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ORIGINAL ARTICLE

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How biological diversity influences ecosystem function: a test with a tropical stream detritivore guild

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Abstract We investigated the relationship between diversity and ecosystem function, which is controversial and has rarely been examined for consumer assemblages, for the process of leaf breakdown by the shredder guild in a tropical stream. We manipulated species richness, evenness and identity of four macroinvertebrate shredder species (three caddisflies and one mayfly) in microcosms and tested their effect on leaf breakdown rates measured as leaf mass loss per capita and per milligram of animal. Species richness, evenness and species identity all affected leaf breakdown rates. Breakdown rates tended to increase with higher richness, but only for the three caddisflies, probably through a release of intraspecific interference, although other mechanisms such as niche complementarity or facilitation cannot be discarded. Leaf breakdown by the caddisflies was reduced in the presence of the mayfly, possibly because of its mode of movement by swimming instead of crawling and its similarity to some predators that are common in leaf litter. Species identity was more important than species richness in determining leaf breakdown rates, indicating that some species within the shredder guild are not redundant, and suggesting important consequences of particular species loss for the functioning of the ecosystem.

Keywords Evenness · Leaf breakdown · Shredders · Species identity · Species richness

Introduction

The relationship between biological diversity and ecosystem function has emerged as a major scientific issue motivated by concerns about the potential ecological consequences of species loss (Loreau 2000). This issue, which has caused considerable controversy over the last decade (Duffy 2002), is considered of great importance not only from a scientific perspective, but also as a guide for environmental policy and resource management (Huston 1997). Most experimental tests of the relationship between diversity and ecosystem function have been performed with terrestrial plant assemblages (Emmerson and Raffaelli 2000) and have reached varying conclusions about the contribution of diversity to ecosystem function (Cardinale et al. 2000). While some consensus is being reached regarding the influence of plant diversity on productivity (Loreau et al. 2001), the influence of diversity of consumer assemblages on community processes has hardly been investigated. Two fundamental problems that need to be addressed concern the form of the relationship between species richness and ecosystem functioning, and the mechanisms that cause this relationship (Cardinale et al. 2000).

Four mechanisms could explain a positive relationship between species richness and ecosystem function, measured as the rate of some ecosystem process: (i) the *sampling effect*, in which a higher number of species increases the probability of encountering a species with higher processing rate; (ii) *niche complementarity*, in which different ways of resource use by different species produce more-efficient processing rates; (iii) *interspecific facilitation*, in which processing by one species facilitates processing by another; and (iv) *release from intraspecific interference*, in which an increase in species number causes a decrease in the number of individuals of the same species, so intraspecific competition or interference is reduced and the processing efficiency of that species is enhanced (Loreau 2000; Fridley 2001; Adler and Bradford 2002). The relative importance of these mechanisms in the interaction between species richness and ecosystem functioning is still not clear, even though they have received some attention in different ecosystems and with different guilds or functional groups (Giller and O'Donovan 2002).

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The second component of diversity, evenness (i.e., the relative abundance of species), has been mostly neglected, although its effect on ecosystem function is an important consideration; a change in evenness without a change in species richness allows the examination of the relationship between diversity and ecosystem function without the confounding effect of species identities (Wilsey and Potvin 2000). However, studies with plant assemblages have found contradictory patterns (Wilsey and Potvin 2000; Polley et al. 2003) and studies with consumers are again scarce (but see Dangles and Malmqvist 2004).

In this study, we experimentally examined the relationship between diversity and ecosystem function in two tropical Australian streams using a guild of stream insects known as *shredders*, which consume terrestrially derived leaf litter. In streams, the effect of species richness on ecosystem processes has received little attention, and recent studies have produced variable results. Jonsson and Malmqvist (2000) found a positive relationship between the number of stonefly shredder species and the rate of leaf breakdown when the number of species was increased from one to three, but this relationship disappeared when species richness was increased from three to six (Jonsson and Malmqvist 2003a). For filter-feeders (Simuliidae), Jonsson and Malmqvist (2003b) found no clear trend in filtration rates when the number of species was increased from one to three, while Cardinale et al. (2002) showed a positive effect of increasing species richness of filter-feeders (Hydropsychidae) on filtration rates in treatments comparing processing by one and three species. While consistent trends have been found within studies, there have been contrasting results between studies for consumption rates in grazers (Jonsson and Malmqvist 2003b; Poff et al. 2003). Regarding evenness, Dangles and Malmqvist (2004) found that, for a given level of shredder species richness, higher evenness caused lower leaf breakdown rates.

