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Effects of litter traits, soil biota, and soil chemistry on soil carbon stocks at a common garden with 14 tree species

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Abstract Tree species interact with soil biota to impact soil organic carbon (C) pools, but it is unclear how this interaction is shaped by various ecological factors. We used multiple regression to describe how ~100 variables were related to soil organic C pools in a common garden experiment with 14 temperate tree species. Potential predictor variables included: (i) the abundance, chemical composition, and decomposition rates of leaf litter and fine roots, (ii) species richness and abundance of bacteria, fungi, and invertebrate animals in soil, and (iii) measures of soil acidity and texture. The amount of organic C in the organic horizon and upper 20 cm of mineral soil (i.e. the combined C pool) was strongly negatively correlated with earthworm abundance and strongly positively correlated with the abundance of aluminum, iron, and protons in mineral soils. After accounting for these factors, we identified additional correlations with soil biota and with litter traits. Rates of leaf litter decomposition, measured as litter mass loss, were negatively correlated with size of the combined soil organic C pool. Somewhat paradoxically, the combined soil organic C pool was also negatively related to the ratio of recalcitrant compounds to nitrogen in leaf litter. These apparent effects of litter traits probably arose because two independent components of litter "quality" were controlling different aspects of decomposition. Leaf litter mass loss rates were

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positively related with leaf litter calcium concentrations, reflecting greater utilization and depolymerization of calcium-rich leaf litter by earthworms and other soil biota, which presumably led to greater proportional losses of litter C as CO_2 or dissolved organic C. The fraction of depolymerized and metabolized litter that is ultimately lost as CO_2 is an inverse function of microbial C use efficiency, which increases with litter nutrient concentrations but decreases with concentrations of recalcitrant compounds (e.g. lignin); thus, high ratios of recalcitrant compounds to nitrogen in leaf litter likely caused a greater fraction of depolymerized litter to be lost as CO_2. Existing conceptual models of soil C stabilization need to reconcile the effects of litter quality on these two potentially counteracting factors: rates of litter depolymerization and microbial C use efficiency.

Keywords Soil organic matter · Decomposition · Lignin · Litter quality · Substrate use efficiency · Earthworm

Introduction

Tree species have large and variable impacts on organic carbon (C) pools in soil, yet the causes of this variability are not well known (Vesterdal et al. 2013). This uncertainty is important because the composition of tree species is changing in temperate and boreal forests (Ellison et al. 2005; Lovett et al. 2006; Iverson et al. 2008; Garbelotto and Pautasso 2012) and tree plantations occupy an increasing amount of land (Paquette and Messier 2009). To estimate the impact of tree species composition on forest C budgets, more information is needed on the relationships between the size of soil C pools and the factors that influence C input and retention, including (i) the abundance and chemical composition of plant-derived inputs (e.g. leaf litter and dead roots), (ii) decomposition, mineralization, and redistribution of plant-derived inputs by soil bacteria, fungi, and animals, and (iii) stabilization of plant-derived inputs via physical and chemical protection in soils. The chemical composition of plant-derived inputs likely plays a central role because it can impact the fate of plant inputs through every step: ingestion by soil fauna, enzymatic depolymerization and mineralization, conversion into biomass and byproducts of decomposers, and stabilization of organic matter.

For years, ecologists focused on how litter chemistry influenced litter decomposition rates. This work was typically justified by predictions of non-specific effects of litter decomposition on soil C cycling (Prescott 2010), although many authors hypothesized or implied that litter decomposition rates were negatively correlated with soil C pools (Wardle et al. 2004; De Deyn et al. 2008). Faster decomposition rates were observed for plant species with leaf litter of higher "quality" as a substrate for decomposers (high quality litter often is characterized by low lignin and/or high nutrient concentrations; Cornwell et al. 2008). Thus, tree species with high quality litter and high decomposition rates might have negative effects on soil C pools (Finzi et al. 1998; Vesterdal et al. 2008; but see Berg et al. 2010). In contrast, the prevailing view of geochemists is that soil physico-chemical

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properties, such as aggregation, mineral surface area, and cation composition, are largely responsible for the stability and variability of soil organic C stocks, implying minimal impacts of litter quality and decomposition rates on soil C pools (Lützow et al. 2006; Schmidt et al. 2011). Presently, the relevance of litter decomposition rates to soil C storage remains uncertain (Prescott 2005, 2010) for two reasons. First, litter decomposition rates are estimated via measurements of litter mass loss, without accounting for how much of the "lost" mass is partitioned to respiration, decomposer biomass, and soluble decomposition byproducts (Rubino et al. 2007, 2010). Second, despite myriad studies of litter decomposition rates and soil organic C stocks, a quantitative relationship between the two has not been documented.

Attempting to bridge the gap between ecologists and geochemists, Cotrufo et al. (2013) suggested that higher litter quality and short-term decomposition rates could result in larger soil C pools due to both: (i) greater C use efficiency during microbial metabolism of high quality litter (i.e. a greater fraction of the C substrate is converted to microbial biomass and a smaller fraction is lost during respiration), and (ii) potential for preferential retention of microbial-derived C in stable soil organic matter. However, it is also plausible that high litter quality could have counteracting effects on soil organic C stocks by increasing the proportion of litter that is depolymerized and subsequently mineralized or leached from soil (consistent with positive effects of litter quality on leaf litter decomposition rates), while also reducing the proportion of metabolized litter that is mineralized (consistent with positive effects of litter quality on microbial C use efficiency). This modification of Cotrufo's hypothesis seems consistent with field observations: while reviewing the results of temperate common garden experiments, Vesterdal et al. (2013) noted that organic C pools in organic and mineral soils are often inversely correlated among tree species. For example, Vesterdal et al. (2008) showed that tree species with lower C:N ratios in leaf litter had smaller C pools in the organic horizon but larger C pools in mineral soils. If higher litter decomposition rates are accompanied by proportionally greater losses of litter-derived C to the atmosphere and/or to the mineral soil, Vesterdal et al. (2008) results could reflect a positive effect of litter quality on leaf litter decomposition rates and a negative effect of litter decomposition rates on C stocks in the organic horizon. Combined with a positive effect of leaf litter quality on microbial C use efficiency and stabilization of microbial biomass and byproducts in mineral soil, such variation in litter C:N among tree species would result in a minimal effect on total soil organic C stocks but a large effect on the vertical distribution of organic C (accounting for the inverse correlation between C pools in the organic and mineral soil layers).

