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Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics

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Summary

1. The chemical composition of plant litter is commonly considered to indicate its quality as a resource for decomposer organisms. Litter quality, defined in this way, has been shown to be a major determinant of litter decomposition rates both within and across terrestrial ecosystems. Notably, the structure of the microbial community that is directly responsible for primary decomposition is rarely considered as an empirical predictor of litter decay rates.

2. Microbial communities are generally assumed to perceive litters of the same chemical composition to be of equivalent resource quality but evidence from field studies suggests that these same communities may adapt to the prevalent litter types at a given site. Here, we tested this assumption by assessing how microbial communities sourced from different forest- and herbaceous-dominated ecosystems perceive the quality of novel, foliar litters derived from a tree (*Rhododendron maximum*) and from a grass (*Panicum virgatum*) species. Based on chemical composition, we would expect *R. maximum* litter to be of lower quality than *P. virgatum* litter.

3. We used an experimental litter–soil system which employs a 'common garden' approach and measured rates of CO_2 production across 50 days; higher rates of production were assumed to indicate higher quality (i.e. more easily degradable) litter.

4. We found that communities sourced from habitats under differing plant cover perceived litter quality differently. Those communities sourced from herbaceous habitats perceived the grass litter to be of higher quality than the tree litter, whereas communities from forest habitats decomposed both litter types similarly. Within a litter type, differences in both community composition and nutrient availability of the source habitat were related to decomposition rates.

5. Our results suggest that litter quality cannot necessarily be predicted solely from chemical characteristics; instead the perceived quality is dependent on the quality of past resource inputs a community has experienced and the structure of those microbial communities responsible for the initial stages of litter decomposition.

Key-words: bacteria, carbon mineralization, fungi, resource history, soil properties

Introduction

The decomposition of plant litter by soil microbial and faunal communities is one of the most heavily researched areas in modern ecology and this process is one of the primary pathways in the terrestrial carbon cycle (Raich & Schlesinger 1992; Couteaux *et al.* 1995; Aerts 1997). Research on litter decomposition has shown that, at the global scale, decomposition rates of plant litter are strongly related to mean annual temperature and precipitation (Meentemeyer 1978; Vitousek *et al.* 1994; Aerts 1997). Within individual ecosystem or biome types, litter quality becomes a better determinant of decomposition rates than climate (Meentemeyer 1978; Aerts 1997). At the ecosystem scale, litter quality is most often related to the chemical characteristics of the litter, for example carbon : nitrogen ratios and/or lignin content (Aber *et al.* 1990; Aerts 1997). Support for this relationship is derived from a multitude of litter decomposition studies which often

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employ experimental set-ups in which a range of litter types are decomposed across a variety of different biomes (Vitousek *et al.* 1994; Gholz *et al.* 2000; Hobbie *et al.* 2006, 2007; Parton *et al.* 2007). Based on this evidence most models of ecosystem carbon dynamics rely heavily on the effects of climate (i.e. mean annual temperature and mean annual precipitation) as well as estimates of quality based on litter chemistry (Parton *et al.* 1983; Heal *et al.* 1997).

Models of decomposition based on climate and litter chemistry effectively ignore the potential influence of microbial community structure on rates of litter decomposition (Zak *et al.* 2006; Reed & Martiny 2007). This omission is partly due to the difficulty associated with manipulating microbial communities *in situ* and is also largely based on the assumption that given their abundance, diversity, and ubiquity, soil microbial communities are, for the most part, redundant with regard to their functional attributes (Cardinale *et al.* 2007; Jiang 2007; Verity *et al.* 2007). This assumption has been questioned (Schimel 1995; Martiny *et al.* 2006; Zak *et al.* 2006; Ramette & Tiedje 2007; Reed & Martiny 2007) but there are surprisingly few studies directly testing how distinct microbial communities may perceive the decomposability of a given litter type. Indeed, we do know that microbial communities are not homogeneous, varying across space and time in composition due to environmental factors and/or historical contingencies (Andrén & Balandreau 1999; Behan-Pelletier & Newton 1999; Wall & Virginia 1999; Fierer & Jackson 2006; Martiny *et al.* 2006; Ramette & Tiedje 2007; Reed & Martiny 2007). Furthermore recent work has demonstrated both implicitly and explicitly that structural differences in the microbial community can influence ecosystem function (Balser & Firestone 2005; Reed & Martiny 2007; Strickland *et al.* 2008). Such results demonstrate that, like comparisons between individual species of microorganisms (Newell 1984; Dowson *et al.* 1989; Osono & Takeda 2002), whole microbial communities also differ with regard to their functional capacity and these differences may influence the process of litter decomposition.

The specific mechanisms which lead to functional dissimilarity (*see* Strickland *et al.* 2008) in litter decomposition among microbial communities remains poorly understood. One possible reason that functional dissimilarity may arise is due to a microbial community's past exposure to litters of differing chemistry (Hunt *et al.* 1988; Gholz *et al.* 2000). Implicit evidence of this phenomenon has been shown for both the degradation of subsequent applications of pesticides and litter residues (Taylor *et al.* 1996; Laha & Petrova 1997; Cooksonet *al.* 1998) as well as in reciprocal litter transplant experiments (Hunt *et al.* 1988; Gholz *et al.* 2000; Castanho & de Oliveira 2008; Vivanco & Austin 2008). However, it is unknown whether or not the past exposure of a microbial community to litter inputs of differing chemistry also relates to that community's ability to decompose novel litters which themselves differ chemically. Such knowledge will improve our ability to understand, and possibly predict, the factors which influence litter decomposition rates.