All these studies have been performed in temperate or boreal streams, while tropical streams have been neglected, as is usually the case (Boyero 2000). Tropical streams offer an excellent opportunity to examine links between biodiversity and ecosystem function because they typically exhibit high diversity of animal species and guilds (Vanni et al. 2002). Tropical Australian streams have some of the highest reported values for biodiversity of any streams globally (Pearson et al. 1986; Vinson and Hawkins 2003) and are therefore of great interest in providing insight into ecological relationships in high-biodiversity systems. The shredder guild, which has been generally reported as very scarce or nonexistent in tropical streams (e.g., Dobson et al. 2002; Mathuriau and Chauvet 2002; Dudgeon and Wu 1999), is abundant in these Australian streams (Cheshire et al. 2005) and has a major role in leaf litter processing (Pearson and Tobin 1989; Pearson et al. 1989; Nolen and Pearson 1993). It is composed of 14 species (Cheshire et al. 2005), of which four make up more than 90% of total shredder biomass and perform the majority of the leaf processing in the stream (Boyero et al. 2006): *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae), *Lectrides varians* Mosely, *Triplectides gonetalus* Morse and Neboiss (Trichoptera: Leptoceridae) and *Atalophlebia* sp. (Ephemeroptera: Leptophlebiidae).

We examined the relationship between diversity (species richness and evenness) of stream shredders and ecosystem functioning by performing two experiments to test the hypotheses that an increase in (1) shredder species richness (with constant abundance and evenness) or (2) shredder evenness (with constant abundance and species richness) causes an increase in the rate of leaf breakdown, indicating the existence of a sampling effect, niche complementarity, interspecific facilitation, and/or release from intraspecific interference.

Methods

Shredders were collected in August and September 2003 from Birthday Creek (18° 59′S, 146°10′E) and Camp Creek (18° 58′S, 146°10′E), both upland rainforest streams (~800 m a.s.l.) located in the Burdekin River catchment within the Paluma Range National Park, north-eastern Queensland, Australia. The collection period was in the cool dry season when flow velocities in the stream were low and constant (generally 0–25 cm s^{-1}) and water temperature ranged from 12 to 18°C.

We used the four most common shredder species in Birthday and Camp Creeks (see above): *A. kirramus*, *L. varians*, *T. gonetalus* and *Atalophlebia* sp. (hereafter we refer to the species by their generic names only). The three caddisfly species are specialist shredders, with >90% of their gut contents being vascular plant tissue (organic matter > 1 mm), while the mayfly species has a more generalist diet but still with an average of 46% of its gut contents being vascular plant tissue (Cheshire et al. 2005). Similar-sized larvae of each species were used in the experiments, avoiding early and final instars: 1.7 mg ± 0.8 SD for *Anisocentropus*, 1.1 mg ± 0.3 SD for *Lectrides*, 2.4 mg ± 0.8 SD for *Triplectides* and 4.7 mg ± 0.8 SD for *Atalophlebia*.

Larvae were acclimated in the laboratory for 2 days before the experiment started. They were placed in plastic containers (25 × 11 cm) filled with stream water to a depth of about 5 cm. Temperature was maintained at 15°C, and a 12:12 h light–dark photoperiod was used to mimic natural conditions. Containers were not aerated, as the animals were collected from still or slow-flowing water. Larvae were provided with leaves of *Apodytes brachystylis* Mueller (Icacinaceae), which were collected from the vicinity of the streams and air-dried. This species was abundant along Birthday and Camp Creeks and was palatable for shredders (Pearson and Connolly 2000).

