Predation and facilitation determine chironomid emergence in a bromeliad-insect food web

BRIAN M. STARZOMSKI,* DARYL SUEN
and DIANE S. SRIVASTAVA　Biodiversity Research Centre and Department of Zoology,
The University of British Columbia, Vancouver, BC V6T 1Z4, Canada

Abstract. 1. Ecological theory has focused on negative interactions, such as competition and predation, to explain species' effects on one another. This study demonstrates the importance of considering both positive and negative interactions in explaining how species influence abundances at the local scale.

2. Two experiments were conducted using the aquatic insect food web in Costa Rican bromeliad phytotelmata. Manipulations contrasted the strength of predation between trophic levels versus facilitation within a trophic level on the emergence of detritivore chironomids.

3. Predation had a strong negative effect on chironomids, reducing emergences by 81% overall. Most predation was as a result of the top predator, the odonate *Mecistogaster modesta*; the intermediate predator, a tanypodine chironomid, had little effect. In the absence of predators, shredder and scraper detritivores (tipulid and scirtid larvae) increased the emergence rate of chironomid larvae by 86%. The mechanism of facilitation was likely the processing, by tipulids and scirtids, of intact detritus into fine particles that the detritivore chironomids consume or use to build protective cases.

4. This study is among the first demonstrations of a processing chain in a multi-species context, and in bromeliad-insect food webs. Our finding that top-down effects are of similar magnitude to facilitative effects suggests that the relative importance of processing chains in nature will depend on food web context.

Key words. Bromeliad, chironomid, *Mecistogaster modesta*, phytotelmata, processing chain.

Introduction

Ecological studies have documented a wide variety of interactions by which species in a food web affect other species, including vertical (between-trophic level) effects, such as predation (e.g. Paine, 1966) and parasitism (e.g. Lafferty *et al*., 2006; 2008), and horizontal (within trophic-level) effects such as competition (e.g. Polis & Strong, 1996) and facilitation (e.g. reviewed in Bruno *et al*., 2003). However, few studies have examined the relative importance of vertical and horizontal processes on the fitness of individual species (Wootton, 1993; Bertness & Callaway, 1994; Heard, 1994a; Fox, 2004),

although examples continue to accumulate. Even rarer are contrasts of positive horizontal (within trophic level: facilitation) and negative vertical (between trophic level: predation) effects on species abundance (but see Stachowicz & Hay, 1999). More progress has been made comparing the effects of vertical and horizontal interactions on the biomass of entire trophic levels. The intriguing conclusion is that vertical interactions are at least as strong, if not stronger, than horizontal interactions (Duffy, 2003; Srivastava & Vellend, 2005).

In this study, we compare the effects of predation and facilitation on one fitness component of a detritivore insect. We examine in detail processing chains, a type of facilitation, in which at least one species conditions, or prepares, a resource for another species. The conditioning species has been termed the *upstream* species (it is at the beginning of the resource processing), and the receiving species is termed the *downstream* species (this species is at the receiving end of the flow of resources, in this case smaller particles of detritus – Heard,

Correspondence: Brian M. Starzomski, Biodiversity Research Centre and Department of Zoology, The University of British Columbia, 6270 University Blvd. Vancouver, BC V6T 1Z4, Canada. E-mail: starzom@uvic.ca

*Current address: School of Environmental Studies, University of Victoria, Victoria, British Columbia V8P 5C2, Canada

1994a). Heard (1994b) lists more than 50 putative processing chains, from microorganisms to vertebrates. Most of these examples, however, come from observational accounts that await experimental confirmation (Heard & Richardson, 1995). Arguably the best experimental evidence of processing chains comes from studies of detritivorous aquatic insects, in either streams (Dieterich *et al.*, 1997; Jonsson & Malmqvist, 2005) or phytotelmata such as treeholes (Paradise & Dunson, 1997; Paradise, 1999; 2000, but see Daugherty & Juliano, 2002), Heliconia bracts (Seifert & Seifert, 1979), and pitcher plants (Beaver, 1983; Heard, 1994a). While these experiments show that *upstream* species increase the growth, mass, or survival of *downstream* species, few have demonstrated the process (Heard, 1994a; Daugherty & Juliano, 2002, 2003). Heard and Richardson (1995) argue that evidence for a processing chain should include evidence not only of facilitation, but of a mechanism based on resource processing. Other authors describe several experiments indicating that processing chains may result in biologically significant inter-specific interactions only under specific conditions (Paradise, 1999; 2000; Daugherty & Juliano, 2002).

