

Placing biodiversity and ecosystem functioning in context: environmental perturbations and the effects of species richness in a stream field experiment

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Abstract Greater biodiversity is often associated with increased ecosystem process rates, and is expected to enhance the stability of ecosystem functioning under abiotic stress. However, these relationships might themselves be altered by environmental factors, complicating prediction of the effects of species loss in ecosystems subjected to abiotic stress. In boreal streams, we investigated effects of biodiversity and two abiotic perturbations on three related indices of ecosystem functioning: leaf decomposition, detritivore leaf processing efficiency (LPE) and detritivore growth. Replicate field enclosures containing leaves and detritivore assemblages were exposed to liming and nutrient enrichment, raising pH and nutrient levels. Both treatments constitute perturbations for our naturally acidic and nutrient-poor streams. We also varied detritivore species richness and density. The effects of the abiotic and diversity manipulations were similar in magnitude, but whereas leaf decomposition increased by 18% and 8% following liming and nutrient enrichment, respectively, increased detritivore

richness reduced leaf decomposition (6%), detritivore LPE (19%) and detritivore growth (12%). The detritivore richness effect on growth was associated with negative trait-independent complementarity, indicating interspecific interference competition. These interactions were apparently alleviated in both enriched and limed enclosures, as trait-independent complementarity became less negative. LPE increased with detritivore density in the monocultures, indicating benefits of intra-specific aggregation that outweighed the costs of intra-specific competition, and dilution of these benefits probably contributed to lowered leaf decomposition in the species mixtures. Finally, the effects of liming were reduced in most species mixtures relative to the monocultures. These results demonstrate how environmental changes might regulate the consequences of species loss for functioning in anthropogenically perturbed ecosystems, and highlight potential influences of biodiversity on functional stability. Additionally, the negative effects of richness and positive effects of density in our field study were opposite to previous laboratory observations, further illustrating the importance of environmental context for biodiversity–ecosystem functioning relationships.

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Introduction

Concern that environmental degradation is compromising important ecological services has stimulated research into the factors governing ecosystem functioning, which is typically quantified as one or more ecosystem-level process rates (e.g. primary production or detritus decomposition;

Gessner and Chauvet 2002; Srivastava and Vellend 2005). Such research falls into two broad but distinct fields: functional bioassessment, which addresses the impacts of environmental degradation on important ecosystem processes (e.g. Doroszuk et al. 2007; McKie and Malmqvist 2009); and biodiversity–ecosystem functioning research, which focuses on the influences of species richness and other biodiversity components (e.g. Balvanera et al. 2006; Cardinale et al. 2006). However, human activities often alter both biodiversity and abiotic environmental parameters simultaneously (e.g. Huryn et al. 2002; McKie et al. 2006), with potentially complex outcomes for ecosystem functioning (Cardinale et al. 2000; Vinebrooke et al. 2004). Abiotic stressors can interact synergistically or antagonistically to produce effects on ecosystem functioning that differ from expectations based on the action of each stressor alone (e.g. Doroszuk et al. 2007), and biodiversity change can further enhance or offset such effects (Vinebrooke et al. 2004). The limited understanding of such interactions hinders application of biodiversity–ecosystem functioning research to environmental conservation and management (Srivastava and Vellend 2005; Thompson and Starzomski 2007).

Maintenance of functioning in an ecosystem under abiotic stress is in part dependent on the environmental tolerances of the biota (Vinebrooke et al. 2004), with diverse communities more likely to include tolerant species able to compensate for those negatively affected by a given stressor (“insurance effects”; Loreau et al. 2002). Furthermore, functioning should be inherently less variable in species-rich systems, as the responses of extreme species are diluted over a more diverse community (i.e. “statistical averaging”; Doak et al. 1998), an idea that has received recent empirical support (Dang et al. 2005; Lecerf et al. 2007; Tilman et al. 2006). Accordingly, impacts of stressors on ecosystem processes are expected to be more variable in species-poor systems.

Furthermore, species loss might impact ecosystem functioning directly, by reducing the overall capacity of biota to maintain a process at a given rate. Results from biodiversity–ecosystem functioning research indicate that average process rates are often higher for more species-rich assemblages (Balvanera et al. 2006; Cardinale et al. 2006), reflecting one or more of three mechanisms: niche partitioning, with process rates enhanced when the activities of species with differing niche requirements complement one another; facilitation, whereby activities of some species enhance activities of other species; the sampling effect, with species-rich communities more likely to include taxa with attributes that strongly influence process rates (Huston 1997; Loreau and Hector 2001). However, the strength of these effects can vary with environmental context (Biles et al. 2003; Vinebrooke et al. 2004). For example, increases in resource availability may increase scope for resource

partitioning and facilitation (Dzialowski and Smith 2008; Fridley 2002), and physical disturbance can reduce dominance of strong competitors, and thus also increase scope for positive species interactions (Cardinale and Palmer 2002; Mulder et al. 2001). Consequences of species loss for functioning in anthropogenically impacted ecosystems might similarly depend on how associated environmental changes alter interactions among the remaining biota.

Effects of both biodiversity change and abiotic stressors on ecosystem functioning have been investigated in running waters, which supply essential ecosystem goods and services to humans (e.g. food, water, and waste removal), but are heavily impacted by anthropogenic stressors worldwide (Malmqvist and Rundle 2002). Particular attention has been given to leaf litter decomposition, a pivotal component of energy flow in stream ecosystems that is often altered by anthropogenic activities (Gessner and Chauvet 2002; McKie et al. 2008). A variety of responses have been observed to different stressors. For example, decomposition is usually depressed in acidified streams (Dangles et al. 2004) but is stimulated by moderate nutrient enrichment (Huryn et al. 2002), though this can be offset by increased sediment loads in agricultural streams affected by bank and catchment erosion (Pascoal et al. 2005). The extent to which such interactions are further modified by changes in decomposer diversity is not clear (Lecerf et al. 2005; McKie et al. 2006; Woodcock and Huryn 2005), though multiple relationships between decomposition and the diversity of both detritivores and microbes have been observed in the laboratory (Dang et al. 2005; Jonsson and Malmqvist 2003; McKie et al. 2008).

In boreal streams, we investigated how variation in detritivore species richness and two environmental perturbations interact to affect three parameters related to litter dynamics: litter decomposition, detritivore leaf processing efficiency (LPE), and detritivore growth. The assessed environmental perturbations were nutrient enrichment and liming, representing widespread anthropogenic impacts, particularly in farmland and plantation forest catchments (Haynes and Naidu 1998; Rosberg et al. 2006). Moderate nutrient enrichment increases microbial activity (Gulis and Suberkropp 2003) and can also stimulate detritivore feeding and growth, probably by enhancing leaf palatability (Robinson and Gessner 2000). In a similar vein, liming raises pH and changes cation composition and concentration, also stimulating microbial activity (Jenkins and Suberkropp 1995). However, in Swedish boreal streams, which are often naturally acidic (Laudon et al. 2004), liming has been associated with reduced decomposition by detritivores (McKie et al. 2006). We hypothesised that by enhancing leaf conditioning (Bärlocher and Kendrick 1975; Gulis and Suberkropp 2003), nutrient enrichment would increase litter use by all detritivore species, leading

to faster decomposition overall. The general increase in quality of the litter resource should also reduce competition and increase scope for resource partitioning and/or facilitation, with positive richness–ecosystem functioning relationships thereby favoured. In contrast, we expected the effects of liming to vary among the detritivore species, reflecting differences in their pH preferences (Lillehammer 1988; McKie et al. 2006). Both positive and negative responses were anticipated (see **Materials and methods**), implying potential for species mixtures to buffer the effects of liming on ecosystem functioning.

