

Habitat structure, trophic structure and ecosystem function: interactive effects in a bromeliad–insect community

Diane S. Srivastava

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Abstract Although previous studies have shown that ecosystem functions are affected by either trophic structure or habitat structure, there has been little consideration of their combined effects. Such interactions may be particularly important in systems where habitat and trophic structure covary. I use the aquatic insects in bromeliads to examine the combined effects of trophic structure and habitat structure on a key ecosystem function: detrital processing. In Costa Rican bromeliads, trophic structure naturally covaries with both habitat complexity and habitat size, precluding any observational analysis of interactions between factors. I therefore designed mesocosms that allowed each factor to be manipulated separately. Increases in mesocosm complexity reduced predator (damselfly larva) efficiency, resulting in high detritivore abundances, indirectly increasing detrital processing rates. However, increased complexity also directly reduced the per capita foraging efficiency of the detritivores. Over short time periods, these trends effectively cancelled each other out in terms of detrital processing. Over longer time periods, more complex patterns emerged. Increases in mesocosm size also reduced both predator efficiency and detritivore efficiency, leading to no net effect on detrital processing. In many systems, ecosystem functions may be impacted by strong interactions between trophic structure and habitat structure, cautioning against examining either effect in isolation.

Keywords Aquatic insects · Decomposition · Habitat size · Habitat complexity · Predation

Introduction

Although ecosystem functions, as measured by energy and nutrient flux, are known to be affected by both habitat structure (Klein 1989; Didham et al. 1996; Wardle et al. 1997; Gonzalez and Chaneton 2002; Tewksbury et al. 2002) and trophic structure (McQueen et al. 1989; Schindler et al. 1997; Carpenter et al. 2001; Wardle et al. 2001), there has been little investigation of how habitat structure and trophic structure might interact to affect ecosystem functions. Habitat structure may affect ecosystem functions not only through direct effects on the species performing the function, but also through indirect effects acting via other trophic levels. This study examines how trophic structure mediates the effects of two aspects of habitat structure (habitat complexity and size) on detrital processing in a bromeliad–insect ecosystem. ‘Habitat complexity’ is a term used in many different ways in the literature; here I define it as the spatial subdivision of habitat at a scale smaller than the mobility of individuals.

Habitat structure could directly affect ecosystem function by changing the density or diversity of species carrying out that function (Schwartz et al. 2000; Loreau et al. 2002). Increases in species diversity resulted in higher rates of ecosystem functioning in >60% of studies (Srivastava and Vellend 2005) because higher diversity communities had complementary functional niches, included more facilitative interactions, or were more likely to contain functional keystone species (Loreau et al. 2002). Increasing habitat complexity can increase both

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D. S. Srivastava (✉)
Department of Zoology and Biodiversity Research Centre,
University of British Columbia, 6270 University Blvd.,
Vancouver, BC, Canada V6T 1Z4,
e-mail: srivast@zoology.ubc.ca

density and diversity by creating new niches for species (MacArthur 1972; Denno and Roderick 1991; Uetz 1991) or reducing rates of competitive encounters (Beck 2000; Young 2001). Increases in habitat size may result in increased density and diversity because of greater opportunities for specialization or increased likelihood of immigration (MacArthur and Wilson 1967). For example, forest fragmentation in the Amazon results in reduced dung decomposition rates, likely due to reductions in density, species richness and body size of dung and carrion beetles (Klein 1989). Habitat complexity and size could also affect the per capita efficiency of organisms performing the function. For example, increasing the complexity of saltmarsh vegetation results in greater efficiency of wolf spiders in herbivore suppression—an ecosystem function (Denno et al. 2002).

Habitat structure could also have indirect effects on ecosystem functions, by changing either top-down or bottom-up control of the trophic level performing the function. Habitat complexity and size have often been shown to affect predation rates, for example by providing absolute or stochastic refuges to prey (Luckinbill 1974; Crowder and Cooper 1982; Beukers and Jones 1997; Nemeth 1998; Floater 2001; Almany 2004; Langellotto and Denno 2004). Such predator-mediated effects of complexity on prey densities can cascade through multiple trophic levels, affecting ecosystem functions carried out by lower trophic levels (Power 1992; Denno et al. 2002; Finke and Denno 2002). Even the threat of predation is enough to potentially affect ecosystem functions when prey species respond by modifying their foraging behavior (Lima 1998; Warfe and Barmuta 2004).

The direct and indirect effects of habitat structure are examined here in a bromeliad–insect ecosystem. A broad suite of aquatic insect larvae and microbes colonize water trapped by the tightly interlocking leaves of phytotelm bromeliads (Picado 1913; Laessle 1961; Frank 1983; Richardson 1999; Armbruster et al. 2002). The insects include both detritivores and their predators. Phytotelm bromeliads are usually composed of multiple compartments, with each leaf collecting a separate compartment of water and detritus. Most aquatic insects (except mosquitoes) can move between compartments by traversing the juncture between overlapping leaves. Thus bromeliads can provide highly complex habitats for insects. An useful index of habitat complexity in this system is the number of leaves subdividing a standard volume of water into compartments. Detritus is the basal resource of the insect and microbial food webs in bromeliads (Richardson 1999), and the main source of nitrogen for epiphytic bromeliads (Reich et al. 2003). Processing of detritus by insects, when coupled with predation, facilitates the uptake of

nitrogen by bromeliads (J. Ngai and D. Srivastava, unpublished results). Detrital processing—the loss of intact detritus through insect feeding—is therefore a key process in this miniature ecosystem.

Growth of bromeliads, conversely, affects their aquatic insect communities. In bromeliads in northwest Costa Rica, increases in bromeliad size covary with changes in both habitat and trophic structure. Larger bromeliads have lower detritivore densities, reduced habitat complexity (defined as the number of leaves subdividing a standard volume of water) and increased incidence of predacious damselfly larvae (Fig. 1). Other phytotelm studies show covariance between habitat size, habitat complexity and insects. Macrofaunal richness in Ecuadorian bromeliads is positively correlated with both bromeliad complexity and bromeliad size (Armbruster et al. 2002). Larger treeholes are reported to have higher occurrence of predatory damselfly larvae (Finke 1992) and predatory mosquito larvae (Bradshaw and Holzapfel 1988).

