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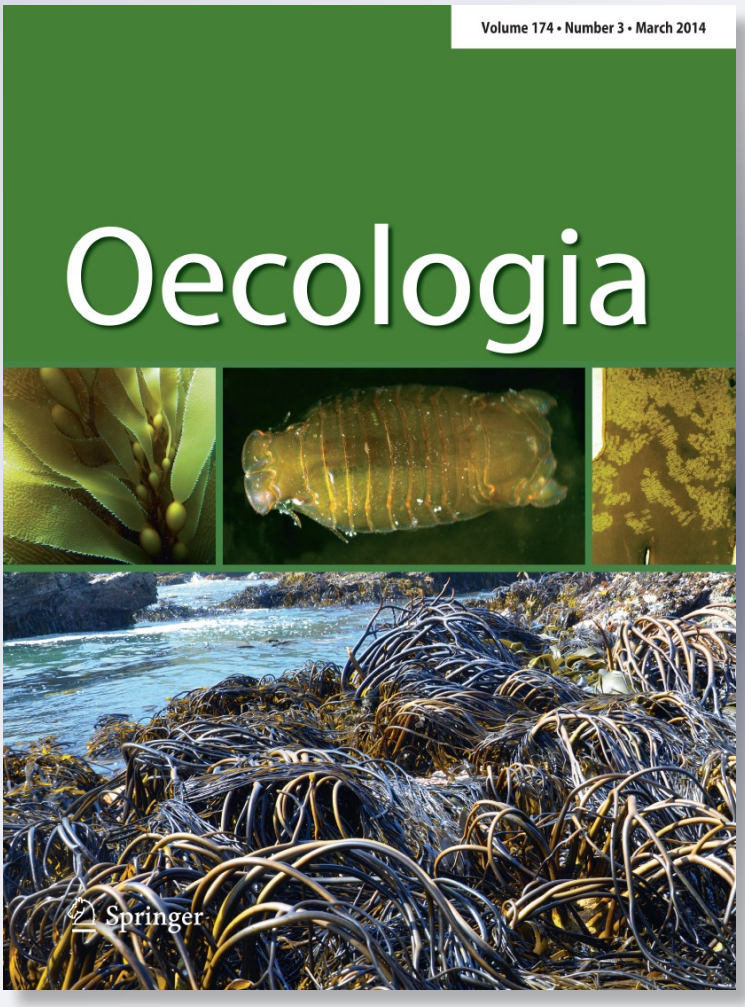

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Genotypic diversity of an invasive plant species promotes litter decomposition and associated processes

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Abstract Following studies that showed negative effects of species loss on ecosystem functioning, newer studies have started to investigate if similar consequences could result from reductions of genetic diversity within species. We tested the influence of genotypic richness and dissimilarity (plots containing one, three, six or 12 genotypes) in stands of the invasive plant *Solidago canadensis* in China on the decomposition of its leaf litter and associated soil animals over five monthly time intervals. We found that the logarithm of genotypic richness was positively linearly related to mass loss of C, N and P from the litter and to richness and abundance of soil animals on the litter samples. The mixing proportion of litter from two sites, but not genotypic dissimilarity of mixtures, had additional effects on measured variables. The litter diversity effects on soil animals were particularly strong under the most stressful conditions of hot weather in July: at this time richness and abundance of soil animals were higher in 12-genotype litter mixtures than even in the highest corresponding one-genotype litter. The litter diversity effects on decomposition were in part mediated by soil animals: the abundance of Acarina, when used as covariate in the analysis, fully explained the litter diversity effects on mass loss of N and P. Overall, our study shows that high genotypic richness of *S. canadensis* leaf litter positively affects richness and abundance of soil animals, which in turn accelerate litter decomposition and P release from litter.

Keywords Decomposer diversity · Decomposition rates · Genotypic dissimilarity · Genotypic richness · Litter diversity

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Introduction

The current rapid loss of biodiversity at several levels from ecosystems to species and genotypes and at global, regional and local scales is considered to be one of the major threats to the continued good functioning of ecosystems and the biosphere at large (Cardinale et al. 2012; Hooper et al. 2012). Among the best-studied effects of biodiversity on ecosystem functioning are a positive relationship between plant species richness and primary production and decomposition (Balvanera et al. 2006; Cardinale et al. 2006, 2011; Schmid et al. 2009; Gessner et al. 2010). Because these two ecosystem processes occur in sequence, the effect of plant diversity on decomposition may be due to increased litter

mass (indirect effect) or to increased litter diversity independent of mass (direct effect).

To study the mass-independent effects of litter diversity on decomposition, experiments using litter samples of equal mass but different species (Blair et al. 1990; Gartner and Cardon 2004; Shen et al. 2007; Ball et al. 2008; Cornwell et al. 2008; Hoorens et al. 2010; Lecerf et al. 2011) or genotypic compositions (Madritch and Hunter 2002, 2003; Hughes et al. 2009) can be carried out. Such experiments have demonstrated direct effects of litter diversity on decomposition, but often with a large influence of the presence of particular species in the litter on decomposition (e.g., Ball et al. 2008). However, because the different species are not easy to separate within decomposing litter, their contribution to a mixture's decomposition cannot be analyzed by the additive partitioning method commonly used in the analysis of diversity–productivity relationships (Loreau and Hector 2001), such that alternative approaches like the comparison of mixtures with monocultures have to be used (Loreau 1998; Cardinale et al. 2006).

In addition to these approaches for statistical explanations of biodiversity effects on decomposition, the recording or biological variables such as litter element concentrations and soil animals colonizing litter samples may allow for a better understanding of the involved mechanisms. For example, differences in litter chemical composition among coexisting species can affect decomposition processes (Wardle et al. 1997; Smith and Bradford 2003; Cornwell et al. 2008). Decomposition rates may be increased by nutrient transfer from high- to poor-quality litter types (McTiernan et al. 1997; Schimel and Hättenschwiler 2007; Hoorens et al. 2010). On the other hand, if mixing increases the amounts of secondary compounds (e.g., phenolics) in the litter (Wardle et al. 1997; Hättenschwiler and Vitousek 2000; Hoorens et al. 2003), decomposition may be slowed down. All these effects very likely involve the activity of soil organisms (Hättenschwiler et al. 2005; Gessner et al. 2010). Therefore, future litter decomposition experiments should try to record litter element concentrations and soil animals, as we did in the present study.

