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Helga Van Miegroet

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Forest Overstory Effect on Soil Organic Carbon Storage: A Meta-analysis

Antra Boča*
Helga Van Miegroet
Dep. of Wildland Resources and
Ecology Center
Utah State Univ.
Logan, UT 84322-5230

Marie-Cécile Gruselle
School of Forest Resources
Univ. of Maine
Orono, ME 04469-5722

A meta-analysis using 77 studies from 28 countries was performed to assess the effect of hardwood vs. conifer overstory on soil organic C (SOC) storage in forest floor (FF), mineral soil, and whole soil (FF + mineral soil). Overall, FF stocks were 38% higher under conifers, mineral SOC stocks were similar, and whole soil SOC was 14% higher under conifers. An analysis with six of the seven most reported tree genera reaffirmed higher FF and whole soil C stocks under conifer stands. Analysis with all seven of the genera showed more pronounced variability in mineral SOC results compared with the overall results. *Eucalyptus* was the only hardwood that stored significantly (17%) more SOC in the mineral soil than adjacent conifers. *Picea* was the only conifer that stored significantly (7%) more SOC in the mineral soil than hardwoods. Differences in FF SOC stocks had a limited predictive power in explaining the variability of mineral SOC stock differences, suggesting that they are not very closely linked with regard to SOC storage. Only when comparing FF SOC stocks among genera did precipitation, age difference, soil texture, and previous land use moderate SOC storage differences between conifers and hardwoods. In other cases, neither climate nor soil variables could explain differences between SOC stocks. Our findings suggest that using plant-trait-driven vegetation categories may be a more descriptive way of detecting vegetation effects on SOC.

Abbreviations: CI, confidence interval; FF, forest floor; MAT, mean annual temperature; MAP, mean annual precipitation; SOC, soil organic carbon.

Globally, forest soils play an important role in the terrestrial greenhouse gas balance because they store many times more C than the tree biomass (de Vries, 2003). Forest soil organic C (SOC) stocks are influenced by biotic and abiotic factors, such as climate and soil properties, that often interact and regulate C inputs to and losses from the soil. Tree species connect to forest soils in two important ways: the distribution and growth of various species depends on climate and soil properties, and soil properties may be strongly influenced by the tree species occupying a site.

In the past, the main interest of tree species effects on soils has focused on soil fertility parameters and possible environmental issues, e.g., following atmospheric deposition and heavy metal accumulation (Vesterdal et al., 2008). From the numerous studies that have investigated the effects of tree species on soil properties across a range of climates (e.g., Binkley and Valentine, 1991; Finzi et al., 1998; Binkley and Menyailo, 2005; Vesterdal et al., 2008; Hansson et al., 2011), including comprehensive reviews (Binkley and Giardina, 1998; Augusto et al., 2002; Vesterdal et al., 2013), only a few have explicitly focused on SOC storage effects (Vesterdal

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*Corresponding author (antraboca@gmail.com)
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et al., 2002, 2013). In many instances, the findings were seldom equivocal. With an ongoing debate about climate change and C sequestration, the potential of forests to store C has become of increasing interest in science, policy, and management (Jandl et al., 2007; Vesterdal et al., 2013). This has led to more efforts to quantify vegetation effects on soil C storage because soils constitute the largest terrestrial reservoirs (Schlesinger, 1977), and small changes in SOC pools may influence atmospheric CO_2 levels.

Forest management, including a change in tree species, has been proposed as a measure for mitigating atmospheric CO_2 in national greenhouse gas budgets (Vesterdal et al., 2008). Many European countries currently experience a change in forest policy toward the use of native tree species adapted to local climates with natural regeneration (Larsen and Nielsen, 2007). Historically, in areas with high population density, forests have been highly shaped by human influence. For example, the need to counteract wood shortages in some European countries caused forest management to focus on regenerating highly productive forests, often associated with the expansion of coniferous forests beyond the limits of their natural ranges (Spiecker, 2003). Forest use for wood fuel and timber and forest clearing for agriculture as well as the alteration of disturbance regimes has also caused shifts in forest composition in the United States during the last 300 yr (McKinley et al., 2011). Current predictions suggest that in many parts of Europe and North America, hardwood species may expand their potential distribution ranges into areas currently dominated by conifers (Thuiller et al., 2006; McKenney et al., 2007; Price et al., 2013). The opposite pattern can also be observed in areas dominated by pioneer hardwood species like aspen (*Populus tremuloides* Michx.) where disturbance suppression has resulted in the expansion of conifers (Rehfeldt et al., 2009; Rogers et al., 2010). Understanding the ecological consequences of these vegetation shifts on the global C balance requires accurate knowledge of forest type effects on SOC storage and stabilization mechanisms.

The differentiation between hardwoods (or broadleaves) and conifers is one of the most basic and most commonly used categorization in forestry. It implies broad differences in plant traits between the two groups and has been the source of extensive and often heated debate among foresters on the impact of tree species on soil properties. Conifers, for example, are generally thought to produce more acidic soils and cation depletion (Dambrine et al., 1998; Berger et al., 2006). However, conclusive evidence of systematic vegetation effects on soils are often lacking (Binkley and Giardina, 1998; Binkley and Fisher, 2012, p. 191–212), especially as it pertains to soil C pools (Vesterdal et al., 2013).

The most consistent findings of overstory effects on SOC stocks relate to the forest floor (FF). Many studies have found that the forest floor under conifer stands accumulates more C than under hardwood stands (Vesterdal et al., 2008), for the most part due to the differences in the persistence of foliage litter (Binkley and Giardina, 1998). Conifer needles consist of highly concentrated C forms in nutrient-poor tissues, resulting in slower decomposition of needles than hardwood litter (Augusto et al., 2002; Vesterdal et al., 2002; Hansson et al., 2011), which leads to higher C accumulation rates in the forest floor of conifer stands than hardwood stands.

Published data on SOC stocks in mineral soils have not yet yielded such consistent results. For example, Ovington (1956) found no significant differences between 20-yr-old conifer and hardwood SOC stocks in southeastern England; Oostra et al. (2006) found higher SOC stocks under hardwoods than under spruce in southern Sweden. In dry montane forests in Utah, Woldeselassie et al. (2012) found that aspen store more mineral SOC than adjacent conifer stands. In the more mesic conditions in Canada, however, aspen store less SOC overall than adjacent conifer stands, but when comparing different depths, aspen store more C in the deeper horizons (Laganière et al., 2013). This raises several questions: (i) does more C in the forest floor imply greater SOC storage in the mineral soil; (ii) does more rapid turnover of hardwood foliage lead to lower SOC stocks in the mineral soil; and (iii) is the effect consistent geographically?

