The response of decomposers (earthworms, springtails and microorganisms) to variations in species and functional group diversity of plants

Alexandru Milcu, Stephan Partsch, Reinhardt Langel, Stefan Scheu

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The responses of three decomposer groups (earthworms, springtails and microorganisms) to manipulations in plant species diversity (1, 2, 4, 8), plant functional group diversity (1, 2, 3, 4) and functional group identity (grasses, legumes, small herbs, tall herbs) were studied in a microcosm experiment. Separate and combined treatments with earthworms and springtails were set up. Two earthworm species representing major functional groups of earthworms in grasslands were investigated, the endogeic species *Aporrectodea caliginosa* (Savigny) and the anecic species *Lumbricus terrestris* L. For springtails three species were investigated, the hemiedaphic species *Heteromurus nitidus* (Leleup), *Folsomia candida* (Willem) and the euedaphic species *Protaphorura fimata* (Gisin). Plant species and functional group diversity beneficially affected *A. caliginosa* (increase in body weight and incorporation of ^{15}N from labelled litter) and *P. fimata* (density), presumably by changing the quality of belowground resources. In contrast, the biomass of *L. terrestris* decreased with plant species diversity but only in presence of legumes. For *H. nitidus* and *F. candida* the identity of plant functional groups was more important than plant species diversity per se. Also, the response of *F. candida* depended on earthworms. Microbial respiration was reduced by earthworms in more diverse plant communities, which correlated with root biomass. In contrast, microbial biomass was not affected by plant species diversity. The results suggest that belowground resource inputs from plant roots strongly modify decomposer performance and that the quality of the resources that enter the belowground subsystem is more important than their quantity. The responses of decomposers generally were not correlated with below- or aboveground plant productivity. In addition, the results document that effects of plant community composition on the performance of decomposer species depend on the presence of other decomposers.

A. Milcu, S. Partsch and S. Scheu, Institut für Zoologie, Technische Universität Darmstadt, Schnittspahnstr. 3, DE-64287 Darmstadt, Germany (amilcu@bio.tu-darmstadt.de). – R Langel, Forschungszentrum Waldökosysteme, Kompetenzzentrum Stabile Isotope, Büsgenweg. 2, DE- 37077 Göttingen, Germany.

Decomposers are crucial for transforming complex organic materials into inorganic forms without which dead organic material would accumulate irreversibly (Schlesinger 1997). The inextricable decomposer – producer co-dependency constitutes of the mineralization of organic matter by decomposers making nutrients available for producers to rebuild complex organic matter. Despite the fact that decomposer microorganisms also immobilize inorganic nutrients which may result in competition with producers, the two compartments essentially complement each other (Harte and Kinzig 1993).

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In attempts of linking below- and aboveground communities the feedback of plant communities to the decomposer food web is often neglected. The quantity and quality of resources produced by plant communities strongly influence the structure of soil food webs and their functioning (Wardle 2002, Scheu et al. 2003, De Deyn et al. 2004). Plant species effects manifests not only through the amount of litter returned to the soil (Wardle et al. 1995, Groffman et al. 1996) but also through the amount of soluble carbon compounds liberated via root exudates (Bais et al. 2004, Li et al. 2004), root and leaf chemical composition (Satchell 1967, Hendriksen 1990, Tian et al. 1993) and the extent to which they deplete nutrients in the soil (Grime 1994, Fransen et al. 1999).

Earthworms and springtails are key decomposers affecting plant performance (Scheu et al. 1999, Wurst et al. 2003). Earthworms as soil macrofauna decomposers modify the physical structure of the soil (Lee and Foster 1991, Lavelle et al. 1997), alter soil microbial community composition and functioning (Brown 1995, Scheu 2002), increase nutrient cycling (Parmelee et al. 1989, Edwards and Bohlen 1996) and affect plant growth and vegetation development (Thompson et al. 1993, Schmidt and Curry 1999, Zaller and Arnone 1999, Scheu 2003). Springtails are important microbial grazers which affect the structure and functioning of the microbial community in the rizosphere and plant nutrient availability (Rusek 1998, Gange 2000). Soil microorganisms compete with plants for nutrients (Kaye and Hart 1997, Hodge et al. 2000) and it has been documented that interactions between soil microorganisms and soil invertebrates significantly affect plant performance (Bonkowski and Scheu 2004). However, little is known how decomposers respond to differences in plant species and functional group diversity. The studies that investigated the effect of plant species diversity on the soil decomposer communities showed positive (Zaller and Arnone 1999, Spehn et al. 2000, Stephan et al. 2000) or no consistent effects (Wardle et al. 1999, Gastine et al. 2003, Hedlund et al. 2003, Salamon et al. 2004).

In this study we established a microcosm experiment to investigate the response of different functional groups of decomposers to variations in plant species and plant functional group diversity. We expected changes in plant biomass, root exudation and microbial community composition caused by reductions in plant diversity to strongly affect the structure of the decomposer community and interactions between decomposer functional groups. Specifically we hypothesized that (1) an increase in plant species and functional group diversity beneficially affect decomposer performance, (2) decomposer performance varies with functional group and plant species identity, and (3) interactions between soil macrofauna decomposers and fungal grazing soil invertebrates depend on plant community composition. Using microcosms these hypothesis were evaluated under controlled conditions and well defined manipulations of the decomposer community. The use of ^{15}N labelled litter allowed to track nutrient fluxes from dead organic matter into plants and animals.

Material and methods

Experimental set-up

The experiment was set up in microcosms consisting of PVC tubes (inner $\varnothing$ 10 cm, height 25 cm) which were sealed at the bottom with 40 μm mesh. The microcosms were filled with 1.4 kg of sieved (4 mm) soil (water content 13%). The soil (Eutric Fluvisoil, FAO Unesco (1997); pH 8.1, carbon content 4.6%, C/N ratio 15.7, sand content 15%, water content 13%) was taken from the northeast corner of the Jena Biodiversity Experiment field site (Thuringia, Germany; cf. Roscher et al. 2004). Prior to use the soil was defaunated by freezing at $-22^{\circ}C$ for 14 d. Defaunation by freezing effectively kills meso- and macrofauna, whereas microfauna (nematoda, protozoa) in large survive (Huhta et al. 1989). A layer of ^{15}N labeled roots of *Lolium perenne* (250 mg, 30 atom% ^{15}N; fragmented <1 mm) was placed 2 cm below the soil surface. After placing in the microcosms the soil was irrigated by adding two 50-ml portions of deionized water every second day for 8 d to leach nutrients released as a result of the defaunation procedure. Subsequently, microcosms were kept moist for another 14 d by adding 50 ml deionized water every third day; weeds germinating during this period were removed.

