

# Do evergreen and deciduous trees have different effects on net N mineralization in soil?

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**Abstract.** Evergreen and deciduous plants are widely expected to have different impacts on soil nitrogen (N) availability because of differences in leaf litter chemistry and ensuing effects on net N mineralization ( $N_{\min}$ ). We evaluated this hypothesis by compiling published data on net  $N_{\min}$  rates beneath co-occurring stands of evergreen and deciduous trees. The compiled data included 35 sets of co-occurring stands in temperate and boreal forests. Evergreen and deciduous stands did not have consistently divergent effects on net  $N_{\min}$  rates; net  $N_{\min}$  beneath deciduous trees was higher when comparing natural stands (19 contrasts), but equivalent to evergreens in plantations (16 contrasts). We also compared net  $N_{\min}$  rates beneath pairs of co-occurring genera. Most pairs of genera did not differ consistently, i.e., tree species from one genus had higher net  $N_{\min}$  at some sites and lower net  $N_{\min}$  at other sites. Moreover, several common deciduous genera (*Acer*, *Betula*, *Populus*) and deciduous *Quercus* spp. did not typically have higher net  $N_{\min}$  rates than common evergreen genera (*Pinus*, *Picea*). There are several reasons why tree effects on net  $N_{\min}$  are poorly predicted by leaf habit and phylogeny. For example, the amount of N mineralized from decomposing leaves might be less than the amount of N mineralized from organic matter pools that are less affected by leaf litter traits, such as dead roots and soil organic matter. Also, effects of plant traits and plant groups on net  $N_{\min}$  probably depend on site-specific factors such as stand age and soil type.

**Key words:** decomposition; genera; inorganic nitrogen; leaf; litter; mineralization; mycorrhizal fungi; nutrients; plant functional trait; plant functional type.

## INTRODUCTION

Many ecologists have suggested that deciduous plants increase soil fertility while evergreens reduce soil fertility (Monk 1966, Aerts 1995, 1999, Cornelissen et al. 1999, Aerts and Chapin 2000, Berendse and Scheffer 2009). This hypothesis, henceforth the “different impacts” hypothesis, is often invoked to explain evergreen dominance on infertile soils (Monk 1966, Givnish 2002). It also has implications for the ability of earth system models to accurately couple the carbon and nitrogen (N) cycles because most models rely on parameterization of plant functional types defined partly by leaf habit (Ostle et al. 2009). Yet, robust evidence of plant functional type effects on soil N cycling is lacking.

Although conceptually appealing, the different impacts hypothesis is based on assumptions that could be problematic. The hypothesis presumes that soils beneath

deciduous species have higher rates of net N mineralization than soils beneath evergreens, and thus greater N availability (Aerts 1999, Cornelissen et al. 1999, Aerts and Chapin 2000, Berendse and Scheffer 2009), due to higher concentrations of N in deciduous leaf litter and faster rates of deciduous litter decomposition (Cornwell et al. 2008). However, litter decomposition rates are questionably relevant to net N mineralization rates ( $N_{\min}$ ) in whole-soil horizons or profiles (Prescott 2005). For example, immobilization of N by microbes can decouple N release from decomposition rates. In addition, mineralization of N from soil organic matter is substantial and potentially unrelated to litter traits and litter decomposition (Knops et al. 2002). Finally, the different impacts hypothesis also overlooks effects of other plant traits (e.g., root N concentrations) and N fluxes (e.g., throughfall N) that can influence soil N cycling (Hobbie 1992, Knops et al. 2002). These traits and processes can also vary independently of leaf traits (Withington et al. 2006, Alexander and Arthur 2010).

Based on qualitative analyses of empirical studies in temperate forests (e.g., Binkley and Valentine 1991, Gower and Son 1992), several review papers have highlighted a lack of support for the predictions of the

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different impacts hypothesis (Stone 1975, Binkley and Giardina 1998, Prescott 2002, Mueller et al. 2010). The only quantitative syntheses conducted to date focused on stands of evergreen and deciduous trees in north-central USA and showed that these tree types had similar rates of net  $N_{\min}$  (Reich et al. 1997, 2001b). To better evaluate the hypothesis that deciduous tree stands have higher net  $N_{\min}$  rates in soil than evergreen stands, a larger synthesis with better controls for environmental factors is required. Hence, we compiled published data on net  $N_{\min}$  rates in soils beneath deciduous and evergreen trees in temperate and boreal zones. To account for climate and soil type effects, we limited our compilation to sites where nearly monotypic stands of deciduous and evergreen trees co-occurred on similar soil types. In addition, to assess whether alternative functional groups of trees have consistent effects on net  $N_{\min}$ , we compared co-occurring trees according to their genera and their association with types of mycorrhizal fungi.

