



Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species



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ABSTRACT

Management of biodiversity and ecosystem services requires a better understanding of the factors that influence soil biodiversity. We characterized the species (or genera) richness of 10 taxonomic groups of invertebrate soil animals in replicated monocultures of 14 temperate tree species. The focal invertebrate groups ranged from microfauna to macrofauna: Lumbricidae, Nematoda, Oribatida, Gamasida, Opilionida, Araneida, Collembola, Formicidae, Carabidae, and Staphylinidae. Measurement of invertebrate richness and ancillary variables occurred ~34 years after the monocultures were planted. The richness within each taxonomic group was largely independent of richness of other groups; therefore a broad understanding of soil invertebrate diversity requires analyses that are integrated across many taxa. Using a regression-based approach and ~125 factors related to the abundance and diversity of resources, we identified a subset of predictors that were correlated with the richness of each invertebrate group and richness integrated across 9 of the groups (excluding earthworms). At least 50% of the variability in integrated richness and richness of each invertebrate group was explained by six or fewer predictors. The key predictors of soil invertebrate richness were light availability in the understory, the abundance of an epigeic earthworm species, the amount of phosphorus, nitrogen, and calcium in soil, soil acidity, and the diversity or mass of fungi, plant litter, and roots. The results are consistent with the hypothesis that resource abundance and diversity strongly regulate soil biodiversity, with increases in resources (up to a point) likely to increase the total diversity of soil invertebrates. However, the relationships between various resources and soil invertebrate diversity were taxon-specific. Similarly, diversity of all 10

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invertebrate taxa was not high beneath any of the 14 tree species. Thus, changes to tree species composition and resource availability in temperate forests will likely increase the richness of some soil invertebrates while decreasing the richness of others.

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1. Introduction

Soils house a large proportion of species on Earth and soil biota, including invertebrate animals, contribute to ecosystem services via their key role in processes like decomposition and nutrient cycling (Anderson, 1975; Giller, 1996; Wardle, 2002; Decaëns, 2010). Yet, uncertainty regarding the fundamental controls of soil animal diversity makes it difficult to explain the enormous diversity of soil animals (Maraun et al., 2003) or predict how soil animal communities will change as the environment continues to change (Sylvain and Wall, 2011; Bardgett and van der Putten, 2014). Knowledge of soil animal diversity remains limited, to a great extent, because very few studies have simultaneously assessed diversity of many types of soil animals; this is due to the number and complexity of methods needed to study such cryptic organisms (Sylvain and Wall, 2011). Up to the present, even the more comprehensive surveys of soil organisms (e.g. van der Wal et al., 2009; Scherber et al., 2010; Postma-Blaauw et al., 2012) typically survey less than half of the taxonomic groups (families, orders, or classes) that represent common types of soil invertebrates (Bardgett and van der Putten, 2014). Since land management often occurs within local and regional scales, effective conservation of soil biodiversity and management of ecosystem services requires more information on the controls of soil biodiversity at those scales. More specifically, to maintain or increase soil biodiversity at these scales, land managers must have *quantitative* knowledge of how soil biodiversity is influenced by the ecological factors associated with management practices, including characteristics of vegetation, soil properties, and microclimatic conditions.

The species composition of plant communities is one ecological factor that impacts soil animal communities, likely because plant community composition shapes the diversity and abundance of resources available to soil animals (Sylvain and Wall, 2011). When comparing zones of influence beneath single plants, monocultures, and/or mixed-species communities, plant species often have divergent impacts on the diversity of soil animal communities; this “plant species identity” effect is often larger than effects of plant species richness (Wardle et al., 2003, 2006; De Deyn et al., 2004; Ball et al., 2009; Eissfeller et al., 2013b). Thus, as plant community composition shifts in response to global environmental changes (Iverson et al., 2008; Garbelotto and Pautasso, 2012) and management practices (Augusto et al., 2002; Fox et al., 2007), there will be corresponding impacts on the diversity of soil animals. Yet, the tremendous diversity of plant species also makes it difficult to widely estimate the impact of plant species and plant community composition on soil animal diversity. Given practical constraints on the number of plant species and communities that can be studied, a predictive framework of plant impacts on soil animal diversity must be based on studies that encompass a relatively small number of plant species. Development of such a predictive framework requires a better understanding of which ecological factors mediate the impact of plant species on soil animal diversity, including plant functional traits and various characteristics of plant communities and soils. Previous studies indicate that two general factors are most likely to mediate the effect of plants on soil animal diversity: resource availability and resource diversity (Hooper et al., 2000;

Wardle, 2006). In this context, one must not only consider plant effects on metabolic resources, such as substrates for energy production and mineral nutrients, but also plant effects on other ecological factors that further shape soil habitats and niche space, including the presence and abundance of ecosystem engineers (Lavelle et al., 1997; Eisenhauer, 2010), microclimatic conditions, and general soil properties.

Theoretical and empirical studies support the idea that plant impacts on soil animal diversity will be determined by how plants affect the quantity and diversity of soil resources (Hooper et al., 2000). As the *quantity* of resources increases, the diversity of soil animals is expected to increase through at least intermediate levels of resource availability because of higher population densities and thus lower probability of local extinction (Bardgett, 2002). As resource availability increases to high levels, theory suggests that competitive exclusion could lead to declines in soil animal diversity; this could be exacerbated by constraints on niche differentiation among soil animals (Anderson, 1975; Maraun et al., 2003). However, a synthesis of available evidence suggests that competition does not have large impacts on many taxa of soil organisms, perhaps due to spatial or temporal niche differentiation (Wardle, 2002, 2006; but see Giller, 1996; Decaëns, 2010). Several observational and experimental studies report a positive effect of resource availability on soil animal diversity (van der Wal et al., 2009; Mulder et al., 2012; Sayad et al., 2012). As the *diversity* of resources increases, diversity of soil animals is expected to rise due to enhanced opportunities for niche differentiation with respect to habitat use and sources of energy and nutrients (Anderson, 1978; Wardle, 2006; Coleman, 2008). Consistent with the hypothesis that resource diversity can mediate the impact of plant species on soil animal diversity, Eissfeller et al. (2013b) showed that oribatid mite diversity was higher beneath tree species that fostered development of more substantial organic horizons, perhaps because niche overlap was reduced by the increased depth, mass, and heterogeneity of the organic horizon.

Ecosystem engineers, such as earthworms, can influence diversity of other soil animals by regulating the availability, diversity, and spatial distribution of resources available to soil animals (Lavelle et al., 1997; Eisenhauer, 2010). Plants are expected to influence the presence and abundance of invertebrate ecosystem engineers, partly through variation of litter quantity and quality among plant species (Lavelle et al., 1997; Schwarz et al., 2015). Common garden experiments confirm this link; Reich et al. (2005) and Sayad et al. (2012) showed that variability of earthworm biomass across plantations of different tree species was positively correlated with the amount of calcium in leaf litter.

Similar to the role of ecosystem engineers, soil microclimate and other general soil properties might regulate soil animal diversity in conjunction with plants through the links between these factors and soil resources or other niche dimensions. For example, soil pH is known to influence the relative abundance and diversity of soil bacteria and fungi (Mulder et al., 2005, 2009; Fierer et al., 2009) as well as the activity of soil enzymes (Sinsabaugh et al., 2008), which could cascade into bottom-up effects on soil animal diversity. Additionally, the metabolic activities of soil microbes and animals are sensitive to soil temperature, with potential consequences for

resource availability and soil animal diversity (Brown et al., 2004). Generally, abiotic conditions that favor the diversity or productivity of bacteria and/or fungi, which form the basis of soil food webs, could also increase the diversity of soil animal communities.

Here, we study the controls of soil animal diversity in a long-term common garden experiment that contains, within a single location, replicated monocultures of 14 common temperate tree species. At this experiment, the monocultures of different tree species have divergent effects on soil resource availability and quality, earthworm abundance, microclimate, and understory plant communities (Reich et al., 2005; Knight et al., 2008; Dickie et al., 2010; Trocha et al., 2012; Mueller et al., 2015). Thus, we can simultaneously assess how variation in these local scale factors is correlated with soil animal diversity and evaluate the role of tree species identity and traits. We sampled soil animals ~34 years after establishment of the monocultures and determined the richness of species (or genera), for earthworms (Lumbricidae), nematodes (Nematoda), oribatid mites (Oribatida), gamasid mites (Gamasida), harvestmen (Opilionida), spiders (Araneida), springtails (Collembola), ants (Formicidae), carabid beetles (Carabidae), and staphylinid beetles (Staphylinidae). In addition, we measured ~125 abiotic and biotic factors that could influence the diversity of these soil invertebrates. In subsequent analyses, we sought to identify which of these potential explanatory variables were the most useful predictors of variation in soil invertebrate diversity across the different monocultures. We hypothesized that soil invertebrate diversity is significantly influenced by tree species identity due to the effects of tree species on i) resource availability, quality, and diversity, and ii) the biotic and abiotic environment, as characterized by earthworm ecosystem engineers, understory plant community structure, microclimate, and soil properties such as pH.