Demonstrating the existence of processing chains is only one part of showing their importance to community structure. Previous experiments have often been conducted with only two or three species (the upstream and downstream components), rather than within a food web context where other factors, such as predation, can be measured (Heard 1994b; Paradise, 1999; 2000). However, new work has expanded this to include more components of the food web (Hoekman, 2007; Hoekman *et al.*, 2009). Predation can also have important impacts on community structure in container habitats (Griswold & Lounibos, 2005; Ngai & Srivastava, 2006), through changing prey behaviour (Juliano & Reminger, 1992), reducing growth rate and body size (Hechtel & Juliano, 1997), and reducing prey abundances and changing intra-guild interactions (Griswold & Lounibos, 2006). In our bromeliad system, previous observations suggest both efficient predation by the top predator and a probable processing chain between its detritivorous prey (Srivastava, 2006). In this study we present the first contrast of the strength of top-down effects of predation versus the strength of a commensal processing chain.

Our experimental manipulations used naturally derived abundances of species in a bromeliad food web. We chose emergence of two common collector species of chironomids (those that collect detritus for feeding and construction of protective cases) as a proxy for the strength of the processing chain versus predation. Previous work in similar systems has shown that collectors are often the beneficiaries of processing chains initiated by shredders and scrapers (Dieterich *et al.*, 1997; Paradise & Dunson, 1997). We first examined the effect of upstream detritivore species on the production of fine detrital particles, an important resource for chironomids. We then manipulated three trophic levels of a bromeliad insect food web to examine separately the effects of predation and facilitation on chironomid emergence. We hypothesised that (i) the upstream components of the processing chain (tipulids and scirtids) will produce detrital particles in the size range usable by collector chironomids, (ii) reductions in the abundance of upstream components of the processing chain will reduce the emergence rate of downstream chironomids, (iii) predation will also reduce chironomid emergence, but the strength of top-down effects may differ between the top predator, an odonate, and the intermediate predator, a tanypodine chironomid, and (iv) the strength of the top-down effect will be much greater than that of facilitative effects.

Materials and Methods

Study site and system

The experiments were performed at the Estación Biológica Pitilla within the Área de Conservación Guanacaste, Costa Rica (10°59′N, 85°26′W). Bromeliads are common in primary and secondary forest surrounding the station (Srivastava *et al.*, 2005). The food webs of phytotelm bromeliads (*Vriesea gladioliflora* H. Wendl, *Guzmania scherzeriana* Mez, and *Vriesea sanguinolenta* Cogn. and Marchal) are based on a detritus resource of fallen vegetation, and the insect larvae and other invertebrates found within the water-filled tanks form a regional food web of more than 70 invertebrate species. Individual bromeliads contain a subset (ranging from 5 to 20 species) of the regional pool. Our experimental food web (Fig. 1) includes six of the most regionally common insect species, with abundances of each species
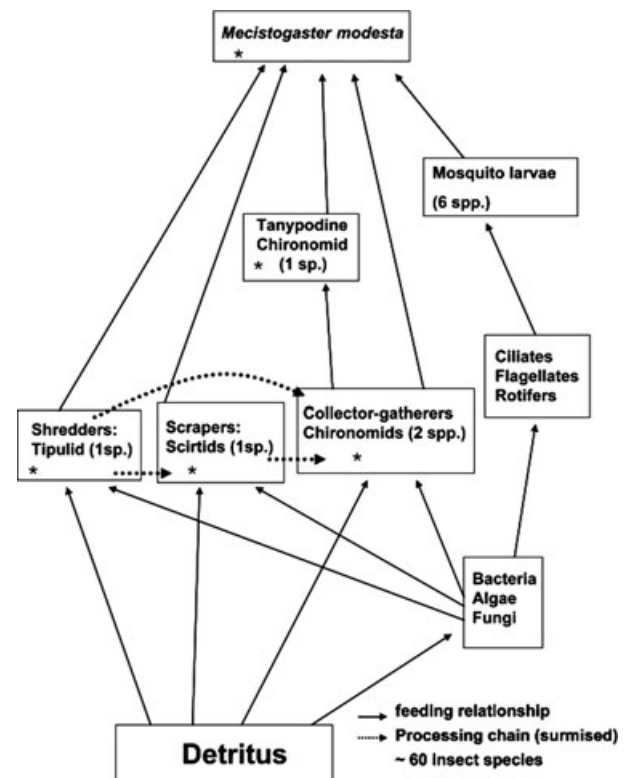
Fig. 1. Simplified bromeliad tank food web showing common species found at Estación Biológica Pitilla, Costa Rica. Species marked with an asterisk (*) are the focus of this study.

based on field observations spanning 7 years (Srivastava, 2006; Srivastava *et al.*, 2008, and D.S. Srivastava unpubl. data). Detritivores in the benthos of the food web included: a tipulid (*Trentepholia* sp., undescribed: Diptera), one scirtid species (*Scirtes* sp. Coleoptera), and two chironomid species including *Polypedilum* sp.: Diptera, which feeds on detritus particles, as well as using them to build protective cases, and an Orthocladiinae species. Predators include the top predator, the damselfly *Mecistogaster modesta* Selys. (Pseudostigmatidae: Odonata), and the intermediate predator, a chironomid of family Tanypodinae (Chironomidae: Diptera). This chironomid was identified as a Tanypodinae based on morphological characteristics of this family (retractile antennae, a weakly sclerotized mentum, a toothed ligula, and an elongate head capsule), as well as the distinctive movement of larvae.

