Simulating species loss following perturbation: assessing the effects on process rates

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We removed stream-living macroinvertebrate shredder species in the sequences in which they are predicted to disappear, in response to two common types of anthropogenic disturbances: acidification and organic pollution, and analysed the effects on leaf breakdown rates. The experiment was performed in field microcosms using three shredder species.

Species identity significantly affected leaf breakdown rates, while species richness *per se* was non-significant. The simulated sequential species loss showed large effects on leaf breakdown rates, with observed rates being significantly higher than expected from single-species treatments in two, out of four, two-species, and in all four three-species treatments. The invertebrates used in this study were taxonomically distinct (Insecta: Plecoptera and Trichoptera; Crustacea: Amphipoda), and of different sizes, hence a high degree of complementarity was probably present. A method to study the effects of species loss, characteristic of perturbation type, could be more useful than a random approach when investigating the impact of perturbation. Our results may have general applicability for investigations on the effects of diversity loss on ecosystem functioning in any ecosystem exposed to human perturbations, given that the order of extinction is known or can easily be assessed.

Keywords: species loss; ecosystem function; streams; perturbation; acidification; organic pollution

1. INTRODUCTION

The issue of whether species loss is important for ecosystem function is a critical one, as biodiversity is declining rapidly worldwide as a consequence of various human activities (Chapin *et al.* 2000). Previous studies on the effects of species richness on ecosystem functioning have tested effects by using (i) non-random species assemblages drawn from the species pool (Naeem *et al.* 1994, 1995); (ii) non-random species assemblages with exhaustive species combinations (Jonsson & Malmqvist 2000); or (iii) random species assemblages (Hector *et al.* 1999) complying with criticism on study design (Huston 1997). Random species assemblages are used to avoid testing for effects of particular sets of species only, and to enable general conclusions about biodiversity loss to be drawn. However, when species go extinct in nature, as a result of anthropogenic perturbation, they often do so in a non-random, approximate sequence as a consequence of differences in body size, trophic position, habitat specialization, physiology, morphology and life history (Patterson & Atmar 2000; Tilman & Lehman 2001). Hence, if species loss caused by perturbation has an effect on the function of a system, it is not the result of random species loss. The order of species loss following perturbation may have strong implications for ecosystem functioning. The kind of perturbation, and the original species composition (Ruesink & Srivastava 2001), are important factors in pre-

dicting the consequences of species loss, but so far few studies have focused on the loss of particular species and related processes.

In streams, the effects of many anthropogenic kinds of perturbation on aquatic invertebrate communities are fairly well known, e.g. at what levels of perturbation species are affected, and when they may become locally extinct (Hildrew & Townsend 1987; Reice & Wohlenberg 1993; Metcalfe 1994). However, the effects of species loss on important stream processes remain virtually unknown. Owing to physiological differences and constraints, aquatic invertebrates tolerate perturbations differently. Differences in sensitivity among macroinvertebrate taxa have also been used to construct indices for assessments of both acidification (Raddum & Fjellheim 1984; Lien *et al.* 1996) and organic pollution (e.g. Kolkwitz & Marsson 1909; Woodiwiss 1964; Chandler 1970). Therefore, it is also possible to rank species, or groups of species, at least approximately, according to the extent to which they are affected by particular perturbations. Both acidification and organic pollution have globally altered many stream communities from their original species composition. How this has affected the function of the streams is generally not well understood (Covich 1996).

Among detritivorous shredders in acidified streams, euholognathan plecopterans dominate while some trichopterans and dipterans, but very few crustaceans, are found (Dangles & Guérol 1999). In circumneutral streams plecopterans may be less numerous, while crustaceans and other acid-sensitive species are often abundant (Griffith & Perry 1993; Dangles & Guérol 1999).

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Figure 1. (a) Design of experiment with species identities nested under species richness and with the species used. (b) The sequences in which the species disappear following (i) acidification or (ii) organic pollution. Abbreviations: Gf, *Gammarus fossarum*; Sp, *Sericostoma personatum*; Np, *Nemurella picteti*.

In organically polluted streams the opposite pattern to that found in acidified streams is generally observed (Woodiwiss 1964), since most plecopterans are sensitive, some trichopterans are fairly tolerant and crustaceans often dominate in systems where they occur (Metcalf 1994). Species richness in streams shows a strong decrease following acidification—up to 60% of the species become extinct (Guérol *et al.* 2000)—and since the sensitivity to this perturbation varies more between higher than lower taxa of aquatic invertebrates (Otto & Svensson 1983), the result is often an even greater loss of higher taxonomic levels. Diversity at higher taxonomic levels may be crucial for the function of a system as positive interactions, facilitating process rates, are more likely to exist between more distantly related taxa (Morse 1977; May 1982).

