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The use of fossil fuels and fertilizers has increased the amount of biologically reactive nitrogen in the atmosphere over the past century. As a consequence, forests in industrialized regions have experienced greater rates of nitrogen deposition in recent decades. This unintended fertilization has stimulated forest growth, but has also affected soil microbial activity, and thus the recycling of soil carbon and nutrients. A meta-analysis suggests that nitrogen deposition impedes organic matter decomposition, and thus stimulates carbon sequestration, in temperate forest soils where nitrogen is not limiting microbial growth. The concomitant reduction in soil carbon emissions is substantial, and equivalent in magnitude to the amount of carbon taken up by trees owing to nitrogen fertilization. As atmospheric nitrogen levels continue to rise, increased nitrogen deposition could spread to older, more weathered soils, as found in the tropics; however, soil carbon cycling in tropical forests cannot yet be assessed.

Atmospheric deposition of reactive nitrogen, originating mainly from fossil-fuel burning and artificial fertilizer applications1, has increased three- to fivefold over the past century[2]. In many areas of the globe, nitrogen deposition is expected to increase further[3,4], with global deposition rates projected to increase by a factor of 2.5 by the end of the century[5]. Atmospheric deposition of nitrogen has many negative ecological effects in terres-trial and aquatic ecosystems, such as eutrophication and the loss of biodiversity[6–8]. Excessive nitrogen deposition can also result in soil acidification, loss of base cations and nitrate leaching into ground-water[9–11]. However, low levels of atmospheric nitrogen deposition can have one positive effect: the stimulation of plant growth and the associated increase in the uptake of carbon from the atmosphere — which contributes to climate change mitigation[12–15]. In 2007, Magnani and co-workers even revealed nitrogen deposition to be the dominant driver of carbon sequestration in forest ecosystems[16]. The publication by Magnani and colleagues generated an intense debate about the magnitude and sustainability of the nitro-gen-induced carbon sink and its underlying mechanisms[17–19]. Two mechanisms contribute to the enhanced carbon-sink strength in forests under elevated atmospheric nitrogen deposition: increased wood formation[13,14,20], and the accumulation of surface litter and soil organic matter (SOM)[14,21,22]. Accumulation of SOM could result from an increase in soil carbon inputs, but this is not com-monly observed in forests exposed to nitrogen deposition[14]. In contrast, decreased rates of plant litter and SOM decomposition, owing to enhanced soil nitrogen inputs, have frequently been reported[23,24]. Using a meta-analysis of measurements in nitrogen-addition experiments (see Supplementary Information S1), and a comparison of study sites exposed to elevated or background atmospheric nitrogen deposition (see Supplementary Information S2), we show that the negative effect of nitrogen on soil respiration is widespread, albeit not universal, in temperate [**Au: OK?**] for-est ecosystems. Despite the long history of evidence that nitrogen deposition slows decomposition, this effect has not been included in current carbon-cycle models.

Empirical evidence

Low-quality litter. It is well established that leaf litter with higher nitrogen concentrations (or high nitrogen to lignin ratios) decom-poses faster than its lower nitrogen counterpart[25–27], although this difference [**Au: what difference?**] may revert during later stages of the decomposition process[28]. However, adding nitrogen to low-nitrogen litter does not accelerate its decomposition. In an early review of more than 60 experiments examining the effect of nitro-gen applications on the decomposition of various types of organic matter, Kåre Fog[23] concluded that "when all these papers are con-sidered together, it is evident that no effect, or even a negative effect, of the addition of nitrogen to decomposing organic material is a very widespread phenomenon."

Literature reviews have indicated distinct decomposition responses to nitrogen additions in litter with low- versus high-lignin contents[23,29]. In agreement with earlier studies on leaf-litter decomposition, nitrogen addition accelerates decomposition of low-lignin litter. However, in contrast to the response of low-lignin litter, Fog[23] concluded that "in recalcitrant substrates the situa-tion is completely different. Here negative effects of the addition of nitrogen are much more common, especially if the lignin con-tent is high, in direct contrast to the case above. Thus, the higher the lignin content, the smaller the amount of nitrogen tolerated".
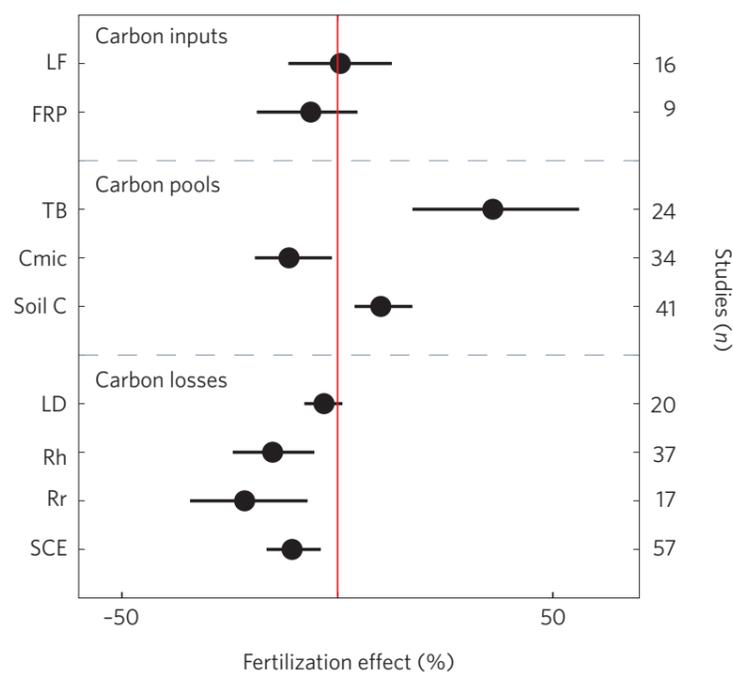
Figure 1 | Effect of experimental nitrogen addition on various forest carbon pools and fluxes as calculated by meta-analysis. Positive values indicate that nitrogen addition had a positive effect, negative values indicate a decrease. Error bars indicate the 95% confidence interval. Data are the weighted means for n data points (right axis). Parameters listed are carbon inputs (left axis): litter fall (LF) and fine‑root production (FRP); carbon pools: total tree biomass (TB), microbial biomass (Cmic) and soil carbon content (Soil C); and carbon losses: litter decomposition (LD), heterotrophic respiration (Rh), root respiration (Rr) and soil carbon dioxide efflux (SCE). Exact numbers can be found in Supplementary Table S1.