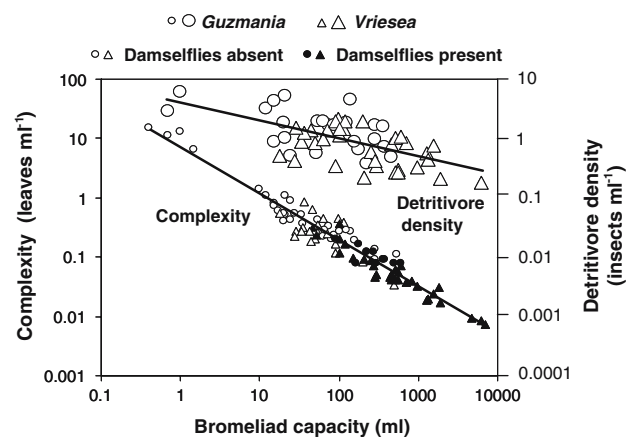


Fig. 1 Bromeliad architecture and the aquatic insect community change over a gradient in bromeliad water-holding capacity. Habitat complexity (measured as the number of bromeliad leaves subdividing a standard volume of water) decreases as bromeliad capacity increases (ANCOVA $F_{1,87}=1,193$, $P<0.0001$, both variables log-transformed). Detritivore density also declines as bromeliad capacity increases (ANCOVA, $F_{1,52}=32.2$, $P<0.0001$, both variables log-transformed). The two main genera of tank-forming bromeliads, *Guzmania* (circles) and *Vriesea* (triangles), differ slightly in complexity (ANCOVA $F_{1,87}=11.6$, $P=0.001$, small symbols) but not in detritivore density (genera: $F_{2,51}=0.003$, $P=0.96$; genera \times capacity: $F_{2,50}=0.54$, $P=0.46$, large symbols). Damselfly occurrence increases with bromeliad capacity (open small symbols damselflies absent, solid small symbols damselflies present). Bromeliad complexity and damselfly occurrence data are from 92 bromeliads collected in 1997 (22 bromeliads), 2000 (51 bromeliads including 31 previously reported in Melnychuk and Srivastava 2002) and 2002 (19 bromeliads). Detritivore density data were recorded for 58 of these bromeliads (20 bromeliads in both 1997 and 2000, and 18 in 2002). Methods for bromeliad measurements and insect surveys followed those described in Melnychuk and Srivastava (2002)

This strong covariance between habitat characteristics and the insect community precludes any observational analysis of how each factor affects detrital processing rates. Instead, I designed mesocosms to disentangle the potential influences of habitat size, habitat complexity, and predator presence on detrital processing rates. These factorial experiments examine the effects of changing habitat structure on a constant community of insects, allowing any treatment effects to be unambiguously attributed to changes in habitat structure rather than covarying changes in insect abundance. Note that detritivore density is thus manipulated solely by changing mesocosm size. I predicted that bromeliad structure would affect detrital processing through both direct effects on detritivore insects (changes in detritivore foraging rates) and by indirect effects via predatory insects (changes in predation rates on detritivores). Specifically, I hypothesized that: (1) increased habitat complexity—but not size—will impede the mobility of the detritivores and therefore their efficiency in locating resources, directly reducing rates of detrital processing; and (2) both increased habitat complexity and size will reduce the rate at which predators encounter detritivores, thus reducing top-down control of detrital processing.

Materials and methods

Study site and system

All experiments and surveys were carried out at the Estación Biológica Pitilla (10°59'N, 85°26'W) in the Área de Conservación Guanacaste, north-western Costa Rica. The mid-elevation tropical rainforest surrounding the station has high densities of bromeliads, particularly in the genera *Guzmania* and *Vriesea* (Melnichuk and Srivastava 2002). The species pool for bromeliad-dwelling insects in this region is in excess of 50 species. Aquatic insects occur only as larvae in the bromeliad; the adults are all winged and terrestrial except in the case of a rare hydrophilid beetle (aquatic larvae and adults). The dominant detritivores in the system are larvae of tipulids (*Trentepholia* spp., undescribed: Diptera), chironomids (especially *Polypedilum* sp.: Diptera), and scirtids (Coleoptera). The dominant predator in the system is *Mecistogaster modesta* Selys (Pseudostigmatidae: Odonata), common in bromeliads > 100 ml in capacity (Fig. 1). This damselfly larvae accounts for 85–90% of total predator biomass in bromeliads where it occurs; the remaining predator biomass is composed of tabanids, tanypodine chironomids, ceratopogonids and hydrophilid beetles.

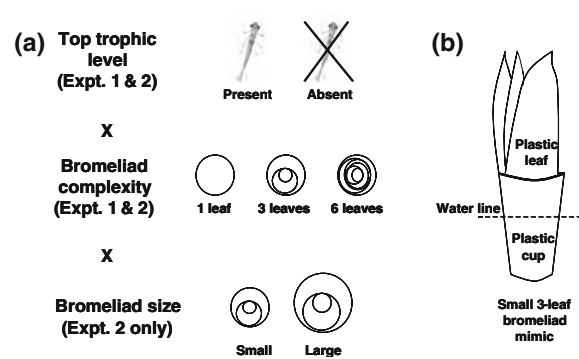


Fig. 2a, b The experimental design for both experiments described in this study. The artificial bromeliad mesocosms are shown from the top (a) or side (b)

Mesocosms as experimental units

Two experiments were conducted in artificial mesocosms that mimicked bromeliad structure (Fig. 2). Mesocosms were necessary to allow assembly of replicate insect communities as it is impossible to remove all insects from a real bromeliad without destroying the water-holding capability of the plant. Insect growth appears roughly comparable between artificial and natural bromeliads. For example, the damselfly larvae in the experiments grew in mass from 0 to 2.2% per day (mean = 0.45%, SD = 0.67, $n = 46$) in mesocosms. In natural bromeliads we have measured growth rates of similar range, 0–2.1% per day, but with a higher mean (mean = 1.20%, SD = 0.98, $n = 10$; D. Srivastava, J. Ware and J. Huff, unpublished data). Mesocosms were placed in a random array on a 1.3 × 1.3 m table, and kept on a shaded outdoor veranda, that is, at ambient conditions similar to those in the adjacent rainforest but with no natural detrital or insect inputs.

Experiment 1: complexity, predation and decomposition rate

In this experiment, two levels of predation (predator present or absent) were crossed with three levels of mesocosm complexity (one, three or six leaves), with six replicates per treatment.