We investigated how species loss following acidification and organic pollution of streams affects detrital breakdown rates. We did this by ‘removing’ species of detritivorous shredders, in the sequence in which they are expected to disappear in nature, following these two perturbation types (figure 1b). We propose not only that the loss of species might be important but also that the presence or absence of particular species might affect breakdown rates, as species differ in their breakdown efficiency, competitive ability and ways of utilizing the food resource. We used two different leaf species, one of presumed higher quality as food for shredders (alder) and one of poorer quality (beech) (Otto 1974; Friberg & Jacobsen 1994), to test whether food quality influences the effects of species loss.

2. MATERIAL AND METHODS

Three species of aquatic invertebrates were used as detritivorous shredders: *Nemurella picteti* Klapalek (Plecoptera), *Sericostoma personatum* (Kirby & Spence) (Trichoptera) and *Gammarus*

Table 1. Water properties in the experimental pool in April 2001.

variable	water properties
temperature (°C)	5.50
pH	6.85
conductivity (µS cm ⁻¹)	50.00
alkalinity (µeq. L ⁻¹)	350.00
hardness (mg CaCO ₃ l ⁻¹)	26.00
Cl ⁻ (mg l ⁻¹)	8.00
SO ₄ ²⁻ (mg l ⁻¹)	6.98
NO ₃ ⁻ (mg l ⁻¹)	4.48

fossarum Koch (Amphipoda). As the food resource, leaves of alder (*Alnus glutinosa* (L.) Gaertn.) and beech (*Fagus sylvatica* L.) were used. Leaves of the two leaf species were collected at autumn shedding, close to the study site, and were air dried. The invertebrates were collected from a single stream system in the Vosges mountains, northeastern France, just prior to the start of the study, and kept under natural conditions in a large container with stream water flowing through. The leaves were conditioned for three weeks in a circumneutral, unpolluted stream to be properly colonized by aquatic microbes. After conditioning, the leaves were retrieved and cut into leaf discs (2 cm in diameter) to produce an identical area of resources in both leaf treatments. Mesh bags (11 cm × 13 cm, 0.3 mm mesh) were used as microcosms and 30 leaf discs (initial ash-free dry mass (AFDM) for alder was 0.333 ± 0.002 g and for beech 0.247 ± 0.006 g) were placed in each bag together with the invertebrates. Initial dry mass (DM) was 1.12 ± 0.27, 5.73 ± 0.96 and 2.16 ± 0.16 mg for *N. picteti*, *S. personatum* and *G. fossarum*, respectively. For each leaf species eight treatments were replicated 10 times: three single-species treatments with 12 individuals of *N. picteti* and *G. fossarum* and six individuals of *S. personatum*, three two-species treatments with *N. picteti* and *G. fossarum* (6 + 6 individuals), *N. picteti* and *S. personatum* (6 + 3 individuals) and *G. fossarum* and *S. personatum* (6 + 3 individuals), one three-species treatment with *N. picteti*, *G. fossarum* and *S. personatum* (4 + 4 + 2 individuals), and one control treatment without macroinvertebrates. The densities of each species in the bags were representative of those found in detrital pools of local streams (Dangles 2000). We used half the density of *S. personatum* to that of the other two species to approximately balance the species mass differences. To estimate initial masses of leaves and animals, 10 samples, each with 30 leaf discs, and 10 individuals of each invertebrate species preserved in 70% alcohol, were used.

The experiment was conducted in a concrete outdoor pool (3 m × 2 m) with natural stream water flowing through. Water quality was typical of circumneutral streams flowing over granite rock in the area (table 1). The bags, containing leaf discs and animals, were attached randomly to a horizontal screen submerged in the pool. When the bags were retrieved after 14 days, leaf discs and animals were immediately separated. The animals were counted and preserved in 70% alcohol, dried at 50 °C for 48 h and weighed. The leaf discs were dried at 50 °C for 48 h, weighed, ashed at 550 °C for 1 h and weighed again to obtain AFDM.