Materials and methods

Field sites

Northern Sweden's boreal region is characterised by streams with high concentrations of dissolved organic C and low pH (Laudon et al. 2004). Many are artificially limed to raise pH levels, though acidity in the region is now known to reflect the runoff of humic compounds naturally present in the soils rather than anthropogenic causes (Laudon et al. 2004). Liming in northern Sweden has been linked to reduced rates of leaf decomposition mediated by detritivores, reflecting a loss of large-bodied species (McKie et al. 2006), and possibly suboptimal pH conditions for a fauna that may prefer soft humic waters (Petrit et al. 2007, 2008). These streams are also typically nutrient poor (Münster 1999), and even moderate fertiliser runoff associated with low intensity agriculture in the region can double dissolved N and P concentrations (B. G. McKie and B. Malmqvist, unpublished data).

Our experiment was conducted during October–November 2004 in two streams (Table 1) north of the city of Umeå (63.8°N, 20.2°E). Data from a third stream were discarded following severe flooding and losses of 60% of our experimental units. The study streams were second order (4–6 m in bankful width), with rocky substrates and forested riparian strips consisting mainly of conifers [especially *Picea abies* (L.)], grey alder *Alnus incana* (L.)

and birches (*Betula* spp.). Ambient nutrient levels were low (Table 1). Both streams have been limed since the early 1990s using a dosing tower, which releases lime powder during periods of elevated runoff to mitigate flood-associated acid episodes (Ahlström 2006). Two 100-m reaches were delineated in each stream: an unlimed reference reach located 50–150 m upstream of the dosing tower, and a limed reach approximately 4 km downstream of the tower at the point where a clear pH change was achieved. Unlimed and limed reaches within each stream were highly comparable in width, depth, flow and substrate characteristics (McKie et al. 2006). Lime powder was released throughout the study period, ceasing only when the streams were ice-covered during the final week of the experiment (B.G. McKie, personal observation), raising mean pH and alkalinity (Table 1). However, these differences were not constant, with the lowest pH values observed in unlimed reaches during an acid pulse early in the experiment (Table 1). McKie et al. (2006) give more information on the study streams and liming in northern Sweden.

Field enclosures and nutrient enrichment

Our experimental units were enclosures constructed from two pieces of opaque polyvinyl chloride drainage pipe (7.5 cm inner diameter), fitted together to form a 25-cm-long tube, and closed at either end with 300- μ m nylon mesh. Additional nylon mesh was wedged between the two tube pieces, dividing each enclosure into two sections. The enclosures were deployed with the mesh perpendicular to the current, so that the first section was positioned upstream from the second. The downstream section contained 1.5 ± 0.1 g of air-dried grey alder leaves, collected just prior to abscission, and an assemblage of detritivorous insects of varying species composition. Slow-release fertiliser pellets were added to half the enclosures in the upstream section, to raise nutrient levels in the downstream section. The fertilizer pellets were a mixture of 50.0 g Osmocote 23 + 00 + 00 (11.5% NO_3^- -N and 11.5% NH_4^+ -N in a clay matrix) and 14.5 g Osmocote Exact 15 + 9 + 9 + 3 MgO + Te (7.1% NO_3^- -N, 7.9% NH_4^+ -N, 9% P as P_2O_5 , 9% K_2O , 3% Mg as

Table 1 Water chemistry (mean \pm SE) at limed and unlimed stream sites between 9 October and 26 November 2004

Stream	Site	pH ^a		Alkalinity ^a ($\mu\text{Eq l}^{-1}$)	Conductivity ($\mu\text{S cm}^{-1}$)	TON ^b ($\mu\text{g l}^{-1}$)	SRP ^b ($\mu\text{g l}^{-1}$)
		Mean	Range				
Oxbäcken	Unlimed	5.1 ± 0.4	4.6–6.5	24.0 ± 23.9	22.6 ± 2.0	74.6 ± 9.7	2.3 ± 1.6
	Limed	6.4 ± 0.13	6.0–6.7	72.0 ± 28.2	30.9 ± 0.7	52.5 ± 10.5	3.1 ± 1.9
Vadbäcken	Unlimed	5.3 ± 0.3	4.8–6.2	25.1 ± 15.0	23.2 ± 0.8	27.8 ± 11.1	1.1 ± 0.6
	Limed	6.3 ± 0.2	5.9–6.6	65.0 ± 13.2	26.1 ± 0.8	27.5 ± 7.5	2.0 ± 0.7

^a pH and alkalinity data are derived from Ahlström (2006); all pH minima occurred during an acid pulse during the first 2 weeks of the study

^b Total oxidised N (TON) and soluble reactive P (SRP) data are site averages of samples taken from a subset of unenriched enclosures 3 and 35 days after starting the experiment (see **Materials and methods**)

MgO, and trace elements), corresponding to a molar N:P ratio of 23:1. On deployment, the pellets sank to the bottom of the enclosures, and did not impede more than 10% of the mesh netting. As a result, there was no difference in flow through 32 paired unenriched (mean \pm SE: $8.3 \pm 0.8 \text{ m s}^{-1}$) and enriched ($7.9 \pm 0.9 \text{ m s}^{-1}$) enclosures measured under various flow conditions by injecting fluorescent dye at the upstream end (paired *t*-test, $t_{15} = -0.802$, $P = 0.43$).

Detritivores and treatments

The studied detritivores were all stoneflies (Plecoptera), reflecting the dominant taxonomic composition of local streams during autumn (McKie et al. 2006): *Protonemura meyeri* (Pictet) and *Nemurella pictetii* Klapalek (both Nemouridae), and *Taeniopteryx nebulosa* (L.) (Taeniopterygidae). At the start of the experiment, individuals of *N. pictetii* ($0.20 \pm 0.03 \text{ mg}$) were smaller than those of *T. nebulosa* ($0.28 \pm 0.04 \text{ mg}$) and *P. meyeri* ($0.29 \pm 0.04 \text{ mg}$). These species were expected to differ in their responses to liming, given that the mean abundance of *T. nebulosa* triples following liming, whereas *P. meyeri* declines by 96% in limed stream sections (McKie et al. 2006). *N. pictetii* is a characteristic species of small, often highly acid, streams in northern Sweden (Pettrin et al. 2007), but is tolerant of a broad range of environmental conditions (Lillehammer 1988).

