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Legacies of plant litter on carbon and nitrogen dynamics and the role of the soil community

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ABSTRACT

There is increasing awareness of the importance of ecological legacies in contemporary ecosystem processes. Decomposition is regulated by a set of interacting hierarchically organized factors. As spatial and temporal scales decrease, decomposition is largely dependent on the quality of resources and the decomposer community, but whether and how these factors manifest via historical legacy effects is not well understood. We tested whether the history of plant litter inputs had short-term legacy effects on contemporary litter and soil organic matter carbon (C) and nitrogen (N) mineralization. Using a field/laboratory microcosm approach, we exposed soils to two litters of contrasting chemistry and, after adding fresh substrates, we monitored C and N dynamics. In a parallel experiment, we manipulated the soil community to reduce litter-history impacts on its composition and size to investigate whether the soil community could be an important contributor to legacy effects We found strong short-term litter legacy effects on contemporary litter and soil N mineralization, the duration of which was dependent on the contemporary substrate for decomposition. These strong effects were not consistent with the home field advantage phenomenon, as exposure to a specific litter did not favor the decomposition of the same litter when it was applied as a contemporary substrate. Reduction of the litter-history effects on soil biota decreased the impact of litter history on N immobilization, suggesting that plant litter impacts on the soil community may be an important component of plant litter legacies on N decomposition. In contrast to N, litter legacies appeared to be much less important for C decomposition, suggesting that legacy effects might uncouple contemporary C and N dynamics.

Introduction

Plant litter decomposition is regulated by a suite of interacting hierarchically organized factors, including climate, soil mineralogy, nutrient status, resource quality, and the activity of soil organisms (Lavelle et al. 1993; Adair et al. 2008; Wall et al. 2008). As temporal and spatial scales decrease, the importance of resource quality and the decomposer community as regulators of decomposition increases. Many studies demonstrate a strong relationship between the chemical composition of substrates and their decomposition rates (e.g. Meentemeyer 1978; Aerts 1997). The impact of the soil community on contemporary decomposition and mineralization rates is also amply supported (Setälä et al. 1991; Bradford et al. 2002; Wardle 2002; Heemsbergen et al. 2004; Carrillo et al. 2011). However, whether and how these factors manifest via historical legacies is not well understood. The chemical composition of organic matter inputs to soil can affect soil chemical variables (Bulluck et al. 2002; Tirol-Padre et al. 2007). It has also been shown that the chemical composition of plant litter influences the structure of the soil microbial (Schutter and Dick 2001) and faunal (Parmelee et al. 1989; Hansen and Coleman 1998) communities. These changes in the chemical and biotic environment in soil may have direct impacts on future soil function. However, the link between the change brought about in the soil environment by the chemical quality of plant material and its legacy on soil processes has not been addressed by many studies.

Whether legacies on function arise mainly via changes in the soil biota or the chemical environment in soil is a matter of debate. Wardle (2002) proposed that plant species indirectly affect ecosystem processes by their influence on soil community structure. This suggests that historical legacies of plant litter occur mainly via the soil community. Strickland et al. (2009a,b) found evidence that plant species can modify the soil community to influence decomposition. Further, several studies provide support for the idea that

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plant species can impact decomposition by altering communities to favor the decomposition of their own litter (Hunt et al. 1988; Cookson et al. 1998; Gholz et al. 2000; Vivanco and Austin 2008; Castanho and de Oliveira 2008; Ayres et al. 2009b; Keiser et al. 2011). In contrast, Ayres et al. (2006) and Orwin et al. (2006) found little support for historical legacies mediated via changes in the soil community. Instead, Orwin et al. (2006) proposed that apparent legacy effects of substrate on decomposition processes were mediated mostly via changes in soil chemistry, not the biota. The available studies addressing legacies of litter on function tend to focus on carbon (C) dynamics only, despite the expectation that C and nitrogen (N) dynamics are intimately coupled in decomposition processes (Ball et al. 2008; Finzi et al. 2011). Also, few studies directly address the impact that plant litter inputs have on decomposition via legacies on the soil biota because they fail to manipulate the biota in conjunction with litter type. Moreover, few studies directly address the impact that historical effects of plant litter inputs have on decomposition in terms of the whole soil community, as they have mainly focused on the microbial components of the community (Ayres et al. 2006; Strickland et al. 2009a,b).