Almost exactly the same results were obtained in a recent quantitative meta-analysis on the effects of nitrogen additions on litter decomposition[29]. Moreover, the overall mean response to nitrogen addition tended to be positive in short-term studies, but a signifi‑cant decrease in decomposition rate (17%) was detected in stud‑ies lasting longer than two years. Given that forest litter contains a substantial fraction of low-quality litter (litter with high-lignin and low-nitrogen content that decomposes very slowly), and the clear evidence that low-quality litter is negatively affected by nitrogen additions, it is to be expected that atmospheric nitrogen deposition would typically reduce litter decomposition in forest ecosystems.

Our statistical meta-analysis[30], applied to data from 20 nitro-gen-manipulation experiments in forests, suggested only a small and statistically insignificant decline in leaf-litter decomposition rate (Fig. 1). However, in agreement with the previous studies, we found that nitrogen additions tend to accelerate decomposi-tion in genera producing easily degradable leaf litter (for example, *Acer*, *Populus*, *Betula*), whereas they clearly reduce decomposi-tion rates in species with more recalcitrant litter (for example, *Pinus*, *Picea*, *Fagus*, *Quercus*; Supplementary Fig. S1). Moreover, all forests produce large quantities of lower-quality litter, such as twigs, branches and seed pods, which may be more strongly affected by added nitrogen; however, there are insufficient data to test this hypothesis.

Reductions in heterotrophic respiration. Respiration in aerobic soils involves the breakdown of organic molecules, with CO_2 as the main end-product. Release of CO_2 is therefore commonly used as a proxy for respiratory activity. Here, we define respiration by organisms obtaining their energy from the decomposition of litter and SOM as heterotrophic respiration. Heterotrophic respiration is thus an integrator of the decomposition of organic matter in all stages of decomposition, and in all soil layers, making its response to nitrogen additions more relevant to soil carbon cycling than

that of leaf-litter decomposition alone. To mitigate variations due to methodological differences[31,32], we focus on heterotrophic res-piration estimates obtained in laboratory incubations, or using the trenching technique[31] — both of which physically separate the soil from root inputs.

Our statistical meta-analysis revealed that the average response of heterotrophic respiration to nitrogen addition is much more pronounced than that of leaf-litter decomposition alone. Averaged over 36 nitrogen-manipulation studies in forest ecosystems, heterotrophic respiration declined by 15% when nitrogen was added (Fig. 1). Variation between experiments was high, with responses ranging from a reduction of 57% to a stimulation of 63% (Fig. 2). Forests exposed to elevated atmospheric nitrogen depo-sition are also observed to have lower heterotrophic respiration than forests receiving background levels of nitrogen deposition (wet deposition <5.5 kg N ha^{-1} yr^{-1}; Fig. 3a). For forests with an annual biomass production of around 600 g C m^{-2} yr^{-1}, the reduc-tion amounts to roughly 100 g C m^{-2} yr^{-1} (Fig. 3a). The different slopes of the two regressions in Fig. 3a further suggest that nitro-gen deposition has a stronger negative effect at highly productive sites, where nitrogen is unlikely to be the most limiting nutrient, than at less productive sites, where nitrogen immobilization is likely to be higher, and the negative effect on heterotrophic respi-ration is only marginal. It can be concluded that both the episodic addition of high amounts of fertilizer, and the chronic deposition of small amounts of nitrogen, induce a decline in heterotrophic soil respiration in most, but not all, forest ecosystems.

Reductions in soil carbon dioxide efflux. Soil carbon dioxide efflux (SCE) is an important indicator of below-ground carbon cycling[33]. Although heterotrophic respiration constitutes a substantial part of SCE, two important carbon fluxes, related to the presence of roots in soils, differentiate SCE from heterotrophic respiration. First, a major component of SCE is autotrophic in nature (root, mycorrhizal and rhizosphere respiration), coupling temporal variations in SCE to variations in below-ground carbon allocation and, ultimately, photosynthesis[34–36]. Second, rhizodeposition — the transfer of root-derived carbon compounds to soil — can stimulate microbial activity and thus prime decomposition of SOM[37–39]. This priming mechanism alters heterotrophic respiration, but could not have con-tributed to the heterotrophic respiration measurements presented above, which were all made in the absence of live roots.