Plant species were selected from a species pool representing central European Arrhenatherion grasslands. A total of 43 plant species were used, grown from seeds in the defaunated soil and transplanted into the microcosms when the plants had grown to a height of 2–6 cm. Eight plant individuals consisting of four functional groups (grasses, legumes, small herbs, tall herbs) were transplanted into each microcosm in different combinations following the design of the Jena Biodiversity Experiment (Roscher et al. 2004). Plant functional groups were assessed using three groups of attributes: (1) above- and below ground morphological traits (2) phenological traits and (3) the ability for N_2 fixation. The seventeen variables created from the selected species attributes were analysed by a multivariate cluster method (Ward's method, Euclidian distance; Kaufman and Rousseeuw 1990) in order to identify species functional groups (Roscher et al. 2004). Monocultures and species mixtures were established forming a plant species and functional group diversity gradient as given in Table 1. A total of 64 different plant species mixtures were set up.

Two grams of litter material consisting mainly of grass leaves was placed on top of the soil subsequently to the

Table 1. Scheme of the 64 plant species mixtures set up in the experiment varying in species identity, number of species and composition of functional groups (grasses (G), small herbs (Sh), tall herbs (Th) and legumes (L)). Four animal treatments were set up per plant species mixture (control without animals, with earthworms, with Collembola, with earthworms and Collembola). (G): Ao = *Anthoxantum odoratum* L., Ap = *Alopecurus pratensis* L., Be = *Bromus erectus* HUDS., Bh = *Bromus hordeaceus* L., Cc = *Cynosurus cristatus* L., Dg = *Dactylis glomerata* L., Fp = *Festuca pratensis* HUDS., Fr = *Festuca rubra* L., Hl = *Holcus lanatus* L., PHp = *Phleum pratense* L., Pp = *Poa pratensis* L., Pt = *Poa trivialis* L., Tf = *Trisetum flavescens.* (Sh): Bp = *Bellis perennis* L., Gh = *Glechoma hederacea* L., La = *Leontodon autumnalis* L. Lh = *Leontodon hispidus* L., Pl = *Plantago lancelolata* L., Pm = *Plantago media* L., Pv = *Prunella vulgaris* L., To = *Taraxacum officinale* WEBER, Vc = *Veronica chamaedrys* L. (Th): Am = *Achillea millefolium* L., Cb = *Crepis benis* L., Cj = *Centaurea jacea* L., Co = *Cirsium oleraceum* L., Cp = *Cardamine pratensis* L., Dc = *Daucus carota* L., Ga = *Galium mollugo* L., Ka = *Knautia arvensis* L., Lv = *Leucanthemum vulgare* Lam., Ra = *Rumex acetosa* L., TRp = *Tragopogon pratensis* L. (L): Lp = *Lathyrus pratensis* L., Lc = *Lotus corniculatus* L., Ml = *Medicago lupulina* L., Ms = *Medicago x varia* MARTYN, Ov = *Onobrychis viciifolia* SCOP., Td = *Trifolium dubium* SIBTH., Th = *Trifolium hybridum* L., Tr = *Trifolium repens* L., Tp = *Trifolium pratense* L., VIc = *Vicia cracca* L.

Species mixture	Species diversity	Functional group diversity	Functional group composition	Species
1–16	1	1	4 G, 4 Sh, 4 Th, 4 L	monoculture of Cc; Fp; Fr; Pp; Pl; Bp; Pv; Gh; Co; Dc; Cb; Gm; Lp; Vic; Ov; Ms
17–18	2	1	2G	Fp, Dg; Fr, Tf
19–20	2	1	2 Sh	Bp, To; Pl, Bp
21–22	2	1	2 Th	Cb, Dc; Cj, Ra
23–24	2	1	2 L	Ov, Tr; Lc, Tp
25	2	2	GSh	Tf, To
26	2	2	GSh	Pp, Pl
27	2	2	ThL	Cj, Td
28	2	2	ThL	Dc, Ms
29	2	2	GTh	Fp, Cj
30	2	2	GTh	Ap, Dc
31	2	2	ShL	La, Tr
32	2	2	ShL	Pl, Td
33	4	1	G	Ap, Pt, Ao, Be
34	4	1	Sh	Pv, Pm, Pl, Lh
35	4	1	Th	Am, Dc, Cp, Ka
36	4	1	L	Lc, Ov, Ms, Tr
37	4	2	GSh	Pt, Be, Pl, Pv
38	4	2	ThL	Cp, Cb, Tr, VIc
39	4	2	GTh	Fp, Pt, Am, Cb
40	4	2	ShL	To, Pl, Tr, Lp
41	4	3	GShTh	Ao, Pt, Pv, Am
42	4	3	GThL	Tf, TRp, Cb, Ms
43	4	3	GShL	Php, Bp, Th, VIc
44	4	3	ShThL	Bp, La, Ka, VIc
45	4	4	GShThL	Bh, La, Lv, Ml
46	4	4	GShThL	Ao, Pl, Co, Td
47	4	4	GShThL	Ao, Pv, Ka, Tp
48	4	4	GShThL	Fp, Pl, Am, Ov
49	8	1	G	Hl, Cc, Pt, Dg, Ao, Fr, Ap, Tf
50	8	1	Sh	Bp, To, Lh, La, Gh, Vc, Pm, Pv
51	8	1	Th	Ka, Ra, Dc, Lv, Co, Gm, Cb, Cj,
52	8	1	L	Tp, Ov, Ms, Td, Lp, Th, Tr, Lc
53	8	2	GSh	Ao, Fr, Bh, Cc, Pl, Lh, Gh, To
54	8	2	ThL	Cp, Ka, Cb, Am, Lc, Td, Ml, Th
55	8	2	GTh	Php, Fr, Be, Ap, Ra, Cj, Cb, Cp
56	8	2	ShL	Bp, Vc, To, La, Ml, Lp, VIc, Td
57	8	3	GShTh	Fp, Be, Pm, Pv, Lh, Am, Cj, TRp
58	8	3	GThL	Ao, Pt, Be, Co, Lv, Ov, Th, Lc
59	8	3	GShL	Cc, Php, Tf, Gh, Vc, Pm, Tr, Lc
60	8	3	ShThL	Bp, Lh, Cb, Gm, Ra, Lc, Tr, Ov
61	8	4	GShThL	Pt, Php, Lh, Gh, Ka, Ra, Td, Th
62	8	4	GShThL	Php, Pt, To, Pm, Ra, Co, Ml, Td
63	8	4	GShThL	Pt, Tf, Pl, Lh, Dc, Co, Td, Ml
64	8	4	GShThL	Hl, Bh, Pl, La, Lv, Cb, Tr, Ov

transplantation of plant seedlings. The litter material (2.53% N, C/N ratio 17.3) was collected near the site from which the soil had been taken, dried at 60°C and cut into pieces about 3 cm in length.