Using a combined field/laboratory microcosm approach, we manipulated litter history and the soil community to test for legacy effects on C and N mineralization and to evaluate the contribution of the soil biota to the legacy effect. We exposed a mineral soil to continuous amendments of two plant litters of contrasting chemical composition (pine needles and legume leaves, termed 'litter history' treatments) for 18 months. To assess effects of litter history on contemporary litter and soil processes (legacy effects) we monitored the initial stages of N and C mineralization of two freshly amended litters and resident soil organic matter (SOM). We hypothesized that the changes brought about in the soil environment by the chemical composition of litter would influence the mineralization of newly added litters and organic materials already present in the mineral soil. Observed differences in C and N process rates when the same fresh litter was applied to soil with different litter histories would be evidence that litter chemical composition can control decomposition via its historical effects on the soil chemical and/or biotic environment. To assess whether legacy effects manifest themselves through the soil community we conducted a second experiment under identical conditions and treatments, except that the soil sourced from different litter histories was deep-frozen prior to addition of fresh litter. This enabled us to reduce litter history effects on the soil community, mainly by reducing the abundance and richness of the faunal community and thereby homogenizing communities.

Materials and methods

Litter history treatments

Litter history was manipulated for the same soil across the course of 18 months, initially in the field for 8 months followed by 10 months in the lab. The field site was located in an old field (previously abandoned conventional farm) in the Piedmont region of Georgia, USA (33°57′N, 83°19′W) surrounded by currently cultivated plots, secondary growth pine stands and mixed hardwood forest. Soil is classified as a Pacolet sandy clay loam (kaolinitic, thermic typic hapludult), with 0.7% C and 0.1% N by content. In early summer, a 100 m^2 plot was cleared by hand removing standing vegetation. The plot was kept vegetation free throughout the duration of the study by pulling out any sprouting vegetation every 1–2 weeks. Surface soils from the top 5 cm of 10 randomly selected 25 cm × 50 cm areas within this plot were sieved (4 mm), homogenized, replaced, and then exposed to surface-applied litter of one of two litter species (5 plots for each). Litter was applied (300 g m^{-2}, approximately 3 cm in depth) to each area and its surroundings (at least 20 cm in all directions). Additional details of the field experiment can be found in Carrillo et al. (2011). Litter consisted of air-dried leaflets of *Amorpha fruticosa* L., a leguminous shrub (*Amorpha* from here on), and air-dried needles of loblolly pine (*Pinus taeda* L.). We chose these litters because pine is a more chemically recalcitrant litter (0.68% N, 0.086% P, 30% lignin, C:N = 76) whereas *Amorpha* is a more chemically labile litter (3.1% N, 0.32% P, 11% lignin, C:N = 12.6). *P. taeda* is native to the Southeastern United States where it occupies large tracts of land; and its needles are used as mulch in agroecosystems. *Amorpha* is also native to North America and has potential as a hedgerow species in agroforestry applications, where its leaves are used as green manure and mulch (Jordan 2004). After 8 months of exposure to surface-litter, distinct soil microbial and faunal communities had been generated in the mineral soil underlying the two litter types (Carrillo et al. 2011). At this point, soils from the top 5 cm were removed and brought back to the laboratory, where they were placed in 20-L plastic pots and surface-amended with fresh, air-dried litter (500 g m^{-2}) from the same species to which they had been exposed in the field. Laboratory conditions maximized exposure of soil to litter treatments by preventing litter loss due to wind or run-off and by allowing us to maintain optimal soil moisture and temperature. Soils were maintained in these pots for 8 months at ca. 70% field capacity and at 20 °C to promote decomposition and biological activity in the litter/soil interface.

Microcosm set-up

To test for legacy effects, we set up controlled microcosms using the same soils that had been exposed to the two litter types (first in the field, later in the lab, see above). Soil was removed from the top 5 cm under the litter layer and homogenized. Microcosms were constructed by adding ca. 80 g dry wt soil to 0.4-L jars covered with 40-μm stainless steel mesh to prevent colonization by foreign soil fauna. In total, 120 microcosms were constructed (60 with soil exposed to pine litter and 60 with soil exposed to *Amorpha* litter). For the experiment involving reduced/homogenized biota, 30 of the microcosms from each litter type were frozen (−80 °C for 5 days, thawed, and frozen again for 2 days). Freezing acts mainly on the soil fauna by decreasing the abundance and species richness of faunal groups (Bruckner et al. 1995; Zechmeister-Boltenstern et al. 1998; Kampichler et al. 1999; Haase et al. 2008; Schutz et al. 2008), but it is expected to have little impact on microbial community and function (Wallenius et al. 2010). So that the flush of C and nutrients expected to follow freezing would not interfere with the interpretation of our results, we continued exposing the soil in each microcosm to its respective litter treatment (3 g of air-dried litter to both frozen and unfrozen) for a further 2 months. These litters were sterilized (autoclaved twice for 20 min at 120 °C) to prevent contamination of the microcosms with foreign fauna. Microcosms were kept at ca.20 °C and between 80% and 100% field capacity. Therefore, soils were exposed to the same litter type for a total of 18 months.