When considering the interactions between litter quality and soil biota, and how these interactions mediate the impact of plants on soil organic C, it is perhaps necessary to consider the quality of both leaf litter and fine roots for several reasons. First, it is likely that some plant species have high quality leaf litter but low quality root litter (or vice versa) because the chemical composition of roots varies at least somewhat independently of that of leaves and leaf litter (e.g. Hobbie et al. 2010). Second, vertical gradients in soil community composition (e.g. the relative abundance of fungi and bacteria) and in the composition of the soil matrix (e.g. the presence and composition of soil minerals) could alter the nature of litter quality effects, regardless of the similarity of leaf and root litter quality.

Although litter decomposition rates can be useful in studying the interaction between litter quality and soil biota, the full impact of this interaction on soil organic C pools cannot be represented by decomposition rates inferred from litter mass loss due to methodological issues (e.g. the limited duration of most studies and exclusion of macrofauna from litter bags). The net, long-term effect of the interaction between litter quality and soil biota will depend on variability among soil bacteria, fungi, and fauna with respect to the type and amount of plant litter they consume, their C use efficiency, the stabilization potential of their biomass and metabolic byproducts, and their capacity for bioturbation (Brown et al. 2000; Six et al. 2006; Osler and Sommerkorn 2007). For example, land use changes that result in bacterial-dominance of soil microbial communities typically also result in smaller soil C pools (Strickland and Rousk 2010; de Vries et al. 2013). More diverse soil biotic communities are expected to increase the rate and efficiency of litter decomposition, with potential impacts on soil C pools, through mechanisms such as facilitation and complementarity of resource use (Gessner et al. 2010).

To clarify how the "quality" of plant inputs and soil biota interact to regulate soil organic C stocks, and to

advance the trait-based framework for predicting the impact of tree species on soil C, we evaluated the covariance of soil C pools with a variety of ecological factors at a 32-year-old common garden experiment with 14 tree species. Previous studies at this site in Poland documented much variability among tree species for the abundance, chemical composition, and decomposition rates of leaf litter and fine roots (Reich et al. 2005; Withington et al. 2006; Hobbie et al. 2006, 2010; Goebel et al. 2010). Across tree species, decomposition rates and indices of litter quality for leaf litter and fine roots were uncorrelated, such that leaf and root traits could have independent effects on soil organic C pools (Hobbie et al. 2010). The composition of bacterial, fungal, and faunal communities in soil was also variable among tree species (Reich et al. 2005; Dickie et al. 2010; Skorupski 2010; Trocha et al. 2012, Table 1). Prior studies at this site reported aspects of the C cycle in organic and mineral soils separately (C stocks in the organic horizon have not been published previously). Reich et al. (2005) and Hobbie et al. (2006) showed that beneath trees with higher calcium concentrations in leaf litter, soils had higher earthworm biomass, and consequently, lower concentrations of C in the organic horizon and higher rates of organic horizon turnover. Focusing on mineral soils, Mueller et al. (2012) showed that tree species with higher nitrogen (N) concentrations in roots also had higher total acidity in soil (i.e. more protons and hydrolyzing Al and Fe cations); this likely influenced mineral soil C pools via complexation of organic matter with Al and Fe and negative effects of acidity on C mineralization (Hobbie et al. 2007). We expanded upon these prior studies by focusing on the combined pool of organic C in organic and mineral soils and by relating the combined C pool to a broader suite of variables than examined previously (e.g. prior studies did not evaluate covariance of soil C pools with litter decomposition rates or soil biotic predictors other than earthworm biomass). Specifically, we used an information-theoretic style, regression-based approach to evaluate the following hypotheses: (i) decomposition rates, i.e. mass loss rates, of leaf litter and fine roots are negatively correlated with soil organic C stocks, (ii) the chemical quality of leaf litter and fine roots is positively correlated with soil organic C stocks (as described above, these first two hypotheses are potentially counteracting) and (iii) soil organic C stocks are negatively correlated with the relative abundance of bacteria and with soil biodiversity. To gain additional insight into these hypotheses, we also evaluated whether C pools in the organic horizon varied independently of C pools in mineral soils.

Methods

Replicate monoculture plantations of 14 tree species were established in 1970 and 1971 near Siemianice, Poland (51°14.87′N, 18°06.35′; mean annual precipitation is 591 mm; mean annual temperature is 8.2 °C; soils formed on glacial outwash with less than 10 % clay in the upper 20 cm of mineral soil). Prior to planting, the site was prepared by clear-cutting an ~80-year-old *Pinus sylvestris* L. stand with subsequent stump removal and plowing, typically to a depth of 30–40 cm. Ten tree species were planted in three plots and four species in six plots (20 × 20 m), with plots distributed in two adjacent blocks (Reich et al. 2005). Trees were planted in 1 m intervals (400 individuals per plot). Planted species included eight deciduous angiosperms, five evergreen gymnosperms, and one deciduous gymnosperm (Fig. 1). Thirty years after planting, basal area ranged from ~6 to 36 m^2 ha^{-2} (Reich et al. 2005). One plot for *Abies alba* was excluded from sampling and analysis due to high initial tree mortality. When sampling litter, soils, roots and soil biota, areas within several meters of a plot boundary were avoided so that each sample was more representative of the tree species planted in each plot. Based on spatially dispersed sampling in each plot (Reich et al. 2005), on average 14 % of leaf litterfall (SD = 13 %) was derived from unplanted species (e.g. from tree species planted in adjacent plots) and only 6 plots had more than 30 % of annual leaf litterfall attributed to unplanted species.