The detritivores were collected from local streams during the first week of October 2004, and held in laboratory aquaria under autumn temperature and light regimes. One day prior to field deployment, individuals were divided randomly among the enclosures according to one of four species richness treatments: controls with no detritivores, all three species monocultures, all three two-species mixtures, and the three-species mixture. Animal density was fixed at 12 individuals, divided evenly among species in the mixtures. A richness of three species represents levels of detritivore diversity often observed at local (leaf patch) scales (Dangles and Malmqvist 2004), while a density of 12 individuals on 3 g of litter corresponds to that observed on litter packs after 3 weeks of colonisation in northern Sweden (McKie et al. 2008). The enclosures were kept immersed and aerated overnight, and transported moist to the study streams the following day. Four evenly spaced riffles were chosen to constitute four blocks at each limed and unlimed site, within which the enclosures were fixed in place using iron bars. Thirty-two nutrient-enriched and unenriched enclosures were placed in each limed and unlimed stream section (128 total in each stream). Every species composition \times nutrient treatment combination was represented once in each riffle. An additional set of monocultures containing only six individuals of each

species was deployed to assess possible density-dependent variation in process rates (McKie et al. 2008). These extra enclosures were handled identically and exposed to the same abiotic treatments as those from the main experiment.

Physico-chemical data

Temperature was measured continuously at each site using Smart Button (ACR Systems, Surrey, BC, Canada) data loggers, while conductivity was measured using a Mettler-Toledo (Greifensee, Switzerland) MX-300 probe at the beginning, midpoint, and end of the study. Dissolved nutrient concentrations were measured from a randomly selected subset of enriched and unenriched enclosures on day 3 and 35 after deployment ($n = 24$ and 32 per site, respectively). Water samples (20 ml) were extracted using a hypodermic needle inserted through the downstream net. These samples were filtered (Millipore Millex-HA, mixed cellulose membrane filters, 0.45- μm pore size, SLHA 025 OS) in the field into 20-ml scintillation vials, and frozen on return to the laboratory. Total oxidised N (TON = $\text{NO}_2\text{-N} + \text{NO}_3\text{-N}$) was later analysed by diazotisation of NO_2^- , after NO_3^- reduction in the presence of Cu^{2+} and Zn^{2+} , and soluble reactive P (SRP) was analysed with the molybdate blue method (DEV 1985).

Enclosure retrieval and laboratory procedures

The enclosures were retrieved after 6 weeks (Table 1) and transported to the laboratory where the leaf litter was separated from the detritivores, dried to constant mass at 50°C, weighed and then ignited at 550°C in a muffle furnace to determine ash free dry mass. The detritivores from each enclosure were sorted into the component species and dried to constant mass at 50°C for final biomass determination. Initial biomass was estimated identically, based on 12 individuals of each species randomly selected prior to animal allocation among the enclosures.

Indices of ecosystem functioning

Three indices of ecosystem functioning were calculated for each experimental unit:

1. Leaf decomposition rates were calculated using the negative exponential decay model:

$$k = \frac{\ln(\text{mass}_{\text{remaining}}/\text{mass}_{\text{initial}})}{\text{time in days}}$$

where k is the decomposition rate coefficient. This represents the standard measure of litter decomposition reported from streams (Gessner and Chauvet 2002).

2. Detritivore LPE (leaf processing per unit insect biomass) was quantified by first calculating the rate of decomposition attributable to detritivore feeding ($k_{\text{detritivore}}$), using the negative exponential model given above, but with the $\text{mass}_{\text{initial}}$ term adjusted to exclude losses attributable to microbes and leaching (estimated from the control microcosms for each nutrient treatment within each block). LPE was then calculated by dividing $k_{\text{detritivore}}$ by M , which is the mean of final and initial detritivore biomass, summing across all individuals and species in each enclosure.
3. Detritivore relative growth rate (RGR) was also calculated using an exponential model:

$$(\text{RGR} = \text{LN}(\text{mass}_{\text{final}}/\text{mass}_{\text{initial}})/\text{time}).$$

All three indices were further corrected for minor temperature variation among sites using allometric equations derived from metabolic theory (Brown et al. 2004), with all rates consequently reported per unit Kelvin. The LPE and RGR measures were also adjusted for the allometric relationship between body mass and metabolic (and hence feeding) rate (Brown et al. 2004; Gillooly et al. 2001). Accordingly, the equations for each index are:

1. Decomposition rate: $k(T) = k(e^{E_i(T-T_0)/k_b(TT_0)})$
2. LPE: $\text{LPE}(T) = k_{\text{shredder}}(M^{-0.25})(e^{E_i(T-T_0)/k_b(TT_0)})$
3. RGR: $\text{RGR}(T) = \text{RGR}(M^{-0.25})(e^{E_i(T-T_0)/k_b(TT_0)})$

where E_i is the activation energy for metabolism (approximately 0.63 across all organisms), k_b is the Boltzmann constant, T is the mean temperature during the study period, and T_0 is a reference temperature (1°C, within the range observed during the study period) used to standardise all rates (Gillooly et al. 2001). The exponent of -0.25 used to adjust M describes a general relationship between body size and metabolism across all organisms (Brown et al. 2004).

Availability of biomass data for individual species in the mixtures allowed us to employ Loreau and Hector's (2001) additive partition of the effect of diversity on growth. Firstly, the net effect of species richness on growth in the mixtures was calculated by summing differences between observed and expected growth across species (Loreau and Hector 2001). Expected growth of a species was calculated based on that observed in the monocultures, following adjustment for mortality. The net effect was then divided into three underlying components following Fox (2005):

1. Trait-independent complementarity, which is positive when species perform better than expected based on

their monoculture performance and without cost to other species.

2. Trait-dependent complementarity, which is positive when species with high monoculture growth perform well in the mixtures without cost to other species.
3. The dominance effect, which is positive when species with high monoculture growth perform well in mixtures but at the expense of other species.

To facilitate comparison with previous studies, we restore Loreau and Hector's (2001) nomenclature and term the dominance effect the "selection effect", since it quantifies the NE fraction attributable to processes analogous to natural selection (Fox 2005).

Statistical analyses

Our hypotheses were primarily assessed using ANOVA, with a particular focus on interactive effects of the abiotic and detritivore assemblage (richness or composition) manipulations on the process rates. Additionally, changes in underlying mechanisms related to interspecific interactions and resource partitioning were assessed through the diversity effect partition, while the monoculture density manipulations were used to evaluate the role of intraspecific interactions (McKie et al. 2008). All statistical analyses were conducted using JMP for Macintosh (version 7.0.2; SAS Institute, Cary, N.C.), with square-root transformation of response variables applied where necessary to satisfy assumptions of parametric statistical tests.