To test whether or not past exposure of microbial communities to high or low quality litters influences the decomposition of novel litters (to those communities), we used a 'common garden' experimental approach. We paired one of 12 soil inocula, six sourced from herbaceous habitats and six sourced from forest habitats, with one of two litters which differed in their litter chemistry. We hypothesized that soil microbial inocula from forested habitats would perceive the lower-nutrient, higher-lignin litters, taken from a tree species, to be of higher 'quality' than would incoula sourced from habitats dominated by herbaceous cover. Similarly, we reasoned that the higher-nutrient, lower-lignin litters, taken from a grass species, would be perceived of equivalent 'quality' by all inocula. This hypothesis was based on the expectation that microbial communities which develop in forest habitats will be adapted (or pre-adapted) to decompose lower-nutrient, higher-lignin litters due to a history of exposure to them, which will have acted as a selection pressure and/or an environmental filter (*sensu* Lambers *et al.* 1998). Hunt *et al.* (1988) present field data which may be explained by this hypothesis. To test the hypothesis our microcosm, experimental design permits effects associated with the microbial community to be separated from co-varying factors in the field. Henceforth, we use the term 'perceived quality'. This is, essentially, a biotic definition of litter quality (see Fierer *et al.* 2005) because a litter's decomposition rate in our experiment is a function of how it is 'perceived' by the microbial community.

Methods

MICROCOSM DESIGN

The tree foliar litter was taken from *Rhododendron maximum* collected from the Coweeta Long Term Ecological Research (LTER) site, North Carolina, USA (35°00′ N, 83°30′ W) as recent, senesced litter fall. The herbaceous litter was taken from *Panicum virgatum* and was collected from the University of Georgia, Georgia, USA (33°53′ N, 83°21′ W) as recent, standing dead material. We chose these species because they have litters of low and high chemical quality, respectively (Table 1). That is, *R. maximum* litter had a C : N ratio which was nearly twice as great as, and a lignin concentration greater than twice that of, *P. virgatum* litter. Neither litter was present at the sites from

Table 1. Initial C%, N%, C : N ratios, Lignin% and pH of the litters

Litter type	C%	N%	C : N	Non-fibrous%	Hemi-cellulose%	Cellulose%	Lignin%	pH
R. maximum	48·9 ± 0·24	0·42 ± 0·01	116 ± 1·70	60·91 ± 1·23	8·81 ± 0·22	17·73 ± 0·22	12·54 ± 1·15	4·5 ± 0·01
P. virgatum	41·8 ± 0·07	0·62 ± 0·02	68 ± 2·32	38·14 ± 0·25	27·53 ± 0·52	29·08 ± 0·18	5·24 ± 0·38	5·2 ± 0·03

Values shown are means ± 1 SE (n = 3).

where the inocula were sourced. This design ensured that effects of differing litter chemistries were not confounded by prior exposure to the litter species used (i.e. 'home-field advantage', *sensu* Gholz *et al.* 2000). Litters were air-dried, passed twice through a Wiley mill (2 mm mesh), and then sterilized by autoclaving twice in succession and again 24 h later (121 °C, 20 min), before being dried to constant mass at 65 °C. The milling was done to increase surface area for microbial colonization, to make the material between replicates more homogenous, and to remove the influence of physical litter structure on decomposition rates. For example, the slow decomposition rate of *R. maximum* foliar litters in the field (e.g. Ball *et al.* 2008) is thought to result from both its chemical composition and physically-tough leaves.

Soils for use as inocula were collected from, or adjacent to, the Calhoun Experimental Forest (CEF), which is managed by the US Department of Agriculture and located in the Piedmont region (approximately 34·5° N, 82° W) of northwestern South Carolina, USA (Gaudinski *et al.* 2001; Callaham *et al.* 2006). Twelve soil inocula were collected from four land-uses (cultivated, pasture, pine, and hardwood) within this region, each land-use being represented three times (4 land-uses × 3 locations = 12 inocula). This provided six inocula from forest habitats (pine and hardwood) and six from habitats dominated by herbaceous vegetation (cultivated and pasture). Each inoculum was a subsample from soil samples composed of 10 individual A horizon soil cores (8 cm diameter, 0–7·5 cm depth), which were collected from a 100 m^2 plot within each of the 12 sites using a stratified random sampling approach. Soils were sieved (4 mm), homogenized, and stored at +5 °C until use.

Microcosms were constructed by adding 0·5 g dry mass equivalent of soil inoculum to 1 g of litter, which was then mixed by vortexing in a 50 mL plastic centrifuge tube. The mixture was adjusted to and maintained at 50% water-holding capacity, which is favourable for microbial activity. Tubes were incubated at 20 °C and 100% humidity during the experiment. Our design was a 2 × 12 combinatorial set-up (i.e. all litters crossed with all soil inocula) plus additional 'no-litter' soils. This resulted in two inocula treatments, herbaceous and forest. The herbaceous inocula were composed of three inocula sourced from cultivated sites and three sourced from pasture sites giving a total of 6 herbaceous replicates. The forest inocula were composed of three inocula sourced from hardwood stands and three inocula sourced from pine stands giving a total of six forest replicates. Six analytical repeats were constructed for each inoculum × litter combination giving 144 experimental units (*i.e.* 12 inocula × 2 litters × 6 analytical repeats). To avoid pseudoreplication the mean was taken across the six analytical repeats for a given inoculum × litter combination resulting in six herbaceous and six forest replicates per litter type. The soil inocula accounted for an average of *c.* 5% of the total carbon dioxide (CO_2) flux across all treatment combinations and soil C (much of which is not likely to be bioavailable) accounted for < 20% of total C in each microcosm (see Table 1, see Table S1 in Supporting Information).

