

LETTER

Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions

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Abstract

Species loss can result in secondary extinctions and changes in ecosystem functions at distant trophic levels. Such effects of species loss are predicted to be affected by both the number of species lost within a trophic level (horizontal diversity) and the number of trophic levels lost (vertical diversity). We experimentally manipulated horizontal and vertical diversity within an aquatic insect community, and examined responses throughout the food web. Horizontal and vertical diversity both impacted ciliates: reduction of detritivorous insect diversity resulted in secondary extinctions and decreased density of ciliates, but only when an insect predator was simultaneously absent. Horizontal and vertical diversity differed in their effect on other foodweb processes, including detrital processing, predator growth, and densities of rotifers, flagellates and flatworms. These results caution that foodweb effects of multitrophic species loss may not be reliably predicted from manipulations of just one dimension of diversity.

Keywords

Bromeliad, ciliates, damselfly, decomposition, detritivore, ecosystem functions, extinction cascades, secondary extinctions, species diversity, trophic structure.

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INTRODUCTION

Species loss has been predicted to have profound effects on the structure and functioning of food webs (Hooper *et al.* 2005). Recent meta-analyses show that reductions of diversity within a trophic level generally reduce the standing stock of and resource capture by the manipulated trophic level (Balvanera *et al.* 2006; Cardinale *et al.* 2006). It is less clear how species loss at multiple trophic levels in a food web will affect ‘ecosystem functions’, defined as the flux of energy and nutrients through food webs and the production or maintenance of biomass (Srivastava & Vellend 2005; Duffy *et al.* 2007). In this study, we examine both the causes and consequences of extinctions at multiple trophic levels.

In natural communities, species often simultaneously go extinct at multiple trophic levels because they share a threatened habitat (e.g. intact Amazonian forest: Laurance *et al.* 2002), or because a stressor affects a broad spectrum of organisms (e.g. lake acidification: Vinebrooke *et al.* 2003). Species may also go extinct in tandem because of tight, coevolved interactions. For example, recent estimates suggest that 6300 species of specialist pollinators, parasites

and herbivores are endangered because their host is at risk of extinction (Koh *et al.* 2004). More generally, loss of a single species may trigger a cascade of further (secondary) extinctions throughout the food web.

There is growing evidence that extinction cascades occur in nature. For example, loss of a keystone predator can lead to local competitive exclusion amongst prey (e.g. Paine 1966). Similarly, local reductions in plant diversity have been linked to decreased herbivore diversity (Siemann *et al.* 1998; Haddad *et al.* 2001). Secondary extinctions have also been documented at distant trophic levels (Estes & Palmisano 1974; Crooks & Soulé 1999; Ebenman & Jonsson 2005). For example, the loss of wolves in parts of North America has led to increased moose populations, whose herbivory has reduced the local richness of passerines (Berger *et al.* 2001). Foodweb models also often show the potential for extinction cascades under certain conditions (e.g. Borrvall *et al.* 2000; Dunne *et al.* 2002; Ebenman *et al.* 2004; Ebenman & Jonsson 2005; Thébault *et al.* 2007). These models have all been developed for ‘green’ (living plant based) food webs rather than the ‘brown’ (detrital based) food web we describe shortly. Moreover, models of

extinction cascades have largely stopped short of examining consequences for ecosystem function (but see Thébault *et al.* 2007).

The loss of species at multiple trophic levels, for example through secondary extinctions, presents a challenge for predicting the effects on ecosystem function because two dimensions of foodweb diversity may change simultaneously: the number of species within a trophic level (horizontal diversity) and the number of trophic levels (vertical diversity). Top trophic levels often disappear first because they tend to be the most vulnerable to perturbations (Petchey *et al.* 2004; Duffy *et al.* 2007). Such changes in vertical diversity could modify the effects of horizontal diversity on function. For example, several models predict that herbivores could alter the effects of plant diversity on plant biomass, particularly if the herbivores are generalists or plants do not experience a resistance-growth tradeoff (Holt & Loreau 2002; Thébault & Loreau 2003). Indeed, experiments demonstrate that losing a higher trophic level changes the effect of horizontal diversity on function (Mulder *et al.* 1999; Duffy *et al.* 2005; Hättenschwiler & Gasser 2005; Wojdak 2005).

Conversely, horizontal diversity could modify the effects of vertical diversity on functions. For example, increasing prey diversity could increase predation because diverse prey communities provide a more balanced diet (DeMott 1998). The opposite pattern could occur if high prey diversity reduces the searching efficiency of specialist predators (Root 1973), or increases the likelihood of including a predation-resistant but slow-growing prey species (e.g. Fox 2004). Similarly, high predator diversity could increase net prey consumption if predators differ spatially or temporally in abundance (Losey & Denno 1998; Otto *et al.* 2008), but decrease prey consumption if predators interfere with or consume each other (Rosenheim *et al.* 1993; Finke & Denno 2005; Otto *et al.* 2008). Such effects of horizontal diversity on predation rates could affect the strength of trophic cascades, as shown within studies (Finke & Denno 2005; Snyder *et al.* 2006; Otto *et al.* 2008) but not between studies (Borer *et al.* 2005).

In studies of how species loss affects either function or secondary extinctions, an important challenge has been to distinguish between the effects of losing a particular species vs. interrupting interactions between species. In the diversity-function literature, the effects of species identity are encapsulated in the idea of selection (also called sampling) effects: if the probability of including any given species in a community increases with species richness, then positive (negative) covariance between species dominance and effect on function leads to function increasing (decreasing) with richness (Huston 1997; Tilman *et al.* 1997). By contrast, complementarity effects refer to species mixtures having higher function than expected from additive effects of

monocultures, usually attributed to niche complementarity or facilitation (Tilman *et al.* 1997). There is a parallel with extinction cascade theory, which also contrasts effects of the number of primary extinctions vs. the identity of the primary extinction. Most models predict that the likelihood of secondary extinctions increases with the number of primary extinctions (reviewed by Ebenman & Jonsson 2005). However, the likelihood of secondary extinctions also depends on characteristics of the primary extinction, with greatest effects predicted for loss of autotrophs and highly-connected species (e.g. Borrvall *et al.* 2000; Dunne *et al.* 2002).