For the present study we chose a single plant species as a model to test whether genotypic richness and dissimilarity of samples of leaf litter would increase decomposition rates and nutrient release, and whether such an effect could be mediated by increased richness and abundance of soil animals. The model species, *Solidago canadensis* L. (Asteraceae), often dominates plant communities in which it occurs, in particular in its invasive range in Eurasia where it can form almost monospecific stands (Weber and Schmid 1998; Dong et al. 2006a). Typically this species has high genotypic diversity within populations, even in introduced ranges (Schmid and Bazzaz 1990; Weber and Schmid 1998). Genotypically diverse leaf litter, therefore, can be expected to commonly occur in nature; and fast decomposition of this litter could benefit further dominance of the species. Furthermore, previous studies have demonstrated various effects of genotypic diversity in this and related species on disease levels (Schmid 1994), primary production, decomposition and arthropod communities (Crutsinger et al. 2006, 2008, 2009).

That genotypes of a single plant species can differ in traits affecting litter decomposition has been shown previously (Treseder and Vitousek 2001; Schweitzer et al. 2004, 2005a; Madritch et al. 2006; LeRoy et al. 2007). Thus, depending on the mixture of genotypes present, decomposition can be expected to be slowed down or accelerated compared with genetically uniform litter. During litter decomposition, soil animals play a key role in litter fragmentation, and then provide new habitats for microbe colonization and further nutrient release (González and Seastedt 2001; Crutsinger et al. 2008). As food of soil animals, leaf litter of different quality from different genotypes may support different decomposers (resource specialization hypothesis), or the richness of soil animals can also increase due to more individuals in diverse leaf litter [more individuals hypothesis (Crutsinger et al. 2006)].

Using a field experiment with leaf litter from 20 different genotypes assembled in samples of increasing genotypic richness from one to three to six to 12, and of different genotypic composition and dissimilarity within richness levels, we explored the effects of litter diversity on decomposition processes over five monthly time intervals. We found positive effects of genotypic litter richness on richness and abundance of soil animals, which in turn mediated faster litter decomposition.

Materials and methods

Plant species

Solidago canadensis is a perennial herb native to North America and introduced intentionally to Shanghai in 1935 as an ornamental plant (Li and Xie 2002). It produces leaves along an unbranched stem in spring until inflorescence initiation in summer (Schmid and Bazzaz 1994). Leaves senescence proceeds from the bottom up along the stem as N concentrations decline from ca. 2 to 1 % of leaf dry mass (Egli and Schmid 2000). Senesced leaves drop in the fall. In China, *S. canadensis* grows more than 2 m tall in one growing season, seriously threatening native biodiversity and ecosystems (Lu et al. 2007).

Collection of leaf litter

In October 2007, twenty patches of *S. canadensis* at least 20 m apart from each other were marked and dug out in Minhang (31°02′N, 121°26′E) and Putuo (31°13′N, 121°21′E) near Shanghai, China. Roots were washed and carefully separated by clones (defined as connected rhizome systems). The largest clone in each of the 20 patches was picked out and two to three least senesced leaves of each of these 20 clones were collected and dried with silica gel for later genotyping. All other pre-senescent leaves of each clone were collected and separately put into paper bags, dried at relatively low temperature (60 °C) and weighed as samples for the decomposition experiment. Subsamples from each clone were retained for determining initial contents of elements.

Genotyping

Genomic DNA was extracted from ~50 mg of the collected two to three leaves per clone using the modified mini-prep cetyltrimethylammonium bromide procedure (Fan et al. 2004). Each sample was genotyped at seven microsatellite loci [SS1B, SS19C, SS20E, SS4F, SS19D, SS24F and SS4G (Wieczorek and Geber 2002)]. Approximately 100 ng of DNA was used to seed a 20-μl polymerase chain reaction (PCR) and amplify following the manufacturer's instruction in a PTC-220 PCR machine (MJ Research, Waltham, MA). Amplification conditions were as follows: an initial 5 min of pre-denaturation at 95 °C followed by 34 cycles of 30 s denaturation at 95 °C, 30 s annealing at 48–61 °C and 45 s extension at 72 °C and a final extension step at 72 °C for 7 min. PCR products were resolved by 6 % polyacrylamide gel electrophoresis, visualized using silver nitrate staining, and manually scored against a sequence ladder of pUC19 DNA/MspI (HpaII) marker 23 (Fermentas). The 20 clones we collected could all be distinguished from each other based on the seven microsatellite loci and are therefore treated as 20 different genotypes in this paper. To characterize the genetic dissimilarity of the genotypes we calculated a pair-wise genetic distance D_{ij} using the software GenAlEx version 6.3 (Peakall and Smouse 2006). The genotypic dissimilarity within each litter sample was calculated as $\text{Dissim} = \frac{\sum_{i=1}^{n}\sum_{j=i}^{n} D_{ij}}{C_n^2}$ (Jousset et al. 2011), where n is the number of genotypes, D_{ij} is genetic distance between pairs of genotypes and C_n^2 is the number of distinct genotype pairs within samples. The genetic relationship of the 20 genotypes is illustrated in Fig. S1 (Electronic Supplemental Material). It should be noted that genotypic dissimilarity as calculated here reaches its maximum in a two-genotype mixture with the two most dissimilar genotypes. Therefore, the measure of genotypic dissimilarity is here only used to compare litter samples of different genotypic composition but equal richness. This is achieved by fitting genotypic dissimilarity after genotypic richness in the statistical analysis (see below).

Design of the field experiment

The field decomposition experiment was set up in April 2008 in an abandoned farmland with a low-C (1.4 % mass) mineral soil (Shenya Farm Garden of Fengxian, Shanghai; 31°55′N, 121°33′E). This region has a subtropical maritime monsoon climate with an annual average precipitation of 1,249 mm, and the highest and lowest monthly average temperatures were 29.8 and 3.5 °C in July 2008 and February 2008, respectively (Shanghai Almanac Editorial Board 2009). The vegetation on the ground was cleared before conducting the experiment. We assembled samples of leaf litter of four genotypic richness levels (see Table S1, Electronic Supplemental Material), the highest level reflecting typical values of genotypic diversity in stands of *S. canadensis* in the Shanghai region (Dong et al. 2006b): 20 replicates with leaf litter of one genotype, each replicate containing a different genotype and seven replicates each with mixed leaf litter of three, six or 12 genotypes, each replicate containing litter from a set of genotypes chosen randomly from the 20 clones (if a particular set was randomly selected more than once the duplicate set was rejected). Each of the 41 unique genotypic combinations was applied to one of 41 plots.