As with heterotrophic respiration, there is convincing evidence that SCE declines following nitrogen addition, either through fertilization (-10%; Fig. 1) or through atmospheric nitrogen depo-sition (Fig. 3b). In most studies, this negative effect appears almost instantaneously, and the negative responses persist for years after the addition of nitrogen has ceased[24,40,41]. Although the average response of SCE in fertilization experiments was clearly negative, SCE was found to be positively affected by nitrogen addition in roughly 25% of the 57 manipulation studies (Fig. 2). A closer look at the experiments where SCE increased following nitrogen fer-tilization revealed that these were mainly studies where nitrogen addition has the potential to strongly enhance photosynthesis. Specifically, SCE increased in [**Au: OK?**] very young plantations (<4 yr), where nitrogen addition may have accelerated canopy development, and in CO_2-fumigated forest stands, where extra nitrogen helps to sustain the stimulatory effect of CO_2 on pho-tosynthesis (Fig. 2 and Supplementary Fig. S2; refs 42–44). Part of the increased carbon availability was probably allocated below ground, stimulating rhizosphere respiration and microbial activ-ity. We therefore predict that the increase in SCE observed in a subset of studies (Fig. 2) is attributable to enhanced photosynthe-sis following nitrogen enrichment.

Excluding the very young and CO_2-fumigated sites, the average decline in SCE amounted to -17% (Supplementary Fig S2), roughly
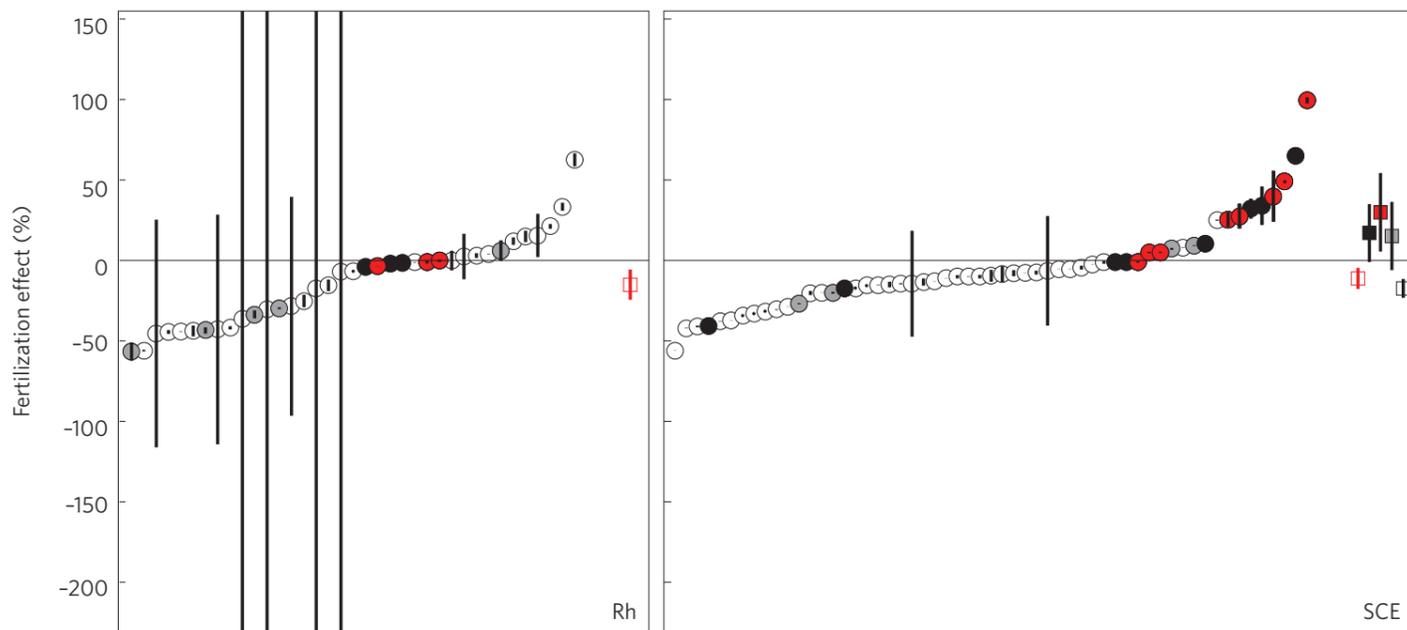
Figure 2 | Relative effect of nitrogen addition on heterotrophic respiration and soil carbon dioxide efflux. The manipulation experiments included in the statistical meta-analysis are indicated by circles, and the overall size of the mean effect is indicate by open red squares. Open black circles are forest stands more than four years old that received no additional CO_2 and their mean is represented by the open black square. Filled grey circles are forest stands more than four years old exposed to elevated atmospheric CO_2 concentrations. Filled black circles are forests of four years or younger, and filled red circles are forest stands of four years old or younger that also received CO_2 fumigation. Error bars indicate the 95% confidence interval. In these young and/or CO_2 fumigated forests, nitrogen deposition favours SCE (positive response, see the overall means represented by the squares on the right hand side), whereas in forests older than five years, nitrogen deposition has a negative effect on SCE almost consistently. The effect of nitrogen addition on heterotrophic respiration (Rh), in contrast, is more consistently negative and does not differ between very young and/or CO_2 fumigated and older forests. Site information, data and references to all studies included in this analysis are given in Supplementary Information S1. [Au: OK?]