Experimental Design

Experiment 1

An experiment was conducted in September and October 2003 to examine the role of tipulid and scirtid insect larvae in creating detritus particles of two sizes: >102 μm but <1720 μm (hereafter referred to as *large*), and <102 μm (hereafter referred to as *small*). The <102 μm particle size range was assumed to contain the particles that were collected and used by chironomids because in a gut analysis of 15 *Polypedilum* chironomids, particles were smaller than the mentum width (which never exceeded 97 μm). The experiment was a factorial design of chironomids (present, absent) by upstream species (none, scirtids only, tipulids only) for a total of six treatments. Chironomid present treatments included five medium *Polypedilum* chironomids (body length: 7 mm) and five small *Polypedilum* chironomids (5 mm) per replicate. Treatments with scirtids had six scirtids per replicate (four of 5 mm body length and two of 4 mm). Treatments with tipulids had three tipulids per replicate (one >18 mm body length, one 13–16 mm and one 8–10 mm).

We used artificial microcosms (*n* = 5 per treatment, except for the treatment without insects, which had 10 replicates) as model bromeliad tanks. Each consisted of a 100-ml plastic cup covered in light-blocking black plastic, with a single bromeliad leaf attached to the inside to provide a route for insect emergences. Microcosms were placed under a rain shelter. Detrital input consisted of three dead and oven-dried leaves collected from the tree *Conostegia xalapensis* Bonpl. (Melastomataceae) [mean dry weight of 0.675 g ± 0.032 (SE) per leaf], and one *C. xalapensis* leaf (dry weight 0.6 g) collected from a wild bromeliad (used to introduce natural populations of micro-organisms -algae, bacteria, and fungi feeding on the leaves- from the bromeliad tank). Each microcosm was inoculated with 55 ml of stream water and 7 ml of bromeliad water (mosquito larvae were removed by picking out individuals, and filtering through Nytex™ mesh). Mesh coverings were placed over each microcosm to prevent oviposition, and the escape of larval insects and emerged adults. The experiment ran from 15 September to 15 October, with daily examination for emerged insects.

Harvesting of the experiment was completed in a single day. Detrital fragments were collected, and the sediment from each microcosm separated into two size ranges: <102 μm and >102 μm (*small* and *large*), by filtering each sample through a 1720-μm sieve stacked over a 102-μm sieve and finally through a qualitative Whatman™ (Piscataway, New Jersey) filter disc (small sediment). Debris caught in the 1720-μm sieve, composed mostly of unusable twigs, was discarded. Sediment trapped in the 102-μm Nytex™ (SEFAR Inc. Ville St. Laurent, Quebec, Canada) sieve was transferred onto another weighed Whatman™ filter disc. The filter discs were dried at 70 °C for 24 h, and then weighed.

Experiment 2

Experiment 2 was conducted in October and November of 2004. Aquatic insect larvae comprising the most common members of the food web of water-filled bromeliad phytotelmata (Fig. 1), were manipulated to form five treatments (Fig. 3) to look for an effect on the abundance and size of emerging detritivore chironomids. Abundances of predators (*M. modesta* and a tanypodine chironomid), upstream processors (shredder: tipulid species and scraper: scirtid species), and downstream collector gatherers (*Polypedilum* chironomids and Orthocladiinae chironomids) were based on the natural range of abundance in eight *Vriesia* sp. bromeliads sampled in October 2003, between 15 and 103 ml in volume (mean abundances ± SD: *M. modesta*, 0.5 ± 1.32; tanypodine chironomid: 0.25 ± 0.66; tipulid: 14.88 ± 16.04; scirtid: 33.13 ± 26.05; *Polypedilum* chironomids: 12.13 ± 14.93; Orthocladiinae chironomids: 1.13 ± 1.05).

By sequentially removing species, we tested for the strengths of predation and facilitation (Fig. 3). At first glance, it might seem that adding a treatment with just *M. modesta* and chironomids would allow for a factorial design of predators crossed by upstream components. However, removing tipulids and scirtids would have the unfortunate side effect of reducing total prey biomass, and so increase predation pressure on chironomids. *Mecistogaster modesta* would also be unlikely to survive the experiment on so little prey. Such effects would confound any interpretation of reduced chironomid fitness in terms of processing chains. Instead, we carefully designed our experiment so the effects of predation and resource processing could be determined using nested planned contrasts (Fig. 3).