2. Materials and methods

2.1. Experimental site

This study was conducted in a common garden experiment established in 1970 and 1971 near Siemianice, Poland (51°14.87' N, 18°06.35', elev. 180 m). Average annual precipitation is 591 mm, and average annual temperature is 8.2 °C. Surface soils are glacial outwash (>80% sand) overlying clay-rich subsoils. The site was prepared by clear-cutting an 80-year-old *Pinus sylvestris* L. stand, followed by stump removal and soil plowing. 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). Planted species included eight deciduous angiosperms (*Acer platanoides* L., *Acer pseudoplatanus* L., *Betula pendula* Roth., *Carpinus betulus* L., *Fagus sylvatica* L., *Quercus robur* L., *Quercus rubra* L., *Tilia cordata* Mill.), five evergreen gymnosperms (*Abies alba* Mill., *Picea abies* (L.) Karst., *Pinus nigra* Arn., *P. sylvestris* L., *Pseudotsuga menziesii* Franco), and one deciduous gymnosperm (*Larix decidua* Mill.). Due to tree mortality, only two plots of *A. alba* were investigated in this study. Previous studies documented much variability among tree species for microclimatic conditions, understory plant communities, litter production, litter chemistry, biomass production, leaf and root growth and phenology, soil chemistry, and dynamics of soil nutrients and organic matter (Reich et al., 2005; Hobbie et al., 2006; Knight et al., 2008; Mueller et al., 2015).

2.2. Sampling of invertebrate animals in soil

Between 2002 and 2006, or approximately 34 years after planting, in each monoculture plot ($n = 53$) we sampled 10 taxonomic groups (orders and families) of invertebrate animals: Lumbricidae, Nematoda, Oribatida, Gamasida, Opilionida, Araneida,

Collembola, Formicidae, Carabidae, and Staphylinidae. In May and October 2004, nematodes were extracted from three soil subsamples (each 100 cm³) per plot; each subsample was composited from 10 soil cores (to 20 cm depth) and each subsample represented one of three sets of soil horizons (the organic horizon, the A horizon or the shallowest mineral horizon, and deeper horizons, including A2, AB, B and E horizons). We used the centrifugal method of nematode extraction (Jenkins, 1964), which yields ~80% of total individuals. Nematodes were killed and fixed in hot 2% formaldehyde solution, then identified and counted at the genera level using a microscope. Soil microarthropods, including gamasid and oribatid mites as well as Collembola, were extracted by heat from cores of the upper 5 cm of soil collected 4 different times: November 2003, June and October 2004, and June 2005. All microarthropods were identified to the species or genus level (Skorupski, 2010). Epigeic fauna, including carabid and staphylinid beetles, ants, spiders, harvestmen, were collected with pitfall traps (250 mL plastic pots filled with 4% formaldehyde and covered to exclude rain). In May and October of 2004, ten traps were distributed randomly in the center of each study plot, with a minimum distance of 50 cm between traps. The traps remained in place for two weeks prior to collection. The epigeic fauna were then transferred to 70% ethyl alcohol, sorted, counted and identified to species level. In summer 2002 and fall 2004, earthworm populations were censused using mustard liquid extraction (40 g powdered mustard/4 L water) in two to four randomly located subplots (35 cm × 35 cm). After preservation in 10% formalin, earthworms were identified to species level and, for each species, the number of individuals was counted and biomass was measured (on an ash-free dry weight basis to account for soil contamination; Reich et al., 2005). For any group (family or order) of soil animals that was sampled more than once, we averaged data from each sampling event to produce a single estimate of taxonomic/species richness.

2.3. An integrated, standardized metric of soil invertebrate diversity

To evaluate invertebrate diversity across the taxonomic groups we sampled, but avoid bias toward taxa with high richness, for each plot we calculated an index of diversity (hereafter we refer to this index as “integrated soil invertebrate diversity”). First, we standardized taxon richness (i.e. richness of species or genera) for each taxon by subtracting the minimum richness value across all plots from the richness value of each plot and dividing the resulting value by the difference between the minimum and maximum richness values across all plots. For each taxon, this serves to set the minimum standardized richness value across plots at zero and to set the maximum standardized richness value across plots at 1. Then for each plot, we averaged the standardized taxon richness values for the nine focal taxa of soil animals (including Nematoda, Oribatida, Gamasida, Opilionida, Araneida, Collembola, Formicidae, Carabidae, and Staphylinidae). We calculated integrated soil invertebrate diversity in this manner for three reasons: i) to give each group similar weight in the estimate of integrated richness, ii) because different soil volumes and depths were sampled for the different taxa, and iii) because taxon richness measures differed between the different groups (e.g., number of nematode genera versus ant species richness). Earthworm richness was excluded from the calculation of integrated diversity of soil invertebrates because earthworms are dominant ecosystem engineers (Lavelle et al., 1997; Eisenhauer, 2010); consequently, we hypothesized that earthworm richness and abundance could be important predictors of the diversity of other soil invertebrates. Further, because earthworm richness varied between 0 and 3 species, the contribution to total soil invertebrate diversity would have been low. Integrated

soil invertebrate diversity (unstandardized) ranged between 91 and 132 taxa per plot and was closely correlated with the standardized index of integrated soil invertebrate diversity ($R^2 = 0.73$, $P < 0.001$). For subsequent statistical analyses, we used the standardized version of integrated soil invertebrate diversity. Finally, although our survey of soil invertebrates was extensive, this index of integrated soil invertebrate diversity is not representative of *total* invertebrate diversity because we did not sample some groups of soil invertebrates (e.g., protozoans, enchytraeids, centipedes, and millipedes).

2.4. Potential predictors of soil invertebrate diversity

We assessed the ability of ~125 abiotic and biotic variables to explain the variation of invertebrate richness across plots. The potential predictors included microclimatic properties of the understory and of soils, general soil properties such as texture and acidity, characteristics of the understory plant community and of the canopy trees, properties of plant litter inputs (e.g., the quantity and chemical composition of leaf litter and root biomass) and of organic substrates in soil (e.g., percent carbon in the organic and mineral soil horizons), the amount of nutrients in plant-derived tissues and soils (including phosphorus, nitrogen, and base cations), and characteristics of bacterial and fungal communities in soil. The supplementary appendix includes a brief description of the methods for key predictors and a full list of the predictors we evaluated (Table A1), including references.

2.5. Statistics

For integrated soil invertebrate diversity and the richness of each group of invertebrates, we performed best subsets regression using the *leaps* package (Lumley, 2009) in R (R Development Core Team, 2012). The list of potential predictors for each taxonomic group was identical, except that invertebrate density was excluded from the models of richness within the same taxonomic group (e.g., density of oribatid mites was not a potential predictor of oribatid mite richness). Density information was only available for mites and nematodes. To limit multicollinearity issues and produce a practical number of models and predictors to compare, a maximum of 6 predictor variables was allowed in the best subset analysis. Issues of multicollinearity were also minimized by carefully selecting the possible predictors from a list of several hundred variables related to vegetation, soil, and microclimatic properties (e.g. the mass of C in the forest floor is a function of the forest floor mass and the %C of the forest floor, so this potential predictor was excluded from regression analyses while forest floor mass and forest floor %C were retained). The six best models of each size, from one to six predictors, are reported and discussed in this manuscript. For each dependent variable, these 36 best models were selected from a pool of up to 90 best models (up to 15 of each size) after screening each model for issues related to multicollinearity or outliers. To be conservative with respect to multicollinearity (Allison, 1999), any model with a variance inflation factor (VIF) greater than 2.5 for any predictor was rejected and the next best model was selected (a VIF ≥ 2.5 indicates that $\geq 60\%$ of the variability in the predictor can be explained by the other predictors in the model). Perhaps more importantly, a low VIF cutoff is useful because it prevents correlated predictors from frequently co-occurring in models, allowing a broader evaluation of predictors. We used this VIF criteria to reject 4 multiple regression models (compared to 330 multiple regression models ultimately reported here) and to remove one variable (mineral soil organic carbon) from the pool of potential predictors of oribatid mite richness (due to its strong positive correlation with soil acidity; Mueller et al.,

2012). For a few predictors that had potential outliers, models containing those predictors were rejected if, for the majority of best models containing that predictor, the P value for the predictor was >0.05 after running the model with alternative transformations or after excluding the outliers. We used the Bayesian Information Criterion (BIC) to compare models with different numbers of predictors. In one instance (nematode richness), the average BIC value of the best 6 models with 6 predictors was not more than 2 BIC units lower than the best 6 models with 5 predictors; thus we excluded the models of nematode richness with 6 predictors from consideration. Similar to Goodenough et al. (2012), for each dependent variable we ranked predictor variables according to their frequency of occurrence in the best 36 models. We then used these frequencies of occurrence in the best 36 models and, to a lesser extent, the average standardized beta coefficients, to compare the predictors that were included in at least one of the best 36 regression models. The standardized beta coefficients show how much the dependent variable is predicted to change, as a proportion of the SD of the dependent variable, if the value of the predictor variable is changed by one SD of the predictor (Bring, 1994).

We used additional statistical methods to supplement the best subsets regression analysis. Simple linear least-squares regression was used to assess correlations among some predictors. One-way ANOVA was used to assess the effects of tree species identity and leaf habit on invertebrate richness. Structural equation modeling (Eisenhauer et al., 2015) was used to further evaluate the strong correlation between understory light availability and integrated soil invertebrate diversity. Specifically, we used structural equation modeling to assess the role of other factors that covaried with understory light availability, including spatial and temporal light variability, soil temperature, and characteristics of the understory plant community (plant cover and species richness). Following Grace (2006), we limited the total number of exogenous and endogenous variables to eight (due to constraints related to the number of plots) and we used model modification indices to improve the models when relationships between variables were supported by prior knowledge. Model adequacy was determined via χ^2 tests and relative model fit was determined using AIC in Amos 5 (Amos Development Corporation, USA).