The meta-analyses and reviews by Guo and Gifford (2002), Paul et al. (2002) and Laganière et al. (2010) concluded that afforestation with coniferous species resulted in lower SOC stocks than afforestation with hardwood species. However, these reviews compared stands under varying climatic and soil conditions and therefore may not reflect solely the effect of forest overstory type on soil properties like SOC. Furthermore, most reviews acknowledged the difficulty in generalizing or quantifying broad patterns about tree species effects on SOC stocks. This raises the question whether differences across broad groups of tree species such as hardwoods vs. conifers are detectable or whether more specific taxonomic levels, e.g., the genus, would give clearer results?

The aim of this study was to investigate whether overstory type (conifer vs. hardwood or broad taxonomic groups such as tree genera) affects SOC stocks in clear and consistent ways. Specifically, we addressed the following study questions: (i) do hardwood stands consistently store more or less SOC than conifer stands under similar climatic and soil conditions; (ii) are differences in SOC storage patterns between different forest covers consistent throughout the soil profile, i.e., similar in forest floor and mineral soil; (iii) are there tree genera that stand out in terms of higher or lower SOC storage relative to their comparison group; and (iv) are differences in SOC storage between hardwood and conifer stands or among taxonomic groups influenced by abiotic site conditions (e.g., climate, soil properties)?

METHODS

Literature Search

Peer-reviewed and "gray" literature was searched mostly via the online databases ISI Web of Science and Google Scholar. Among others, the keywords used were *tree species*, *forest*, *soil organic carbon*, *pool*, *stock* as well as names of specific countries like South Africa, Russia, New Zealand, and Brazil. We also searched for references in studies that addressed SOC in forest soils. This analysis contains data from six unpublished studies and two studies (one in Japan, one in Brazil) that were obtained after personal communication with researchers from these countries.

The search was done using English keywords; therefore, the hits included only studies that had keywords and abstracts in English. This introduces a language bias and is a major reason for missing data. However, searching with keywords from different languages and national databases was beyond the practical limits of this study. Our search resulted in >10,000 hits, from which we extracted 77 studies that matched the following eligibility criteria: (i) the study reported soil C stocks (or data from which stocks could be estimated) for forest or woodland stands; (ii) the comparison stands were dominated (~80%) by hardwoods or conifers in terms of species composition, stem density, and/or canopy cover; (iii) the comparison stands were adjacent and therefore shared similar climatic and soil/parent material conditions; (iv) the stand age was ≥15 yr; and (v) SOC data were reported for at least 5 cm of mineral soil. The studies originated from 28 countries and reported SOC stocks for adjacent hardwood and conifer stands in 93 sites (see the Appendix). Acceptable comparisons were paired plot designs, single-tree studies (soils under multiple individual tree canopies), and chronosequences that compared adjacent hardwood vs. conifer stands. For our analysis, we used ancillary information provided in the studies to select only those comparison pairs where abiotic factors (climate, elevation, aspect, soils) were as similar as possible.

We used soil C pool size as the response variable for this analysis. When only C concentrations and bulk densities were reported, we calculated the SOC stocks from these values. If the data were reported in a graph, we used Plot Digitizer 2.6.2 (http://plotdigitizer.sourceforge.net/) to extract the relevant information. To explain potential patterns in SOC stock differences between hardwoods and conifers, we also extracted metadata (predictor variables) from each publication (Table 1) for a moderator analysis.

Comparisons of SOC pools were done at the level of the whole soil (FF + mineral soil), FF, mineral soil, surface mineral soil (<30 cm), and deep mineral soil (>30 cm). However, most studies (54 out of 77) reported C pools for <30 cm. In the genus-level analysis, we analyzed differences between individual hardwood and conifer genera for the whole soil, FF, and mineral soil (without separation into surface and deep soils). The decision to analyze the total mineral soil without separation by depth was made so that a sufficient number of response ratios (the effect size that measures the magnitude of difference between SOC stocks under hardwoods and conifers) were obtained for the individual genera. Several studies reported C stock data for the whole depth of 0 to 50 or even 100 cm, excluding them from the surface mineral soil analysis.

The studies we selected encompassed 31 hardwood genera, including a group that contained stands with more than one genus (classified in the data set as Hardwood), and 17 conifer genera, including a group that contained more than one genus (classified in the data set as Conifer). The genera that were reported the most were *Betula*, *Eucalyptus* (mineral soil only), *Fagus*, *Quercus*, *Larix*, *Picea*, and *Pinus* (number of effect sizes (k) > 25). We compared these individual genera with the corresponding comparison group (e.g., *Betula* vs. conifers or *Larix* vs. hardwoods). This analysis could not be performed with other genera due to a low number of effect sizes.

Table 1. Predictor variables tested using meta-analysis.

Factor	Levels
Hardwood genus	*Acer*, *Alnus*, *Betula*, *Brachystegia*, *Carpinus*, *Carya*, *Castanea*, *Castanopsis*, *Eucalyptus*, *Fagus*, *Fraxinus*, *Gleditsia*, *Hyeronima*, *Laurus*, *Liquidambar*, *Liriodendron*, *Michelia*, *Mytilaria*, *Nothofagus*, *Ormosia*, *Pentaclethra*, *Populus*, *Quercus*, *Schima*, *Sclerolobium*, *Tilia*, *Ulmus*, *Virola*, *Vochysia*, hardwood
Conifer genus	*Abies*, *Araucaria*, *Cedrus*, *Chamaecyparis*, *Cunninghamia*, *Cupressus*, *Fokienia*, *Juniperus*, *Larix*, *Picea*, *Pinus*, *Podocarpus*, *Pseudotsuga*, *Thuja*, *Tsuga*, conifer
Soil texture	loamy, sandy, clayey
Soil fine texture	sandy, fine loamy, coarse loamy, fine clayey, very fine clayey
Clay (%)	continuous
Silt (%)	continuous
Soil depth	(l) forest floor, (u) surface soil, (d) deep soil
Previous land use	forest, grassland, cropland (as pairs)
Stand establishment	natural, plantation, afforested
Age difference	continuous (range: −58 to 163 yr)
Elevation	continuous (range: 10–2700 m asl)
Koeppen–Geiger climate class	Af, Am, Aw, BSk, Cfa, Cfb, Cfc, Csa, Csb, Cwa, Cwb, Dfa, Dfb, Dfc, Dwa, Dwb, ET
Mean annual temperature	continuous (range: −3.4 to 25.8°C)
Mean annual precipitation	continuous (range: 29–3960 mm)
Parent material	glacial, igneous, sedimentary, metamorphic, lacustrine, eolian, andic (volcanic ashes and tuffs)
pH difference	continuous (range: −1.2 to 1.54)
Stem density difference	continuous (range: −75 to 1409)
Diameter at breast height difference	continuous (range: −20.62 to 20.6)
Basal area difference	continuous (range: −52.5 to 6.6)
U.S. soil taxonomy	Alfisol, Oxisol, Ultisol, Inceptisol, Spodosol