Ten terrestrial bromeliads (>1500 ml volume) of the species *Vriesea gladioliflora*, a common tank species in Costa Rica (Janzen, 1983), were used as blocks. All were located in secondary forest surrounding the research station. Five leaf wells per bromeliad were used for the experimental treatments (*n* = 1 replicate/treatment/block, for a total of 10 replicates), with each treatment replicated once in each block, although assigned randomly across all bromeliads. Fifty millilitre plastic centrifuge tubes were used to contain our experimental food webs. Two 7-mm holes were drilled in the side of the tubes and covered with 80-μm Nytex™ mesh, to allow water to flow between the tube and the leaf well in which it was placed. The mesh was small enough to prevent insect larvae

from leaving the tube. The top of each tube was also covered with 80-μm mesh, to prevent both re-invasion of the tube by egg-laying adults and dispersal of larvae. Four 2 × 2 cm and eight 1 × 1 cm samples of dead *C. xalapensis* leaves were added as a detritus resource to each treatment. Leaves were conditioned in a bath of stream water for 2 days to allow colonisation by native bacteria, algae, and fungi. Finally, a 10-cm section of popsicle stick was included in the tube to allow emerging insects a place to pupate out of the water.

Experiment 2 sampling

Each replicate was visited daily to check for emerged insects, which were removed for identification and later for analysis. The Nytex^{TM} mesh was checked daily, and at the end of the experiment, for holes and leaks; none were found. The experiment lasted 25 days; after this time, a small number of other insect larvae became apparent, likely by passing through the Nytex^{TM} mesh as eggs or early instars. Dry mass of remaining large detritus was determined at the end of the experiment by oven-drying the detritus on a Whatman filter for 9 h at ~70 °C. All remaining insect larvae were collected and lengths measured at the end of the experiment.

Analysis

Experiment 1 data were log-transformed and analysed using a two-way MANOVA with the masses of small and large sediment as the dependent variables. This was followed by univariate two-way ANOVAS and planned comparisons. Experiment 2 chironomid emergence data were analysed using a generalised linear model ANOVA with a Poisson distribution and a log-link function. Overdispersion was corrected using an empirically determined scale parameter. Orthogonal planned comparisons, to look for differences between individual treatments, are listed in Fig. 3. These contrasts compare chironomid emergence in the presence of a particular species or group of species with emergence in food webs with that species absent, and thus ask which species interactions account for most of the variation between food webs. All analyses were conducted in R 2.0.1 (r-project.org), using an α of 0.05. Insect larvae body size data were log-transformed to conform to ANOVA assumptions of normality and homoscedasticity. Dry leaf detritus mass and larval body size were analysed using an ANOVA (α of 0.05).

Results and Discussion

Experiment 1: analysis of sediment produced in artificial leaf-wells

Manipulation of the bromeliad detritivore community resulted in significant overall differences in the production of small and large detritus particles (two-way MANOVA, $F_{5,34} = 4.11$, $P = 0.005$; Fig. 2). Most of the insect effect on detrital particle production was as a result of manipulation of the
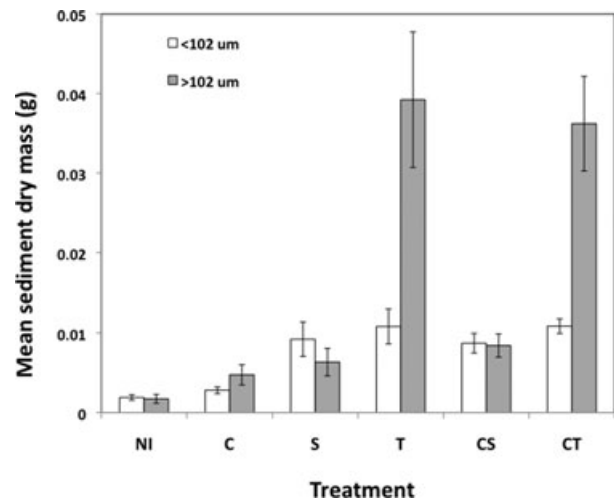
Fig. 2. Average dry mass ±SE of sediment for the treatments *chironomids alone* (C), *chironomid-scirtids* (CS), *chironomid-tipulids* (CT), *no insects* (NI), *scirtids alone* (S), and *tipulids alone* (T).

upstream species; that is, differences exist between treatments with scirtids, tipulids or neither (two-way MANOVA, $F_{2,34} = 8.53$, $P = 0.001$). Chironomids did not affect sediment production (two-way MANOVA, $F_{1,34} = 1.00$, $P = 0.32$). There were no significant interactions in either the MANOVA ($F_{2,34} = 0.73$, $P = 0.49$) or subsequent univariate ANOVAS (large detritus: $F_{2,39} = 3.16$, $P = 0.06$; small detritus: $F_{2,39} = 0.77$, $P = 0.47$).

We performed planned comparisons to look for the effects of presence of processing insects (tipulids and scirtids) and insect type on detrital processing. The presence of the upstream component had a significant impact on overall production of small and large detritus (univariate ANOVAS, small detritus: $F_{1,39} > 4.32$, $P \ll 0.001$; large detritus: $F_{1,39} > 4.32$, $P \ll 0.001$). Tipulids created more large detritus than scirtids, but an equivalent amount of small detritus (univariate ANOVAS; small detritus: $F_{1,19} = 1.60$, $P = 0.12$; large detritus: $F_{1,19} > 4.90$, $P \ll 0.001$).