The experiments were performed in similar plastic containers to those of the acclimation phase, filled with 1.2 l of stream water. One dry leaf of *A. brachystylis* was added to each container (initial mass: 337 mg ± 70 SD), where it was allowed to condition for 2 days before the experiment started. Processing rates at the experimental temperature were such that this was sufficient leaf material and habitat for normal processing to take place through the duration of the experiment (Nolen and Pearson 1993). Shredders commenced feeding on leaves immediately. Temperature and light conditions were identical to those of the acclimation phase.

Experiment I: species richness

We manipulated the number of species from one to three, always with a total of six individuals per container, and the same number of individuals of each species. The experiment consisted of three treatments (one, two, and three species) with different combinations of species and 6–15 replicates each. In the one-species treatments, six individuals of the same species were present; in the two-species treatments, there were three individuals of each species; and in the three-species treatments, there were two individuals per species. Ten containers were provided with one leaf but no animals to serve as a control of leaf mass loss (LML) in the absence of shredders. The experiment was checked daily, and any individual that died or pupated was immediately replaced by another individual. The experiment was terminated after 14 days. Individuals and leaf material were dried at 45°C for 48 h and weighed.

Experiment II: evenness

Evenness was manipulated (high or low), while the total number of individuals (six) was kept constant, and richness was either two or three species. Only the three caddisflies were used in this experiment because of availability. In the two-species treatment, high-evenness consisted of three individuals of each species, while the low evenness consisted of five individuals of one species and one individual of the other species. In the three-species treatment, high evenness consisted of two individuals of each species, while low evenness consisted of four individuals of one species and one individual of each of the other two species. All combinations of species/number of individuals were used and each combination was replicated four times. Ten containers were provided with one leaf but no animals, to serve as a control of LML. The experiment was checked daily and occasional dead or pupated individuals were replaced immediately. The experiment was terminated after 14 days. Individuals and leaf material were dried at 45°C for 48 h and weighed.

Statistical analysis

Leaf breakdown rates were quantified as daily LML, calculated as the initial minus the final leaf mass (corrected by subtracting average LML in controls) divided by 14 days. The variables considered were the LML per capita and the LML per milligram of animal (the latter log-transformed in order to meet the assumptions of parametric analysis).

In experiment I, the effects of species richness and species identity on LML per capita and LML per milligram were tested using two-way nested analyses of variance (ANOVA), where species identity was nested within species richness. We performed two analyses, one including the four shredder species and another one including only the three caddisflies, so our results could be more comparable to results for evenness and to those of Jonsson and Malmqvist (2000), who tested three species from a single insect order (Plecoptera).

Differences between observed and expected LML per capita and LML per milligram were tested for combinations of two or three species through two-way ANOVA, where the factors were the nature of the observation (observed/expected) and species identity. Observed values resulted from the two- and three-species treatments, while expected values resulted from combining appropriate multiples of the values for each species in the one-species treatments. Lower observed than expected rates could indicate the existence of negative interspecific interference, while higher observed than expected rates could indicate the existence of niche complementarity, interspecific facilitation, and/or release from intraspecific interference.

In experiment II, three-way nested ANOVAs were used to test for the effect of species richness, evenness (nested within species richness), and species identity (nested within species richness and evenness), on LML per capita and LML per milligram. Although assessing the interaction between species richness and evenness would be interesting, we considered evenness as a nested factor because it was not constant in the uneven treatments: at the two-species level, 83.3% of all individuals belonged to the dominant species (as the ratio was 5:1 individuals), while at the three-species level, the dominant species had 66.7% of total individuals (the ratio was 4:1:1).

Despite every treatment having equal numbers of individuals, differences in density were expected given the different body mass of the species, so we estimated animal density (mg of animal per cm^2 of container) and explored its variation with species richness and species identity through a nested ANOVA (with species identity nested within species richness).