DETERMINATION OF DECOMPOSITION RATES AND LITTER CHEMISTRY

Litter decomposition rates were estimated by periodic measurement of CO_2 production rates from the microcosms. This was done across 50 days using a 24 h static incubation procedure described in Fierer *et al.* (2003). Before the start of the incubation period, soil–litter mixtures were incubated for 10 days to allow microbial colonization of the litters. Following this period CO_2 production rates were measured on days 1, 5, 10, 20, 30, 40, and 50 and were corrected for soil contributions by subtracting the production rates measured from the corresponding 'no-litter' soils. Cumulative CO_2 production was calculated by integrating values under the curve for the incubation period.

Total percentage C, nitrogen (N), non-fibrous material, hemi-cellulose, cellulose, lignin, and pH, were determined for both litter types (Table 1). Total C and N were determined using an NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy). Non-fibrous material, hemi-cellulose, cellulose, and lignin concentrations were determined using an Ankom A200 Fiber Analyzer (Ankom, Macedon, NY). Litter pH was determined in water (2 : 1 ratio of water : litter) using a benchtop pH meter.

DETERMINATION OF INOCULUM SOURCE EDAPHIC CHARACTERISTICS

For each site from which an inoculum was sourced, we determined a series of edaphic factors. Carbon and nutrient pools, microbial biomass, pH, soil texture, bulk density, and cation concentrations were calculated from three analytical replicates per soil sample from each inoculum source.

Total, particulate organic material (POM) associated, and mineral associated C and N were determined using an NA1500 CHN Analyser (Carlo Erba Strumentazione, Milan, Italy). Carbon and N associated with POM and mineral material were determined using the fractionation method described in Bradford *et al.* (2008). Microbial biomass C and N, and dissolved organic C (DOC), were determined using the method described in Fierer & Schimel (2003). Ammonium (NH_4^+) and nitrate (NO_3^-) were determined colorimetrically following Fierer & Schimel (2002). Extractable phosphorus (P) was measured on an Alpkem auto-analyzer (OI Analytical, College Station, TX) using Murphy-Riley chemistry after extraction with Mehlich I double-acid (H_2SO_4 – HCl) using a 1 : 4 mass : volume ratio (Kuo, 1996). Soil pH was determined in water (1 : 1 ratio of water : soil) using a benchtop pH meter. Silt and clay contents were measured using a simplified version of the hydrometer method as described by Gee & Orr (2002). Soil bulk density was calculated after correcting for the mass and volume of roots and stones (Culley 1993). Exchangeable cations (Ca^+, Mg^+ and K^+) were measured by atomic absorption in the presence of $LaCl_3$ after extraction with 1 M NH_4OAc (pH 7) using a 1 : 10 mass : volume ratio (Sumner & Miller 1996). Edaphic data for each inoculum source are provided in Table S1.

DETERMINATION OF THE STARTING COMMUNITY COMPOSITION OF THE SOIL INOCULA

Soils for community analyses were collected and treated the same as those collected for edaphic characterization. A DNA-based rather than an RNA-based assessment of microbial communities was used because it probably better reflects the potential pool of microbes that might develop on our microcosm litter environments from the soil incolua; also DNA-based assessments are less variable and hence provide a more integrated assessment of differences in microbial community inocula. DNA was isolated from three replicate subsamples of fresh soil per plot using the MoBio Power Soil DNA Extraction kit (MoBio Laboratories, Carlsbad, CA) with the modifications described in Lauber *et al.* (2008). Each DNA sample was amplified in triplicate using both bacterial and fungal specific primer sets described in Lauber *et al.* (2008) to assess bacterial and fungal community composition in each sample. For each plot, we constructed

an individual clone library and sequenced 80–100 cloned amplicons per library following standard protocols. Additional details on the PCR conditions, clone library construction, and sequencing are provided in Lauber *et al.* (2008). To classify the fungal sequences, we used the BLAST algorithm (Altschul *et al.* 1990) to compare the fungal sequences to an in house database of 100 fungal 18S sequences derived from the AFTOL data set (Lutzoni *et al.* 2004). Bacterial sequences were aligned against the Greengenes database <http://greengenes.lbl.gov/cgi-bin/nph-index.cgi> using the NAST alignment utility (DeSantis *et al.* 2006a) and fungal sequences were aligned using MUSCLE 3·6 (Edgar 2004a). The sequences were chimera-checked using utilities available on the Greengenes website (DeSantis *et al.* 2006b). Sequences which were of poor quality or suspected to be chimeric were eliminated from the analysis (< 9% of the sequences). Sequences were aligned using MUSCLE 3·6 (Edgar 2004b) and a neighbour-joining phylogenetic tree containing either all of the bacterial or all of the fungal sequences was generated with PHYLIP 4·0. The phylogenetic distance between the bacterial and fungal communities within each soil inoculum was determined using the weighted-normalized UniFrac algorithm (Lozupone & Knight 2005). For full details and results concerning the composition of microbial communities, see Lauber *et al.* (2008). Briefly, Lauber *et al.* (2008) found that bacterial community composition was related to both soil pH and soil texture whereas fungal community composition was related to both extractable P and soil C : N ratios.