Effects of litter history and freezing on the soil environment

After the 18-month conditioning we destructively sampled four microcosms from each litter and freezing treatment combination to characterize the effects of the litter history and freezing treatments on the mineral soil chemical and biotic environment. After removing the litter layer, soils were analyzed for extractable NH_4^+ and NO_3^-, pH, %C and %N, microbial biomass C and microarthropod community structure. For inorganic N determinations, 4 g of fresh soil were freeze-dried immediately following collection and later extracted by shaking in 20 ml of 2-M KCl for 1 h. Extracts were

analyzed for NO_3^- and NH_4^+ using an Alpkem Continuous Flow Analyzer. pH was measured in a 2:1 water-to-soil ratio and total C and N content was determined via the Dumas combustion method on a Carlo Erba Elemental Analyzer. Microbial C in soil was determined using the chloroform fumigation extraction method (Vance et al. 1987). Five g of 2-mm sieved fresh soil were fumigated for 72 h and then extracted in 20 ml of 0.5-M K_2SO_4. Extracts were filtered and analyzed for total organic C (using a Shimadzu TOC-5000A). Microbial biomass was calculated using $K_c = 0.32$.

Microarthopods were extracted from ca. 25 g of fresh soil for five days on modified Tullgren-type extractors. Mites were identified to suborder (Oribatei, Mesostigmata and Prostigmata). The Collembola detected in samples were assigned to the following families: Isotomidae, Entomobryidae, Onychiuridae, Tomoceridae, Sminthuridae. No differences in the responses of the groups of collembolans were observed so numbers were pooled. To assess the status of the microbiota during incubation conditions, microarthropods were extracted from microcosms eight days after application of litter treatments (see below). They were extracted and identified as described above.

Experimental treatments and process measurements

The remaining 104 microcosms were used to test for legacy effects (52 unfrozen, 52 frozen). Litter was removed from each jar, and within each of the litter history treatments and frozen/unfrozen sets, ten jars were amended with 4 g of pine litter, ten with 4 g of *Amorpha* litter, and six were not amended ("bare soil"). From here on, we refer to the 18-month conditioning with a specific litter type as the "Litter history" treatment (pine vs. *Amorpha*). We refer to the contemporary substrate treatment as "Substrate" and it had three levels (contemporary *Amorpha* and pine litter and bare soil). Immediately after amendment with substrates, jars were covered with 40-μm mesh to prevent contamination with foreign fauna. Jars were kept at 20 °C for 28 days. Moisture was kept between 80 and 100% field capacity via daily water additions.

To assess whether litter history had any legacy effects on contemporary processes we monitored both N and C processes. For N processes, net N mineralization/immobilization rates were calculated across two time periods: 0–8, and 8–28 days following substrate addition to the microcosms. To calculate these rates, extractable inorganic N concentrations were determined for the microcosms at 8 and 28 days as described above. The difference between final and initial, extractable inorganic N concentration was divided by the number of days in each incubation period. For the 0–8 day period (Week 1) we used the inorganic N concentrations from the initial characterizations as the initial values, and for the 8–28 day period (Weeks 2–4) the 8-day extractions were used as the initial values. For the 8-day extraction point, we harvested half of the replicates of each of the treatments (5 for contemporary *Amorpha* and pine litter and 3 for bare soil). The remaining half was harvested at 28 days.

For C processes, C-mineralization rates were measured 4, 10, 18 and 27 days after substrate addition on 5 (for contemporary *Amorpha* and pine litter) or 3 (bare soil) replicate samples using a static incubation procedure. This procedure consisted of sealing each microcosm for 3 h with a gas-tight lid modified to accept a septum. We measured CO_2 concentrations immediately after capping each microcosm and at the end of the 3 h incubation period using an infra-red gas analyzer (Li-Cor Biosciences, Model LI-7000). Contemporary litter CO_2 production rates were corrected for the contribution of the soil by subtracting the mineralization rates of the bare soil microcosms with the same litter history and community treatment combination, allowing us to estimate litter-derived CO_2. In all cases soil CO_2 production accounted for less than 20% of total CO_2 production and in most cases accounted for less than 10% of total CO_2 production.

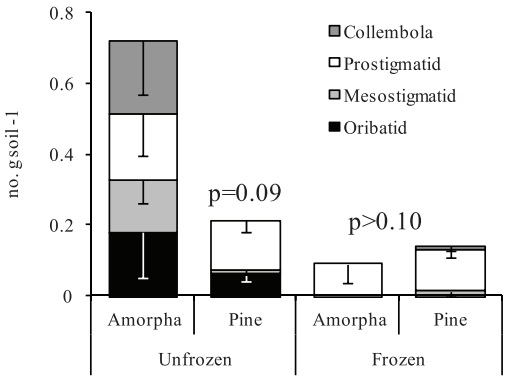

Fig. 1. Densities of microarthropods in microcosm soils after amendment with *Amorpha* and pine litter for 16 months (litter history) in frozen and unfrozen soils and before fresh substrate addition. *P* values are from *t*-tests on total abundances. Values are means ± standard error ($n = 4$).