Correction for effects of animal mortality on breakdown rates was made by assuming that dead individuals had lived for half the experimental time. Further, leaf mass loss per unit animal mass was used in the analyses to account for differences in

Table 2. Breakdown rates, both per capita and per unit biomass, and survival (± 1 s.e.) for each shredder species, on each leaf species.

species	breakdown rate (g per individual)	breakdown rate (g g ⁻¹)	survival (± 1 s.e.)
alder			
<i>S. personatum</i>	0.15 $\pm$ 0.010	2.6 $\pm$ 0.2	97.9 $\pm$ 1.4
<i>N. picteti</i>	0.06 $\pm$ 0.010	3.6 $\pm$ 0.3	71.4 $\pm$ 3.7
<i>G. fossarum</i>	0.05 $\pm$ 0.010	1.5 $\pm$ 0.2	71.4 $\pm$ 4.2
beech			
<i>S. personatum</i>	0.12 $\pm$ 0.010	2.5 $\pm$ 0.3	98.6 $\pm$ 0.9
<i>G. fossarum</i>	0.02 $\pm$ 0.008	1.0 $\pm$ 0.7	51.4 $\pm$ 3.6
<i>N. picteti</i>	0.01 $\pm$ 0.010	0.5 $\pm$ 0.4	72.5 $\pm$ 3.3

Table 3. Nested ANOVAs on breakdown of alder and beech, including all species identity treatments.

	source	sum of squares	d.f.	mean squares	<i>F</i>	<i>p</i>
alder	species richness	0.000 0023	2	0.000 001 15	0.23	0.80
	species identity	0.000 0200	4	0.000 005 01	10.91	< 0.000 001
	error	0.000 0285	62	0.000 000 46		
beech	species richness	0.000 0142	2	0.000 007 10	0.69	0.55
	species identity	0.000 0415	4	0.000 010 37	7.96	< 0.0001
	error	0.000 0821	63			

biomass. Expected values for each multispecies treatment in the sequential-loss data were based on average breakdown values of the different single-species treatments. The expected values in the random-loss experiments are equal to the average of the single-species treatments.

(a) Statistical methods

The experiments were set up in a nested fashion with each species identity treatment nested under a species richness treatment (Jonsson & Malmqvist 2000). This design allowed us to separate the effects of species richness and species identity using nested ANOVA, including all species combinations in each species richness treatment (figure 1a). Analyses were performed using SYSTAT 8.0 for Windows. In the analyses, where species loss following perturbation (figure 1b) was simulated, observed breakdown rates were compared with expected breakdown rates, derived from single-species treatments, using two-tailed, paired *t*-tests.

3. RESULTS

Survival was high, except for *G. fossarum*, in the beech treatment, with just over 50% remaining at the end of the experiment (table 2). The most efficient shredder on alder was *S. personatum*, followed by *N. picteti* and *G. fossarum*, and for beech *S. personatum* was the most efficient shredder, followed by *G. fossarum* and *N. picteti* (table 2). Taking biomass into account, *N. picteti* was the most efficient shredder on alder, followed by *S. personatum* and *G. fossarum* (table 2). In the beech treatment, *S. personatum* was the most efficient shredder per unit biomass, followed by *N. picteti* and *G. fossarum* (table 2). Alder breakdown was significantly affected by species identity but not by richness (nested ANOVA; table 3; fig-

ure 2a). For the simulated species loss following acidification, breakdown rate was significantly higher than expected in the three-species treatment ($t = 2.47$, $p < 0.05$) where the 95% confidence interval did not bracket the expected value (figure 2b). The same results were obtained in the three-species treatment for species loss following organic pollution (figure 2c) as this treatment was identical in both sequences.

Beech breakdown rate was not significantly affected by species richness when all species treatments were included, whereas species identity was highly significant (nested ANOVA; table 3; figure 3a). The observed breakdown rates predicted from acidic perturbation in both the two- and three-species treatments were significantly higher than expected ($t = 6.44$ and 2.36 , $p < 0.001$ and $p < 0.05$; figure 3b). For the simulated effect of organic pollution (figure 3c), the breakdown values observed were again significantly higher than expected for both the two- and three-species treatments ($t = 3.28$ and 2.36 , $p < 0.01$ and $p < 0.05$), the three-species treatment again being identical in both types of simulated perturbation.

4. DISCUSSION

Our results showed that species number was important for the detrital breakdown rates, although only through species combinations, as species richness *per se* showed no significant effect. The effect of species loss on leaf breakdown rate is similar to previous results (Jonsson & Malmqvist 2000) although the species were more closely related, and species richness *per se* was significant. Species identity effects in the present study are different from the situation when a single species has exceptionally large effects on process rates (i.e. the 'sampling effect'; Huston

Figure 2. Species richness versus alder leaf breakdown rate with (a) all species identity treatments included; (b) species loss following acidification; and (c) species loss following organic pollution. Black dots represent expected breakdown based on the single-species treatments. Error bars represent ± 1 s.e. in (a) and 95% confidence intervals in (b) and (c). Abbreviations as in figure 1.