Statistical Analyses of Response Ratios

Meta-analysis encompasses statistical methods used to summarize research findings across disparate studies (Gurevitch and Hedges, 1999) by using relative effect sizes, i.e., standardized, directional measures of the mean change (Harrison, 2011). This is typically done between a "control" and a "treatment." The groups compared in this study do not constitute true experimental controls or treatments; however, vegetation is the only variable that is different between the comparable sites. Because the overarching goal was to find patterns in SOC storage differences among vegetation groups, we selected hardwoods as our control or norm against which to evaluate relative changes in SOC storage by conifers.

We measured the magnitude of difference in the SOC stocks between hardwoods and conifers across studies using the natural-logarithm-transformed response ratio (R) as the effect size:

$$\ln R = \ln\left(\frac{X_{\text{hardwood}}}{X_{\text{conifer}}}\right)$$

where X_{hardwood} represents the mean SOC stock value of hardwood stands and X_{conifer} represents the mean SOC value of conifer stands for a given site. After back transformation ($\exp[\ln(R)]$), R can be conceptualized as the proportional or percentage change in SOC stocks relative to its control value (as per Nave et al., 2013).

When analyzing data at the genus level, R was based on the mean SOC stock value of a specific hardwood genus over the mean SOC stock value of different conifer genera for a site or the SOC stock value of different hardwood genera over the mean SOC stock value of a specific conifer genus for a site. Consider, for example, a study reporting SOC pools for *Betula*, *Acer*, *Populus*, *Pinus*, and *Picea* on one site. In the general hardwood–conifer meta-analysis, X_{hardwood} was the mean SOC pool value for *Betula*, *Acer*, and *Populus* for the analyzed depths (whole soil, FF, mineral soil, surface mineral soil, and deep mineral soil) and X_{conifer} was the corresponding mean SOC pool value for *Pinus* and *Picea*. Consequently, in this case, the number of response ratios (k) is 1 (i.e., one comparison for the mean SOC pool under hardwoods vs. the mean SOC pool under conifers) per analyzed depth. Some studies reported data for two separate sites with adjacent conifer and hardwood stands. For example, Olsson et al. (2012) reported data for one site in southwestern Sweden and one site in northern Finland. For that study, $k = 2$, one for Sweden and one for Finland. When the genus effect was evaluated, k depended on the number of genera compared. In the above example, k would be 6 because three hardwood genera (*Betula*, *Acer*, and *Populus*) were compared against two conifer genera (*Pinus* and *Picea*). In reporting the results by hardwood genus, response variables against all conifers were averaged; if reported as conifer genus, responses of all hardwoods against this conifer genus were averaged.

A parametric, weighted meta-analysis should always be the first choice when error terms and sample size data are reported (Gurevitch and Hedges, 1999). Unfortunately, many of the identified studies did not report these data, mostly lacking information on variance. To include as many studies as possible, we performed an unweighted meta-analysis, where all studies in a data set were assigned an equal variance. Distributional statistics were generated by bootstrapping using the package "boot" in the software R (Canty and Ripley, 2013). Bootstrapping allows estimation of the distributional statistics by iteratively permuting and resampling the data set. Because it makes no parametric assumptions and generates distributional statistics from the available data, bootstrapping typically produces wider, more conservative confidence intervals (Adams et al., 1997). The difference between SOC pools was considered significant when the 95% confidence intervals (CIs) did not overlap, with 0% change (i.e., no change) in SOC pools.

Our data synthesis generated 93 response ratios for mineral soils in the general analysis, 248 response ratios for mineral soils in the genus-level comparison, 44 response ratios for forest floors in the general analysis, and 195 response ratios for forest floors in the genus-level comparison.

Significance of Predictor Variables

Much as one can partition variance in an analysis of variance (ANOVA), one can also partition the total heterogeneity (Qt) in the distribution of observations into within-class (Qw) and between-class (Qb) homogeneity (Gurevitch and Hedges, 2001). To define factors that drive the difference between SOC pools under hardwoods and conifers, Qb is a measure of the variation in mean effect size between classes (i.e., between classes of the predictor variables, such as previous land use, parent material, etc.), which is distributed as a χ^2 statistic with degrees of freedom equal to the number of classes minus 1 (Gurevitch and Hedges, 2001). A categorical factor that defines groups of R with large Qb is a better predictor of variation than a categorical factor with low Qb and accordingly has a lower P value. In this study, we used Qb and P statistics to check for the best predictors of variation.

Categorical (e.g., soil texture, previous land use) and continuous (e.g., mean annual temperature [MAT], mean annual precipitation [MAP], clay content) predictors were used in the analysis to explain SOC stock differences between hardwoods and conifers at the general or genus level (Table 1). Because the description of parent material and mineralogy across studies was often vague, we had to use broad descriptors for this category (e.g., sedimentary, glacial, andic, etc.; Table 1). Likewise, we attempted to use soil taxonomic units to the extent possible, which resulted in using only U.S. taxonomic soil orders, and ended up excluding many studies from the soil taxonomy analysis that used different classification systems due to the difficulty in reconciling different soil classification systems.

In the general analysis (i.e., hardwood vs. conifer comparisons), continuous variables that differed among stands from one site (e.g., soil pH, stem density, etc.) were averaged for each site. Other variables like MAT, MAP, climate class, parent material, and soil texture had to be similar a priori for a site to be included in this analysis and could be used unmodified. Previous land use was often only coarsely or incompletely described. Only sites where all hardwood stands shared the same previous land use and all conifer stands shared the same previous land use were included in the general moderator analysis (no averaging possible). For the specific genus-level analysis on SOC stock differences between individual hardwood or individual conifer genera, all variables from Table 1 were considered without modification.