Artificial bromeliads (Fig. 2) were constructed from green plastic cut into leaf shapes and sequentially glued together using aquarium-safe silicon, replicating as much as possible the architecture of natural bromeliads. The outer leaf of each plastic bromeliad was glued to the inside of a 220 ml plastic cup, this mesocosm size will be referred to as “small”. Bromeliad mesocosms were constructed out of one, three or six leaves, all with a total mesocosm volume of 95 ml water (i.e. the

one-leaf mesocosms had one large compartment whereas the six-leaf mesocosms had six small compartments). Recently fallen dead leaves, representing a variety of species, were collected from nearby rainforest and dried at low temperature for 2 h. The dried leaves were hand-crumbled and separated using soil sieves into three size categories: large (2 cm–7 mm), medium (7 mm–850 μ m), and fine (850–250 μ m).

A total of 2.2 g (weighed ± 0.002 g) of leaves was added to each mesocosm, based on surveys of detrital to volume ratios in natural bromeliads (D. Srivastava, unpublished data). The size of detrital fragments added to each individual leaf was: 45.5% large fragments, 45.5% medium and 9% fine, simulating the size distribution of detritus in natural bromeliads (D. Srivastava, unpublished data). Detritus was distributed between leaves of the same mesocosm to obtain a coefficient of variation of 0.333, similar to that observed in natural bromeliads (D. Srivastava, unpublished data). On 28 September 1999, each mesocosm received debris, 85 ml settled stream water and 10 ml water extracted from nearby natural bromeliads as a microbial inoculant (all insects were first removed from this water under $\times 10$ magnification). Water levels were maintained during the course of the experiment by adding appropriate amounts of stream water.

Three of the most common species of detritivorous insect larvae were added to each mesocosm at densities comparable to that observed in nature (Table 1). Insects were added between 30 September and 2 October (day 1 staggered to allow for harvesting over a period of days): ten chironomid larvae (*Polypedilum* sp., 4 mm), one tipulid larva (an undescribed *Trentepohlia* sp., 11–12 mm long), and two

scirtid beetle larvae (unidentified sp. 4 and 5 mm long). Detritivores were randomly distributed among mesocosm compartments. Twenty-four hours after all detritivores were added, one damselfly larva (*M. modesta*, 13–16 mm long, excluding caudal lamellae) was added to the central compartment of half the bromeliads. A second round of detritivore insects was added mid-experiment, to simulate natural colonization: a tipulid larva (12–20 mm long) was added to all mesocosms on day 14, and on day 25 a scirtid larva (5–6 mm long) was added. Damselflies were not added mid-experiment as oviposition by *M. modesta* is rare in the wet season; oviposition occurs primarily in April and May at this site, and the larval period lasts more than half a year (D. Srivastava and J. Ngai, unpublished results).

The experiment was destructively sampled on day 33. This experimental duration allowed measurable loss of detrital mass while minimizing loss of detritivores through pupation (all detritivores in this study have larval stages greater than 1 month). Plastic leaves were removed from each mesocosm, separated, and all larvae were retrieved. Body lengths of larvae were measured, and converted to biomass using empirically derived relationships. Pupal cases were recorded. The quantity of detritus remaining at the end of the experiment was measured by sieving the detritus-water mixture through an 850 μ m soil sieve. Particles retained on the sieve were dried for 2 days at 55°C and weighed (± 0.0001 g).

Growth rates were estimated for tipulid larvae, the only detritivore species with enough difference in initial size between individuals to allow individuals to be tracked through time. I restricted the analysis to bromeliads without predators; otherwise growth and

Table 1 Comparison of insect densities in natural bromeliads and experimental mesocosms

	Insect densities (individuals per gram dry detritus) ^a			
	<i>Polypedilum</i> chironomid larvae	Scirtid beetle larvae	<i>Trentepohlia</i> tipulid larvae	<i>Mecistogaster modesta</i> damselfly larvae
Natural bromeliads with damselfly larvae				
1997 (mean \pm SE, $n=9$)	5.96 \pm 1.43	7.08 \pm 1.11	1.60 \pm 0.41	0.56 \pm 0.17
2000 (mean \pm SE, $n=5$)	14.25 \pm 4.38	7.15 \pm 3.21	1.72 \pm 0.59	0.17 \pm 0.05
2002 (mean \pm SE, $n=11$)	6.84 \pm 2.36	3.27 \pm 0.97	0.97 \pm 0.18	0.75 \pm 0.20
Experimental mesocosms				
Experiment 1	4.54	0.9–1.4	0.45–0.91	0.45 ^b
Experiment 2	10–13	3–5	2	1 ^b

^a Only data for bromeliads that contained at least one damselfly larva are reported here. Bromeliads were collected in both primary and secondary forest in 1997, entirely in primary forest in 2000, and entirely in secondary forest in 2002. Insect densities in experimental mesocosms are given as a range, where appropriate, to represent net densities before and after mid-experiment addition of further larvae

^b Predator treatments

development estimates could be biased towards size classes not detected by the predator. Larval growth rates were calculated only for tipulid larvae added at the start of the experiment; many of the tipulids larvae added mid-experiment were later instars and so pupated near the end of the experiment.

Experiment 2: size, complexity, predation and decomposition rate

In this experiment, three levels of the insect community (detritivores and predators, detritivores only, no insects) were crossed with three levels of mesocosm complexity (one, three or six leaves) and two levels of mesocosm size (small or 50% larger); there were five replicates per treatment. Experiment 2 is thus an expanded version of Experiment 1, with the additional factors of mesocosm size and no-insect controls. The no-insect controls allowed the amount of detritus processed by insects to be calculated as the difference in detritus between treatments with and without insects.

Bromeliad mesocosms were constructed as described earlier. “Small” mesocosms were constructed from 220 ml plastic cups (diameter 4.7–7.1 cm, height 9.0 cm) with a total water volume of 133 ml. “Large” mesocosms were constructed in 440 ml cups (diameter 5.5–9.0 cm, height 11.0 cm) with a total water volume of 195 ml (50% more habitat volume than small mesocosms). Note that the “small” mesocosms of Experiment 2 were exactly the same size as the “small” mesocosms of Experiment 1, but were filled with more water so that the small and large bromeliads of Experiment 2 had the same water height (6 cm). Any difference in water height could have affected the distance insects needed to travel out of water from one compartment to the other, potentially confounding effects of mesocosm volume. Dead leaves were obtained from windfall branches of a *Quina schippii* (Quinaceae) tree; a single detrital source was used to reduce between-mesocosm variation in rates of leaching. On 3 October 2000, 1.0 g oven-dried, crumbled dead leaves (weighed to the nearest 0.002 g) was added to each mesocosm. Detrital distribution amongst compartments followed the same rules as in Experiment 1. Insect densities (per gram detritus) were higher than in Experiment 1 but still within the range naturally observed (Table 1). Differences between the experiments in the abundance of individual species simply reflect variation between years in the availability of specific instars harvested from natural bromeliads. The following detritivore insects were added between 4 and 6 October 2000 (day 1): two tipulid larvae (one 15–20 mm long, one 9–13 mm long), three