In 2002, ~32 years after planting, organic and mineral soil horizons were sampled in all plots as described by Hobbie et al. (2007). Organic horizons were sampled in their entirety, including O_i, O_e, and O_a horizons, at three locations per plot. The upper 100 cm of mineral soil was sampled by genetic horizon via large soil pits (1 m wide × 1.8 m long × 2 m deep; 1 per plot). Soil samples were collected across the horizontal extent of each genetic horizon in the pit and then composited for each horizon. The depth and bulk density of each genetic

Table 1 Potential predictors of variability in soil C pools beneath tree species

Soil organism diversity and abundance				Tree-species characteristics				Soil and stand properties			
Potential predictor	CV	Maximum difference (% of min.)	Ref.	Potential predictor	CV	Maximum difference (% of min.)	Ref.	Potential predictor	CV	Maximum difference (% of min.)	Ref.
Soil animal *spp*. rich.	0.18	118	*	Root cell-solubles	0.19	129	1,5	pH Oa horizon	0.08	32	4
Carabid beetle *spp*. rich.	0.47		*	Root hemicellulose	0.23	170	1,5	exchangeable Fe Oa horizon	0.26	245	4
Staphylinid beetle *spp*. rich.	0.52		*	Root cellulose	0.19	141	1,5	exchangeable Mn Oa horizon	0.06	23	4
Oribatid mite *spp*. rich.	0.35		*	Root recalcitrant compounds	0.14	97	1,5	ex. base cations Oa horizon	0.14	75	4
Oribatid mite density	0.13	60	*	Root C	0.04	17	1,5	exchangeable Mn min. soil	0.23	211	1,8
Gamasid mite *spp*. rich.	0.40		*	Root N	0.23	158	1,5	ex. base cations min. soil	0.14	79	1,8
Gamasid mite density	0.11	56	*	Root P	0.22	159	1,5	exchangeable Al min. soil	0.31	317	1,8
Nematode *spp*. rich.	0.39		*	Root C:N	0.06	27	1,5	exchangeable Fe min. soil	0.26	211	1,8
Nematode density (combined)	0.08	44	*	Root N:P	0.15	101	1,5	saturated paste Mn min. soil	0.73	408	1,8
Nematode density (O horizon)	0.09	56	*	Root recalcitrant comp. to N	0.08	47	1,5	sat. paste base cations min. soil	0.18	102	1,8
Nematode density (min. soil)	0.13	75	*	Root biomass	0.09	52	1,5	saturated paste Al min. soil	0.43	1581	1,8
Bacterial-feeding nemat. density	0.10	62	*	Root density	0.11	64	6	saturated paste Fe min. soil	1.13	170	1,8
Fungal-feeding nemat. density	0.13	61	*	Root production	3.02	203		pH min. soil (saturated paste)	0.12	75	1,8
Plant-feeding nematode density	0.13	89	*	Root turnover	0.26	346		pH min. soil (1:1 water)	0.05	26	1,8
Ant *spp*. rich.	0.42		*	Leaf litter cell-solubles	0.21	170	1,7	total acidity min. soil	0.26	259	8
Arachnid *spp*. rich.	0.39		*	Leaf litter hemicellulose	0.17	122	1,7	percent clay min. soil	0.60	1500	8
Opilionid *spp*. rich.	0.49		*	Leaf litter cellulose	0.06	25	1,7	ammonium-oxalate Al min. soil	0.21	130	8
Collembola *spp*. rich.	0.49		*	Leaf litter recalcitrant comp.	0.11	59	1,7	pyrophosphate Al min. soil	0.50		8
rich. of bacterial PLFAs	0.55		*	Leaf litter C	0.05	23	1,7	citrate-dithionate Al min. soil	0.03	16	8
Fungal PLFAs:Bacterial PLFAs	0.18	56	*	Leaf litter N	0.30	238	1,7	ammonium-oxalate Fe min. soil	0.32	664	8
C:N microb. biomass (O horizon)	0.25	1068	1	Leaf litter P	0.31	447	1,7	pyrophosphate Fe min. soil	0.19	161	8
C:N microb. biomass (min. soil)	0.13	86	1	Leaf litter C:N	0.08	37	1,7	citrate-dithionate Fe min. soil	0.65		8
Ectomycorrh. sporocarp *spp*. rich.	0.46		2,3	Leaf litter N:P	0.16	89	1,7	Soil temperature (Apr to Nov)	0.01	8	7
Ectomycorrhizal root *spp*. rich.	0.42		3	Leaf litter recalc. comp. to N	0.12	67	1,7	Soil temperature (May to Sep)	0.01	8	7
Total ectomycorrhizal *spp*. rich.	0.31	439	2,3	Leaf litterfall mass	0.07	38	4,7	Soil temperature (Winter)	0.18	150	7
Ectomyco. sporocarp biomass	0.41		*	Woody litterfall mass	0.08	41		Soil temperature (annual)	0.01	8	7
Saprotrophic *spp*. rich. (soil)	0.37	425	2	Specific leaf area	0.62	788		Soil moisture (gravimetric)	0.08	27	7
Sapro. *spp*. rich. (woody debris)	0.18	100	2	*Acer* leaf litter *k*	0.22	221		Soil moisture (volumetric)	0.17	129	
Sapro. sporocarp biomass (soil)	0.32	567	*	Home leaf litter *k*	0.20	59	7				
Earthworm *spp*. rich.	0.55		4	Common plot leaf litter *k*	0.18	61	5,7	Tree density	0.06	31	4
Dendrobaena octaedra biomass	0.25	57	4	*Acer* root *k*	0.32	79		Tree DBH	0.34	280	4
Dendrobaena octaedra presence	0.52		4	*Pinus* root *k*	0.17	139		Tree height	0.31	903	
Lumbricus terrestris biomass	1.50		4	Average root *k*	0.21	63		Tree basal area	0.41	795	4
Lumbricus terrestris presence	1.03		4	Common plot root *k*[a]	0.18	110	5	Tree woody biomass	0.36	574	8
Total earthworm biomass	0.62		4								

The coefficient of variation (CV) and the standardized difference between the maximum and minimum observed value across plots (n = 53) for each predictor are shown. To better reflect variability as it relates to the potential role of each predictor in the regression models, the CVs and maximum differences are based on log or square-root transformed data when transformations improved normality. Maximum differences are not shown when the minimum value was zero

1 Hobbie et al. 2007, 2 Dickie et al. 2010, 3 Trocha et al. 2012, 4 Reich et al. 2005, 5 Hobbie et al. 2010, 6 Dauer et al. 2007, 7 Hobbie et al. 2006, 8 Mueller et al. 2012

* See Online Resource 1 for methods of characterizing soil biota

[a] Common plot root *k* (mass loss rates of roots from different tree species and plots placed in a single plot) was measured for only 11 tree species