Results

Survival was high in the experiments, viz.: *Anisocentropus*, 93%; *Lectrides*, 93%; *Triplectides*, 88%; *Atalophlebia*, 92%. Thus, replacement of individuals was low during the experiment. Daily LML in control leaves was 6.84 mg ± 1.99 SD in experiment I and 6.47 mg ± 1.17

SD in experiment II, which corresponded to approximately 2% of initial leaf mass.

Experiment I: species richness

When the four shredder species were included in the analysis, species richness had no effect on either LML per capita or LML per milligram, while the effect of species identity was marginally non-significant for LML per capita and highly significant for LML per milligram (Table 1; Fig. 1). When only the three caddisflies were included in the analysis, neither species richness nor species identity affected LML per capita (Table 1; Fig. 1). However, the effect of both factors on LML per milligram was marginally non-significant (Table 1), LML per milligram tending to be higher in three-species treatments than in one- and two-species treatments (Fig. 1).

For combinations of two or three species, differences between observed and expected LML per capita and per milligram were significant, as was the variation among species combinations (Table 2). For both variables, observed values were lower than expected for all the species combinations including *Atalophlebia*, and higher than expected for the combination *Anisocentropus—Lectrides—Triplectides* (Fig. 2).

Experiment II: evenness

LML per capita varied significantly with evenness, but not with species richness or identity (Table 3). Student's *t* post hoc tests showed that LML was higher with high evenness but only in the three-species treatments ($P < 0.0050$; Fig. 3). On the contrary, LML per milligram did not vary with evenness, but it was higher with three than two species (Fig. 3) although this result was marginally non-significant (Table 3). Variation of LML per milligram with species identity was also marginally non-significant (Table 3).

Density

Dry animal mass (mean ± SD) per individual at the end of the experiments was: *Anisocentropus*, 1.64 ± 0.62 mg; *Lectrides*, 1.02 ± 0.13 mg; *Triplectides*, 2.17 ± 0.62 mg; and *Atalophlebia*, 4.04 ± 1.41 mg. Density (mg/cm^2) varied with species identity but not with species richness (Table 4). Student's *t* post hoc tests showed that treatments with *Atalophlebia* and *Atalophlebia—Anisocentropus* had higher densities than all other treatments, while treatments with *Anisocentropus*, *Lectrides*, *Anisocentropus—Lectrides*, *Anisocentropus–Triplectides*, and *Anisocentropus—Lectrides—Triplectides* had the lowest densities.

Discussion

Our results show that species richness, evenness and species identity all have some effect on leaf breakdown rates, especially when corrected by animal mass. However, the effect of species richness on leaf breakdown rates was only evident for the three caddisflies, disappearing when *Atalophlebia* was included. The only comparable study on the effect of shredder species richness on leaf breakdown rates was performed with three stonefly species from two families and also found a positive effect of species richness on leaf breakdown rates when corrected by animal mass (Jonsson and Malmqvist 2000).

Leaf breakdown rates for two- and three-species combinations were different from those expected from one-species treatments. Breakdown rates were always lower than expected when *Atalophlebia* was present, suggesting the existence of interference between the mayfly and the caddisflies. This could be explained simply by an increase in density when *Atalophlebia* is present, as larger individuals could interfere with others more than would smaller individuals (assuming that intraspecific and interspecific interference were equal). However, the apparent size of the three caddisfly species

Table 1 Results of two-way nested ANOVA (with species identity nested within species richness) exploring the effect of species richness and species identity on leaf breakdown rates, measured as leaf mass loss (LML) per capita and per milligram of animal

	df	SS	*F*	*P*		*df*	SS	*F*	*P*
LML per capita (all spp.)					LML per capita (3 caddisflies)				
Species richness	2	0.23	1.05	0.3529	Species richness	2	0.16	0.82	0.4479
Species identity	10	2.01	1.88	0.0583	Species identity	4	0.38	0.96	0.4368
Error	92	9.86			Error	42	4.15		
LML per mg (all spp.)					LML per mg (3 caddisflies)				
Species richness	2	0.011	1.53	0.2211	Species richness	2	0.02	2.45	0.0986
Species identity	10	0.22	4.57	< 0.0001	Species identity	4	0.05	2.51	0.0561
Error	92	0.44			Error	42	0.21		