Experiment 2: food web manipulation and chironomid emergences

Detritivore chironomid emergences were strongly negatively affected by predation by *M. modesta*, and positively affected by the processing chain, although only with natural abundances of the upstream component (tipulid and scirtid species; Fig. 3). There was a significant difference among treatments (generalized linear model ANOVA, $F_{4,45} = 3.117$, $P = 0.024$). Predation by *M. modesta* significantly reduced the number of emerging detritivore chironomids [planned comparison, *M. modesta* treatment (treatment A) versus all other treatments (treatments B, C, D, and E); $F_{1,45} = 6.339$, $P = 0.015$], whereas predation by the tanypodine chironomid had no effect [planned comparison, tanypodine treatment (B) versus no predator treatments (C, D, and E); $F_{1,45} = 0.014$, $P = 0.905$; Fig. 3]. Natural abundances of tipulids and scirtids significantly increased the
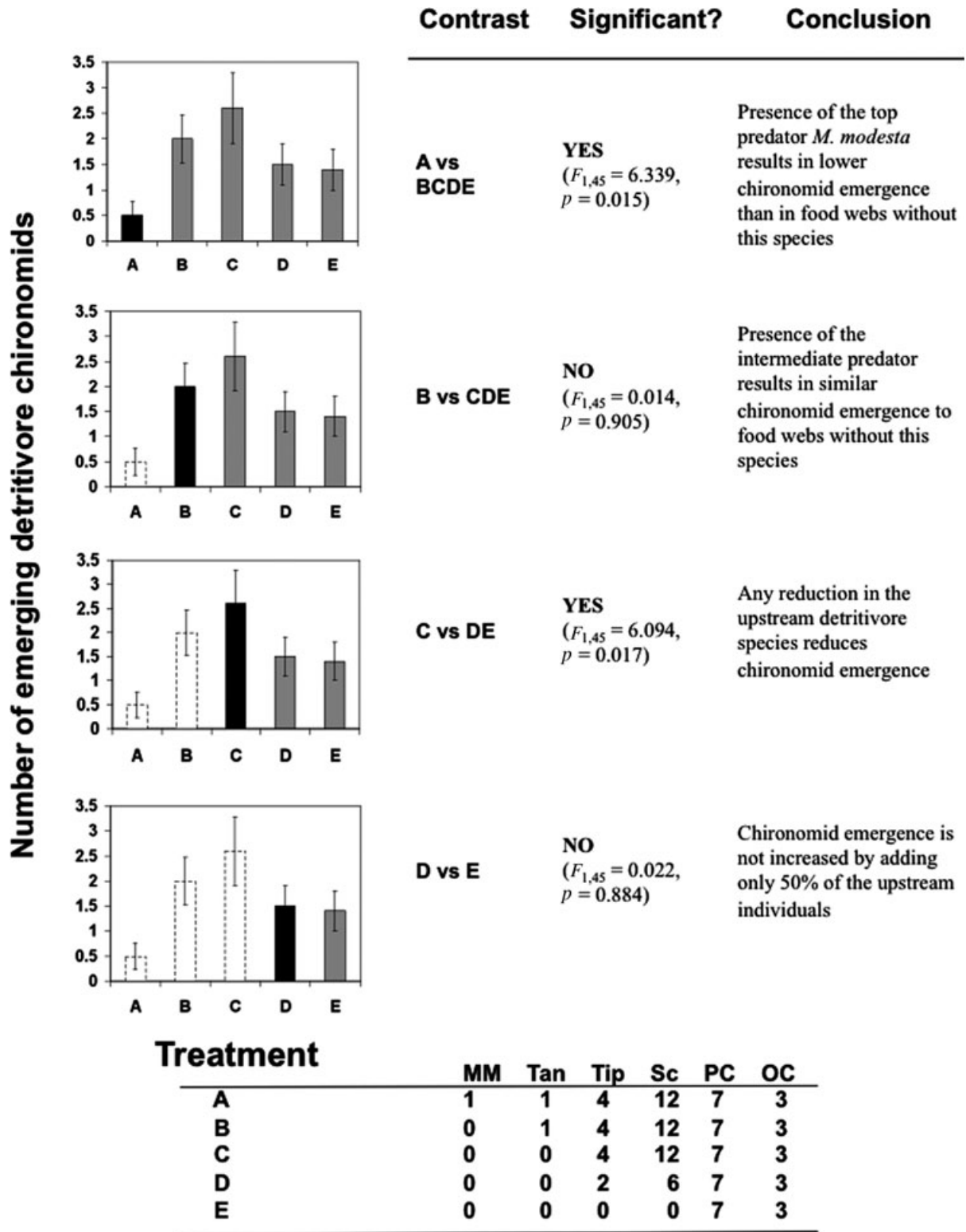
Contrast	Significant?	Conclusion
A vs BCDE	**YES** ($F_{1,45} = 6.339$, $p = 0.015$)	Presence of the top predator *M. modesta* results in lower chironomid emergence than in food webs without this species
B vs CDE	**NO** ($F_{1,45} = 0.014$, $p = 0.905$)	Presence of the intermediate predator results in similar chironomid emergence to food webs without this species
C vs DE	**YES** ($F_{1,45} = 6.094$, $p = 0.017$)	Any reduction in the upstream detritivore species reduces chironomid emergence
D vs E	**NO** ($F_{1,45} = 0.022$, $p = 0.884$)	Chironomid emergence is not increased by adding only 50% of the upstream individuals