For each plot, five nylon litterbags (10 × 10 cm, with 1 × 0.7-mm mesh size) with the same genotypic composition of leaf litter were prepared for five retrieves. On 30 April 2008 all five litterbags were placed on the soil surface at a minimum distance of 20 cm from each other and were linked to the same bamboo stake with lines of 20 cm in length. Each bag had the same total amount of dried leaf litter, i.e., 6 g, and different genotypes in mixture treatments had equal mass. From May to September 2008, we collected one litterbag per plot every month. Original litter samples as put out to the field in April 2008 were also analyzed.

Extraction of soil animals

Soil animals were extracted by drying each sample under a 60-W lamp placed over a modified Tullgren funnel for 24 h with a stop of 15 min every 4 h to avoid excessive heating. Soil animals were collected using a beaker, filled with 75 % ethanol, under the funnel. The soil animals were identified to order and counted under a stereomicroscope (Yin et al. 1998). For Coleoptera we made two groups, one containing larva and one containing adults. The groups of animals contained litter feeders and other trophic guilds, which for

soil animals are difficult to assess (Schneider et al. 2004) (Table S2, Electronic Supplemental Material).

Analyses of mass and element contents of leaf litter

After extracting soil animals, litter samples were carefully taken out of the funnels. After removing sundries, such as soil and excrement of soil animals, the samples were oven dried at 80 °C to constant mass, weighed and ground for element analysis. Total N and C of the litter were analyzed with a Vario MICRO cube elemental analyzer (Elementar, Hanau, Germany). Total P content was analyzed using the molybdenum blue method after digestion by H_2SO_4–H_2O_2 (Institute of Soil Science 1978).

Data analyses

We tested the effects of three aspects of genotypic diversity of leaf litter, genotypic richness (log transformed), proportion of genotypes collected at site Minhang and genotypic dissimilarity on mass of C, N and P, on N:C and P:C mass ratios and on richness and abundance of soil animals with repeated-measures ANOVA using mixed models. We used mass of C instead of total litter mass because the latter declined more slowly, indicating increasing contamination of samples with mineral soil over time. It should be noted that because leaf litter was collected in the field, the three aspects of genetic diversity include potential environmental effects on leaf litter quality. This is particularly likely for effects of the proportion of litter from the two sites, although genotypes from the two sites also seemed to be genetically separated to some degree (see Fig. S1, Electronic Supplemental Material). Diversity variables, time as multilevel factor and interactions between diversity variables and time were treated as fixed terms in the model; diversity main effects were then tested against the random term plot (corresponding to the different genotypic compositions of samples) and diversity × time interactions against the residual. We checked whether genotypic richness effects deviated from a log-linear relationship by adding a 4-level factor for genotypic richness after the (log-) linear richness term. Furthermore, in alternative analyses we included terms for the presence of any particular genotype in leaf litter to check if "identity" effects could partly explain diversity effects. All mixed-model analyses were done with the residual maximum likelihood approach as implemented in the statistical software GenStat (VSN International, Hemel Hempstead, UK).

Richness of soil organisms per sample was simply calculated as the number of groups of soil animals listed in Table S2 (Electronic Supplemental Material), taking Coleoptera larva and Coleoptera adults as separate groups but otherwise each order as a single group. Although this is a very crude richness measure, its strong dependence on genotypic richness of litter suggested that it did reflect aspects of functionally relevant soil organism diversity. Abundance of soil animals was calculated as number of individuals per sample and additionally as number or individuals per gram C per sample. Abundance measures were also calculated separately for Acarina, which were the most abundant by far (Table S2, Electronic Supplemental Material) and for all other soil animals combined. All abundance variables were square-root transformed to ensure homoscedasticity and obtain normally distributed residuals. The same transformation was made when abundance variables were used as explanatory covariates to analyze litter decomposition variables (C, N, P). We only analyzed June to September data for soil animals because there were almost no individuals found in May. The statistical models followed the repeated-measures, mixed-model ANOVA approach as mentioned above for the decomposition variables.

To look at relationships between dependent variables we calculated correlations and added covariates to the mixed-model ANOVAs. In particular, we tested whether the inclusion of richness and abundance of soil organisms as covariates could explain all or part of the effects of litter diversity on decomposition variables (C, N, P). Conversely, we also analyzed if C, N or P could explain all or part of the litter-diversity effects on richness and abundance of soil organisms.

Following the repeated-measures analyses we also analyzed the influence of genotypic richness on the first-order decomposition rate constants of C, N and P over time, calculated for each of the 41 plots separately. These decomposition rate constants were calculated as the absolute value of the slope of the logarithmically transformed elemental mass in a litter sample over the six equally spaced sample dates (t_0–t_5, 0–153 days). A first-order decomposition rate constant corresponds to k in the negative exponential model $M_t = M_o e^{-kt}$ (Olson 1963). M here is the mass of C, N or P in the litter bags. We used this simple decay model because average values of C, N and P declined exponentially over the observation period. Effects of the proportion of genotypes from the two sites and of genotypic dissimilarity on decomposition rate constants of C, N and P were also analyzed but not significant and thus not further discussed. Finally, the effect of the presence of particular genotypes was tested in alternative models of the type k ~ genotypic richness + genotype i and k ~ genotype i + genotypic richness to test if identity effects could, respectively, add to or replace variation in decomposition rate constants explained by genotypic richness.