Continuously varying factors were tested as predictors of variation using continuous meta-analyses, which is similar to the variance-partitioning process of Qb analysis in that the heterogeneity among *k* observations is partitioned into a fraction explained by a linear model (Qm) and that which constitutes the residual error variance (Qe). As such, continuous meta-analysis is the same as the ANOVA *F*-test for significance of linear regression models (Hedges and Olkin, 1985, from Nave et al., 2013). In all tests, we accepted results with $P < 0.05$ as statistically significant. The meta-analysis statistics for the moderator analysis were performed using the R package "metafor" (Viechtbauer, 2010).

RESULTS AND DISCUSSION

Patterns of Soil Organic Carbon Stock Differences

The SOC stocks in the FF were significantly higher (38%) under conifer than hardwood stands (Fig. 1). This statistically significant difference in the FF affected the whole soil C results, with conifers having overall higher SOC stocks (14%) than hardwood stands. The SOC stocks in the mineral soil (0–30, 30–100, and 0–100 cm) showed no significant difference between hardwoods and conifers.

None of the potential moderator variables selected (Table 1) proved significant in explaining the variability of the effect sizes among hardwood–conifer comparisons across studies in the general analysis of FF, mineral soil, and whole soil (FF + mineral soil) (data not shown). In other words, the difference between hardwood and conifer FF or mineral soil SOC stocks could not be explained by any other (constrained and unconstrained) sources of variation.

When each of the most commonly reported genera was compared with its comparison group, FF SOC stocks were consistently lower under the hardwood genera than conifers, with differences ranging from 28% to up to two times lower (Fig. 2b). The same pattern was observed, albeit less pronounced, in the mineral soil (8–20% lower) and whole soil (17–32% lower) (Fig. 2a and 2c). For the conifer genera, SOC stocks were higher in the forest floor (up to two times) and whole soil (up to 30%), but, except for *Picea*, no significant difference in the mineral soil was found compared with the hardwood comparison group (Fig. 2c).

Betula stored significantly less SOC than adjacent conifers at all soil levels (Fig. 2), indicated by the lack of overlap between the 95% CI and zero, with differences more pronounced in the forest floor (76% lower) than in the mineral soil (14% lower). Studies reporting SOC stocks for *Betula* stands were mostly located in the temperate, boreal, and arctic zones, with *Larix*, *Picea*, or *Pinus* as the main comparison groups. While across all studies, *Betula* stands on average contained less SOC in the whole soil, forest floor, and mineral soil than conifer stands in these climatic zones, this was not always the case, and the opposite pattern was found for some plots at individual sites (Alriksson and Eriksson, 1998; Hansson et al., 2011; Mueller et al., 2012).

A similar pattern was observed for *Fagus*-dominated stands, where SOC stocks were on average 26% lower in the FF and 19% lower in the mineral soil than adjacent conifer stands (Fig. 2). The SOC stock comparisons were predominantly reported in the temperate zone and against stands dominated by *Abies*, *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*. Once again, the overall effect across all experimental units was not always reflected in individual sites, with several studies reporting the opposite pattern (Ladegaard-Pedersen et al., 2005; Zhiyanski et al., 2008; Mueller et al., 2012).

Quercus-dominated stands showed the largest differences in FF SOC stocks (nearly half) and the smallest differences in mineral SOC stocks (8% less) compared with adjacent conifer stands, with all effects statistically significant (Fig. 2). Among the four hardwood genera analyzed, *Eucalyptus* stood out as the only hardwood genus with significantly higher SOC stocks (17% more) in the mineral soil than adjacent conifer stands

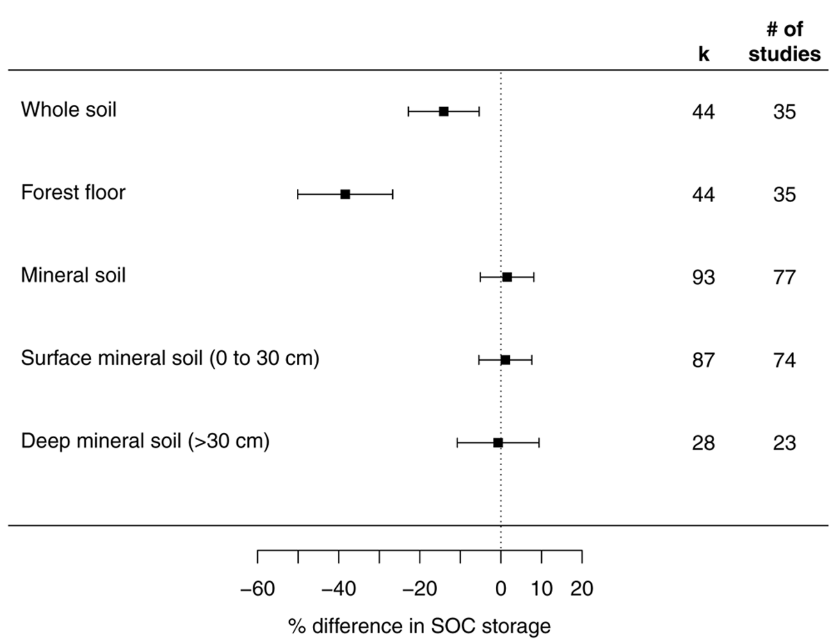

Fig. 1. Soil organic C (SOC) stock differences between conifer and hardwood stands. Negative values indicate more C stored under conifer stands and positive values indicates more C stored under hardwood stands (*k* is the number of response ratios).