STATISTICAL ANALYSES

Statistical analyses of cumulative CO_2 production were performed in S-Plus 7·0 (Insightful Corp., Seattle, WA), using ANOVA with litter type and inoculum source as discrete variables that were permitted to interact. Using this approach, a significant inoculum or inoculum by litter type interaction would support our hypothesis that resource history influences the perception of litter quality whereas only a litter type effect would refute this hypothesis. We further explored our results using correlation and regression approaches (see below). For statistical significance we assumed an α-level of 0·05. When reported as such, data were $\log_e$-transformed to conform to assumptions of homoscedasticity (verified using model checking).

Relationships between cumulative CO_2 production, edaphic characteristics of the source environment, and the starting community composition of the inocula were assessed using Plymouth Routines in Multivariate Ecological Research v5 software (Primer v5, Lutton, UK). Mantel tests were performed to determine if there were significant correlations between community function on either *R. maximum* or *P. virgatum* litter, edaphic characteristics of the source environment, and the starting whole fungal or whole bacterial community composition of the inoculum (individual taxa were examined using regression analyses, see below). Correlations between these factors were considered significant when $P < 0{\cdot}05$.

Linear regression analyses were performed to look at the relationships between cumulative CO_2 production on either *R. maximum* or *P. virgatum* and the starting edaphic characteristics of the inocula. This was only conducted for those edaphic characteristics which Mantel tests showed were significantly correlated to cumulative CO_2 production. Regression analyses were also used to look at relationships between cumulative CO_2 production and the dominant bacterial and fungal taxa in the starting inocula. We were able to look at the relationships between cumulative CO_2 production and the dominant bacterial and fungal taxa by performing phylogenetic independent analyses which recorded the distribution of taxa for each site and normalized these values to represent the percentage of each taxon within a given inoculum. Regression analyses, like ANOVAS, were performed using S-Plus 7·0.

Results

LITTER DECOMPOSITION

During this 50-day incubation, between 2·4% and 3·1% of *R. maximum* litter C was lost as CO_2 and between 3·1% and 4·2% of *P. virgatum* litter C was lost as CO_2. When examining cumulative CO_2 production, we found a significant inoculum by litter type interaction ($P < 0{\cdot}01$; Fig. 1). This interaction suggested that the quality of past resources influences how the community inocula perceive the quality of the two litters. This difference is clearly represented in Fig. 1 – cumulative CO_2 production differs from one litter type to the other for the different inocula. Specifically, cumulative CO_2 production was nearly identical for the forest inoculum on either litter resource suggesting that there was no difference in perceived quality. In contrast, the herbaceous inocula perceived the *P. virgatum* litter to be of higher quality than the *R. maximum* litter. To further explore this interaction we examined each litter type separately. We did not detect a significant inoculum effect on cumulative CO_2 production for *P. virgatum* litter ($F_{1,10} = 2{\cdot}40$; $P = 0{\cdot}15$) but did detect a significant inoculum effect on cumulative CO_2 production for *R. maximum* litter ($F_{1,10} = 25{\cdot}80$; $P < 0{\cdot}001$). This suggested that the interaction between inoculum and litter type was driven by minimal differences in CO_2 production on *P. virgatum* litter while CO_2 production did differ between inocula on *R. maximum* litter.

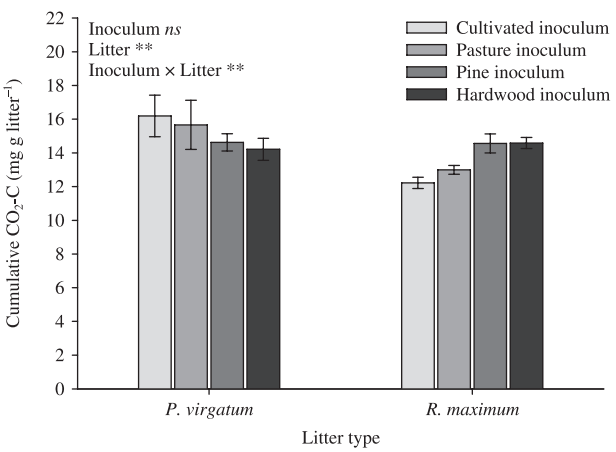

Fig. 1. Cumulative CO_2 production from microcosms consisting of microbial inocula sourced from four land-uses representing two cover-types combined with either *R. maximum* or *P. virgatum* litters. Land-uses representing herbaceous cover-types are the cultivated and pasture inocula and land-uses representing forest cover-types are the pine and hardwood inocula. Values are means ± 1SE ($n = 6$). ANOVA results are based on cover-type. A significant interaction between inoculum and litter was detected for cumulative CO_2 production ($F_{1,20} = 12{\cdot}71$; $P < 0{\cdot}01$). Main effects of litter type and inoculum were significant ($F_{1,20} = 10{\cdot}39$; $P < 0{\cdot}01$) and not significant ($F_{1,20} = 0{\cdot}583$; $P = 0{\cdot}454$), respectively.