3. Results

3.1. Relationships among soil invertebrate groups and effects of tree species

None of the pairwise correlations between richness of one invertebrate group and another had a Pearson coefficient (r) greater than $|0.41|$. Further, none of the taxonomic groups had significant correlations ($P < 0.05$) with richness more than three other taxonomic groups (Table 1). Consequently, the identity of the tree species with the highest or lowest richness for a given soil invertebrate group was typically different than the identity of the tree species with the highest or lowest richness for other invertebrate groups. Tree species identity had a significant influence on the richness of four soil invertebrate groups, including both groups of beetles surveyed (Carabidae and Staphylinidae) as well as nematodes (Nematoda) and oribatid mites (Oribatida; Table 2). Deciduous tree species had higher average taxon richness for both types of beetles, nematodes, and gamasid mites, but evergreen tree species had higher average taxon richness for oribatid mites (Fig. 1).

Due to the lack of strong relationships among the richness of different soil invertebrate groups, no single taxon could be used to represent the integrated richness of the nine invertebrate groups surveyed in this study (excluding Lumbricidae). Therefore, our

Table 1
Correlation matrix for taxon richness (i.e. species or genera richness) of different soil invertebrate groups. Bold print indicates correlations with $P < 0.05$ and italic print indicates correlations with $0.05 < P < 0.10$.

	 Nemat.	 Lumbr.	 Oribat.	 Gamas.	 Opilion.	 Araneid.	 Collemb.	 Formicid.	 Carabid.	 Staphyl.
Nematoda	1.00	-0.37	0.00	0.29	-0.01	<i>0.24</i>	-0.29	0.35	0.13	-0.05
Lumbricidae	-0.37	1.00	-0.23	0.19	-0.21	-0.31	<i>0.30</i>	-0.39	0.17	0.25
Oribatida	0.00	-0.23	1.00	0.13	-0.03	0.19	0.09	0.01	-0.32	-0.41
Gamasida	0.29	0.19	0.13	1.00	-0.04	0.16	0.23	0.12	0.26	0.16
Opilionida	-0.01	-0.21	-0.03	-0.04	1.00	0.01	-0.03	0.11	-0.10	-0.05
Araneida	<i>0.24</i>	-0.31	0.19	0.16	0.01	1.00	-0.09	0.37	0.29	-0.26
Collembola	-0.29	<i>0.30</i>	0.09	0.23	-0.03	-0.09	1.00	-0.16	-0.05	0.17
Formicidae	0.35	-0.39	0.01	0.12	0.11	0.37	-0.16	1.00	0.12	-0.11
Carabidae	0.13	0.17	-0.32	0.26	-0.10	<i>0.29</i>	-0.05	0.12	1.00	0.08
Staphylinidae	-0.05	<i>0.25</i>	-0.41	0.16	-0.05	-0.26	0.17	-0.11	0.08	1.00

standardized, integrated estimate of the taxon richness of soil invertebrates is the best, albeit incomplete, proxy for soil invertebrate diversity in this study. The integrated soil invertebrate diversity index was significantly variable among monocultures of different tree species (Table 2) and was also 15% higher in soils beneath deciduous species as compared to evergreens (Fig. 1).

3.2. Potential predictors of soil invertebrate diversity: an overview of regression results

In this section, we summarize a variety of statistics for two purposes: *i*) to show that the multiple regression analyses were useful both for identifying key predictors of soil invertebrate richness and for explaining variation in soil invertebrate richness, and *ii*) to provide a broader context for interpretation of specific results, such as the frequency of occurrence for a given predictor in regression models of invertebrate richness.

For regression models of integrated soil invertebrate diversity and of taxon richness of individual groups, as the number of predictors included increased up to 6, the coefficient of determination (R^2) increased and the Bayesian Information Criterion (BIC) decreased, by at least 2 BIC units on average (Fig. 2A and B; Table 3; Tables A2–A11 in the supplementary appendix). There was one exception; for nematode richness, the BIC of the best models with 6 predictors was not lower than that of best models with 5 predictors (Fig. 2B). Similarly, except for models of nematode richness with 6 predictors, the regression coefficients were significantly different from zero ($P < 0.05$) for every predictor in each of the best 36 models for integrated soil invertebrate diversity and taxon richness of the 10 invertebrate groups. Across the different invertebrate groups, the best single predictor of taxon richness explained between 15 and 44% of the variation in richness, while the best multiple regression model explained between 53 and 78% of the variation in richness (Tables A2–A11; Fig. 2A).

For each group of invertebrates and for integrated soil invertebrate diversity, there was at least one predictor that occurred in 65% of the best regression models. The mean frequency of the top ranked predictor across the 11 dependent variables was 83%, while the second and third most frequently included predictors had mean frequencies of 60 and 42%. After the third ranked predictor, the potential predictors overlapped much more with respect to their frequency of occurrence in models (Fig. 2C). However, even the fifth and sixth ranked predictors were included in 31 and 27% of the best regression models (on average across the 11 dependent variables). In summary, for each taxonomic group of soil animals, one to three predictors were observed to be present in more than 50% of the best regression models and a set of 5–6 predictor variables were

observed to be present in ~20% or more of the best regression models.

Although the frequency of occurrence in best models is a useful tool to *qualitatively* compare the utility of potential predictors, we caution against a strict *quantitative* interpretation of predictor frequency in the models because some predictors are not independent (e.g. the lignin:N ratio and N concentration of leaf litter). For brevity and to be cautious of spurious correlations, below we do not report instances when a predictor was present in fewer than 11 of the best models (~35% of the best models) *unless*: *i*) the predictor in question was frequently correlated with other dependent variables in the same manner or *ii*) two or more related predictors were correlated with the dependent variable in the same manner (e.g. when two independent estimates of nitrogen availability showed similar relationships to the dependent variable). For a complete summary of best subsets regression results for each taxonomic group of soil invertebrates, see Tables A2–A11 in the supplementary appendix.

3.3. Microclimatic predictors

The predictor that was most strongly correlated with integrated soil invertebrate diversity was the average light availability in the understory between April and November ($R^2 = 0.35$, $P < 0.0001$; Fig. 3A). Understory light availability was included in 90% of the best regression models and the correlation was strongly positive (evident by the relatively large, positive β coefficient; Table 3). Integrated soil invertebrate diversity was also significantly positively correlated with spatial and temporal variability in understory light (Fig. 3B and C), but these relationships were weak or negligible after accounting for covariance between average light availability and its spatial and temporal variability (Fig. 3E). When comparing alternative models with only one predictor (Table 3), average soil temperature between April and November was the second best predictor of integrated soil invertebrate diversity. Soil temperature during this time period was positively correlated with understory light availability ($R^2 = 0.58$, $P < 0.0001$) and integrated soil invertebrate diversity (Fig. 3D). Three of the best *multiple* regression models included soil temperature but not light availability, such that either average light availability or soil temperature between April and November were included in all of the best multiple regression models of integrated invertebrate diversity (Table 3).

Average understory light availability between April and November was positively correlated not only with soil temperature, but also with spatial variability (SD) of understory light ($R^2 = 0.44$, $P < 0.0001$), temporal variability of understory light ($R^2 = 0.41$, $P < 0.0001$), understory plant cover ($R^2 = 0.51$, $P < 0.0001$), and understory plant species richness ($R^2 = 0.35$, $P < 0.0001$). Structural

Table 2 Variability of standardized taxon richness of soil invertebrate groups among plots planted with different tree species. Reported values are means ± standard deviation (sd). For each taxonomic group of soil invertebrates, the highest and lowest values of standardized taxon richness are highlighted in bold. Also shown are P values of one-way ANOVAs of tree identity effects on taxon/species richness of each taxa, with bold print indicating $P < 0.05$. Species and taxonomic abbreviations are defined below.

Tree species	n	Nematoda		Lumbricidae		Oribatida		Camasida		Opilionida		Araneida		Collembola		Formicidae		Carabidae		Staphylinidae		Integrated soil invertebrate diversity	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
<i>Abies alba</i> Mill.	2	0.48	0.15	0.67	0.47	0.52	0.29	0.59	0.13	0.25	0.12	0.25	0.28	0.42	0.27	0.56	0.44	0.08	0.04	0.47	0.08	0.40	0.06
<i>Acer platanoides</i> L.	3	0.53	0.14	0.56	0.19	0.13	0.05	0.39	0.11	0.28	0.10	0.22	0.33	0.28	0.19	0.46	0.07	0.67	0.15	0.51	0.09	0.38	0.04
<i>Acer pseudoplatanus</i> L.	3	0.56	0.08	0.56	0.38	0.06	0.09	0.45	0.22	0.33	0.17	0.23	0.08	0.31	0.35	0.54	0.26	0.54	0.16	0.82	0.16	0.43	0.03
<i>Betula pendula</i> Roth.	3	0.85	0.18	0.33	0.00	0.27	0.09	0.80	0.19	0.44	0.10	0.58	0.21	0.31	0.33	0.79	0.26	0.91	0.11	0.43	0.27	0.61	0.09
<i>Carpinus betulus</i> L.	3	0.81	0.14	0.22	0.19	0.52	0.35	0.61	0.24	0.39	0.10	0.37	0.43	0.23	0.33	0.54	0.36	0.25	0.30	0.55	0.07	0.49	0.19
<i>Fagus sylvatica</i> L.	3	0.58	0.24	0.67	0.00	0.24	0.10	0.59	0.11	0.33	0.17	0.30	0.23	0.54	0.27	0.46	0.26	0.63	0.05	0.47	0.27	0.46	0.06
<i>Larix decidua</i> Mill.	6	0.54	0.18	0.33	0.21	0.45	0.25	0.48	0.20	0.36	0.25	0.53	0.26	0.44	0.13	0.60	0.23	0.60	0.08	0.28	0.16	0.48	0.11
<i>Picea abies</i> (L.) Karst.	6	0.40	0.18	0.50	0.18	0.58	0.33	0.56	0.22	0.42	0.14	0.29	0.14	0.63	0.31	0.38	0.26	0.37	0.26	0.47	0.17	0.45	0.11
<i>Pseudotsuga menziesii</i> (Mirb.)	6	0.34	0.28	0.50	0.35	0.45	0.20	0.32	0.23	0.47	0.29	0.18	0.13	0.63	0.10	0.50	0.14	0.26	0.12	0.30	0.11	0.38	0.04
<i>Pinus sylvestris</i> L.	3	0.58	0.16	0.33	0.00	0.46	0.17	0.41	0.15	0.28	0.19	0.38	0.29	0.54	0.00	0.42	0.14	0.56	0.06	0.53	0.31	0.46	0.03
<i>Pinus sylvestris</i> L.	3	0.45	0.08	0.33	0.00	0.49	0.02	0.42	0.24	0.39	0.19	0.52	0.25	0.15	0.13	0.71	0.14	0.44	0.13	0.12	0.20	0.41	0.07
<i>Quercus robur</i> L.	6	0.59	0.16	0.61	0.33	0.30	0.12	0.64	0.19	0.36	0.13	0.37	0.18	0.49	0.17	0.73	0.17	0.64	0.19	0.60	0.28	0.53	0.05
<i>Quercus rubra</i> L.	3	0.43	0.07	0.33	0.00	0.12	0.13	0.53	0.12	0.28	0.10	0.27	0.38	0.69	0.08	0.54	0.19	0.65	0.20	0.76	0.21	0.47	0.07
<i>Tilia cordata</i> Mill.	3	0.45	0.13	0.67	0.33	0.32	0.09	0.54	0.15	0.17	0.00	0.33	0.19	0.44	0.25	0.46	0.26	0.67	0.12	0.49	0.21	0.43	0.04