By emphasizing net  $N_{\min}$  rates as both a foundation for the different impacts hypothesis and as a metric for evaluating the hypothesis, important effects of plant functional types on soil N cycling and availability could be overlooked. This is because net  $N_{\min}$  has limitations as an index of soil N cycling and N availability to plants (Schimel and Bennett 2004, Frank and Groffman 2009). It is measured, in the absence of plant roots, as the difference between gross inorganic N release during organic matter decomposition and inorganic N immobilization in microbial biomass. As such, it could underestimate the availability of recycled organic N if plant uptake of organic N is substantial or if rhizosphere processes stimulate N mineralization. To partly counter these limitations and to expand the scope of our assessment, in the *Discussion* section we briefly review how additional components of the soil N cycle are influenced by temperate and boreal tree species. Insufficient data were available to evaluate tree effects on dissolved organic N in soil, so we focused on inorganic N abundance in soil and plant N uptake.

## METHODS

### Data

All data in our compilation were extracted from peer-reviewed articles identified using ISI Web of Science (Appendix A). Net N mineralization ( $N_{\min}$ ) data were derived from short-term laboratory or field incubations. All laboratory incubations and most field incubations were 6 weeks or less. When soil bulk density and the soil depth were reported, we converted net  $N_{\min}$  estimates from units of soil mass to units of ground area. We excluded data expressed per mass unit of soil N or organic matter (when these could not be converted to units of soil mass or area).

We only included studies with co-occurring stands of more than one plant functional type. We defined plant functional type by the combination of leaf habit

(evergreen or deciduous) and phylogeny (angiosperm or gymnosperm). Each study in our final data set also met the following criteria: stands were at least 10 years old, had similar age, grew in close proximity on the same soil type and topography, and had similar management (e.g., thinning). Some natural stands were of uncertain age, but were described as mature. For each site we also collected data on environmental variables, including mean annual precipitation, mean annual temperature, and atmospheric N deposition (Appendix A). The compiled data are available in the Supplement.

### Calculations of effect size

For each set of co-occurring stands (i.e., for each site), mean values of net  $N_{\min}$  for each species were used to calculate average net  $N_{\min}$  for deciduous angiosperms (DAs) and evergreen gymnosperms (EGs). Then, for each site, we calculated the difference between DA and EG means, and divided this value by the absolute value of the EG mean: [DA  $N_{\min}$  deviation = (DA mean  $N_{\min}$  – EG mean  $N_{\min}$ )/|EG mean  $N_{\min}$ |  $\times$  100]. This estimate of effect size, henceforth “DA deviations” (from EGs), standardizes the data while highlighting the contrast between DAs and EGs. It is equivalent to the ratio of the DA and EG means minus one when both means are positive. Values above zero indicate higher net  $N_{\min}$  beneath DAs, negative values indicate lower net  $N_{\min}$  beneath DAs, and zero indicates equivalence of DAs and EGs.

We used additional calculations to compare net  $N_{\min}$  rates beneath co-occurring genera. For each combination of two genera that co-occurred at more than three sites, we calculated the deviation of average net  $N_{\min}$  of one genus relative to the other genus in the pair: [genus Y  $N_{\min}$  deviation from genus Z = (genus Y mean  $N_{\min}$  – genus Z mean  $N_{\min}$ )/|genus Z mean  $N_{\min}$ |  $\times$  100].

### Focal data “populations”

We evaluated DA deviations from EGs separately for plantations and natural stands, given the greater control of soil type, topography, and stand age in adjacent plantations. However, because the number of replicates for each pairwise combination of genera was frequently small, we combined plantations and natural stands for genera comparisons. Due to the low number of sites with deciduous gymnosperms (e.g., *Larix* spp.) present, we did not broadly compare deciduous gymnosperms with either EGs or DAs. To maintain independence of data for statistical analyses, each soil horizon at each site was represented by either a mass-based estimate of net  $N_{\min}$  or an area-based estimate, but not both. When net  $N_{\min}$  rates were available for combined organic and mineral horizons (i.e., a single measurement of net  $N_{\min}$  across both horizons), we excluded data from individual organic and mineral horizons. Otherwise, net  $N_{\min}$  rates from both mineral and organic soil horizons were included as separate data points.

### Hypothesis testing

We used the lower 95% confidence interval (CI) to determine if DA deviations from EGs were significantly greater than zero (Curtis 1996). We estimated 95% CIs using two different methods that account for the non-normal distribution of DA deviations. First, following Adams et al. (1997), we estimated 95% CIs by resampling each population, with replacement, 10 000 times and determining the value of the 2.5th percentile of the resampled means. We also estimated 95% CIs derived from natural-log-transformed response ratios (Hedges et al. 1999) when this estimate of effect size produced distributions that were more normal (i.e., when  $P > 0.1$  for the Shapiro-Wilk  $W$  test). Confidence intervals for the response ratios were then back-transformed to equivalent DA deviations from EGs by taking the antilog and subtracting one (because  $[DA - EG]/EG = DA/EG - 1$ ; see Hedges et al. 1999).

