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REVIEW AND SYNTHESIS

Global patterns in belowground communities

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Abstract

Although belowground ecosystems have been studied extensively and soil biota play integral roles in biogeochemical processes, surprisingly we have a limited understanding of global patterns in belowground biomass and community structure. To address this critical gap, we conducted a meta-analysis of published data (> 1300 datapoints) to compare belowground plant, microbial and faunal biomass across seven of the major biomes on Earth. We also assembled data to assess biome-level patterns in belowground microbial community composition. Our analysis suggests that variation in microbial biomass is predictable across biomes, with microbial biomass carbon representing 0.6–1.1% of soil organic carbon (r^2 = 0.91) and 1–20% of total plant biomass carbon (r^2 = 0.42). Approximately 50% of total animal biomass can be found belowground and soil faunal biomass represents < 4% of microbial biomass across all biomes. The structure of belowground microbial communities is also predictable: bacterial community composition and fungal : bacterial gene ratios can be predicted reasonably well from soil pH and soil C : N ratios respectively. Together these results identify robust patterns in the structure of belowground microbial and faunal communities at broad scales which may be explained by universal mechanisms that regulate belowground biota across biomes.

Keywords

Acari, Collembola, nematodes, 16S rRNA, soil bacteria, soil faunal biomass, soil food webs, soil fungi, soil microbial biomass.

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INTRODUCTION

For centuries ecologists have mapped the distribution and abundance of plants and animals across terrestrial biomes. This work has provided key insights into the factors that structure plant and animal communities across the globe and such surveys have been critical to advances in a wide range of disciplines, including biogeochemistry, global change ecology and biogeography. In contrast, we lack a similar global perspective on the distribution of non-plant biomass in soil and the distribution of individual soil taxa across biomes.

Although the long history of soil ecological research has revealed variations in belowground fauna and microbes across sites, there have been few comprehensive cross-biome comparisons. Of course, there are some notable exceptions, including work by Petersen & Luxton (1982) (a product of the International Biosphere Project) as well as a number of other studies that have compared soil biota and community characteristics across a broad range of ecosystem types (e.g. Wardle 1992; Zak *et al.* 1994; Boag & Yeates 1998; Cleveland & Liptzin 2007). Likewise, global-scale variations in belowground biota have been synthesized in several textbooks (Lee 1985; Lavelle & Spain 2001; Wardle 2002; Coleman *et al.* 2004; Bardgett 2005), but such

summaries were generally generated by extrapolating data from studies which focused on a few sites or a few select taxa. It is thus reasonable to conclude that a comprehensive, cross-biome analysis of soil microbial and faunal community composition and abundance has not been conducted. As a result, a number of fundamental questions in soil ecology remain unanswered. Such questions include: (a) Which microbial taxa are most abundant in soils from different biomes? (b) How does the 'average' belowground microbial and faunal biomass vary across biomes? (c) Are there predictable changes in the structure of belowground communities across biomes? Although such broad-scale biogeographical questions have long been examined by plant and animal biologists, similar information describing global patterns of soil faunal communities is less comprehensive or, in the case of soil microbes, essentially non-existent.

Several factors have impeded our ability to generate biome-scale comparisons of belowground, non-plant biomass and community composition. For example, logistical and financial constraints often force ecologists to focus on single sites or groups of organisms. There are also a number of methodological issues associated with obtaining accurate estimates of soil faunal and microbial biomass (Martens 1995; André *et al.* 2002; Jenkinson *et al.* 2004; Coleman & Wall 2007), with little agreement on the suitability of various methods. Likewise, only in recent years have researchers developed the high-throughput molecular techniques that permit the characterization and comparison of a sufficiently large number of soil microbial communities without introducing the biases associated with cultivation-dependent approaches (Kirk *et al.* 2004; Thies 2007). Despite these limitations, the ability to compare the structure of belowground communities across broad scales would allow us to describe general patterns and test paradigms in soil ecology that are widely accepted but often supported by only limited direct evidence. For example, one reasonable hypothesis is that belowground faunal and microbial biomass, like the biomass of aboveground herbivores (McNaughton *et al.* 1989), is strongly correlated with net primary production. Likewise, one might predict that the overall composition of soil communities – like plant communities – should be more variable between distinct biomes than within a given biome.

In this study, we synthesized published data to generate estimates of total belowground biomass, and used that information to compare soil microbial and faunal biomass to estimates of plant biomass, plant productivity and soil organic carbon (SOC) concentrations across biomes. In addition, because there have been few attempts to analyse broad-scale patterns in microbial community composition we present data describing changes in soil bacterial community structure and bacterial : fungal ratios across biomes. Finally, we highlight the major uncertainties in our extrapolations and discuss the predictability of patterns in soil microbial biomass and community structure at the global scale.

METHODS

Estimates of soil microbial biomass

Microbial biomass was estimated from data collected on *c.* 400 individual soils (see references in Appendix S1). Individual soils were grouped into one of seven general biome categories: boreal forest, desert, temperate coniferous forest, temperate deciduous forest, temperate grassland, tropical moist forest or tundra. We excluded biomes from which there were insufficient data and cultivated soils (or soils that were intensively managed). We excluded cultivated soils because they do not represent a unique biome classification, they can represent diverse plant cover types (e.g. pine plantations or annual crops), and management practices can vary widely with large anticipated effects on belowground communities (e.g. Hendrix *et al.* 1986). On a per-biome basis, the resulting database included a minimum of 38 (boreal forest) and a maximum of 91 (temperate grassland) individual soil microbial biomass estimates. We only used microbial biomass estimates obtained using the chloroform fumigation–extraction (CFE) technique (Vance *et al.* 1987; Tate *et al.* 1988) as this is the most commonly used method and it should provide an index of total microbial biomass in soil (including both bacteria and fungi). The CFE technique is subject to some biases and may under- or over-estimate microbial biomass C (Mic_c) in soils with low porosity and high organic matter concentrations respectively (Badalucco *et al.* 1997; Jenkinson *et al.* 2004). However, no microbial biomass measurement approach is error-free and other techniques have not been used as frequently across a wide range of soil types. We excluded biomass estimates that were exclusively obtained from litter or organic horizons in the database. Limiting our analysis to mineral soils led to an underestimation of microbial biomass, but because most data are for mineral soil horizons alone, this was necessary to have consistent comparisons between biomes. Finally, where microbial biomass was estimated at multiple time points at the same location, we calculated an arithmetic mean of reported values and if experimental treatments were included in a study, we only used those data from the 'control' (unmanipulated) plots.

Microbial biomass C values are usually calculated using the following equation:

$$\mathrm{Mic_c} = K_\mathrm{c}/E_C \quad (1)$$

where K_c represents the difference between fumigated and unfumigated extractable C concentrations and E_c represents

the extraction efficiency (Vance *et al.* 1987). To determine K_c for each soil, we either used the reported K_c value or we calculated K_c from the reported biomass C value and the E_c coefficient that was applied. We then used a constant E_c value of 0.4 to calculate Mic_c concentrations for all soils as this E_c value is within the range of E_c values (0.35–0.45) most commonly reported in the literature (Jenkinson *et al.* 2004; Kandeler 2007). Although different soils or methodologies result in variable extraction efficiencies, E_c values are rarely determined experimentally for individual soils and using a standard E_c value allowed us to compare estimates across studies.