Tree species identity $P = 0.02$ $P = 0.29$ $P = 0.03$ $P = 0.16$ $P = 0.68$ $P = 0.41$ $P = 0.12$ $P = 0.33$ $P = 0.001$ $P = 0.005$ $P = 0.03$

equation modeling revealed that understory light availability remained a significant predictor of soil invertebrate diversity even after accounting for covariance of both light availability and invertebrate diversity with spatial and temporal variability in understory light, soil temperature, and understory plant characteristics (Fig. 3E; Table A12).

Similar relationships were frequently observed between these microclimatic predictors and the taxon richness of individual soil invertebrate groups (Tables A2–A11; Fig. 4). The availability or variability of understory light was positively correlated with taxon richness of several invertebrate groups, most notably carabid beetles (100% of best models) and arachnids (34% of best models). Average soil temperature between April and November was positively correlated with taxon richness of arachnids (74% of best models) and ants (74% of best models). In contrast, the taxon richness of oribatid mites was negatively correlated with both average soil temperature between April and November (16% of best models) and temporal variability in understory light (66% of best models).

3.4. Biotic predictors

Characteristics of plant community structure were not included as a predictor in any of the best 36 regression models for integrated soil invertebrate diversity (Table 3). However, the taxon richness of some groups of soil invertebrates was related to various characteristics of understory plant communities or canopy trees, including the richness or abundance of plants in the understory, tree density, average diameter at breast height (DBH), and basal area. Except for species richness of ants (Fig. 4), characteristics of understory plants were infrequently included as predictors in the best 36 models of taxon richness (Tables A2–A11); perhaps inclusion of light availability in the best regression models precluded the inclusion of understory plant characteristics due to their covariance with light availability (Fig. 3E). Characteristics related to the density and size of canopy trees were positively correlated with taxon richness of some invertebrate groups, including carabid beetles (68% of best models included basal area or both of its components, DBH and tree density) and Collembola (58% of best models included basal area). Conversely, basal area, DBH, or tree density was negatively correlated with taxon richness of several invertebrate groups, especially with species richness of ants (48% of best models; Fig. 4).

The biomass of *Dendrobaena octaedra*, an epigeic earthworm, was positively correlated with integrated soil invertebrate diversity in 87% of the best 36 models (Table 3). Nearly half of the variability in integrated soil invertebrate diversity could be explained by the model with both *D. octaedra* biomass and understory light availability (April to November; Table 3). Variation in *D. octaedra* biomass alone could explain 19% of the variation in integrated soil invertebrate diversity ($P < 0.001$; Table 3). The biomass of *D. octaedra* or the presence of *D. octaedra* was also positively correlated with taxon richness of harvestmen (100% of best models) and carabid beetles (35% of best models; Fig. 4; Tables A2–A11).

For several of the groups of soil invertebrates, taxon richness was correlated with the richness or abundance of soil invertebrates from other groups (Tables A2–A11; Fig. 4). Notably, arachnid richness was positively correlated with the abundance of nematodes in the organic horizon (39% of best models) and earthworm richness was positively correlated with richness of Collembola (42% of best models).

The abundance or diversity of fungi or bacteria was correlated, positively in most cases, with soil invertebrate richness (Table 3; Tables A2–A11). Integrated soil invertebrate diversity was

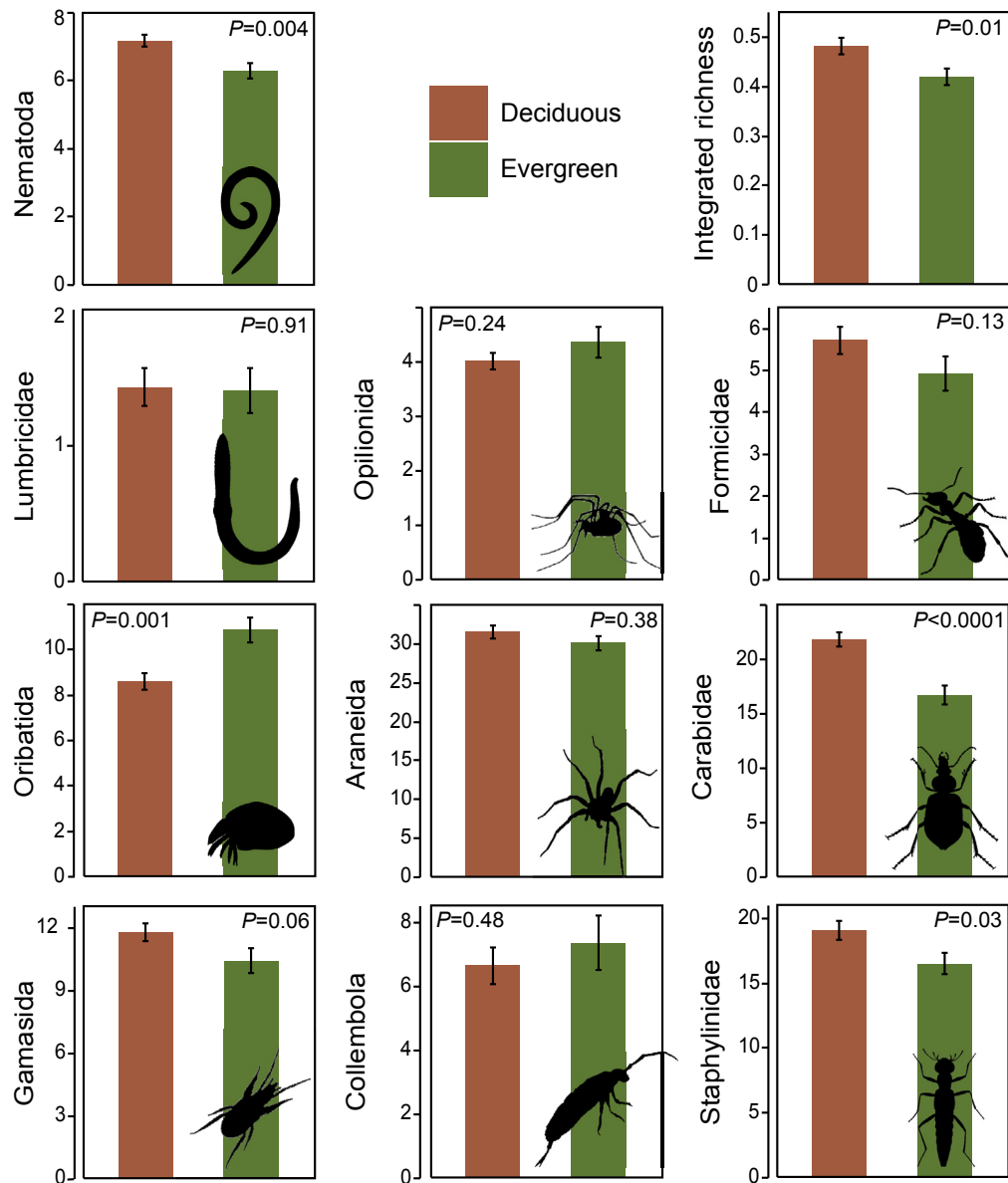


Fig. 1. Effects of leaf type on the taxon richness of 10 groups of soil invertebrates and on the standardized taxon richness as integrated across 9 of the groups (excluding earthworms). For each group of soil invertebrates, the Y-axis shows the number of species or genera.

positively correlated with microbial C in the uppermost mineral soil horizon (in 23% of best models). Estimates of fungal or microbial abundance were also positively correlated with taxon richness of four invertebrate groups, most notably for nematodes (96% of best models included biomass of ectomycorrhizal sporocarps; Fig. 4). Estimates of fungal species richness or the number of bacterial PLFA types were positively correlated with taxon richness of four of the invertebrate groups, including staphylinid beetles (90% of best models included richness of fungi that inhabit woody litter). In contrast, earthworm species richness was negatively correlated with the number of bacterial PLFA types in soil (77% of best models; Fig. 4).