Some authors suggest that the mean effect size should be weighted by the standard error of effect size estimates from each study or by the level of replication within individual studies (Adams et al. 1997, Hedges et al. 1999). We did not use weighted effect sizes for two reasons. First, error estimates were not available for several studies (regardless, error-weighted CIs are probably too narrow when  $n < 20$ , (Hedges et al. 1999), as was the case for each of our data populations). Second, weighting by replication assumes that the value of effect sizes of individual studies is influenced more by precision (i.e., replication) than by other factors. This is not likely to be true in our compilation because sites diverged substantially with respect to factors that could directly influence the value of DA deviations, such as the identity and number of DAs and EGs present.

We also performed paired Wilcoxon signed-rank tests to evaluate the hypothesis that the median difference in net  $N_{\min}$  between co-occurring DA and EG stands was zero. First, we standardized the mean net  $N_{\min}$  of DAs and EGs at each site by the median value for all tree species at each site. Standardization was necessary because populations of interest (Table 1, Fig. 1) contained data expressed as concentrations (e.g., mg N/kg soil) and as pools (e.g., mg N/m<sup>2</sup> ground area); thus, values of plant type differences were not comparable across sites before standardization.

For each population of interest, we also determined values for the upper and lower quartiles. These nonparametric, descriptive statistics are not indicative of the likelihood that the mean or median of DA deviations or genera-level deviations is different from zero. Rather, they provide information regarding the proportion of co-occurring stands for which DAs had higher net  $N_{\min}$  rates than EGs. Specifically, if the lower quartile is negative, at least 25% of stand pairs in the population of interest had net  $N_{\min}$  rates that were lower in DAs relative to EGs.

With the exception of the statistics describing populations of resampled means, all statistics were

generated using JMP version 7.0.2 (SAS Institute 2007). Following Christie (2004), Microsoft Excel was used to produce the population of resampled, mean DA deviations and to calculate the mean and CIs of the resampled population.

## RESULTS

### Data breadth

All sites in our data set were in temperate or boreal zones. The final data set contained data from 21 studies, 35 unique combinations of site and soil type or site and stand age (some sites had stand comparisons for multiple soil types or stand ages), and 43 different tree species from 17 genera. Six genera collectively accounted for 77% of species–site combinations (*Acer*, *Betula*, *Fagus*, *Picea*, *Pinus*, and *Quercus*). There were 16 and 19 independent stand contrasts available for comparing net  $N_{\min}$  rates beneath deciduous angiosperms (DAs) and evergreen gymnosperms (EGs) as plantations and natural stands, respectively (Table 1). Stand age ranged from 10 to 123 years ( $41 \pm 20$  years, mean  $\pm$  SD; median = 33 years). Our compiled data are largely independent of previously published regional-scale compilations (Reich et al. 1997, 2001b) because only two sites from these studies met our criteria for inclusion.

### Comparing deciduous angiosperms and evergreen gymnosperms

The differences in net N mineralization ( $N_{\min}$ ) rates between DAs and EGs were highly variable. For example, DAs had average net  $N_{\min}$  rates that were as much as 400% greater than EGs at some sites and 100% lower than EGs at other sites. For data populations containing all independent soil horizons (i.e., containing data from both mineral and organic horizons), the lower quartile of DA deviations from EGs was –39% for plantations and –10% for natural stands; Table 1). Thus, for at least 25% of DA–EG contrasts, DAs had lower average net  $N_{\min}$  than EGs. The lower quartile of DA deviations was also consistently negative when data were separated by soil horizon (Fig. 1). In contrast, the results of hypothesis tests for net  $N_{\min}$  rates depended on whether DAs and EGs were compared as natural stands or as plantations. The lower 95% CI of DA deviations was negative for net  $N_{\min}$  of plantations, but positive for natural stands (Table 1). Likewise, the median difference between paired DA and EG stands was not significantly different from zero for plantations, but was significantly different from zero ( $P < 0.05$ ) and positive for net  $N_{\min}$  in natural stands.

### Comparing genera

Differences in net  $N_{\min}$  rates between genera were highly variable. For several pairs of DA and EG genera, net  $N_{\min}$  was not consistently higher beneath the DA genus (e.g., *Acer*, *Betula*, *Populus*, *Quercus*, and *Tilia* compared to *Picea*; also *Acer*, *Betula*, and *Quercus*

TABLE 1. Percentage deviations of net N mineralization ( $N_{\min}$ ) beneath deciduous angiosperms (DAs) from the average beneath evergreen gymnosperms (EGs).