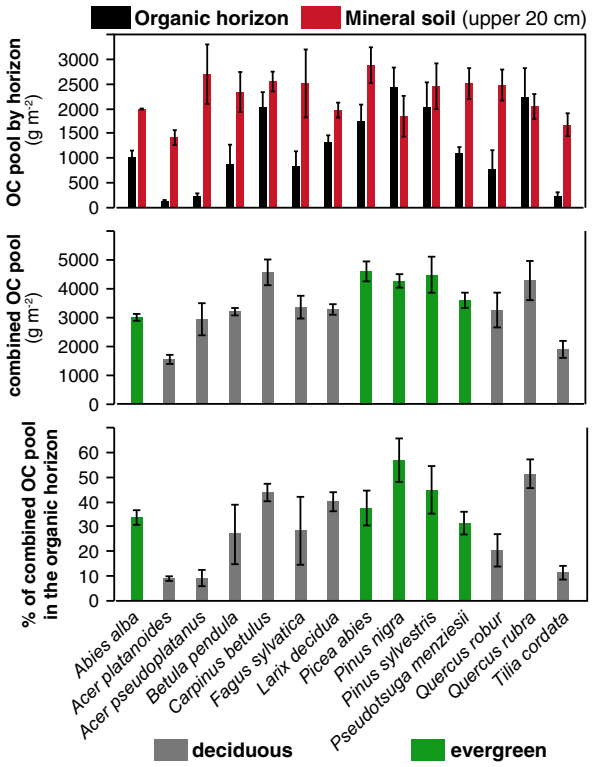

Fig. 1 Organic carbon (OC) pools are shown separately for the organic horizon (*black bars*) and upper 20 cm of mineral soil (*red bars*) in the *top panel* (error bars show SE). The *middle panel* shows the combined OC pool that includes the organic horizon and the upper 20 cm of mineral soil. The *bottom panel* shows the percent of the combined OC pool that is present in the organic horizon. According to ANOVA models, plantations of different tree species varied significantly ($P < 0.001$) with respect to OC in the organic horizon, the combined OC pool including the organic horizon and upper 20 cm of mineral soil, and the percent of the combined OC that was present in the organic horizon. Tree species was also a significant factor ($P < 0.003$) when combining C pools in the organic horizon with the upper 60 cm of mineral soil (not shown). (Color figure online)

horizon was used to estimate the pools of organic C and other elements to depths of 20 and 60 cm below the transition from organic to mineral soil (Dauer et al. 2007; Mueller et al. 2012). There was more variability among tree species for the pool of organic C in the organic horizon as compared to that in mineral soils (Fig. 1). Vesterdal et al. (2013) noted this pattern is typical of other common garden experiments, perhaps because of the longer mean residence time of organic C in mineral soils or increased spatial variability with soil depth. However, there was still substantial variability among tree species for the combined soil organic C pool that included both organic and mineral horizons (Fig. 1).

We evaluated ~100 potential predictors of variability in soil C pools; most potential predictors were measured between 1999 and 2006 and the methods and data have been previously published (Table 1, Online Resource 1). Decomposition rates of leaf litter and fine roots were estimated from mass loss rates (k) derived from overlapping litterbag studies (~2 and 1.5 year, respectively; Hobbie et al. 2006, 2010). The abundances of individual base cations in leaf litter, roots, and soils were not considered as predictors for several reasons. First, in acidic soils such as at our study site (pH < 5.2 in the upper 20 cm of mineral soil), hydrolyzing cations such as Al and Fe are more likely to play a role in complexation and stabilization of organic matter than base cations (Mueller et al. 2012), such that direct, causative links between base cation abundance and soil C stabilization are not expected. Second, previous studies at this site show the abundance of base cations, particularly calcium, covaries tightly with earthworm abundance and soil pH, which are expected to be directly related to variation in soil C pools (Reich et al. 2005; Mueller et al. 2012). Thus, due to multicollinearity issues, inclusion of base cations as potential predictors of variability in soil C pools could hinder our ability to quantify the role of factors more directly related to soil C pools and to our hypotheses. However, we discuss the role of base cations when relevant in the Results and Discussion. All variables were screened for normality and transformed when necessary by a square-root or log transformation.

We used best subsets regression in *R* (Lumley 2009) to identify predictors of the mass of organic C contained in the organic horizon, the upper 20 cm of mineral soil, and the combined organic horizon and mineral soil (from this point forward, we refer to this as the combined soil C pool). We focused on the upper 20 cm of mineral soil because this depth increment falls entirely within the plowing depth, such that tree species effects below the upper 20 cm of mineral soil are more likely to be confounded with variability in plowing depth. However, for comparison, we also analyzed the combined soil C pool based on the upper 60 cm of mineral soil. Consistent with the information-theoretic approach and similar to Goodenough et al. (2012), we compiled information from a subset of regression models (42 models), rather than

identifying one or few best models. To limit multicollinearity and make the model output practical, we evaluated models with a maximum of 7 predictors. We also took a markedly conservative approach to multicollinearity by removing models from consideration if any predictor had a variance inflation factor (*VIF*) greater than 2.5. A low VIF cutoff is useful because it prevents correlated predictors from frequently co-occurring in models, allowing a broader evaluation of predictors. Regardless, few models were excluded due to VIFs. To compare predictors, each was ranked according to its frequency of occurrence in the best 42 models (6 models of each size up to 7 predictors per model) and the average standardized beta coefficient across the best 42 models was calculated for each predictor (Bring 1994). We focused on the best 6 models of each model size because a comparison of the Bayesian Information Criterion (*BIC*) across models showed that differences among models were minimal beyond the best 6 models of each size. The average *BIC* of the best six models with $n + 1$ predictors was always at least 2 *BIC* units lower than the average of the best six models with n predictors. For each of the best models, leverage plots of each predictor and residual plots were checked for issues related to outliers and heteroskedasticity.

Results and discussion

Consistent with our prior studies at this site (Reich et al. 2005; Hobbie et al. 2006, 2007; Mueller et al. 2012), the combined soil C pool was negatively related to earthworm abundance and positively related to metrics of mineral soil acidity, especially exchangeable Fe and total acidity (including Al, Fe, and protons; Tables 2, 3). According to their frequency in the best models and standardized beta coefficients, earthworm abundance and mineral soil acidity were the most important predictors of the combined soil C pool. All of the best 36 multiple regression models (i.e. models with more than one predictor) contained one, but never more than one, predictor associated with earthworm abundance (Table 2). Similarly, at least one metric of soil acidity was included in each of the best 36 multiple regression models (Table 2). Together, earthworm abundance and mineral soil acidity explained about half of the variance in the combined soil C pool (see models with two predictors in Table 2), highlighting the potential to reveal additional mechanisms through which tree species can impact soil C pools.