One subadult *Aporrectodea caliginosa* (Savigny) and one juvenile of *Lumbricus terrestris* L. were added to half of the microcosms. *A. caliginosa* is an endogeic geophagous earthworm species, whereas *L. terrestris* is an anecic litter feeding species. Both species are among the dominant species at the Jena Biodiversity Experiment field site. Earthworms were weighed prior to placement in the microcosms (average fresh weight 863 and 927 mg for *A. caliginosa* and *L. terrestris*, respectively). Twenty individuals of each of three Collembola

species, *Heteromurus nitidus* (Leleup), *Folsomia candida* (Willem) and *Protaphorura fimata* (Gisin), were added to half of the microcosms creating four treatments in a two factorial design (control, with earthworms, with Collembola, with earthworms and Collembola). The Collembola species were taken from laboratory cultures, where they were kept at constant temperature (17°C) and fed on bakery yeast. *Folsomia candida* and *Heteromurus nitidus* are hemiedaphic species dwelling in the litter layer and upper soil layers. *H. nitidus* is present at the Jena field site. *Protaphorura fimata* is an euedaphic species living in deeper soil layers. In total 256 microcosms were set up.

During the experiment the microcosms were kept in a temperature controlled greenhouse at a day–night regime of 16–8 h and 20°C ± 2. During the experiment the water regime was increased from irrigating three times per week with 25 (week 1–2), 40 (week 3–5), 50 ml (week 5–7) deionized water to 50 (week 8–9) and 80 ml daily (week 9–11).

Sampling and analytical procedure

After 11 weeks the earthworms were collected by hand sorting, washed, dried for 1 min on filter paper and weighed. Then, earthworms were killed by freezing, dried at 60°C for three days and stored in a desiccator. The anterior end of *A. caliginosa* without gut content was used for analysing total nitrogen concentration and ^{15}N signatures which were determined by a coupled system consisting of an elemental analyzer (NA 1500, Carlo Erba, Milan) and a gas isotope mass spectrometer (MAT 251, Finnegan; Reineking et al. 1993). For ^{15}N atmospheric N_2 served as primary standard and acetanilide (C_8H_9NO; Merk, Darmstadt) as internal calibration.

Collembola were sampled taking a soil core of a diameter of 5 cm from each of the microcosms to a depth of 5 cm. Collembola were extracted by heat (Macfadyen 1961), separated into species and counted.

Microbial biomass was measured using the substrate-induced respiration (SIR) method (Anderson and Domsch 1978). The microbial respiratory response to addition of glucose was measured at hourly intervals in an electrolytic O_2 microcompensation apparatus for 24 h at 22°C (Scheu 1992). Microbial biomass (C_{mic}; $\mu g\ C\ g^{-1}$ soil) was measured after the addition of a sufficient amount of glucose as substrate in order to saturate the catabolic activity of microorganisms (4 mg glucose g^{-1} soil dry weight). The maximum initial respiratory response (MIRR; $\mu g\ O_2\ g^{-1}$ soil dry weight h^{-1}) was calculated as the average of the lowest three readings within the first 11 h and microbial biomass was calculated as $C_{mic} = 38 \times MIRR$ ($\mu g\ C_{mic}\ g^{-1}$ soil dry weight) (Anderson and Domsch 1978, Beck et al. 1997). Soil basal respiration ($\mu l\ O_2\ g^{-1}$ soil dry weight h^{-1}) was measured as mean of the O_2 consumption rates of unamended soil of hours 15 to 20 after start of the measurements.

We used analysis of variance (ANOVA) as part of the GLM procedure in SAS 8 (SAS Inst., Cary, Florida, USA) to test in a hierarchical order (type I sum of squares) the effects of earthworms (E), Collembola (C), plant species diversity (S), plant functional group diversity (FG) and presence/absence of legumes (L), grasses (G), small herbs (Sh) and tall herbs (Th) as treatment factors. The experimental design does not allow to fully separate the effects of S and FG which are partially confounded; the F-values given in text and tables for the effects of S (log-linear and deviation) and FG (linear and deviation), and their interactions with other factors refer to those where the respective factor (and interaction) was fitted first (Neter and Wasserman 1974, Schmid et al. 2002). No interaction term between S and FG was calculated. The effects of presence/absence of legumes (L), grasses (G), small herbs (Sh) and tall herbs (Th) and there interactions with earthworms and Collembola always were fitted after fitting S and FG. F-values of L × G interactions refer to those fitting the interaction before functional groups. In analyses of covariance (ANCOVA) plant shoot, root and total biomass were fitted as covariables to separate the effects driven by changes in plant primary production from diversity effects; covariables always were fitted before fitting S and FG (and their interactions with other factors). Microbial biomass and respiration were also analysed by ANCOVA using the soil water content as covariable to control for differences caused by soil moisture. Interactions between factors that were not significant were excluded from the model. Prior to ANOVA data were inspected for homogeneity of variance and log-transformed if required.

Results

Earthworms

Survival and body weight

In total, 92% of the 128 individuals of *A. caliginosa* added survived until the end of the experiment. On average, the biomass of *A. caliginosa* increased by 17%, however, the increase was significantly more pronounced in presence (+25%) than in absence of Collembola (+9%; Table 2). Furthermore, the body weight of *A. caliginosa* increased with plant species and FG diversity but only in treatments without Collembola (Fig. 1a, 1b). Shoot, root and total plant biomass (fitted as covariables) did not significantly affect the biomass of *A. caliginosa* ($P = 0.32$, $P = 0.83$ and $P = 0.34$, respectively),

Table 2. ANOVA table of F-values on the effect of Collembola (C), number of plant species (S), number of plant functional groups (FG) and presence of legumes (L), grasses (G), small herbs (Sh) and tall herbs (Th) on changes in body weight, tissue nitrogen concentrations and ^{15}N atom% in *Aporrectodea caliginosa*.