In this study, we examine how horizontal and vertical diversity interact in causing secondary extinctions and affecting ecosystem functions. We base our experiment on the aquatic food web within bromeliad plants (Fig. 1), consisting of a basal resource of detritus (passively captured by the bromeliad) which is processed by detritivorous insects and decomposed by bacteria and fungi. The detritivores are preyed upon by predatory insects, especially damselfly larvae, while the bacteria and fungi also support microfauna (ciliates, rotifers, flagellates and flatworms). We manipulated the diversity of insect detritivores (horizontal diversity) and the presence of damselflies (vertical diversity) in a fully factorial design and measured effects on ciliate extinctions and six ecosystem functions. This experiment tests the following hypotheses: (1) reduction in horizontal diversity results in secondary extinctions, and changes in both standing stocks (densities of individuals) and rates of resource capture throughout the food web; (2) reduction in vertical diversity also results in secondary extinctions, and changes in standing stocks and rates of resource capture; (3) these effects of horizontal and vertical diversity interact; (4) effects of species loss depend on disrupting interactions between species (i.e. species complementary or facilitative effects) rather than losing a particular species (i.e. selection effects).

METHODS

Experimental design

Our experiment was designed to determine the effect of predators and detritivore richness and composition on secondary extinctions and foodweb processes. Our factorial design crossed two predator levels (present and absent) with 11 detritivore community compositions. Detritivore communities consisted of one, two or four detritivore species, with all possible combinations at each richness level from a species pool of four detritivores ($n = 5$). Three-species detritivore communities would have been useful in examining transitive effects, but were not included because of limits on the total number of replicates we could run. There

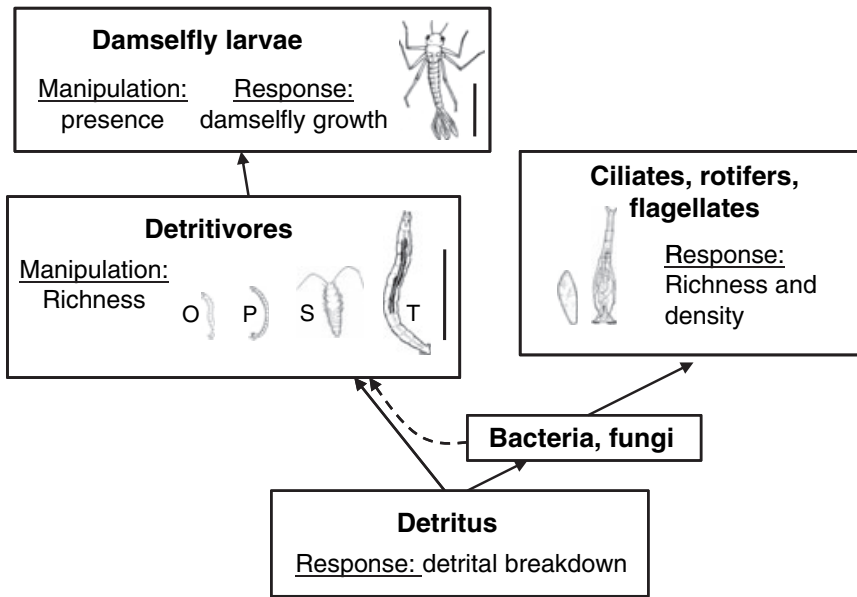


Figure 1 The aquatic food web used in this experiment (shown) is based on the food web in Costa Rican bromeliads. Two trophic levels were factorially manipulated and the response of three trophic levels was measured, as indicated. Detritivores used in this experiment included Orthocladiinae chironomids (O), *Polypedilum* sp. chironomids (P), *Syrtes* sp. scirtid beetle larvae (S), and *Trentepholia* sp. tipulid larvae (T). The scale bar placed next to insects represents 1 cm. The ciliate and rotifer illustrated are microscopic.

is a tradeoff between number of treatments and the number of replicates per treatment, and we emphasized the latter to maximize power in detecting detritivore diversity effects.

The experiment followed a substitutive design, that is, the total amount of detritivores in each treatment was the same. Substitutive designs ensure that differences between monocultures and polycultures reflect real differences in composition (presence and relative abundance of species), not differences simply in the amount of insects. In our design, all treatments had the same net metabolic capacity (i.e. biomass standardized for allometric effects on metabolic requirements), and within a treatment, species contributed equally to net metabolic capacity (Table S1). By standardizing for metabolic capacity we ensured that any difference between detritivore communities must represent traits of detritivores other than body size (Ruesink & Srivastava 2001; Wilby *et al.* 2005).

Study site and organisms

This study was conducted at Estación Biológica Pitilla in the Área de Conservación Guanacaste, Costa Rica (10°59' N, 85°26' W, 700 m elevation). Bromeliad fauna were collected from tropical moist (3000 mm precipitation year⁻¹) forest surrounding the station.

Damselfly (*Mecistogaster modesta* Selys) larvae (Fig. 1) are generalist predators in bromeliads, and consume all detritivores used in this experiment. Damselflies occur in larger or exposed bromeliads (Srivastava 2006) where they represent > 85% of total predator biomass (D.S. unpublished data).

We also used the four most abundant detritivore species (Fig. 1): larvae of each of a crane fly (*Trentepholia* sp.,

Tipulidae: Diptera), a beetle (*Syrtes* sp., Scirtidae: Coleoptera), a large chironomid (*Polypedilum* sp., Chironomidae: Diptera) and a smaller chironomid (Orthocladiinae, Chironomidae: Diptera). Together, these four species represent 81 (± 3 SE) % of detritivore biomass in bromeliads ($n = 18$).

Experimental conditions

We constructed mesocosms that approximated the natural architecture of bromeliads. Each artificial bromeliad consisted of three plastic leaf shapes glued with aquarium-safe silicon to form nested compartments within a 220-mL plastic cup (see Fig. 2 of Srivastava 2006). We covered each artificial bromeliad with 1.5-mm mesh bags to capture emerging adults. As in natural bromeliads, insects could move slowly between compartments by crawling out of the water to where 'leaves' overlapped. Insect growth is broadly comparable between natural and artificial bromeliads (Srivastava 2006).

