Stability of pitcher-plant microfaunal populations depends on food web structure

M. Kurtis Trzcinski, Sandra J. Walde and Philip D. Taylor

Enrichment (increasing K) destabilizes simple consumer–resource interactions, but increasing food web complexity in various ways can remove this paradox of enrichment. We varied resources and number of omnivorous predators (mosquitoes) and tested for effects on the stability (persistence and temporal variability) of microfaunal populations living in pitcher plants. Top-down (omnivorous) effects were destabilizing, decreasing the persistence time of a rotifer, *Habrotrocha rosa,* and perhaps a microflagellate, *Bodo* sp. Enrichment effects were more complex, in part due to effects of shredding midges on resource availability, and in part due to interactions with predation. The persistence of *Bodo* increased with resource availability (more bacteria due to shredding by midges; no paradox of enrichment). Increasing resources by adding ants decreased persistence of *H. rosa* when mosquitoes were rare (paradox of enrichment), but the effect was reversed in leaves with significant colonization by mosquitoes. Thus, in the microfaunal community of pitcher plants, omnivorous predation tends to be destabilizing, and also tends to remove the paradox of enrichment.

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The relative importance of top-down vs bottom-up factors in determining population stability has stimulated much debate, and at least part of the resolution of this debate involves consideration of food web structure (Power 1992, Strong 1992, Schmitz et al. 2000). The ultimate effect of top-down and bottom-up factors on population stability is related to the community or trophic structure in which the interactions are embedded (Abrams 1993, Scheffer and de Boer 1995, Leibold 1996, McCann et al. 1998, Fussman and Heber 2002). In simple consumer–victim models, increases in victim carrying capacity (bottom-up effects) are destabilizing, and can result in the extinction of one or both species – the 'paradox of enrichment' (Rosenzweig 1971). Similar results can be obtained for models with three trophic levels (Abrams and Roth 1994). However, increasing the complexity of the food web by modeling multiple victim types (especially inedible species), spatial heterogeneity or consumer interference, can eliminate destabilizing bottom-up effects (Arditi and Ginzburg 1989, Ruxton et al. 1992, Grover 1995, Jansen 1995, Abrams and Walters 1996, Huxel and McCann 1998). Empirically, there exists both confirmation of the paradox of enrichment phenomenon in simple systems, and documentation of its absence in at least some webs (McCauley et al. 1988, McCauley and Murdoch 1990, Kaunzinger and Morin 1998, Kirk 1998, Holyoak 2000, Persson et al. 2001).

One important food web characteristic is the prevalence of omnivory. Early theory indicated that food webs with omnivory would tend to be unstable (May 1974, Pimm and Lawton 1978), but more recent models, with

slightly more complex webs containing omnivores, can be stable (Law and Blackford 1992, McCann and Hastings 1997). Enrichment of an omnivorous food web (with resource, consumer and omnivore) produces a range of possible outcomes (Holt and Polis 1997, Diehl and Feißel 2000). As enrichment increases, there are expected to be transitions in community types: basal species only, basal and consumer species, basal, consumer and omnivorous species, and finally, only basal species and the omnivore (Diehl and Feißel 2000). Empirical tests are few. In laboratory microcosms omnivores have been shown to influence the temporal variability and persistence of protist prey (Lawler and Morin 1993, Holyoak and Sachdev 1998, Morin 1999). Some of the predicted transitions with increased enrichment have been observed in laboratory protist systems, along with greater temporal variability and shorter persistence times (Morin 1999, Diehl and Feißel 2000). In an elegant field study, Fagan (1997) found that increasing the degree of omnivory in an insect community increased stability (recovery after disturbance) for about half of the species. So far as we know, no study has attempted to determine the combined effects of enrichment and omnivory on population stability for a naturally occurring community.

Our objective is to test the effects of enrichment and omnivory on the stability of microfaunal populations living within the purple pitcher plant (*Sarracenia purpurea*; Fig. 1). Pitcher plant leaves contain small aquatic communities that reassemble each year. Variation in colonization produces communities that differ in species composition (Trzcinski et al. 2003). The top trophic level consists of omnivorous mosquito larvae,

which feed on microfauna (rotifers and protists) as well as on bacteria. The microfauna feed on the bacteria (basal species). The abundance of bacteria is affected by resources (insects captured by the plant) and decomposition rates (influenced by the abundance of shredding midges; Bradshaw and Holzapfel 1986, Naeem 1988, Heard 1994). As a consequence, enrichment in this system depends on both resource levels and decomposition rates. Previous studies have shown significant, though sometimes contradictory top-down and bottom-up effects on abundance and species diversity (Addicott 1974, Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002, 2003). In this study we manipulated resources and predators in a system open to colonization, with the objective of examining how enrichment and variation in food web structure (omnivory) influences the dynamics of the microfauna.