Our experiment was established as a split-plot design, with liming applied to sites within stream blocks, and the remaining treatments applied to individual enclosures within riffles and stream sites. To account for the hierarchical nature of this design, mixed-model ANOVA employing multiple error terms was used for all analyses (Quinn and Keough 2002). Fixed factors included liming (two levels: unlimed or limed), nutrients (unenriched or enriched), and detritivore species richness (one, two or three species). Detritivore species composition (comprising all seven possible species combinations) was also fitted as a fixed factor, since we chose our study species to test specific hypotheses rather than represent a random subset of all possible species. Species composition was nested within richness, to partition the effects of richness per se from those of the particular species present (e.g. Jonsson 2006). Random factors included the two stream blocks, two sites nested within each stream, and four riffle blocks nested within each site. The error terms incorporated the appropriate random effects for each level of the design: liming was tested against sites within streams, while the other factors were tested against terms including

Table 2 Analyses of leaf decomposition, detritivore leaf processing efficiency (*LPE*) and detritivore relative growth rates (*RGR*)

Source of variation	df_N^a	Decomposition			LPE			RGR		
		df_D^a	<i>F</i>	<i>P</i>	df_D^a	<i>F</i>	<i>P</i>	df_D^a	<i>F</i>	<i>P</i>
Lime	1	2.6	71.7	0.006	1.0	0.30	0.68	1.0	2.83	0.33
<i>Site(Stream × Lime)</i>										
Nutrients	1	28.7	4.36	0.046	18.6	0.69	0.43	22.3	3.46	0.076
Nutrients × Lime	1	28.7	0.27	0.61	18.6	3.57	0.075	22.3	2.21	0.15
<i>Nutrients × Riffle[Site(Stream × Lime)]</i>										
Richness	2	32.7	4.18	0.024	31.1	4.83	0.015	24.9	3.88	0.034
Richness × Lime	2	32.7	1.41	0.26	31.1	1.89	0.17	24.9	0.69	0.5
<i>Richness × Riffle[Site(Stream × Lime)]</i>										
Richness × Nutrients	2	30.3	0.42	0.66	28.2	0.35	0.71	26.2	0.63	0.54
Richness × Nutrients × Lime	2	30.3	0.06	0.95	28.2	0.01	0.99	26.2	4.76	0.017
<i>Richness × Nutrients × Riffle[Site(Stream × Lime)]</i>										
Comp(Richness)	4	57.0	14.0	<0.001	57.8	13.5	<0.001	51.2	54.6	<0.001
Comp(Richness) × Lime	4	57.0	3.01	0.023	57.8	3.48	0.013	51.2	1.28	0.29
<i>Comp(Richness) × Riffle[Site(Stream × Lime)]</i>										
Comp(Richness) × Nutrients	4	53.0	1.10	0.37	52.9	1.01	0.41	60.8	0.62	0.65
Comp(Richness) × Nutrients × Lime	4	53.0	1.80	0.14	52.9	1.57	0.2	60.8	1.15	0.34
<i>Comp(Richness) × Nutrients × Riffle[Site(Stream × Lime)]</i>										

Output from mixed-model ANOVAs testing the fixed effects of liming (*Lime*), nutrient enrichment (*Nutrients*), detritivore richness (*Richness*), and detritivore species composition (*Comp*) nested within richness [*Comp(Richness)*]. Random effect error terms for the preceding fixed factors are shown in *italics*

^a Numerator *df* (df_N) were identical across all analyses, whereas the effective denominator *df* (df_D) differed

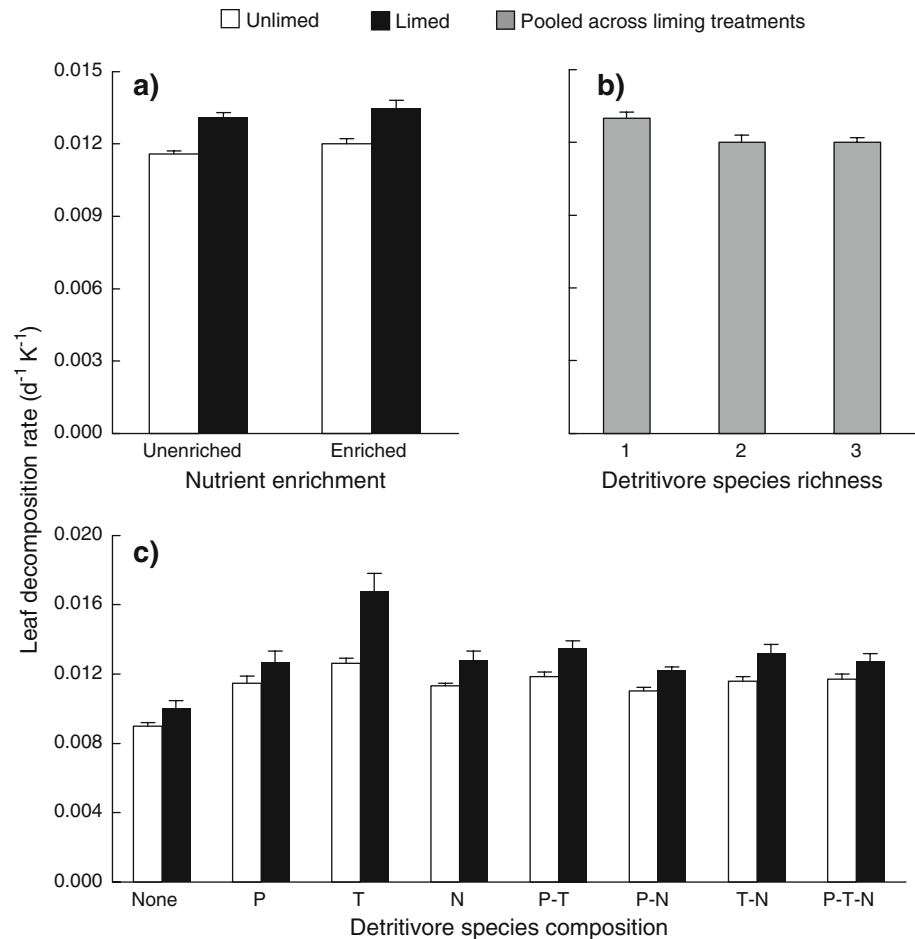
the riffle, site and stream block factors (see Table 2). Across all analyses, the bulk of random variation (69–96%) was associated with the riffle block error terms, while the remainder was associated with the streams and sites within streams.

Our experimental design was unbalanced, reflecting the different numbers of species combinations within each richness level, and replicate losses during the experiment. To account for this, we used restricted maximum likelihood (REML) estimation to model our error terms. REML gives asymptotic maximum likelihood estimations of the true mean and variance for random factors, and is reliable even when data are unbalanced, unlike traditional ANOVA approaches based on expected mean square estimation (Searle et al. 1992). Denominator *df* are also modelled separately for each fixed effect test, which are then termed “effective *df*” (Kenward and Roger 1997). REML cannot provide direct tests of interactions between fixed and random factors, but in our study these represent background “block” variation for which we had no particular hypotheses. The assumption of sphericity was fulfilled for all our mixed model analyses (Mauchly’s criterion, all $\chi^2 < 10.1$, $P > 0.076$), indicating that any interactions between fixed and random factors were unlikely to pose interpretational difficulties (Quinn and Keough 2002).