Statistical analyses

The frozen and unfrozen sets were analyzed as separate experiments. Within each experiment, *t*-tests were used to analyze the effects of litter history treatments on initial soil chemical and biotic characteristics. Microarthropods abundance at day 8 was analyzed with two-factor ANOVA (litter history, substrate). Microarthropod abundances were log ($n + 1$) transformed prior to analysis. N mineralization data were analyzed with three-factor ANOVA (incubation period, litter history and substrate) and subsequently with two-factor analyses for each incubation period. C mineralization rates were analyzed via two-factor (litter history, substrate) repeated measures ANOVA and subsequently for each substrate. Litter history effects on N mineralization by substrate and incubation time were evaluated with *t*-tests. We report significant effects as $P < 0.05$ and marginally significant effects as $P < 0.10$. Analyses were performed with JMP (version 8, SAS Institute, Cary, NC, USA).

Results

Effects of litter history on the soil environment

After 18 months of exposure to litter (and prior to addition of contemporary litter treatments), soil mineral N concentrations were substantially greater in soils exposed to *Amorpha* than pine litter. As a result, C to N ratios were significantly lower in *Amorpha* treated soils (Table 1). Soil pH was higher in soils exposed to pine (Table 1). There was no significant effect of litter history on microbial biomass C (Table 1). Total microarthropod abundance was higher under *Amorpha* litter in unfrozen soil (Fig. 1). Notably, the collembolans and mesostigmatids were absent or extremely rare in soils exposed to pine (Fig. 1). One week into the incubation microarthropod abundances continued to be greater in soils with *Amorpha* litter history (Fig. 2a and b).

Microarthropod densities were negatively affected by freezing before substrate addition and continued to be 1 week after addition (Figs. 1 and 2). Importantly, total microarthropod abundance in frozen soils did not differ between litter history treatments before substrate addition (Fig. 1) or 1 week after substrate addition (Fig. 2). Hence, our goal of deep-freezing soils to reduce the biotic differences due to litter history was achieved in terms of faunal abundance.

Table 1
Chemical and biotic characteristics in microcosm soil after 16 months of exposure to pine or *Amorpha* litter (litter history treatment) and community treatment (frozen/unfrozen soils) but before fresh litter amendment.

Frozen/unfrozen	Litter history	$NO_3^- + NH_4^+$ ($\mu g\ g\ soil^{-1}$)	C/N	pH	Microbial C ($mg\ g\ oil^{-1}$)
Unfrozen	*Amorpha*	153 (24)a	6.56 (0.4)a	4.77 (0.05)a	0.49 (0.08)a
	Pine	4.4 (1.8)b	8.31 (0.7)b	4.97 (0.05)b	0.47 (0.06)a
Frozen	*Amorpha*	104 (13)a	6.18 (0.2)a	4.89 (0.05)a	0.83 (0.19)a
	Pine	2.8 (0.8)b	7.16 (0.5)b	5.00 (0.07)a	0.87 (0.06)a

Values are means with standard error in parentheses. Same letters indicate no significant difference (*t*-test). $n = 4$.

Legacies of litter history on C and N processes and the role of the soil community

The effects of litter history and substrate on net soil N mineralization or immobilization were dependent on the incubation period ($P < 0.05$ for the interactions of litter history and substrate with incubation period). Hence, to evaluate these interactions we assessed litter history and substrate treatment effects per incubation period. In the first period, both unfrozen (Fig. 3a) and frozen (Fig. 3b) microcosms exhibited very low mineralization and in the great majority of cases, net N immobilization, the magnitude of which was not dependent on contemporary substrate. Significant litter history effects were present in both unfrozen and frozen soils likely because soils with *Amorpha* litter history exhibited greater net N immobilization than soils that had been exposed to pine. In the second incubation period, soils under *Amorpha* litter showed net N mobilization, soils under pine litter showed net immobilization, while mineralization/immobilization in bare soil was dependent on litter history treatment. Although generally smaller, litter history effects were still present in the second period and were still due to greater immobilization/mineralization under *Amorpha* litter history as in the first period. However, the magnitude of these effects was highly dependent on contemporary substrate, such that litter history effects were only significant for the pine litter and bare soil.