Microbial biomass is most commonly reported as units of microbial C per gram dry soil. To facilitate comparisons across biomes and between different taxa, we converted all microbial biomass to units of Mic_c m^{-2} using bulk density values (where reported) or estimating bulk density values for individual soils by matching the soil description (or site location if no soil description was provided) to those soils included in the global soil profile database (Batjes 1995). Because most studies estimate microbial biomass in only the top 15–25 cm of the soil profile, we used the following equation to estimate the total amount of biomass found in the top meter of the soil profile for each soil included in the database:

$$\text{Microbial biomass C (to 1 m)} = (-0.132) \times \log(x) + 0.605) \times B \quad (2)$$

where x = the depth interval sampled and B = measured microbial biomass. This equation is based on the biomass depth distributions reported in the few studies that have measured microbial biomass to a depths of at least 1 m (Dictor *et al.* 1998; Blume *et al.* 2002; Fierer *et al.* 2003; Agnelli *et al.* 2004; Castellazzi *et al.* 2004) and it assumes that *c.* 60% of the microbial biomass is in the top 5 cm, 70% in the top 10 cm and 80% in the top 20 cm, down to 1 m. This extrapolation of microbial biomass estimates through the soil profile is likely to lead to an over- and under-estimation of total microbial biomass in very shallow and deep soils respectively. However, we extrapolated to 1 m depth to facilitate comparisons across studies and to compare microbial biomass estimates to published estimates of root biomass and SOC concentrations.

Estimates of faunal biomass

We collected biomass estimates for five major groups of soil fauna (Acari, Collembola, Enchytraeids, Nematoda and earthworms) across all seven biomes. Other taxa that may also contribute significantly to soil faunal biomass (e.g. termites, ants and isopods) were excluded from the analysis due to insufficient data on their biomass levels across biomes. Together the faunal biomass database consisted of *c.* 930 individual datapoints (see references in Appendix S2) but there were more data for certain biomes and taxa than others leading to variability in the confidence of our estimates (Table 1). As with the microbial biomass estimates, all data were converted to units of biomass C m^{-2} and we excluded data obtained strictly from litter material but many of the biomass estimates may have included litter material. In most cases, faunal biomass data were reported as numbers of individuals or mg of faunal biomass m^{-2} (dry weight basis), but if biomass data were reported on a per gram soil basis, estimates were converted using a bulk density value appropriate to each soil type. To convert numbers of individuals to biomass we used estimates from Petersen & Luxton (1982) with average dry weights per individual as follows: nematodes (0.1 μg), Acari (5 μg), Collembola (5 μg), enchytraeids (50 μg) and earthworms (10 mg). We assumed that all organisms have a carbon content of 50% C (Sohlenius 1979; Ferris *et al.* 1997; Elser *et al.* 2000). Note that using average dry weights per individual per taxa may introduce error given variation in some taxa across biomes (see Petersen & Luxton 1982). We did not extrapolate faunal biomass through the entire soil profile as sampling depths were not recorded for > 30% of the samples (most biomass estimates were only reported as individuals or unit of faunal biomass m^{-2}) and because biomass depth distributions are likely to vary considerably across faunal taxa and within individual taxa across biomes. Since the majority of soil faunal biomass is likely to be restricted to the top 10–15 cm of the soil profile (Lavelle & Spain 2001), this is unlikely to lead to a significant underestimation of faunal biomass in most soils (although desert soils may be the exception, see Results and discussion). Likewise, because we did not adjust the faunal biomass estimates to account for efficiencies of faunal extraction, our estimates are likely conservative. There is a high degree of variability in the efficiency of extracting faunal biomass from soil (André *et al.* 2002; Coleman & Wall 2007) and correcting for differences in extraction efficiencies between studies would be very difficult given that efficiencies are highly dependent on the taxon in question, soil characteristics and the specific extraction technique utilized.

Other estimates of biome-level characteristics

Biome-level estimates of aboveground and belowground net primary productivity were based on estimates published in Saugier *et al.* (2001), assuming tissue is 49% C by mass (Jackson *et al.* 1997). Plant root and shoot biomass values were obtained from Jackson *et al.* (1996). The biome-level estimates of average SOC concentrations follow those

Table 1 Estimated mean microbial and faunal biomass by biome

Biome	Group of organisms	No. data points	Mean (1 SEM)	Median	Confidence in estimate
Boreal forest	Acari	35	0.20 (0.02)	0.14	Medium
	Collembola	33	0.06 (0.01)	0.05	Medium
	Enchytraeids	21	0.32 (0.06)	0.28	Medium
	Nematoda	14	0.08 (0.02)	0.06	Low
	Earthworms	5	0.28 (0.18)	0.10	Low
	Microbes	38	57 (6)	51	High
Desert	Acari	12	0.01 (0.00)	0.01	Low
	Collembola	12	0.01 (0.00)	0.01	Low
	Enchytraeids	ND	ND	ND	
	Nematoda	105	0.01 (0.00)	0.03	High
	Earthworms	ND	ND		
	Microbes	40	43 (8)	19	High
Temperate coniferous forest	Acari	12	0.35 (0.12)	0.15	Medium
	Collembola	14	0.24 (0.06)	0.17	Medium
	Enchytraeids	48	0.80 (0.10)	0.56	High
	Nematoda	100	0.10 (0.01)	0.06	High
	Earthworms	12	1.2 (0.6)	0.13	Low
	Microbes	49	175 (26)	89	High
Temperate deciduous forest	Acari	29	0.23 (0.03)	0.16	Medium
	Collembola	36	0.12 (0.03)	0.06	Medium
	Enchytraeids	26	0.64 (0.16)	0.30	Medium
	Nematoda	44	0.25 (0.11)	0.05	High
	Earthworms	28	2.0 (0.4)	1.19	Low
	Microbes	75	116 (9.4)	82	High
Temperate grassland	Acari	37	0.18 (0.03)	0.09	High
	Collembola	38	0.16 (0.05)	0.05	High
	Enchytraeids	18	0.31 (0.07)	0.26	Medium
	Nematoda	44	0.36 (0.08)	0.17	High
	Earthworms	22	3.8 (1.9)	0.79	Medium
	Microbes	91	131 (10)	114	High
Tropical Forest	Acari	16	0.16 (0.05)	0.13	Medium
	Collembola	13	0.02 (0.01)	0.01	Medium
	Enchytraeids	ND	ND	ND	
	Nematoda	5	0.01 (0.00)	0.01	Low
	Earthworms	22	4.9 (1.78)	0.48	Low
	Microbes	59	203 (20.84)	167	High
Tundra	Acari	41	0.13 (0.02)	0.07	Medium
	Collembola	34	0.10 (0.02)	0.05	Medium
	Enchytraeids	27	0.99 (0.16)	0.83	Medium
	Nematoda	17	0.18 (0.05)	0.11	Medium
	Earthworms	8	1.4 (0.80)	0.09	Low
	Microbes	40	136 (20)	74	Medium