Leaf litter traits

After accounting for earthworm abundance and mineral soil acidity, several leaf litter traits were significantly correlated with the combined soil organic C pool, including aspects of litter quality, the annual litterfall flux, and litter decomposition rates (estimated as short-term litter mass loss rates given by k). Nearly 25 % of best models identified a negative relationship between leaf litter decomposition rates and the size of the combined C pool (Table 2); 14 % of models included k measured in a common plot (isolating effects of litter quality), 8 % of models included k of a common litter (*Acer pseudoplatanus*) placed in all plots (isolating effects of soil microclimate, soil chemistry, and soil organisms), and 5 % of models included k measured by placing the litter of each tree species onto soil beneath the same species (allowing for effects of both litter quality and soil properties). Leaf litter decomposition rates measured in a common plot were also negatively related to the C pool in the organic horizon (32 % of best models; Table 3). This quantitative link between litter decomposition rates and soil C pools, which has not been reported previously, provides support for the common assumption among ecologists that litter decomposition rates estimated in litterbag studies have consequences for soil C stocks. A negative relationship between litter decomposition rates and soil organic C stocks is, however, partly inconsistent with the more recent conceptualization of Cotrufo et al. (2013). Tree species with high leaf litter decomposition rates likely had negative effects on soil organic C pools due to greater mineralization of litter-derived C by soil organisms and/or leaching of dissolved organic C derived from litter. However, as described below, the potential negative effects of litter decomposition rates on soil C stocks might be partly mitigated by retention of dissolved organic C or microbial-derived C in soil; perhaps this explains the somewhat lower β coefficients observed for litter mass loss rates as compared to other predictors (Tables 2, 3).

The size of the combined soil C pool was also negatively related to the ratio of recalcitrant compounds to N in leaf litter (43 % of best models) and the

Table 2 Results of best subsets regression for the combined soil organic C pool (including the organic horizon and the upper 20 cm of mineral soil)

no. of pred.	*BIC*	R^2	***L. terr.* presence**	earth-worm biomass	*L. terr.* biomass	earth-worm *spp.* rich.	**bact. feeding nemat.**	carabid beetle richness	**ex. Fe (0-20)**	**acidity (0-20)**	soluble Fe (0-20)	soluble Al (0-20)	**leaf litter recalc:N**	leaf litter recalc.	**leaf litter cellul.**	leaf litterfall mass	leaf litter *k* (1 plot)	*Acer* leaf litter *k*	leaf litter *k* (home)	specific leaf area	soil °C (spring to fall)	soil pH (O_a)
2	-29.9	0.55	-0.61							0.50												
2	-26.2	0.51		-0.41					0.46													
2	-25.9	0.51	-0.59								0.46											
2	-24.9	0.50		-0.57						0.41												
2	-24.2	0.49	-0.38						0.48													
2	-23.3	0.48							0.51											-0.35		
3	-34.0	0.61	-0.55							0.40		0.28										
3	-33.9	0.61	-0.62							0.36	0.29											
3	-33.5	0.61	-0.49						0.30	0.38												
3	-32.4	0.60	-0.61							0.48							-0.23					
3	-32.1	0.60	-0.40						0.37													
3	-32.0	0.60	-0.57						0.44													
4	-37.5	0.66	-0.51						0.33	0.33											-0.24[b]	
4	-37.4	0.66	-0.56							0.40		0.34				0.24						
4	-37.1	0.66	-0.65							0.32	0.31										-0.23[b]	
4	-36.9	0.66		-0.42				-0.38	0.46							0.34						
4	-36.5	0.65	-0.47						0.34	0.32											-0.23[c]	
4	-36.4	0.65	-0.61							0.44				-0.28			-0.38					
5	-45.7	0.73	-0.44				-0.46		0.55				-0.32		0.36							
5	-44.5	0.72		-0.39			-0.38		0.53				-0.33		0.39							
5	-43.2	0.72	-0.46				-0.33		0.50				-0.32							-0.30		
5	-41.9	0.71			-0.35		-0.37		0.56				-0.38		0.45							
5	-41.5	0.71		-0.57				-0.43			0.40					0.35						
5	-41.0	0.71	-0.61							0.31	0.27			-0.29			-0.34					
6	-50.2	0.77	-0.38				-0.41		0.52				-0.36		0.29					-0.24		
6[a]	-48.6	0.76	-0.42				-0.42		0.55				-0.33		0.38			-0.19				
6	-47.9	0.76	-0.35				-0.43		0.54				-0.40		0.35							
6	-47.8	0.76	-0.47				-0.38		0.55				-0.33		0.35							
6	-47.6	0.76	-0.51				-0.38		0.55				-0.33		0.41							
6	-47.5	0.76	-0.48				-0.39		0.44	0.21			-0.28		0.33							
7	-51.5	0.79	-0.31					-0.33	0.46				-0.29			0.49			-0.26			-0.38
7	-51.1	0.79	-0.30				-0.42		0.49				-0.37		0.29					-0.29		
7	-50.2	0.79	-0.37				-0.39		0.53				-0.36		0.32			-0.14		-0.19		
7	-50.1	0.79				-0.35			0.53				-0.34			0.42			-0.20		-0.31[c]	-0.42
7	-50.0	0.79	-0.43				-0.37		0.49				-0.39		0.38		-0.18	-0.19				
7	-49.9	0.79	-0.49				-0.33		0.36	0.23			-0.34		0.32		-0.20					
% of models			**78**	16	5	3	**38**	8	**70**	**38**	14	8	**43**	5	**35**	14	14	8	5	16	11	5
mean stand. *β*			**-0.49**	-0.49	-0.41	-0.35	**-0.39**	-0.38	**0.48**	**0.36**	0.34	0.38	**-0.34**	-0.29	**0.35**	0.37	-0.26	-0.17	-0.23	-0.31	-0.25	-0.40

Standardized beta coefficients are shown when a predictor was included in the model. With one exception, predictors are not shown if they occurred in only one model (earthworm spp. richness is shown in one instance when other predictors associated with the earthworm community were not included in the best model). Bold type is used to highlight the six predictors that were most frequently included in the best models