scirtid larvae (one 4–5 mm, two 5–6 mm), and ten chironomids (4 mm). A single larvae of *M. modesta* (12–14 mm) was added to the central compartment of half of the mesocosms on day 4. At the mid-point of the experiment, day 21, a second round of detritivores (to simulate natural colonization), consisting of three chironomid larvae (4 mm) and two scirtid larvae (5–6 mm), was added to all mesocosms. The experiment was harvested after 38–41 days, as described earlier. Mesocosms were carefully searched for cadavers of larvae in this experiment, to quantify non-predation mortality. Growth of tipulids in the small mesocosms was calculated as in Experiment 1. There were not enough tipulids remaining in the large, one-leaf mesocosms at the end of the experiment to permit growth analysis for the large mesocosms. Damselfly length was measured at the start and end of the experiment, and converted to wet mass using an empirical relationship ($r^2=0.96$, $n=46$)

Analysis of experiments

Loss of detrital mass was measured at the end of both experiments. Detrital loss includes effects of insect processing as well as passive leaching and microbial decomposition. In Experiment 2, detrital processing by insects was calculated as detrital loss in the insect-containing replicate minus mean detrital loss in the corresponding no-insect control. In Experiment 1, there were no treatments without insects, so detrital processing could not be directly calculated; instead, detrital loss was used as the response variable. The results were similar regardless of whether detrital loss or detrital processing was considered the response variable in Experiment 2.

Complexity could have been analyzed as either a categorical or continuous variable in these experiments. By analyzing complexity as a continuous variable, I am able to examine how—not just if—complexity affects insects and energy flux. Note that my hypothesized mechanisms involve directional change in insect behavior over a complexity gradient. I also avoid any loss in power associated with post hoc comparisons of means. Regression analysis is generally recommended over ANOVA because it affords greater power and provides more quantitative information about causal patterns (Cottingham et al. 2005). All data were analyzed with regression models. Categorical terms of predator presence and bromeliad size were coded as either 1 or 0, and nonlinear effects of complexity were tested using a quadratic model. Most data was modeled with normal errors. The pupation and cadaver data had substantial

heteroscedasticity, so Poisson errors with a log-link function were used in a generalized linear model. The pupation but not the cadaver data was initially under-dispersed (residual deviance: $df=0.65$), and this was corrected with an empirical scale parameter. Analyses used GENSTAT 5, release 3.2 (Lawes Agricultural Trust) and R version 1.8.0 (<http://www.r-project.org>).

Results

Two experiments were conducted. Experiment 1 examined the effects of habitat complexity on detrital loss and predation. Experiment 2 examined the effects of both habitat complexity and habitat size on detrital processing and predation. Similar results between the two experiments indicate robustness of the conclusions, whereas different results suggest either low power or strong context-dependence. To facilitate such comparisons, I have grouped results from both experiments under several themes.

Net effects of habitat and predation on detrital processing

In Experiment 1, the effects of habitat complexity on detrital loss depended on whether predators were present or absent (Fig. 3a). In the presence of predators, rates of detrital loss were constantly low, irrespective of complexity. In the absence of predators, rates of detrital loss were much higher in the one-leaf mesocosms than either the three- or six-leaf mesocosms. The effects of complexity were thus dependent on trophic structure, and were non-linear in nature (Table 2: predator \times complexity and predator \times complexity² interactions).

Table 2 Reduced regression models (backwards elimination) for the response variables measured in Experiment 1. Only significant ($P < 0.05$) explanatory variables are shown, no variables were marginally significant ($0.10 > P > 0.05$). For the response variables of detrital loss and detritivore abundance, the full model included predator, complexity, complexity², predator \times complexity, and predator \times complexity². The full model for tipulid growth, examined in no-predator mesocosms, included complexity and complexity²

Response variable	Explanatory variables	F ratio	P value
Detrital loss	Predator \times complexity	$F_{1,31}=5.73$	0.022
	Predator \times complexity ²	$F_{1,31}=7.43$	0.010
Detritivore abundance	Predator	$F_{1,32}=70.19$	< 0.0001
	Predator \times complexity	$F_{1,31}=19.1$	< 0.0001
Tipulid growth	Complexity	$F_{1,31}=64.3$	0.021

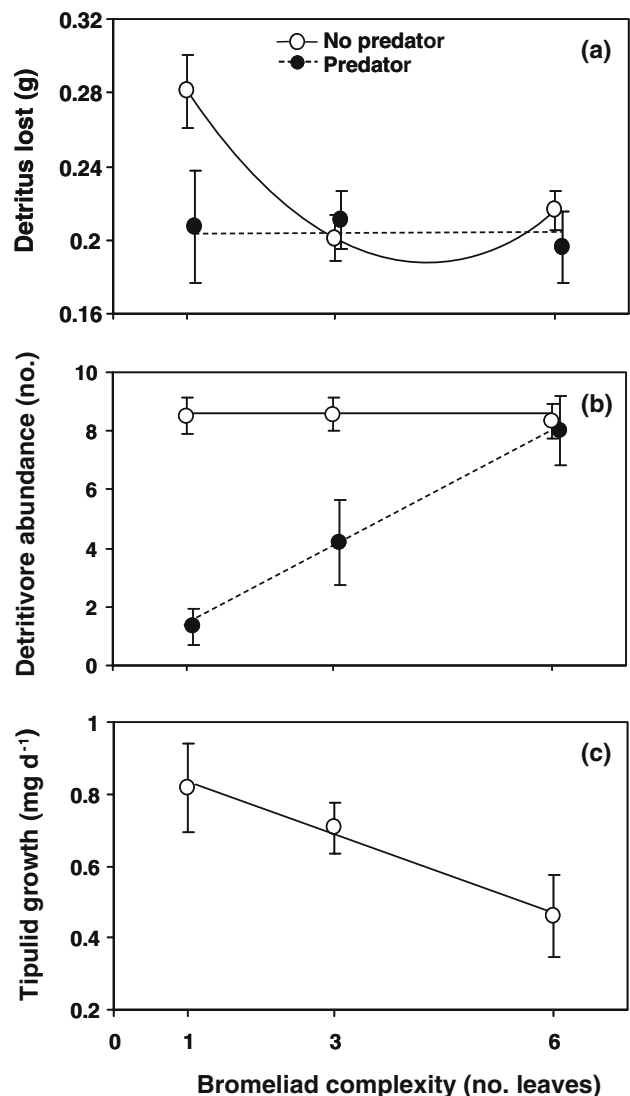


Fig. 3 Effects of predation by damselfly larvae (*Mecistogaster modesta* Selys) and bromeliad complexity in small mesocosms (Experiment 1) on **a** detrital loss over 4 weeks, **b** final detritivore abundance, and **c** growth of tipulid larvae. Tipulid growth is presented only for mesocosms without predators, as growth estimates could otherwise be biased towards size classes not detected by the predator. Lines Best-fit regression models (see Table 2), symbols mean \pm SE for each treatment