Methods

Experimental manipulations

We manipulated resources (dead insects) and mosquitoes (omnivorous predators) in the leaves of pitcher plants in a coastal bog in eastern Canada (44°29′N, 63°32′W) (Fig. 1). We monitored, in situ, the densities of three common microfaunal taxa twice a week over two months, then collected the leaves, and counted the arthropods present. Finally, we tested for the effects of our manipulations, as well as several co-variates, on microfaunal abundance, temporal variability and persistence.

The manipulation was a fully crossed design, with nine treatment categories (three levels each of resources and mosquitoes). On 17–18 May 1999, we selected ten newly-opened leaves (on separate plants) in each of six zones (approx. 80×80 m), and assigned them to one of the nine treatment categories, with two replicates in the unmanipulated category (n = 60). Resource levels were: 0, 1 or 2, dead harvester ants added bi-weekly (*Pogonomyrmex*, Wards biology), and mosquito levels were 0, 5 or 10 larvae added once. Mosquito larvae were collected from 100 leaves at the study site, and gently transferred through three baths of deionized water to reduce the associated transfer of protozoa. We introduced the larvae to the study leaves on 12 Aug (just after the peak period of mosquito oviposition), together with 2 ml of water from the last bath (2 ml of bath water was also added to control leaves).

Estimating abundance

We monitored the abundance of the three dominant taxa in the microfaunal assemblage, *Bodo* sp., a small flagellate (8–10 μm), *Cyclidium* sp., a ciliate (25–30 μm), and *Habrotrocha rosa*, a bdelloid rotifer (usually >150 μm)
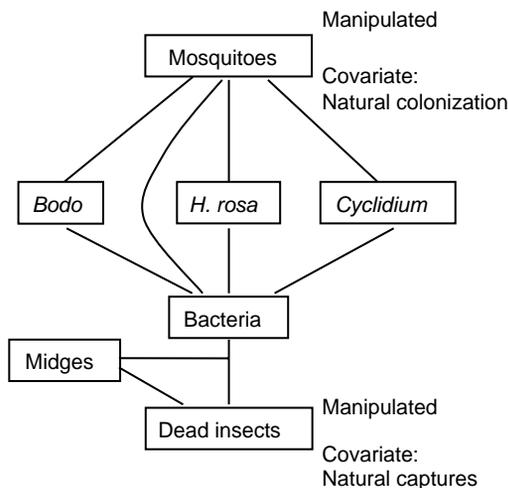

Fig. 1. Food web of the pitcher plant community considered in this study. We manipulated the top predators (mosquitoes) which are omnivorous, feeding on microfauna and bacteria. Microfauna feed on bacteria. Bacterial abundances are affected by the amount of dead insect biomass (manipulated in this study) in the leaf and by the shredding activity of midges (measured as a covariate).

over the course of the experiment. We focused on these taxa because they were common and easy to identify, and because they have been the focus of other recent studies (Bledzki and Ellison 1998, Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002). We collected samples from each leaf twice a week from 2 June until 2 Sept, first measuring water depth, and then pipetting three water samples (170 µl) from mid-way between the water surface and the bottom, touching the edge of the leaf with the tip. An effort was made to avoid disturbing the leaf contents, and removed liquid was replaced with distilled water. Samples were preserved with 10 µl $HgCl_2$ (saturated), and refrigerated until analyzed. We reduced sampling effort when water level was low: depth <5 mm: no sample, 5–10 mm: 1 sample, 11–20 mm: 2 samples.

Densities were frequently low, and we therefore concentrated samples prior to counting, centrifuging lightly (500 G for 10 min), and then discarding the top 145 µl. After re-suspension, we loaded a hemocytometer with two 10 µl drops. For each drop, we scanned 0.016 µl at $400 \times$ for *Bodo*, and 0.9 µl at $100 \times$ for *Cyclidium* and *H. rosa*, resulting in detection limits of 343 individuals per ml (unconcentrated fluid) for *Bodo*, and 3.3 ml^{-1} for *Cyclidium* and *H. rosa*.