To test whether mixed leaf litter of different genotypes had stronger effects than average effects of these single genotypes or even than the genotype with the highest performance, we calculated log ratios of dependent

variables between 12-genotype litter samples and single-genotype litter samples according to Cardinale et al. (2006): $LR_{net} = \ln \frac{I_{\tilde{p}i}}{I_{\tilde{m}i}}$ and $LR_{trans} = \ln \frac{I_{\tilde{p}i}}{I_{\min_i}}$ or $LR_{trans} = \ln \frac{I_{\tilde{p}i}}{I_{\max_i}}$, where $I_{\tilde{p}i}$ is the value of a 12-genotype litter, $I_{\tilde{m}i}$ is the mean value of all 12 corresponding single-genotype litters and $I_{\min_i}(I_{\max_i})$ is the value of the most extreme single-genotype litter contained in the corresponding 12-genotype litter (i.e., the least remaining mass of C, N or P or the highest richness and abundance of soil animals). We refer to LR_{net}-values as net effects and to LR_{trans}-values as transgressive effects, e.g., transgressive over-decomposition. For interpretation, the calculated log ratios were plotted with SEs versus time, but no formal statistical tests were made because of the derived and aggregated nature of these values.

Results

On average the total mass of litter samples of *Solidago canadensis* declined from 6.00 > 5.43 > 4.47 > 3.40 > 2.48 > 1.23 g over the six equally spaced sample dates of the 153-day decomposition period. C declined from 2.54 > 1.68 > 0.68 > 0.45 > 0.16 > 0.08 g, N declined from 105 > 79 > 44 > 32 > 13 > 6 mg and P declined from 15.50 > 9.71 > 3.27 > 1.32 > 0.81 > 0.28 mg over the same time span (Time, Table 1). As mentioned above, we used mass of C instead of total litter mass as the reference because the latter likely included increasing amounts of contamination from mineral soil over time. There was no indication that N was initially immobilized in the litter as the N:C mass ratio continually increased over the entire observation period (0.0414 < 0.0472 < 0.0640 < 0.0714 < 0.0776 < 0.0794) whereas the P:C mass ratio decreased over the first three time intervals and then increased and decreased over the last two (0.00610 > 0.00588 > 0.00515 > 0.00332 < 0.00505 > 0.00361). The decomposition of the leaf litter was enhanced by increasing genotypic richness of the litter, the effect being marginally significant in the repeated-measures analysis for mass of C and N and significant for mass of P [Log(genotypic richness), Table 1]. Increasing genotypic richness of litter also resulted in lower P:C mass ratios (0.00363 for average 12-genotype vs. 0.00545 for average single-genotype litter; Table 1) but did not significantly affect the N:C mass ratio (0.0618 for average 12-genotype vs. 0.0640 for average single-genotype litter; $P > 0.1$). For single time points the effect of genotypic richness varied in strength as exemplified for the June sampling date in Fig. 1 and for the other sampling dates in Fig. S2 (Electronic Supplemental Material). However, interactions between genotypic richness and time were only significant for mass of P and P:C mass ratios [Log(g.r.) × time interaction, Table 1]. More diverse litter initially contained more P than less

Table 1 Results of repeated-measures ANOVAs using mixed models for mass of C, N and P and N:C and P:C mass ratios in leaf litter of *Solidago canadensis* from the start (30 April 2008) to the end (30 September 2008) of the experiment

Fixed-term effects	Mass of C			Mass of N			Mass of P			N:C			P:C		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Log genotypic richness (GR)	3.64	1, 38	0.064	3.21	1, 38	0.081	5.38	1, 38	0.026	–	–	–	8.92	1, 39	0.005
Percentage minhang (PM)	0.04	1, 38	0.838	0.27	1, 38	0.608	11.53	1, 38	0.002	–	–	–	–	–	–
Genotypic dissimilarity	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Time	2,461	5, 195	<0.001	484	5, 195	<0.001	545	5, 190	<0.001	91.1	5,200	<0.001	5.45	5, 195	<0.001
Log GR × time	–	–	–	–	–	–	12.45	5, 190	<0.001	–	–	–	2.57	5, 195	0.028
PM × time	5.59	5, 195	<0.001	4.18	5, 195	0.001	3.96	5, 190	0.002	–	–	–	–	–	–

Only fixed terms with $P < 0.1$ (or main effects occurring in fixed-term interactions with $P < 0.1$) were included in models; genotypic combination was used as random term to test the following diversity effects of the leaf litter: genotypic richness (logarithm of the number of different genotypes), percentage of genotypes from site Minhang (the other genotypes originating from site Putuo) and genotypic dissimilarity (calculated as explained in "Genotyping" in the "Materials and methods"; here, never significant)