In Experiment 2, insects processed the most detritus in mesocosms of intermediate complexity (Fig. 4a). For all four treatment combinations in this experiment (large and small mesocosms, with and without predators), there were therefore strong non-linear relationships between complexity and detritus processed (Table 3: complexity² effect). The form of these non-linear relationships depended on habitat size, predation and their interaction (Table 3; Fig. 4a). Specifically, in the absence of predators, small mesocosms had higher detrital processing rates than large mesocosms (effect of combining these treatments: $F_{1,54}=67.2$,

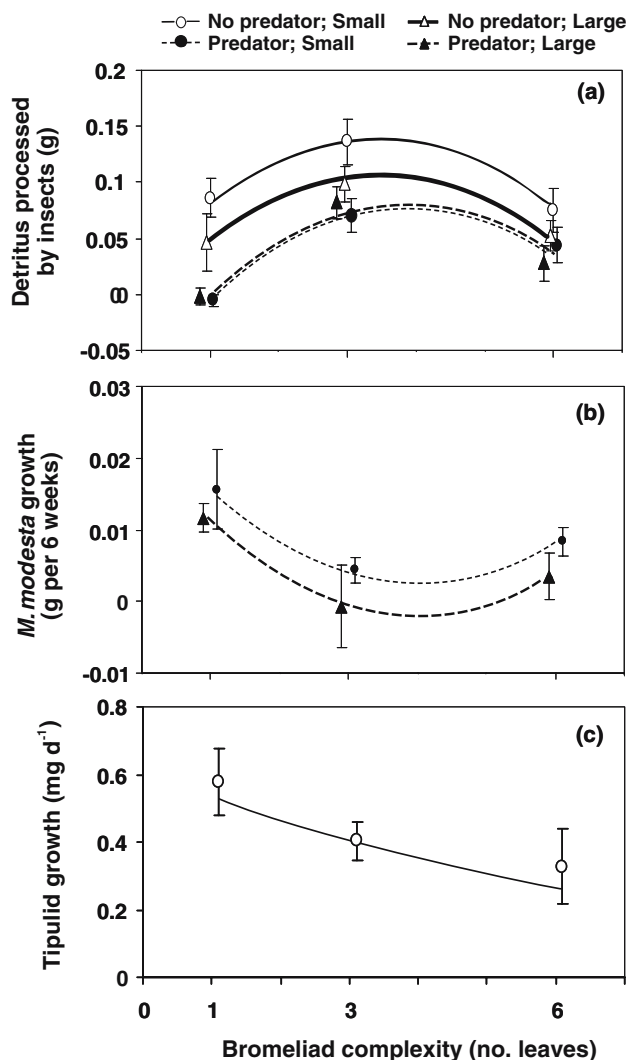


Fig. 4 Effects of predation, bromeliad complexity and bromeliad size in Experiment 2 on **a** detrital processing over 6 weeks, and growth rate of **b** *M. modesta* larvae and **c** tipulid larvae. Tipulid growth is presented only for mesocosms without predators, as growth estimates could otherwise be biased towards size classes not detected by the predator. There were not enough tipulids remaining in the large, one-leaf mesocosms at the end of the experiment to permit growth calculations. *Lines* Best-fit regression models (see Table 3) and, in the case of the small and large mesocosms with predators in (a), are so similar as to be indistinguishable; *symbols* mean \pm SE for each treatment

$P < 0.0001$, Fig. 5b), but in the presence of predators, this difference disappeared (effect of combining these treatments: $F_{1,53} = 0.008$, $P = 0.92$; Fig. 5b).

At first glance, the effect of habitat complexity on detrital processing appears quite different between the experiments: maximal detrital processing occurred in one-leaf mesocosms in Experiment 1 but in three-leaf mesocosms in Experiment 2. It will be argued later that such differences in patterns of detrital processing are an artifact of differences between experiments, such as

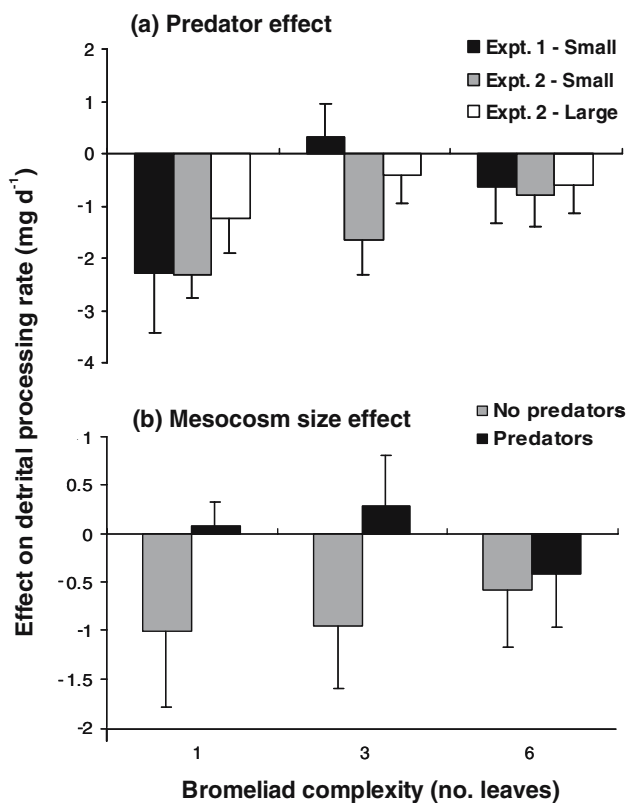


Fig. 5 a Effects of predation on detrital processing over a gradient in bromeliad complexity, for both experiments. *Negative values* indicate that predators reduce detrital processing. **b** Effects of habitat size on detrital processing over a gradient in complexity for Experiment 2. *Negative values* indicate that increasing habitat size reduces detrital processing. *Bars* Mean (\pm SE) differences between appropriate treatments

duration. However, there are important similarities between the experiments. In Experiment 1 mesocosms and the similar-sized small mesocosms of Experiment 2, predators reduced daily rates of detrital processing by comparable amounts (Fig. 5a), and this predator effect depended on habitat complexity (Tables 2, 3: predation \times complexity interactions). Specifically, predation reduced detrital loss in the one-leaf mesocosms marginally in Experiment 1 (two-tailed t test: $t_{10} = 2.00$, $P = 0.073$) and substantially in Experiment 2 ($t_8 = 5.06$, $P = 0.0010$), but as complexity increased, the effects of predation on detrital loss diminished to insignificant in six-leaf mesocosms (Experiment 1: $t_{10} = 0.89$, $P = 0.39$; Experiment 2: $t_8 = 1.25$, $P = 0.25$).