The diversity effect partition for detritivore growth was first analysed by testing for deviation between observed and expected growth using a paired *t*-test. Variation in the three diversity effect fractions was then assessed using a similar mixed model ANOVA design to that described above. However, REML estimation failed to converge on reliable solutions when species richness was included in these models, reflecting the very restricted variance around some mean estimates and the small sample size of the three-species treatment (both potentially undermining REML estimation; see Kenward and Roger 1997; Searle et al. 1992). Analyses of the diversity effect fractions therefore focussed on the two-species combinations only, with the liming and nutrients fixed factors tested against the appropriate random-effects error terms (see Table 2). These simpler analyses fulfilled the distributional requirements for reliable REML estimation, and still allowed assessment of the effects of the abiotic perturbations on potential mechanisms underlying the diversity effect.

Density effects were assessed through analysis of data from the six- and 12-individual monocultures. A mixed-model ANOVA was used, with liming, nutrient enrichment, detritivore density and species identity fitted as fixed factors.

Fig. 1 Effects of liming and a nutrient enrichment, b detritivore species richness and c detritivore species composition on leaf decomposition rate (k), corrected for temperature in Kelvin (K) (mean \pm SE). Data from the non-insect controls (None) in c are shown for reference only, and were not included in a, b. See Table 2 for main and interaction effect significance levels. *P* *Protonemura meyeri*, *T* *Taeniopteryx nebulosa*, *N* *Nemurella pictetii*, $d^{-1} K^{-1}$



Results

Nutrient enrichment

Nutrient concentrations were higher in enriched than unenriched enclosures on both day 3 and 35 after deployment (mixed model ANOVA: all $F > 10.2$, all $P \leq 0.007$). On day 3, concentrations (mean \pm SE) of TON ($49.6 \pm 8.5 \mu\text{g l}^{-1}$) and SRP ($6.3 \pm 2.7 \mu\text{g l}^{-1}$) in enriched enclosures exceeded levels in unenriched enclosures (TON, $31.4 \pm 4.2 \mu\text{g l}^{-1}$; SRP, $0.8 \pm 0.3 \mu\text{g l}^{-1}$). After 35 days, these differences increased to sixfold for TON (348.2 ± 143.8 vs. $55.6 \pm 6.0 \mu\text{g l}^{-1}$), and 20-fold for SRP (71.2 ± 26.3 vs. $3.6 \pm 0.6 \mu\text{g l}^{-1}$). However, there was considerable variation among enriched enclosures, with nutrient concentrations little elevated above unenriched levels in 17% of those sampled. Nutrient concentrations did not vary with liming (all $F < 0.2$, $P > 0.69$).

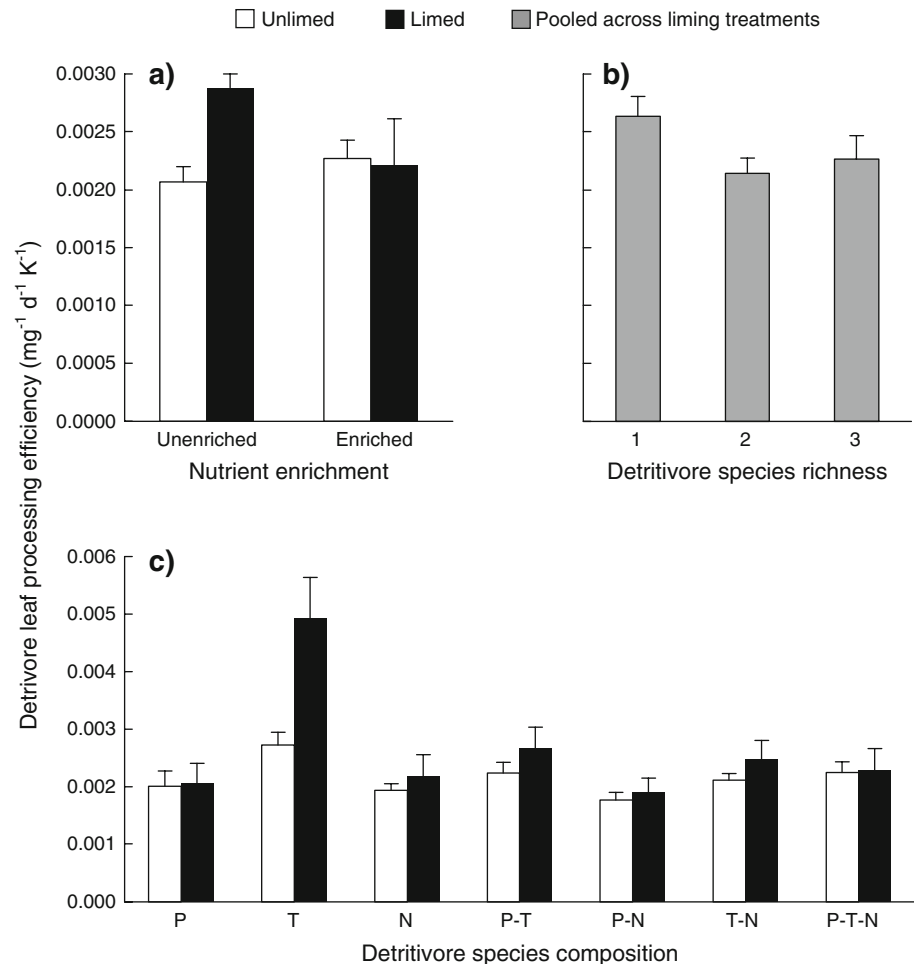
Temperature and animal survivorship

Slight temperature differences between unlimed ($1.6 \pm 0.2^\circ\text{C}$) and limed ($1.2 \pm 0.3^\circ\text{C}$) sites were not significant overall (all $F_{1,22} = 1.2$, $P = 0.29$). While both streams froze during the last week of the experiment, water flow continued under the ice and most enclosures were unaffected. However, 26 of 256 chambers were frozen solid or otherwise damaged, and were excluded from statistical analyses. Detritivore survivorship in the remaining enclosures was $80.1 \pm 1.1\%$, and did not vary for any species with any treatment (all $F < 2.2$, $P > 0.15$).

Leaf decomposition

Leaf decomposition rates were higher in limed ($0.013 \pm 1.67 \times 10^{-6} \text{ mg day}^{-1} \text{ K}^{-1}$) than unlimed ($0.011 \pm 1.87 \times 10^{-4} \text{ mg day}^{-1} \text{ K}^{-1}$) enclosures (Fig. 1a), with this result significant despite the low power of this test (Table 2).