In a few instances (Table 3; Tables A2–A11), we observed correlations between taxon richness of soil invertebrates and two potential indicators of the relative abundance of fungi and bacteria: the ratio of fungal to bacterial PLFAs and the ratio of C to N in microbial biomass (fungal biomass typically has higher C:N than

bacterial biomass; Strickland and Rousk, 2010). A negative correlation between microbial C:N in the organic horizon and taxon richness of gamasid mites was the only such relationship that was frequently included in the best models (58%; Fig. 4).

3.5. General soil properties

General soil properties, including measures of soil texture, soil acidity, and size of the organic horizon, were not included as predictors in any of the best 36 models for integrated soil invertebrate diversity. However, some of these predictors, especially various indices of soil acidity, were frequently included in the best models of taxon richness of individual invertebrate groups (Tables A2–A11). As indices of soil acidity increased, i.e., as pH decreased or the quantity of hydrolyzing cations such as H^+ and Al^{3+} increased, taxon richness decreased for nematodes (58% of best models) and staphylinid beetles (35% of best models).

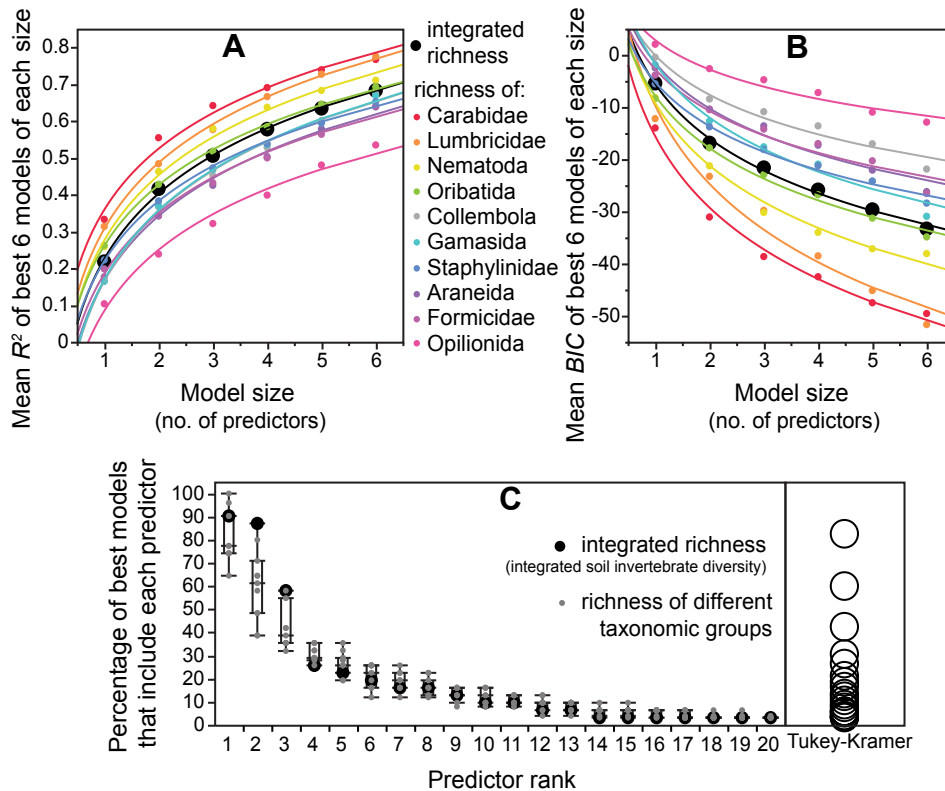


Fig. 2. Changes in the coefficient of determination (R^2 ; panel A) and Bayesian Information Criterion (BIC; panel B) with the size of the best 36 models of each soil invertebrate group. The best 36 models were determined by best subsets regression (see [Methods](#)) and include 6 models of each size up to a maximum size of 6 predictors. In panel C, for each dependent variable (i.e. each soil invertebrate group and integrated invertebrate diversity), each predictor included in at least one of the best 36 models was ranked according to its frequency of inclusion in the best 36 models, such that a predictor rank of 1 was given to the predictor most frequently included the best 36 models for each dependent variable. Separate box plots are shown for each predictor rank to display the distribution of inclusion frequency across the 11 dependent variables (species or genera richness of 10 taxonomic groups of soil invertebrates and standardized taxon richness as integrated across 9 of those groups). The ends of the whiskers show the maximum and minimum frequency of predictor inclusion across the different dependent variables, the upper and lower bounds of the box indicate the upper and lower quartiles of frequency of predictor inclusion, and the median frequency of predictor inclusion is shown by the horizontal bar within the box.

Conversely, other groups of soil invertebrates showed evidence of higher richness in monocultures with more acidic soils, including oribatid mites (74% of best models), ants (66% of best models), and harvestmen (38% of best models; [Fig. 4](#)).

3.6. Predictors related to nutrient availability

According to the frequency of predictors in the best 36 regression models, the third best predictor of integrated soil invertebrate diversity was phosphorus (P) availability in mineral soils as measured by the Bray extraction (58% of best models; [Table 3](#)). Bray-extractable P in mineral soils was positively correlated with integrated soil invertebrate diversity. Bray-extractable P in soil or other indices of P availability (e.g., total soil P, P concentrations in leaf litter or roots) were also positively correlated with taxon richness of oribatid mites (72% of best models) and arachnids (35% of best models; [Fig. 4](#)).

Integrated soil invertebrate diversity was also positively correlated with the amount of base cations in mineral soil (41% of best models included the amount of Mg or Ca in water-extracts of mineral soil; [Table 3](#)). Similar to the results for indices of soil acidity, some invertebrate groups were strongly positively associated with the amount of base cations in plant tissues or soils (e.g., earthworms [47% of best models] and carabid beetles [45% of best models]), while other groups were strongly negatively associated with the amount of base cations in plant tissues or soils (e.g., oribatid mites [52% of best models] and ants [36% of best

models]; [Fig. 4](#)). The taxon richness of arachnids and gamasid mites showed diverse relationships with the amount of base cations in different locations. For example, arachnid richness was positively correlated with water-extractable Ca in mineral soil (39% of models) and with Ca concentrations in fine roots (one model), but 18% of best models showed a negative correlation between arachnid richness and K or Ca concentrations in leaf litter or humus from the organic horizon.

Integrated soil invertebrate diversity was only modestly positively related to indices of soil nitrogen (N) availability (22% of best models; [Table 3](#)). This is perhaps because taxon richness of some invertebrate groups was strongly positively related to indices of N availability (e.g., gamasid mites [91% of best models included either leaf litter N concentration or C:N, 71% included the N:P ratio of fine roots] and nematodes [81% of best models included mineral soil total N or C:N, 20% included both total N in mineral soil and total N in humus from the organic horizon]), while richness of other groups was strongly negatively correlated with indices of N availability (e.g., earthworms [69% of best models included either total N or NH_4 in mineral soil] and staphylinid beetles [66% of best models included NH_4 in organic or mineral horizons]; [Fig. 4](#)).

3.7. Predictors related to the quantity and quality of organic substrates

Taxon richness of soil invertebrates also showed diverse relationships with the dynamics and quantity of various organic

Table 3
Best subsets regression results for integrated soil invertebrate diversity (excluding earthworm richness).^a

No. pred.	R ²	BIC	Light availab.	D. oct. biomass	Soil P (0–20)	Soil Mg (0–20; SP)	Microb. C (A _h)	Soil temp. (winter)	Soil Ca (0–20; SP)	Soil C:N (0–20)	Soil temp. (Apr–Nov)	Root prod.	Microb. C:N (A _h)	Root cell solubles	Light variab. (Spatial SD)
1	0.35	-15.0	0.59												
1	0.23	-5.8													
1	0.21	-4.9								0.48					0.46
1	0.19	-3.3		0.44											
2	0.46	-21.2	0.53	0.34											
2	0.42	-16.7	0.62												
2	0.41	-16.4	0.55												
2	0.41	-15.8	0.70			0.26									
2	0.40	-15.6		0.42							0.46				
2	0.40	-15.3	0.63												
3	0.52	-23.0	0.47	0.38									0.24		
3	0.52	-22.7	0.45	0.36	0.24										
3	0.50	-21.1	0.55	0.34											
3	0.50	-20.9	0.55	0.39								0.20			
3	0.50	-20.9	0.62	0.31		0.21									
3	0.50	-20.8		0.38							0.39				0.32
4	0.59	-27.5	0.41	0.40	0.38		0.30								
4	0.58	-25.7	0.43	0.33	0.33										
4	0.58	-25.7	0.55	0.33	0.30	0.28									
4	0.58	-25.6	0.55	0.38	0.32				0.28						
4	0.57	-25.5	0.44	0.39	0.48										
4	0.57	-24.9	0.46	0.43	0.28							0.24			
5	0.64	-30.4	0.43	0.41	0.35			-0.32	0.41						
5	0.64	-30.4	0.36	0.41	0.44			0.33		-0.23					
5	0.64	-30.0	0.57	0.40	0.35	0.29						0.26			
5	0.63	-29.5	0.50	0.37	0.42	0.24	0.27								
5	0.63	-29.0	0.44	0.43				-0.33	0.37				0.32		
5	0.63	-28.3	0.51	0.33	0.35	0.30				-0.23					
6	0.69	-35.1	0.38	0.45	0.29			-0.36	0.45				0.26		
6	0.69	-34.9	0.45	0.37	0.49	0.27	0.29			-0.25					
6	0.69	-33.9		0.29	0.51					-0.39	0.47			0.34	
6	0.68	-32.3	0.38	0.44	0.44		0.23	-0.30	0.34						
6	0.68	-31.8	0.40	0.38	0.43	0.30	0.27	-0.24							
6	0.67	-31.7	0.46	0.39	0.46		0.27			-0.26				0.23	
Mean beta coefficient:			0.50	0.38	0.38	0.27	0.28	-0.33	0.37	-0.27	0.45	0.23	0.27	0.28	0.39
% of Best models:			90	87	58	26	23	19	16	16	13	10	10	6	6