In summary, detrital processing was reduced by large habitat size and high habitat complexity and—particularly in small, low-complexity habitats—by predation. To understand the mechanisms underlying these patterns, I now examine the effects of habitat structure on the foraging efficiency of both predators and detritivores.

Table 3 Reduced regression models (backwards elimination) for the response variables measured in Experiment 2. Only explanatory variables significant ($P < 0.05$) or marginally significant (in parentheses, $0.10 > P > 0.05$) are shown. The full model for all response variables except damselfly and tipulid growth included predator, size, complexity, complexity², and all two- and three-way interactions between predator, size and complexity (linear and quadratic forms). The full model for both tipulid and damselfly growth included size, complexity, complexity², size \times complexity, size \times complexity². Tipulid growth was examined only in small mesocosms without predators, damselfly growth was examined only in mesocosms with predators

Response variable	Explanatory variables	F ratio	P value
Detrital processing	Complexity	$F_{1,53} = 3.14$	< 0.0001
	Complexity ²	$F_{1,53} = 35.6$	< 0.0001
	Size	$F_{1,53} = 6.64$	0.013
	Predator	$F_{1,53} = 20.8$	< 0.0001
	Predator \times complexity	$F_{1,53} = 3.34$	(0.072)
Damselfly growth	Predator \times size	$F_{1,53} = 3.20$	(0.080)
	Complexity	$F_{1,26} = 8.59$	0.007
	Complexity ²	$F_{1,26} = 7.09$	0.013
Tipulid growth (in absence of predators)	Complexity	$F_{1,12} = 4.67$	0.05
Pupation rate (all species)	Complexity \times size	$F_{1,58} = 6.32$	0.01
Non-predation mortality (all species)	Complexity	$F_{1,58} = 17.2$	< 0.0001

Effects of habitat on predation rates

High habitat complexity reduced predation rates. This can easily be seen in Experiment 1, in which predators reduced larval abundance by 85% in one-leaf bromeliads, 50% in three-leaf bromeliads, and not at all in six-leaf bromeliads (Fig. 3b, significant predator \times complexity effect: Table 2). Larvae were also lost in the absence of predators (due to other causes of mortality and pupation), but final abundances were similar across complexity levels. The frequency of pupation was greater in the longer-running Experiment 2. Pupation rates were not independent of predator presence, as described later, preventing the estimation of predation rates as simply the difference in abundance between treatments with and without predators (as in Experiment 1). However, predation rates could be measured indirectly by examining the growth rate of the damselfly, *M. modesta*. Damselfly growth rates were significantly higher in the one-leaf mesocosms than in more complex mesocosms in Experiment 2 (Fig. 4b, Table 3: complexity effects). Although damselflies tended to grow more slowly in large than small mesocosms, this size effect was not significant (Table 3, Fig. 4b, $F_{1,25} = 2.72$, $P = 0.11$).

Effects of habitat on detritivore foraging efficiency

High habitat complexity also reduced the foraging efficiency of detritivores. In Experiment 1, in the absence of predators, total detrital processing decreased as complexity increased yet detritivores maintained a constant abundance across the complexity gradient; in other words, each individual detritivore consumed less detritus as complexity increased. In the presence of predators, detritivore abundance increased with complexity, yet total detritus processed remained constant over the complexity gradient. Thus, again, per capita foraging efficiency must have decreased as complexity increased.

These reductions in foraging efficiency as a result of high habitat complexity had important consequences for detritivores: slower growth, lower pupation rates, and higher mortality rates. In both experiments, tipulids had slower growth rates in the more complex mesocosms (Figs. 3, 4; Tables 2, 3). In Experiment 2, pupation rates of all species declined with increasing mesocosm complexity, particularly in the small mesocosms, and non-predation deaths increased with mesocosm complexity (Table 3; Fig. 6; comparable data is not available for Experiment 1). A likely cause of non-predation deaths is starvation due to low foraging efficiency, though further experiments are required for confirmation. In general, each extra compartment in the mesocosm resulted in an additional 1.47 larval cadavers, and a reduction of 1.43 pupal cases.

Predation also affected pupation rates in Experiment 2. In the absence of predators, one-leaf mesocosms had higher pupation rates than more complex mesocosms (57% of all pupations) but, in the presence of predators, had no pupations since as many detritivores were consumed as larvae. Thus, the low detrital processing rates in one-leaf mesocosms in Experiment 2 (Fig. 4a) was due to loss of detritivores to pupation when predators were absent, but loss of detritivores to predation when predators were present. The low detrital processing rates in six-leaf mesocosms (Fig. 4a) was due to high detritivore mortality in both cases. The combination of both patterns resulted in maximum detrital processing in the three-leaf mesocosms of Experiment 2 (Fig. 4a).

Discussion

In manipulations with bromeliad mesocosms, habitat structure had both direct (detritivore-mediated) and indirect (predator-mediated) effects on detrital processing. Increasing habitat complexity reduced the

foraging efficiency of detritivores, and so directly reduced rates of detrital processing. However, increasing habitat complexity simultaneously increased rates of detrital processing by decreasing the efficiency of damselflies preying on detritivores. Thus, increasing habitat complexity resulted in opposing effects on detrital processing rates: more surviving detritivores (due to reduced predation) but less processing per detritivore (Fig. 3). These opposing effects of complexity were of similar magnitude in Experiment 1—there was no net effect of complexity on detrital loss in the presence of predators (Fig. 3a)—but not in Experiment 2 (Fig. 4a). Habitat size may have also had similar direct and indirect effects on detrital processing; increasing habitat size led to reductions in detrital processing in the absence, but not in the presence, of predators (Fig. 5b). However, the corollaries of reduced predator and detritivore growth with increased habitat size are not as well supported as with increased habitat complexity. Note that habitat structure affected not only detrital processing, but more generally the flux of energy from detritus to detritivores to damselfly larvae: complex mesocosms had lower growth rates of both detritivores and damselfies.