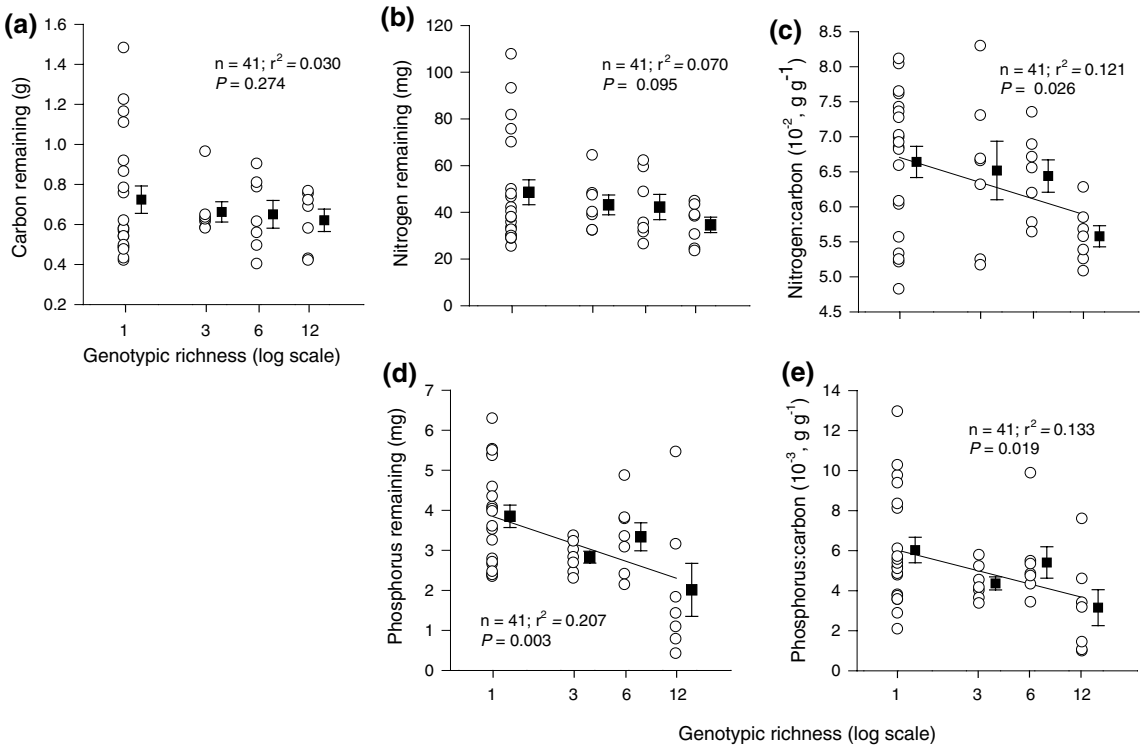

Fig. 1 Relationship between genotypic richness of *Solidago canadensis* leaf litter and **a** total amount of C, **b** total amount of N, **c** N:C mass ratio, **d** total amount of P and **e** P:C mass ratio—all per litter sample of initially 6 g dry mass—61 days after decomposition in the field (30 June 2008). Corresponding graphs for the start of the experiment and other dates are presented in Fig. S2 (Electronic Supplementary Material). *Circles* represent individual samples (see Table S1, Electronic Supplementary Material), *squares* and *bars* represent means (±SE) for each genotypic richness level (note that these are slightly displaced to avoid overlapping with circles). Sample size (*n*), r^2- and *P*-values from linear regression analyses are shown for each panel. *Regression lines* are shown in graphs with significant relationships

diverse litter, a relationship that reversed as decomposition proceeded (see Fig. S2). Litter with a large proportion of Minhang genotypes (percentage Minhang) had more mass of C, N and P initially and during the early but not the later sampling dates than litter with a large proportion of Putuo genotypes (P.M. × time interaction, Table 1). The genotypic dissimilarity of litter samples did not significantly affect decomposition variables (Table 1). It should be noted that genotypic compositions within richness levels varied more with regard to proportions Minhang:Putuo than with regard to genotypic dissimilarity (Table S1, Electronic Supplemental Material). Deviations from log linearity of genotypic richness were very small for all tested variables ($P > 0.1$).

The analysis of first-order decomposition rate constants of C, N and P showed the positive effects of genotypic richness of litter on decomposition over time more clearly than did the repeated-measures ANOVA reported above. This was probably due to the integration of different time points into a single dependent variable and the good fit of individual data points to exponential decay curves for the 41 plots. For all three elements, decomposition rate constants increased significantly with the logarithm of genotypic richness of litter (Fig. 2).

Soil animals had colonized the litter samples in June, then were scarce at the end of July and back in larger numbers in August and September (Table 3), leading to highly significant variation over time (Time, Table 2). Increasing genotypic richness of litter samples had a positive effect on the richness and abundance of soil animals, the latter both if expressed per sample or per gram C in the sample [Log(genotypic richness), Table 2]. However, as decomposition proceeded over time, the positive effect of genotypic richness of litter on soil animals declined and at the final date was no longer visible [Table 3; Log(g.r.) × time interaction, Table 2]. Acarina abundance at the final date was even lower for the average 12-genotype litter than for the average single-genotype litter, both if expressed per sample (Table 3) and if expressed per gram C (146 g^{-1} for average 12-genotype vs. 226 g^{-1} for average single-genotype litter). Using mass of C, N or P as covariates in the analyses did not reduce the positive effects of genotypic richness of the litter on the richness and abundance of soil animals per sample, indicating that these effects were not

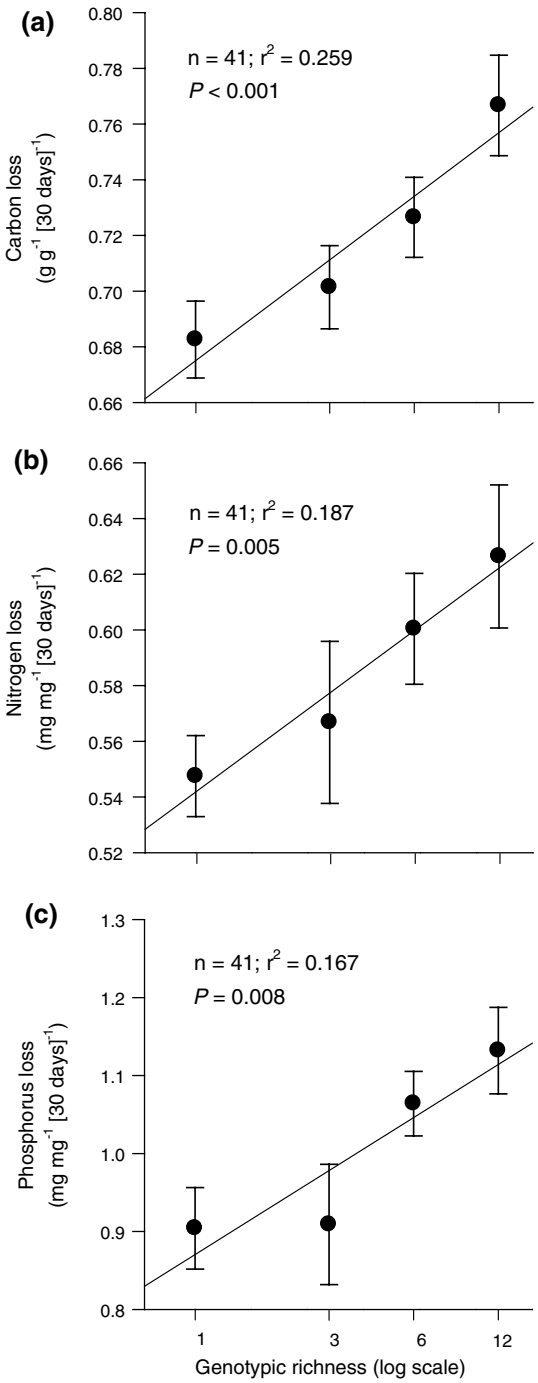

Fig. 2 Relationship between genotypic richness of *S. canadensis* leaf litter and first-order decomposition rate constant of **a** C, **b** N and **c** P. Decomposition rate constants were calculated as the absolute value of the slope of the log-transformed elemental mass in a litter sample over the six sampling dates (0–153 days; see "Data analysis" section of "Materials and methods"). *Filled circles* represent mean (±SE) values. *Regression lines*, sample size (*n*), r^2- and *P*-values are shown for each relationship

due to litter diversity-related differences in element contents. However, the covariates did explain the positive effect of genetic diversity on the abundance of Acarina per