Each artificial bromeliad was filled with 85 mL of sterile water, plus 10 mL of water from natural bromeliads (to seed our experiment with microbiota). Bromeliad water was cleared of insect larvae under 10 \times magnification prior to inoculation. Each artificial bromeliad received 2 g of dried (60 °C), recently dead leaves from nearby *Conostegia xalapensis* Bonpl. (Melastomataceae) trees, pre-conditioned in water for 10 days.

The experiment ran from 26 October to 23 November, 2001. During this period, detritivores showed typical dynamics: they survived as larvae, emerged as adults or died (often due to predation). Emerging adults were recorded daily, removed and replaced with late instar larvae of the same species to maintain treatments. To offset

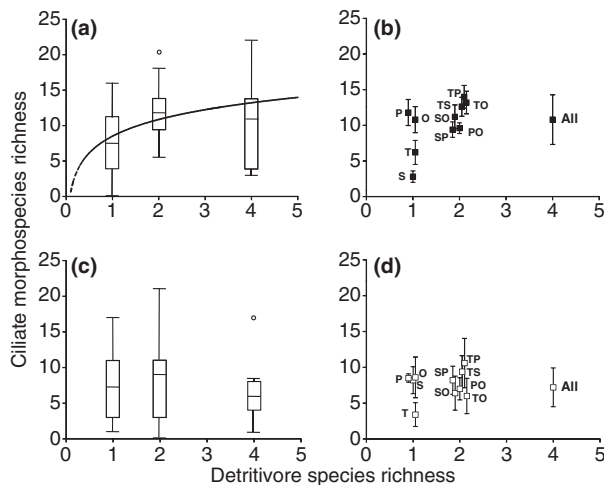


Figure 2 Richness of ciliate morphospecies as affected by the richness and composition of detritivore species, in either the absence (a, b) or presence (c, d) of predacious damselflies. In (a, c), the distribution of data is shown using box-whisker plots where the box bounds the interquartile range (middle 50% of data), the inner line of the box denotes the median, whiskers show range of data which exceeds the interquartile box by $< 1.5 \times$ interquartile range and open circles show outliers (data $> 1.5 \times$ interquartile range beyond box). Dashed lines indicate significant regression models predicting ciliate richness as a function of detritivore richness, irrespective of detritivore composition. In (b, d), detritivore monocultures are labelled as in Fig. 1. Two-species communities are designed with the two letters corresponding to their component species. Four-species communities are designed as 'all'. Mean values and SE are shown. Treatments are jittered horizontally slightly to reveal all data.

reductions in metabolic capacity due to larval mortality, we added additional detritivores on 2 November (50% of original metabolic capacity) and 13 November (25% of original metabolic capacity), with each species again contributing equally to total metabolic capacity. These inputs also ensured that the damselfly had adequate prey to survive. Four replicates with damselfly mortality were excluded from the analysis.

Response variables

At the end of the experiment, we dismantled the mesocosms and recorded the number and body length of detritivores. Damselfly growth was assessed by mass change over the experiment (± 0.001 g). After the insects were removed, we washed the mesocosm and detritus with Lugol's solution (200 g potassium iodide, 100 g crystalline iodide, 2000 mL of distilled water, 190 mL of glacial acetic acid) to kill and dislodge attached microorganisms. The detritus was rinsed through 1.5-mm mesh, and retained particles were dried for

24 h prior to mass (± 0.0001 g) determination. Detrital loss was calculated as mass change over the experiment. Liquid from each artificial bromeliad was transferred to a 100-mL cylinder, additional Lugol's solution was added, and after 48 h of settling the liquid was decanted until 10 mL remained. Lugol's solution binds to microorganisms so that they lose buoyancy. In Canada, a 2 mL of subsample of the 10 mL of liquid was examined at $200\times$ magnification. Ciliates were identified to morphospecies based on gross morphological characteristics. Ciliates, rotifers and rhabdocolle worms were counted in the entire 2 mL of sample and flagellates in 20 fields of view.

Statistical analysis

We modelled the response of each ecosystem variable (EV) to our foodweb manipulations as follows:

$$EV_i = \beta_0 + \beta_1 \text{detritivore variable(s)} + \beta_2 \text{predator} + \beta_3 \text{detritivore variable(s)} \times \text{predator} + \varepsilon_i$$

where 'detritivore variable(s)' refers to one or more detritivore parameters as described shortly, 'predator' refers to the presence or absence of the damselfly, and ε_i refers to the residual error for replicate i . As initial analyses showed that damselflies affected variances, we also conducted separate analyses of detritivore effects in treatments with vs. without damselflies:

$$EV_i = \beta_0 + \beta_1 \text{detritivore variable(s)} + \varepsilon_i$$

We first examined the effect of the number of detritivore species [i.e. detritivore variable(s) = detritivore richness] on each EV. We then examined the effect of detritivore identity and detritivore polycultures on each EV:

$$\text{detritivore variable(s)} = \beta_T T + \beta_S S + \beta_P P + \beta_O O + \text{detritivore polycultures}$$

In this equation, T, S, P and O indicate the proportion of total metabolic capacity (0, 0.25, 0.5 or 1) represented by, respectively, tipulids, scirtids, *Polydora* chironomids and Orthoclaadiinae chironomids in a particular community. If the effects of species are purely additive, then the expected EV value of a polyculture will simply be equal to the mean of the monocultures of its constituent species ($\beta_T T + \beta_S S + \beta_P P + \beta_O O$). In this case, the 'detritivore polycultures' term will be nonsignificant. If species effects are non-additive, then the 'detritivore polycultures' term will be significant. This type of analysis, which compares polyculture response with the weighted mean of the monoculture responses, is the norm for assessing antagonistic or synergistic effects of multiple consumers in substitutive designs (e.g. Wilby *et al.* 2005). If non-additive effects were important in explaining variation in the

response variable, then the effect of 'detritivore polycultures' could be further decomposed, first by comparing two species vs. four species polycultures, and then by examining the significance of particular two-species communities (Wilby *et al.* 2005). Note that non-additive effects preclude us from examining effects of individual species as main effects cannot be separated from interactions.