Variables analysed Treatment factors	Changes in body weight		Tissue N (%)		^{15}N atom%	
C	**$F_{1/97}=15.75$**	**$P=0.0001$**	$F_{1/82}=0.39$	$P=0.5361$	**$F_{1/82}=4.54$**	**$P=0.0361$**
FG	$F_{3/97}=1.39$	$P=0.2499$	$F_{3/82}=2.21$	$P=0.0937$	**$F_{3/82}=3.61$**	**$P=0.0167$**
FG linear	$F_{1/124}=2.63$	$P=0.1075$	$F_{1/109}=0.01$	$P=0.9334$	$F_{1/109}=3.34$	$P=0.0704$
FG deviation	$F_{2/124}=0.12$	$P=0.8883$	$F_{2/109}=3.00$	$P=0.0541$	$F_{2/109}=3.00$	$P=0.0540$
S	**$F_{3/97}=5.78$**	**$P=0.0011$**	$F_{3/82}=0.81$	$P=0.4915$	$F_{3/82}=2.62$	$P=0.0561$
S log-linear	$F_{1/124}=8.25$	$P=0.0048$	$F_{1/109}=0.21$	$P=0.6493$	$F_{1/109}=3.64$	$P=0.0590$
S deviation	$F_{2/124}=2.30$	$P=0.1048$	$F_{2/109}=0.99$	$P=0.3749$	$F_{2/109}=1.49$	$P=0.2292$
L	$F_{1/97}=0.56$	$P=0.4543$	$F_{1/82}=3.65$	$P=0.0597$	**$F_{1/82}=5.33$**	**$P=0.0235$**
G	$F_{1/97}=0.12$	$P=0.7249$	$F_{1/82}=0.31$	$P=0.5767$	$F_{1/82}=1.59$	$P=0.2105$
Sh	$F_{1/97}=0.16$	$P=0.6879$	$F_{1/82}=1.29$	$P=0.2586$	$F_{1/82}=0.04$	$P=0.8370$
Th	$F_{1/97}=0.49$	$P=0.4847$	$F_{1/82}=0.06$	$P=0.8049$	$F_{1/82}=1.87$	$P=0.1757$
C × FG	**$F_{3/97}=4.31$**	**$P=0.0068$**	**$F_{3/82}=3.09$**	**$P=0.0315$**	$F_{1/82}=0.74$	$P=0.5287$
C × S	**$F_{3/97}=8.24$**	**$P<0.0001$**	$F_{3/82}=1.04$	$P=0.3804$	$F_{1/82}=1.00$	$P=0.3990$
C × L	$F_{3/97}=0.78$	$P=0.3779$	**$F_{1/82}=7.03$**	**$P=0.0096$**	**$F_{3/82}=8.44$**	**$P=0.0047$**
C × G	$F_{3/97}=0.14$	$P=0.3779$	$F_{3/82}=3.12$	$P=0.0812$	$F_{3/82}=3.28$	$P=0.0738$
C × Sh	$F_{3/97}=1.43$	$P=0.2345$	$F_{3/82}=0.18$	$P=0.6739$	$F_{3/82}=2.74$	$P=0.1017$
C × Th	$F_{3/97}=0.46$	$P=0.4979$	$F_{3/82}=2.10$	$P=0,1510$	$F_{3/82}=0.25$	$P=0.6188$
S × L	**$F_{3/97}=2.93$**	**$P=0.0372$**	$F_{3/82}=0.64$	$P=0.5905$	$F_{3/82}=2.65$	$P=0.0541$
S × G	**$F_{3/97}=3.17$**	**$P=0.0277$**	$F_{3/82}=1.40$	$P=0.2497$	$F_{3/82}=1.13$	$P=0.3407$
S × Sh	$F_{3/97}=0.64$	$P=0.5910$	$F_{3/82}=0.61$	$P=0.6127$	$F_{3/82}=1.10$	$P=0.3534$
S × Th	**$F_{2/97}=2.90$**	**$P=0.0391$**	$F_{2/82}=1.72$	$P=0.1695$	$F_{2/82}=0.65$	$P=0.5864$

suggesting that the plant species and functional group effects were not due to increased plant biomass.

The percentage of *L. terrestris* individuals collected at the end of the experiment was only around 60%; despite the 10 cm transparent fences used, some individuals managed to escape form the pots in the last weeks of the experiment when the plants were used to evade. On average, the biomass of the surviving individuals had increased by 34%. In contrast to *A. caliginosa* the presence of Collembola did not affect the body weight of *L. terrestris*, but it decreased with plant species diversity in treatments with legumes, whereas in treatments without legumes it was at a maximum at the maximum plant species diversity (S × L interaction $F_{3,42}=4.06$, $P=0.0128$; Fig. 1c).

Tissue nitrogen

Tissue nitrogen concentration was only analysed for *A. caliginosa*. It was affected by plant functional group diversity but only in the treatment with Collembola being at a minimum at the three functional group diversity level (significant C × FG interaction; Table 2). The effect of plant functional group diversity likely was caused by legumes (significant C × L interaction; Table 2); without legumes Collembola decreased the concentration of nitrogen in earthworm tissue from 13.1% to 12.8% suggesting that Collembola and earthworms competed for nitrogen resources but only if there were no legumes (Fig. 2a).

^{15}N incorporation

Incorporation of ^{15}N from the litter was only analysed for *A. caliginosa*. Similar to tissue nitrogen concentration the ^{15}N atom% in *A. caliginosa* depended on Collembola and plant functional group diversity, with legumes contributing most to this effect (Table 2). In presence of legumes and without Collembola earthworm tissue ^{15}N atom% slightly increased; in contrast, in presence of Collembola it decreased (Fig. 2b). Again, this suggests that presence of legumes provided additional nitrogen that diminished the competition for nitrogen between *A. caliginosa* and Collembola that occurred in the absence of legumes. As a result the total earthworm N tissue content did not decrease but the ^{15}N atom% declined, presumably in part through assimilation of nitrogen with low ^{15}N signature typical for legume fixed nitrogen.

Collembola

Collembola densities increased during the experiment reaching the upper range occurring in temperate grasslands (average of 220.000 ind. m^{-2}). Total number of Collembola was reduced by earthworms (−20%) and in the presence of legumes (−23%), but was increased in the presence of grasses (+66%). Collembola species responded differently to plant species diversity, functional group diversity, identity of functional groups and the presence of earthworms. Numbers of *P. fimata* increased with plant species and functional group diversity, while that of *F. candida* was at a minimum in the two species mixtures (Table 3). Including plant root biomass as covariable the effect of plant diversity on the density of *F. candida* declined ($F_{1,94}=2.41$, $P=0.0720$) whereas in *P. fimata* it increased ($F_{1,94}=8.00$, $P=0.0057$) suggesting that the plant diversity effect in part was due to differences in root biomass in *F. candida* but