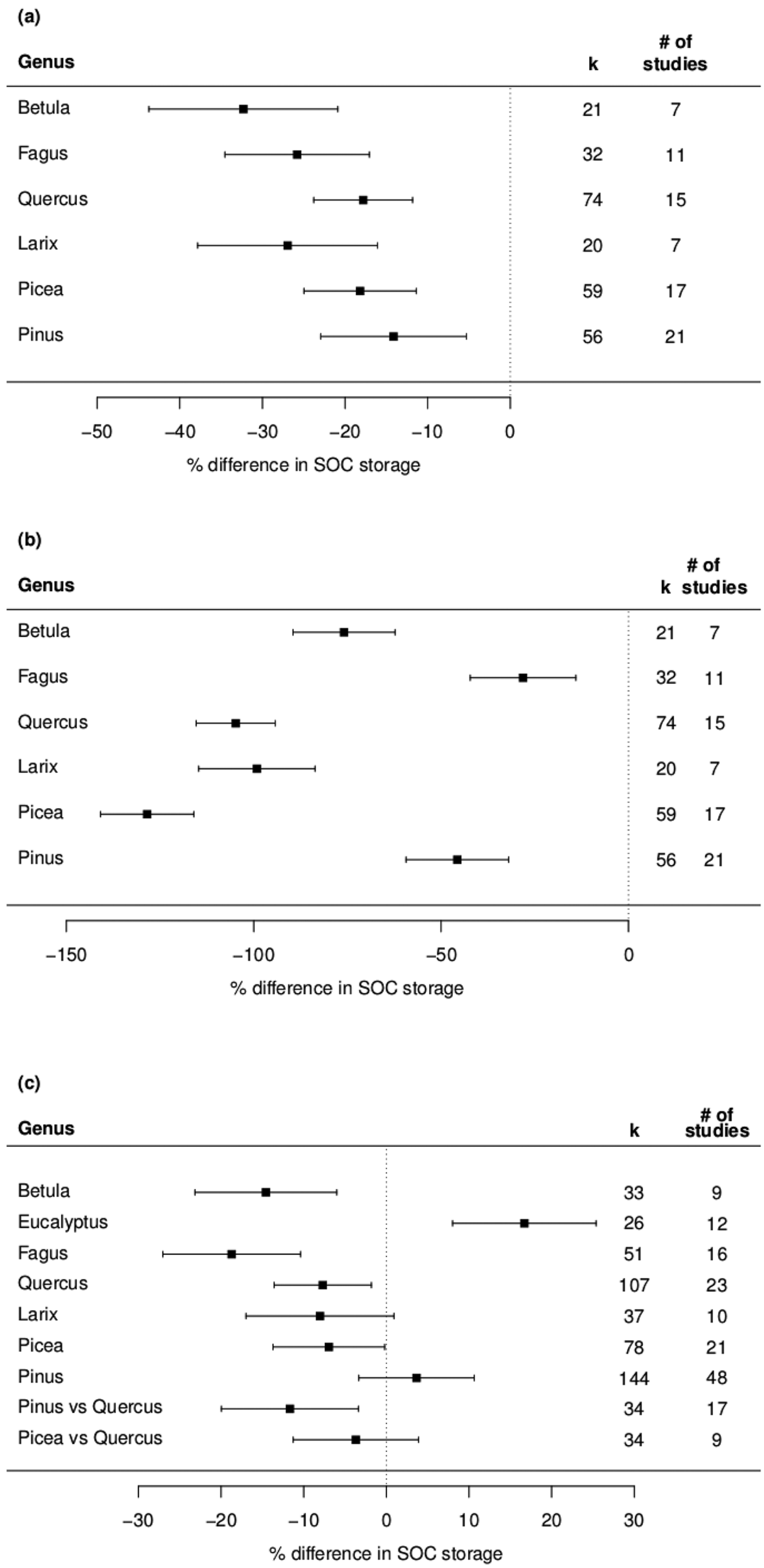

Fig. 2. Soil organic C (SOC) stock differences in (a) whole soil (forest floor + mineral soil), (b) forest floor, and (c) mineral soil under stands of specific tree genera compared with the comparison group. Negative values indicate more SOC under conifer stands; positive values indicate more SOC under hardwood stands. In (c), the comparison between two genera is given for *Pinus* vs. *Quercus* and *Picea* vs. *Quercus* stands as these were the only paired genera with a sufficient number of response ratios (*k*).

(Fig. 2c). The majority of values (k = 21 out of 26) for *Eucalyptus* soils were derived from the temperate zone, and these stands were mostly compared with soils under *Pinus*. Exclusion of this genus from the general hardwood–conifer analysis (k = 83) or from genus-level comparison with *Pinus* (k = 123) did not alter the overall conclusion, i.e., the SOC stocks under hardwoods were lower than SOC stocks under conifers. This is most likely due to the comparatively small number of response ratios for *Eucalyptus*, i.e., 10 in the general analysis and 21 in the *Pinus*-based analysis.

Forest floor SOC stocks under *Larix* were almost twice as large as under the hardwood comparison group. In the mineral soil, this difference was reduced to only 8% and was no longer statistically significant (Fig. 2). *Larix* stands were mostly compared with stands dominated by *Betula*, *Fagus*, and *Quercus*, as well as with seven other genera stands, and were located mostly in temperate climates; some values were reported in the boreal and arctic zones.

Forest floor SOC stocks under *Pinus* were about 46% higher than under hardwoods. Mineral SOC stocks, on the other hand, showed no significant difference relative to the hardwood comparison groups (Fig. 2). Interestingly, when mineral soils under *Pinus* were compared specifically with *Quercus*, we found significantly more SOC (∼12%) under *Pinus*.

Only *Picea* stands stored significantly more mineral SOC (7%) than adjacent hardwood stands, with the CI remaining below zero. In the FF, *Picea* stored more than twice the amount of C as the hardwood comparison group (Fig. 2). When *Quercus* stands were compared with *Picea* stands, however, no statistically significant difference in SOC stocks in the mineral soil was observed.

To our knowledge, this is the first broad-scale analysis of forest overstory composition effects on SOC pools that used a quantitative approach. Our analysis numerically reaffirmed earlier findings in the literature of higher FF C accumulation under conifer stands (e.g., Binkley and Giardina, 1998; Vesterdal et al., 2013). Even though we found that whole soil (FF + mineral soil) C stocks under conifer stands were often higher than under hardwood stands, this was not always the case. Several studies (e.g., Finzi et al., 1998; Oostra et al., 2006; Vesterdal et al., 2008) have shown that differences in FF C stocks can be countered by an opposite accumulation pattern of C in the mineral soil, resulting in total SOC stocks that are not significantly different among overstory types.

Relationship between Predictor Variables and Forest Floor Carbon Stock Differences

As was the case with the general hardwood–conifer comparison, none of the predictor variables used in the genus-level analysis tested as significant (data not shown) for SOC stocks in the mineral soil. In the FF genus-level analysis, age difference (hardwood age minus conifer age), elevation, MAT, MAP, previous land use, and soil texture initially emerged as significant. When hardwood stands were older than adjacent conifer stands, the difference between SOC stocks in the FF was smaller, and in some cases hardwood stands stored more SOC in the FF. While statistically significant, this positive effect of age difference was mostly driven by 49 response ratios (i.e., 25% of the data set) where the age among comparison stands was indeed different (Fig. 3a). However, the variability in effect size was very large when there were no differences in age among the comparison stands, which encompassed the majority of the data set. Therefore, the ecological relevance of age as a predictor of difference in SOC stocks among compared groups is questionable.