^a For brevity, only the four best models with one predictor are shown. Predictor variables that were present in only one of the best 36 possible models are also not shown; those predictors, followed by their beta coefficients were: total N in the upper 20 cm of mineral soil (0.26), microbial biomass C in the organic horizon (-0.26), fine root turnover (0.20), richness of ectomycorrhizal fungi based on root samples alone (0.26) and based on both root and sporocarp samples (0.42), richness of fungi observed on woody litter (0.40), root cellulose concentration (-0.23), and exchangeable Mg in the upper 20 cm of mineral soil (0.34). Microbial biomass C:N was present in 11 of the 36 best models (i.e. 11 of 31 possible best models since it can only be included in one of the best 6 models with only one predictor), but is not shown here because its inclusion in the models was dependent on three potential outliers; when those three potential outliers were excluded, the coefficient estimated for this parameter was only significantly different from zero in 3 of those 11 models ($P < 0.05$). **SP** = saturated paste. **A_h** = A horizon. **SD** = standard deviation. **0–20** = upper 20 cm of mineral soil.

substrates, including leaf litter, fine roots, and soil organic matter (Tables A2–A11). However, none of these predictors was frequently included in the best models of integrated soil invertebrate diversity (Table 3). Measures of fine root mass, density or dynamics were positively correlated with the taxon richness of some groups (e.g., staphylinid beetles [65% of best models included root density], oribatid mites [41% of best models included fine root production or fine root turnover], and harvestmen [35% of best models included dead root mass]), but negatively related to taxon richness of other groups, including earthworms (50% of best models included living or dead mass of fine roots, root density or root production) and Collembola (35% of best models included fine root density). Similarly, taxon richness was positively related to leaf litterfall for some invertebrate groups (e.g., 19% of best models for gamasid mites), but negatively related to leaf litterfall for other groups (e.g., 39% of best models for opilionids; Fig. 4). The amounts of lignin, cellulose, hemicellulose, and cell-solubles in leaf litter and fine roots were frequently included in the best models of soil invertebrate richness (Table 3; Tables A2–A11), except for one invertebrate group: root hemicellulose or cellulose was negatively correlated with the richness of Collembola (88% of best models for Collembola).

4. Discussion

The identity and leaf habit (evergreen vs. deciduous) of common temperate tree species had substantial impacts on both *i*) the richness of species (or genera) within individual groups of soil invertebrate animals, and *ii*) richness integrated across nine soil invertebrate groups (“integrated soil invertebrate diversity”). Importantly, no single taxonomic group of soil invertebrates was representative of integrated soil invertebrate diversity. Consequently, a broad understanding of soil invertebrate diversity will require greatly increased efforts to sample soil invertebrates in a taxonomically comprehensive manner. Similarly, none of the monospecific tree plantings was consistently associated with high or low levels of taxon richness across the nine invertebrate groups, and leaf habit had divergent effects on richness of different invertebrates. Thus, as land management and climate change induce shifts in the tree species composition of temperate forests, the diversity of some soil invertebrate groups will likely increase, but the diversity of other groups will likely decrease.

Consistent with conceptual frameworks of the constraints on soil biodiversity (Bardgett, 2002; Wardle, 2006; Bardgett and van der Putten, 2014), our results suggest that tree species identity

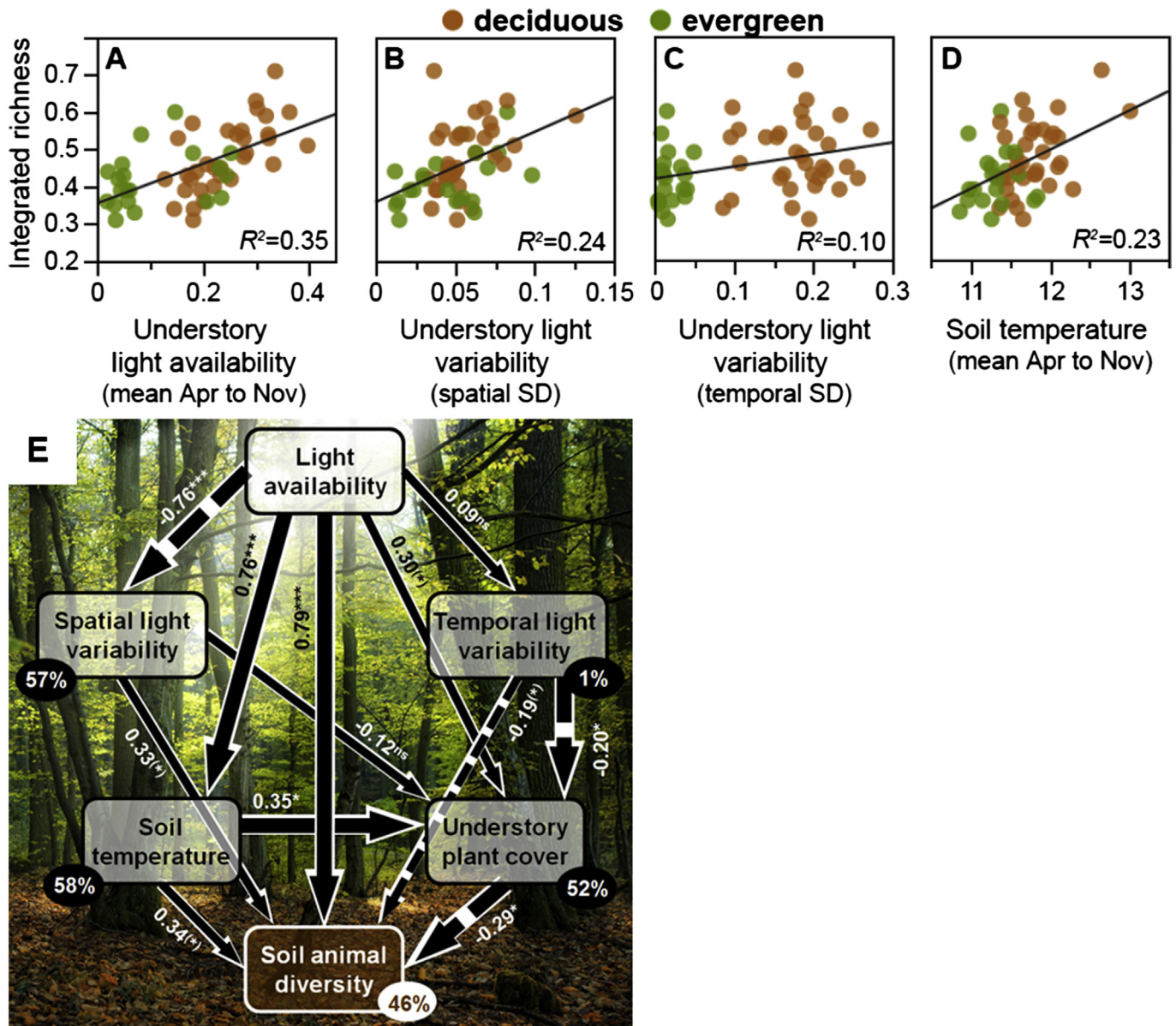


Fig. 3. Relationships between integrated soil invertebrate diversity (standardized) and various microclimatic properties of each plot, including understory light availability (A), spatial and temporal variability in understory light (B and C respectively), and soil temperature (D). Panel E shows the results of structural equation modeling that aims to describe the covariance structure among these and other interrelated variables, including characteristics of the understory plant community, in order to identify how understory light availability and variability impact soil invertebrate diversity. The data did not significantly deviate from the model (χ^2 -test, $P > 0.1$). Numbers on arrows are standardized path coefficients. Solid (positive) and dashed (negative) arrows with bold path coefficients (with asterisks) indicate significant ($P < 0.05$) relationships; asterisks in brackets indicate marginally significant ($P < 0.1$) relationships; unresolved relationships between endogenous variables are not displayed to improve readability but details are given in the main text. Percentages in black and white ellipses represent the variance explained by the model. Note that the coefficient of variation of spatial light availability (spatial light variability) and of temporal light availability (temporal light variability), respectively, yielded a better model than using standard deviation.

and leaf habit influenced soil invertebrate diversity by regulating resource availability and resource diversity in soils. We also identified other key ecological factors, at least partially regulated by trees, that further explain variability in soil invertebrate diversity across monocultures of different tree species. These key factors included earthworms as ecosystem engineers, soil acidity, and microclimate; their influence is likely partly associated with their role in regulating soil resources. Soil acidity and nutrient availability, which are also sensitive to management and environmental change, were positively correlated with the taxon richness of some soil invertebrate groups, but negatively correlated with the taxon richness of other groups. Accordingly, shifts in soil acidity and

nutrient availability at regional and global scales (Bouwman et al., 2002), irrespective of shifts in tree species composition, are also likely to induce increases in diversity within some soil invertebrate groups while causing diversity loss within other groups.