We multiplied densities by water volume to obtain abundance. We produced a regression model to estimate water volume by adding known volumes of water (vol) at 5 ml increments to a set of 50 leaves, and measured water depth (h), leaf length, and maximum diameter (d). Our best predictive model underestimated volume by less than 10%, and included only depth and diameter:

$$vol = 0.2619 \ h + 0.004252 \ h^2 + 0.1511 \ d - 6.28$$

$$(r^2 = 0.89)$$

We began recording bacterial densities on 12 Aug, when we manipulated mosquitoes. We did rough counts at $400 \times$ in the samples scanned for *Bodo*, and then used five density categories: none, low, medium, high, and extremely high (0, 1–5, 6–99, 100–500, >500 cells per 0.004 µl of concentrated fluid).

At the end of the experiment, we collected and measured the 60 leaves, (length, maximum diameter), and then filtered the contents through an 85 µm mesh. We counted the mosquitoes, midges, mites, and head capsules of other arthropods (resources) at $25 \times$ power.

Statistical analysis

We tested for effects of our manipulations, along with three covariates, on three measures of dynamics: mean abundance, persistence and temporal variability of the three microfaunal taxa. Estimates of abundance, persistence and temporal variability were obtained for each taxon in each leaf (time series of 20 sampling dates over 64 days).

Population persistence was defined as the maximum number of days between the appearance of a taxon and its disappearance, over the entire time series. Disappearance was defined as three consecutive zero counts. For the estimation of mean abundance and temporal variability, we divided the time series into two time periods: before (40 days) and after (22 days) the mosquito manipulation. Mean abundance was the average, and temporal variability the coefficient of variation (CV), of counts over each period. As sampling variability inflates estimates of temporal variability (McArdle and Gaston 1995, Stewart-Oaten et al. 1995), we used a linear mixed effects model to separate the within and between date variance components, and then used only the between dates component to calculate CV.

We used a mixed effects analysis to test for effects on persistence and a mixed effects repeated measures analysis (pre- and post-mosquito manipulation) for abundance and CV. Zone was treated as a random effect, and treatments and covariates within zone were fixed effects. We used a consistent structure in our statistical models, first entering covariates to remove the effects of other possibly correlated factors, and then testing for treatment effects. Covariates were natural levels of mosquito colonization, midge colonization and resources. Abundance was added as a covariate to the persistence models, so as to test for effects on persistence after removing the correlation between persistence and abundance. We tested other orders, but order of entry made little quantitative difference, and no difference to any conclusions drawn. F-tests on deviances, scaled by their degrees of freedom, were used to assess the significance of explanatory variables (Venables and Ripley 1999).

Covariates were estimated as follows: colonization by mosquitoes was a categorical variable based on the deviation from expected mosquito densities based on manipulations. We classified leaves as those with (i) mortality (fewer mosquitoes than expected), (ii) little colonization or mortality (0 to 2 'extra' mosquitoes), or (iii) significant colonization (3 or more 'extra' mosquitoes). Natural resource level was a continuous variable, calculated as the difference between the observed and expected (based on ant additions) number of head capsules. Midge colonization was simply the number of larvae found at the end of the experiment.

Mean abundance and persistence appeared to follow an over-dispersed Poisson distribution with many small values and a few large values. We therefore log-transformed these response variables and assumed a Gaussian error distribution. In the analysis of abundance, we substituted the lowest estimated abundance for zeroes prior to transformation (Turchin 2003). Estimates of temporal variability (CV) tended to follow

a Gaussian distribution, so we used the raw estimates and assumed a Gaussian error distribution for these analyses. Bacterial density in the second period was analyzed using the same statistical model as for persistence.

Two leaves with aberrant mosquito densities were excluded from all analyses (a leaf with 0 mosquitoes should have had 10, and one with 15 should have had 0). Models were sensitive to the inclusion of a leaf with uncommonly high midge densities (88 when next highest was 65), it was therefore also excluded. Diameter was not obtained for three leaves, and thus these were excluded from analyses of abundance and variability, but retained for the analyses of persistence time. Only occupied leaves were used for analyses of CV and persistence.

Results

The microflagellate, *Bodo*, was both the most abundant and the most widely distributed of the three microfaunal taxa, occurring in all of the leaves examined. The ciliate, *Cyclidium*, and the rotifer, *H. rosa*, were found in 45% and 73% of the leaves respectively (Table 1). *Bodo* populations were also the most persistent and least variable over time (Table 1). Leaves used in this study were from 87 to 189 mm long, petiole to tip, (mean $\pm$ sd 129 $\pm$ 19), and from 18 to 40 mm wide (mean $\pm$ sd 27 $\pm$ 5). An average of 24 ($\pm$ 17) midges (range 0 to 88), and 113 ($\pm$ 80) mites (range 14 to 450) were present in the leaves at the end of the experiment.