In the analysis with all species, we included *Anisocentropus kirramus*, *Lectrides varians*, *Triplectides gonetalus* and *Atalophlebia* sp., while in the analysis with only caddisflies, the first three species were included. Degrees of freedom, sum of squares, *F* statistic and probability values are shown

Fig. 1 Variation of LML (leaf mass loss) per capita and LML per milligram with shredder species richness, from one to three species, in experiment I. The species included in the analysis were *Anisocentropus kirramus*, *Lectrides varians*, *Triplectides gonetalus* (Trichoptera) and *Atalophlebia* sp. (Ephemeroptera) (*left*), or only the three caddisflies (*right*)

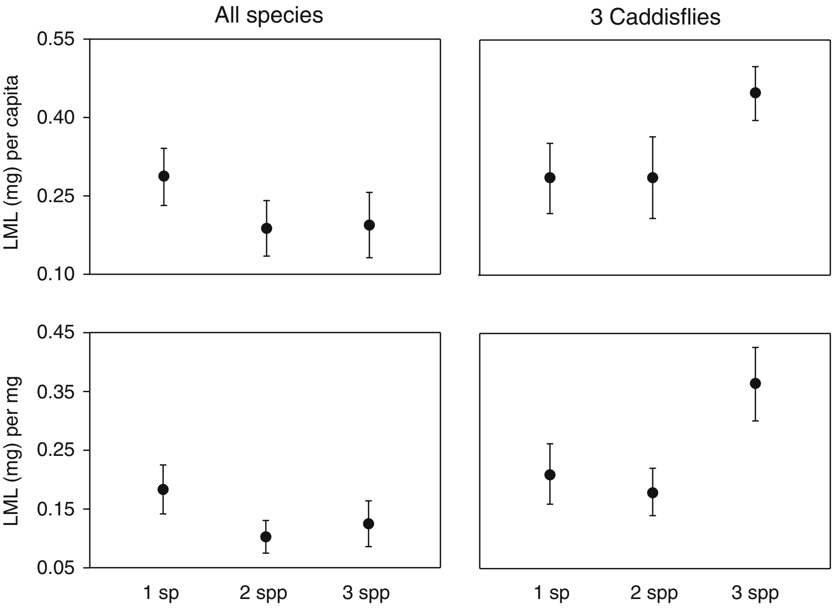

Table 2 Results of two-way ANOVA exploring the difference between observed and expected values of leaf breakdown (see Table 1) and the effect of species identity

	df	SS	*F*	*P*
LML per capita				
Obs./exp.	1	0.55	5.81	0.0167
Spp. identity	8	1.53	2.04	0.0436
Obs./exp. × spp. identity	8	1.09	1.46	0.1751
Error	217	20.32		
LML per mg				
Obs./exp.	1	0.31	7.16	0.0080
Spp. identity	8	1.19	3.45	0.0009
Obs./exp. × spp. identity	8	0.52	1.52	0.1525
Error	217	9.34		

Degrees of freedom, sum of squares, *F* statistic and probability values are shown

is not that of their body, as they have portable cases made of leaf pieces in *Anisocentropus* and *Lectrides* and of a hollow stick in *Triplectides*, which increase their size markedly (up to twofold in *Lectrides* and *Anisocentropus* and more than threefold in *Triplectides*). Thus, total animal size is not very different among species, and individuals of *Triplectides* are usually bigger than those of *Atalophlebia*. *Atalophlebia* individuals are swimmers, in contrast to the caddisflies, which are crawlers, and they could be confused with some predators that are common in the leaf litter such as damselflies (see Cheshire et al. 2005), or they could simply inhibit caddisfly feeding with their movement. Aggressive encounters between *Atalophlebia* and the other species are also possible but they were never observed.

Observed breakdown rates were higher than expected for the combination of three caddisfly species but not for combinations of two species. Consistently, leaf breakdown by caddisflies was similar in one-species and two-species treatments and higher in three-species treatments, suggesting the existence of at least one of three mechanisms (niche complementarity, interspecific facilitation, or release from intraspecific interference) occurring only when the three caddisfly species were all present.