Notably, with one exception (harvestmen), at least 60% of the variability in taxon richness of each invertebrate group could be explained by the combination of six or fewer predictors directly or indirectly related to soil resources (Fig. 2). Similarly, despite the range in size (over five orders of magnitude) and life strategies (detritivores, herbivores, predators) among the nine taxonomic groups included in our index of integrated soil invertebrate diversity, nearly 70% of the variation in integrated invertebrate

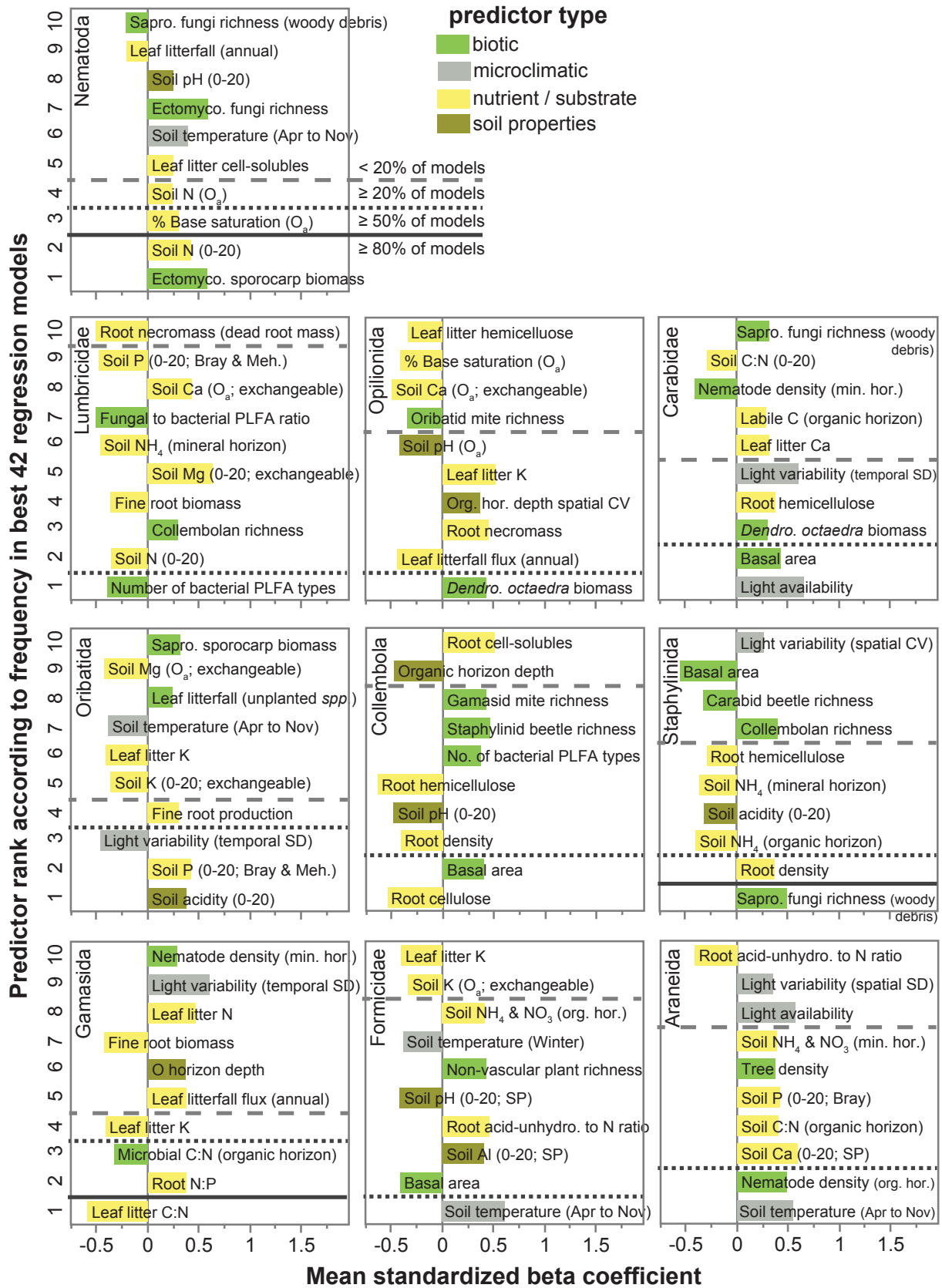


Fig. 4. Mean beta coefficient values for the ten predictors that were most frequently included in regression models of taxon richness for each group of soil invertebrates. For each group of soil invertebrates, the predictors are arranged from bottom to top in order of decreasing frequency of occurrence in the best 36 regression models. Solid and dashed lines are used to separate predictors according to their frequency of inclusion in best models (>80%, between 80 and 50%, between 50 and 20%, and less than 20%). In a few instances, we show the sum of the frequency of inclusion for two predictors and the average beta coefficients for two predictors when those two predictors were associated with highly similar measurements of the same soil layer (e.g. Bray and Mehlich extractable phosphorus in soil; nitrate and ammonium accumulation on ion-exchange resins).

diversity could be explained by six predictors. This suggests that our model results could be useful as a guide for management of soil biodiversity in temperate forests. Below, we discuss the role of different types of predictors of soil invertebrate diversity.

4.1. Microclimatic predictors

Surprisingly, the average understory light availability between April and November was the single best predictor of soil invertebrate diversity; light availability (or variability) during this time period was positively correlated with integrated soil invertebrate diversity and with the taxon richness of most individual invertebrate groups (particularly carabid beetles; Fig. 4). In this study, much of the variation across plots in light availability was due to leaf habit, with deciduous species having higher understory light availability and higher soil invertebrate diversity (Fig. 3). Oribatid mites were a notable exception; species richness of oribatid mites was lower beneath deciduous trees and was negatively correlated with the temporal variability of understory light.

The positive relationship between understory light availability and soil invertebrate diversity is likely derived from a variety of ecological factors that covary with understory light availability, including soil temperature, characteristics of understory plant communities (Barbier et al., 2008), and spatial and temporal variation in light. First, higher light availability in the understory can warm understory air, plants and soil (Ritter et al., 2005; Prévost and Raymond, 2012), potentially increasing the energy available to and utilized by soil invertebrates. Indeed, our regression models often identified soil temperature as an important correlate of soil invertebrate diversity, particularly for taxon richness of arachnids and ants (Fig. 4) and when light availability was not also included in the model (Table 3; Tables A2–A11 in the supplementary appendix). Soil temperature effects might be due to higher resource use efficiency of ectothermic soil organisms and/or due to increased rates of metabolism. For example, in a study of the same monocultures in Poland, Hobbie et al. (2006) observed a positive correlation between soil temperature and decomposition rates of leaf litter, which could lead to higher resource availability with trophic cascade effects. Second, higher light levels in the understory could also influence the amount, chemical composition, or diversity of plant-derived inputs to soil food webs. For example, understory light can impact carbon assimilation by understory plants (Pfutsch and Pearcy, 1989; Ellsworth and Reich, 1992), carbon allocation to roots and short-lived leaves of understory plants (Euliss et al., 2007), and total understory plant cover and diversity (Reich et al., 2012). In this study, understory light availability was positively correlated with understory plant cover and species richness. Plant species richness may have fueled the soil food web with diverse organic inputs and thereby increased soil biodiversity (Hooper et al., 2000; Wardle, 2006). Finally, spatial and temporal variation in understory light probably contributes to variation in microclimatic conditions (e.g. soil temperature and moisture), which might facilitate species co-existence by creating spatiotemporal microhabitats for soil organisms (Huston, 1979). In this study, average understory light availability from April to November was positively related to spatial and temporal understory light variability, which were higher under deciduous trees than under evergreen ones (especially temporal variability; Fig. 3). Indeed, within evergreen species, integrated soil invertebrate diversity was more strongly correlated with spatial light variability ($R^2 = 0.32$, $P < 0.001$, $n = 20$) than with mean light availability ($R^2 = 0.17$, $P = 0.07$, $n = 20$; Fig. 3); this might indicate that patches of high light are more important when average light availability is low, as was the case beneath evergreens. The direct path between light availability and integrated soil animal diversity in the structural equation model

indicates that the indirect effects of light availability on soil animal diversity were only partly explained by other measured variables such as soil temperature; this result highlights that the mechanisms of light impacts on soil biodiversity require further investigation (sensu Eisenhauer et al., 2015).

Light availability in the understory is a function of many aspects of forest composition and structure that are subject to forest management, including overstory species composition and stand age and density (Liefvers et al., 1999; Augusto et al., 2002; Barbier et al., 2008). Consequently, we expect that forest management practices could have large potential consequences for soil biodiversity in temperate and boreal forests. For example, in Europe, evergreen species that tend to cast deep shade, such as *P. abies*, *P. menziesii*, *P. sylvestris*, and *A. alba*, have been extensively planted in the last 150 years, including in areas previously occupied by native deciduous trees (Augusto et al., 2002). A similar expansion of evergreen plantations is occurring rapidly in the southeastern United States (Fox et al., 2007). Globally, plantations are expected to account for an increasing fraction of total forest cover and timber production (Paquette and Messier, 2010), such that potential effects of species identity and light on soil invertebrate diversity will likely be even more important in the future.

4.2. “Bottom-up” biotic predictors

We documented many positive relationships between soil invertebrate diversity and the richness and abundance of biota from lower trophic levels, including plants, bacteria, and fungi (Fig. 4). These relationships support the hypothesis that resource abundance and diversity have positive effects on soil biodiversity (Hooper et al., 2000; Wardle, 2006). Integrated soil invertebrate diversity was positively related to fine root production and carbon in microbial biomass, consistent with other observations that belowground resources can be more important for soil food webs than leaf litter (Pollierer et al., 2007). However, the effects of above- and belowground plant inputs on soil diversity are likely to be taxa specific (Pollierer et al., 2007; Eisenhauer and Reich, 2012; Eissfeller et al., 2013a). For example, gamasid mite richness was higher in plots with high leaf litter inputs and low root biomass, while the richness of harvestmen showed the opposite pattern (Fig. 4). Characteristics of the understory plant community, including percent cover and diversity of vascular plant species, were rarely included in the best models of invertebrate richness (except for ant species richness; Fig. 4). This provides evidence for the mass-ratio hypothesis, which purports that effects of plant communities on ecosystem properties can be largely attributed to abundant plant species (Grime, 1998). This conclusion is also supported by observations that much of the variability in understory plant communities in our study was associated with the traits and identity of the overlying tree species (see also Knight et al., 2008).