150–200 g C m^{-2} yr^{-1}. Sites receiving more than 50 kg N ha^{-1} yr^{-1} showed a stronger decline in SCE (-21%) than sites receiving doses of less than 50 kg N ha^{-1} yr^{-1}, which better mimics the effects of atmospheric nitrogen deposition. Nevertheless, the response of SCE in this latter group remained significantly negative (-10%). Per unit of nitrogen added, the reduction in SCE amounts to 36 g C per g N added. At a small number of sites older than five years, and not enriched with CO_2, SCE responded positively, or not at all, to nitrogen addition. At these few sites, we speculate that nitrogen might be limiting microbial growth and thus heterotrophic respiration (see above).

Soil carbon increases as microbial biomass decreases. The response of plant-litter inputs (leaf-litter fall and fine-root production) to nitrogen addition is variable; both increases and decreases are frequently observed, and on average litter inputs are not affected (Fig. 1). In nitrogen fertilization experiments, the combination of reduced heterotrophic carbon losses and unaltered plant-litter inputs results in substantial soil carbon accumulation (relative increase of 10%; Fig. 1), corresponding to 19 g C per g N added. Thus, on average, about half of the reduction in SCE in the manipulation experiments may be due to carbon accumulating in the soil. This substantial increase in soil carbon should be interpreted with caution, however, because most studies report carbon-pool changes only for the uppermost soil layers. Furthermore, in a comprehensive review of results from ^{15}N field experiments, long-term low-dose nitrogen fertilization experiments and ecosystem models, de Vries and co-workers[45] also reported that nitrogen deposition substantially stimulated soil carbon sequestration. Taking all the evidence into account, soil carbon sequestration in European forests in response to nitrogen deposition was estimated to range from 5 to 23 g C per g N (ref. 45), agreeing well with our estimate. Sequestration rates of a similar magnitude were also reported in other, more limited, multi-site analyses[14,46]. The efficiency of soil carbon storage per unit of nitrogen deposited declines with the amount of nitrogen added or deposited to the forest[46]. This trend is expected, because as nitrogen availability increases, a larger fraction will be lost to groundwater and the atmosphere, and the probability of adverse

effects of nitrogen saturation occurring increases proportionally.

Caution is needed, however, when interpreting spatial correlations between nitrogen deposition and soil carbon sequestration across forests (P. Högberg, personal communication). Within Europe, for example, nitrogen deposition co-varies with natural soil-nutrient availability. Human population centres have developed in the more fertile regions, with a good climate for nitrogen mineralization (not too dry, not too cold), and nitrogen deposition has increased with population. Hence, soil carbon accumulation may be partly attributable to the more favourable, natural nutrient availability in these areas.

In agreement with the declines in heterotrophic respiration and SCE, we observe a statistically significant decline (-11%) in microbial biomass (Fig. 1). A review on the effects of nitrogen deposition on microbial biomass showed that the average decline exceeded 20% in both temperate and boreal forests[47]. When excluding very young forests and elevated CO_2 treatments from our analysis, we observe an average reduction in microbial biomass of 16% (Supplementary Fig. S1), in line with the review by Treseder[47] and with the response of SCE.

Processes underlying the reduction in soil respiration [Au: OK?]

Empirical evidence thus tells us that various aspects of below-ground carbon cycling are negatively affected by nitrogen addition and that these effects are widespread, but that there are also conditions under which nitrogen addition accelerates decomposition and soil respiration (severe nitrogen limitation, young forests and elevated CO_2 experiments). The following mechanisms have been put forward in the literature to explain these observations (Box 1).