High habitat complexity likely reduced predation rates by providing detritivores with a stochastic refuge:

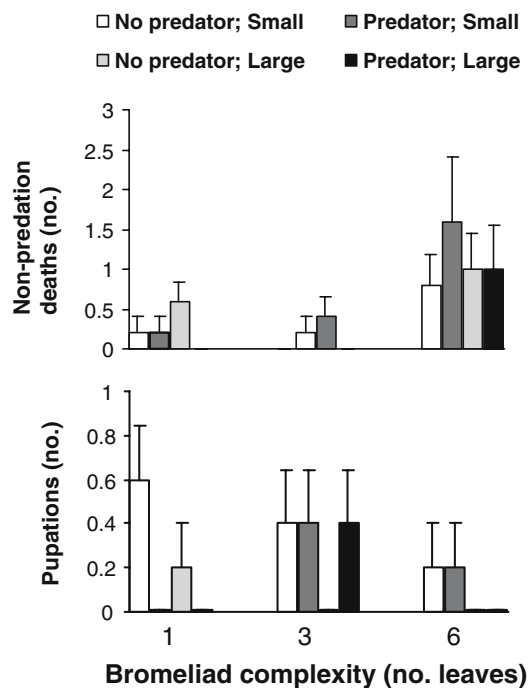


Fig. 6 Effects of bromeliad complexity, size and predator presence on the number of detritivore larvae that **a** died due to non-predation causes or **b** reached pupation. Values are mean (+ SE) number of occurrences per mesocosm measured over the 6 weeks of Experiment 2

reduced probability of detritivores and damselfies co-occurring in the same leaf compartment. Co-occurrence probably occurs when detritivores, not damselfies, move compartments in search of resources. *M. modesta* damselfies are sit-and-wait predators, and have been recorded residing in the same leaf compartment for at least 2 weeks at a time, whereas detritivores normally move compartments within 2 weeks (D. Srivastava, unpublished observation). Effects of habitat complexity on predation rates have been shown for many other aquatic communities (Crowder and Cooper 1982; Heck and Crowder 1991; Sebens 1991; Nemeth 1998; Warfe and Barmuta 2004), as well as terrestrial insect communities (Casas and Djemai 2002). In a few cases, such as the current study, complexity effects have been documented to cascade through multiple trophic levels. For example, increases in the complexity of *Spartina* tussocks improve predator efficiency in reducing planthopper abundance, which in turn increases *Spartina* biomass (Denno et al. 2002). Similarly, rock size in stream beds affects the strength of a fish–damselfly–chironomid–algae trophic cascade, as the complex habitat provided by gravel creates refuges for invertebrates from fish predation (Power 1992).

High habitat complexity also reduced detritivore foraging rates, even in the absence of predators. Complexity may reduce the ability of detritivores to find high-quality patches of resources (detritus in the mesocosms was heterogeneously distributed amongst compartments, as in natural bromeliads). Detritivores in complex bromeliads may also delay moving to a new compartment to search for better resources, trading-off the benefits of finding new resources against the energetic costs of moving, or the risk of encountering a predator. Such trade-offs between feeding and predator avoidance have been shown for many organisms (Lima 1998).

Increasing habitat size also reduced detrital processing rates in the absence of predators. The mechanism is not clear here, for detritivores might be expected to easily find detritus within 6 weeks in even the largest compartment (though arguably at a slower rate, due to reduced density of both insects and detritus). This study was designed so that increases in habitat size resulted in reduced detritivore density, to mimic patterns in real bromeliads (Fig. 1). Reduced encounter rates between detritivores in large mesocosms might have been expected to reduce interference competition, promoting detrital processing, but the opposite trend was observed. This experiment does not allow a direct assessment of resource competition, but note that detritivores consumed only a fraction of the detritus

provided. In general, detritivore species in phytotelmata have more often been shown to have facilitative than competitive interactions (Bradshaw and Holzapfel 1992; Heard 1994a; Paradise and Dunson 1997).

The patterns in detrital processing observed in this study may, in addition to the mechanisms already addressed, involve disruption of two types of facilitative interactions. First, damselfly predation on detritivores reduced the fragmentation of detritus, and may have thus reduced the colonization of detritus by bacteria and fungi. Microbial decomposition, which is essential to the breakdown of detritus, may be facilitated by insects (Cummins and Klug 1979). Second, increases in either predation or complexity may have disrupted detrital processing chains. A processing chain occurs when some detritivores convert intact detritus into finer organic particles (by shredding detritus or scraping mesophyll layers), facilitating other detritivores that collect or filter fine particulate matter (Heard 1994b). Processing chains have been documented in phytotelmata, but only under certain conditions (Heard 1994a; Paradise and Dunson 1997; Paradise 1999; Daugherty and Juliano 2002). We have recently found evidence for processing chains in bromeliads (B. Starzomski, D. Suen and D. Srivastava, unpublished results). Tipulids are particularly vulnerable to damselfly predation and loss of this dominant shredder may have disrupted any processing chain. Spatial partitioning of both insects and detritus in complex mesocosms may have also disrupted potential processing chains; this could have resulted in the observed reduction in detritivore efficiency. Such mechanisms can only be tested with additional experiments.

The two experiments exhibited very different patterns between complexity and detrital loss (processing), despite similar underlying mechanisms. In the absence of predators, maximal detrital loss occurred at the lowest complexity in Experiment 1. By contrast, maximal detrital processing occurred at intermediate complexity in Experiment 2. The proximate reasons for these differences were more pupations (especially in one-leaf bromeliads) and more non-predation deaths (especially in six-leaf bromeliads) in Experiment 2. Both of these effects probably occurred because of the longer duration of Experiment 2 (38–41 days for Experiment 2 vs 33 days for Experiment 1), although this cannot be isolated from other differences between the experiments (year, detritus type and amount, detritivore abundances). The contrast between the two experiments suggests that, in natural bromeliads, net effects of complexity on detrital processing may be quite sensitive to seasonal variation in oviposition rates and detrital inputs.