Factors describing fungal communities were strong predictors of the taxonomic richness of nematodes, carabid and staphylinid beetles, and to a lesser extent, oribatid mites. Sporocarp biomass and species richness of ectomycorrhizal fungi, which were tightly positively correlated ($R^2 = 0.68$, $P < 0.0001$), were the strongest positive correlates of nematode richness (Fig. 4); this is consistent with the use of plant roots and fungi as the primary food source for many nematodes (Yeates et al., 1993) and a strong role of resource abundance and diversity in regulating nematode diversity (but see Brussaard et al., 2001). The effects of fungal diversity might also “cascade” into the upper trophic levels of soil food webs; two predatory taxa of soil invertebrates, staphylinid and carabid beetles, were positively correlated with the species richness of saprotrophic fungi that inhabit woody debris (Fig. 4). Sporocarps and mycelium of wood inhabiting fungi are an important food resource for

different groups of invertebrates (Swift and Boddy, 1984). Further, many invertebrates show preferences for particular fungal species (Jonsell and Nordlander, 2002) or for substrates interwoven with fungal mycelium or partly degraded by fungal enzymes (because the presence and activity of fungi lower the C:N and C:P ratios of the substrates; Maraun et al., 2003; Boddy and Jones, 2008).

4.3. Earthworms as ecosystem engineers

According to its frequency in the best regression models, the biomass of the epigeic earthworm *D. octaedra* was the second most important predictor of integrated soil invertebrate diversity (Table 3). Consistent with our results, a review (Eisenhauer, 2010) showed that moderate densities of epigeic earthworms can positively influence the density and diversity of soil microarthropods. This was ascribed to creation of an increased number and diversity of microhabitats and the fragmentation of litter material, paving the way for decomposition processes driven by other soil organisms. McLean and Parkinson (1998) suggested the effects of epigeic earthworms on soil organisms might be density dependent, with positive effects on soil mites at moderate earthworm densities and negative effects at high earthworm densities. In our study, we also observed that the biomass of *D. octaedra* was positively correlated with the species richness of carabid beetles and harvestmen (Fig. 4), suggesting that epigeic earthworms might also positively influence the diversity of soil macroarthropods. Regardless of the mechanisms, our results further highlight the role of earthworms as potential ecosystem engineers (Lavelle et al., 1997) and the role of tree traits as regulators of earthworm communities.

For at least two reasons, it is likely that some correlates of *Lumbricidae* species richness in our study (Fig. 4) reflect the effects of the earthworm community on soil resources (as opposed to the effects of soil resources on earthworm diversity). First, previous reports from the same field experiment in Poland (Reich et al., 2005; Hobbie et al., 2006; Mueller et al., 2015) suggest that *Lumbricus terrestris* is a likely ecosystem engineer with respect to decomposition rates of leaf litter and carbon cycling in soil. Second, earthworm species richness is low in our study (Fig. 1) and is positively correlated with earthworm biomass ($R^2 = 0.51$, $P < 0.0001$), most of which is attributable to *L. terrestris* (Reich et al., 2005). Species richness of *Lumbricidae* was also negatively related to fine root biomass and necromass (dead root biomass), the amount of nitrogen in mineral soils, the fungal to bacterial ratio in soil, and the number of different types of bacterial PLFAs (Fig. 4). These relationships are consistent with previous studies that show earthworms can lead to lower root biomass due to consumption and soil disturbance (Scheu, 2003), to lower soil organic matter stocks due to consumption and low substrate use efficiency (Eisenhauer et al., 2007), and to dominance of the microbial community by bacteria (Brown, 1995; McLean et al., 2006). Indices of root abundance and of fungal abundance relative to bacteria (e.g., C:N ratios of microbial biomass) were frequently included in the best models of integrated soil invertebrate diversity and of the richness of individual soil taxa. Thus, earthworm diversity, and likely the dominant earthworm *L. terrestris*, probably affected the diversity of other soil animals by mediating the availability of root-derived resources and the composition of fungal and bacterial communities (Brown, 1995). Two other soil properties impacted by *L. terrestris*, soil C stocks and the depth of the forest floor (Reich et al., 2005; Mueller et al., 2015), were rarely included in the best models of soil invertebrate diversity, although the role of these factors could be masked by their correlation with other predictors (such as soil acidity; see below).

Across the monocultures we studied, variability in the presence and abundance of *L. terrestris* was strongly positively correlated

with soil pH and the amount of base cations in leaf litter and soils, likely due to the high calcium requirement of this earthworm species (Reich et al., 2005; Hobbie et al., 2006). Thus, the positive relationships between earthworm species richness and both soil calcium and magnesium (Fig. 4) likely reflect the role of base cation availability in regulating earthworm diversity. Further, although *L. terrestris* presence (or abundance) was very rarely included as a predictor in the best models of soil invertebrate diversity, we cannot rule out a coincident effect of *L. terrestris* when predictors related to soil pH and base cation availability were included in the best models (Fig. 4).

4.4. General soil properties and soil nutrients

The taxon richness of individual soil invertebrate groups was often strongly correlated with measures of soil acidity. However, soil acidity was not identified as a strong correlate of integrated soil invertebrate diversity; this is because plots with more acidic soils had higher taxon richness within some groups (ants, oribatid mites, Collembola, harvestmen) but lower taxon richness within other groups (nematodes, staphylinid beetles; Fig. 4). The cause of these correlations is uncertain, in part because many other factors co-vary with soil acidity across these plots (e.g., as soil acidity increases, earthworm biomass and base cation availability decrease but the amounts of organic C and nitrate in soil rise; Reich et al., 2005; Mueller et al., 2012, 2015). The species richness of oribatid mites was particularly strongly and positively correlated with soil acidity. Other studies have documented that oribatid mite densities are higher in more acidic soils (Kaneko and Kofuji, 2000; Erdmann et al., 2012), although the mechanism is uncertain. Regardless of the underlying causes, this study identifies soil acidity as a potentially strong predictor of the diversity of several soil invertebrate groups.

Integrated soil invertebrate diversity was positively related to indices of the availability of P, base cations, and N, suggesting that the net effect of soil nutrient availability on soil invertebrate diversity might be positive. However, as for soil acidity, taxon richness of some invertebrate groups was positively correlated with soil nutrient availability (e.g., nematodes and gamasid mites), richness of some groups was negatively correlated with soil nutrients (e.g., staphylinid beetles), and richness of other groups was positively correlated with some soil nutrients but negatively correlated with others (e.g., oribatid mites; Fig. 4). Thus, alterations in the nutrient availability of temperate forests, much like shifts in soil acidity, might increase the diversity of some soil invertebrate groups while decreasing the diversity of others. The negative relationships between soil nutrients and taxon richness within some soil invertebrate groups might arise if: i) the overall relationship between soil nutrients and diversity is hump-shaped for those groups of soil invertebrates (Bardgett, 2002), and ii) the plots in our study occupy only the decreasing part of the hump-shaped curve for those groups of soil invertebrates.

Importantly, soil acidity and soil nutrient availability are sensitive to environmental change and land management, including shifts in tree species composition (Augusto et al., 2002; De Schrijver et al., 2007; Mueller et al., 2012) and pollution of the atmosphere with nitrogenous and sulfurous compounds (Bouwman et al., 2002). Our results show that these regional scale phenomena have likely had, and will continue to have, substantial consequences for soil biodiversity, with those consequences being unevenly distributed across taxonomic groups of soil invertebrates.

4.5. Conclusions

Collectively, the results of this unique study were strikingly consistent with the idea that resource abundance, quality, and

diversity are the fundamental controls of soil biodiversity. Although the richness of individual groups of soil invertebrates was sometimes negatively correlated with the abundance of soil resources, when species (or genera) richness was integrated across nine taxonomic groups of soil invertebrates, the apparent effects of resource abundance were consistently positive. This highlights the possibility that total soil invertebrate diversity will rise with increasing resource availability despite potential trade-offs across individual taxa of soil invertebrates (i.e., despite the likelihood that richness within some invertebrate groups will decline with increasing soil resources even as other groups show increasing richness). Future studies should test this hypothesis using even more comprehensive surveys of soil biota and, ideally, surveys across a larger range of variability in soil resources and abiotic conditions.

The relationships reported in this study provide opportunities for predicting the effects of environmental change and land management on soil invertebrate diversity in temperate forests, even if the mechanisms underlying each relationship are not known. The relationship between understory light availability and soil invertebrate diversity is particularly promising given the pervasive effects of forest management on light conditions and the relative ease of measuring understory light availability. Future studies should identify whether similar relationships between light conditions and soil biodiversity exist at other sites and evaluate the underlying mechanisms.

It is unlikely that diversity of all or most types of soil invertebrates can be maximized under any scenario of environmental change or land management. This is supported by our observations that co-occurring changes in the identity of dominant tree species (including leaf habit), soil acidity, and soil nutrient availability had positive apparent effects on the diversity of some soil invertebrate groups and negative apparent effects of the diversity of other invertebrate groups. These apparent trade-offs are likely a function of trait dissimilarities and trophic interactions among different soil invertebrate groups that serve to constrain to composition and diversity of the entire soil community.

Author contributions

JO, PBR and SEH designed and conducted the experiment; AMJ, AR, AW, BK-R, CMH, DME, IK, JC, JM, JO, JW, KEM, LS, LKT, MK, MS, MS, MT, OAC, PBR, SEH, and TD collected and analyzed the samples; KEM and NE analyzed the data; KEM and NE wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2015.10.010>.

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