Niche complementarity and facilitation are most likely when species have different feeding abilities but we have no evidence that this occurred in the studied species or of any change in feeding behaviour of any species when the others were present. Jonsson and Malmqvist (2003a) suggested the existence of niche complementarity among stonefly shredder species and demonstrated the facilitation of leaf breakdown by *Taeniopteryx nebulosa* (Taeniopterygidae) when *Protonemura meyeri* (Nemouridae) was already present, although the opposite did not occur (leaf breakdown by *P. meyeri* was not enhanced when *T. nebulosa* was already present). Facilitation has also been demonstrated within other functional feeding groups such as filter-feeders (Cardinale et al. 2002), but has been mostly found between functional feeding groups, such as shredders facilitating the action of filter-feeders (Usio et al. 2001).

Release from intraspecific interference has been previously found in the four studied species (Boyero and Pearson 2006) and it has also been shown for stonefly shredders (Jonsson and Malmqvist 2003a). Moreover, the positive effect of evenness on leaf breakdown rates in the three-species treatment suggests that intraspecific interference is important as the three species were all present in the different treatments, only varying the number of individuals of each species. The richness experiment suggests that intraspecific interference occurs even with a low number of individuals, as breakdown rates were lower in the two-species treatment (three individuals per species) than in the three-species treatment (two individuals per species).

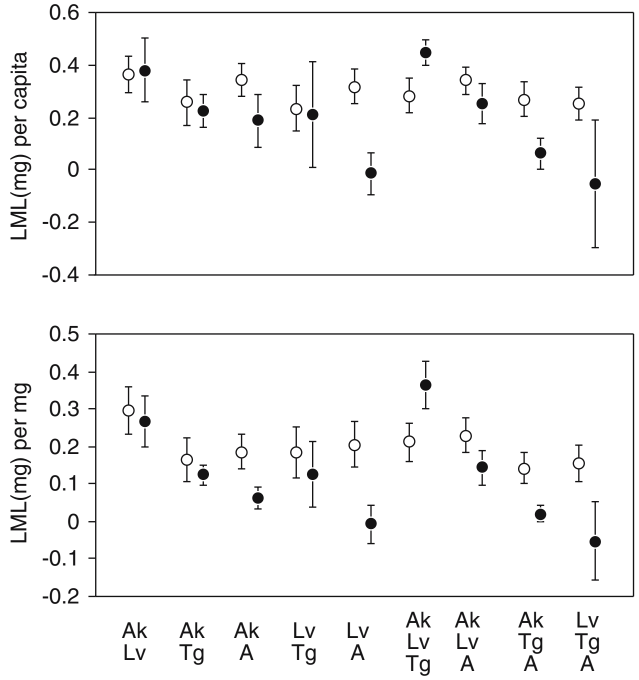

Fig. 2 Expected (*open circles*) and observed (*closed circles*) values for LML per capita and LML per milligram for two-species and three-species combinations. Observed values resulted from the two- and three-species treatments, while expected values resulted from combining appropriate multiples of the values for each species in the one-species treatments. Ak: *Anisocentropus kirramus*; Lv: *Lectrides varians*; Tg: *Triplectides gonetalus*; A: *Atalophlebia* sp.

Table 3 Results of three-way nested ANOVA (with evenness nested within species richness and species identity nested within species richness and evenness) exploring the effect of species richness, evenness and species identity on leaf breakdown rates (see Table 1)

	df	SS	*F*	*P*
LML per capita (3 caddisflies)				
Species richness	1	0.16	2.29	0.1381
Evenness	2	0.57	4.11	0.0245
Species identity	9	0.76	1.21	0.3185
Error	37	3.92		
LML per mg (3 caddisflies)				
Species richness	1	0.03	3.16	0.0835
Evenness	2	0.05	2.34	0.1101
Species identity	9	0.17	1.90	0.0833
Error	37	0.56		

Degrees of freedom, sum of squares, *F* statistic and probability values are shown