All regression analyses were based on generalized linear models, using the statistical program R (version 2.6.2). Error distributions were chosen based on the nature of the data; identifying the actual error distributions – a task for future studies – would yield greater insights into the underlying ecological processes. Species richness and density data are both count data (for which Poisson errors are appropriate), but in some situations are better modelled as continuous data (for which Gaussian errors are appropriate). We chose either Poisson or Gaussian errors for such data based on residual diagnostic plots. Detritus decays exponentially over time, and Gamma errors are often appropriate for such multiplicative processes. Damsel fly growth was a continuous measure, thus modelled with Gaussian errors. The per capita emergence rate of detritivores is proportion data, and thus modelled with binomial errors. Standard link functions and transformations were used to ensure residuals had constant variance and were uncorrelated with linear predictors. Over- or under-dispersion in Poisson models was corrected using the procedure `dispmod` (package MASS; <http://www.r-project.org>).

We tested for effects of detritivore richness on ciliate composition in subsets of treatments with vs. without damsselfies, using the Analysis of Similarity (ANOSIM) routine of PRIMER 5 for Windows (Plymouth Marine Labs, Plymouth, UK). ANOSIM uses a randomization test (999 permutations) to assess the significance of Global R , the standardized difference (between treatments and within treatments) in pairwise similarity.

RESULTS

Ciliates richness, density and composition

Overall, damsselfies and detritivores affected ciliates. In the full dataset, the richness of ciliate morphospecies was reduced by damsselfy presence, but unaffected by either detritivore richness or the interaction between detritivore richness and damsselfy presence (Table 1). However, when just treatments without the damsselfy were considered, ciliate richness increased with detritivore richness (Fig. 2a; Table 1). In the presence of damsselfies, detritivore richness did not affect ciliate richness (Fig. 2c; Table 1). Note that the significance of detritivore richness differed substantially between treatments with and without damsselfies, yet there was no interaction between detritivore richness and dam-

selfy presence in the full data set. We interpret this to mean that detritivore richness generally affected ciliate richness, but noise in treatments with the damsselfy prevented this pattern from being significant.

Ciliate density increased with detritivore richness in the full dataset, but was unaffected by either damsselfy presence or the interaction between detritivores richness and damsselfies (Table 1). The effect of detritivore richness on ciliate density was, like ciliate richness, stronger in the absence of damsselfies (Table 1). Note that effects of detritivore richness on ciliate density, unlike ciliate richness, are marginal after correction for multiple tests. Similarly, ciliate composition differed significantly among treatments with one, two or four detritivore species in the absence of damsselfies (ANOSIM, Global $R = 0.112$, $P = 0.036$) but not in the presence of damsselfies (ANOSIM, Global $R = 0.045$, $P = 0.19$).

One reason detritivore polycultures have more species than detritivore monocultures (11.22 vs. 8.32 species on average) is that they simply tend to have more individuals (59.1 vs. 36.5 mL⁻¹). However, this is not the only reason, as correlations between ciliate and detritivore richness persist even after rarefying ciliate richness to the lowest sample size: six individuals ($F_{1,52} = 6.06$, $P = 0.017$). We investigated whether demographic traits of ciliates (mean abundance or frequency in detritivore polycultures) explained which ciliates were lost from a monoculture, but found no significant correlations ($r < 0.25$, $P > 0.05$, $n = 34$ ciliate morphospecies).

The preceding analyses establish an effect of detritivore richness on ciliates, but are unable to distinguish between two potential causes: synergistic effects of detritivore species in polycultures, or sampling effects. We now investigate these two causes by explicitly incorporating detritivore composition into our analysis (see Methods). In these models the main and interactive effects of damsselfies and detritivores were qualitatively similar to the previous results (Table 2), allowing us to examine polyculture effects in more detail.

Detritivore polycultures had more ciliate species and individuals than detritivore monocultures largely because of non-additive effects of detritivores in two-species combinations (Table 2). Specifically, in the absence of damsselfies, most two-species detritivore communities had significantly more ciliate species (50% more on average) than predicted from their monocultures (Fig. 3). This pattern did not result from the presence of a particular species (e.g. tipulids) causing high ciliate richness or density: the fit of the models is reduced by replacing relevant polyculture terms by a binary presence term for a single species (repeated for all four detritivore species; ciliate richness: $F_{8,99} > 2.4$, $P < 0.02$, ciliate density: $\chi^2 > 17$, d.f. = 8, $P < 0.03$). Thus, detritivore polycultures appear to have truly synergistic effects on both ciliate richness and density.

Table 1 Generalized linear models explaining effects of detritivore richness and damselfly presence on response variables, for the full dataset and two subsets

Response	Full dataset	No. damselflies subset	Damselflies present subset	Model details
Ciliate richness	Detritivore richness × damselfly: $F_{1,106} = 2.46$ (0.12) Detritivore richness: $F_{1,107} = 2.46$ (0.12) Damselfly: $F_{1,108} = 6.98$ (0.0095)	Detritivore richness: $F_{1,53} = 5.69$ (0.021)	Detritivore richness: $F_{1,53} = 0.0001$ (0.99)	Gaussian errors Log(detritivore richness)
Ciliate density	Detritivore richness × damselfly: $\chi^2 = 0.018$ (0.89) Detritivore richness: $\chi^2 = 4.68$ (0.031) Damselfly: $\chi^2 = 0.26$ (0.610)	Detritivore richness: $\chi^2 = 4.49$ (0.034)	Detritivore richness: $\chi^2 = 1.14$ (0.23)	Poisson errors Log(detritivore richness) Log link for ciliate density
Rotifer density	Detritivore richness × damselfly: $\chi^2 = 0.150$ (0.70) Detritivore richness: $\chi^2 = 2.8$ (0.094) Damselfly: $\chi^2 = 1.46$ (0.23)	Detritivore richness: $\chi^2 = 1.09$ (0.30)	Detritivore richness: $\chi^2 = 1.86$ (0.17)	Poisson errors Exp(detritivore richness) Log link for rotifer density
Flagellate density	Detritivore richness × damselfly: $\chi^2 = 0.057$ (0.81) Detritivore richness: $\chi^2 = 1.94$ (0.16) Damselfly: $\chi^2 = 3.00$ (0.08)	Detritivore richness: $\chi^2 = 0.60$ (0.44)	Detritivore richness: $\chi^2 = 1.47$ (0.23)	Poisson errors Log link for flagellate density
Flatworm density:	Detritivore richness × damselfly: $F_{1,106} = 1.95$ (0.16) Detritivore richness: $F_{1,108} = 3.82$ (0.053) Damselfly: $F_{1,107} = 1.38$ (0.24)	Detritivore richness: $F_{1,53} = 0.137$ (0.71)	Detritivore richness: $F_{1,53} = 6.94$ (0.011)	Gaussian errors $\sqrt{\text{flatworm density}}$
Detrital breakdown	Detritivore richness × damselfly: $\chi^2 = 0.00025$ (0.678) Detritivore richness: $\chi^2 = 0.00007$ (0.83) Damselfly: $\chi^2 = 0.00427$ (0.086)	Detritivore richness: $\chi^2 = 0.0003$ (0.68)	Detritivore richness: $\chi^2 = 0.00003$ (0.87)	Gamma errors Log(detritivore richness) Log link for detrital breakdown
Damselfly growth	NA	NA	Detritivore richness: $F_{1,47} = 0.95$ (0.36)	Gaussian errors

