon in ECM plots. Although there were no significant differences in net N mineralization rates between AM- and ECM-dominated plots ($P = 0.64$), the concentration of ammonium was greater in AM-dominated plots – a process which was likely promoted greater nitrification rates in these plots ($P = 0.002$; Table 1). Additionally, two important indices of organic N and P cycling differed. The activity of NAGase (*N*-acetyl-β-D-glucosaminidase) – an enzyme involved in N acquisition from the organic N form, chitin – was two-fold greater in ECM plots ($P = 0.033$). Phosphatase enzyme activity – an index of P release from SOM – was 62% greater in ECM-dominated plots indicating enhanced mining of organic-bound P (Table 1). In general, differences between AM and ECM plots declined with depth such that few of the measured variables were significantly different 15 cm below the surface (data not shown).

Collectively, the results from Moores Creek suggest that distinct trait-integrated biogeochemical syndromes in AM and ECM stands may exist as a result of differences in their 'nutrient economies' (i.e. the primary forms of nutrients utilized by plants and microbes). We refer to this framework as the Mycorrhizal-Associated Nutrient Economy (hereafter the MANE framework; Fig. 2), and speculate that this framework provides a useful way to characterize the biogeochemical attributes of AM- and ECM-dominated temperate forests. The MANE framework predicts that, in soils where AM trees are dominant, an 'inorganic' nutrient

Table 1 Arbuscular mycorrhizal (AM)- and ectomycorrhizal (ECM)-dominated soils at Moore's Creek, IN, USA (for methods and site description, please see Supporting Information Methods S1)

	AM	ECM	*P* value
Leaf litter			
Decomposition rate (% mass loss)	17.7 (2.8)	9.8 (1.6)	0.0002
C cycling			
Extractable DOC (mg organic C g^{-1} soil)	0.32 (0.04)	0.64 (0.06)	0.0007
N cycling			
Organic N : inorganic N	159 (28)	277 (50)	0.0768
NAGase enzyme activity (μmol h^{-1} g^{-1})	0.006 (0.0004)	0.014 (0.003)	0.0328
Nitrification (μg NO3^{-} N g^{-1} soil d^{-1})	1.05 (0.21)	< 0.001	0.0023
P cycling			
Phosphatase enzyme activity (μmol h^{-1} g^{-1})	0.034 (0.004)	0.055 (0.004)	0.0009
Other variables			
Soil pH	5.23 (0.24)	4.27 (0.09)	0.0027

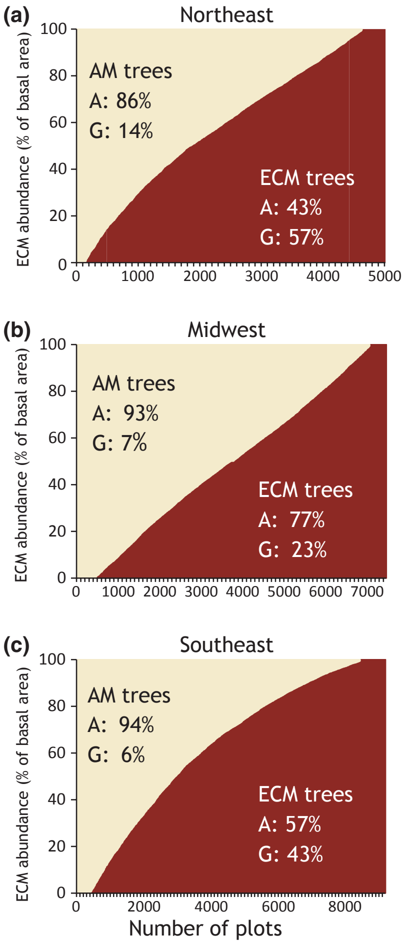

Fig. 1 Plot of the distribution of arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) trees in forests across the eastern (a), midwestern (b), and (c) southeastern USA. For each plot, the relative abundance of trees from each mycorrhizal group (based on basal area) was summed and the plots were sorted based on the percentage of ECM trees (left to right, lowest to highest). Numbers in the legend refer to the mean percentage of angiosperms (A) and gymnosperms (G) within each mycorrhizal group across the 5017 (northeast), 7469 (midwest) and 9189 (southeast) plots. All data used in this analysis were collected from the forest inventory analysis (FIA) data repository.

economy occurs (Fig. 2a). The inorganic nutrient economy results from rapid rates of C mineralization owing to the high chemical quality of AM leaf litter (Cornelissen *et al.*, 2001), root exudates (Smith, 1976) and mycorrhizal litter (Staddon *et al.*, 2003; Drigo *et al.*, 2010). As a consequence, N is rapidly transformed from organic forms (e.g. proteins, chitin and amino acids) to inorganic forms (ammonium and nitrate) by a microbial community dominated by free-living bacteria and fungi. Nitrification is likely promoted by the amelioration of soil acidity by AM litter (Finzi *et al.*, 1998a) and increases in the ammonium pool owing to the rapid decomposition of the AM litter. In the AM nutrient economy, inorganic N is the dominant source of N available to plants and the dominant form of N lost through leaching. The primary role of the AM fungal hyphae is to scavenge for inorganic nutrients released from litter and SOM by saprotrophic microbes.

The MANE framework predicts that in forests where ECM trees are dominant, an 'organic' nutrient economy will occur (Fig. 2b). We speculate that the slow decomposition of litter in these soils results in a greater accumulation of SOM, such that a significant fraction of nutrients exist in organic forms (Table 1). Thus, a large proportion of C allocated belowground is used by ECM fungi to acquire N and P from SOM. ECM hyphae have greater enzymatic capabilities relative to AM hyphae (Olsson *et al.*, 2002; Read & Perez-Moreno, 2003) and thus, ECM-associated plants can access some forms of organic N and P directly. Because of the conservative cycling of N through this pathway and the acidifying nature of most ECM tree species' litter (Finzi *et al.*, 1998a; Reich *et al.*, 2005), little N becomes available for ammonium oxidizers, and nitrification rates and nitrate leaching losses are low. The large pool size of the dissolved organic N pool and low soil pH select for a fungal-dominated microbial community (including ECM fungi), and the turnover of organic N forms controls N availability to plants and microbes. ECM fungi influence these dynamics by producing proteases and chitinases that hydrolyse N in SOM and in microbial necromass (Fernandez & Koide, 2012). In addition, the ECM fungi produce phosphatase enzymes and release low-molecular-weight organic acids, which are used to increase P availability (Jansa *et al.*, 2011). The resulting phosphate esters, including the inositol phosphates and phosphate ions are then acquired by fungi and roots (Antibus *et al.*, 1997; Turner, 2008). The N and P acquired by roots and fungi are released to soil in the form of slowly decomposing ECM litter. Thus, we speculate that the organic nutrient economy of the ECM-dominated forest is driven primarily by a tight coupling of plant C allocation and nutrient uptake.