In our FF data set, elevation, MAT, and MAP were highly correlated, and when colinearity was accounted for, MAP was the only significant variable in the model. The results showed that differences between conifer and hardwood FF C stocks were bigger with lower precipitation (Fig. 3b). This relationship, however, was based on two-thirds of the FF response ratios data set in temperate and boreal climatic zones. Keeping in mind that MAP was positively related to MAT in this analysis, these results indicate that there are fewer differences between hardwood and conifer FF SOC stocks on warmer moister sites than on colder drier sites. Fissore et al. (2008) found that the difference in mineral SOC stocks between hardwoods and conifers decreased with increasing temperature. They suggested that forests with higher MAT experience higher decomposition rates. Liu et al. (2004) found that litterfall increased more under hardwoods than conifers with increasing temperature and precipitation. They suggested that conifers are better adapted to low-temperature climates, therefore having a higher productivity than hardwoods and resulting in higher litterfall. They did not find productivity differences in production in temperate regions and hypothesized that higher litterfall in hardwood forests was due to differences in biomass allocation patterns.

In the FF analysis among genera, previous land use was reduced to only two levels (cropland and forest) due to the limited number of response ratios in the other categories. Nevertheless, the results showed that the differences in FF C stocks among genera were more pronounced when stands had been converted from agricultural land than when stands had been under forest cover previously (either the same or different) (data not shown, $P < 0.001$). Most of the stands (38 out of 44) were 20 to 40 yr old, and all were on loamy or clayey soils. Conversion of agricultural land to forest offers more homogenous initial soil conditions among the comparison groups because no FF is present, and FF C stocks more clearly reflect differences in litter chemistry and decomposition rates among the planted species. Our results suggest that, when managing forests for increasing SOC storage, species choice may be a more critical decision during afforestation than in the case of forest conversion. However, this applies only to the FF, which is a more labile C pool than mineral SOC. We found no effect of previous land use on mineral SOC stock differences.

Finally, soils emerged as a modifier in terms of texture, such that differences between conifer and hardwood FF C stocks were smaller on sandy soils than loamy and clayey soils.

It is difficult to distinguish between the effect of previous land use and soil texture on FF C stocks because all sandy soils for the FF analysis had been previously under forest cover. However, Vesterdal and Raulund-Rasmussen (1998) reported increasing FF C contents with decreasing mineral soil nutrient status in Danish stands of oak (*Quercus robur* L.) and Norway spruce [*Picea abies* (L.) H. Karst.] and attributed this mainly to differences in decomposition rates.

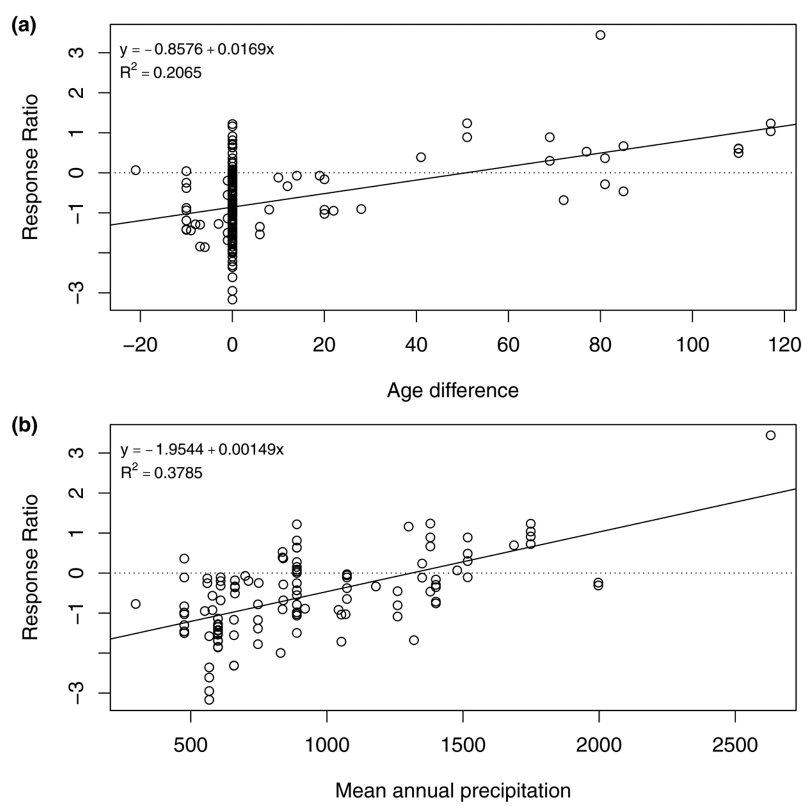

Fig. 3. Relationship between hardwood and conifer genera forest floor C response ratios and (a) age difference (calculated as hardwood stand age minus conifer stand age; number of response ratios [*k*] = 192, with about 40 values being non-zero), and (b) mean annual precipitation (*k* = 123, with most comparisons being located in the temperate and boreal zones).

Contrast between Forest Floor and Mineral Soil Organic Carbon Stock Differences

Our meta-analyses indicated pronounced differences in FF SOC storage between hardwood and conifer stands, but these were highly variable in the genus analysis. Mineral SOC stock differences, on the other hand, were far less pronounced (nonsignificant in the general analysis) and considerably less variable, suggesting that SOC in the mineral soil is more robust and less sensitive to changes in the aboveground vegetation cover. The FF has traditionally been considered as the main source of organic C to the mineral soil (Schmidt et al., 2011), and recent ^{13}C studies have provided evidence for this aboveground litter contribution (Rubino et al., 2010). However, mineral SOC has also been shown to correlate more with fine root growth and turnover and less with foliage input (Russell et al., 2004). Unfortunately, root data are seldom reported, and this gap in our data set did not allow us to analyze the effect of fine root mass and turnover on mineral SOC stocks. Furthermore, as Schmidt et al. (2011) pointed out, C dynamics in the FF and mineral soils are subject to quite different controls. Environmental conditions and biochemical recalcitrance, i.e., litter origin, primarily control microbial decomposition rates in the litter layer. On the other hand, the presence of a mineral matrix further regulates the persistence of SOC in the mineral soil through physical and chemical protection mechanisms (Six et al., 2002), and biochemical characteristics (associated with vegetation composition) are thought to play a secondary role (Rovira et al., 2010). When testing the FF as a predictor variable, it explained only 6% of the variability in mineral SOC stocks in the general analysis and <1% in the genus-level analysis. This lack of predictive power, together with the somewhat divergent accumulation patterns of FF vs. mineral SOC stocks under hardwood and conifer stands suggests that the two ecosystem compartments are not that closely linked with regard to SOC storage.