Fig. 2 Effects of liming and a nutrient enrichment, **b** detritivore species richness and **c** detritivore species composition on the leaf processing efficiency (of detritivores ($k_{\text{detritivore}}$, mg^{-1}), corrected for temperature in K (mean + SE). See Table 2 for main and interaction effect significance levels. For abbreviations, see Fig. 1



Decomposition was also higher in enriched ($0.013 \pm 2.35 \times 10^{-4} \text{ mg day}^{-1} \text{ K}^{-1}$) than unenriched enclosures ($0.012 \pm 2.70 \times 10^{-4} \text{ mg day}^{-1} \text{ K}^{-1}$), though this effect was small (see Fig. 1a) and only just significant at the 5% level (Table 2). Leaf decomposition further varied with both detritivore species richness and composition, and an interaction apparent between liming and composition was also apparent (Table 2). Decomposition rates declined with increasing detritivore species richness (Fig. 1b), and were highest overall for monocultures of *T. nebulosa* (Fig. 1c). Liming also had the strongest effect on decomposition in the *T. nebulosa* monocultures, whereas responses in *P. meyeri* monocultures and most species mixtures barely exceeded that observed in the control enclosures (Fig. 1c).

Detritivore LPE

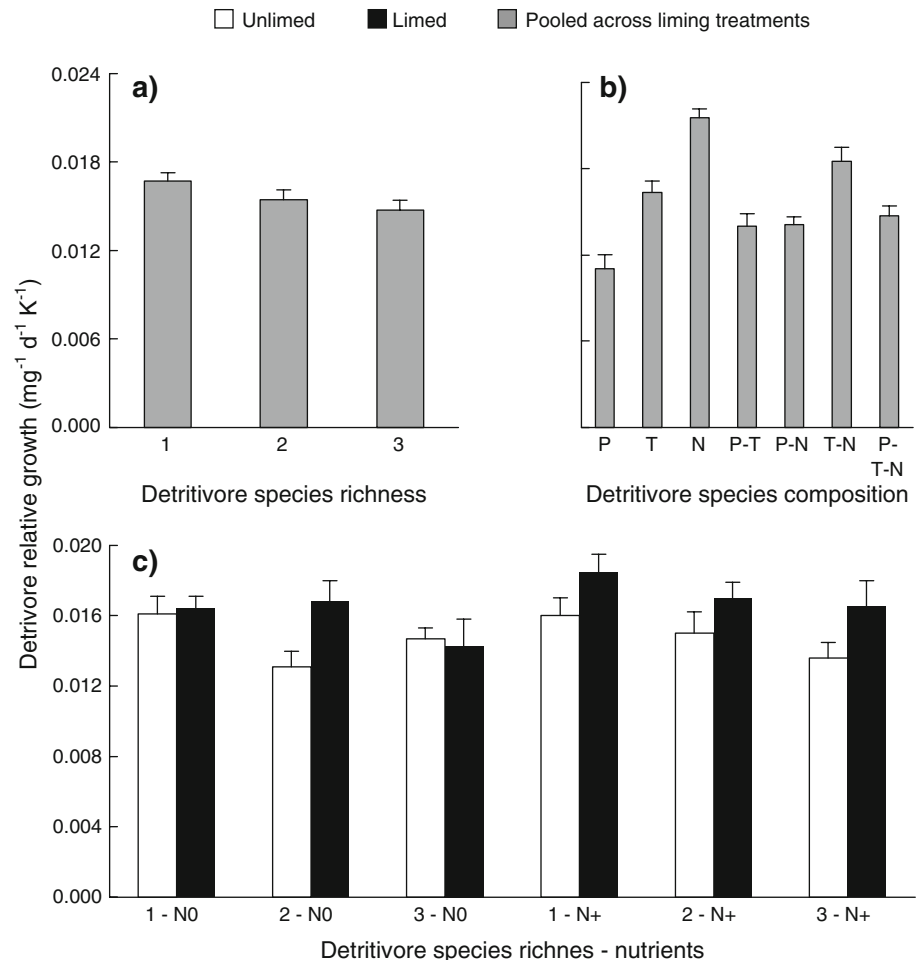
Similar to leaf decomposition, detritivore LPE varied with species richness and composition, and an interaction between liming and composition was also apparent (Table 2). LPE declined with increasing detritivore

richness (Fig. 2b). *T. nebulosa* was the most efficient species, and its feeding activity was markedly stimulated by liming (Fig. 2c). LPE for the remaining species combinations was much less affected by liming, if at all (Fig. 2c). A trend for a positive effect of liming in unenriched but not enriched enclosures (Fig. 2a) was not significant at the 5% level ($P = 0.075$, Table 2).

Detritivore growth

RGRs of detritivores declined with increasing species richness (Table 2; Fig. 3a), similar to observations for both leaf decomposition and LPE (Figs. 1b, 2b). Growth rates also varied with detritivore species composition (Table 2), with the highest rates observed for *N. pictetii*, and the lowest for *P. meyeri* (Fig. 3b). A tendency for faster detritivore growth in enriched than unenriched enclosures ($0.016 \pm 5.08 \times 10^{-4}$ vs. $0.015 \pm 5.74 \times 10^{-4} \text{ mg}^{-1} \text{ day}^{-1} \text{ K}^{-1}$) was not significant at the 5% level ($P = 0.076$; Table 2). However, there was a complex interaction between nutrients, liming and detritivore richness

Fig. 3 Effects of **a** detritivore species richness, **b** detritivore species composition and **c** interactions between detritivore richness, liming and nutrients on the relative growth rate of detritivores, corrected for temperature in K (mean + SE). See Table 2 for main and interaction effect significance levels. *NO* Unenriched (ambient) nutrient concentrations, *N+* enriched nutrient concentrations; for other abbreviations, see Fig. 1



(Table 2). This largely reflected growth rates of the two-species mixtures, which were most reduced relative to monoculture levels in the unenriched enclosures (Fig. 3c).

The net effect of detritivore richness on growth was significant (paired *t*-test, $t_{117} = -4.10$, $P < 0.001$) and negative overall (mean -0.74 ± 0.18 mg). The net effect comprised a large negative trait-independent complementarity fraction (-0.71 ± 0.19 mg) and smaller negative trait-dependent complementarity (-0.10 ± 0.04 mg) and selection effect (0.08 ± 0.07 mg) fractions. Trait-independent complementarity in the two-species mixtures was affected by nutrients ($F_{1,9.6} = 10.96$, $P = 0.008$), becoming less negative in enriched (-0.90 ± 0.35 mg) than unenriched (-0.18 ± 0.24 mg) enclosures. Additionally, an interaction between nutrients and liming was apparent ($F_{1,9.6} = 5.59$, $P = 0.041$). Liming and nutrient enrichment caused trait-independent complementarity to be less negative when applied separately (Fig. 4), but no further reduction occurred in enclosures subjected to liming and nutrient addition simultaneously (Fig. 4). Neither trait-dependent complementarity nor the selection effect varied with the liming or nutrient treatments (all $F < 1.7$, $P > 0.22$).