Table 2. Mantel test results showing correlations between either inoculum source edaphic factors or initial inoculum community composition and cumulative CO_2 production on either *R. maximum* or *P. virgatum* litter. Spearman's correlation coefficients relate the calculated Euclidian distance between cumulative CO_2 production and edaphic factors; UniFrac distance is used for the community factors. Significant correlation coefficients are reported in bold ($P < 0.05$)

	R. maximum litter		*P. virgatum* litter	
	Spearman's correlation coefficient	*P*-value	Spearman's correlation coefficient	*P*-value
Edaphic factors				
DOC (mg g dry weight soil^{-1})	0·104	Ns	–0·063	Ns
NO_3^- (μg g dry weight soil^{-1})*	**0·750**	**< 0·01**	0·044	Ns
NH_4^+ (μg g dry weight soil^{-1})*	**0·480**	**< 0·01**	–0·20	Ns
Total C (mg g dry weight soil^{-1})	0·089	Ns	–0·137	Ns
POM C (mg g dry weight soil^{-1})	0·034	Ns	–0·108	Ns
Mineral C (mg g dry weight soil^{-1})	–0·072	Ns	–0·029	Ns
Total N (mg g dry weight soil^{-1})	–0·013	Ns	–0·012	Ns
POM N (mg g dry weight soil^{-1})	0·069	Ns	–0·073	Ns
Mineral N (mg g dry weight soil^{-1})	0·062	Ns	0·203	Ns
Extractable P (μg g dry weight soil^{-1})*	**0·314**	**< 0·05**	–0·032	Ns
Ca^+ (mg g dry weight soil^{-1})	0·026	Ns	0·034	Ns
Mg^+ (mg g dry weight soil^{-1})	–0·03	Ns	0·120	Ns
K^+ (mg g dry weight soil^{-1})*	**0·251**	**< 0·05**	**0·379**	**< 0·05**
C : N	0·094	Ns	0·114	Ns
C : P	0·152	Ns	–0·14	Ns
N : P	0·101	Ns	–1·38	Ns
Sand (%)	0·134	Ns	0·032	Ns
Silt (%)	–0·145	Ns	–0·196	Ns
Clay (%)*	**0·244**	**< 0·05**	0·189	Ns
Ph	–0·061	Ns	–0·014	Ns
SIR (μg g dry weight soil^{-1})	0·088	Ns	–0·077	Ns
Microbial C (μg g dry weight soil^{-1})	0·060	Ns	–0·145	Ns
Microbial N (μg g dry weight soil^{-1})	0·136	Ns	–0·167	Ns
Community factors				
Bacteria	**0·417**	**< 0·01**	**0·356**	**< 0·05**
Fungi	**0·327**	**< 0·05**	0·017	Ns

*Data were $\log_e$-transformed for both litters, except for K^+ which was only transformed for *R. maximum*.

To further explain these results and to asses other cover-type related differences in the perception of litter quality, we explored relationships between cumulative CO_2 production and the edaphic and microbial community characteristics of each inoculum (see next).

RELATIONSHIP OF LITTER DECOMPOSITION RATES TO INOCULUM CHARACTERISTICS

When examining how cumulative CO_2 production from *R. maximum* litter was related to the microbial community composition of the inocula, we found significant relationships with both fungal and bacterial community composition ($P < 0·05$ for fungi and $P < 0·01$ for bacteria; Table 2). Regression analyses showed that the relative abundances of Sordariomycete, Leotiomycete, Chaetothyriomycete and Agaricales (the dominant fungal taxa in these inocula; Lauber *et al.* (2008)) were significantly related to cumulative CO_2 production (Fig. 2a–d). The relative abundances of Leotiomycete and Sordariomycete were negatively related to cumulative CO_2 production (Fig. 2a,b). The relative abundances of Agaricales and Chaetothyriomycete were positively related (Fig. 2c,d). Of the bacterial taxa, the relative abundances of Acidobacteria in the starting inocula were positively related to cumulative CO_2 production on *R. maximum* (Fig. 2e).

We also found that site specific differences in the soil chemical and physical characteristics from which an inoculum was sourced were related to cumulative CO_2 production on *R. maximum* (Table 2). More specifically, we found that NO_3^-, NH_4^+, extractable P, K^+ and percentage clay were all significantly related to cumulative CO_2 production on *R. maximum* ($P < 0·01$ for NO_3^- and NH_4^+, $P < 0·05$ for P, K^+ and % clay; Table 2). All except for NH_4^+ were negatively related to cumulative CO_2 production on *R. maximum* (Fig. 3).

When examining how cumulative CO_2 production from *P. virgatum* litter was related to the microbial community composition of the inocula, we found that only the composition of the bacterial community was significantly related ($P < 0·05$; Table 2), whereas the fungal community composition was not (Table 2). Regression analyses of bacterial taxa showed that only the relative abundance of Actinobacteria was positively related to cumulative CO_2 production (Fig. 2f). Of the soil chemical and physical characteristics, only K^+ concentration was positively related to cumulative CO_2 production ($P < 0·05$; Table 2, Fig. 3f).