Relationship between Predictor Variables and Mineral Soil Carbon Stock Differences

Our analysis failed to show a relationship between abiotic site conditions (climate, soil texture, previous land use, etc.) and SOC stock differences in the mineral soil and the general hardwood vs. conifer analysis. This does not imply that these factors are not important because several studies have shown the effect of climate and soil texture on SOC stocks (Jobbágy and Jackson, 2000; Six et al., 2002; Fissore et al., 2008). We think that the lack of any relationship arose from the coarseness of the data available. For example, data on the exact proportions of clay and silt by depth were scarce, and we had to rely on broad texture descriptors or use values that were averaged across the entire site. In addition, the depth increments measured varied among all studies (0 to 5, 10, 15, or 20 cm), as did the final depths for which SOC data were reported. This might result in different effect sizes than if all studies had reported data to the same depth. A study by Baritz et al. (2010), comparing C stocks in forest soils in Europe, also showed that the effect of climate and soil texture could not be detected across a broader geographic area. Finally, variables like previous land use, parent material, or soil order were probably too general to enable detection of their influence on the reported SOC stocks.

Potential Limitations of This Study

Overall, our analysis shows that it is difficult to detect the influence of biotic and abiotic factors on mineral SOC stocks across a wide geographical range. Potential reasons for this are that the number of studies used in this analysis is not sufficiently large to draw clear conclusions and/or that the information provided in the studies is reported at too coarse of a scale. A more extensive analysis, using databases like the International Soil Carbon Network would be a great source of data for answering these kinds of questions, provided that they contain specific (genus-level) vegetation descriptions. Such information is seldom available in large databases.

Furthermore, the search method introduced a language bias in this analysis and therefore limited the number of studies conducted outside of Europe and North America. Also, an unweighted analysis, as performed in this study, is very conservative and of low sensitivity; thus, one has to be careful in interpreting the results. Increases in analysis power of 50 to 100% can easily be obtained in a weighted analysis compared with unweighted tests of the significance of the mean (Gurevitch and Hedges, 1999). However, using the weighted approach would have excluded one-third of all studies due to the lack of information on variance. We made the decision to give higher priority to the inclusion of more studies because it would provide more information on the variability in SOC stocks across a broader geographical scale. This was of greater interest than more precisely quantifying the variability within individual sites.

Most studies reported sample sizes, which allowed an approximation of the sampling variance (see, e.g., Hedges and Olkin, 1985). However, the definition of replicates turned out to be more problematic than expected. Evaluating true replication for all studies, and hence weighting according to sample size, was not possible due to limited information.

CONCLUSIONS

Our whole soil analysis showed that conifer stands generally store more SOC than hardwood stands, mostly driven by higher FF C accumulation under conifers. However, at the level of the mineral soil, no differences in SOC storage between conifer and hardwood stands were found, irrespective of whether the focus was on surficial or deeper soil layers. This shows that a broad generalization of a hardwood vs. conifer overstory effect on SOC storage in the mineral soil is not possible based on the information available and methods used. One has to be careful in interpreting the "whole soil" data because the SOC pool estimates in many studies did not extend beyond 30 cm, with some going only to the 5-cm depth.

The individual genus-level analysis revealed more pronounced differences in mineral SOC stocks between hardwood and conifer stands not observed in the general analysis. It also highlighted genus differences in FF C accumulation. This implies that broad categories such as hardwoods and conifers may not be appropriate groupings for understanding vegetation composition effects on soil properties such as C storage. Vegetation affects soil properties by its morphology and dominant plant traits (De Deyn et al., 2008). Therefore, it would probably be more useful to divide vegetation using plant-trait-driven categories. Using genus was a first attempt in that direction. Further analyses may reveal better surrogates for plant traits than the genus level used in this study. By understanding the mechanisms and drivers for SOC sequestration under different species, genera, or families, we could make better predictions of different ecosystem services and implement these findings into forest policy and management practices.

This study utilized the limited number of basic variables that were available and known from observational and experimental studies to influence SOC storage. Additional parameters, such as above- and belowground detritus input, type of clay minerals, etc., might be worth considering in future analyses, provided that such information is available. The number of studies reporting aboveground litterfall, for example, was insufficient for this variable to be included in this analysis. Carbon fluxes were not explicitly part of this investigation, and large knowledge gaps remain concerning the sources of litter, decomposition, mixing, leaching, or stabilization of organic matter through aggregation and sorption in soils. A more consistent approach toward sampling and analysis across studies, as well as availability of more detailed data, would allow improvement of this type of analysis. Data from common garden experiments, where all factors except vegetation are similar, give us the most insights into C pathways in forest ecosystems.

We did not detect a relationship between FF and mineral SOC stocks, suggesting that different factors control C fluxes in these two ecosystem compartments. In addition, our results suggest that mineral SOC stocks might be more influenced by belowground litter inputs than the FF.

Finally, as did Guo and Gifford (2002), we concluded that because the quantity of available data is not large and the methodologies used are diverse, the conclusions drawn must be regarded as working hypotheses from which to design future targeted investigations that expand the database.

APPENDIX

Data sources used in the meta-analysis of SOC storage differences between hardwood and conifer stands.