Effects of litter history on C mineralization were dependent on incubation periods and contemporary substrate ($P < 0.05$ for interactions of incubation period × substrate × litter history for both frozen and unfrozen microcosms). Hence, to evaluate these interactions we assessed litter history per contemporary substrate. In microcosms amended with contemporary pine litter, significant litter history effects that differed over time were apparent (Fig. 4a and b). This effect arose because, over the first days of decomposition, microcosms that had been exposed to *Amorpha* had higher rates of litter C mineralization than those with a pine litter history. A marginally significant interaction between litter history and time for *Amorpha* litter (Fig. 4d) also suggests increased C mineralization of *Amorpha* litter with *Amorpha* litter history early in the incubation. In contrast, for bare soils there was no significant effect of litter history (alone or in interaction with time; Fig. 4e and f), suggesting that mineralization of resident SOM C was unaffected by previous exposure.

Discussion

Legacy effects

Our aim was to determine if contemporary C and N dynamics were affected by legacies of litter inputs. We found that the type of litter to which soil was exposed significantly influenced N and C dynamics suggesting that history played an important role in contemporary dynamics. N mineralization/immobilization rates of both contemporary litter substrates as well as resident SOM were greater in microcosms with soils that had been treated with *Amorpha*. This effect is likely partially due to the greater availability of mineral N in soils after being exposed to *Amorpha*, as a greater pool of mineral N available for microbial uptake could make more N immobilization possible. That the magnitude of the litter history effect on N dynamics tended to decrease with time is consistent with the differences in soil mineral N concentrations becoming smaller with time due to the influence of the freshly added litter (data not presented). The high C to N ratio of freshly added pine litter would be expected to generate high demand for soil N, leading to higher immobilization rates. However, after a week of incubation there was no difference in N immobilization rates between *Amorpha* and pine as contemporary substrates (Fig. 3) indicating that litter history, and not the contemporary substrate, was the main factor driving the responses of immobilization rates and notably, that the effects of litter history on N immobilization superseded the effect of the quality of contemporary substrates, at least during the initial phase of decomposition. Importantly, that litter history effects remained strong in the second incubation period only for pine and bare soil, the most resistant substrates, may indicate that the duration of legacy effects is related to the quality of the contemporary substrate.

In contrast to N processing, C mineralization rates from contemporary litters were only significantly affected by litter history

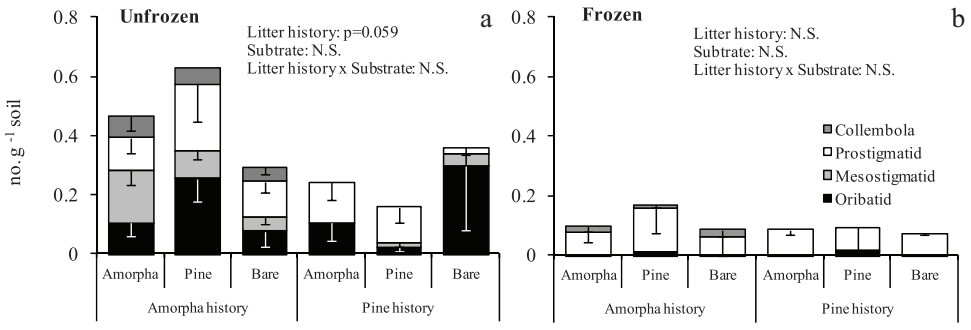

Fig. 2. Densities of microarthropods in unfrozen and frozen microcosm soils with *Amorpha* and pine litter history 1 week after fresh substrate addition (*Amorpha* litter, pine litter) or no addition (Bare soil). *P* values are from two-factor ANOVA on total abundances; values are means ± standard error ($n = 5$).