Discussion

We initially hypothesized that resource quality history would influence how microbial communities perceived litters which

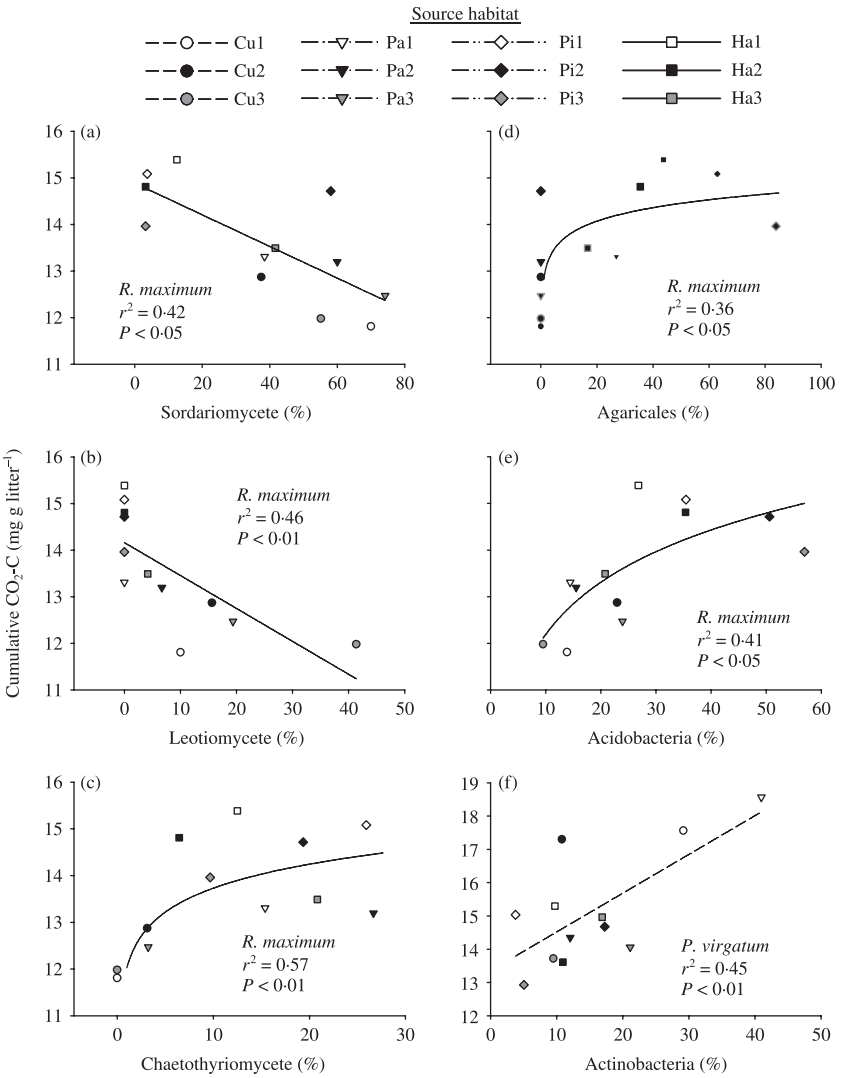

Fig. 2. Relationships between cumulative CO_2 production and the relative abundances of three fungal taxa (Sordariomycete, Leotiomycete and Agaricales) and two bacterial taxa (Acidobacteria and Actinobacteria) on *R. maximum* (a–e) and *P. virgatum* litter (f). Circles, inverted triangles, diamonds, and squares represent cultivated, pasture, pine, and hardwood land-uses, respectively. Each individual plot within a given land-use is indicated by a different shade (e.g. Cultivated plot 1 (Cu1 in the legend) is represented by a white circle).

differed in chemical quality. Our expectation was that microbial communities which develop in forest habitats will be adapted (or pre-adapted) to decompose lower chemical quality litters due to their history of exposure to lower quality litters (Hunt *et al.* 1988; Gholz *et al.* 2000). We also expected that microbial communities, regardless of their previous history, would be equally well-adapted to decompose high chemical quality litters (Hunt *et al.* 1988). As hypothesized, we found that those microbial communities sourced from forest habitats perceived the low chemical quality *R. maximum* litter to be of higher quality than did the communities sourced from herbaceous habitats (Fig. 2). This result is similar to results from reciprocal litter transplant studies which have shown that litters often decompose more rapidly when placed in their native forests (Cookson *et al.* 1998; Castanho & de Oliveira 2008; Vivanco & Austin 2008). Also confirming our original hypothesis was the observation that communities sourced from either habitat generally perceived the high chemical quality *P. virgatum* litter equally (Fig. 2), a result also observed in studies which have found no differences in decomposition rates across sites for the same litter type (Prescott *et al.* 2000; Ayres *et al.* 2006).