[a] See Fig. 2

[b] Average soil temperatures measured between May and September

[c] Average soil temperatures measured between April and November

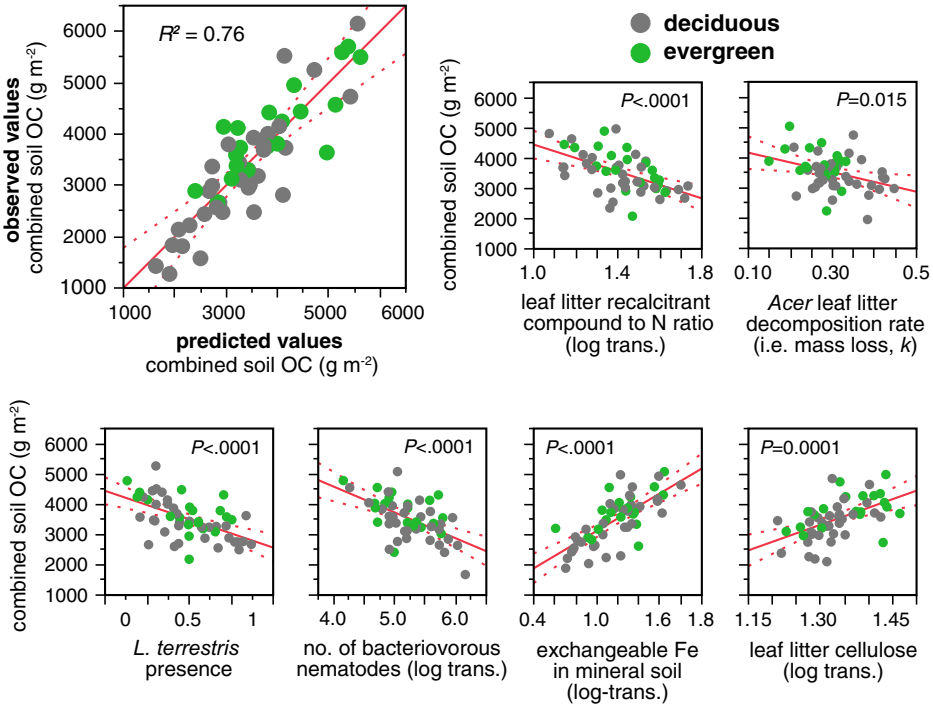

Fig. 2 Predicted values and leverage plots of individual predictors from a representative regression model of the combined soil organic C pool (including the organic horizon and the upper 20 cm of mineral soil). This model, marked as 6[a] in Table 2, was selected because it was the simplest model that included leaf litter decomposition rates as a predictor as well as the 'best' predictors related to soil acidity, soil biota, and litter quality (according to their frequency of inclusion in the best 42 models of the combined soil organic C pool; Table 2). For *L. terrestris* presence, 0 = absent and 1 = present. Leverage plots show the relationship between each predictor and the dependent variable, using the residuals of both the predictor and the dependent variable (based on regression with the other predictors)

concentration of recalcitrant compounds in leaf litter (5 % of best models; we define recalcitrant as non-hydrolyzable in strong acid), but the combined soil C pool was positively related to the concentration of cellulose in leaf litter (35 % of best models; Table 2). Fungi likely dominate cellulose decomposition (Strickland and Rousk 2010; Koranda et al. 2014); thus for tree species with more cellulose in leaf litter, a greater fraction of litter-derived C is likely funneled through fungal-based energy channels, with potential consequences for retention of litter-derived C in soils (see below). Although "lignin" to N ratios are often strongly correlated with litter decomposition rates (Prescott 2010), in our study the recalcitrant compound to N ratio of leaf litter was only weakly negatively correlated with litter decomposition rates ($R^2 = 0.05$, $P = 0.13$ in "home" soils; $R^2 = 0.14$, $P = 0.006$ in a common plot); consequently, instead of reflecting an effect on decomposition rates, the effect of this ratio on combined soil C pools is likely related to the fate of litter C during or after decomposition by soil organisms. It is probable that a greater fraction of leaf litter C was mineralized to CO_2 during microbial decomposition of litter with high recalcitrant compound to N ratios: the C use efficiency of microbes is lower for complex C substrates such as lignin (more CO_2 and less microbial biomass are produced per mass of C substrate metabolized), and the C use efficiency of microbes also decreases as the ratio of C to nutrients increases in substrates (Keiblinger et al. 2010; Manzoni et al. 2012; Koranda et al. 2014).

Finally, annual leaf litterfall mass was positively correlated with the combined soil C pool (14 % of best models; Table 2) and its standardized β coefficient was similar in magnitude compared to predictors related to litter quality (Tables 2, 3). Vesterdal et al. (2013) noted that, across studies, a relationship between litterfall flux and soil organic C pools was not always apparent, likely because of limited variability of litterfall fluxes among tree species. The

Table 3 Summary of best subsets regression for organic C pools in the organic horizon, the top 20 cm of mineral soil, and the organic and mineral horizons combined

	Organic horizon			Mineral horizon (top 20 cm)			O + mineral horizon (top 20 cm)			O + mineral horizon (top 60 cm)		
	Predictor	Frequency (%)	Mean st. β	Predictor	Frequency (%)	Mean st. β	Predictor	Frequency (%)	Mean st. β	Predictor	Frequency (%)	Mean st. β
Soil acidity	pH Oa horizon	72	−0.54	Total acidity min. soil	100	0.82	Exchangeable Fe min. soil	70	0.48	Total acidity min. soil	100	0.71
	Exchangeable Fe Oa horizon	40	−0.33	Saturated paste Fe min. soil	49	0.28	Total acidity min. soil	38	0.36	Saturated paste Al min. soil	49	0.41
				Exchangeable Fe min. soil	46	0.27	Saturated paste Fe min. soil	14	0.34	pH min. soil (1:1 water)	5	−0.35
Soil biota	*L. terrestris* presence	84	−0.52	Oribatid mite spp. rich.	59	−0.21	*L. terrestris* presence	78	−0.49	*L. terrestris* presence	68	−0.55
	Total earthworm biomass	20	−0.66	Gamasid mite density	49	0.19	Total earthworm biomass	16	−0.49	*D. octaedra* presence	16	−0.20
	Fungal:Bacterial PLFAs	20	0.30	*D octaedra* presence	24	−0.16	Bacterial-feeding nemat. density	38	−0.39	Earthworm spp. rich.	5	−0.32
				Fungal:Bacterial PLFAs	3	0.18	Fungal:Bacterial PLFAs	3	0.17			
Litter or root traits	Common plot leaf litter *k*	32	−0.27	Leaf litterfall mass	11	0.14	Leaf litter recalcitrant:N	43	−0.34	Root P	35	0.33
	Leaf litter cellulose	8	0.30	Leaf litter N:P	3	0.13	Leaf litter cellulose	35	0.35	Root N:P	22	−0.28
	Leaf litterfall mass	4	0.23				Leaf litterfall mass	14	0.37	Leaf litter recalcitrant:N	35	−0.27
							Common soil leaf litter *k*	14	−0.26	Leaf litter N:P	27	0.33
							Acer leaf litter *k*	8	−0.17	*Acer* leaf litter *k*	8	−0.17
Other	Soil temperature (May to Sep)	24	−0.29	Woody litterfall mass	57	−0.19	Specific leaf area	16	−0.31	Percent clay min. soil	14	−0.71
	Tree DBH	20	−0.30	Soil moisture (gravimetric)	8	−0.22	Soil temperature (Apr to Nov)	5	−0.27	Specific leaf area	5	−0.38
	Tree height	8	−0.26	Percent clay min. soil	5	−0.18	Soil temperature (May to Sep)	5	−0.23			