Taken together, the MANE framework predicts that an inorganic nutrient economy occurs in AM-dominated stands owing to rapid mineralization of plant-derived C and nutrients, whereas an organic nutrient economy occurs in ECM-dominated stands owing to the slow turnover of plant-derived C and enhanced root/rhizosphere couplings. Given that most forests include mixtures of AM and ECM trees (Fig. 1), the utility of this framework depends on whether the relative abundance of AM or ECM trees in a plot or stand reflect gradients in the nutrient economy. To test this, we randomly located 30 plots (15 m × 15 m) in a mixed hardwood forest located at the Griffy Woods Research and Teaching Preserve in south central Indiana (Methods S1). For each plot, we calculated the relative abundance of AM and ECM trees based on basal area. Most trees in Griffy Woods are 70–80 yr old, and the site contains a rich assemblage of both AM and ECM tree species. Dominant AM tree species include sugar maple, tulip poplar, white ash, black walnut, black cherry and sassafras, while dominant ECM trees include northern red oak, black oak, American beech, shagbark hickory (*Carya ovata* P. Mill.), white oak and bitternut hickory (*Carya cordiformis* Wangenh.). Similar to Moores Creek, Griffy Woods is also on the unglaciated plateau, and has soils consisting of silty-loams derived from sandstone, shale and, to a lesser extent, limestone.

Similar to Moores Creek, multiple indices of C and nutrient cycling differed between AM- and ECM-dominated plots, and

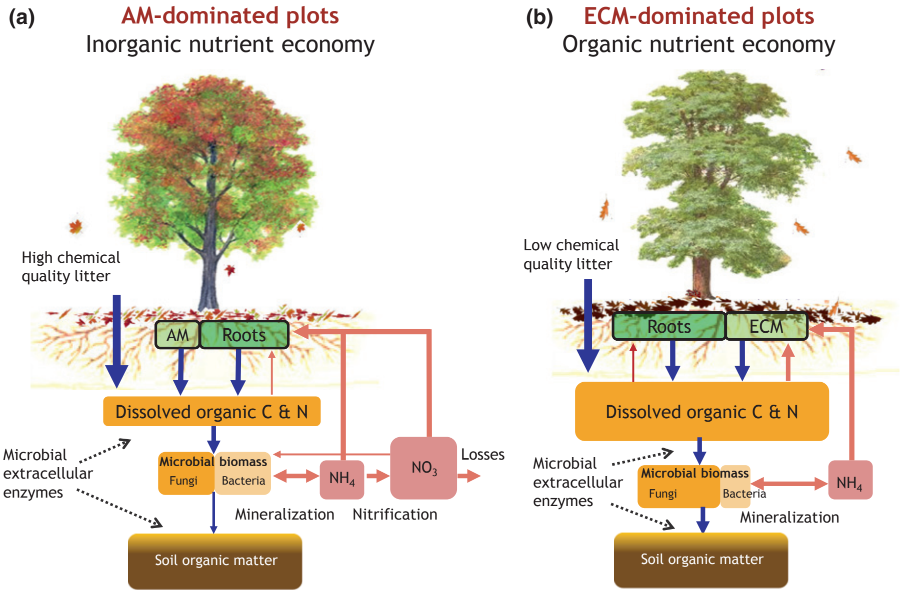

Fig. 2 Conceptual model of the nutrient economies of arbuscular mycorrhizal (AM)- and ectomycorrhizal (ECM)-dominated stands of the Mycorrhizal-Associated Nutrient Economy (MANE) framework for temperate forests. In AM-dominated stands (a), an inorganic nutrient economy is predicted as a result of the fast decomposition of high-quality litter pools and elevated rates of carbon (C) and nitrogen (N) mineralization. In ECM-dominated stands (b), an organic nutrient economy is predicted as a result of low-quality litter pools and slow rates of C and N turnover, resulting in limited losses of inorganic nutrients. Within a mycorrhizal group, the size of the boxes and arrows indicates relative importance of pools and fluxes, respectively. The phosphorus cycle (not depicted here) is hypothesized to have an inorganic nutrient economy (AM) mediated by litter decomposition and an organic nutrient economy (ECM) driven by a tight coupling between root C allocation and nutrient uptake. Blue arrows, C fluxes; red arrows, N fluxes.

such differences tracked the shifts in the relative abundance of AM and ECM trees (i.e. resulting in a nutrient economy gradient). Here we present a subset of these data for key aspects of the nutrient economy. First, the ratio of organic N to inorganic N in the upper surface soil was highly correlated with the percentage of ECM trees at the plot-scale (Fig. 3a; see Methods S1 for methods). Organic forms of N increased in importance as ECM trees increased in abundance across the landscape. Nitrification rates followed the opposite pattern: plots with increasing amounts of AM trees had greater rates of nitrification whereas plots with increasing abundance of ECM trees had little if any net nitrification (Fig. 3b). Nitrification is a critical ecosystem process that governs N loss in forest ecosystems, and differences across the gradient suggest that N losses may be greater as the percentage of AM trees increases. Elevated nitrification and nitrate leaching, while often attributed to individual tree species such AM sugar maple (Finzi *et al.*, 1998b; Lovett *et al.*, 2002; Templer *et al.*, 2005) have rarely been related to functional groups of trees. We found no significant relationship between the percentage of sugar maple in our plots and nitrification rates ($r^2 = 0.27$; $P = 0.19$). In fact, some of the highest nitrification rates occurred in plots where sugar maple comprised < 5% of the basal area of the plot. This indicates that our results cannot be attributed to a single species. Rather, nitrification appears to be governed by a suite of factors, which relate to the traits of the dominant species (e.g. nutrient use efficiency and litter chemistry) and their interaction with the broader nutrient economy (Pastor *et al.*, 1984). As a consequence, tree species from different mycorrhizal groups, a are likely contributing to these spatially distinct biogeochemical patterns.