All mean and median biomass values in units of g biomass C m^{-2} with one standard error of the mean indicated in parentheses. Confidence in the estimate is a qualitative description of our confidence in the reported mean value for each taxon and is based on the number of data points that go into each estimate, the geographic breadth of the samples used for the biome-level biomass estimates, the range in the biomass values, and the difficulties associated with obtaining accurate biomass estimates for the group in question. ND, no data or insufficient data to warrant reporting any estimates; either the group is largely absent from that biome or the group has been insufficiently studied.

reported in Jobbagy & Jackson (2000) and those soil respiration rates reported in Raich & Schlesinger (1992). We used estimates of average total faunal biomass (sum of aboveground plus belowground animal biomass) provided in Whittaker (1975). These estimates of total faunal biomass across biomes are similar to those reported elsewhere

(McNaughton *et al.* 1991) but provide estimates for a broader range of biomes.

Determination of soil bacterial community structure and fungal : bacterial ratios

To complement the estimates of microbial biomass across the biomes, we also examined biome-level variability in soil bacterial community composition and soil fungal : bacterial ratios. We used soil bacterial community composition data from Lauber *et al.* (2009), who analysed 88 soils collected from across North and South America using a barcoded pyrosequencing approach. Fungal : bacterial ratios were estimated across a subset of these 88 soils using the quantitative PCR technique described in Fierer *et al.* (2005). Briefly, copy numbers of bacterial 16S rRNA genes and fungal 18S rRNA genes were determined in separate assays for each individual soil (78 soils in total) with each assay conducted in quadruplicate. We report the average ratio of fungal to bacterial copy numbers for each soil because using a ratio reduces the biases associated with different soil DNA samples having different amplification efficiencies (Fierer *et al.* 2005). For each of these soils analysed, we collected a wide range of soil and site characteristics (see Fierer *et al.* (2007) and Fierer & Jackson (2006) for details on the soil/site characteristics that were measured and how they were measured). We used regression models implemented in SYSTAT [Systat Software Inc. (2004)] to test relationships between fungal : bacterial ratios and individual soil parameters.

RESULTS AND DISCUSSION

Global patterns in belowground microbial biomass

Across all soils included in our database, estimates of microbial biomass ranged from 2 to 806 g C m^{-2} with some of the highest concentrations from those soils in temperate coniferous and tropical forests. On a per gram soil basis, the highest microbial biomass concentrations were in tundra soils, but soil bulk density was often lower in tundra soils than in soils from other biomes. Although microbial biomass concentrations were highly variable across soils within a given biome (Table 1), there were distinct differences in average microbial biomass values across biomes. For example, we found that desert and boreal forest soils harboured the lowest average microbial biomass per area (43 and 57 g C m^{-2} respectively) and that tropical and temperate coniferous forest soils had the highest average biomass (203 and 175 g C m^{-2} respectively).

Variation in microbial biomass across biomes was most strongly related to SOC concentrations (Fig. 1a; $r^2 = 0.91$) confirming the results of a previous analysis using > 100 individual paired microbial C and SOC concentration data obtained from multiple biomes (Cleveland & Liptzin 2007). In our analysis we used biome-level means of Mic_c, not individual datapoints per site, because this allowed us to assess the potential role of other variables in explaining variation in microbial C across biomes. These other variables are not typically available from the same study (hence the use of biome-level means). Specifically, we also found significant, though weaker, relationships between microbial biomass and soil respiration rates (Fig. 1b), total plant productivity (Fig. 1c), belowground plant productivity (Fig. 1d), total plant biomass (Fig. 1e) and belowground plant (root) biomass (Fig. 1f). The patterns shown in Fig. 1 are qualitatively similar to those reported in other studies that have compared soil microbial biomass values across ecosystems using smaller datasets (e.g. Insam 1990; Wardle 1992; Zak *et al.* 1994; Wright & Coleman 2000; Santruckova *et al.* 2003). At the simplest level, these patterns suggest that globally, microbial biomass parallels the well-established patterns of plant biomass and productivity (Chapin *et al.* 2002). However, SOC concentrations could explain more of the variance in microbial biomass than plant productivity or plant biomass (Fig. 1). In particular, at our global scale of inquiry, mean microbial biomass in the tundra was higher than would be predicted based on plant productivity and soil respiration rates, but very close to expectations based on SOC concentrations (Fig. 1). There are a number of possible explanations for this observation. First, high annual variability in microbial biomass levels in tundra soils (Wardle 1998), combined with the fact that a disproportionate number of samples were obtained during the growing season (when microbial biomass is probably highest; Grogan & Jonasson 2005) may be leading to an overestimation of total microbial biomass in tundra soils. If so, we would expect actual annual average soil microbial biomass in tundra soils to be lower than those depicted in Fig. 1 and more closely correlated with annual rates of plant primary production or respiration. An alternative hypothesis is that extreme temperature and moisture conditions in tundra soils strongly limit decomposition rates. As a result, relatively undecomposed and unprotected organic matter accumulates (Weintraub & Schimel 2003; Davidson & Janssens 2006) and provides the dominant C source for tundra soil microbes. In other environments, where decomposition is less constrained by climatic conditions, SOC stocks may be more advanced in their decay and hence more chemically and/or physically protected (Davidson & Janssens 2006) with microbes deriving a larger percentage of their C from recent plant inputs. If so, this hypothesis would suggest a temporal decoupling of plant inputs and standing stocks of microbial biomass in tundra ecosystems, highlighting the importance of documenting temporal variability to better understand C dynamics in certain biomes (Bardgett *et al.*