Statistic	DA deviations from average EG net $N_{\min}$ (as % of EG mean)	
	Plantations	Natural stands
Range	-134 to +244	-41 to +472
Upper quartile (75%)	22	76
Lower quartile (25%)	-39	-10
Median	5	42
Mean (from resampling)	13	59
Mean (from $\ln[\text{DA}/\text{EG}]$ )	1	36
Lower 95% CI (from resampling)	-14	17
Lower 95% CI (from $\ln[\text{DA}/\text{EG}]$ )	-23	6
$n$	16†	19

Notes: Within each column, data used to calculate statistics were independent combinations of plant type with site, soil type, and stand age (i.e., at some sites, DA-EG contrasts were available for two different stand ages or two soil taxonomic orders). For comparison, confidence intervals (CIs) were calculated based on a resampled population of mean DA deviations ( $n = 10\,000$ ) and on ln-transformed response ratios calculated for each site (see *Methods*).

† For CIs derived from response ratios,  $n = 14$  because two DA-EG contrasts had negative values for one of the plant type means, and these values could not be ln-transformed (these two contrasts had the most extreme DA deviations, -134% and 244%, respectively).

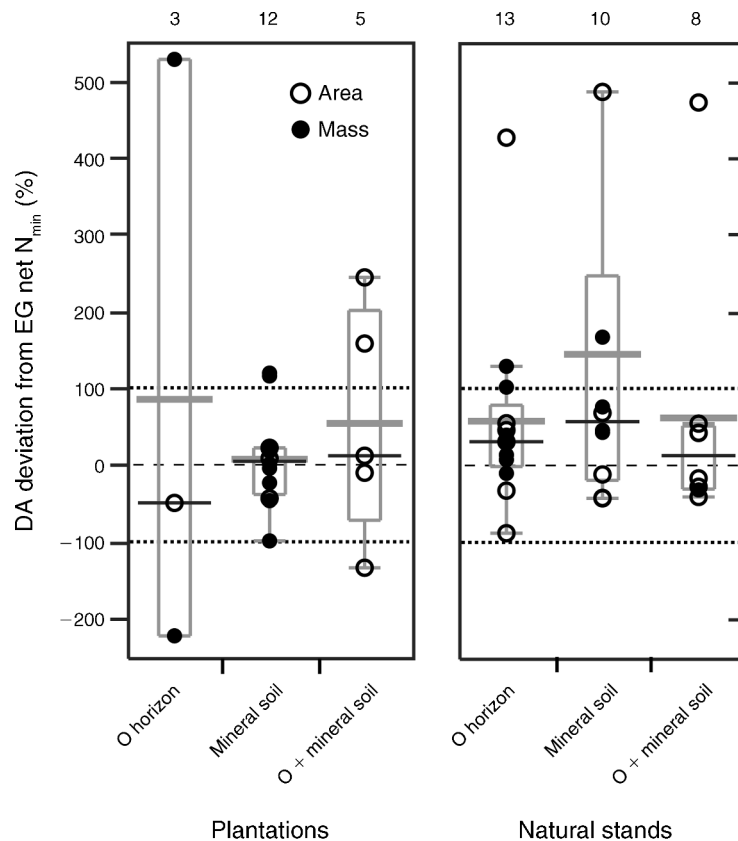


FIG. 1. Percentage deviations of net N mineralization ( $N_{\min}$ ) in soil beneath deciduous angiosperms (DAs) from the average beneath evergreen gymnosperms (EGs). Net  $N_{\min}$  was measured both per unit of soil mass (solid circles) and per soil surface area (open circles). Positive values indicate that DAs have higher net  $N_{\min}$  than EGs; negative values indicate higher net  $N_{\min}$  beneath EGs. For each soil horizon, the number of independent DA-EG contrasts is listed above the boxplot. Boxplots show the median (horizontal black bar), mean (horizontal gray bar), and 25% and 75% quartiles. The whiskers extend from each quartile to the maximum and minimum values or to the outermost point that does not extend beyond the upper or lower quartile by a value more than 1.5 times the interquartile range. Dashed and dotted lines, respectively, denote 0%, +100%, and -100% on the y-axis.