The MANE framework as a lens for considering global change impacts

Given predicted changes in forest composition owing to invasive insects (Twery & Patterson, 1984), altered disturbance regimes (Abrams, 1992) and climate (Iverson & Prasad, 1998; Iverson *et al.*, 2004), the MANE framework provides a conceptual framework for considering the impacts of tree species gains and losses. Tulip poplar, red maple and sugar maple – all AM species – are becoming increasingly dominant in hardwood forests due the poor regeneration and selective harvesting of ECM oak species (Woodall *et al.*, 2011; Lister *et al.*, 2012). To the extent that the increased abundance of AM trees promotes a more inorganic nutrient economy, the biogeochemical attributes of these forests will also change (e.g. faster rates of C and N cycling; greater nitrate leaching losses, etc.). Likewise, the biogeochemical consequence of tree species declines owing to invasive insects may depend on the mycorrhizal association of the replacement trees. White ash (an AM tree species) is currently in decline across much of the central hardwood region as a consequence of the emerald ash borer. If ash trees are replaced by other AM species, nitrate leaching losses may continue to be high. If, on the other hand, ashes are replaced by ECM species, nitrate leaching losses may be reduced. Thus, the MANE framework can provide a lens for developing testable hypotheses about the biogeochemical consequences of shifts in forest composition.

Additionally, there is accumulating evidence that AM and ECM forests may respond differently to global change drivers. Here we describe several examples of how differences in the nutrient economies of AM and ECM-dominated forests may impact how

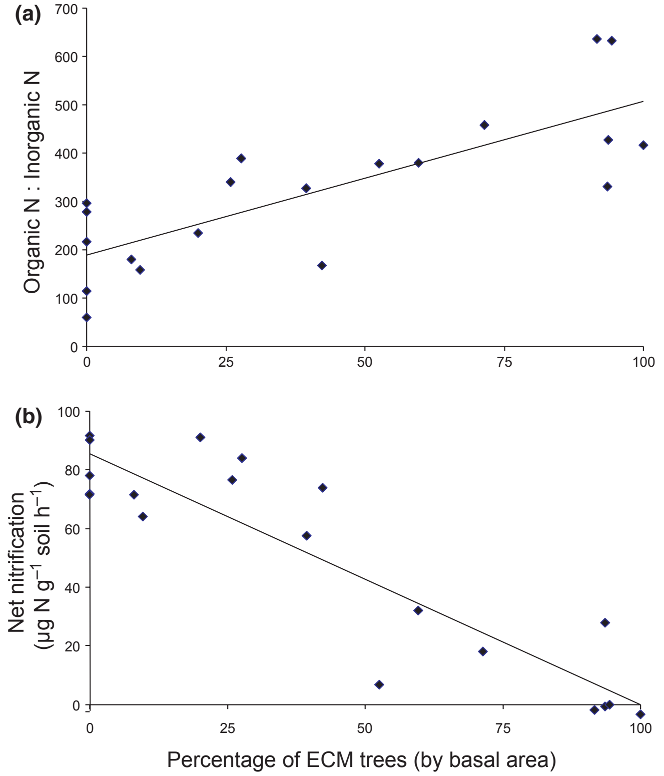

Fig. 3 The relationship between the percentage of ectomycorrhizal (ECM) trees and soil nitrogen (N) cycling. As the percentage of ECM trees in a plot increases, the organic N to inorganic N ratio increases (a; $r^2 = 0.62$; $P < 0.001$), while net nitrification rates decrease (b; $r^2 = 0.82$; $P < 0.0001$). Data are averages of two sampling dates at Griffey Woods (IN, USA) from 2009 (See Supporting Information Methods S1 for Methods). This establishes that the relative abundance of AM and ECM trees is an excellent indicator of the nutrient economy of forest plots, as plots dominated by ECM trees have soil pools dominated by organic N and low nitrification rates.

these forests respond to global changes. Although factors such as soil type and land use history may also mediate ecosystem responses, we present several recent studies that support the MANE framework as a useful construct for predicting the magnitude and direction of forest responses.

Effects of N deposition

Temperate forests receive some of the highest rates of N deposition on earth (Holland *et al.*, 1999; Galloway & Cowling, 2002; Elliott *et al.*, 2007). To date, most N deposition studies in temperate forests have been conducted in ECM-dominated forests, especially in *Pinus*-dominated stands (LeBauer & Treseder, 2008; Lu *et al.*, 2011; Templer *et al.*, 2012). These studies have reported increases, decreases and no effects of N on net primary productivity (NPP) (Magill *et al.*, 2004; McNeil *et al.*, 2007; Wallace *et al.*, 2007). Interestingly, many N-enrichment studies conducted in AM forests have shown positive NPP responses (Boggs *et al.*, 2005; McNeil *et al.*, 2007; Pregitzer *et al.*, 2008b). A differential response between AM and ECM trees to N deposition was also reported by Thomas *et al.* (2010) who examined the species-specific responses of tree species to N deposition for tens of thousands of trees in the FIA database. All five of the tree species which showed increased growth in response to N were AM tree species whereas ECM trees exhibited more variable responses (i.e. some increased, some decreased, and some were unaffected).

Differences in the responses of AM and ECM trees to N enrichment may relate to their nutrient economies. AM trees generally occur in soils with low organic N to inorganic N ratios. Accordingly, the positive response of AM trees to N enrichment may be driven by the extent to which these trees are adapted to exploit pulsed supplies of inorganic N (Veresoglou *et al.*, 2012). ECM trees, in contrast, may respond differently from AM trees, especially if the N deposition is in the form of nitrate – a form of N which is generally not produced in ECM-dominated forests (Vitousek *et al.*, 1982).