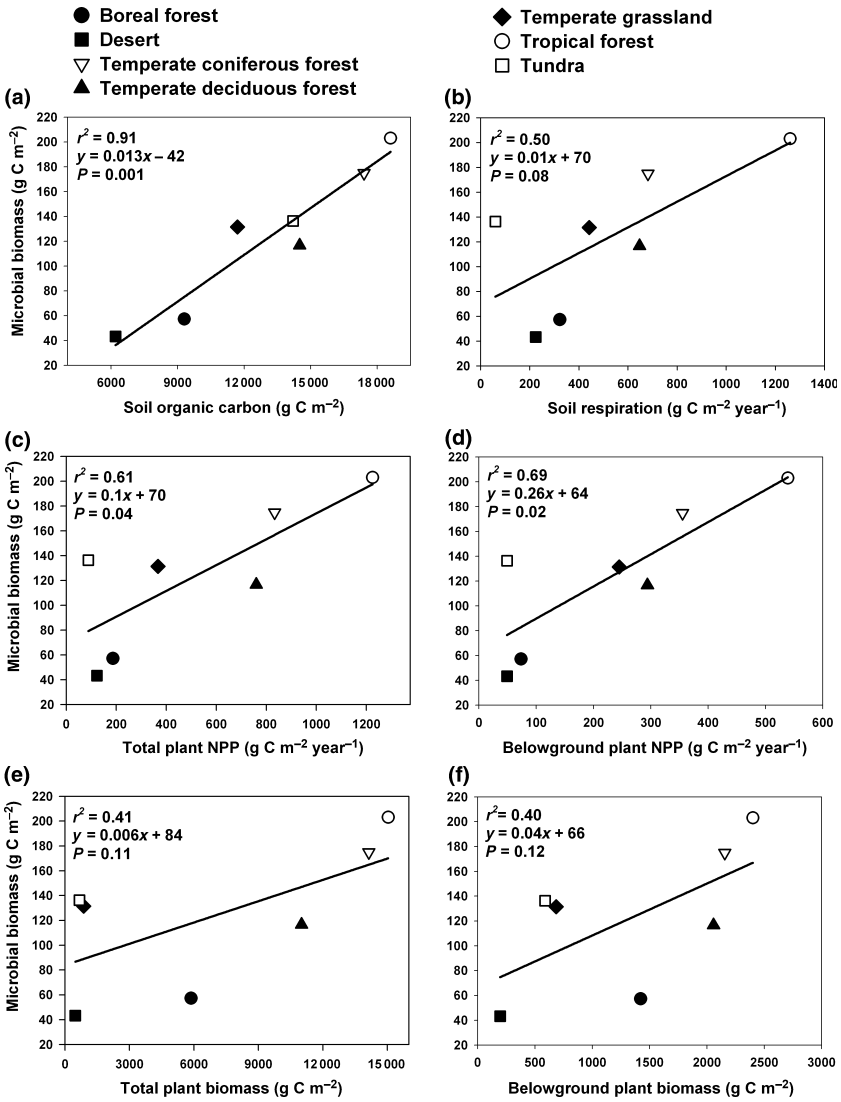

Figure 1 Relationships between microbial biomass and soil organic carbon (a), soil respiration rates (b), total net primary production (NPP) (c), belowground NPP (d), total plant biomass (both aboveground and belowground) (e), and belowground plant (root) biomass (f) across biomes. Note that we used biome-level averages to determine these relationships because rarely are the parameters shown on the *x*-axes of panels (b–f) reported together with the microbial biomass measurements.

2005). These competing mechanistic hypotheses demand the attention of soil microbial ecologists.

Microbial biomass was strongly constrained across biomes ranging from 0.6% to 1.1% of total SOC concentrations (Fig. 1a). These percentages of microbial biomass vs. SOC levels are similar to those reported elsewhere: including those reported by Wardle (1992) (1–3%), Insam (1990) (1–5%) and Zak *et al.* (1994) (0.3–3%). Our percentages are probably at the lower end of these previously reported ranges because we compared microbial biomass and SOC concentrations to 1 m, not just within surface soil horizons. Deeper horizons often present environmental limitations (e.g. low O_2 tensions) to microbial biomass accumulation and often contain relatively more organic C than Mic_c owing to the lower quality of the organic C stores at depth (Paul *et al.* 1997; Trumbore 2000; Fierer *et al.* 2003). Nonetheless, the relatively consistent ratio of Mic_c to SOC across biomes is remarkable given the likely variations in SOC quality, plant C inputs and rates of C turnover. The consistency suggests a number of potential explanations for the close correlation between microbial biomass and SOC levels across biomes (Fig. 1a). First, these results may lend support to the observation that SOC quality, defined as the availability of SOC to microbial mineralization, is often fairly constant across biomes due to similarities in SOC characteristics under different vegetation types (Grandy & Neff 2008) or similarities in the abiotic controls on SOC availability (Sollins *et al.* 1996; Six *et al.* 2002). Alternatively, different C inputs may not necessarily lead to 'high'- or 'low'-quality SOC pools because C quality may partly be a function of the resource input history experienced by the resident microbial community, i.e. the 'litter quality is in the eye of the beholder' hypothesis (Strickland *et al.* 2009a,b). Alternatively, SOC may simply be

a better predictor of microbial biomass than other site characteristics because it provides an integrated measure of the biotic and abiotic factors that regulate the size of the microbial biomass pool. Future research comparing the relationships between SOC quantity, quality, and microbial biomass across ecosystem or vegetation types will be required to elucidate the specific mechanisms contributing to the pattern evident in Fig. 1a.

Across all biomes, microbial biomass averaged 7% of total plant biomass (both aboveground and belowground), but the percentages varied widely across biomes (ranging from 1% to 20%; Fig. 2). Relative to plant biomass, microbial biomass was higher in desert, tundra and temperate grassland biomes (9–20% of plant biomass) than in forested biomes (1–1.4% of plant biomass). This discrepancy may result from our exclusion of the microbial biomass contained in litter from the biome estimates or the larger amounts of woody plant tissue and larger diameter roots in forests relative to grasslands. We would expect estimates of non-woody plant biomass to be more closely correlated with microbial biomass as structural C decomposes relatively slowly and is not likely to represent important short-term resource pools fuelling microbial biomass accumulation. Future work should evaluate whether non-woody plant biomass inputs to soils provide a better predictor of microbial biomass than total plant biomass inputs.

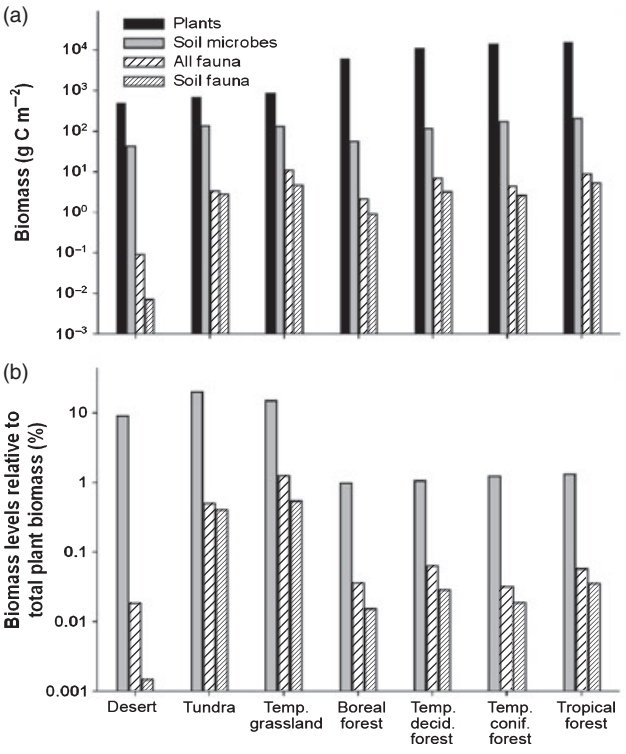

Figure 2 Total plant biomass, faunal biomass, soil faunal biomass and soil microbial biomass per biome (a) with (b) showing faunal and microbial biomass values as a percentage of total plant biomass (percentages calculated by comparing biomass in g C m^{-2}). Sources for biomass estimates are described in the Methods. Note that the *y*-axes are on a log-scale.