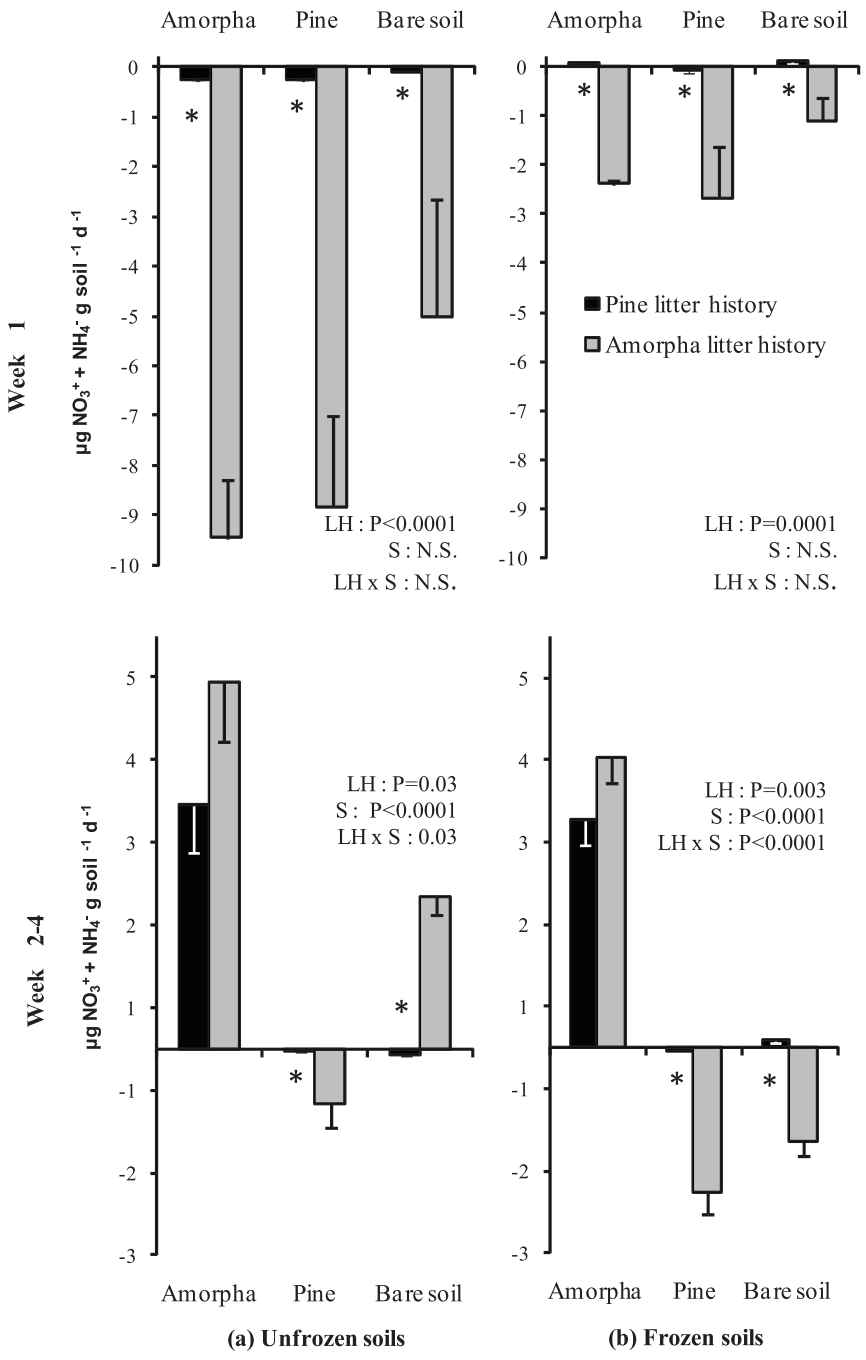

Fig. 3. Average net N mineralization (positive values) or immobilization (negative values) rates in microcosms with soils with pine and *Amorpha* litter history, and in frozen and unfrozen soils in two incubation periods. Categories on the x axes represent the contemporary substrate in the microcosms: *Amorpha* litter, pine litter or no litter (resident soil organic matter in bare soil). *P* values are from two-factor ANOVA (LH, litter history; S, substrate; LH × S, interaction of litter history and substrate; N.S., not significant, $P > 0.05$). Asterisks represent significant differences between litter histories (*t*-test). Values are means ± standard error; $n = 5$ for *Amorpha* and pine litter; $n = 3$ for bare soil. Note the different scales of the y-axes between the incubation periods.

at early measurement points and to a much lesser magnitude than N processes while C release from resident SOM was not influenced by litter history at all (Fig. 4). Greater release of C from contemporary litter at the beginning of the incubation in soils that had been exposed to *Amorpha* could, again, be explained by a greater N availability, which is often found to have a positive effect early in decomposition (Berg and Matzner 1997). The smaller magnitude and duration of the litter history effects on C (vs. N dynamics) suggests that contemporary C mineralization dynamics are influenced far less by legacies than net N dynamics are, suggesting a potential uncoupling between contemporary C and N dynamics.