The best predictors in each category (e.g. soil acidity) are listed for each dependent variable, along with the frequency of predictor occurrence in the selected subset of best regression models and the average standardized β coefficient for each predictor. Predictors with a frequency of less than 10 % are not shown unless: (i) the predictor was particularly relevant to our hypotheses AND (ii) results were consistent for other dependent variables or related predictors. Online Resource 2 includes a complete summary of regression results for the organic horizon, mineral horizon, and combined horizons including the upper 60 cm of mineral soil

annual leaf litterfall flux varied substantially among species in our study, from 1152 kg ha^{-1} for *Abies alba* to 6225 for *Quercus rubra*.

Fine root traits

None of the measured fine root traits were frequently included in the best models of the organic C pool in the organic horizon, the upper 20 cm of mineral soil, or the organic horizon combined with the upper 20 cm of mineral soil (Tables 2, 3; Online Resource 2). This is somewhat surprising given: (i) considerable variability among plots and species with respect to root abundance, chemical composition, and decomposition rate (Table 1, Withington et al. 2006; Hobbie et al. 2010) and (ii) the hypothesis that root-derived C is preferentially stabilized in mineral soils due to the proximity of roots to mineral surfaces and aggregates that can protect organic matter from microbial metabolism (Rasse et al. 2005; Schmidt et al. 2011). However, measured decomposition rates of fine roots (Hobbie et al. 2010) are perhaps not representative of actual rates because: (i) the conditions in litterbags are unlike undisturbed soils, where roots decompose in closer proximity with soil minerals and interactions with mycorrhizal fungi and other organisms are undisturbed (Dornbush et al. 2002), and (ii) fine roots (<2 mm diameter) include a wide range of root orders with different rates of mortality and decomposition (Goebel et al. 2010). Regarding root chemical "quality", we previously reported that root N concentrations were positively correlated with mineral soil acidity due to positive effects of root N on N transformations and losses that generate protons (Mueller et al. 2012); thus, root N was likely not included in our best models due to its correlation with soil acidity. We do not have an explanation for the lack of other apparent effects of root chemical composition. Across the 14 tree species in this study, fine root chemical traits were typically not significantly correlated with leaf litter chemical traits (Hobbie et al. 2010), so covariance of leaf litter and root traits does not explain the lack of apparent effects of root chemical traits.

Interestingly, for the combined organic C pool integrated to a depth of 60 cm in the mineral soil, we identified a positive relationship between root phosphorus concentrations and the size of the combined C pool (Table 3). This could indicate that the relative importance of root traits increases with depth in the soil profile, as would be expected given decreasing inputs of leaf-litter derived C with depth. The C use efficiency of microbes, and particularly bacteria, has been shown to increase with increasing substrate P (Keiblinger et al. 2010; Manzoni et al. 2012), such that a greater fraction of root-derived C is perhaps retained in soils during decomposition of roots with high P. The sensitivity of microbial C use efficiency to P might increase with soil depth because the abundance of bacteria relative to fungi can increase with depth in forest soils (Leckie 2005); this could further explain why effects of root P concentrations were not apparent for C pools in the organic horizon, the upper 20 cm of mineral soil, or the combination of these horizons. With the exception of this difference, regression results were very similar for the combined organic C pools integrated over different depths of the mineral soil (to 20 versus 60 cm, Table 3).

Soil biota

The combined soil organic C pool was negatively related to the abundance of nematodes that feed on bacteria (38 % of best models; Table 2). This suggests that less C is stored in soils beneath tree species that foster bacterial dominated food webs, an interpretation that is consistent with other studies (Strickland and Rousk 2010; de Vries et al. 2013) and other observations from this study. Specifically, the ratio of fungal to bacterial PLFAs was positively related to the C pool in the organic horizon (20 % of the best models) and in the combined soil C pool (3 % of best models; Table 3). Here, as in other studies, it is uncertain whether the link between fungal dominance and higher soil C pools is causative and, if it is, what mechanism underlies the pattern (Strickland and Rousk 2010). Two plausible explanations for this pattern are a possibly higher C use efficiency of fungi as compared to bacteria (but see Strickland and Rousk 2010 and Six et al. 2006) and a potentially greater stabilization potential for fungal biomass and byproducts as compared to bacterial biomass and byproducts.

Few of the best regression models included predictors that describe soil biodiversity (Tables 2, 3; Online Resource 2). The absence of apparent effects of soil biodiversity could be due to an incomplete survey of soil taxa (e.g. enchytraeids and wood lice were not sampled), limitations of the methodology used for surveys (e.g. for some taxa we lack data on abundance and functional composition), or covariance of diversity metrics with

other predictors. Total species richness of soil animals was positively correlated with soil temperature ($P < 0.002$, $R^2 = 0.20$) and biomass of the earthworm *Dendrobaena octaedra* ($P < 0.001$, $R^2 = 0.22$), which were both negatively related to the combined soil C pool (Tables 2, 3). Likewise, species richness of ectomycorrhizal fungi was positively correlated with the decomposition rate of *Acer* leaf litter in all plots ($P < 0.01$, $R^2 = 0.13$), which was negatively related to the combined soil C pool (Tables 2, 3). Thus, it is possible that there were negative relationships between soil biodiversity and the combined soil organic C stocks that were masked by covariance of soil biodiversity with other predictors.

The vertical distribution of soil organic C

The size of the C pool in the organic horizon was not correlated with the size of the C pool in either the top 20 or top 60 cm of mineral soil ($R^2 \leq 0.1$ and $P > 0.25$), regardless of whether correlations were assessed using plots (n = 53) or species means (n = 14). This is likely a consequence of three characteristics of our experiment as elaborated below: (i) the composition of the earthworm community, (ii) the primary mechanism of organic matter stabilization in mineral soils, (iii) and the lack of correlations among key litter traits across tree species.