(1997)), as all species were included in all species richness treatments. Instead, certain combinations of species had disproportionately large effects on the leaf breakdown rates.

The simulation of species loss both following acidification and after organic pollution (figure 1b) showed significant effects on the breakdown rates. In the alder treatment there was, however, only a significant effect in the three-species treatment, where the observed breakdown was higher than expected (figure 2b,c). In the beech treatment, the effect of species loss was larger than in the alder treatment and significant in both the two- and three-species treatment (figure 3b,c). Loss of species thus led to decreased breakdown rates because combinations of species performed better than single species. Our predictions are conservative, as it is conceivable that the perturbation has negative effects on the performance of the remaining species.

Species differed somewhat in the way they fed on the detrital discs, which suggests niche partitioning, and hence facilitation between species. *Nemurella picteti* appeared to feed on the surface of the leaves, *G. fossarum* on the edges

Figure 3. Species richness versus beech leaf breakdown rate with (a) all species identity treatments included; (b) species loss following acidification; and (c) with species loss following organic pollution. Black dots represent expected breakdown based on the single-species treatments. Error bars represent ± 1 s.e. in (a) and 95% confidence intervals in (b) and (c). Abbreviations as in figure 1.

whereas *S. personatum* cut the discs into smaller pieces. The most obvious case of facilitation would, in our study, be between *G. fossarum* and *S. personatum*, since *S. personatum*, through cutting, greatly increased the availability of edges, which *G. fossarum* seemed to prefer. The probability of including seemingly important species, such as *S. personatum*, increases with species richness. Because of its large size and powerful mouthparts, *S. personatum* was able to feed on the detritus, independently of quality or conditioning, thus making the resource more accessible to the other detritivores. Such facilitation could be particularly important when the detritus is of low quality. Consequently, we observed that the effect of species loss was greater when poor-quality beech detritus was used than when alder was used.

The performance of different shredder species changed with leaf species. *Sericostoma personatum* went from being the second most efficient shredder in the alder treatment to being more than twice as efficient as the second most efficient shredder in the beech treatment, per unit biomass

(table 2). Thus, the most important species may shift between different systems if properties, such as perturbation type or level, vary. This suggests that species composition may determine process rates not only following perturbation but also in the event of changed food quality. Food quality changes could occur independently of chemical perturbation, for example through the invasion of exotic plant species. Thus, decreasing species richness and/or changing food quality could affect process rates.

Our study was performed under field conditions using naturally co-occurring species, in typical abundances and with a natural food level. Furthermore, the species used have an unambiguous and expected order of extinction following acidification and organic pollution. Hence, our results may provide important clues to what may happen in natural stream systems if these species, or others with similar tolerances, were lost following these perturbations. Simulating sequential species loss to measure the consequences of perturbations may be useful in environmental management, and may work for any systems where perturbation tolerance levels are known, e.g. organic pollution and marine benthos (Bellan & Bellan-Santini 1972), acidification and zooplankton (Locke 1991), airborne pollutants and microbial soil communities (Rusek & Marshall 2000) and airborne pollutants and lichens (Richardson 1991). To our knowledge, previous studies have rarely tested the effects of species loss occurring in an order that can be expected, and comparing it with random loss (although note Petchey *et al.* (1999)). Testing specific species loss requires, of course, a good knowledge of the system and how species are affected by different types of perturbation, but also that the order of species loss remains constant. If these criteria are met, useful indications of the effects of species loss in virtually any type of ecosystem may be derived using experiments similar to ours.

Investigating random species loss, or loss of species richness *per se*, may also be useful to predict the consequences of species loss and reveal the mechanisms behind species richness effects, especially if patterns of species loss are unknown. Such an approach might, however, be of little practical use, since species loss in nature is not random but often occurs in a predictable sequence following perturbation (Huston *et al.* 2000). If the sequence for a particular perturbation type is known it may be quite possible to perform useful experiments, whereas when the effects, or the animal responses, are unknown preliminary experiments should be performed to suggest extinction orders. Thus, it is crucial to understand how anthropogenic perturbations affect species—which species are affected and to what degree—to be able to predict the consequences of losing species for system processes.

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