Although the decomposition dynamics of contemporary litter species were influenced by litter history, thus showing strong legacy effects, exposure to a specific litter species did not appear to favor decomposition of the same litter species when it was applied as a contemporary substrate. The idea that it might has been dubbed "home-field advantage" (HFA) and has been observed in a number of studies (Hunt et al. 1988; Cookson et al. 1998; Hansen 1999; Gholz et al. 2000; Ayres et al. 2009a) suggesting the soil community adapts to resource inputs (Strickland et al. 2009a,b). Recent studies have suggested that HFA is more important for low quality litters (Milcu and Manning 2011; Osanai et al. 2012) and under low

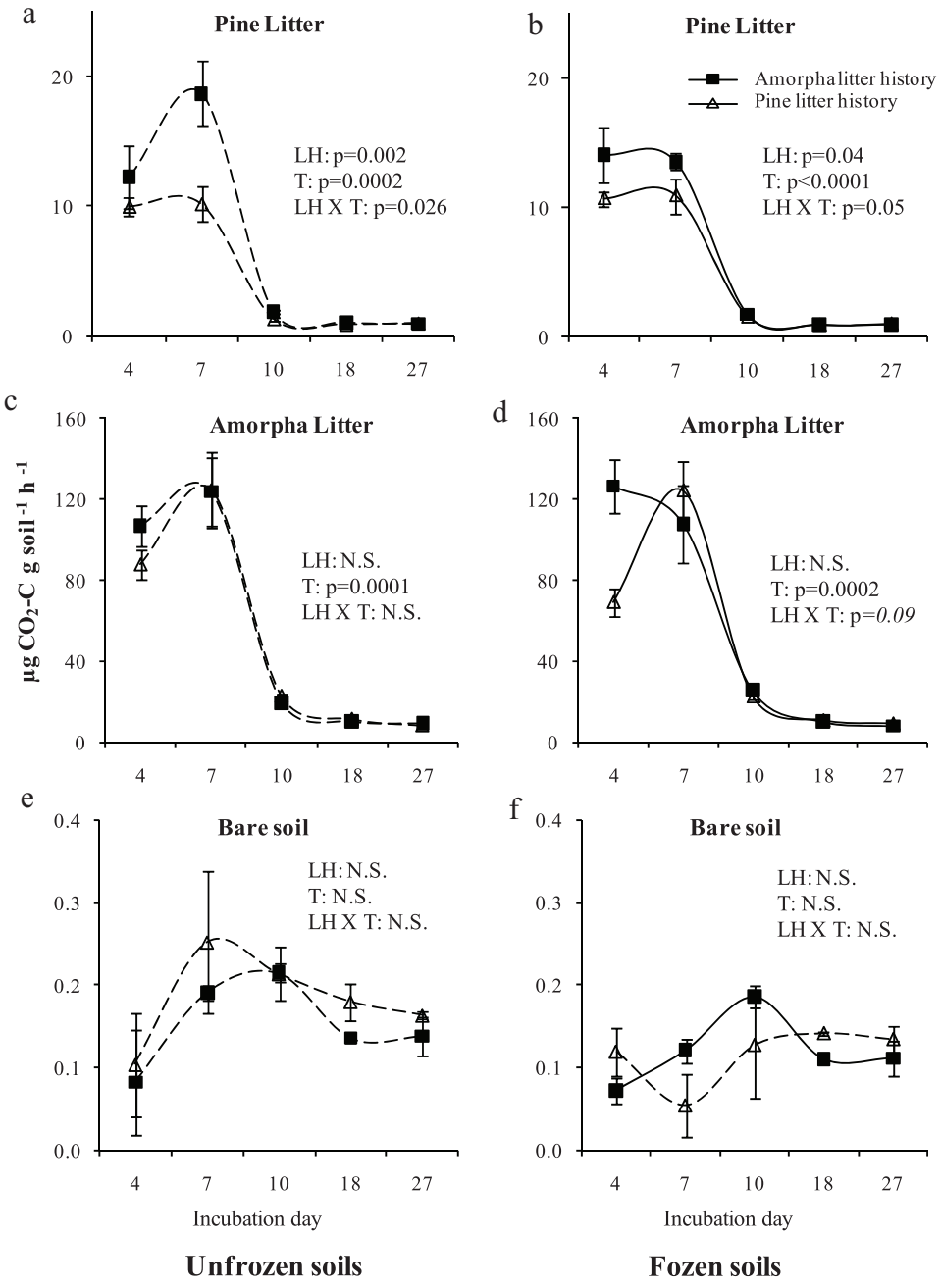

Fig. 4. CO_2–C flux from contemporary pine and *Amorpha* litter (µg CO_2–C g litter^{-1} h^{-1}) and from bare soil (µg CO_2–C g soil^{-1} h^{-1}) in microcosms with soils with *Amorpha* and pine litter history in unfrozen and frozen soils. Values are means ± standard error; $n = 5$ for *Amorpha* and pine litter; $n = 3$ for bare soil. *P* values presented are from repeated measures ANOVA testing for the effect of litter history (LH), time (T) and their interaction (LH × T). Degrees of freedom for *Amorpha* and pine litter were: LH: 1:8; T: 4:5; LH × T: 4:5 and for Bare soil: LH: 1:4; T: 4:1; LH × T: 4:1. Note the different scales of the *y*-axes.