In our experiment, the dominance of anecic earthworms and dearth of endogeic species probably contributed to the lack of an inverse correlation between organic C pools in the organic and mineral horizons. The most abundant earthworm at our site was the anecic species *Lumbricus terrestris* (maximum biomass observed was 10 g m^{-2}); its presence was negatively related to combined soil organic C stocks (78 % of best models; Table 2). Anecic earthworms consume large quantities of leaf litter and the leaf litter C that is not mineralized or converted to earthworm biomass is likely concentrated within earthworm middens on the soil surface or within permanent vertical burrows in the mineral soil (Brown et al. 2000; Wilcox et al. 2002; Curry and Schmidt 2007; Don et al. 2008). If *L. terrestris* middens or burrows were under-sampled during soil sampling, the soil C pool could be underestimated in plots with higher *L. terrestris* densities, but the impact would likely be minimal because the mass of midden and burrow soil per m^2 is small relative to the rest of the soil matrix. The second most abundant earthworm across plots was the epigeic (surface dwelling) species *Dendrobaena octaedra* (maximum observed biomass was 0.23 g m^{-2}). The presence of *D. octaedra* was negatively related to the size of the organic C pool in mineral soil and the combined organic and mineral soils (Table 3; note the smaller β coefficient compared to *L. terresris* presence). Total earthworm biomass was included in the best models of soil C pools more frequently than biomass of *L. terrestris* alone (Table 3), providing further evidence for a potential effect of *D. octaedra*. Neither *L. terrestris* nor *D. octaedra* are associated with widespread mixing of organic and mineral soil matrices, such that earthworm utilization of litter-derived C at this site likely causes a net loss of litter-derived C and minimal transfer of litter-derived C to mineral soils. Endogeic species, which can increase mixing of organic and mineral horizons (Edwards and Bohlen 1996), were much less abundant when present (maximum biomass of *Aporrectodea* spp. was 0.08 g m^{-2}).

An inverse relationship between C pools in the organic and mineral horizons is perhaps more likely to occur when microbial-derived C is selectively stabilized in mineral soils, allowing the positive effect of litter quality on microbial C use efficiency to further counteract the positive effect of litter quality on decomposition (i.e. allowing retention of microbial C produced during leaf litter decomposition to further counterbalance mineralization of litter C). Preferential stabilization of microbial C is more likely to occur in fine-textured soils due to the increased abundance of microaggregates and clay-surfaces (Plaza et al. 2013; Cotrufo et al. 2013). Our site has sandy soils dominated by particulate organic matter (across plots, particulate organic matter accounted for 66 % of organic C in the upper 20 cm; K. E. Mueller unpublished). Thus, our site likely has limited capacity for selective retention of microbial C.

The effect of tree species on the vertical distribution of soil organic C also appeared to be dependent on the nature of relationships among various traits that define litter quality. Earthworm biomass at our site is closely correlated with variability of calcium concentrations in leaf litter among tree species (Reich et al. 2005), such that consumption of leaf litter, and litter depolymerization and subsequent mineralization, is likely determined to a great extent by the amount of calcium in leaf litter (Hobbie et al. 2006). However, the C use

efficiency of leaf litter decomposers is likely more a function of substrate complexity and C:N ratios, as indicated by the negative relationship between the combined soil C pool and the ratio of recalcitrant compounds to N in leaf litter (Tables 2, 3). Finally, stabilization of organic C in mineral soils at our site appears to be limited by the availability of Al and Fe, which is likely influenced more by root N concentrations (and subsequent N transformations) than other litter traits (Mueller et al. 2012). Notably, root N concentrations were not correlated with leaf litter Ca concentrations ($P \geq 0.25$, $R^2 \leq 0.07$; among species and among plots) or the ratio of recalcitrant compounds to N in leaf litter ($P \geq 0.80$, $R^2 \leq 0.01$). Further, leaf litter Ca was only modestly negatively correlated with the ratio of recalcitrant compounds to N in leaf litter ($P = 0.1$, $R^2 = 0.21$ across species; $P = 0.005$, $R^2 = 0.15$ across plots). Thus, three different aspects of litter quality apparently had largely independent impacts on the three most important phases of litter C dynamics, namely litter consumption and depolymerization, conversion of litter-derived C to CO_2 and biomass of decomposers, and stabilization of plant and microbial-derived C in mineral soils.

Further consideration of Vesterdal's results (2008) reinforces our interpretation of how site conditions constrain the nature of tree species effects on combined soil organic C pools and their vertical distribution (see also Prescott and Vesterdal 2013). In that study, which included several of the same tree species, the primary factor influencing litter decomposition rates and microbial C use efficiency was apparently the same (leaf litter C:N) and the average clay content of soils was higher. We hypothesize that these conditions allowed the negative effect of litter quality on organic horizon C stocks (mediated by positive effects of litter quality on losses of litter-derived C during decomposition) to be counteracted by the positive effect of litter quality on mineral soil C stocks (mediated by positive effects of litter quality on microbial C use efficiency and subsequent retention of microbial-derived C on clay surfaces).

Conclusions

Our results are partly consistent with the hypothesis that high plant litter quality has a positive effect on soil C sequestration via positive effects on microbial C use efficiency. Yet, the complexity of the observed litter quality effects on soil organic C pools suggests that current conceptual models of litter quality impacts on soil C are overly simplistic. Specifically, we suggest that conceptual models need to better account for positive effects of litter quality on two factors with potentially counteracting impacts on soil C: microbial C use efficiency and the rate at which microbes and soil fauna consume and depolymerize litter (as partly reflected in litter mass loss rates, which were negatively related to soil C stocks in our study). Conceptual models should also consider effects of litter quality on the capacity for organic matter stabilization (e.g. by modifying soil pH, the abundance of polyvalent cations, or soil aggregation). Across sites, we suggest the net effect of litter quality on soil organic C pools depends on the composition of the soil microbial community, the nature of variance and covariance among litter quality traits (including root traits), and the characteristics of the dominant mechanisms of C stabilization in soil at each site (determined in part by soil texture). To better predict how tree species composition impacts soil organic C pools, yielding more accurate estimates of forest C budgets, future research must address the context-dependency of relationships between soil C pools and variability in litter quality, litter inputs, soil biota, and soil properties. This will require that data of similar scope as in our study (Table 1) be collected and analyzed at multiple common garden experiments (or similarly constrained field studies), with the data collectively encompassing common soil types and tree species.

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