Reductions in below-ground carbon allocation. Nitrogen is the most important macronutrient. With the exception of regions where other nutrients are more limiting, a large increase in nitrogen availability reduces the need for trees to invest carbon in nutrient-absorbing systems. This induces a shift in carbon allocation in favour of above-ground tissue production, at the expense of the root system[48].
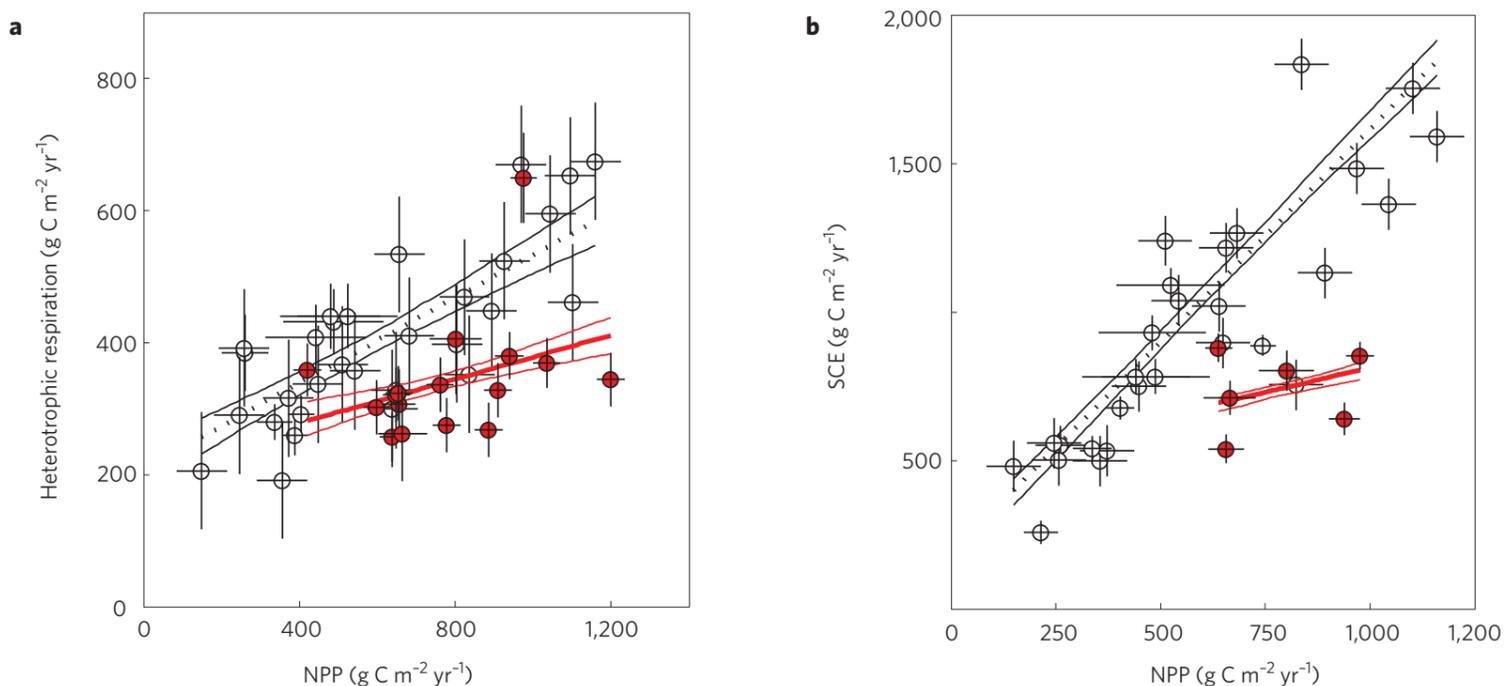
Figure 3 | Observed annual heterotrophic respiration rates and soil carbon dioxide efflux as a function of annual biomass production (NPP) in forests exposed to elevated or background nitrogen deposition. a, Open black circles and dotted black line ($y = 212 + 0.32x$) represent forests with wet nitrogen deposition < 5.5 kg N ha^{-1} yr^{-1} (the current average deposition rate in unaffected forests). Filled red circles and solid red line ($y = 217 + 0.16x$) reflect forests with nitrogen deposition > 5.5 kg N ha^{-1} yr^{-1} (affected by nitrogen deposition). The thinner lines surrounding the regression lines represent the 67% confidence intervals (one standard deviation). The data support the hypothesis that intercepts are equal ($p = 0.475$), but reject the hypothesis that slopes are equal ($p = 0.965$). b, Open black symbols and dotted black line ($y = 153 + 1.47x$) represent forests with wet nitrogen deposition < 5.5 kg N ha^{-1} yr^{-1} (the current average deposition rate in unaffected forests). Filled red circles and solid red line ($y = 483 + 0.32x$) reflect forests with nitrogen deposition > 5.5 kg N ha–1 yr–1 (affected by nitrogen deposition). The thinner lines surrounding the regression lines represent the 67% confidence intervals (one standard deviation).

In absolute values, our data do not show clear differences in fine-root annual biomass production between nitrogen-fertilized and control plots (Fig. 1). However, the nutrient acquisition system is not limited to the root system, and there is abundant evidence that nitrogen enrichment spectacularly affects the activity of the rhizosphere, and of mycorrhizal root symbionts in particular[49]. In a nitrogen-supply gradient study, carbon allocation to fungal symbionts was the process that responded most to nitrogen addition[50]. Drastic declines in the production of fruiting bodies by mycorrhizal fungi[51], the contribution of mycorrhizae to total microbial biomass[52], mycorrhizal diversity (see Treseder[47] for a review), mycorrhizal infection rates and survival[53], and arbuscular mycorrhizal biomass, hyphal length and storage structures[54,55] have all been reported in response to nitrogen addition. These results reflect reduced reliance of trees on fungal symbionts under high nitrogen deposition, which underlies the strong reduction in below-ground carbon allocation.