Initial litter decomposition rates with inocula sourced from herbaceous sites confirmed the expectation (Aber *et al.* 1990; Aerts 1997) that litter chemistry is a good predictor of decomposition rates. That is, the *R. maximum* litter with its greater C : N ratio and higher lignin content decomposed more slowly than the *P. virgatum* litter with its lower C : N ratio and lower lignin content (Fig. 1). In contrast to the inocula sourced from the herbaceous sites, the decomposition rates observed with the forest inocula were similar for the two litter types (Fig. 1). This result agrees with those studies which have found that litter chemistry is not a strong predictor of litter decomposition rates (Hunt *et al.* 1988; Gholz *et al.* 2000) and provides empirical support for the suggestion from these previous studies that the decomposer community characteristics affect litter decomposition rates. Overall, our results imply that an understanding of the microbial community and/or its past resource environment may increase our ability to predict decomposition dynamics. Indeed, the community or the resource history of that community may account for some of the unexplained variation in decomposition models where climate and litter quality are used as explanatory variables (e.g. Gholz *et al.* 2000; Parton *et al.* 2007). Our microcosm

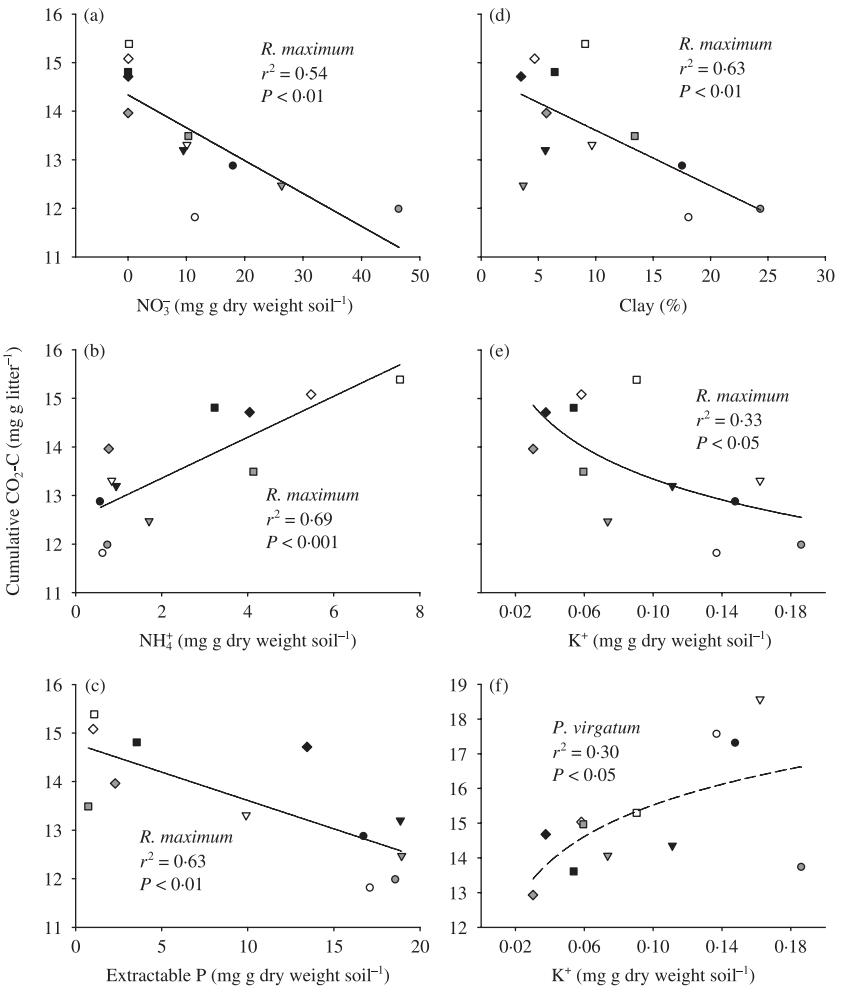

Fig. 3. Relationships between cumulative CO_2 production and the edaphic characteristics of the site from which the inocula were sourced on *R. maximum* (a–e) and *P. virgatum* litter (f). Symbols are as in Fig. 2.

experiment demonstrates the potential for both decomposer communities and the resource history of the decomposer community to influence decomposition rates, but it remains to be determined if our results are relevant to decomposition dynamics observed in the field.

To further explore how differences in microbial community structure and resource quality history impact the perception of litter quality we assessed the relationship between cumulative CO_2 production of both litter types and the biological, chemical, and physical characteristics of the sites from which each inoculum was sourced. When examining the biological factors of the inocula sources which were related to cumulative CO_2 production from either *R. maximum* or *P. virgatum* litters, we found that both fungal and bacterial community composition was related to the cumulative CO_2 production from *R. maximum* litter but only the bacterial community composition was significantly related to the cumulative CO_2 production from *P. virgatum* litter (Table 2). The fact that the fungal community was related to cumulative CO_2 production on *R. maximum* but not on *P. virgatum* litter may be due to the ability of fungi to degrade litters of lower-nutrient and higher-lignin content, or at least out-compete bacteria in such environments (Six *et al.* 2006). When more closely examining the fungal community, we found that four fungal taxa (Sordariomycete, Leotiomycete, Chaetothyriomycete and Agaricales) of the inocula sources were related to the cumulative CO_2 production on *R. maximum* litter. We found that those inocula sources which had comparably higher relative abundances of either Sordariomycetes or Leotiomycetes had lower cumulative CO_2 production on *R. maximum* litter than sites with lower abundances of these groups (Fig. 2a,b). Conversely, those inocula sourced from sites having a higher relative abundance of Chaetothyriomycete or Agaricales tended to have higher cumulative CO_2 production on *R. maximum* litter than did sites with lower abundances of either of these fungal taxa (Fig. 2c,d). This finding is similar to observations which have demonstrated differences in the litter degrading abilities of fungal phyla (Osono & Takeda 2002). Our observations suggest that such differences may also occur within phyla given that within the phylum Ascomycota the abundance of one taxon (Chaetothyriomycete) was positively related, whereas two other taxa (Sordariomycetes and Leotiomycetes) were negatively related, to cumulative CO_2 production from *R. maximum* litter (Fig. 2a–d).