Understanding the direct and indirect effects of habitat structure on ecosystem function is not just important in pristine systems like the bromeliad–insect food web. Whether habitat structure is changed through natural or anthropogenic effects, systems experiencing reductions in habitat structure may be expected to show concomitant decreases in trophic structure. For example, extinction of predator species has been linked to reductions in habitat size (Luckinbill 1974; Holt et al. 1999; Brashares et al. 2001) and increases in habitat fragmentation (Gilbert et al. 1998). Similarly, decreases in habitat complexity lead to reductions in predator abundance (meta-analysis: Langellotto and Denno 2004). The bromeliad example shows that, when trophic structure and habitat structure covary, it will be particularly important to understand how the two factors interact to affect ecosystem functions. Despite interest in biotic regulation of ecosystem function (Loreau et al. 2002) and the ecological consequences of changed habitat structure (Langellotto and Denno 2004), there is still remarkably little research on the combined effects of species loss and habitat change on function (Srivastava 2002; Srivastava and Vellend 2005).

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References

- Tewksbury JJ et al (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc Natl Acad Sci USA* 99:12923–12926
- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- Armbruster P, Hutchinson RA, Cotgreave P (2002) Factors influencing community structure in a South American tank bromeliad fauna. *Oikos* 96:225–234
- Beck MW (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. *J Exp Mar Biol Ecol* 249:29–49
- Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- Bradshaw WE, Holzapfel CM (1988) Drought and the organization of tree-hole mosquito communities. *Oecologia* 74:507–514

- Bradshaw WE, Holzapfel CM (1992) Resource limitation, habitat segregation, and species interactions of British tree-hole mosquitoes in nature. *Oecologia* 90:227–237
- Brashares JS, Arcese P, Sam MK (2001) Human demography and reserve size predict wildlife extinction in West Africa. *Proc R Soc Lond B Biol Sci* 268:2473–2478
- Carpenter SR et al (2001) Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecol Monogr* 71:163–186
- Casas J, Djemai I (2002) Canopy architecture and multitrophic interactions. In: Tschamntke T, Hawkins BA (eds) *Multitrophic level interactions*. Cambridge University Press, Cambridge, pp 174–196
- Cottingham KL, Lennon JT, Brown BL (2005) Knowing when to draw the line: designing more informative ecological experiments. *Front Ecol Environ* 3:145–152
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Cummins KW, Klug MJ (1979) Feeding ecology of stream invertebrates. *Annu Rev Ecol Syst* 10:147–172
- Daugherty MP, Juliano SA (2002) Testing for context-dependence in a processing chain interaction among detritus-feeding aquatic insects. *Ecol Entomol* 27:541–553
- Denno RF, Roderick GK (1991) Influence of patch size, vegetation texture, and host plant architecture on the diversity, abundance, and life history styles of sap-feeding herbivores. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, New York, pp 169–196
- Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458
- Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. *Trends Ecol Evol* 11:255–260
- Fincke OM (1992) Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. *Ecology* 73:449–462
- Finke DL, Denno RF (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83:643–652
- Floater GJ (2001) Habitat complexity, spatial interference, and “minimum risk distribution”: a framework for population stability. *Ecol Monogr* 71:447–468
- Frank JH (1983) Bromeliad phytotelmata and their biota, especially mosquitoes. In: Frank JH, Lounibos LP (eds) *Phytotelmata: terrestrial plants as hosts of aquatic insect communities*. Plexus, Medford, pp 101–128
- Gilbert F, Gonzalez A, Evans-Freke I (1998) Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proc R Soc Lond B* 265:577–582
- Gonzalez A, Chaneton EJ (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J Anim Ecol* 71:594–602
- Heard SB (1994a) Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology* 75:1647–1660
- Heard SB (1994b) Processing chain ecology: resource condition and interspecific interactions. *J Anim Ecol* 63:451–464
- Heck KL Jr, Crowder LB (1991) Habitat structure and predator-prey interactions in vegetated aquatic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, New York, pp 281–299
- Holt RD, Lawton JH, Polis GA, Martinez ND (1999) Trophic rank and the species-area relationship. *Ecology* 80:1495–1504
- Klein BC (1989) Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* 70:1715–1725
- Laessle AM (1961) A micro-limnological study of Jamaican bromeliads. *Ecology* 42:499–517
- Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139:1–10
- Lima SL (1998) Non-lethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34
- Loreau M, Naeem S, Inchausti P (eds) (2002) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford
- Luckinbill LS (1974) The effects of space and enrichment on a predator-prey system. *Ecology* 55:1142–1147
- MacArthur RH (1972) *Geographical ecology*. Harper and Row, New York
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton
- McQueen DJ, Johannes MRS, Post JR, Stewart TJ, Lean DRS (1989) Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol Monogr* 59:289–309
- Melnichuk MC, Srivastava DS (2002) Abundance and vertical distribution of a bromeliad-dwelling zygopteran larva, *Mecistogaster modesta*, in a Costa Rican rainforest (Odonata: Pseudostigmatidae). *Int J Odonatol* 5:81–97
- Nemeth RS (1998) The effect of natural variation in substrate architecture on the survival of juvenile bicolor damselfish. *Environ Biol Fishes* 53:129–141
- Paradise CJ (1999) Interactive effects of resources and a processing chain interaction in treehole habitats. *Oikos* 85:529–535
- Paradise CJ, Dunson WA (1997) Insect species interactions and resource effects in treeholes: are helodid beetles bottom-up facilitators of midge populations? *Oecologia* 109:303–312
- Picado C (1913) Les broméliacées épiphytes considérées comme milieu biologique. *Bull Sci Fr Belg* 47:215–360
- Power ME (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* 73:1675–1688
- Reich A, Ewel JJ, Nadkarni NM, Dawson T, Evans RD (2003) Nitrogen isotope ratios shift with plant size in tropical bromeliads. *Oecologia* 137:587–590
- Richardson BA (1999) The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. *Biotropica* 31:321–336
- Schindler DE, Carpenter SR, Cole JJ, Kitchell JF, Pace ML (1997) Influence of food web structure on carbon exchange between lakes and atmosphere. *Science* 277:248–251
- Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122:297–305
- Sebens KP (1991) Habitat structure and community dynamics in marine benthic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, New York, pp 211–234
- Srivastava DS (2002) The role of conservation in expanding biodiversity research. *Oikos* 98:351–360
- Srivastava DS, Vellend M (2005) Biodiversity-ecosystem function research: is it relevant to conservation? *Annu Rev Ecol Syst* 36:267–294
- Uetz GW (1991) Habitat structure and spider foraging. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, New York, pp 325–348

- Wardle DA, Zackrisson O, Hörnberg G, Gallet C (1997) The influence of island area on ecosystem properties. *Science* 277:1296–1299
- Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecol Monogr* 71:587–614
- Warfe DM, Barmuta LA (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171–178
- Young K (2001) Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids. *Oikos* 95:87–93