The mere reduction in below-ground carbon allocation has been shown to produce a direct negative effect on rhizosphere respiration and thus SCE[56]. The reduction of carbon inputs into the soil is an important mechanism through which decomposition and soil respiration may be altered (Box 1). Mycorrhizal root symbionts have the capacity to degrade organic matter[57], and their decline would therefore be expected to directly reduce decomposition. Furthermore, fine roots, and especially mycorrhizal hyphae, exude substantial amounts of soluble organic compounds[58] — and these compounds serve as a carbon and energy source for saprotrophic organisms — that subsequently decompose organic matter while searching for nutrients[59]. The stimulation of saprotrophic organisms by root and mycorrhizal exudates is known as the priming effect, and is widely accepted to exert a major control over SOM decomposition[38,60–64]. By supplying less substrate to the decomposers, the nitrogen-induced reduction of below-ground carbon allocation can thus be expected to impede the decomposition of soil organic carbon.

The reduction in below-ground carbon allocation thus contributes to the reduction in SCE (on average, 36 g C per g N; see section on SCE above), but cannot explain the substantial increase in soil carbon (on average, 19 g C per g N; see section on soil carbon increases above). Soil carbon accumulation on this scale can only be explained by mechanisms that directly reduce the activity of saprotrophs.

Shifts in the saprotrophic community. There are several ways in which nitrogen-induced changes in microbial community structure or function could affect the decomposition of SOM. Saprotrophic organisms could switch food source — from nitrogen-containing recalcitrant SOM to energy-rich rhizodeposits (preferential substrate theory[63,65–67]) — following nitrogen addition. Alternatively, less efficient microbial populations (which assimilate less carbon and emit more carbon dioxide per gram of litter decomposed) that require little nitrogen might be out-competed by populations that are nitrogen limited, but more efficient[41]. Indeed, Ågren and co-workers[41] postulated that a shift towards more efficient nitrogen-demanding species could explain the observed reductions in SCE. Their model would also be consistent with observed increases in soil carbon stocks and reduced microbial biomass if the new microbial populations also produced more recalcitrant organic matter.

Numerous other studies have reported microbial community shifts following nitrogen addition. In the early 1960s, Mangenot & Reymond[68] noted that several species of wood-decomposing basidiomycetes lost their competitive ability following nitrogen additions. And there is ample recent evidence that nitrogen additions to forest soils induce shifts in microbial community composition[47,69–71].

Whatever the exact mechanism explaining nitrogen-induced reductions in the decomposition of recalcitrant soil organic carbon and litter, alterations in the activity or expression of enzymes involved

Box 1 | Conceptual scheme depicting the mechanisms that explain the nitrogen-induced response of below-ground carbon cycling and its variation.
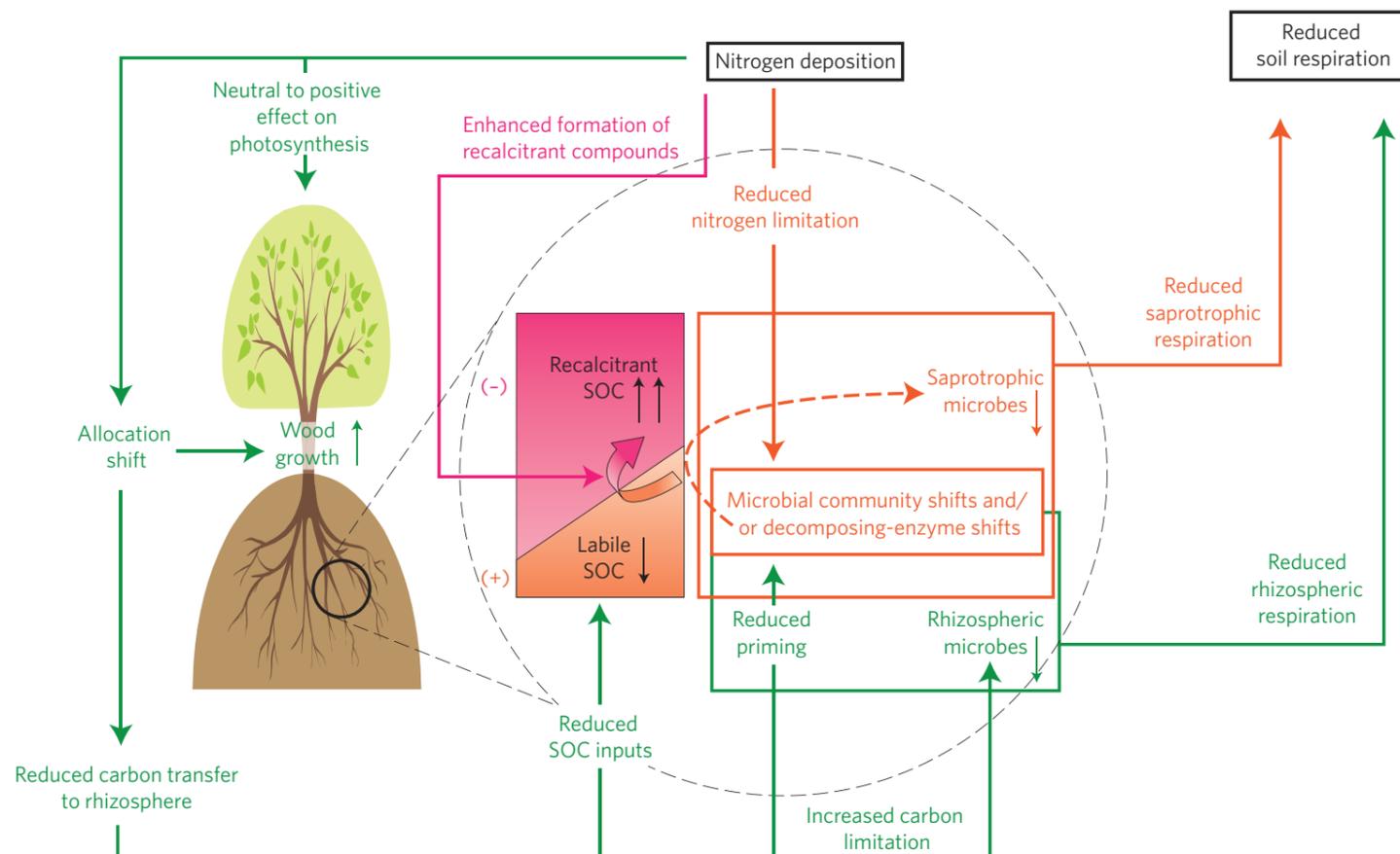
The effects of nitrogen deposition on the saprotrophic system may be related to two, mutually non-exclusive, mechanisms: enhanced chemical stabilization of organic matter into recalcitrant compounds, resistant to microbial decay (magenta arrow); and shifts in microbial enzyme synthesis and activity towards preferential decomposition of labile, energy-rich compounds, coupled with reduced decomposition of recalcitrant substrates (orange arrows).