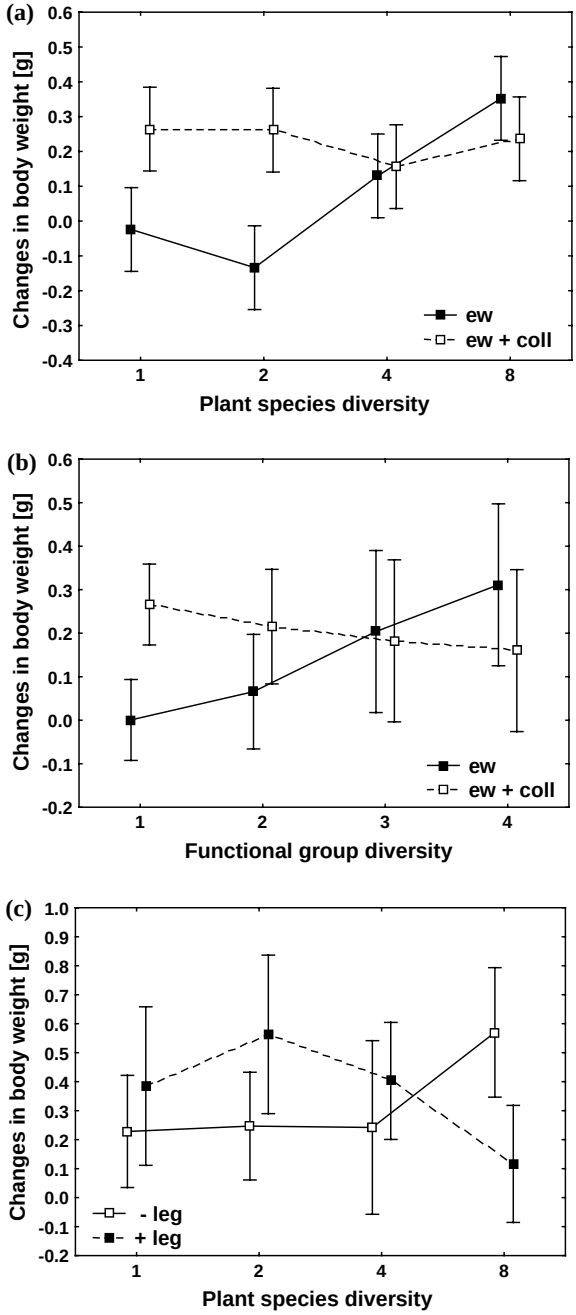

Fig. 1. (a) Body weight of *Aporrectodea caliginosa* as affected by plant species diversity and Collembola and (b) plant functional group diversity and Collembola, and (c) body weight of *Lumbricus terrestris* as affected by plant species diversity and presence of legumes. Error bars represent ±SE.

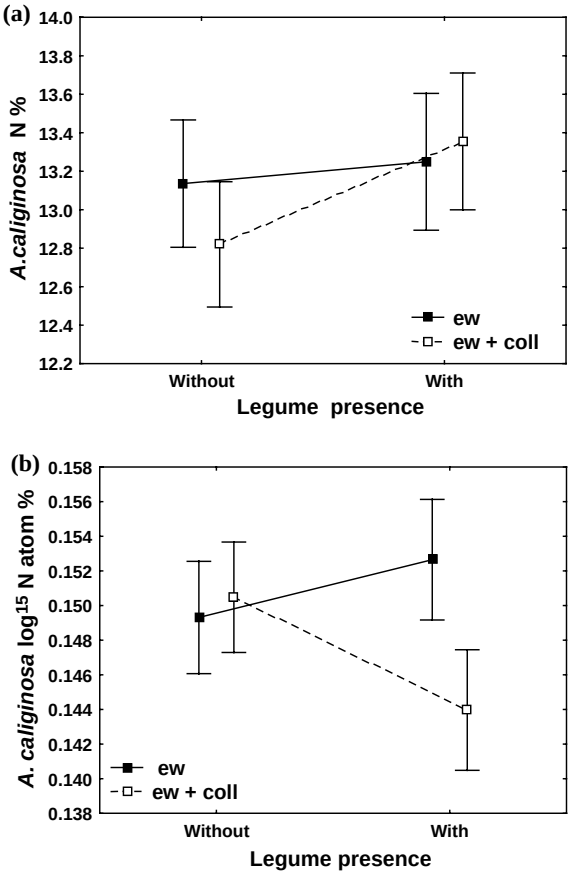

Fig. 2. (a) Tissue nitrogen concentration and (b) ^{15}N atom% of *Aporrectodea caliginosa* as affected by Collembola and presence of legumes. Error bars represent ±SE.

not in *P. fimata*. Using shoot biomass, total plant biomass or the biomass ratio between different plant fuctional groups per pot as covariables did not affect the plant diversity effect on *P. fimata* suggesting that neither of these factors contributed to the observed effect of plant species diversity on the numbers of *P. fimata.*

Presence of legumes reduced the density of *F. candida* (−23%) and *H. nitidus* (−49%), whereas grasses increased the density of these Collembola species (+146 and +90% for *P. fimata* and *H. nitidus*, respectively). However, for *H. nitidus* the effect depended on the presence of earthworms. In the presence of earthworms grasses lead to a more than four fold higher density of *H. nitidus* (significant Ew × G interaction, Table 3, Fig. 3a). Also, legumes affected the density of *H. nitidus* but again, the effect depended on the presence of earthworms. In the presence of earthworms legumes reduced the density of *H. nitidus* by 70% (significant Ew × L interaction, Table 3, Fig. 3b).

Of the grass species, mixtures containing *T. flavescens, F. rubra* and *F. pratensis* strongly increased the density of *P. fimata,* suggesting that certain combinations of plant species affected the reproduction and survival of Collembola. The significant interaction between legumes and grasses reflects that the increase in Collembola density in presence of grasses was less pronounced if legumes were also present. Tall herbs also affected the

Table 3. ANOVA table of F-values on the effect of earthworms (E), number of plant species (S), number of plant functional groups (FG) and presence of legumes (L), grasses (G), small herbs (Sh) and tall herbs (Th) on the density of the Collembola species studied (*Folsomia candida*, *Protaphorura fimata* and *Heteromurus nitidus*).