Table 2 Results of repeated-measures ANOVAs using mixed models for number of orders of soil animals (*Richness*), number of individuals of Acarina[a] (*Abundance Acarina*, square-root transformed) and number of individuals of other orders of soil animals[b] (*Abund. other animals*, square-root transformed) per litter sample

Fixed-term effects	Richness			Abundance Acarina			Abund. other animals			Acarina g^{-1} C			Others g^{-1} C		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Log genotypic richness (GR)	19.00	1, 38	<0.001	24.86	1, 37	<0.001	22.78	1, 39	<0.001	7.78	1, 39	0.008	16.92	1, 39	<0.001
Percentage minhang (PM)	1.88	1, 38	0.178	2.75	1, 37	0.106	–	–	–	–	–	–	–	–	–
Genotypic dissimilarity	–	–	–	7.56	1, 37	0.009	–	–	–	–	–	–	–	–	–
Time	65.93	3, 114	<0.001	141.9	3, 114	<0.001	61.26	3, 117	<0.001	154.5	3, 117	<0.001	34.43	3, 117	<0.001
Log GR × time	5.77	3, 114	0.001	13.05	3, 114	<0.001	8.45	3, 117	<0.001	5.06	3, 117	0.002	5.59	3, 117	<0.001
PM × time	3.47	3, 114	0.019	3.06	3, 114	0.031	–	–	–	–	–	–	–	–	–

Only fixed terms with $P < 0.1$ (or main effects occurring in fixed-term interactions with $P < 0.1$) were included in models; genotypic combination was used as random term to test the following diversity effects of leaf litter: genotypic richness (logarithm of the number of different genotypes), percentage of genotypes from site Minhang (the other genotypes originating from site Putuo) and genotypic dissimilarity (calculated as explained in "Genotyping" in the "Materials and methods" section). Because of initially very low numbers of animals, only four monthly recordings (30 June–30 September 2008) could be included in the analyses

P Error probability

[a] Also expressed per gram of remaining C in litter samples of *S. canadensis* (Acarina g^{-1} C, square-root transformed)

[b] Also expressed per gram of remaining C in litter samples of *S. canadensis* (Others g^{-1} C, square-root transformed)

Table 3 Changes in richness and abundance of soil animals over time on leaf litter of *S. canadensis* varying in genotypic richness

Genotypic richness	30 June	30 July	30 August	30 September	Number of samples
Richness (number of orders of soil animals)					
1	3.65 ± 0.33	0.30 ± 0.11	2.10 ± 0.19	2.70 ± 0.30	20
3	4.14 ± 0.55	1.71 ± 0.18	2.43 ± 0.30	2.43 ± 0.37	7
6	5.14 ± 0.55	1.57 ± 0.30	3.71 ± 0.42	2.71 ± 0.64	7
12	4.29 ± 0.47	1.57 ± 0.30	4.14 ± 0.14	2.43 ± 0.43	7
Abundance Acarina (number of individuals)					
1	5.50 ± 0.77	0.30 ± 0.13	26.50 ± 1.84	18.45 ± 2.92	20
3	12.71 ± 2.91	2.00 ± 0.38	35.57 ± 2.86	13.57 ± 3.64	7
6	14.29 ± 1.44	1.29 ± 0.36	45.86 ± 5.25	9.43 ± 2.10	7
12	23.00 ± 2.76	1.43 ± 0.37	36.71 ± 7.16	7.29 ± 1.69	7
Abundance other animals (number of individuals)					
1	6.10 ± 1.01	0.05 ± 0.05	1.25 ± 0.20	3.35 ± 0.69	20
3	6.14 ± 1.22	1.29 ± 0.36	2.86 ± 0.46	1.86 ± 0.55	7
6	9.29 ± 1.58	1.00 ± 0.31	4.86 ± 0.51	3.14 ± 1.20	7
12	10.86 ± 1.01	0.86 ± 0.26	6.86 ± 1.60	2.43 ± 0.92	7

The experiment was carried out in 2008 at Shenya Farm Garden of Fengxian, Shanghai, 31°55′N, 121°33′E. Values are means (±SE)

gram C. That is, the most diverse litter samples had the lowest mass of C, N or P (averaged over time) and these samples also had the most Acarina individuals per gram C (averaged over time).

Given the effects of genotypic richness on both decomposition variables (more rapid mass loss) and soil animals (higher richness and abundance), we asked if the two were connected in a way that the increased richness and abundance of soil animals on more diverse litter may have influenced the faster decomposition in terms of mass loss of C, N and P from litter. Because soil animals were very few at the first two sampling dates, we only analyzed June–September dates for the following correlation analyses. First, richness of soil animals was not correlated with C and N ($P > 0.1$), but was positively correlated with P ($r^2 = 0.083$, $P < 0.001$), indicating that higher P favored colonization of the litter by more animal groups. Second, abundance of Acarina per sample or per gram C was negatively correlated with C ($r^2 = 0.083$, $P < 0.001$ and $r^2 = 0.429$, $P < 0.001$, respectively), N ($r^2 = 0.123$, $P < 0.001$ and $r^2 = 0.404$, $P < 0.001$, respectively) and P ($r^2 = 0.033$, $P < 0.021$ and $r^2 = 0.202$, $P < 0.001$, respectively). This indicated that the litter-diversity effect on mass loss of C, N and P might be explained by the increased abundance of Acarina on litter with higher genotypic richness. Indeed, using abundance of Acarina (per sample or per gram C) as covariates in the repeated-measures ANOVAs for the decomposition variables C, N and P removed the effect of genotypic richness on C and N completely, as it was no longer significant if fitted after the covariate ($P > 0.1$). That is, the genotypic richness of litter had increased the abundance of Acarina, which in turn led to increased loss of C and N. However, regarding P, using the abundance of Acarina as covariate slightly increased the negative effect (lower remaining mass) of genotypic richness fitted afterwards (with abundance of Acarina per sample, genotypic richness $P = 0.002$; with abundance of Acarina per gram C, genotypic richness $P = 0.010$).