Global patterns in belowground faunal biomass

Across all biomes, soil faunal biomass averaged 2% of microbial biomass (Fig. 3; Table 1), a percentage that is similar to that reported for individual soils where both microbial and faunal biomass have been estimated simultaneously (Paustian *et al.* 1990; Zwart *et al.* 1994; Hunt & Wall 2002). Although we have likely underestimated soil faunal biomass due to the limited amount of data on soil macrofauna, our estimate that faunal biomass averages 2% of microbial biomass is reasonable given that it is similar to what we would expect based on detrital foodweb models (Cebrian 2004). While the ability to correct for differences in faunal extraction efficiencies or biomass depth distributions may alter our absolute estimates of soil faunal biomass, our overall conclusion that soil faunal biomass is a small percentage of microbial biomass is still likely accurate given the magnitude of the difference between faunal and microbial biomass. However, it is important to note the faunal : microbial biomass ratio was far lower in desert soils (faunal biomass C is < 0.02% of Mic_c) than in the other six biomes where faunal biomass ranged from 1.5% to 3.6% of microbial biomass. This may suggest that the desert biome represents a (relatively) more inhospitable environment for soil fauna than for microbes given that a larger portion of the belowground biomass is microbial. However, a more parsimonious explanation is that this disparity simply reflects an underestimation of faunal biomass in desert soils since we excluded larger fauna that are likely to be important

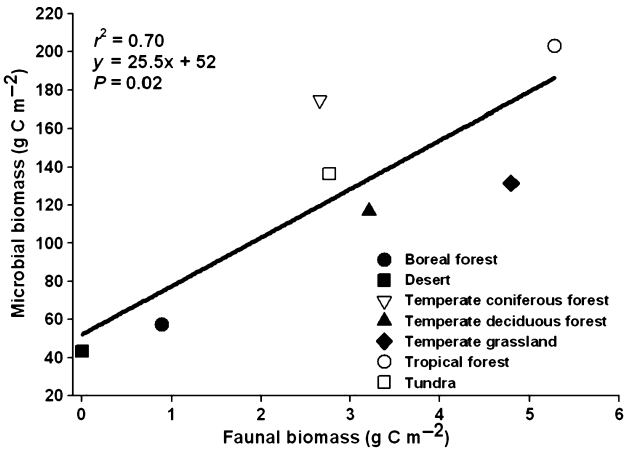

Figure 3 Relationship between soil microbial biomass and faunal biomass across biomes.

contributors to desert soil biomass (Petersen & Luxton 1982) and did not include fauna residing in deeper soil depths where desert fauna may be relatively more abundant due to moisture/temperature constraints or the limited amount of organic matter on the soil surface (Freckman & Virginia 1989; Lavelle & Spain 2001).

Soil faunal biomass across the biomes was not strongly associated with either total plant biomass ($r^2 = 0.15$) or root biomass ($r^2 = 0.20$). These weak relationships are driven by the high faunal : plant biomass ratios in tundra and temperate grasslands (Fig. 2); these two biomes support relatively high levels of soil faunal biomass (relative to plant biomass). While the exact mechanistic explanation for this is unclear, unique vegetation characteristics, climate and/or soil properties in tundra and temperate grasslands are speculated to contribute to the pattern (Lavelle & Spain 2001). A pattern that was consistent across biomes, except for the desert, was that 40–80% of the total animal biomass within biomes can be found in the soil (Fig. 2), confirming results from work conducted at individual locations (Zlotin & Khodashova 1980; Paustian *et al.* 1990). This finding emphasizes the need to consider the belowground environment when investigating factors (e.g. global change) that may influence the biomass and distribution of organisms within and across ecosystems. Studies restricted to the aboveground may omit the responses of a significant component of the biomass in terrestrial ecosystems.

We used the estimates of soil faunal biomass to assess changes in faunal community composition across biomes (Fig. 4a). Although the estimates are poorly constrained (Table 1), we observed major differences in the composition of soil fauna across biomes. For example, we find that nematodes, although numerous in most soils, represented a small portion of the total faunal biomass in all biomes except for the desert (see also Petersen & Luxton 1982). Enchytraeids and earthworms have relatively large body sizes and thus, although they are generally less numerous in terms of numbers of individuals per unit area than smaller fauna, they represent the majority of faunal biomass in all non-desert biomes we assessed. Enchytraeids were particularly abundant in tundra, temperate forests and boreal forests; earthworms dominated in the tropical forest and temperate grassland biomes. Although these biome-level patterns do confirm those reported elsewhere (Petersen & Luxton 1982; Lavelle & Spain 2001; Coleman *et al.* 2004), the low confidence in our biome-level faunal biomass estimates, even with our much larger dataset, highlights an important knowledge gap in our understanding of the global distribution of soil fauna. This is particularly true for soil

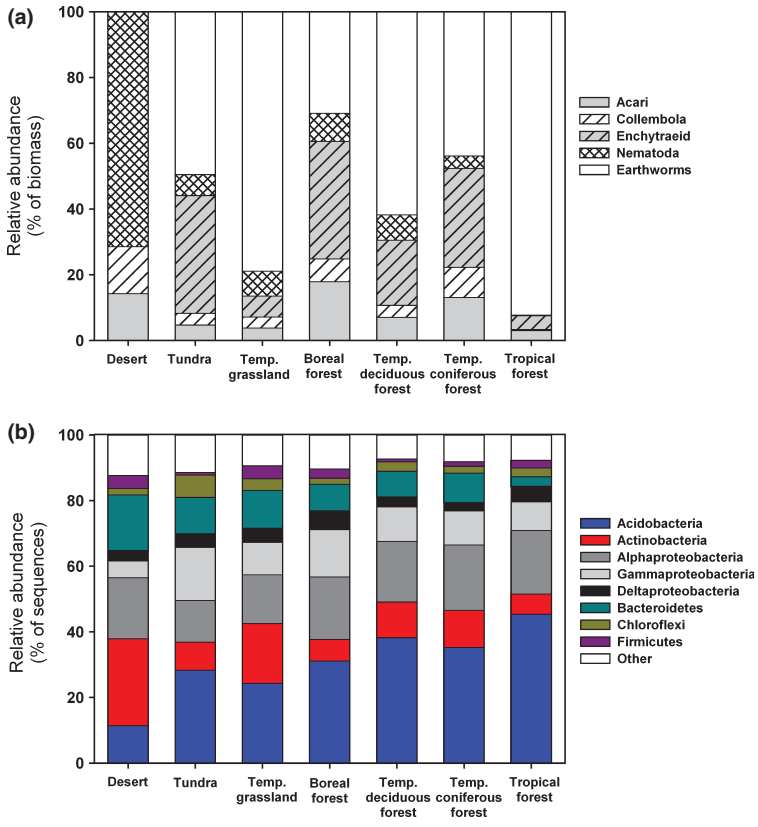

Figure 4 Estimates of the relative abundances of the major fauna within soils of different biomes (a) and relative abundances of the major soil bacterial phyla across biomes (b). Faunal community composition determined from the faunal biomass estimates provided in Table 1. Bacterial community composition determined using a pyrosequencing-based analysis of 88 individual soils.

macrofaunal biomass which can be difficult to estimate given that many macrofauna are not strictly soil dwellers, spending only a portion of their life-cycle belowground, and macrofauna often exhibit distributions that are spatially and/or temporally patchy due to localized colonies or infrequent emergence events.