Collembola	*F. candida*		*P. fimata*		*H. nitidus*		All three species	
Treatment factors								
E	$F_{1/94}=3.30$	$P=0.0725$	$F_{1/94}=2.55$	$P=0.1138$	$F_{1/94}=0.10$	$P=0.7535$	**$F_{1/94}=6.04$**	**$P=0.0158$**
FG	$F_{3/94}=0.53$	$P=0.6634$	**$F_{3/94}=3.41$**	**$P=0.0208$**	$F_{3/94}=0.93$	$P=0.4301$	$F_{3/94}=0.87$	$P=0.4587$
FG log linear	$F_{3/94}=3.11$	$P=0.0805$	**$F_{1/122}=5.66$**	**$P=0.0189$**	$F_{1/122}=0.01$	$P=0.9163$	$F_{1/122}=1.25$	$P=0.2655$
FG deviation	$F_{3/94}=2.08$	$P=0.1293$	$F_{1/122}=0.84$	$P=0.4335$	$F_{1/122}=1.12$	$P=0.3309$	$F_{1/122}=0.37$	$P=0.6904$
S	**$F_{3/94}=3.18$**	**$P=0.0274$**	**$F_{3/94}=4.57$**	**$P=0.0050$**	$F_{3/94}=0.20$	$P=0.8932$	$F_{3/94}=2.69$	$P=0.0506$
S log linear	$F_{1/122}=3.17$	$P=0.0775$	**$F_{1/122}=5.63$**	**$P=0.0192$**	$F_{1/122}=0.28$	$P=0.5967$	$F_{1/122}=2.57$	$P=0.1113$
S deviation	$F_{2/122}=2.38$	$P=0.0967$	$F_{1/122}=2.22$	$P=0.1128$	$F_{1/122}=0.10$	$P=0.9028$	$F_{1/122}=1.65$	$P=0.2017$
L	**$F_{1/94}=5.24$**	**$P=0.0243$**	$F_{1/94}=1.92$	$P=0.1688$	**$F_{1/94}=9.19$**	**$P=0.0031$**	**$F_{1/94}=6.44$**	**$P=0.0128$**
G	$F_{1/94}=0.82$	$P=0.3678$	**$F_{1/94}=39.35$**	**$P<0.0001$**	**$F_{1/94}=23.17$**	**$P<0.0001$**	**$F_{1/94}=21.02$**	**$P<0.0001$**
Sh	$F_{1/94}=2.87$	$P=0.0934$	$F_{1/94}=3.46$	$P=0.0662$	$F_{1/94}=0.06$	$P=0.8123$	$F_{1/94}=0.36$	$P=0.5488$
Th	$F_{1/94}=2.24$	$P=0.1375$	**$F_{1/94}=9.16$**	**$P=0.0032$**	$F_{1/94}=2.38$	$P=0.1260$	$F_{1/94}=2.08$	$P=0.1522$
L × G	**$F_{3/94}=4.80$**	**$P=0.0037$**	**$F_{3/94}=16.28$**	**$P<0.0001$**	**$F_{3/94}=7.92$**	**$P<0.0001$**	**$F_{3/94}=7.07$**	**$P=0.0002$**
E × FG	$F_{3/94}=0.04$	$P=0.9889$	$F_{3/94}=0.46$	$P=0.7089$	$F_{1/94}=1.46$	$P=0.2304$	$F_{1/94}=0.47$	$P=0.7042$
E × S	$F_{3/94}=2.62$	$P=0.0554$	$F_{3/94}=2.21$	$P=0.0923$	$F_{1/94}=2.15$	$P=0.0987$	$F_{1/94}=1.92$	$P=0.1319$
E × L	$F_{3/94}=2.45$	$P=0.1209$	$F_{1/94}=0.10$	$P=0.7528$	**$F_{3/94}=6.52$**	**$P=0.0123$**	$F_{1/94}=1.11$	$P=0.2948$
E × G	$F_{3/94}=1.08$	$P=0.3005$	$F_{3/94}=0.03$	$P=0.8715$	**$F_{3/94}=6.63$**	**$P=0.0116$**	$F_{3/94}=0.76$	$P=0.3861$
E × Sh	$F_{3/94}=2.27$	$P=0.1350$	$F_{3/94}=0.00$	$P=0.9587$	$F_{3/94}=0.51$	$P=0.4778$	$F_{3/94}=1.22$	$P=0.2728$
E × Th	$F_{3/97}=1.21$	$P=0.2747$	$F_{3/94}=0.18$	$P=0.6710$	$F_{3/94}=0.48$	$P=0.4908$	$F_{3/94}=0.67$	$P=0.4136$
S × L	$F_{3/94}=1.32$	$P=0.2718$	$F_{3/94}=0.85$	$P=0.4722$	$F_{3/94}=1.95$	$P=0.1264$	$F_{3/94}=1.84$	$P=0.1541$
S × G	$F_{3/94}=0.14$	$P=0.9363$	$F_{3/94}=0.79$	$P=0.5013$	$F_{3/94}=0.16$	$P=0.9210$	$F_{3/94}=0.63$	$P=0.6001$
S × Sh	$F_{3/94}=1.28$	$P=0.2872$	$F_{3/94}=0.54$	$P=0.6555$	$F_{3/94}=1.01$	$P=0.3936$	$F_{3/94}=0.60$	$P=0.6134$
S × Th	**$F_{3/94}=4.56$**	**$P=0.0050$**	$F_{2/94}=2.07$	$P=0.1089$	$F_{2/94}=0.96$	$P=0.4138$	**$F_{3/94}=4.38$**	**$P=0.0062$**

density of *P. fimata*; in presence of tall herbs the density was reduced by 25%.

Presence of earthworms generally tended to affect each of the Collembola species but their effect varied with plant species diversity ($P<0.1$) for each of the three species (E × S interactions; Table 3). On average, the presence of earthworms reduced the density of *F. candida* (−47%; Table 3) which was most pronounced in the two plant species treatment (−59%) and least pronounced in the one plant species treatment (−28%), however, the effects were only marginally significant (E × S interaction, Table 3). In contrast to *F. candida*, *P. fimata* was less sensitive to the presence of earthworms.

Microorganisms

Microbial basal respiration but not microbial biomass was significantly affected by soil water content as indicated by ANCOVA (Table 4). The presence of earthworms reduced microbial basal respiration by 17%, whereas Collembola did not affect microbial respiration (Fig. 4a). Microbial basal respiration but not microbial biomass was significantly affected by plant species and functional group diversity, decreasing log-linearly and linearly, respectively, with the increase in species and functional group diversity (Fig. 4b, 4c). Basal respiration was at a maximum in the two species treatment and at a minimum in the eight species treatment with the one and four species treatment being intermediate. In the presence of tall herbs basal respiration was increased by ca 5%.

Microbial biomass was only affected by earthworms; in the presence of earthworms it decreased on average by approximatively 4%. Including root biomass, total plant biomass and the biomass ratio between plant functional groups per pot as covariables suggest that root biomass contributed to the plant diversity effect on basal respiration (drop of P-values to 0.0644), but these parameters did not contribute to the reduction in microbial biomass in the presence of earthworms nor to the effect of tall herbs on soil respiration.

Data on the response of plants to decomposer manipulation is subject to another paper (S. Partsch, A. Milcu and S. Scheu, unpubl.). We did not find unnaturally high root biomass in the microcosms as compared with the field conditions.

Discussion

Earthworms

Earthworms are considered to be strongly influenced by the amount of plant residues entering the soil (Edwards and Bohlen 1996). Since most of the biomass produced by plants ultimately enters the detrital system earthworms should benefit from increased primary production. Since primary production increases with plant species richness in grassland communities (Hector et al. 1999, Tilman et al. 2001) plant species diversity likely also impacts earthworms and other decomposers. In fact, in field experiments Zaller and Arnone (1999) and Spehn et al. (2000) found the biomass of earthworms to increase with increasing plant species richness.

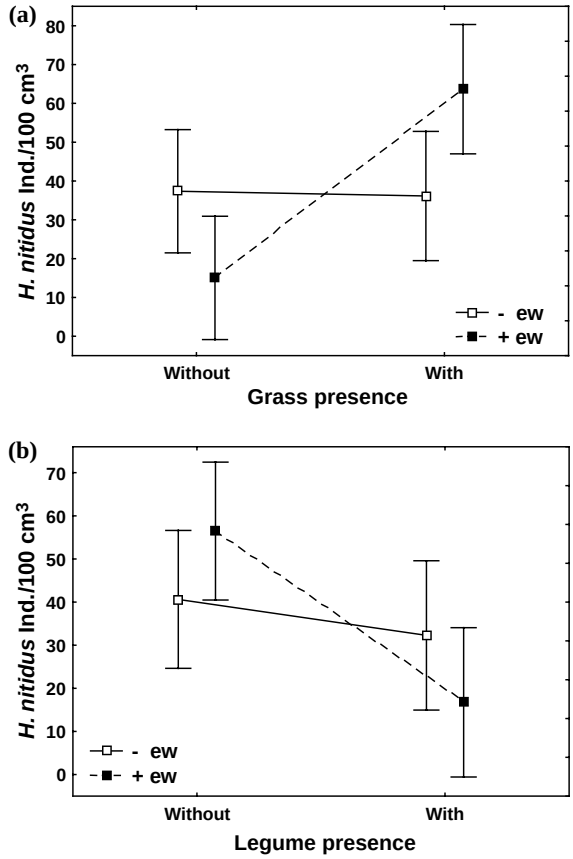

Fig. 3. Densities of *Heteromurus nitidus* as affected by (a) earthworms and presence of grasses and (b) earthworms and presence of legumes. Error bars represent ±SE.