Additionally, soil processes in AM and ECM stands may respond differently to N enrichment. Waldrop *et al.* (2004) reported that N deposition increased decomposition in AM-dominated forests but decreased decomposition in ECM-dominated forests. These effects were attributed to differences in soil microbial communities, particularly the presence of N-sensitive white-rot fungi that decompose recalcitrant SOM commonly found in ECM-dominated stands (Fog, 1988; Carreiro *et al.*, 2000; Frey *et al.*, 2004). Differences in nutrient economies also appear to drive the magnitude and the direction of the response of nitrate leaching to N deposition. In a recent meta-analysis, mycorrhizal association was found to be the most important biological factor predicting the response of nitrate leaching to experimental N deposition (M. G. Midgley and R. P. Phillips, unpublished). N deposition induced higher nitrate leaching in AM-dominated stands than in ECM-dominated stands. Greater nitrate leaching losses in the AM stands likely reflect their inorganic nutrient economy, with N deposition leading to more nitrate produced but also more nitrate lost (Goodale *et al.*, 2002; Lovett *et al.*, 2002). Whether faster decomposition and greater nitrate leaching in AM stands will eventually minimize the growth-enhancing effects of N deposition on AM tree growth warrants further study.

Elevated CO_2 and nitrogen limitation

The progressive N limitation (PNL) hypothesis states that the growth-enhancing effects of elevated atmospheric CO_2 will decline over time, as N accumulates in slow-turnover biomass and soil pools (Luo *et al.*, 2004). The results of several long-term free air carbon dioxide enrichment (FACE) experiments suggest that differences in the degree to which trees species delay PNL may depend, in part, on the mycorrhizal association of the dominant trees. At the Oak Ridge FACE site – the only FACE site dominated by AM trees (*Liquidambar styraciflua* L.) – increases in the productivity of fine roots under elevated CO_2 were not sustained over time, resulting in no NPP enhancement several years after the start of the experiment (Norby *et al.*, 2010). The exacerbation of N limitation in these soils may have occurred owing to the inability of AM trees to mine N from SOM (Cheng *et al.*, 2012), especially the N-rich particulate and mineral-associated SOM pools that occur at depth (Iversen *et al.*, 2012).

In contrast, ECM trees have demonstrated a greater ability to delay PNL and sustain forest productivity, presumably by mining SOM for N. Much of the N in forest soils is bound to SOM and this N must be depolymerized by microbial extracellular enzymes before it can be taken up by roots (Schimel & Bennett, 2004). The Rhizosphere Accelerated Mineralization and Priming (RAMP) hypothesis predicts that under elevated CO_2, roots modify the availability of growth-limiting nutrients by stimulating the microbial breakdown of SOM in the rhizosphere (Phillips *et al.*, 2012). Multiple lines of evidence suggest that RAMP sustained elevated forest productivity at the Duke Forest FACE site over 15 yr (Drake *et al.*, 2011), as elevated CO_2 increased fine root production (Pritchard *et al.*, 2008a), exudation (Phillips *et al.*, 2011) and mycorrhizal turnover (Pritchard *et al.*, 2008b; Phillips *et al.*, 2012) in ECM-associating loblolly pine (*Pinus taeda* L.). These findings are generally consistent with those in other ECM-dominated systems. At the Rhinelander FACE site, the dominant tree species is aspen (*Populus* spp.) – a dual colonist that is primarily colonized by ECM fungi (Andrew & Lilleskov, 2009). The productivity of these stands was sustained with elevated CO_2, as increases in belowground C allocation (Pregitzer *et al.*, 2008a) enhanced soil C turnover (Talhelm *et al.*, 2009) and accelerated N cycling (Zak *et al.*, 2011). Similarly, Langley *et al.* (2009) reported that the sustained productivity response of three ECM-associating oaks (*Quercus* spp.) to elevated CO_2 resulted from enhanced mineralization and priming effects.

Research needs for testing the MANE framework

The MANE framework builds on previous classifications for forests such as 'mull' vs 'mor' (Mueller, 1878; Handley, 1954), 'open' vs 'closed' ecosystems (Odum, 1969), 'fungal' vs 'bacterial' energy channels (Wardle *et al.*, 2004) and ecosystems with 'extravagant' vs 'conservative' traits (Chapman *et al.*, 2006). A key distinction is that the MANE framework is predictive, as the mycorrhizal associations of nearly all temperate tree species are known, and the relative abundance of trees at the plot, stand or regional scale can be calculated relatively easily. While the appeal of the MANE framework is its simplicity, we recognize several aspects of this framework require more evidence and experimental testing before it can be applied more broadly. In this section, we highlight a few of these considerations.

A critical question relates to whether the nutrient economy differences are controlled by plant traits, microbial traits or some interaction of these two with soil factors (Wurzburger & Hendrick, 2009). There has been a paucity of work conducted on trees which can associate with both AM and ECM fungi (Chen *et al.*, 2000; Egerton-Warburton & Allen, 2001), particularly for field-grown trees (Querejeta *et al.*, 2009). Many of the species which can associate with both AM and ECM (e.g. *Salix, Populus, Eucalyptus*) are currently being used in short-rotation biomass plantations. Taking advantage of species which associate with AM and/or ECM fungi may enhance our understanding of the extent to which the mycorrhizae contribute to nutrient economy differences, and may aid in the development of soil inoculum that enhances forest biomass production while minimizing environmental impacts (e.g. nitrate leaching). Functional trait differences among taxa of mycorrhizal fungi may also influence how nutrient economies differ from site to site. ECM taxa differ in their exudation rates, enzyme activities and nutritional mode (Courty *et al.*, 2010; Fransson & Johansson, 2010) and AM taxa have variable effects on nutrient acquisition and soil biogeochemistry (Smith & Smith, 2011). The degree to which mycorrhizal functional groups (e.g. ECM species' exploration strategies (Agerer, 2001) and successional stages (Twieg *et al.*, 2007) and AM species' phylogenies) interact with plant traits to drive the nutrient economy warrants further study.

A second question is whether the nutrient economy gradients observed in our study are driven by some unique characteristics of particular tree species. Many ECM stands in the central hardwood region (Fig. 1b) are dominated by closely related species (e.g. *Quercus* and *Carya* are both in the order Fagales), and it is possible that the ECM nutrient economy is driven more by phylogenetic similarities than mycorrhizal status (Koele *et al.*, 2012). Further, the ECM stands in this region include few gymnosperms. While ECM gymnosperms and angiosperms both have slowly decomposing leaf litter that contributes to SOM accumulation and soil acidity, other traits such as foliar chemistry (Koele *et al.*, 2012), root morphology (Comas & Eissenstat, 2009) and root turnover (Hobbie *et al.*, 2010; McCormack *et al.*, 2012) generally differ between these groups. Such differences may be sufficient to warrant a separate category or secondary axis of variation to separate gymnosperms and angiosperms in forests. Along the same lines, it is unclear whether AM gymnosperms (e.g. *Juniperus, Taxodium* and *Thuja*) have leaf and root traits that overlap more with AM angiosperms or ECM gymnosperms. These questions are relevant for current plant functional type classifications, as gymnosperms are currently lumped together as needleleaf conifers in land surface models. Many of these questions can likely be addressed through the further development of plant trait databases (Kattge *et al.*, 2011), and by using community-weighted trait-based approaches to link plant traits with ecosystem processes (Laughlin, 2011) and landscape-level patterns of soil microbial communities (de Vries *et al.*, 2012).