Changes in microbial community composition across biomes

In contrast to the soil faunal communities, which exhibit marked biome-level differences in composition (Fig. 4a), we found few differences in the general structure of soil bacterial communities across biomes (Fig. 4b). All biomes were dominated by the same soil bacterial phyla (Acidobacteria, Actinobacteria, Proteobacteria and Bacteroidetes), and in proportions that are roughly equivalent across biomes (Fig. 4b). There are likely to be some important differences between biomes at finer scales of taxonomic resolution, but phylogenetic-based analyses show that bacterial community composition is not significantly different across biomes. Instead, soil pH explains the most variance in bacterial community composition (Lauber *et al.* 2009), suggesting that, although distinct biomes typically harbour distinct plant communities, the same is not true for bacterial communities. To phrase this another way, the variability in bacterial community composition within a given biome is higher than that between biomes and this spatial pattern is a product of variance in soil pH levels. The net effect is that biogeography is distinctly different for plant and bacterial communities at broad spatial scales (Fierer & Jackson 2006).

Extending the microbial community composition analyses, we observed that across the five biomes for which we had sufficient data, fungal : bacterial ratios were highly variable ranging from 0.007 to 0.34. Soils from coniferous forests had particularly high fungal : bacterial ratios, with soils from deserts and grasslands having the lowest measured ratios (Fig. 5). These patterns are further exemplified by the differences in mean fungal : bacterial ratios across individual biomes with forest biomes having the highest mean fungal : bacterial ratios (Fig. 5, inset). These data confirm the assumed pattern that in general grasslands are more bacterial-dominated than forested soils (Paul & Clark 1989; Lavelle & Spain 2001; Bardgett 2005; Joergensen & Wichern 2008). The low fungal : bacterial ratios in deserts suggests that fungi may not necessarily be more resistant to desiccation than bacteria, as is often assumed (Harris 1981; Zak *et al.* 1995). This observation highlights the need to ensure that taxonomic classifications for soil microbes are not simply used as surrogates for ecological classification (see Fierer *et al.* (2007).

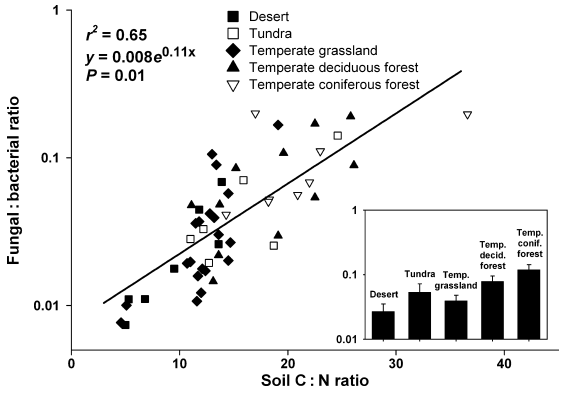

Figure 5 Fungal : bacterial ratios estimated using quantitative polymerase chain reaction vs. measured soil C : N ratios. A fungal : bacterial ratio of 1 means that fungal and bacterial rRNA gene copies are in equal abundance. The bar chart in the insert shows averages and standard errors of the fungal : bacterial ratios determined for each of the five biomes.

The range of fungal : bacterial ratios we report (Fig. 5) is approximately similar to the range of fungal : bacterial ratios reported for individual studies that have used a similar molecular technique (Boyle *et al.* 2008; Lauber *et al.* 2008; Nemergut *et al.* 2008). Although all of the ratios are < 1, this does not imply that bacterial biomass always exceeds fungal biomass. Instead, the values represent ratios of fungal to bacterial small-subunit rRNA gene copies and it is the relative differences in ratios that are important.

Across the range of soils examined only one factor, soil C : N ratio, was significantly correlated ($P < 0.05$; Fig. 5) with fungal : bacterial ratios. There are a number of possible mechanisms that may explain the positive correlation between fungal : bacterial ratios and soil C : N ratios (Fig. 5). Soil C : N ratio may directly influence the relative abundance of fungi due to stoichiometric constraints as bacteria are generally considered to require more nitrogen per unit biomass C accumulation than fungi (Bardgett & McAlister 1999; Kuijper *et al.* 2005; DeDeyn *et al.* 2008). Conversely, higher fungal : bacterial ratios may lead directly to higher soil C : N ratios given the wider C : N ratio of fungal biomass and the possibility that dead microbial biomass represents a major fraction of the organic matter in mineral soils (Guggenberger *et al.* 1999; Six *et al.* 2006; Simpson *et al.* 2007). Alternatively, there may be only a weak mechanistic link between fungal : bacterial ratios and soil C : N ratios; instead soil C : N ratios may reflect the integrated effects of a suite of other soil characteristics, including soil pH, SOC quality, quality of plant C inputs and plant community composition, that may drive differences in fungal : bacterial ratios across sites (Wardle *et al.* 2004; Six *et al.* 2006; DeDeyn *et al.* 2008; van der Heijden *et al.* 2008).

Clearly, detailed cross-site research is required to elucidate the mechanism, or set of mechanisms, responsible for the apparent relationship between soil C : N and fungal : bacterial ratios (Fig. 5).

Data limitations

In addition to documenting biome-level patterns in belowground biomass levels and community composition, this data compilation highlights key gaps in our current knowledge of belowground biota and the associated data needs. In particular, there are relatively few studies that have simultaneously quantified total faunal and microbial biomass in individual soils. Such studies would enable more robust comparisons of belowground foodweb structure, particularly if coupled with detailed information on microbial and faunal community composition, biomass depth distributions and the changes in biomass across seasons. Likewise, to make robust comparisons between plant productivity, plant biomass and belowground faunal and microbial biomass, it would be useful to have measurements on all of these parameters from the same plot (or even better, numerous plots in different biomes). With the emergence of more comprehensive, cross-site studies, such as those proposed by National Ecological Observatory Network (Keller *et al.* 2008) and other continental-scale research efforts, these data may become more readily available. In the datasets compiled here, it is also apparent that some biomes are more thoroughly sampled than others. For example, there is a pronounced bias towards temperate biomes and sites in close proximity to established research centres in the United States and Europe with poor representation from certain biomes (e.g. deserts and tropical rainforests) that make up a large portion of the terrestrial land surface. Although this geographic bias is not unique to surveys of belowground biota, it constrains our ability to describe global patterns.