Treatment

	MM	Tan	Tip	Sc	PC	OC
A	1	1	4	12	7	3
B	0	1	4	12	7	3
C	0	0	4	12	7	3
D	0	0	2	6	7	3
E	0	0	0	0	7	3

Fig. 3. Treatment descriptions (bottom) and effects on the mean number of emerging detritivore chironomids (±SE). Orthogonal contrasts used in Experiment 2 are shown, with the conclusion drawn from each test.

number of emerging detritivore chironomids over the course of the experiment [planned comparison, full processing chain (C) versus half (D) and no processing chain (E) treatments; $F_{1,45} = 6.094$, $P = 0.017$]. The processing chain required full abundances of the upstream components; no facilitation was observed with only 50% of upstream abundances [planned comparison, half processing chain (D) versus no processing chain (E) treatments; $F_{1,45} = 0.022$, $P = 0.884$].

The dry mass of remaining leaves (intact or coarse fragments >102 μm, which we would not expect the insects to have an effect on) showed no significant difference among treatments ($F_{4,49} = 2.096$, $P = 0.097$), nor did the size of the remaining chironomid larvae at the end of the experiment differ among treatments ($F_{4,49} = 1.597$, $P = 0.181$). Due to the presence of a small number of contaminant individuals in some of the centrifuge tubes at the end of the experiment (due, likely, to eggs or very small instars getting through the 80-μm mesh), we did not consider the difference in number of remaining individuals per treatment.

In bromeliad phytotelmata, the positive effect of a processing chain was strong and increased the emergence rate of downstream species by 86%, although only with natural abundances of upstream species. The mechanism by which this occurred was likely through the creation, by upstream species, of detrital particles of a size that could be used by chironomids. This is the first evidence of a processing chain in bromeliads, and is similar to the effects seen in other systems such as streams (Richardson & Neill, 1991; Dieterich *et al.*, 1997; Jonsson & Malmqvist, 2005), pitcher plants (Beaver, 1983; Heard, 1994b), and treeholes (Paradise & Dunson, 1997; Paradise, 1999). Predation was also very strong and resulted in the loss of 81% of chironomids. Most predation was a result of the top predator, the odonate *M. modesta*. Predation by the intermediate predator, a tanypodine chironomid, resulted in only a non-significant 23% reduction in chironomid emergences. Our novel contribution is to demonstrate these processes in a multi-species context, very similar to naturally occurring bromeliad phytotelmata. These results demonstrate that both negative (between trophic level) processes and positive (within trophic level) processes are important in determining chironomid emergence success, and that the strength of these two processes are at least within the same order of magnitude.

Our experiment showed that both tipulids and scirtids create small detritus particles <102 μm, the size below which particles are able to pass through the chironomid mentum. In addition, tipulids create substantial amounts of large detritus particles (>102 μm but <1720 μm), which likely facilitates the growth of increased amounts of bacteria, algae, and fungi as a result of the increase in surface/volume ratio relative to intact detritus (Cummins & Klug, 1979; McArthur & Barnes, 1988). Decreasing the size of the detritus particles may thus have accrued benefits in three ways to the downstream chironomids: (i) smaller detritus particles can pass through the mentum of the chironomid, (ii) smaller detritus particles can be used in protective anti-predator cases, and (iii) increased detritus surface/volume ratio provides increased habitat for bacteria, algae, and fungi, a chironomid food source (Merritt & Cummins, 1996). Although we did not directly test whether fine particles increase chironomid emergence in this study, other experiments with this system show that chironomid survival appears to be resource limited (R. Sargent, S. Iverson & D.S. Srivastava, pers comm.), and this has been demonstrated in other shredder systems (Paradise & Dunson, 1997). In addition, bromeliads with the full complement of processing chain species tend to have more ciliates than bromeliads missing upstream components (Srivastava & Bell, 2009), suggesting that bacterial abundances are elevated in such communities.