Finally, the application of the MANE framework to ecosystems other than temperate forests would be a fruitful area of research. Although most tropical trees associate with AM fungi, large monodominant stands of ECM trees are often surrounded by dense AM-dominated stands (Newbery *et al.*, 1997; McGuire *et al.*, 2008). This presents an opportunity to examine whether there are sharp gradients in forest nutrient economies as one moves from AM-dominated to ECM-dominated stands. Other profitable areas for investigation include whether nutrient economy gradients occur from woody shrub (ECM) encroachment into grasslands (AM) or drought-induced shifts from pinyon (ECM) to juniper (AM). The extent to which the MANE framework can be applied to ecosystems containing both ericoid and ECM species in sub-arctic ecosystems is also an intriguing question. Ericaceous plants have acidifying litter (Cornelissen *et al.*, 2006) and mycorrhizae which have the ability to mine recalcitrant SOM for N (Wurzburger & Hendrick, 2009). Whether these plants represent a further end-member on the organic nutrient economy spectrum is a question worthy of study.

Mycorrhizal associations as plant functional groups in models

Incorporating a mycorrhizal framework into how earth systems models (ESMs) classify plant functional types (PFTs) has the potential to improve our ability to predict the response of C–N couplings to global change. Earth system models are global climate models that include representations of biogeochemical processes such that feedbacks between the physical climate and the biological and chemical processes on earth can be predicted. Current ESMs predict C and N dynamics using prescribed physiological parameters for each PFT (Oleson *et al.*, 2010). In the latest version of the Community Land Model (CLM 4.0), there are three PFTs that capture temperate forests, needleleaf evergreen, broadleaf evergreen, and broadleaf deciduous (Lawrence & Chase, 2007). Each temperate forest PFT has set C : N for leaves, roots, wood, and litter that impact SOM decomposition and C and N allocation (Thornton *et al.*, 2007). However, the C : N of leaves and litter are the only parameters that differ across temperate forest PFTs (Oleson *et al.*, 2010; Brovkin *et al.*, 2012). In addition, the ratio for the amount of C allocated to stem vs leaves increases as a function of annual NPP, but the allocation of C to leaves and roots is assumed to be equal across all PFTs. Thus, there is generalization of physiological differences across temperate forest PFTs and it is an open question whether a single set of physiological parameters for temperate broadleaf forests is sufficient.

Incorporating the MANE framework into ESMs could be accomplished in two steps. First, new PFTs could be developed based on well documented differences between ECM and AM trees in the C : N ratio of leaves and roots, and the chemical quality of litter (Langley & Hungate, 2003). These mycorrhizal PFTs could be further refined by including organic to inorganic nutrient ratios, by incorporating differences in microbial function based on fungal to bacteria ratios or C-use efficiency terms, and by testing the hypothesized differences in belowground C allocation (i.e. root C : leaf C ratios) between ECM and AM trees. We acknowledge that the utility of mycorrhizal-based PFTs in models will require the ability to remotely sense and map AM and ECM distributions. This is currently not possible but recent advances in the remote sensing of individual tree species in temperate forests suggests that remote sensing of mycorrhizal association is feasible (Plourde *et al.*, 2007; Kokaly *et al.*, 2009; Ustin & Gamon, 2010).

Conclusions

There is a critical need to develop new approaches for measuring belowground processes and to develop conceptual frameworks that enable the up-scaling of these processes. These unmet needs represent key obstacles to developing improved projections of how forests mediate global C cycle–climate feedbacks. Here we present evidence to support the development of a new framework that classifies temperate forests based on the mycorrhizal associations of the dominant trees and their contrasting effects on the nutrient economy. The framework is based on evidence that forests dominated by AM trees have an inorganic nutrient economy (characterized by rapid turnover of plant-derived C by saprotrophs and the rapid cycling of inorganic nutrient forms), whereas forests dominated by ECM trees have an organic nutrient economy (as a result of the slow turnover of plant-derived C and enhanced root-rhizosphere utilization of root-induced increases in the availability of organic forms of nutrients). While there are certainly some exceptions to the rule (e.g. ECM species that have leaf litter traits that are more ‘AM-like’ and vice versa), the framework should be useful as a starting point for exploring variation in forest biogeochemical syndromes across a wide of range of forest types and ecosystems. Finally, our results suggest that this new conceptual framework may facilitate an improved understanding of the context dependence of forest responses to global changes and increase the degree to which we can predict the biogeochemical consequences of shifts in forest composition.

Acknowledgements

This project was supported by a grant from the National Science Foundation (DEB, Ecosystem Studies; #1153401), the Department of Energy (BER, TES), Indiana University’s Center for Research in Environmental Sciences (CRES) and the Indiana Academy of Sciences. We thank Daniel Lehman, Zach Brown and Anna Rosling for field and lab assistance, and Josh Fisher, Ina Meier, Alex Eilts, Keith Clay, Luke Flory, Justin Wright and Tom Evans for insightful suggestions on refining the ‘mycorrhizal gradient’ concept. We also thank Dan Johnson for providing guidance on FIA data processing. Finally, we thank the three reviewers and handling editor Ian Alexander for their helpful comments and suggestions on how to improve the manuscript.

References

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM. 1989. Nitrogen saturation in northern forest ecosystems. *BioScience* 39: 378.

Abrams MD. 1992. Fire and the development of oak rorests – in Eastern North-America, oak distribution reflects a variety of ecological paths and disturbance conditions. *BioScience* 42: 346–353.

Agerer R. 2001. Exploration types of ectomycorrhizae – a proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza* 11: 107–114.

Allen MF, Swenson W, Querejeta JI, Egerton-Warburton LM, Treseder KK. 2003. Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. *Annual Review of Phytopathology* 41: 271–303.