Density effects

Density significantly affected both LPE ($F_{1,8} = 134.3$, $P < 0.001$) and RGR ($F_{1,10} = 21.8$, $P < 0.001$) for all three detritivore species. However, whereas LPE was substantially higher in 12- than six-individual microcosms, growth rates were lower in 12-individual microcosms (Table 3). A tendency for LPE to differ more between six- and 12-individual microcosms in limed ($0.0017 \pm 4.75 \times 10^{-5}$ vs. $0.0030 \pm 9.64 \times 10^{-5}$ day $^{-1}$ mg $^{-1}$ K $^{-1}$) than unlimed enclosures ($0.0016 \pm 2.34 \times 10^{-4}$ vs. $0.0023 \pm 9.63 \times 10^{-5}$ day $^{-1}$ mg $^{-1}$ K $^{-1}$) was not significant at the 5% level ($F_{1,8} = 4.6$, $P < 0.065$). No further interactions between density and liming or nutrient enrichment were apparent for either LPE or relative growth (all $F < 1.6$, $P > 0.23$).

Discussion

The importance of consumer biodiversity relative to other potential controls of ecosystem functioning has been unclear (Fridley 2002; Srivastava and Vellend 2005),

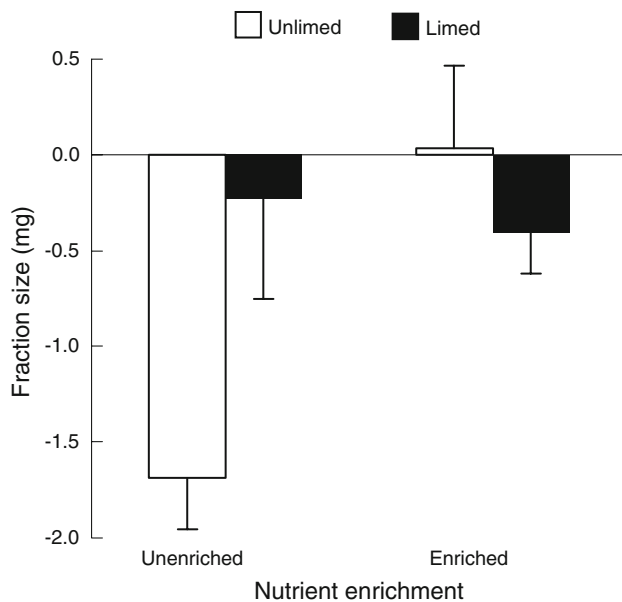


Fig. 4 Effects of liming and nutrients on the trait-independent complementarity fraction of the diversity effect across two-species mixtures

though variation in herbivore species richness had comparable effects to nutrient and predator manipulations in a pond study (Wojdak 2005). Similarly, ecosystem functioning in our field enclosures was affected as much by variation in detritivore species richness as by the abiotic perturbations. Leaf decomposition rates increased by 18% and 8% following liming and nutrient enrichment, respectively, whereas increasing detritivore richness was associated with 6%, 19% and 12% reductions in rates of leaf decomposition, detritivore LPE and detritivore relative growth, respectively. Interactions between detritivore richness and the perturbations were also apparent, with the negative richness effect on detritivore growth altered by both liming and enrichment, and the effects of liming on the *T. nebulosa* monocultures notably weakened in the multispecies mixtures. Furthermore, the overwhelmingly negative effects of increased detritivore richness in our field study were opposite to observations from previous laboratory microcosm experiments (e.g. Jonsson and Malmqvist 2003). Taken together, these results are indicative of the potential for local environmental conditions to

alter species interactions and resource use, and hence biodiversity–ecosystem functioning relationships.

Liming and nutrient enrichment

Comparison of the relative effects of the abiotic and biotic treatments requires consideration of the success of the abiotic manipulations (Wojdak 2005). The positive effect of liming on decomposition in our study matched expectations based on previous litterbag experiments, in which leaf mass loss rates increased by 12% following liming (McKie et al. 2006; data rescaled for comparison with results from the present study). In part, this probably reflects the stimulation of key fungal enzymes (i.e. pectin lyases) that have neutral or alkaline pH optima and require divalent cations such as Ca as a cofactor (Jenkins and Suberkropp 1995). Additionally, liming was associated with increased LPE for *T. nebulosa*, in line with the markedly high background abundances of this species in limed stream reaches (McKie et al. 2006). Together, these results indicate that liming improves habitat conditions for *T. nebulosa*, though corresponding effects on growth did not become apparent over the time scales of this study. No similar effects were apparent for *P. meyeri*, which declines in abundance following liming (McKie et al. 2006), or *N. pictetii*, a characteristic acid-stream species (Petrin et al. 2007). These findings demonstrate that blanket ecosystem interventions, such as palliative liming, can have contrasting effects even on taxonomically and functionally similar species, and on processes mediated by these species.

The 8% increase in decomposition following nutrient enrichment was substantially lower than levels observed in many previous studies elsewhere (typically more than 30%; e.g. Gulis and Suberkropp 2003; Pascoal et al. 2005; Robinson and Gessner 2000), particularly given the low ambient nutrient concentrations. Furthermore, the evidence for a transfer of the nutrient stimulus through the detrital food web was limited, with positive effects on detritivore growth not significant at the 5% level ($P = 0.076$). These weak responses might partly reflect the inconsistency among enclosures in the level of enrichment we achieved. However, these results might also indicate that nutrients were less limiting in our systems than indicated by ambient

Table 3 LPE and RGR of detritivores in monocultures containing six or 12 individuals (mean \pm SE)

Species	LPE ($k_{\text{detritivore}} \text{ mg}^{-1} \text{ day}^{-1} \text{ K}^{-1}$)		RGR ($\text{mg}^{-1} \text{ day}^{-1} \text{ K}^{-1}$)	
	Six individuals	Twelve individuals	Six individuals	Twelve individuals
<i>Protonemura meyeri</i>	0.0014 \pm 0.0002	0.0020 \pm 0.0002	0.014 \pm 0.001	0.011 \pm 0.001
<i>Taeniopteryx nebulosa</i>	0.0022 \pm 0.0001	0.0038 \pm 0.0005	0.021 \pm 0.001	0.016 \pm 0.001
<i>Nemurella pictetii</i>	0.0013 \pm 0.0002	0.0021 \pm 0.0002	0.023 \pm 0.001	0.021 \pm 0.001

For abbreviations, see Table 2

concentrations, possibly because microorganisms were able to utilise the abundant P and N bound in humic complexes, as observed in other boreal streams and lakes (Jansson et al. 2001; Münster 1999). If so, the observed effects of not only liming but also nutrient enrichment might be typical for our humic streams.