A reduction in the number of upstream insects below natural abundances resulted in the disappearance of the processing chain. It appears that the decrease in the abundance of the tipulid and scirtid component of the processing chain decreases the production of smaller particles of detritus, to the extent that any positive effect on the growth rate of the chironomids is below detection limits. Scirtids are also important facilitators in treeholes, resulting in increased growth of ceratopogonid midges (Paradise & Dunson, 1997) and mosquitoes (Paradise, 1999; 2000; but see Daugherty & Juliano, 2003). The mechanism behind this facilitation is likely (but not unequivocally: Heard & Richardson, 1995) a detrital processing chain resulting in fine detrital and faecal particles. For example, both artificial reductions in particle size and additions of scirtid faeces have been shown to increase survivorship of mosquitoes (Daugherty & Juliano, 2002, 2003). Treehole scirtids increase the production of fine particles, particularly those <100 μm (Daugherty & Juliano, 2002), similar to our results for bromeliad scirtids.

We expected tanypodine predators to have been efficient predators of chironomids, but this was not the case. Although the tanypodine species in our system has been observed consuming chironomids as big as, and occasionally bigger than itself (B. Starzomski & D. Srivastava pers. obs.), this may occur at a much lower rate than predation on chironomids by the much larger odonate larvae. Tanypodine predation may be more important on smaller instars of chironomids than used in this experiment.

The effects of predation and facilitation may not be independent in this system. The top predator, *M. modesta*, not only consumed the detritivorous chironomids, but most of all the other insects in the bromeliad enclosures, presumably reducing the strength of the processing chain. Ultimately, *M. modesta* may have both direct and indirect effects on chironomids. This has interesting implications for the ecology of the bromeliad. On the one hand, high *M. modesta* abundance should result in the slowing of the processing chain, and hence reduce the release of detrital nutrients for the bromeliad. However, by feeding on those insect larvae that might also have emerged and left the plant (with their loads of nutrients such as nitrogen), *M. modesta* benefits the plant by releasing some of the nutrients of the predated insect larvae in its faeces. This has been demonstrated experimentally in this system using stable isotopes to track N limitation and availability to bromeliads in both the presence and absence of *M. modesta* (Ngai & Srivastava, 2006). Thus the reduction of an insect–insect facilitation may allow for an insect–plant facilitation. A study involving bromeliad-dwelling spiders

has shown a similar predator–plant relationship (Romero *et al*., 2006).

In natural bromeliads, several water-filled tanks are found in one plant, and insect larvae may move from tank to tank. In our experimental setup, all insect larvae were confined to 50-ml centrifuge tubes, and thus opportunities for avoiding predation through spatial heterogeneity (moving to another tank without *M. modesta*) were reduced. Other experiments have shown that detritivores can evade predators by moving tanks, although they reduce their foraging efficiency in the process (Srivastava, 2006). Thus, the effects of *M. modesta* predation in our enclosures may have been amplified relative to completely natural conditions. On the other hand, in the large Vriesea bromeliads used in this experiment, there is usually a single *M. modesta* larva in every tank (Srivastava *et al*., 2005), so very few predator-free refuges exist. Where spatial refuges exist, however, facilitation may be more important overall than predation. An experiment to test the relative strength of processing chains and predation in the presence of habitat complexity would shed light on this problem.

Studies in phytotelmata systems typically show facilitative rather than competitive effects between detritivores, and processing chains may be a general feature of these systems. Phytotelm processing chains have been shown to be modified by bottom-up effects of resource supply (Heard, 1994a; Paradise & Dunson, 1997; Paradise, 1999; 2000), by shredder diversity (Jonsson & Malmqvist, 2005), and by water chemistry (Paradise, 2000). We take a step beyond the methods of these studies to examine processing chains in a food web context, contrasting top-down with facilitative effects on organisms. We find that both predation and facilitation are important processes in bromeliad food webs. More generally, our results suggest that positive interactions, such as facilitation, can be of similar magnitude to negative interactions, even top-down effects like predation. When examining the processes responsible for co-occurrence and relative abundance of species in communities, both positive and negative interactions should be considered.

Acknowledgements

References

Beaver, R.A. (1983) The communities living in Nepenthes pitcher plants: fauna and food webs. *Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities* (ed. by J. H. Frank), pp. 129–159. Plexus Publishing, Medford, New Jersey.

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Incorporating facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.

Cummins, K.W. & Klug, M.J. (1979) Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics*, **10**, 147–172.

Daugherty, M.P. & Juliano, S.A. (2002) Testing for context-dependence in a processing chain interaction among detritus-feeding aquatic insects. *Ecological Entomology*, **27**, 541–553.

Daugherty, M.P. & Juliano, S.A. (2003) Leaf scraping beetle feces are a food resource for tree hole mosquito larvae. *American Midland Naturalist*, **150**, 181–184.

Dieterich, M., Anderson, N.H. & Anderson, T.M. (1997) Shredder-collector interactions in temporary streams of western Oregon. *Freshwater Biology*, **38**, 387–393.

Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, **6**, 680–687.