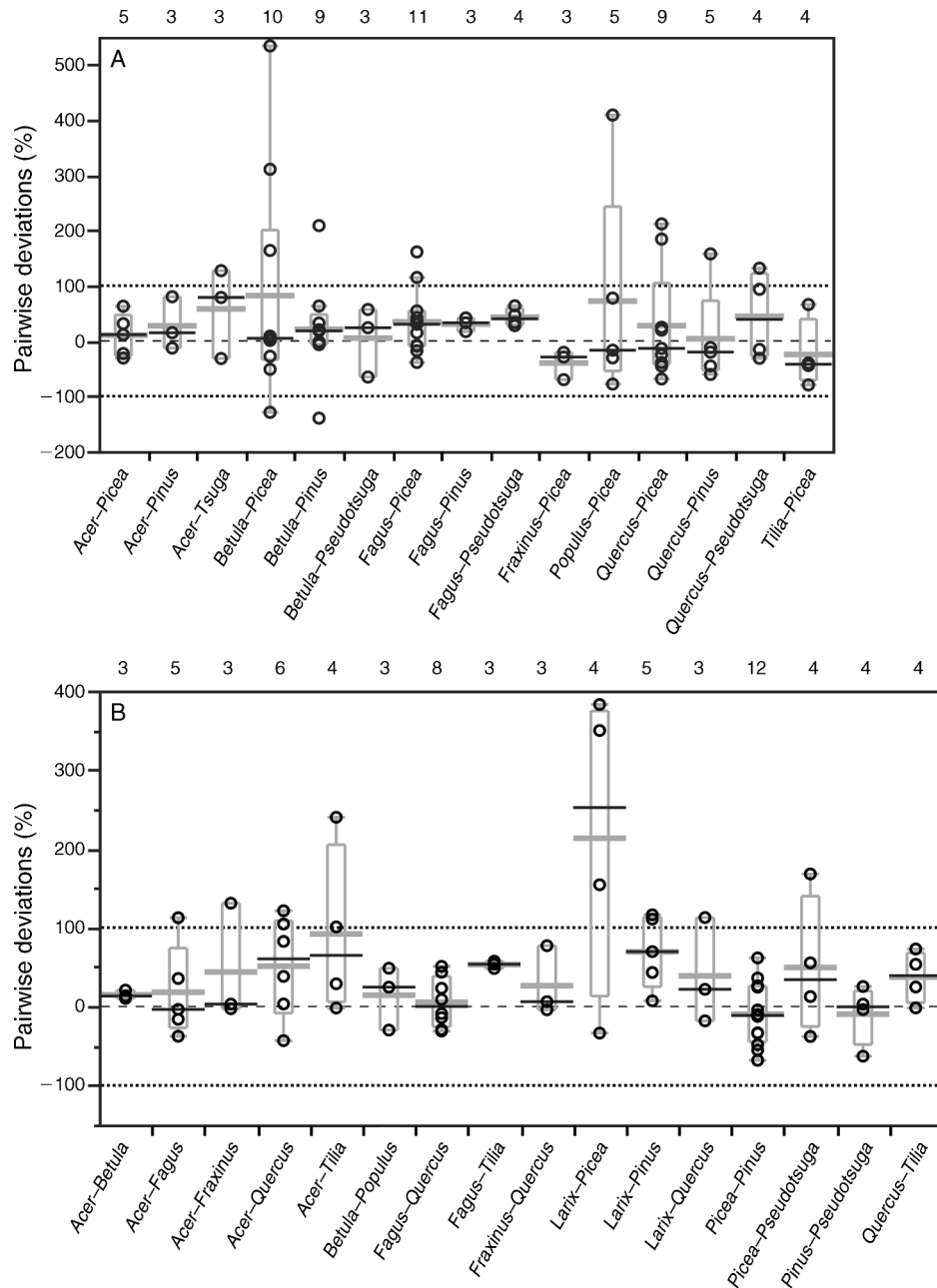


FIG. 2. Differences in net N mineralization ( $N_{\min}$ ) rates between co-occurring genera. Positive deviations indicate higher net  $N_{\min}$  beneath the first genus listed in the pair (e.g., *Betula* in the *Betula-Picea* pair). Panel (A) shows DA-EG genus pairs only, with the DA genus always listed first. Panel (B) shows DA-DA and EG-EG pairs, plus pairs of *Larix*, a deciduous conifer genus, with other genera. For each pair of genera, the number of independent contrasts is listed above the boxplot. Boxplots show the median (horizontal black bar), mean (horizontal gray bar), and 25% and 75% quartiles. Whiskers extend from each quartile to the maximum and minimum values or to the outermost point that does not extend beyond the upper or lower quartile by a value more than 1.5 times the interquartile range. Dashed and dotted lines, respectively, denote 0%, +100%, and -100% on the y-axis.

compared to *Pinus*; Fig. 2A; note that all *Quercus* spp. in this study were deciduous). *Tilia* spp. tended to have lower net  $N_{\min}$  than other genera, regardless of leaf habit or phylogeny (Fig. 2A, B). *Larix* spp., the only deciduous gymnosperm genus in our data set, generally had higher net  $N_{\min}$  than co-occurring e.g., genera (Fig. 2B).

#### Environmental effects

Precipitation, temperature, and atmospheric N deposition were not statistically related to DA deviations from EGs or pairwise genera deviations (data not shown). Sites with both high and low N deposition had DA deviations from EGs that were above and below

zero (i.e., EGs had equivalent or higher net  $N_{\min}$  at some sites with very low N deposition). The same was true for common genera contrasts.