Anderson IC, Cairney JWG. 2007. Ectomycorrhizal fungi: exploring the mycelial frontier. *FEMS Microbiology Reviews* 31: 388–406.

Andrew C, Lilleskov EA. 2009. Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO_2 and O_3. *Ecology Letters* 12: 813–822.

Blum JD, Klaue A, Nezat CA, Driscoll CT, Johnson CE, Siccama TG, Eagar C, Fahey TJ, Likens GE. 2002. Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. *Nature* 417: 729–731.

Boggs JL, McNulty SG, Gavazzi MJ, Myers JM. 2005. Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests. *Canadian Journal of Forest Research* 35: 1901–1913.

van Breemen N, Finlay R, Lundstrom U, Jongmans AG, Giesler R, Olsson M. 2000. Mycorrhizal weathering: a true case of mineral plant nutrition? *Biogeochemistry* 49: 53–67.

Brovkin V, van Bodegom PM, Kleinen T, Wirth C, Cornwell WK, Cornelissen JHC, Kattge J. 2012. Plant-driven variation in decomposition rates improves projections of global litter stock distribution. *Biogeosciences* 9: 565–576.

Brundrett M, Murase G, Kendrick B. 1990. Comparative anatomy of roots and mycorrhizae of common Ontario trees. *Canadian Journal of Botany* **68**: 551–578.

Burns RG, Honkala BH. 1990. *Silvics of North America.* Washington, DC, USA: United States Department of Agriculture, Forest Service.

Carreiro MM, Sinsabaugh RL, Repert DA, Parkhurst DF. 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology* **81**: 2359–2365.

Chalot M, Brun A. 1998. Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews* **22**: 21–44.

Chapin FS, Matson PA, Mooney HA. 2002. *Principles of terrestrial ecosystem ecology.* New York, NY, USA: Springer-Verlag, Inc.

Chapman SK, Langley JA, Hart SC, Koch GW. 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist* **169**: 27–34.

Chen YL, Brundrett MC, Dell B. 2000. Effects of ectomycorrhizas and vesicular–arbuscular mycorrhizas, alone or in competition, on root colonization and growth of *Eucalyptus globulus* and *E. urophylla. New Phytologist* **146**: 545–556.

Cheng L, Booker FL, Tu C, Burkey KO, Zhou LS, Shew HD, Rufty TW, Hu SJ. 2012. Arbuscular mycorrhizal fungi increase organic carbon decomposition under elevated CO_2. *Science* **337**: 1084–1087.

Comas LH, Eissenstat DM. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* **18**: 388–397.

Comas LH, Eissenstat DM. 2009. Patterns in root trait variation among 25 co-existing North American forest species. *New Phytologist* **182**: 919–928.

Cornelissen JHC, Aerts R, Cerabolini B, Werger MJA, van der Heijden MGA. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* **129**: 611–619.

Cornelissen JHC, Quested HM, Logtestijn RSP, Perez-Harguindeguy N, Gwynn-Jones D, Diaz S, Callaghan TV, Press MC, Aerts R. 2006. Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia* **147**: 315–326.

Courty PE, Buee M, Diedhiou AG, Frey-Klett P, Le Tacon F, Rineau F, Turpault MP, Uroz S, Garbaye J. 2010. The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. *Soil Biology & Biochemistry* **42**: 679–698.

Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML *et al.* 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. *Ecology Letters* **14**: 349–357.

Drigo B, Pijl AS, Duyts H, Kielak A, Gamper HA, Houtekamer MJ, Boschker HTS, Bodelier PLE, Whiteley AS, van Veen JA *et al.* 2010. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. *Proceedings of the National Academy of Sciences, USA* **107**: 10938–10942.

Egerton-Warburton L, Allen MF. 2001. Endo- and ectomycorrhizas in *Quercus agrifolia* Nee. (*Fagaceae*): patterns of root colonization and effects on seedling growth. *Mycorrhiza* **11**: 283–290.

Elliott EM, Kendall C, Wankel SD, Burns DA, Boyer EW, Harlin K, Bain DJ, Butler TJ. 2007. Nitrogen isotopes as indicators of NO(x) source contributions to atmospheric nitrate deposition across the Midwestern and northeastern United States. *Environmental Science & Technology* **41**: 7661–7667.

Fellbaum CR, Gachomo EW, Beesetty Y, Choudhari S, Strahan GD, Pfeffer PE, Kiers ET, Bucking H. 2012. Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences, USA* **109**: 2666–2671.

Fernandez CW, Koide R. 2012. The role of chtin in the decomposition of ectomycorrhizal fungal litter. *Ecology* **93**: 24–28.

Finzi AC, Canham CD, Van Breemen N. 1998a. Canopy tree soil interactions within temperate forests: species effects on pH and cations. *Ecological Applications* **8**: 447–454.

Finzi AC, Van Breemen N, Canham CD. 1998b. Canopy tree soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* **8**: 440–446.

Fog K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. *Biological Reviews of the Cambridge Philosophical Society* **63**: 433–462.

Frank DA, Groffman PM. 2009. Plant rhizospheric N processes: what we don't know and why we should care. *Ecology* **90**: 1512–1519.

Fransson PMA, Johansson EM. 2010. Elevated CO_2 and nitrogen influence exudation of soluble organic compounds by ectomycorrhizal root systems. *FEMS Microbiology Ecology* **71**: 186–196.

Frey SD, Knorr M, Parrent JL, Simpson RT. 2004. Chronic nitrogen enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests. *Forest Ecology and Management* **196**: 159–171.

Galloway JN, Cowling EB. 2002. Reactive nitrogen and the world: 200 years of change. *Ambio* **31**: 64–71.

Goodale CL, Lajtha K, Nadelhoffer KJ, Boyer EW, Jaworski NA. 2002. Forest nitrogen sinks in large eastern US watersheds: estimates from forest inventory and an ecosystem model. *Biogeochemistry* **57**: 239–266.

Govindarajulu M, Pfeffer PE, Jin HR, Abubaker J, Douds DD, Allen JW, Bucking H, Lammers PJ, Shachar-Hill Y. 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature* **435**: 819–823.

Handley WRC. 1954. Mull and mor formation in relation to forest soil. Forestry Commision Bulletin No. 23: 115.