CONCLUSIONS

We find distinct patterns in belowground community biomass and composition across biomes. In particular, these results demonstrate remarkable consistency in the biomass patterns of belowground communities, suggesting that there are similar mechanistic constraints on belowground biota that are shared across biomes, constraints that warrant more detailed study. Our work highlights some key knowledge gaps, particularly with regards to the estimation of faunal biomass in a consistent manner and the characterization of global-scale patterns in soil microbial and faunal community composition. However, cross-biome comparative studies are increasingly tractable, given methodological advances and the globalization of research efforts. Such studies are worthwhile in that they allow us to identify ecological patterns that are not immediately obvious from individual studies focusing on only a few soils or on select taxa.

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REFERENCES

Agnelli, A., Ascher, J., Corti, G., Ceccherini, M.T., Nannipieri, P. & Pietramellara, G. (2004). Distribution of microbial communities in a forest soil profile investigated by microbial biomass, soil respiration and DGGE of total and extracellular DNA. *Soil Biol. Biochem.*, 36, 859–868.

André, H.M., Ducarme, X. & Lebrun, P. (2002). Soil biodiversity: myth, reality or conning? *Oikos*, 96, 3–24.

Badalucco, L., DeCesare, F., Grego, S., Landi, L. & Nannipieri, P. (1997). Do physical properties of soil affect chloroform efficiency in lysing microbial biomass? *Soil Biol. Biochem.*, 29, 1135–1142.

Bardgett, R.D. (2005). *The Biology of Soil: A Community and Ecosystem Approach*. Oxford University Press, Oxford.

Bardgett, R.D. & McAlister, E. (1999). The measurement of soil fungal : bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands. *Biol. Fertil. Soils*, 29, 282–290.

Bardgett, R.D., Bowman, W.D., Kaufmann, R. & Schmidt, S.K. (2005). A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.*, 20, 634–641.

Batjes, N.H. (1995). *A Homogenized Soil Data File for Global Environmental Research: A Subset of FAO, ISRIC and NRCS Profiles* (Version 1.0). ISRIC, Wageningen.

Blume, E., Bischoff, M., Reichert, J., Moorman, T., Konopka, A. & Turco, R. (2002). Surface and subsurface microbial biomass, community structure and metabolic activity as a function of soil depth and season. *Appl. Soil Ecol.*, 592, 1–11.

Boag, B. & Yeates, G. (1998). Soil nematode biodiversity in terrestrial ecosystems. *Biodiver. Conserv.*, 7, 617–630.

Boyle, S.A., Yarwood, R.R., Bottomley, P.J. & Myrold, D.D. (2008). Bacterial and fungal contributions to soil nitrogen cycling under Douglas fir and red alder at two sites in Oregon. *Soil Biol. Biochem.*, 40, 443–451.

Castellazzi, M.S., Brookes, P.C. & Jenkinson, D.S. (2004). Distribution of microbial biomass down soil profiles under regenerating woodland. *Soil Biol. Biochem.*, 36, 1485–1489.

Cebrian, J. (2004). Role of first-order consumers in ecosystem carbon flow. *Ecol. Lett.*, 7, 232–240.

Chapin, F., Matson, P. & Mooney, H. (2002). *Principles of Terrestrial Ecosystem Ecology*. Springer, New York.

Cleveland, C.C. & Liptzin, D. (2007). C : N : P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? *Biogeochemistry*, 85, 235–252.

Coleman, D. & Wall, D. (2007). Fauna: the engine for microbial activity and transport. In: *Soil Microbiology, Ecology, and Biochemistry* (ed. Paul, E.). Academic Press, New York, pp. 163–191.

Coleman, D., Crossley, D. & Hendrix, P. (2004). *Fundamentals of Soil Ecology*, 2nd edn. Elsevier, New York.

Davidson, E.A. & Janssens, I.A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440, 165–173.

DeDeyn, G., Cornelissen, J. & Bardgett, R. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.*, 11, 516–531.

Dictor, M., Tessier, L. & Soulas, G. (1998). Reassessment of the Kec coefficient of the fumigation-extraction method in a soil profile. *Soil Biol. Biochem.*, 30, 119–127.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A. *et al.* (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408, 578–580.

Ferris, H., Venette, R.C. & Lau, S.S. (1997). Population energetics of bacterial-feeding nematodes: carbon and nitrogen budgets. *Soil Biol. Biochem.*, 29, 1183–1194.

Fierer, N. & Jackson, R. (2006). The diversity and biogeography of soil bacterial communities. *Proc. Natl Acad. Sci. USA*, 103, 626–631.

Fierer, N., Schimel, J. & Holden, P. (2003). Variations in microbial community composition through two soil depth profiles. *Soil Biol. Biochem.*, 35, 167–176.

Fierer, N., Jackson, J., Vilgalys, R. & Jackson, R. (2005). The assessment of soil microbial community structure by use of taxon-specific quantitative PCR assays. *Appl. Environ. Microbiol.*, 71, 4117–4120.

Fierer, N., Bradford, M. & Jackson, R. (2007). Toward an ecological classification of soil bacteria. *Ecology*, 88, 1354–1364.

Freckman, D.W. & Virginia, R.A. (1989). Plant-feeding nematodes in deep-rooting desert ecosystems. *Ecology*, 70, 1665–1678.

Grandy, A. & Neff, J. (2008). Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. *Sci. Total Environ.*, 404, 221–446.

Grogan, P. & Jonasson, S. (2005). Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Glob. Chang. Biol.*, 11, 465–475.

Guggenberger, G., Frey, S.D., Six, J., Paustian, K. & Elliott, E.T. (1999). Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. *Soil Sci. Soc. Am. J.*, 63, 1188–1198.

Harris, R. (1981). Effect of water potential on microbial growth and activity. In: *Water Potential Relations in Soil Microbiology* (eds Parr, J., Gardner, W. & Elliott, L.). Soil Science Society of America, Madison, pp. 23–95.

van der Heijden, M.G.A., Bardgett, R.D. & van Straalen, N.M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.*, 11, 296–310.

Hendrix, P.F., Parmalee, R.W., Crossley, D.A., Coleman, D.C., Odum, E.P. & Groffman, P.M. (1986). Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience*, 36, 374–380.

Hunt, H. & Wall, D. (2002). Modelling the effects of loss of soil biodiversity on ecosystem function. *Glob. Chang. Biol.*, 8, 33–50.

Insam, H. (1990). Are the soil microbial biomass and basal respiration governed by the climatic regime? *Soil Biol. Biochem.*, 22, 525–532.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411.

Jackson, R., Mooney, H. & Schulze, E.-D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl Acad. Sci. USA*, 94, 7362–7366.

Jenkinson, D., Brookes, P. & Powlson, D. (2004). Measuring soil microbial biomass. *Soil Biol. Biochem.*, 36, 5–7.

Jobbagy, E.G. & Jackson, R.B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.*, 10, 423–436.

Joergensen, R.G. & Wichern, F. (2008). Quantitative assessment of the fungal contribution to microbial tissue in soil. *Soil Biol. Biochem.*, 40, 2977–2991.

Kandeler, E. (2007). Physiological and biochemical methods for studying soil biota and their function. In: *Soil Microbiology, Ecology, and Biochemistry* (ed. Paul, E.). Academic Press, New York, pp. 53–83.