#### DISCUSSION

Deciduous species are frequently expected to have higher soil N availability than evergreen species due to higher rates of net N mineralization,  $N_{\min}$  (Aerts 1995, Aerts and Chapin 2000, Cornwell et al. 2008). Our results indicate that the evidence to support this hypothesis is, at best, inconsistent; consequently, it seems unreasonable to expect differences in leaf longevity and nutrient concentrations alone to be predictive of plant impacts on soil N supply. Deciduous angiosperms (DAs) did not have significantly higher net  $N_{\min}$  rates than evergreen gymnosperms (EGs) in tree plantations, but net  $N_{\min}$  of DAs was higher when comparing naturally generated stands, where potentially confounding factors were somewhat constrained, but not controlled (Table 1, Fig. 1). The median deviation of DA net  $N_{\min}$  rates from those of EG rates was 42% in natural stands, compared to only 5% in plantations. However, for natural stands and plantations, the lower quartile of DA deviations from EGs was negative (Table 1). Thus, for at least 25% of sites, average net  $N_{\min}$  rates beneath DAs were not higher than those of co-occurring EGs.

The reasons for the contrasting results in plantations and natural stands are uncertain. Many factors could be responsible. One likely explanation is that DAs and EGs tend to colonize and dominate sites with inherently different properties, such as soil type, that create or reinforce the differences in net  $N_{\min}$  between naturally generated stands of DAs and EGs. Other factors that could be responsible for the contrasting results include differences in stand age, climate, and tree species composition in the sampled "population" of plantations and natural stands.

Our pairwise comparisons of co-occurring tree genera are also relevant to the different impacts hypothesis. Deciduous *Acer*, *Betula*, *Populus*, and *Quercus* spp. did not typically have higher net  $N_{\min}$  rates than evergreen *Pinus* or *Picea* spp. (Fig. 2A; *Populus*–*Pinus* not shown). These genera represent some of the most dominant evergreen and deciduous trees in boreal and temperate forests; thus, the lack of consistent differences in net  $N_{\min}$  between these genera casts further doubt on the different impacts hypothesis. In a study of 80 boreal forest stands that were not included in our compilation, Reich et al. (2001a) also showed that dominant deciduous and evergreen trees can have equivalent net  $N_{\min}$  rates; *Populus tremuloides* had net  $N_{\min}$  rates ( $0.35 \pm 0.08 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ ; mean  $\pm$  SE) that were higher than for *Picea mariana* ( $0.12 \pm 0.10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ ) but similar to those of *Pinus banksiana* ( $0.29 \pm 0.09 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ ).

Other evidence also refutes the notion that deciduous trees typically have higher rates of net  $N_{\min}$  than evergreens. A regional study in the north-central United

States showed that deciduous and evergreen trees had similar net  $N_{\min}$  rates when compared on similar soils within a relatively narrow climate envelope (Reich et al. 1997). A global meta-analysis, albeit one without controls for climate or soil type (Booth et al. 2005), showed that deciduous and evergreen temperate trees had similar gross  $N_{\min}$  rates.

#### *Caveats and inferences from other parameters related to soil N availability*

Actual differences in N availability beneath DAs and EGs could be obscured by methodological limitations of net  $N_{\min}$  measurements (Schimel and Bennett 2004). For example, dissolved organic N can be an important source of N to plants (Chapman et al. 2006, Näsholm et al. 2009) and tree species are likely to vary in their ability to utilize organic N and influence its abundance. Yet, lack of sufficient data for dissolved organic N precluded addressing it in our study. Regardless, patterns of net  $N_{\min}$  remain informative because inorganic N represents a substantial portion of plant N uptake in most ecosystems and net  $N_{\min}$  rates have been shown to be correlated with productivity (Zak et al. 1989, Reich et al. 1997). Rhizosphere effects on net  $N_{\min}$  are also important, but were not included in the standard estimates of net  $N_{\min}$  utilized in our data compilation (Frank and Groffman 2009). However, based on the limited data available, rhizosphere effects on net  $N_{\min}$  seem to be dependent on mycorrhizal associations, but not on leaf habit (Phillips and Fahey 2006, Zhao et al. 2010).

Plant N uptake is sometimes considered as an alternative measurement of soil N availability (Schimel and Bennett 2004). We estimated aboveground plant N uptake as the product of annual leaf litterfall and leaf litter N concentration for the few studies in our compilation with suitable data ( $n = 6$  sites). These estimates of plant N uptake were not consistently higher for DAs; mean DA deviations from EGs were 89%, 28%, 22%, 4%, –21%, and –33%. Other studies have also reported similar annual leaf litter N fluxes for DA and EG stands (Perala and Alban 1982, Reich et al. 1997). In contrast, a compilation by Vogt et al. (1986) showed that deciduous forests had higher N fluxes through leaf litterfall than evergreen forests, but this comparison did not account for differences in soil fertility or climate.