Hobbie SE, Ogdahl M, Chorover J, Chadwick OA, Oleksyn J, Zytkowiak R, Reich PB. 2007. Tree species effects on soil organic matter dynamics: the role of soil cation composition. *Ecosystems* **10**: 999–1018.

Hobbie SE, Oleksyn J, Eissenstat DM, Reich PB. 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. *Oecologia* **162**: 505–513.

Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P. 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* **87**: 2288–2297.

Hodge A, Campbell CD, Fitter AH. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* **413**: 297–299.

Hodge A, Fitter AH. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proceedings of the National Academy of Sciences, USA* **107**: 13754–13759.

Holland EA, Dentener FJ, Braswell BH, Sulzman JM. 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* **46**: 7–43.

Iversen CM, Keller JK, Garten CT, Norby RJ. 2012. Soil carbon and nitrogen cycling and storage throughout the soil profile in a sweetgum plantation after 11 years of CO_2-enrichment. *Global Change Biology* **18**: 1684–1697.

Iverson LR, Prasad AM. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* **68**: 465–485.

Iverson LR, Schwartz MW, Prasad AM. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* **13**: 209–219.

Jansa J, Finlay R, Wallander H, Smith FA, Smith SE. 2011. Role of mycorrhizal symbioses in phosphorus cycling. In: Bünemann EK, Oberson A, Frossard E, eds. *Phosphorus in action: biological processes in soil phosphorus cycling.* Heidelberg, Germany: Springer.

Kattge J, Diaz S, Lavorel S, Prentice C, Leadley P, Bonisch G, Garnier E, Westoby M, Reich PB, Wright IJ *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* **17**: 2905–2935.

Koele N, Dickie IA, Oleksyn J, Richardson SJ, Reich PB. 2012. No globally consistent effect of ectomycorrhizal status on foliar traits. *New Phytologist* **196**: 845–852.

Kokaly RF, Asner GP, Ollinger SV, Martin ME, Wessman CA. 2009. Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies. *Remote Sensing of Environment* **113**: S78–S91.

Langley JA, Hungate BA. 2003. Mycorrhizal controls on belowground litter quality. *Ecology* **84**: 2302–2312.

Langley JA, McKinley DC, Wolf AA, Hungate BA, Drake BG, Megonigal JP. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO_2. *Soil Biology & Biochemistry* **41**: 54–60.

Laughlin DC. 2011. Nitrification is linked to dominant leaf traits rather than functional diversity. *Journal of Ecology* **99**: 1091–1099.

Lawrence PJ, Chase TN. 2007. Representing a new MODIS consistent land surface in the Community Land Model (CLM 3.0). *Journal of Geophysical Research-Biogeosciences* 112: G01023.

LeBauer DS, Treseder KK. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**: 371–379.

Lister TW, Gladders G, Barnett CJ, Brand GJ, Butler BJ, Crocker SJ, Domke GM, Griffith DM, Hatfield MA, Kurtz CM *et al.* 2011. *Delaware's forests 2008.* Newtown Square, PA, USA: US Department of Agriculture, Forest Service, Northern Research Station.

Lovett GM, Weathers KC, Arthur MA. 2002. Control of nitrogen loss from forested watersheds by soil carbon: nitrogen ratio and tree species composition. *Ecosystems* **5**: 712–718.

Lovett GM, Weathers KC, Arthur MA, Schultz JC. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry* **67**: 289–308.

Lu M, Yang YH, Luo YQ, Fang CM, Zhou XH, Chen JK, Yang X, Li B. 2011. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. *New Phytologist* **189**: 1040–1050.

Luo Y, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ *et al.* 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* **54**: 731–739.

Magill AH, Aber JD, Currie WS, Nadelhoffer KJ, Martin ME, McDowell WH, Melillo JM, Steudler P. 2004. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management* **196**: 7–28.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist* **195**: 823–831.

McGuire KL, Henkel TW, de la Cerda IG, Villa G, Edmund F, Andrew C. 2008. Dual mycorrhizal colonization of forest-dominating tropical trees and the mycorrhizal status of non-dominant tree and liana species. *Mycorrhiza* **18**: 217–222.

McNeil BE, Read JM, Driscoll CT. 2007. Foliar nitrogen responses to elevated atmospheric nitrogen deposition in nine temperate forest canopy species. *Environmental Science & Technology* **41**: 5191–5197.

Mueller KE, Hobbie SE, Oleksyn J, Reich PB, Eissenstat DM. 2012. Do evergreen and deciduous trees have different effects on net N mineralization in soil? *Ecology* **93**: 1463–1472.

Mueller PE. 1878. Studiero ver SkovjordT. idskr. *Skovbrug* **3**: 1–124.

Nadelhoffer KJ, Emmett BA, Gundersen P, Kjonaas OJ, Koopmans CJ, Schleppi P, Tietema A, Wright RF. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* **398**: 145–148.

Newbery DM, Alexander IJ, Rother JA. 1997. Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. *Ecological Monographs* **67**: 367–409.

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE. 2010. CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences, USA* **107**: 19368–19373.

Odum EP. 1969. Strategy of ecosystem development. *Science* **164**: 262–270.

Oleson KW, Lawrence DM, Bonan GB, Flanner MG, Kluzek E, Lawrence PJ, Levis S, Swenson SC, Thornton PE, Dai A *et al.* 2010. Technical description of version 4.0 of the Community Land Model (CLM). In: *Technical description of version 4.0 of the community land model, NCAR Tech.* Boulder, CO, USA: Climate and Global Dynamics Division.

Olsson PA, Jakobsen I, Wallander H. 2002. Foraging and resource allocation strategies of mycorrhizal fungi in a patchy environment. In: Van der Heijden MGA, Sanders I, eds. *Mycorrhizal ecology.* Berlin, Heidelberg, Germany: Springer-Verlag, 93–115.

Pastor J, Aber JD, Mcclaugherty CA, Melillo JM. 1984. Above-ground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* **65**: 256–268.

Pendall E, Bridgham S, Hanson PJ, Hungate B, Kicklighter DW, Johnson DW, Law BE, Luo YQ, Megonigal JP, Olsrud M *et al.* 2004. Below-ground process responses to elevated CO_2 and temperature: a discussion of observations, measurement methods, and models. *New Phytologist* **162**: 311–322.

Phillips RP, Fahey TJ. 2006. Tree species and mycorrhizal associations influence the magnitude of rhizosphere effects. *Ecology* **87**: 1302–1313.