Negative richness effects

Increasing richness was associated with reduced rates of leaf decomposition, detritivore LPE and detritivore growth in this study. This contrasts markedly with the positive effects of richness on detritivore LPE and growth documented from a previous laboratory experiment using the same stonefly species (Jonsson 2006), though in a further study richness also affected growth negatively in numerically uneven assemblages (McKie et al. 2008). Clearly, effects of detritivore richness on ecosystem processes vary with environmental context, even within a given species pool. Positive richness effects observed in stream microcosms have been attributed to altered antagonistic interactions among conspecifics (or other negative density-dependent effects; McKie et al. 2008), which should decline as richness is increased when total density is held constant (Jonsson and Malmqvist 2003). Consistent with this scenario, strong negative relationships between density and both LPE and growth have been documented for all three of our study species (McKie et al. 2008). Furthermore, *P. meyeri* has previously been found to enhance the feeding activities of *T. nebulosa* via an unknown mechanism of facilitation, contributing to a positive richness effect on LPE (Jonsson and Malmqvist 2003). However, in the present study LPE was greater at the higher density, indicating positive effects of intra-specific aggregation on decomposition, while the negative trait-independent complementarity fraction in the diversity effect partition indicates that inter-specific interactions were predominantly antagonistic (Fox 2005). These contrasting results indicate that the balance of positive and negative inter- and intra-specific interactions differed in our field experiment from previous laboratory studies.

Intra-specific competition should normally be more intense than inter-specific competition, since niche overlap is greater within than between species (Lotka 1932). Despite this, stream detritivores often aggregate with their conspecifics, with a given leaf patch typically dominated by one species (Murphy et al. 1998; Presa Abós et al. 2006). The positive effects of density on LPE in this study indicate advantages to aggregating in the field that outweigh the costs of intra-specific competition. Plausible possibilities include enhanced control of resources not readily available in closed laboratory microcosms (Sommer 1992), or reduced pressure for individuals in larger aggregations to

respond on detecting danger (e.g. via kairomones released by predators; McKie and Pearson 2006), allowing more feeding time (Malmqvist 1993; Rohlf and Hoffmeister 2004). Such effects would be diluted as intra-specific encounter rates decline in more diverse species mixtures, potentially contributing to the negative effect of detritivore richness on decomposition in the present study. Alternatively, the contrasting effects of density between field and laboratory experiments could reflect differences in detritivore–microbe interactions. Detritivorous stoneflies often scrape litter surfaces rather than chew leaves directly (Lieske and Zwick 2007). If biofilm development was more extensive under the field conditions of this study, then the need for stoneflies to consume litter directly in order to gain adequate nutrition might have been reduced (Lieske and Zwick 2007). Such behaviour could drive a positive association between LPE and detritivore density, if more rapid consumption of surficial biofilms at higher densities caused more individuals to feed directly on the litter.

In contrast with LPE, detritivore growth was lower at the higher density, suggesting that any positive effects of aggregation on resource capture were not sufficient to outweigh negative density-dependent effects on energy expenditure. Accordingly, the negative effect of richness on growth is unlikely to reflect altered intra-specific interactions in the mixtures. This result was also not caused by the selection effect, contrary to Jiang et al.'s (2008) suggestion that negative selection effects are the main drivers of negative richness effects in situ. Instead, trait-independent complementarity was negative in the present study, indicating that antagonistic interspecific interactions reduced performance across the species mixtures (Fox 2005). All our study species are relatively aggressive (personal observation and cf. Malmqvist 1993), and the energetic costs of such interactions might be more deleterious when combined with other environmental stresses in situ (e.g. Hemphill 1991), hindering allocation of acquired resources to somatic growth.

Environmental variation and the effects of species richness and composition

Unlike studies focusing on producer–herbivore systems (Dzialowski and Smith 2008; Fridley 2002), nutrient enrichment did not generate positive richness effects in our decomposer system. However, the negative richness effect on detritivore growth was weakened under both the liming and nutrient treatments. This was associated with reductions in negative trait-independent complementarity, indicating that both treatments reduced the intensity of antagonistic inter-specific interactions. This evidently allowed a greater allocation of acquired resources to somatic growth without any alteration of leaf consumption

rates, since the negative richness effect on LPE remained unaffected. Ca (Jenkins and Suberkropp 1995) and nutrients (e.g. Gulis and Suberkropp 2003) have potential to stimulate fungal growth in leaves, and it is possible that the reduction in negative trait-independent complementarity under the liming and nutrient treatments reflects reduced competition for microbially colonized patches. These results demonstrate that environmental factors can alter relationships between biodiversity and ecosystem functioning through effects on species interactions. However, in the present study there were upper limits to the potential for such effects, since there was no further change in trait-independent complementarity when lime and nutrients were applied together, over that observed when these treatments were applied separately.

The marked positive effect of liming on decomposition and LPE in the *T. nebulosa* monocultures was not apparent in the responses of any mixture including this species (Figs. 1c, 2c). This is suggestive of a stabilising influence of species richness on functioning, whereby variability in a process is reduced when more species are present (Loreau et al. 2002; Vinebrooke et al. 2004). Our results might partly reflect an “insurance effect” (Loreau et al. 2002) given that the positive liming effect on LPE for *T. nebulosa* was presumably offset, at least in part, by the weak responses of the other species. However, this cannot explain the full reduction in the responses of all combinations including *T. nebulosa*, indicating that the weaker effect of liming on LPE across the species mixtures also reflects “statistical averaging” (Doak et al. 1998), which is the inherent tendency of processes to fluctuate less as extreme responses are averaged across a more diverse community. Further experiments using higher richness levels are required to assess the extent to which these effects depend on increasing richness per se, given that the present results predominantly reflect the responses of just one species. Nevertheless, the weakened effect of liming on the performance of the species mixtures highlights the potential for a loss of detritivore diversity to compromise maintenance of processes in streams under anthropogenic stress.

Biodiversity, ecosystem functioning and environmental management in a variable world

Results from our field study highlight how changes in community diversity and composition might alter both the magnitude and variability of functioning in anthropogenically perturbed ecosystems, and also indicate that such effects can vary with environmental context. In particular, the consistent negative effects of increasing species richness on functioning in our field enclosures were not expected based on results from experiments conducted in laboratory microcosms (e.g. Jonsson and Malmqvist 2003),

including those where the same three species were studied (Jonsson 2006; McKie et al. 2008). This could reflect a number of differences between field and laboratory experiments that have potential to influence species interactions and resource use (e.g. presence of other organisms, differential accumulation of waste products). Consequently, caution is required in using laboratory results to predict outcomes of species loss for processes occurring in natural ecosystems. These contrasting results also highlight risks in basing cases for biodiversity conservation strongly on positive outcomes for ecosystem functioning observed in simplified experimental environments (Srivastava and Vellend 2005; Thompson and Starzomski 2007). Consequences of species loss for functioning in the real world are likely to vary not only with abiotic environmental characteristics (e.g. this study, Biles et al. 2003), but also with changes in trophic structure (Mulder et al. 1999), the composition of regional species pools (McKie et al. 2008), and the type and number of processes considered (Gamfeldt et al. 2008; Hector and Bagchi 2007). Such variation need not be intractable, but requires explicit consideration, whether biodiversity–ecosystem functioning experiments are conducted in the field or laboratory. Environmental management may best be informed through a stronger focus on how ecosystem functioning varies in response to well-defined and realistic scenarios of species loss and environmental change, with consideration given to both the magnitude and variability of important process rates.

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