The values presented in parentheses are *P*-values.

The 'Model details' column lists any transformations or link functions used in the construction of the model, as well as the type of error distribution specified. Results that remain significant after correction for multiple tests (Bonferroni layering) are indicated in bold type.

NA, not applicable.

Other ecosystem responses

Unlike ciliates, densities of flagellates were unaffected by detritivore richness, irrespective of the presence or absence of damselflies (Table 1; Fig. 4). Rotifer density tended to be negatively correlated with detritivore richness, although marginally (Table 1; Fig. 4). Flatworm density was also negatively correlated with detritivore richness, although only in the presence of damselflies (Table 1, Fig. 4). Densities of rotifers, flagellates and flatworms in detritivore polycultures were not different than densities predicted from the relevant detritivore monocultures (Table 2), although we note that the null expectation for log-linked response variables (rotifer, flagellate density) is a

multiplicative effect, not additive. Detritivore species differed in their effects on rotifers and flagellates, but not flatworms (Table 2). Both rotifer and flagellate density was significantly lower in treatments with scirtids compared with other detritivore species (Fig. 4; rotifers: $\chi^2 = 13.0$, d.f. = 1, $P = 0.0003$; flagellates: $\chi^2 = 15.9$, d.f. = 1, $P < 0.0001$).

Detrital breakdown was unaffected by detritivore richness or detritivore polycultures, but was strongly affected by detritivore identity and damselfly presence (Fig. 4; Tables 1 and 2). Tipulid and scirtids had greater effects on detrital breakdown than chironomids (Fig. 4; tipulid: $\chi^2 = 0.052$, d.f. = 1, $P < 0.0001$; scirtid: $\chi^2 = 0.0039$, d.f. = 1, $P = 0.036$).

Table 2 Generalized linear models explaining effects of detritivore composition and damselfly presence on response variables

Response	Full dataset	No damselflies subset	Damselflies present subset	Model details
Ciliate richness	Composition × damselfly: $F_{10,88} = 1.12$ (0.36) Damselfly: $F_{1,98} = 7.85$ (0.006) Detritivore interactions: $F_{7,98} = 2.49$ (0.022) Four sp. interactions: $F_{1,98} = 0.58$ (0.45) Two sp. interactions: $F_{6,99} = 2.81$ (0.014)	Detritivore interactions: $F_{7,44} = 3.35$ (0.006) Four sp. interactions: $F_{1,44} = 2.21$ (0.145) Two sp. interactions: $F_{6,45} = 3.44$ (0.007)	Detritivore interactions: $F_{7,44} = 0.69$ (0.68) Detritivore identity: $F_{3,51} = 1.05$ (0.38)	Gaussian errors
Ciliate density:	Composition × damselfly: $\chi^2 = 13.1$, d.f. = 10 (0.22) Damselfly: $\chi^2 = 0.268$, d.f. = 1 (0.605) Detritivore interactions: $\chi^2 = 18.02$, d.f. = 7 (0.012) 4 sp interactions: $\chi^2 = 3.64$, d.f. = 1 (0.056) 2 sp interactions: $\chi^2 = 16.0$ (0.014)	Detritivore interactions: $\chi^2 = 12.6$, d.f. = 7 (0.082) Detritivore identity: $\chi^2 = 11.2$, d.f. = 3 (0.011)	Detritivore interactions: $\chi^2 = 10.1$, d.f. = 7 (0.18) Detritivore identity: $\chi^2 = 3.51$, d.f. = 3 (0.32)	Poisson errors $\sqrt{\text{Ciliate density}}$ with a log link
Rotifer density:	Composition × damselfly: $\chi^2 = 14.5$, d.f. = 10 (0.15) damselfly: $\chi^2 = 1.04$, d.f. = 1 (0.31) Detritivore interactions: $\chi^2 = 5.93$, d.f. = 7 (0.55) Detritivore identity: $\chi^2 = 22.5$, d.f. = 3 (< 0.0001) Scirtid effect: $\chi^2 = 13.0$, d.f. = 1 (0.0003)	Detritivore interactions: $\chi^2 = 5.17$, d.f. = 7 (0.64) Detritivore identity: $\chi^2 = 13.2$, d.f. = 3 (0.004)	Detritivore interactions: $\chi^2 = 9.28$, d.f. = 7 (0.23) Detritivore identity: $\chi^2 = 15.3$, d.f. = 3 (0.002)	Poisson errors $\sqrt{\text{Rotifer density}}$ with a log link
Flagellate density:	Composition × damselfly: $\chi^2 = 10.5$, d.f. = 10 (0.40) Damselfly: $\chi^2 = 2.56$, d.f. = 1 (0.097) Detritivore interactions: $\chi^2 = 7.61$, d.f. = 7 (0.37) Detritivore identity: $\chi^2 = 18.7$, d.f. = 3 (0.0003) Scirtid effect: $\chi^2 = 15.9$, d.f. = 1 (< 0.0001)	Detritivore interactions: $\chi^2 = 5.47$, d.f. = 7 (0.60) Detritivore identity: $\chi^2 = 16.7$, d.f. = 3 (0.001)	Detritivore interactions: $\chi^2 = 5.86$, d.f. = 7 (0.56) Detritivore identity: $\chi^2 = 8.58$, d.f. = 3 (0.036)	Poisson errors $\sqrt{\text{Flagellate density}}$ with a log link
Flatworm density:	Composition × damselfly: $F_{10,88} = 0.712$ (0.711) Damselfly: $F_{1,98} = 1.31$ (0.26) Detritivore interactions: $F_{7,99} = 0.95$ (0.48) Detritivore identity: $F_{3,106} = 0.30$ (0.92)	Detritivore interactions: $F_{7,44} = 0.10$ (0.998) Detritivore identity: $F_{3,51} = 1.01$ (0.71)	Detritivore interactions: $F_{7,44} = 1.60$ (0.16) Detritivore identity: $F_{3,51} = 2.11$ (0.27)	Gaussian errors $\sqrt{\text{Flatworm density}}$