Estimates of plant N uptake are, at best, a conservative index of total soil N availability because they cannot account for N that was leached from soils but otherwise could have been available to plants (Schimel and Bennett 2004). Nonetheless, when estimates of plant N uptake are coupled with data on net  $N_{\min}$  rates and inorganic N abundance in soil, a more robust view of soil N cycling and availability is provided. For example, at a common-garden experiment in Poland, the accumulation of inorganic N on buried ion-exchange resins was 66% lower beneath the DAs (Mueller et al. 2012),

despite slightly higher net  $N_{\min}$  beneath DAs (+12%; Hobbie et al. 2007). This discrepancy is at least partially explained by plant uptake for DAs that was, on average, 89% greater than for EGs (Appendix B). Consistent with these results, some studies show that soil nitrate pools and nitrate leaching are lower in tree stands with greater apparent capacity for N uptake (Houlton et al. 2003, Hansen et al. 2007).

*How could DAs and EGs have similar effects on net  $N_{\min}$ ?*

One possible explanation is that leaf litter of DAs and EGs could have less divergent N concentrations when they occur on the same soils. Only seven stand contrasts in our compilation had litter N data available, but with one exception (Paré and Bergeron 1996), differences of leaf litter N between DAs and EGs at these sites were modest (DA deviations from EGs ranged from -8% to 20%). Such moderate differences in leaf litter N can occur even when green leaf N concentrations differ greatly; at a common-garden experiment in Poland, DAs had 76% higher green leaf N concentrations than EGs ( $P < 0.05$ ), but leaf litter N concentrations of DAs were only 20% higher ( $P = 0.3$ ; Appendix B). This suggests that DAs at this site recover a greater proportion of leaf N prior to senescence. A global meta-analysis also reported higher leaf N resorption for deciduous trees and shrubs (Yuan and Chen 2009).

A broader explanation is that net  $N_{\min}$  rates are influenced by too many independently varying factors to be well-predicted by leaf habit alone. For example, species-level variation in fine-root N concentrations can be strongly correlated with net  $N_{\min}$  (Wedin and Tilman 1990, Reich et al. 2001b, Parton et al. 2007) and can vary independently of leaf economic traits (Hobbie et al. 2007, 2010). Also, even if N is immobilized during decomposition of litter with a low N concentration (i.e., litter net  $N_{\min}$  is negative), total soil net  $N_{\min}$  could be positive, and largely independent of litter N, due to mineralization of N from large organic matter pools in organic or mineral soil horizons. Yet, total soil net  $N_{\min}$  rates are obscured when  $N_{\min}$  is expressed per gram of soil (or soil N) instead of per unit of soil surface area; thus, plant effects on soil N availability also can be obscured. For example, at the Poland common garden, DAs had net  $N_{\min}$  rates in the organic soil horizon that were 31% higher than rates of the EGs when expressed per gram of soil, but only 4% higher when expressed per square meter of soil surface (Hobbie et al. 2007). Likewise, at a common garden in British Columbia, DAs had net  $N_{\min}$  rates in the organic horizon that were 33% lower than those of the EGs when expressed per gram of soil and 50% lower when expressed per square meter of soil surface (Thomas and Prescott 2000).

#### ALTERNATIVE HYPOTHESES

Temperate DAs that form associations with arbuscular mycorrhizal (AM) fungi have been suggested to have faster soil N cycling and a greater dependency on

net  $N_{\min}$  for available N as compared to species that form associations with ectomycorrhizal fungi (EM) (Cornelissen et al. 2001, Chapman et al. 2006). Our results tentatively suggest that the nature of mycorrhizal associations formed by a tree is also inadequate for generalizing about plant impacts on net  $N_{\min}$ , even when used in conjunction with leaf life span (this does not mean that mycorrhizal associations do not determine how trees influence other aspects of soil N cycling, such as uptake of organic N). In our compiled data, *Acer* and *Fraxinus* were the only well-sampled genera that are associated with AM fungi. Although *Acer* spp. sometimes had higher rates of net  $N_{\min}$  than co-occurring genera, neither *Acer* nor *Fraxinus* consistently had higher rates of net  $N_{\min}$  than genera that form associations with EM fungi. The median deviation between *Acer* and several EM genera (*Pinus*, *Picea*, *Betula*, and *Fagus*), was close to zero and the median deviation between *Fraxinus* and the two ECM genera with which it commonly co-occurred (*Picea* and *Quercus*) was also near zero or negative (Fig. 2A, B). Other studies also suggest that DAs with AM fungal associations do not have higher rates of net  $N_{\min}$  than do EM-associated species. At a common-garden experiment in New York, six AM-associated species (*Acer saccharum*, *Acer rubrum*, *Fraxinus americana*, *Liriodendron tulipifera*, and *Prunus serotina*) collectively had ~20% lower net  $N_{\min}$  in bulk soils (i.e., non-rhizosphere soils) as compared to the mean of five EM-associated species (*Picea abies*, *Pinus resinosa*, *Pinus strobus*, *Quercus rubra*, and *Tilia americana*) (Phillips and Fahey 2006). In that study, the stimulation of net  $N_{\min}$  in rhizosphere soil was also smaller for AM species. At another common garden in Connecticut, *Fraxinus pennsylvanica* had the lowest net  $N_{\min}$  of three species (Binkley and Valentine 1991).