The effects of genotypic diversity as measured by log ratios between the 12-genotype mixed litter and the average of the corresponding one-genotpye litters (LR_{net}) became more negative with time for remaining mass of C ($-0.003 < 0.012 > -0.190 < -0.137 > -0.236 > -0.548$), N ($-0.056 < -0.048 > -0.380 < -0.176 > -0.201 > -0.584$) and P ($0.171 > -0.394 > -0.978 < -0.446 > -1.684 > -1.977$). That is, mass loss of C, N and P was increased in the most diverse litter compared with the average of the corresponding one-genotype litters. However, the 12-genotype mixed litters only rarely decomposed even faster than the fastest decomposing one-genotype litters contained within them; that is, instances of transgressive over-decomposition ($LR_{trans} < 0$) were rare. The effects of genotypic diversity on the richness and abundance of soil animals (Acarina and others combined) as measured by log ratios were positive ($LR_{net} > 0$), with maximum log ratios for both measured variables in July (Fig. 3a). After that, the effects decreased with time. In this case, transgressive effects occurred from June to August: during these sample dates 12-genotype litter mixtures supported more groups (in July and August) and more individuals (in June and July) of soil animals than even the most animal-beneficial one-genotype litter ($LR_{trans} > 0$; Fig. 3b).

The presence of particular genotypes of *S. canadensis* in the leaf litter had few and generally small effects on the dependent variables. The following effects of the presence of particular genotypes were significant when fitted

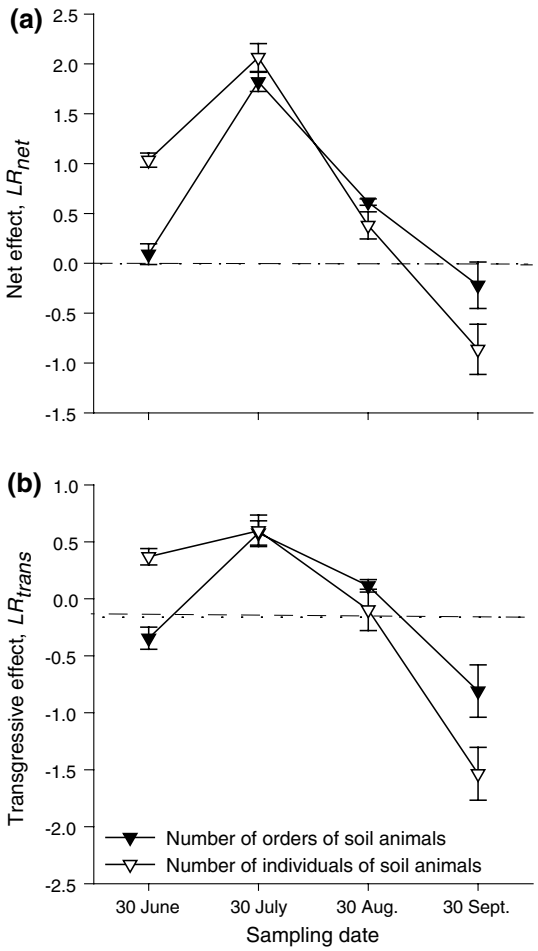

Fig. 3 **a** Mean net effect (LR_{net}) and **b** mean transgressive effect (LR_{trans}) of highest genotypic richness of *S. canadensis* leaf litter (mixture of 12 genotypes) on richness (*filled triangles*) and abundance (*open triangles*) of soil animals after 61–153 days of decomposition in the field. *Triangles* and *bars* represent means (±SE)

before genotypic richness: G16 increased the richness of soil organisms ($P = 0.035$) and the decomposition rate constants of C ($P = 0.012$) and P ($P = 0.002$), G19 affected the abundance of Acarina per sample ($P = 0.005$) but not per gram C ($P > 0.1$).

Discussion

Our results show that leaf litter samples of equal mass of the invasive species *Solidago canadensis* decompose significantly faster the higher their genotypic diversity. This effect was mainly due to a log-linear increase of genotypic richness of the litter, with additional contributions of the mixing ratio of leaf litter from the two sites Minhang and Putuo, but no additional effects of genotypic dissimilarity of litter mixtures of the same genotypic richness. Genotype richness positively affected not only the reduction in mass of C, N and—most strongly—P but also the richness and abundance of soil animals in litter samples.

Previous plant biodiversity experiments have demonstrated positive effects of plant species diversity on litter mass (Hector et al. 1999; Knops et al. 2001; Balvanera et al. 2006; Cardinale et al. 2006) and previous litter decomposition experiments have shown positive effects of litter species diversity on decomposition rates per mass (Gartner and Cardon 2004; Hättenschwiler et al. 2005). Taken together, this suggests that species diversity has a doubly positive effect on nutrient cycling in ecosystems, first via increased litter production and second via increased decomposition rates. The experiment reported here, in combination with other previous studies (Crutsinger et al. 2009; Schweitzer et al. 2005a), extends the second aspect to the level of genotypic richness within a single species. In addition, it provides an example where mixture, dissimilarity and identity effects could be tested together with pure richness effects of genotypic diversity. This contributes to accumulating evidence that the log-linear relationship between plant litter diversity and decomposition has a considerable degree of universality (Hooper et al. 2005; Schmid et al. 2009; Cardinale et al. 2011; Reich et al. 2012). This generality may even extend to different ecosystems such as forests and streams, although habitat conditions and evolutionary trajectories of soil biota may differ between these ecosystem types (Gessner et al. 2010).

In our study we collected leaf litter from different plant genotypes in the field. As a consequence, differences between genotypes not only reflected genetic variation but also environmental variation. Thus the effects of mixing ratio of litter from Minhang and Putuo could reflect environmental variation between sites, but it could also be due to genetic differences between genotypes from the two sites. The absence of additional effects of genotypic dissimilarity of litter samples ("holding constant" genotypic richness and mixing ratio by fitting these explanatory terms first in the ANOVA) on decomposition could suggest that environmental dissimilarity might be more important; but we could not measure this. Whatever the reason for the variation between genotypes, the strong effect of litter diversity within a single species on decomposition can positively affect nutrient recycling in stands of *S. canadensis*.