Fox, J.W. (2004) Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology*, **85**, 549–559.

Griswold, M.W. & Lounibos, L.P. (2005) Competitive outcomes among aquatic container Diptera depend on predation and resource levels. *Annals of the Entomological Society of America*, **98**, 673–681.

Griswold, M.W. & Lounibos, L.P. (2006) Predator identity and additive effects in a treehole community. *Ecology*, **87**, 987–995.

Heard, S.B. (1994a) Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology*, **75**, 1647–1660.

Heard, S.B. (1994b) Processing chain ecology: resource condition and interspecific interactions. *Journal of Animal Ecology*, **63**, 451–464.

Heard, S.B. & Richardson, J.S. (1995) Shredder-collector facilitation in stream detrital food webs: is there enough evidence? *Oikos*, **72**, 359–366.

Hechtel, L.J. & Juliano, S.A. (1997) Effects of a predator on prey size at and time to metamorphosis: plastic response by prey or selective mortality? *Ecology*, **78**, 838–851.

Hoekman, D. (2007) Top-down and bottom-up regulation in a detritus-based aquatic food web: a repeated field experiment using the pitcher plant (*Sarracenia purpurea*) inquiline community. *The American Midland Naturalist*, **157**, 52–62.

Hoekman, D., Winston, R. & Mitchell, N. (2009) Top-down and bottom-up effects of a processing detritivore. *Journal of the North American Benthological Society*, **28**, 552–559.

Janzen, D.H. (ed.) (1983) *Costa Rican Natural History*. University of Chicago Press, Chicago, Illinois.

Jonsson, M. & Malmqvist, B. (2005) Species richness and composition effects in a detrital processing chain. *Journal of the North American Benthological Society*, **24**, 798–806.

Juliano, S.A. & Reminger, L. (1992) The relationship between vulnerability to predation and behavior: Geographic and ontogenetic differences in larval treehole mosquitoes. *Oikos*, **63**, 465–476.

Lafferty, K.D., Dobson, A.P. & Kuris, A.M. (2006) Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 11211–11216.

Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., DeLeo, G. Dobson, A.P. *et al*. (2008) Parasites in food webs: the ultimate missing links. *Ecology Letters*, **11**, 533–546.

McArthur, J.V. & Barnes, J.R. (1988) Community dynamics of leaf litter breakdown in a Utah alpine stream. *Journal of the North American Benthological Society*, **7**, 37–43.

Merritt, R.W. & Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North America*, 3rd edn. Kendal/Hunt Publishing Company, Dubuque, Iowa.

Ngai, J.T. & Srivastava, D.S. (2006) Predators accelerate nutrient cycling in an insect-bromeliad ecosystem. *Science*, **314**, 963.

Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.

Paradise, C.J. (1999) Interactive effects of resources and a processing chain interaction in treehole habitats. *Oikos*, **85**, 529–535.

Paradise, C.J. (2000) Effects of pH and resources on a processing chain interaction in simulated treeholes. *Journal of Animal Ecology*, **69**, 651–658.

Paradise, C.J. & Dunson, W.A. (1997) Insect species interactions and resource effects in treeholes: are helodid beetles bottom-up facilitators of midge populations? *Oecologia*, **109**, 303–312.

Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.

Richardson, J.S. & Neill, W.E. (1991) Indirect effects of detritus manipulations in a montane stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 776–783.

Romero, G.Q., Mazzafera, P., Vasconcellos-Neto, J. & Trivelin, P.C. (2006) Bromeliad-living spiders improve host plant nutrition and growth. *Ecology*, **87**, 803–808.

Seifert, R.P. & Seifert, F.H. (1979) A Heliconia insect community in a Venezuelan cloud forest. *Ecology*, **60**, 462–467.

Srivastava, D.S. & Bell, T. (2009) Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. *Ecology Letters*, **12**, 1016–1028.

Srivastava, D.S. (2006) Habitat structure, trophic structure and ecosystem function: interactive effects in a bromeliad-insect community. *Oecologia*, **149**, 493–504.

Srivastava, D.S. & Vellend, M. (2005) Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution and Systematics*, **36**, 267–294.

Srivastava, D.S., Melnychuk, M.C. & Ngai, J.T. (2005) Landscape variation in the larval density of a bromeliad-dwelling zygopteran, *Mecistogaster modesta* (Odonata: Pseudostigmatidae). *International Journal of Odonatology*, **8**, 67–79.

Srivastava, D.S., Trzcinski, M.K., Richardson, B.A. & Gilbert, B. (2008) Why are predators more sensitive to habitat size than their prey? Insights from bromeliad-insect food webs. *American Naturalist*, **172**, 761–771.

Stachowicz, J.J. & Hay, M.E. (1999) Mutualism and coral persistence in algal-dominated habitats: the role of herbivore resistance to algal chemical defense. *Ecology*, **80**, 2085–2101.

Wootton, J.T. (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *American Naturalist*, **141**, 71–98.