When considering the bacterial community, we found that those inocula sourced from sites with higher relative abundances of Acidobacteria and Actinobacteria were positively related to cumulative CO_2 production on *R. maximum* litter and *P. virgatum* litter, respectively (Figs 2e and 3f). Acidobacteria have recently been associated with resource environments of

lower quality (Fierer *et al.* 2007) and this may explain why a positive relationship was observed on *R. maximum* litter which has both a high C : N ratio and lignin content (Fig. 2e). When considering the Actinobacteria, relatively little is known concerning their ecological attributes. However, due to their filamentous growth form and a presumed ability to effectively scavenge nutrients (Goodfellow & Williams 1983; Steger *et al.* 2007), those inocula which started with a higher relative abundance of Actinobacteria may be better at decomposing *P. virgatum* litter across the course of our experiment.

Many more chemical and physical factors of the inocula sources were related to cumulative CO_2 production on *R. maximum* than on *P. virgatum* (Table 2). Of those factors that significantly correlated with CO_2 production on *R. maximum* litter we found that all but one was negatively related (Fig. 3a–e). Specifically, we observed that NO_3^-, extractable P, K^+, and percentage clay were negatively related to cumulative CO_2 production on *R. maximum* whereas NH_4^+ was positively related. Only K^+ was related to cumulative CO_2 production on *P. virgatum* and this relationship was positive (Table 2, Fig. 3f). Soil physical and chemical factors are often products of management. In the region where our inocula were sourced NO_3^-, extractable P, and K^+ are generally higher in cultivated and pasture sites (than forests) due to annual fertilizer inputs (Richter *et al.* 2000). Percentage clay is generally higher in cultivated sites due to long-term intensive agriculture and weathering (Richter & Markewitz 2001; Callaham *et al.* 2006) and NH_4^+ is generally higher in forest sites due to lower levels of nitrification (Adams 1986). These relationships between chemical and physical variables and the source environments of the soil microbial inocula make it difficult to determine whether the chemistry of the litter inputs in the source environments, the nutrient status of the environments, or both were important factors in structuring the function of the microbial inocula in our litter microcosms. Notably, differences between the inocula in their chemical and physical characteristics, and microbial community composition, did not follow land use differences exactly (Table S1 and Lauber *et al.* 2008). This may suggest that litter chemistry (i.e. herbaceous *vs.* woody plant litters) was the over-riding cause of differences in the functioning of our inocula on the *R. maximum* and *P. virgatum* litters.

Our results provide a foundation upon which future studies can investigate how historical factors that may shape microbial communities may influence their function. In future work, investigation of how microbial community composition develops on different litter types and across time may facilitate a more detailed understanding of the relationships between the taxonomic composition of microbial communities and their function (Osono 2005; Trinder *et al.* 2008; Strickland *et al.* 2008). Such studies might address whether compositionally distinct communities, when faced with similar environments, develop in the same manner. They should consider which characteristics (e.g. lignin content) of litter chemistry likely influence this development both at earlier and later stages of decomposition. They should also ask how long differences in the functioning of microbial communities might persist once different communities are exposed to the same environment. Given the rapid generation times of microbes it seems plausible that microbial community functioning might rapidly converge in the same environment (Strickland *et al.* 2008). Such information will add to our understanding of the process of decomposition and may also enable prediction of how a given microbial community will respond to environmental change.

Our study involved a short-term, laboratory, common garden approach to determine the significance of microbial community structure and its resource history for the initial decomposition rate of leaf litters of differing chemical composition. There are a number of criticisms that can be levelled at our approach. These include the fact that we do not know whether microfauna, which affect the activities of microbial decomposers, were present in our inocula or not. Certainly, the functional symbiosis of plants and mycorrhizal fungi, which may play a crucial role in decomposition (Talbot *et al.* 2008), was absent. In addition autoclaving, as any sterilization technique, impacts soil and potentially litter properties (Berns *et al.* 2008). However, in our study such non-target effects would have been consistent within a given litter type or inoculum and hence would not have been able to explain our most significant finding. That is litter chemistry impacting decomposition rates of litters inoculated with soils from herbaceous but not forested environments.

What our approach did provide was a tightly-controlled experiment which demonstrated that the past resource environment of a microbial community impacted its ability to decompose litters differing in their chemistry. We cannot conclude to what extent this effect influences decomposition rates in the field, but it does offer one explanation for why different litter chemistries do not always lead to expected differences in decomposition rates *in situ* (Hunt *et al.* 1988; Gholz *et al.* 2000; Castanho & de Oliveira 2008; Vivanco & Austin 2008). Our work suggests that the differential perception of litter chemistry by different microbial inocula may be explained by the starting, community composition of microbial inocula and/or the resource status of the environment from which they were derived. To fully understand decomposition dynamics in the environment across space and time may require recognition and further exploration of the role of microbial community composition and that community's resource history as a driving variable.

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Supporting information

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

Table S1. Edaphic characteristics measured at each plot. Cultivated and pasture sites were classified as herbaceous-cover and pine and hardwood plots were classified as forest-cover. Means of three analytical repeats are shown

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