In contrast, our data suggest that mycorrhizal type might help to explain differences among species in their effects on inorganic N pools in soil. At the Polish common-garden experiment, AM *Acer* spp. had the lowest accumulation of inorganic N on buried ion-exchange resins out of 14 species (Mueller et al. 2012). Likewise, at two common gardens in Denmark, inorganic N leaching below the root zone was markedly lower beneath *Acer pseudoplatanus* and *Fraxinus excelsior* than beneath other species present, including three DAs (*Quercus*, *Fagus*, *Tilia*) and one EG, *Picea abies* (Christiansen et al. 2010). Given that net  $N_{\min}$  rates beneath *Acer* and *Fraxinus* spp. at these sites were not low, other factors are required to explain low inorganic N levels. At the Polish common garden, *Acer* spp. had the highest fine-root biomass and root length density of all 14 species, allowing for a relatively high capacity for inorganic N uptake and allocation to roots (Appendix B). Additional studies are needed to evaluate whether this is a common feature of *Acer* spp. or species with AM associations.

## CONCLUSIONS

In our compilation of data from 35 sets of temperate and boreal forest stands, co-occurring tree species from different plant functional types and genera often had net N mineralization ( $N_{\min}$ ) rates in soil that diverged by 50% or more (Figs. 1 and 2). These results provide further evidence that plant species and plant traits can have strong impacts on soil N availability. However, the effects of trees on net  $N_{\min}$  were generally not well predicted by differences in leaf habit, phylogeny, or mycorrhizal associations. For example, net  $N_{\min}$  rates in whole-soil profiles beneath deciduous angiosperms (DAs) were 100% higher than beneath evergreen gymnosperms (EGs) at some sites and 100% lower than beneath EGs at other sites. Similarly, for several pairs of co-occurring tree genera, one of the genera had net  $N_{\min}$  rates that were 50% higher at one site and 50% lower at another site. Even species-level comparisons can yield variable results; differences in net  $N_{\min}$  between *Acer saccharum* and *Tsuga canadensis* were not consistent across sites or between studies conducted at the same site (Mladenoff 1987, Ferrari 1999, Campbell and Gower 2000). This remarkable variation in the effects of species, genera, and plant functional types on net  $N_{\min}$  rates probably arises, in part, because the effect of plant traits on net  $N_{\min}$  depends on environmental factors and stand properties. For example, rankings for net  $N_{\min}$  rates among tree species can depend on stand age (Paré and Bergeron 1996), soil horizon (Thomas and Prescott 2000), and soil type (Ste-Marie et al. 2007, Kooijman and Smit 2009). The relative effects of different plant traits on net  $N_{\min}$  rates also are likely to depend on these and other factors. As organic matter accumulates in soils over time, the effects of litter N concentrations on net  $N_{\min}$  might become less important relative to plant traits that influence soil organic matter dynamics.

Following Eviner and Chapin (2003), we suggest that soil N cycling and N availability are probably influenced by too wide a range of plant traits, biogeochemical processes, and environmental factors to be predicted by simply defined plant groups or single plant traits (e.g., leaf litter N concentration). With respect to the “different impacts” hypothesis, future studies should not simply address the question posed in our title: *Do evergreen and deciduous trees have different effects on net N mineralization?* Rather, the question should be: *Under what conditions do evergreen and deciduous trees have different effects on soil N cycling and availability?* To address this question and the complexity of tree impacts on soils, future studies must consider interactions among site conditions (e.g., soil type, stand age, atmospheric N deposition), multiple plant traits, and multiple soil N forms and fluxes. Under-studied components of plant trait variation, e.g., fine-root N concentrations (Li et al. 2010), and of the N cycle, e.g., dissolved organic N, merit additional consideration. Finally, more common-garden experiments, or otherwise-constrained field

studies, are needed to generate larger data sets for evaluating tree impacts on soil N.

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## SUPPLEMENTAL MATERIAL

**Appendix A**

Additional information regarding the methods used to conduct the literature search, the methods used to extract the data from publications, and individual studies in the meta-analysis (*Ecological Archives* E093-128-A1).

**Appendix B**

Plant traits and stand properties for 14 tree species planted at a common garden in central Poland (*Ecological Archives* E093-128-A2).

**Supplement**

Data presented in Table 1 and Fig. 1 (*Ecological Archives* E093-128-S1).