In both studies this was explained by increased input of resources but also by changes in resource quality. In field experiments it is difficult to disentangle effects of resource quality from those of resource quantity (Scheu and Schaefer 1998, Maraun et al. 2001). Furthermore, it is difficult to differentiate between effects caused by litter materials from above the ground from those caused by root derived resources. Results of the present study suggest that the increase in earthworm biomass with increasing plant species diversity is largely caused by root derived resources since the same aboveground litter resources were added to each of the treatments. However, results of ANCOVAs suggest that the increase in body weight of *A. caliginosa* with increase in plant species richness was not related to root or total plant biomass. Presumably, the increase in earthworm body weight with increasing plant diversity was caused by changes in the quality rather than the quantity of rhizodeposits. Possibly, rhizodeposits are more diverse in more diverse plant communities. In contrast to the study of Spehn et al. (2000), the increase in body weight of *A. caliginosa* was not related to the presence of legumes which provide shoot and root litter resources rich in nitrogen. This supports the conclusion of Tiunov and Scheu (2004) that endogeic earthworms are primarily limited by carbon rather than nitrogen. Interestingly, the increase in biomass of *A. caliginosa* in more diverse plant communities was associated with an increase in the exploitation of the ^{15}N labelled litter material added to the microcosms. This indicates that earthworms in the more diverse plant communities were more active and therefore more efficiently exploited organic resources in soil.

A striking result of the present study was that at low plant diversity the increase in body weight of *A. caliginosa* was more pronounced in presence of Collembola. This suggests that Collembola facilitated the resource acquisition by earthworms. However, as indicated by tissue ^{15}N concentrations this was not the case for the litter resources added to the microcosms. Also, reduced tissue nitrogen concentration of *A. caliginosa* in presence of Collembola (treatments without legumes) suggests that Collembola and earthworms competed for nitrogen resources which is consistent with earlier studies

Table 4. ANCOVA table of F-values on the effect of Earthworms (E), Collembola (C), number of plant species (S), number of plant functional groups (FG) and presence of legumes (L), grasses (G), small herbs (Sh) and tall herbs (Th) on microbial basal respiration and microbial biomass; soil water content was used as covariable.

Variables analysed Treatment factors	Basal respiration		Microbial biomass	
Water	**$F_{1/237}=52.32$**	**$P<0.0001$**	$F_{1/237}=0.28$	$P=0.5947$
E	**$F_{1/237}=43.44$**	**$P<0.0001$**	**$F_{1/237}=7.15$**	**$P=0.0080$**
C	$F_{1/237}=0.01$	$P=0.9218$	$F_{1/237}=0.87$	$P=0.3520$
E × C	$F_{1/237}=1.76$	$P=0.1858$	$F_{1/237}=0.25$	$P=0.6173$
FG	$F_{3/237}=1.34$	$P=0.2606$	$F_{3/237}=1.29$	$P=0.2771$
FG linear	**$F_{1/247}=9.51$**	**$P=0.0023$**	$F_{1/247}=1.79$	$P=0.1827$
FG deviation	$F_{1/247}=0.68$	$P=0.5078$	$F_{1/247}=1.03$	$P=0.3587$
S	**$F_{3/237}=3.13$**	**$P=0.0263$**	$F_{3/237}=1.03$	$P=0.3787$
S log linear	**$F_{1/247}=5.85$**	**$P=0.0163$**	$F_{1/247}=0.71$	$P=0.4017$
S deviation	$F_{1/247}=2.47$	$P=0.0870$	$F_{1/247}=1.15$	$P=0.3169$
G	$F_{1/237}=2,05$	$P=0.1539$	$F_{1/237}=1.53$	$P=0.2176$
Sh	$F_{1/237}=0.52$	$P=0.4733$	$F_{1/237}=3.41$	$P=0.0662$
Th	**$F_{1/237}=6.95$**	**$P=0.0090$**	$F_{1/237}=0.03$	$P=0.8733$
L	$F_{1/237}=0.81$	$P=0.3698$	$F_{1/237}=1.70$	$P=0.1929$

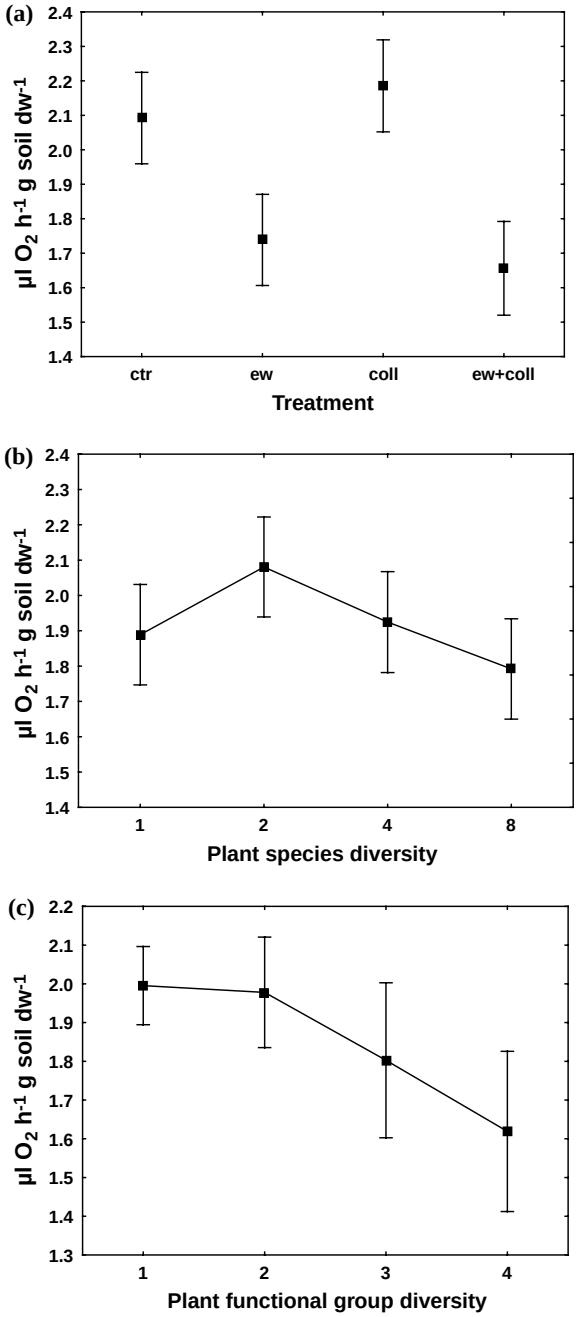

Fig. 4. Microbial basal respiration as affected by (a) decomposers, (b) plant species diversity and (c) plant functional group diversity. Adjusted means and standard deviation calculated using water as covariable (average water content 30.8%). Error bars represent ±SE.