Table 2 continued

Response	Full dataset	No damselflies subset	Damselflies present subset	Model details
Detrital breakdown:	Composition × damselfly: $\chi^2 = 0.010$, d.f. = 10 (0.31)	Detritivore interactions: $\chi^2 = 0.007$, d.f. = 7 (0.30)	Detritivore interactions: $\chi^2 = 0.0027$, d.f. = 7 (0.88)	Gamma errors Log link for detrital breakdown
	Damselfly: $\chi^2 = 0.0041$, d.f. = 1 (0.033)	Detritivore identity: $\chi^2 = 0.048$, d.f. = 3 (< 0.0001)	Detritivore identity: $\chi^2 = 0.019$, d.f. = 3 (< 0.0001)	
	Detritivore interactions: $\chi^2 = 0.0057$, d.f. = 7 (0.49)			
	Detritivore identity: $\chi^2 = 0.061$, d.f. = 3 (< 0.0001)			
Damselfly growth	NA	NA	Detritivore interactions: $F_{7,38} = 1.46$ (0.21) Detritivore identity: $F_{3,45} = 3.20$ (0.032)	Gaussian errors

The values presented in parentheses are *P*-values.

Detritivore composition is composed of the effects of detritivore identity, as well as detritivore interactions (deviances of polycultures from additive expectations based on monocultures). Detritivore interactions can be further decomposed into four species (sp.) interactions (deviances of four species polycultures from monoculture-based expectations) and two species interactions (deviances of two species polycultures from monoculture-based expectations). Detritivore identity effects can only be examined in the absence of higher order interactions. Three datasets were analysed: the full dataset, only treatments without damselflies, and only treatments with damselflies. The 'Model details' column lists any transformations or link functions used in the construction of the model, as well as the type of error distribution specified. Results that remain significant after correction for multiple tests (Bonferroni layering) are indicated in bold type. NA, not applicable.

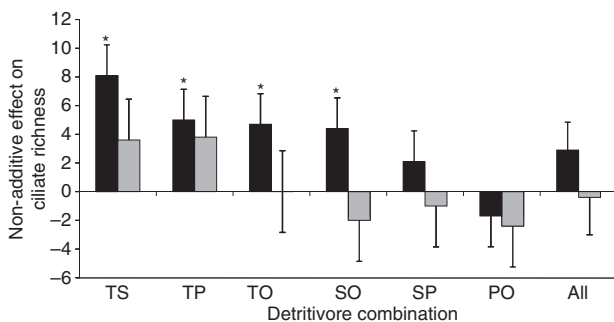


Figure 3 Non-additive effects (\pm SE) of various detritivore combinations on ciliate richness, both in the absence (black bars) and presence (grey bars) of predacious damselflies. Non-additive effect sizes were calculated as the difference in ciliate richness between a detritivore polyculture and the predicted ciliate richness based on monocultures of the component detritivore species. An asterisk indicates those non-additive effects significantly different than zero.

Damselfly growth was also unaffected by detritivore richness and detritivore polycultures, but did differ between detritivore species (Tables 1 and 2). Damselflies lost an average of 7.6 mg biomass in treatments with tipulids (tipulids vs. other species: $F_{1,45} = 7.01$, $P = 0.011$), lost 2.2 mg in treatments with scirtids, and tended to increase

their biomass by 1.6 and 1.3 mg in treatments with *Polypedilum* and Orthoclaadiinae chironomids respectively.

The per capita emergence rate of each detritivore species was equivalent between detritivore monocultures and polycultures, and between treatments with and without damselflies (all main effects and interactions $P > 0.05$, $\chi^2 < 3.0$, Generalized Linear Model with binomial errors).

DISCUSSION

In this study, we examined the response of a food web to the loss of diversity in two dimensions: horizontally (within the detritivore trophic level) and vertically (loss of the top trophic level, represented by damselfly larvae). We discovered that loss of detritivore diversity caused secondary extinctions of ciliates, reductions in ciliate density, and changes in ciliate composition-but only when damselflies were simultaneously absent. Damselflies also caused an overall reduction in ciliate richness. Thus loss of horizontal diversity and loss of vertical diversity both impact ciliates. However, loss of horizontal and vertical diversity did not have consistent effects on other foodweb processes or components. Detrital processing was affected by damselfly presence but not detritivore diversity, rotifer abundance tended to be affected by detritivore diversity but not damselfly presence, flatworm abundance was affected by the interaction between detritivore diversity and damselfly