Phillips RP, Finzi AC, Bernhardt ES. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO_2 fumigation. *Ecology Letters* **14**: 187–194.

Phillips RP, Meier IC, Bernhardt ES, Grandy AS, Wickings K, Finzi AC. 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO_2. *Ecology Letters.*

Plourde LC, Ollinger SV, Smith ML, Martin ME. 2007. Estimating species abundance in a northern temperate forest using spectral mixture analysis. *Photogrammetric Engineering and Remote Sensing* **73**: 829–840.

Pregitzer KS, Burton AJ, King JS, Zak DR. 2008a. Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO_2 and tropospheric O_3. *New Phytologist* **180**: 153–161.

Pregitzer KS, Burton AJ, Zak DR, Talhelm AF. 2008b. Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. *Global Change Biology* **14**: 142–153.

Pritchard SG, Strand AE, McCormack ML, Davis MA, Finzi A, Jackson RB, Matamala R, Rogers HH, Oren R. 2008a. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO_2-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 1–15.

Pritchard SG, Strand AE, McCormack ML, Davis MA, Oren R. 2008b. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO_2-enrichment. *Global Change Biology* **14**: 1252–1264.

Querejeta JI, Egerton-Warburton LM, Allen MF. 2009. Topographic position modulates the mycorrhizal response of oak trees to interannual rainfall variability. *Ecology* **90**: 649–662.

Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* **157**: 475–492.

Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences, USA* **101**: 11001–11006.

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale C, Tjoelker MG. 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecology Letters* **8**: 811–818.

Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94**: 13730–13734.

Schimel JP, Bennett J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* **85**: 591–602.

Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis.* New York, NY, USA: Academic Press.

Smith SE, Smith FA. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annual Review of Plant Biology* **62**: 227–250.

Smith WH. 1976. Character and significance of forest tree root exudates. *Ecology* **57**: 324–331.

Staddon PL, Ramsey CB, Ostle N, Ineson P, Fitter AH. 2003. Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of C^{14}. *Science* **300**: 1138–1140.

Talhelm AF, Pregitzer KS, Zak DR. 2009. Species-specific responses to atmospheric carbon dioxide and tropospheric ozone mediate changes in soil carbon. *Ecology Letters* **12**: 1219–1228.

Taylor LL, Leake JR, Quirk J, Hardy K, Banwart SA, Beerling DJ. 2009. Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. *Geobiology* **7**: 171–191.

Templer PH, Lovett GM, Weathers KC, Findlay SE, Dawson TE. 2005. Influence of tree species on forest nitrogen retention in the Catskill Mountains, New York, USA. *Ecosystems* **8**: 1–16.

Templer PH, Mack MC, Chapin FS, Christenson LM, Compton JE, Crook HD, Currie WS, Curtis CJ, Dail DB, D'Antonio CM *et al.* 2012. Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of ^{15}N tracer field studies. *Ecology* **93**: 1816–1829.

Thomas KD, Prescott CE. 2000. Nitrogen availability in forest floors of three tree species on the same site: the role of litter quality. *Canadian Journal of Forest Research* **30**: 1698–1706.

Thomas RQ, Canham CD, Weathers KC, Goodale CL. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* **3**: 13–17.

Thornton PE, Lamarque JF, Rosenbloom NA, Mahowald NM. 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO$_2$ fertilization and climate variability. *Global Biogeochemical Cycles* **21**: GB4018.

Turner BL. 2008. Resource partitioning for soil phosphorus: a hypothesis. *Journal of Ecology* **96**: 698–702.

Twery MJ, Patterson WA. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New-England. *Canadian Journal of Forest Research* **14**: 565–574.

Twieg BD, Durall DM, Simard SW. 2007. Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytologist* **176**: 437–447.

Ustin SL, Gamon JA. 2010. Remote sensing of plant functional types. *New Phytologist* **186**: 795–816.

Veresoglou SD, Chen BD, Rillig MC. 2012. Arbuscular mycorrhiza and soil nitrogen cycling. *Soil Biology & Biochemistry* **46**: 53–62.

Vesterdal L, Elberling B, Christiansen JR, Callesen I, Schmidt IK. 2012. Soil respiration and rates of soil carbon turnover differ among six common European tree species. *Forest Ecology and Management* **264**: 185–196.

Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA. 1982. A comparative-analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological Monographs* **52**: 155–177.

Vitousek PM, Reiners WA. 1975. Ecosystem succession and nutrient retention – hypothesis. *BioScience* **25**: 376–381.

de Vries FT, Manning P, Tallowin JRB, Mortimer SR, Pilgrim ES, Harrison KA, Hobbs PJ, Quirk H, Shipley B, Cornelissen JHC *et al.* 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecology Letters* **15**: 1230–1239.

Waldrop MP, Zak DR, Sinsabaugh RL, Gallo M, Lauber C. 2004. Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. *Ecological Applications* **14**: 1172–1177.

Wallace ZP, Lovett GM, Hart JE, Machona B. 2007. Effects of nitrogen saturation on tree growth and death in a mixed-oak forest. *Forest Ecology and Management* **243**: 210–218.

Wang B, Qiu YL. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* **16**: 299–363.

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629–1633.

Whiteside MD, Digman MA, Gratton E, Treseder KK. 2012. Organic nitrogen uptake by arbuscular mycorrhizal fungi in a boreal forest. *Soil Biology & Biochemistry* **55**: 7–13.

Woodall CW, Webb MN, Wilson BT, Settle J, Piva RJ, Perry CH, Meneguzzo DM, Crocker SJ, Butler BJ, Hansen MH *et al.* 2011. *Indiana's forests 2008.* Newtown Sqaure, PA, USA: US Department of Agriculture, Forest Service, Northern Research Station.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Wurzburger N, Hendrick RL. 2009. Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. *Journal of Ecology* **97**: 528–536.

Zak DR, Pregitzer KS, Kubiske ME, Burton AJ. 2011. Forest productivity under elevated CO$_2$ and O$_3$: positive feedbacks to soil N cycling sustain decade-long net primary productivity enhancement by CO$_2$. *Ecology Letters* **14**: 1220–1226.

Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Species and mycorrhizal associations of all trees in the FIA plots used to generate Fig. 1

Methods S1 Methods for collecting and processing litter and soil samples from Griffy Woods and Moores Creek, IN, USA.