(Scheu et al. 1999). Overall, the results indicate that the relationship between earthworms and Collembola is complex; depending on the diversity of the plant community and the element considered (C or N). Collembola may facilitate or inhibit earthworm resource acquisition.

Compared to the endogeic species *A. caliginosa* which predominantly feeds on organic resources in the soil, the anecic species *L. terresris* was less responsive to the experimental treatments. Anecic species strongly rely on litter input form above the ground (Edwards and Bohlen 1996). Since each of the treatments was set up with the same litter material, the lower responsiveness of *L. terrestris* was expected. However, changes in body weight of *L. terrestris* were also affected by plant species diversity, but this varied significantly with the presence of legumes. Without legumes earthworm body weight only increased in the highest plant diversity treatment whereas in presence of legumes it was at a maximum in the two species treatment and then declined at higher plant species diversity. The increase in biomass of *L. terrestris* suggests that anecic earthworm species also rely at least in part on belowground resources. The increase in biomass at high plant species diversity (in absence of legumes) supports our conclusion that earthworms may benefit from more diverse rhizodeposits.

Collembola

In contrast to our expectation the density of Collembola did not consistently increase with plant species diversity nor with legume presence. Rather, the Collembola species used differentially responded to the experimental treatments suggesting that functional groups of Collembola differentially respond to plant community composition. The only species which significantly increased in density with plant species diversity was *P. fimata*. Consistently, species of the genus *Protaphorura* have been reported previously to benefit from an increase in species diversity in a field experiment (Salamon et al. 2004). High densities of *Protaphorura* species in the latter study were associated with high fine root biomass, high microbial biomass and high soil water content. As indicated by ANCOVAs using root biomass, microbial biomass and soil water content as covariables these factors were not responsible for the increased density of *P. fimata* in our experiment. Rather, high density of *P. fimata* (and also of *H. nitidus*) was associated with the presence of grasses (but not grass biomass as indicated by ANCOVA), in particular that of *Trisetum flavescens, Festuca rubra* and *Festuca pratensis*. This indicates that the identity of functional groups (grasses) and within functional groups the identity of plant species is more important for Collembolan performance then the diversity of plant species and functional group per se.

Total density of Collembola was reduced in the presence of earthworms (−20%), in particular that of *F. candida* (−46%),. As hemiedaphic species *F. candida* predominantly colonizes the litter layer; the reduced density in the presence of earthworms therefore likely was caused by removal of litter by earthworms, in

particular by *L. terrestris*. In the field, however, *F. candida* and other hemiedaphic Collembola species have been documented to reach high density in middens and burrows of *L. terrestris* (Wickenbrock and Heisler 1997, Maraun et al. 1999) and this was explained by enhanced food supply and increased soil pore space. Since anecic earthworms, such as *L. terrestris*, concentrate litter resources in middens but deplete it in between middens, increased densities of Collembola in middens presumably occurs at the expense of the region in between middens. Since in the present experiment *L. terrestris* consumed the litter material quickly rather than concentrating it in middens, hemiedaphic Collembola were detrimentally affected. In contrast to *F. candida*, *H. nitidus* benefited from the presence of earthworms when grasses were present. In part this might have been due to competitive release caused by the reduced density of *F. candida*. However, since *H. nitidus* has been shown to selectively colonize earthworms casts (Salmon and Ponge 1999, Salmon 2004), more likely *H. nitidus* benefited from resources in earthworm casts deposited on the soil surface and in upper soil layers.

Microorganisms

Microorganisms in soil are primarily limited by the amount of carbon entering the detrital system and hence by plant biomass production (Zak et al. 1994, Spehn et al. 2000). However, in our experiment microbial biomass was not related to total plant biomass production but correlated weakly with root biomass. This suggests that microbial biomass in soil (as measured by substrate-induced respiration) is resistant to plant species composition (and associated belowground resource input) and to the feeding activity of Collembola. In agreement with these findings it has been documented that even massive changes in liquid carbon input (glucose) hardly affect microbial biomass in soil (Joergensen and Scheu 1999, Maraun et al. 2001). The failure of Collembola to control the biomass of microorganisms in soil suggests that most of the microorganisms are inaccessible to microarthropod grazers (Kandeler et al. 1998, Schlatte et al. 1998). In contrast to Collembola, microbial biomass was reduced in presence of earthworms suggesting that either earthworms digested microorganisms or effectively competed with microorganisms for resources. There is increasing evidence that the latter but not the former is in fact the case (Scheu and Schaefer 1998, Schönholzer et al. 1999, Wolter and Scheu 1999, Tiunov and Scheu 2004). Overall, the low responsiveness of microbial biomass to the experimental treatments suggests that the effects of plant species and functional group diversity on the performance of earthworms and Collembola directly resulted from changes in plant resources rather than indirectly from plant-mediated changes in microbial biomass. The low responsiveness of microbial biomass suggests that microorganisms in the soil are rather resistant to changes in belowground resource supply.

In comparison to microbial biomass, the respiratory activity of microorganisms responded more sensitively to the experimental manipulations. Similar to microbial biomass microbial respiration was also reduced by earthworms supporting our conclusion that earthworms effectively competed with microorganisms for resources in the soil. Furthermore, microbial respiration varied with plant species diversity and this likely was in part due to differences in root biomass. However, the significant effect of tall herbs on microbial respiration and the lack of correlation with root biomass suggest that not only belowground productivity but also the quality of rhizodeposits affects microbial activity in the rhizosphere.

Conclusion

The hypothesis that decomposers are beneficially affected by an increase in plant species and functional group diversity appears to be oversimplistic. Rather, the response of decomposers to variations in plant diversity varies with decomposer species with endogeic and euedaphic species, such as *A. caliginosa* and *P. fimata* being more sensitive than anecic (*L. terrestris*) or hemiedaphic species (*F. candida* and *H. nitidus*). Consistent with our expectations, the identity of the plant functional groups strongly affected growth and reproduction of decomposers. Grasses beneficially affected Collembola densities whereas legumes detrimentally affected Collembola densities but beneficially affected total N concentration in *A. caliginosa* tissue. Also consistent with our expectations, soil macrofauna and mesofauna species affected each other and these interactions were modified by plant species diversity, plant functional group diversity and presence of legumes. Both changes in the amount and quality of belowground resources presumably were responsible for these modifications. Future experiments need to further incorporate variations in the input of aboveground litter resources with plant species and functional group diversity to fully capture the complexity of the dependency of decomposers on plant community composition.

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