Keller, M., Schimel, D.S., Hargrove, W.W. & Hoffman, F.M. (2008). A continental strategy for the National Ecological Observatory Network. *Front. Ecol. Environ.*, 6, 282–284.

Kirk, J.L., Beaudette, L.A., Hart, M., Moutoglis, P., Khironomos, J.N., Lee, H. *et al.* (2004). Methods of studying soil microbial diversity. *J. Microbiol. Methods*, 58, 169–188.

Kuijper, L.D.J., Berg, M.P., Morrien, E., Kooi, B.W. & Verhoef, H.A. (2005). Global change effects on a mechanistic decomposer food web model. *Glob. Chang. Biol.*, 11, 249–265.

Lauber, C.L., Strickland, M.S., Bradford, M.A. & Fierer, N. (2008). The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biol. Biochem.*, 40, 2407–2415.

Lauber, C., Knight, R., Hamady, M. & Fierer, N. (2009). Soil pH as a predictor of soil bacterial community structure at the continental scale: a pyrosequencing-based assessment. *Appl. Environ. Microbiol.*, 75, 5111–5120.

Lavelle, P. & Spain, A. (2001). *Soil Ecology*. Kluwer, Boston.

Lee, K. (1985). *Earthworms: Their Ecology and Relationshiops with Soils and Land Use*. Academic Press, New York.

Martens, R. (1995). Current methods for measuring microbial biomass-C in soil – potentials and limitations. *Biol. Fertil. Soils*, 19, 87–99.

McNaughton, S., Oesterheld, M., Frank, D. & Williams, K. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341, 142–144.

McNaughton, S., Oesterheld, M., Frank, D. & Williams, K. (1991). Primary and secondary production in terrestrial ecosystems. In: *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories* (eds Cole, J., Lovett, G. & Findlay, S.). Springer Verlag, New York, pp. 120–139.

Nemergut, D.R., Townsend, A.R., Sattin, S.R., Freeman, K.R., Fierer, N., Neff, J.C. *et al.* (2008). The effects of chronic nitrogen fertilization on alpine tundra soil microbial communities: implications for carbon and nitrogen cycling. *Environ. Microbiol.*, 10, 3093–3105.

Paul, E. & Clark, F. (1989). *Soil Microbiology and Biochemistry*. Academic Press, San Diego.

Paul, E.A., Follett, R.F., Leavitt, S.W., Halvorson, A., Peterson, G.A. & Lyon, D.J. (1997). Radiocarbon dating for determination of soil organic matter pool sizes and dynamics. *Soil Sci. Soc. Am. J.*, 61, 1058–1067.

Paustian, K., Andren, O., Clarholm, M., Hansson, A.C., Johansson, G., Lagerlof, J. *et al.* (1990). Carbon and nitrogen budgets of four agro-ecosystems with annual and perennial crops, with and without N fertilization. *J. Appl. Ecol.*, 27, 60–84.

Petersen, H. & Luxton, M. (1982). A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 39, 287–388.

Raich, J.W. & Schlesinger, W.H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Ser. B*, 44, 81–99.

Santruckova, H., Bird, M.I., Kalaschnikov, Y.N., Grund, M., Elhottova, D., Simek, M. *et al.* (2003). Microbial characteristics of soils on a latitudinal transect in Siberia. *Glob. Chang. Biol.*, 9, 1106–1117.

Saugier, B., Roy, J. & Mooney, H. (2001). Estimations of global terrestrial productivity: Converging towards a single number? In: *Terrestrial Global Productivity* (eds Roy, J., Saugier, B. & Mooney, H.). Academic Press, San Diego, CA, pp. 543–557.

Simpson, A.J., Simpson, M.J., Smith, E. & Kelleher, B.P. (2007). Microbially derived inputs to soil organic matter: are current estimates too low? *Environ. Sci. Tech.*, 41, 8070–8076.

Six, J., Conant, R.T., Paul, E.A. & Paustian, K. (2002). Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil*, 241, 155–176.

Six, J., Frey, S.D., Thiet, R.K. & Batten, K.M. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Sci. Soc. Am. J.*, 70, 555–569.

Sohlenius, B. (1979). A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. *Holarctic Ecol.*, 2, 30–40.

Sollins, P., Homann, P. & Caldwell, B.A. (1996). Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma*, 74, 65–105.

Strickland, M., Lauber, C., Fierer, N. & Bradford, M. (2009a). Testing the functional significance of microbial community composition. *Ecology*, 90, 441–451.

Strickland, M., Osbourn, E., Lauber, C., Fierer, N. & Bradford, M. (2009b). Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. *Funct. Ecol.*, 23, 627–636.

Systat Software Inc. (2004). *Systat for Windows*. In Systat Software, Inc., Richmond, CA.

Tate, K., Ross, D. & Feltham, C. (1988). A direct extraction method to estimate soil microbial C: effects of experimental variables and some different calibration procedures. *Soil Biol. Biochem.*, 20, 329–355.

Thies, J. (2007). Molecular methods for studying soil ecology. In: *Soil Microbiology, Ecology, and Biochemistry* (ed. Paul, E.). Academic Press, New York, pp. 85–118.

Trumbore, S. (2000). Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecol. Appl.*, 10, 399–411.

Vance, E., Brookes, P. & Jenkinson, D. (1987). An extraction method for measuring soil microbial C. *Soil Biol. Biochem.*, 19, 703–707.

Wardle, D.A. (1992). A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biol. Rev.*, 67, 321–358.

Wardle, D.A. (1998). Controls of temporal variability of the soil microbial biomass: a global-scale synthesis. *Soil Biol. Biochem.*, 30, 1627–1637.

Wardle, D. (2002). *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton, NJ.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H. & Wall, D.H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304, 1629–1633.

Weintraub, M.N. & Schimel, J.P. (2003). Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems*, 6, 129–143.

Whittaker, R. (1975). *Communities and Ecosystems*, 2nd edn, MacMillan, New York.

Wright, C.J. & Coleman, D.C. (2000). Cross-site comparison of soil microbial biomass, soil nutrient status, and nematode trophic groups. *Pedobiologia*, 44, 2–23.

Zak, D.R., Tilman, D., Parmenter, R.R., Rice, C.W., Fisher, F.M., Vose, J. *et al.* (1994). Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. *Ecology*, 75, 2333–2347.

Zak, J.C., Sinsabaugh, R. & Mackay, W.P. (1995). Windows of opportunity in desert ecosystems – their implications to fungal community-development. *Can. J. Bot.*, 73, S1407–S1414.

Zlotin, R. & Khodashova, K. (1980). *The Role of Animals in Biological Cycling of Forest-Steppe Ecosystems*. Academic Press, New York.

Zwart, K.B., Burgers, S.L.G.E., Bloem, J., Bouwman, L.A., Brussaard, L., Lebbink, G. *et al.* (1994). Population dynamics in the belowground food webs in two different agricultural systems. *Agric. Ecosys. Environ.*, 51, 187–198.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 References for the soil microbial biomass estimates.

Appendix S2 References for the soil faunal biomass estimates.

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