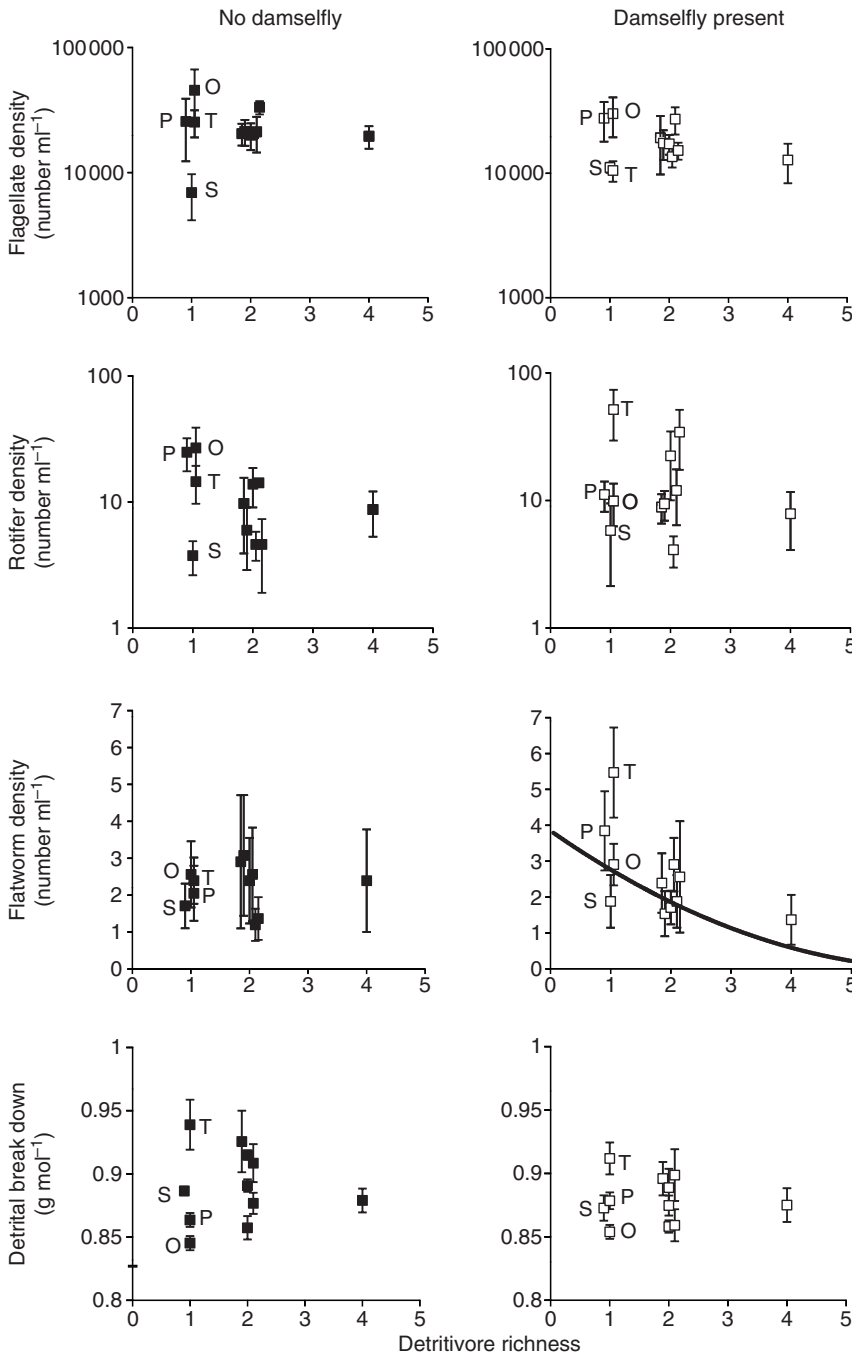


Figure 4 Effects of detritivore richness and composition on various EV, both in the absence (left graphs) and presence (right graphs) of predacious damselflies. Detritivore monocultures are labelled as in Fig. 1. Detritivore polycultures are not labelled as none of the response variables showed significant non-additive effects of combinations of detritivore species. Treatments are jittered horizontally slightly to reveal all data. Curved lines indicate significant regression models predicting response variables as a function of detritivore richness, irrespective of detritivore composition.

presence and flagellate abundance was affected by neither diversity type.

We begin by examining secondary extinctions amongst the ciliates. This extinction cascade is remarkable in that the primary extinctions are within a different arm of the food web (the insect subweb: left side of Fig. 1) than the secondary extinctions (the microfauna subweb: right side of Fig. 1). Although detritivores may passively ingest ciliates in the process of consuming detritus, they do not target ciliates

(e.g. by filter feeding). Instead, the main pathway between insects and ciliates likely involves the detritus. Detritivores differ in how they process detritus. Tipulids shred large pieces of detritus, scirtids scrape the surfaces of detritus, and chironomids collect small detrital particles. This suggests that niche complementarity between pairs of species may result in species mixtures more efficiently fragmenting detritus. This effect may be particularly noticeable in a substitutive experiment, such as this study, where increases

in diversity reduce intraspecific competition (Ruesink & Srivastava 2001). Note that the two species of chironomids have similar feeding modes and did not exhibit synergistic effects.

Facilitation between detritivores could also occur via a detrital processing chain. Processing chains occur when one detritivore processes large pieces of detritus into much finer particles that can be used by other detritivores. In bromeliads at the study site, detrital feeding by tipulids and scirtids releases fine particles (< 100 µm) able to fit in the mentum of chironomids (B. Starzomski, D. Suen and D.S., unpublished data). Chironomids show faster growth in the presence of tipulids and scirtids in other experiments (B. Starzomski, D. Suen and D.S., unpublished data) although we did not detect such an effect in this study. Detrital processing chains have been shown in similar aquatic habitats such as treeholes (Paradise & Dunson 1997) and pitcher plants (Heard 1994). Potentially, high detritivore diversity ensures that multiple links along this processing chain are represented, resulting in more efficient conversion of intact detritus into fine detrital and faecal particles. Fine particles created by invertebrate processing have lower C : N ratios and higher bacterial abundance than intact detritus (Montemarano *et al.* 2007), and so could provide the extra resources needed to maintain high ciliate diversity. Ciliates feed both directly on bacteria, and indirectly through consumption of bacteria-feeding protozoa like heterotrophic flagellates (Epstein *et al.* 1992). Note that such detritivore diversity effects on the production of fine detrital and faecal particles would not be detected in our measures of detrital loss simply because we measured loss of large detrital particles.