In the presence of roots, nitrogen effects through altered rhizosphere carbon inputs (green arrows) influence rhizosphere respiration, but also carbon cycling through the saprotrophic system. Under increasing nitrogen availability, wood production is typically promoted at the expense of below-ground carbon allocation, reflecting the reduced need for an elaborate nutrient acquisition system. Declining availability of energy-rich compounds, combined with excess nitrogen, affects the functioning of the microbial community, producing a different enzyme spectrum. The reduced carbon available for mineralization results in further reductions in saprotrophic biomass; the associated increase in net nitrogen mineralization thus aggravates the above-mentioned, direct, negative, nitrogen effects on decomposition of recalcitrant SOM.

Although retarded below-ground carbon cycling in response to nitrogen addition is the general rule in forests, there are exceptions. In severely nitrogen-limited forests, such as in the northern boreal zone, microbial biomass may grow following nitrogen addition, resulting in enhanced enzyme production and increased soil respiration. More commonly, however, nitrogen deposition may stimulate canopy photosynthesis. In nitrogen-limited, open forests, as well as in very young, accruing plantations, nitrogen deposition can accelerate canopy closure, and thus enhance light interception and photosynthesis. In nitrogen-limited systems, such as boreal forests or CO_2-enriched trees, leaf-level photosynthesis may also be enhanced by nitrogen addition. This increase in photosynthesis may offset the relative decline in below-ground carbon allocation, such that more labile carbon enters the soil, fuelling not only rhizosphere microbes but also saprotrophic microbes and their decomposition of recalcitrant soil organic carbon (SOC). Hence, although these are negative responses, and nitrogen deposition and addition clearly dominate the literature, positive responses do occur.

The scheme presented in this box is, however, not valid for nitrogen-saturated systems where adverse effects such as acidification, cation leaching and altered vegetative composition may induce very different responses.

in the decomposition process are likely to play a key role. For example, cellulose-decomposing and phosphate-acquiring enzymes were reported to increase [**Au: in abundance or activity?**] following nitrogen fertilization, especially in nitrogen-limited ecosystems[72–74], often accelerating cellulose decomposition[74,75]. In contrast, lignin-degrading enzymes, such as phenol oxidases and peroxidases, are frequently down-regulated[23,70,74,76,77] (but see ref. 73). Several white-rot fungi failed to synthesize lignin-degrading enzymes in the presence of low-molecular-weight nitrogen compounds[24,78,79], but

this response varies between species[23,80]. One potential reason for a reduction in the synthesis of lignin-degrading enzymes is that lignolitic fungi are inefficient in their carbon use and grow slowly. They are therefore likely to be out-competed by other microbes when nitrogen is in plentiful supply, resulting in reduced ligninase activity and hence lignin degradation[41,68,81]. Many easily decomposable substrates are embedded in the lignin matrix in fresh plant litter[23]. Thus, by degrading lignin more slowly, decomposition of all compounds within the lignin matrix is reduced[76].

Shifts in the expression and activity of various enzymes are thus likely to explain the observation that more labile litter types or compounds (such as cellulose) decompose faster following nitrogen addition, especially in the short term[23,29]. In the long term, the reduced production or activity of specific enzymes involved in the degradation of more recalcitrant compounds such as lignin may be responsible for the negative effect of nitrogen addition.

Although the concepts of altered microbial community structure and enzymatic spectra are appealing, Keeler *et al.*[73] were not able to find any relationship between the nitrogen-addition effects on decomposition rates and on the activities of six key enzymes involved in decomposition. Moreover, despite the strong evidence that lignin-degrading enzymes are suppressed by nitrogen addition, this mechanism may only be valid in organic surface layers; in mineral soils neither lignin nor lignin-derivatives accumulate in soils exposed to nitrogen addition (see for example ref. 71). It is thus obvious that the molecular transformations in soils, and the role of exo-enzymes in the degradation of the produced recalcitrant compounds, are far from elucidated.