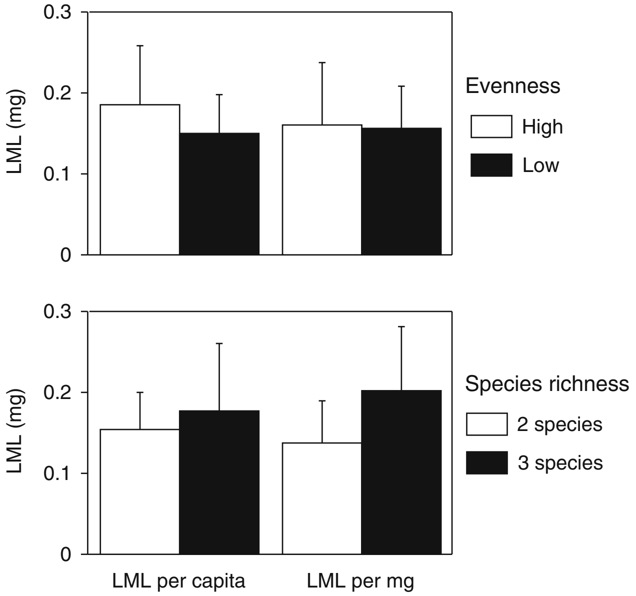

Fig. 3 Variation of LML per capita and LML per milligram with evenness and species richness in experiment II

It is likely that different mechanisms are operating at the same time. Although streams are often considered to be dominated by abiotic events, which keep populations at low densities such that resources are abundant and encounters among individuals are rare (Cross and Benke 2002), this is probably not the case in these tropical streams, for which the dry season presents relatively benign physical conditions as flow diminishes. It is suggested that, under these conditions, biological interactions become more important than physical effects, particularly as habitat area decreases in extent and invertebrate densities increase (Pearson 2004). However, the environmental context can modify the relationship between biodiversity and ecosystem function, so that it may vary even for the same organisms in the same system (Cardinale et al. 2000). The Australian Wet Tropics are distinctly seasonal, with a cool to warm dry season (May–October) and a hot wet season (November–April), so the patterns reported here might be valid only for the dry season, when the experiments were performed. However, the four shredder species are present in both seasons and shredding activity is important all year round (Pearson and Tobin 1989). Further investigations should address the influence of temperature on the relationship between biodiversity and leaf breakdown rates in these streams.

A possible drawback of this study might be the lack of resource heterogeneity, as only one leaf was offered to the shredders. Although shredder movement from leaf to leaf is not common in nature, and various individuals from the same species or from different species can be found on the same leaf (personal observation), further experiments should include a more heterogeneous resource and should address the importance of different mechanisms to explain a positive relationship between shredder species richness and/or evenness and leaf breakdown rates as well as the role of resource heterogeneity in determining the relative importance of these mechanisms. While experiments generally lack strict realism, they do provide clean tests of specific predictions (Daehler and Strong 1996).

Our results suggest that the identity of the shredder species present is more important than the number of species in determining the rates of leaf breakdown in these tropical streams. Vanni et al. (2002) also showed that taxonomic identity of consumers (fish and

Table 4 Results of two-way nested ANOVA (with species identity nested within species richness) exploring the effect of species richness and species identity on animal density (mg/cm^2)

	df	SS	*F*	*P*
Density (all spp.)				
Species richness	2	0.004	0.48	0.6196
Species identity	10	< 0.001	7.77	< 0.0001
Error	92	0.005		
Density (3 caddisflies)				
Species richness	2	< 0.001	1.10	0.3414
Species identity	4	< 0.001	3.95	0.0083
Error	42	0.002		

Degrees of freedom, sum of squares, *F* statistic and probability values are shown

amphibians) is important in determining the rates at which nutrients are recycled in a tropical stream. These results indicate that species within the same guild are not redundant and that the relationship between diversity and ecosystem function is not simply numeric, highlighting the importance of individual species' characteristics and predicting important consequences of loss of at least some species on the functioning of the ecosystem.

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