As detritivore polycultures have both more and different ciliate species even after correcting for ciliate density, we can conclude that detritivore diversity increases ciliate richness not only by creating conditions that support greater ciliate populations, but also by fostering ciliate species that would otherwise be absent. This particular extinction cascade therefore involves the loss of ciliate niches, and represents a substantially different phenomena than what is normally considered 'ecosystem functioning'.

So far, we have proposed niche complementarity or facilitation effects as likely mechanisms for detritivore–ciliate extinction cascades. We can discount two other potential explanations for detritivore diversity effects on ciliates: allometric effects and selection effects. If we based abundances on an inappropriate allometric-scaling equation, then differences between treatments within a richness level would be affected. However, in substitutive experiments, tests of the non-additivity of species effects are independent of the particular allometric equation used, as abundance of any species in a two-species community will always be half of that in monoculture. Selection effects might be important

if diversity effects depended primarily on the inclusion of a functionally important species in high diversity treatments, rather than on the behaviour of species in polycultures. However, our analysis shows that ciliate diversity is increased by non-additive effects of detritivores in polyculture rather than the presence of any particular detritivore. Furthermore, models of positive selection effects require the functionally important species to numerically dominate mixtures in which it occurs (Tilman *et al.* 1997), whereas our experiment did not permit increases in detritivore abundances and mortality rates were roughly equivalent.

The effects of detritivore diversity on the ciliates occur only in the absence of damselflies. Damselflies are voracious predators within bromeliads (Srivastava 2006). Bromeliad structure provides spatiotemporal refuges for detritivores; the sit-and-wait damselflies only prey on detritivores within the same compartment (Srivastava 2006). This stochasticity in predation leads to high variation in the surviving detritivore communities, and this noise has the potential to obscure the relationship between detritivores and ciliates. Specifically, detritivores appear to have the same general effect on ciliates regardless of damselfly predation (detritivore × damselfly interaction not significant) but only in the absence of damselflies is this effect significant.

Unlike ciliates, flagellates and rotifers were either constant or tended to decline as detritivore diversity increased. In other aquatic systems, increased resource productivity causes a shift from flagellate-dominated to ciliate-dominated communities, as observed in lakes (oligotrophic to eutrophic gradient: Berninger *et al.* 1991) and treeholes (low to high detritivory: Paradise & Dunson 1997). Our experiment shows the same pattern if we assume that the detritivore diversity gradient was correlated with a productivity gradient (i.e. higher detritivore diversity led to greater bacterial production). Consumption of flagellates by larger ciliates (Epstein *et al.* 1992) may be an important part of this flagellate to ciliate shift, although we cannot discount other indirect effects (e.g. rotifers and flatworms can also consume small flagellates).

Damselflies had strong top-down effects on detrital processing, confirming previous results (Srivastava 2006). By reducing detrital processing, damselflies must also reduce any positive effects of detritivores on ciliates (for example, via stimulating bacterial growth). Indeed, ciliate richness was lower in treatments with damselflies.

Detritivore identity was much more important than detritivore richness in affecting detrital breakdown and damselfly growth. Strong effects of tipulids and scirtids on detrital loss reflect the inefficiency of shredding and scraping: such detritivores ingest only some of the detrital particles that they create. Differential predation is less likely to explain detrital loss patterns, as detritivore identity effects occurred even in the absence of damselflies. However,

detrivore identity did affect damselfly growth, with growth greatest on the smallest detritivores. Note this pattern occurred despite the fact that small-bodied detritivore communities had lower total biomass than those of large-bodied detritivores, a consequence of standardizing metabolic capacity. Damselflies appear to be more effective predators of small-bodied detritivores, consuming up to 91% of Orthocladiinae chironomids, 74% of *Polyhedilum* chironomids, 65% of scirtids and 37% of tipulids (species ordered smallest to largest).

This experiment reveals that changes in horizontal and vertical diversity in the insect subweb can have profound effects on the entire food web. Importantly, different parts of the food web varied in their sensitivity to horizontal diversity, vertical diversity, or their interaction. Similar conclusions have been reached in two other aquatic mesocosm experiments (Duffy *et al.* 2005; Wojdak 2005). This variety of responses is perhaps not surprising, given that both horizontal and vertical diversity effects are known to depend on foodweb context, including the degree of consumer specialization (Thébault & Loreau 2003; Fox 2004), prey resistance-growth tradeoffs (Thébault & Loreau 2003; Fox 2004), and the trophic position of species loss relative to that of the response (Balvanera *et al.* 2006; Srivastava *et al.* 2009).

One interesting result of our study is the suggestion that horizontal and vertical diversity interact on their effects on ciliate abundance and richness. Stochasticity in damselfly predation on detritivores disrupted the cascading effects of detritivore richness on ciliate richness (although note that this interaction was revealed only in the analyses of data subsets, not the full dataset). Several theoretical studies predict interactive effects of horizontal and vertical diversity on ecosystem functions (Holt & Loreau 2002; Thébault & Loreau 2003; Fox 2004; Duffy *et al.* 2007), but effects on extinction cascades have not been considered previously. The few empirical studies that have tested for interactions between horizontal and vertical diversity on ecosystem functions have generally found significant interactions, including the current study (Mulder *et al.* 1999; Duffy *et al.* 2005; Hättenschwiler & Gasser 2005; Wojdak 2005; Snyder *et al.* 2006; but see Douglass *et al.* 2008; Murtaugh 2008). As real patterns of species endangerment are likely to reduce both dimensions of food webs (Petchey *et al.* 2004; Srivastava & Vellend 2005), any attempts to forecast the effects of impending extinctions needs to consider such interactions. Duffy *et al.* (2007) argue that: 'Whether diversity effects at one trophic level depend on presence or diversity of another level is critical to evaluating the generality of the last decade's research on ecosystem effects of biodiversity'.

Finally, this study highlights the need to integrate research on secondary extinctions with that on biodiversity effects on

ecosystem functions. Such integration is needed because (1) secondary extinctions could have effects on ecosystem functions additional to those of primary extinctions (Thébault *et al.* 2007), and (2) if there is a time lag in secondary extinctions being realized (an extinction debt), then primary species loss may continue to affect ecosystem functions well into the future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Detritivore insects (abundance, live body mass) assembled in experimental detritivore communities.

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