N availability (Vivanco and Austin 2011), and that soil fauna contribute to HFA (Milcu and Manning 2011). However, despite our efforts to maximize exposure to the litter types, we observed no evidence of a HFA on C or N mineralization for either of the contrasting litters used, under intact or frozen communities, or under high or low N environments. Our results agree with studies that have found no evidence of HFA effects and support the notion that whether the HFA occurs is highly dependent on the experimental system (St John et al. 2011; Giesselmann et al. 2011). However, because our system only included litter and soil but no living plants, the absence of a HFA may indicate that a species' litter by itself is not the sole driver of the HFA phenomenon and that other plant species traits and processes, e.g. root-driven chemical and/or biotic changes in the soil environment, are also involved. It is also possible that HFA may only manifest at time scales greater than what we used in our experiment or that it was not expressed under conditions were soil organisms from the surrounding environment could not be recruited (St John et al. 2011; Milcu and Manning 2011).

The role of the soil biota

We also wanted to determine if the impact of litter on the soil biota played a role in generating litter legacy effects. For this, we used deep-freezing of soil to reduce effects of litter history on the soil community. Freezing reduced the size of the microarthropod communities, and more importantly it

homogenized them so that effects of litter history were not detectable in frozen microcosms during incubation (Fig. 2). Thus, frozen microcosms provided us with the opportunity to expose freshly added litters to soils with different litter histories but not-distinguishable microarthropod communities. We did not make statistical comparisons between frozen and unfrozen microcosms but rather treated them as independent experiments as we anticipated that freezing would influence soil physical and chemical properties that could potentially affect C and N mineralization. The fact that litter history, substrates and time impacted N and C mineralization in very similar ways, i.e. same general behavior and the same results of statistical analyses in frozen and unfrozen jars (Figs. 3 and 4), demonstrated that litter history effects are robust to small differences in the soil environment. However, we observed that the absolute magnitude of the effect of litter history on N immobilization was considerably smaller in frozen soils than in unfrozen soils during the first week of incubation for all substrates. That is, while in unfrozen microcosms N immobilization under *Amorpha* litter history was greater by an average of 7 $\mu g\, g\, soil^{-1}\, d^{-1}$ than under pine litter history, in frozen soils this difference was less than a third of that ($2\ \mu g\, g\, soil^{-1}\, d^{-1}$). This observation suggests that the effect of litter history on the microarthropod community was an important contributor to the legacy effects on N mineralization at least in the initial stage of decomposition. In contrast to N dynamics, there was no clear indication that the impact of litter history on C mineralization was altered by freezing, suggesting that the soil community was not an important component of the litter legacies on the C dynamics of either litter or resident SOM C.

We deliberately chose two litters that contrasted markedly in chemical composition to provide a robust test of whether the history of plant litter inputs could impact contemporary decomposition processes. Plant species with contrasting ecological strategies do co-occur and their litter inputs can contrast markedly in chemical composition (Cornwell et al. 2008). In addition, abrupt changes in litter sources are common in managed systems, and rather fast changes in plant species or functional group dominance due to environmental change are commonly observed in natural systems. In this way our experimental design has direct relevance to natural and arable communities. However, although there is indirect evidence in field situations to suggest that decomposition is affected through legacy effects (Hunt et al. 1988; Gholz et al. 2000; Vivanco and Austin 2008; Ayres et al. 2009b), studies focused on the mechanisms underlying these legacies are usually conducted under laboratory conditions (Ayres et al. 2006; Strickland et al. 2009a,b). The next step is to test the role of biotic and chemical legacies, on litter and SOM decomposition processes in field situations. One particularly important question pertains to whether the behavior, magnitude and duration of legacy effects, both chemically and biotically mediated, are sufficient to alter ecosystem functioning in situ.

There is increasing awareness of the importance of ecological legacies in determining the rates of contemporary ecosystem processes (Belnap et al. 2005; Gholz et al. 2000; Strickland et al. 2009a,b) but how legacies operate remains uncertain. Understanding the role of litter chemical composition and the soil decomposer community on legacy effects is of crucial importance as they are critical factors determining the rate of litter and SOM mineralization (e.g. Meentemeyer 1978; Aerts 1997). Further, both of these factors are highly susceptible to alteration under predicted environmental change (Wolters et al. 2000). Our study found strong short-term plant litter legacy effects on N dynamics and early stage C dynamics. The duration of legacy effects appeared to be dependent on the contemporary substrate for decomposition. Our results suggested that the impact of plant litter legacies on the soil biota, specifically the microarthropods, may be an important component of plant litter legacies affecting N decomposition dynamics, but not C dynamics. Legacy effects appeared to be much less important for contemporary C than for N decomposition suggesting that legacy effects could uncouple contemporary C and N dynamics.

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