A novel aspect of our experiment is that we could demonstrate parallel effects of genotypic richness of litter samples on decomposition variables and on the richness and abundance of soil organisms found on the litter. More diverse litter was colonized faster by soil animals, which in turn stayed for longer on less diverse litter. The more rapid colonization was probably caused by higher genotypic richness rather than higher mass of C or N of the litter, because the total mass of litter samples was equal (6 g) at the beginning of the experiment. However, the initially slightly

higher mass of P in litter samples with high genotypic richness might have contributed to their attractiveness to soil animals, even though the positive relationship between litter diversity and P was reversed into a negative one as early as after the first month, when soil animals had barely arrived on the litter. Using the soil animals as covariables in the statistical analysis to explain litter diversity effects on remaining mass of C, N and P, we found that the higher abundance of Acarina—the group of soil animals with the highest number of individuals by far—on the more diverse litter samples fully explained the faster loss of C and N, although not that of P.

Taken together, the parallel effects of litter richness on decomposition variables and soil animals and the explanation of the mass loss of C and N by a diversity-induced higher abundance of Acarina suggest that by supporting higher richness and abundance of soil animals, genotypically more diverse litter leads to increased resource extraction from the litter, similar to the increased extraction of soil resources by more diverse as compared to less diverse plant communities (Balvanera et al. 2006). However, this analogy is not complete, because biodiversity experiments with plant communities so far only manipulated the resource extractors (the plants, corresponding to the soil animals in our case) but not the diversity of resources themselves, which we manipulated here. In addition, soil animals have both direct and indirect effects on litter decomposition (Petersen and Luxton 1982; Bradford et al. 2002). The genotypic litter diversity effects could in part have been mediated by indirect effects of higher richness and abundance of soil animals (in addition to the direct effects of resource extraction), for example, increased surface area for microorganisms or trophic effects between decomposers and predators. Another potential mechanism that has been invoked in biodiversity experiments with plant litter corresponds to facilitation, e.g., between high- and low-quality litter types via nutrient exchange through a water film or fungal hyphae (McTiernan et al. 1997; Hättenschwiler and Vitousek 2000; Hoorens et al. 2003). After decomposition, the decomposers seemed to leave the litter again, as suggested by the reversal of the effect of genotypic litter richness on soil animals towards the end of the experiment (see Table 2).

The generality of the litter diversity–soil animals–decomposition relationship was also reflected in the analyses using log ratios between mixtures and monocultures. Similar to the results compiled by Cardinale et al. (2006) for experiments manipulating species diversity, we found that even in an experiment manipulating genotypic diversity, mixtures typically outperformed the average and in some cases even the most extreme monoculture (Schmid et al. 2008). Transgressive over-performance of mixtures compared with the most extreme single genotype was most consistently observed for the effects of genotypic litter richness on richness and abundance of soil organisms (see Fig. 3). This supports previous views (Schläpfer et al. 1999; Allan et al. 2013) that diversity-begets-diversity effects generally are stronger than diversity-begets-processes effects. Considering the temporal variability of these effects over time found here and reported previously from other studies (Prescott et al. 2000), mixtures may be even more over-performing if multiple times are considered (Hector and Bagchi 2007; Isbell et al. 2011; Wang et al. 2012). Remarkably, the transgressive over-performance of mixtures in relation to richness and abundance of soil organisms occurred during the hottest month (July), suggesting that genotypic litter diversity increases the resistance of the decomposition process under stressful environmental conditions.

Litter diversity-begets-animal diversity effects may be due to specialization of different soil animals on different litter genotypes (resource specialization hypothesis). For example, more than 90 % of herbivorous insects feed on only one or a few types of plants and exhibit some degree of host specialization (Bernays and Graham 1988), leading to an increasing diversity of these insects with increasing diversity of plants. Plant diversity-begets-litter abundance-begets-animal abundance effects have been explained by the more individuals hypothesis (Crutsinger et al. 2006). However, in contrast to the typical biodiversity experiments with plants, where increased diversity also increases the amount of resources available for herbivores (Hunter and Price 1992), in litter decomposition experiments with equal starting mass such as ours more diverse litter obviously does not imply a higher amount of litter. The high abundance of soil animals thus may have been a consequence of litter diversity, i.e., a litter diversity-begets-animal abundance effect.

Compared to the genotypic richness effects, genotypic identity effects in our experiment were weaker than reported in some other studies (Schweitzer et al. 2005b; Madritch et al. 2006; Crutsinger et al. 2009). In our case, differences between individual genotypes, even though apparently large when comparing monocultures (see Fig. 1 and Fig. S2, Electronic Supplemental Material), may not have played out as much in mixtures as they did in the other studies. Also, the variation between individual genotypes in monocultures was quite "regular", without any clearly under- or over-performing genotypes. Perhaps more surprising than the absence of genotypic identity effects was the absence of genotypic dissimilarity effects in our experiment, contrasting, for example, with the strong effects of genotypic dissimilarity found in bacterial communities, where it increased complementary resource use and ecosystem functioning (Jousset et al. 2011). The reason for the absence of dissimilarity effects most likely was the

relatively similar average genotypic dissimilarity between genotypes in all communities (see Table S1, Electronic Supplemental Material). Apparently, our random assembly of litter compositions led to similar degrees of genotypic dissimilarity. This can be seen as a desirable design feature when concentrating on genotypic richness effects, but reduces the opportunities to additionally analyze genotypic dissimilarity effects.

In the context of the invasion ability of *S. canadensis*, it may be speculated whether high litter diversity can increase the invasion success of the species by promoting decomposition. First, the enhanced rate of nutrient release from genotypically more diverse litter may promote rhizome production and emergence of leaf rosettes in autumn, which can increase the shoot population in the next year (Hartnett and Bazzaz 1985). Accelerated litter decomposition can have large effects on soil nutrient availability and thereby other ecosystem processes (Godoy et al. 2010). A study in Long Island, USA, found that litter of exotic woody plants had a much higher rate of decomposition and N release than litter of native plants, thus increasing nutrient turnover in the ecosystem (Ashton et al. 2005). Studies in Linhai, Zhejiang, China, showed that, total P in soil can be significantly decreased in areas invaded by *S. canadensis* (Chen et al. 2012). The increased release from leaf litter of *S. canadensis* caused by genotypic diversity may remove P limitation and promote further invasion. Second, previous studies showed that plants can have greater productivity in the presence of soil animals than in their absence (Bardgett and Chan 1999; Cragg and Bardgett 2001). Thus, the increased richness and abundance of soil organisms during decomposition may have improved soil conditions and nutrient availability.

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