Reference	Location	Dominant hardwood genera	Dominant conifer genera
Alban et al. (1978)	Minnesota	*Populus*	*Picea, Pinus*
Alriksson and Eriksson (1998)	northeastern Sweden	*Betula*	*Larix, Picea, Pinus*
Andreux et al. (2002)	central France	*Fagus*	*Pseudotsuga*
Armas-Herrera et al. (2012)	Canary Islands, Spain	*Laurus*	*Pinus*
Ashagrie et al. (2005)	central Ethiopia	*Eucalyptus*	*Podocarpus*
Berger et al. (2010)	northeastern Austria	*Fagus*	*Picea*
Bini et al. (2013)	southern Brazil	mixed hardwoods	*Araucaria, Pinus*
Borken et al. (2002)	central Germany	*Fagus*	*Picea, Pinus*
Charro et al. (2010)	western Spain	*Quercus*	*Pinus*
Chen et al. (2005)	southeastern China	*Castanopsis*, mixed hardwoods, *Ormosia*	*Cunninghamia, Fokienia*
Chen et al. (2013)	Northeast China	mixed hardwoods	*Cunninghamia*
Cole et al. (1995)	Washington	*Alnus*	*Pseudotsuga*
Compton and Boone (2000)	Massachusetts	mixed hardwoods	mixed conifers
Compton et al. (1998)	Massachusetts	*Populus, Quercus*	*Pinus*
Cook (2012)	southern Brazil	*Eucalyptus*	*Pinus*
Díaz-Pinés et al. (2011)	central Spain	*Quercus*	*Pinus*
Dijkstra and Fitzhugh (2003)	Connecticut	*Acer, Fagus, Fraxinus, Quercus*	*Tsuga*
Gartzia-Bengoetxea et al. (2009)	northeastern Spain	*Fagus, Quercus*	*Pinus*
Goh and Heng (1987)	central New Zealand	*Nothofagus*	*Pinus*
Gomes da Silva et al. (2009)	central Brazil	*Eucalyptus, Sclerolobium*	*Pinus*
Gurmesa et al. (2013)	Denmark	*Fagus, Quercus*	*Larix, Picea*
Hansson et al. (2011)	southwestern Sweden	*Betula*	*Picea, Pinus*
Huygens et al. (2005)	central Chile	*Nothofagus*	*Pinus*
Ichikawa et al. (2004)	central Japan	mixed hardwoods	*Cryptomeria*
Jiang et al. (2010)	southern China	*Liquidambar*, mixed hardwoods, *Schima*	*Pinus*
Kasel and Bennett (2007)	southeastern Australia	*Eucalyptus*	*Pinus*
King and Campbell (1994)	central Zimbabwe	*Brachystegia, Eucalyptus*	*Pinus*
Kulakova (2012)	southeastern Russia	*Quercus*	*Pinus*
Ladegaard-Pedersen et al. (2005)	Denmark	*Fagus, Quercus*	*Abies, Larix, Picea, Pinus, Pseudotsuga*
Laganière et al. (2013)	Ontario and Quebec, Canada	*Populus*	*Picea, Pinus*

continued on next page

Appendix (continued).

Reference	Location	Dominant hardwood genera	Dominant conifer genera
Lakshmanan (1962)	Ohio	*Acer*, *Carya*, *Liriodendron*, mixed hardwoods, *Quercus*	*Pinus*
Lee et al. (2009)	northern South Korea	*Quercus*	*Pinus*
Lemenih et al. (2004)	central Ethiopia	*Eucalyptus*	*Cupressus*, mixed conifers
Lemma et al. (2006)	southwestern Ethiopia	*Eucalyptus*, mixed hardwoods	*Cupressus*, *Pinus*
Li et al. (2005)	northeastern Puerto Rico	mixed hardwoods	*Pinus*
Liang et al. (2007)	Michigan	*Acer*, *Tilia*	*Tsuga*
Luan et al. (2010)	southern China	mixed hardwoods	*Cunninghamia*
Matos et al. (2010)	northeastern Germany	*Quercus*	*Pinus*
Michalzik and Gruselle (unpublished data, 2013)	central Germany	*Fagus*	*Pinus*
Morris et al. (2007)	Michigan	mixed hardwoods	*Pinus*
Mueller et al. (2012)	central Poland	*Acer*, *Betula*, *Carpinus*, *Fagus*, *Quercus*, *Tilia*	*Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*
Nihlgård (1971)	southern Sweden	*Fagus*	*Picea*
Noh et al. (2012)	central South Korea	*Quercus*	*Abies*
Olsen and Van Miegroet (2010)	Utah	*Populus*	Mixed conifers
Olsson et al. (2012)	northern Finland	*Betula*	*Picea*, *Pinus*
Oostra et al. (2006)	southern Sweden	*Carpinus*, *Fagus*, *Fraxinus*, *Quercus*, *Ulmus*	*Picea*
Ovington (1956)	southern United Kingdom	*Alnus*, *Betula*, *Castanea*, *Fagus*, *Nothofagus*, *Quercus*	*Abies*, *Chamaecyparis*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja*, *Tsuga*
Paul et al. (2003)	Ontario, Canada; Ohio	*Acer*, mixed hardwoods	*Pinus*
Priha and Smolander (1999)	southern Finland	*Betula*	*Picea*, *Pinus*
Richards et al. (2007)	eastern Australia	mixed hardwoods	*Araucaria*
Riestra et al. (2012)	central Argentina	*Eucalyptus*, *Gleditsia*	*Pinus*
Ritter (2007)	eastern Iceland	*Betula*	*Larix*
Roman-Dobarco (unpublished data, 2013)	Utah	*Populus*	mixed conifers
Russell et al. (2007)	eastern Costa Rica	*Hyeronima*, *Pentaclethra*, *Virola*, *Vochysia*	*Pinus*
SanClements et al. (2010)	Maine	mixed hardwoods	mixed conifers
Schulp et al. (2008)	central Netherlands	*Fagus*, *Quercus*	*Larix*, *Pinus*, *Pseudotsuga*
Scott and Messina (2010)	Texas	*Quercus*	*Pinus*
Sevgi et al. (2011)	northwestern Turkey	*Quercus*	*Abies*, *Cedrus*, *Picea*, *Pinus*
Shugalei (2005)	central Russia	*Betula*, *Populus*	*Larix*, *Picea*, *Pinus*
Shukla et al. (2006)	New Mexico	*Quercus*	*Juniperus*, *Pinus*
Sigurðardóttir (2000)	eastern Iceland	*Betula*	*Larix*, *Pinus*
Son and Gower (1992)	Wisconsin	*Quercus*	*Larix*, *Picea*, *Pinus*
Stolpe et al. (2010)	central Chile	*Nothofagus*	*Pinus*
Turner and Kelly (1977)	eastern Australia	*Eucalyptus*	*Pinus*
Turner and Kelly (1985)	southeastern Australia	*Eucalyptus*	*Pinus*
Turner and Lambert (1988)	eastern Australia	*Eucalyptus*	*Pinus*
Turner and Lambert (2000)	eastern Australia	*Eucalyptus*	*Pinus*
Ulrich et al. (1971)	central Germany	*Fagus*	*Picea*
Vesterdal et al. (2002)	eastern Denmark	mixed hardwoods, *Quercus*	*Picea*
Vesterdal et al. (2008)	Denmark	*Acer*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia*	*Picea*
Wang and Wang (2007)	southeastern China	mixed hardwoods	*Cunninghamia*
Wang et al. (2007)	southeastern China	*Michelia*	*Cunninghamia*
Wang et al. (2010)	southern China	*Castanopsis*, *Michelia*, *Mytilaria*	*Pinus*
Woldeselassie et al. (2012)	Utah	*Populus*	mixed conifers
Yang et al. (2005)	southeastern China	mixed hardwoods	*Cunninghamia*
Yuste et al. (2005)	northeastern Belgium	*Quercus*	*Pinus*
Zhiyanski et al. (2008)	central Bulgaria	*Fagus*	*Picea*

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