The role of stabilization mechanisms. A large fraction of SOM is chemically or physically protected from microbial decay[82]. If nitrogen additions were to interact with these stabilization mechanisms, decomposition and heterotrophic respiration could well be affected. One hypothesis, often brought forward to explain reductions in decomposition and heterotrophic respiration, is abiotic stabilization of SOM[23,24]. There is evidence for direct chemical incorporation of added nitrogen into organic matter, producing heterocyclic forms of nitrogen (indoles and pyroles)[83] or phenolic compounds polymerized by nitrogen bridges[84] — two groups of compounds that are highly resistant to degradation by microbial enzymes. By chemically protecting part of the organic matter available for decomposition, these abiotic reactions could reduce decomposition and enhance carbon sequestration (see also refs 23,24). However, ^{15}N NMR spectrometry indicates that most of the retained nitrogen is in the amide form, which points towards the dominance of biotically mediated formation of recalcitrant SOM[85–88], possibly in response to a nitrogen-induced shift in microbial community composition[41]. Although this finding downplays the importance of abiotic reactions that have been postulated to have an important role[23,24], it does not rule them out. Also, incorporation of SOM into soil aggregates could help to stabilize SOM. However, aggregate formation correlates positively with rhizodeposition, microbial biomass and microbial activity, all of which decline in response to nitrogen deposition. Hence, aggregate formation is not expected to explain reductions in SOM cycling.

Finally, soil acidification is a stabilization mechanism through which decomposition of plant litter and SOM could be reduced. Given that soil pH is crucial to enzyme functioning[23], acidification could have a detrimental effect on microbial activity, and thus on the decomposition of SOM. Poorly buffered soils where nitrification occurs will tend to have lower pH[23,89], especially after chronic nitrogen deposition. Nonetheless, even where soil acidification does not occur, negative effects of nitrogen addition are frequently observed[23]. Hence, acidification may aggravate the response, but not explain it completely.

Implications

Both the nitrogen-fertilization experiments and the comparison between forest ecosystems exposed to background versus elevated nitrogen deposition, provide evidence for declines in SCE and heterotrophic respiration of the same order of magnitude as net ecosystem productivity (the actual net CO_2 uptake or release by ecosystems) reported elsewhere[90–95]. Thus it is not surprising that Magnani and co-workers[16] identified nitrogen deposition as a better determinant of forest net ecosystem productivity than climate or site productivity. Networks of ecosystem CO_2 flux measurements are commonly used to construct greenhouse-gas balances[90] or to extract information on the determinants of these fluxes[16,91–95]. The fact that nitrogen deposition often reduces heterotrophic respiration and SCE by such vast amounts implies that syntheses of CO_2 flux networks have to take nitrogen deposition into account, for example when analysing the effects of climate on carbon cycling.

Eventually, all forests receiving elevated nitrogen deposition for decades or longer will run into nitrogen saturation, a state in which the forest nitrogen cycle is no longer closed[87]. Although the exact effects remain unclear, a decrease in productivity could be anticipated through the loss of base cations and lower phosphorus availability[9,11,96,97]. Long-term soil carbon responses may therefore differ from the overall response reported here.

So far, nitrogen deposition has been elevated mainly in regions with relatively young nutrient-rich soils, where nitrogen is often limiting plant growth (Eastern US, Europe, China). It remains to be tested whether nitrogen deposition will affect carbon cycling (that is, stimulate wood growth and retard SOM decomposition) similarly in tropical and other regions with older severely weathered soils, where nitrogen may not be the most limiting nutrient[98]. If nitrogen enrichment were to slow down decomposition, then nutrient immobilization in accumulating soil organic carbon could negatively affect tropical forest productivity. Because 70% of global primary productivity is realized in the tropics, a shift in nitrogen deposition towards these regions might alter the global carbon balance in unexpected ways. Current understanding of carbon–nutrient interactions in severely weathered soils, or soils with shortages of other nutrients, remain extremely limited, and nitrogen-addition studies in these areas are too rare to allow statistical meta-analysis.

The evidence for altered below-ground carbon cycling presented here highlights the need to incorporate nitrogen cycling and nitrogen deposition into terrestrial carbon-cycle models; not only potential nitrogen-induced impacts on productivity and interactions with increasing atmospheric CO_2 levels[99,100], but, especially, the negative effects on decomposition, below-ground carbon allocation and the coupling of carbon and nitrogen cycling in ecosystems. To do this properly, more work is needed to fully understand the relative importance of the different mechanisms at play (Box 1), the long-term responses to chronic nitrogen deposition, as well as the responses in tropical areas. Given that the size of the nitrogen-induced inhibition of below-ground respiration is of the same order of magnitude as the forest carbon sink, a better understanding of nitrogen deposition effects should be a strong future research priority.

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I.A.J., W.D. and S.L. conceived the manuscript. S.L., W.D., J.A.S. and B.E.L. provided the data. W.D. and S.L. performed the analyses. All authors collaborated in the writing.