Enrichment (increased K) for the basal species (bacteria) in pitcher plant food webs can occur in two ways: more resources (captured arthropods) and/or higher decomposition rates (influenced by number of midges). We found a weak (non-significant), but positive relationship between number of ants added and bacterial counts ($r^2 = 0.17$, P $= 0.21$, Fig. 2b), and a strong
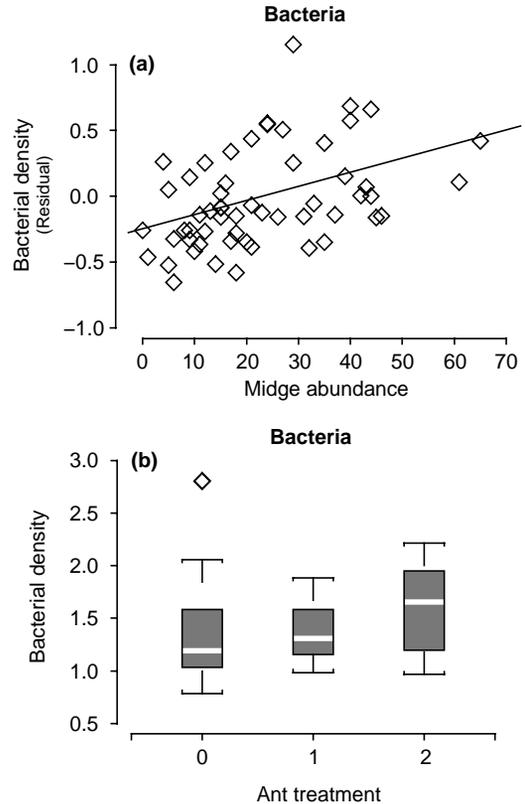

Bacteria

(a)

Bacteria

(b)

Fig. 2. Effects of midges and mosquitoes on bacterial density. Bacterial densities (a) increased with midges, and (b) increased (non-significant) with the addition of ants. Residuals are plotted (mean effect after the other factors have been entered into the model). Box plots illustrate the median (line), interquartile range of the data (box), tails of the distribution (bars = 1.5 × interquartile range), and outliers (points).

association between midge and bacterial abundance (P <0.001, Fig. 2a). The two forms of enrichment had differential effects on the microfaunal taxa. *Bodo* dynamics were only influenced by midges, *Cyclidium* only by resource additions, and *H. rosa* by both.

Effects on abundance

Enrichment affected the abundance of two taxa, *Bodo* and *Cyclidium*, but not the third, *H. rosa*. The highest abundance of *Cyclidium* occurred in the intermediate category of resource (ant) addition. Leaves with more midges had higher *Bodo* numbers (Table 2, Fig. 3a).

Mosquitoes influenced the abundances of *Bodo* and *H. rosa*, but not *Cyclidium*. Addition of mosquitoes depressed abundances of *Bodo* (Fig. 3b), and *H. rosa* was less abundant in leaves colonized naturally by mosquitoes (Fig. 3c, Fig. 4). Natural colonization by mosquitoes correlated positively with bacterial densities (P = 0.02), whereas the mosquitoes added to leaves

Table 1. Population size and stability parameters for the 60 study populations of *Bodo*, *Cyclidium* and *H. rosa*. Incidence: proportion of leaves occupied by a taxon. Mean density: number per ml. Mean abundance: number per leaf. Temporal variability: CV calculated over sampling dates (corrected for sampling variability). Persistence: the interval (in days) with consecutive non-zero counts. Summary statistics were calculated for each leaf, and then averaged across leaves. Temporal variability and persistence were calculated only for occupied leaves.

	Bodo	*Cyclidium*	*H. rosa*
Incidence	1.0	0.45	0.73
Density (SE)	9.24×10^4 (1.4×10^4)	145 (50.7)	22.5 (5.05)
Abundance (SE)	7.40×10^5 (1.3×10^5)	959 (301)	243 (54.5)
Temporal variability (SE)	1.22 (0.06)	1.45 (0.39)	1.85 (0.22)
Persistence (SE)	43.9 (2.1)	6.81 (1.22)	14.45 (2.10)

Table 2. Results of models testing for effects of resource and predator manipulations (Ant trt, Mosq trt) on the log abundance of microfauna for the pre- and post-mosquito manipulation periods. Covariates were mosquito colonization (Mosq col), natural resource level (Nat resource), and midge colonization (Midge). Significant values in bold.

|	NDf	*Bodo*			*H. rosa*			*Cyclidium*		
		DDf	F value	Pr(F)	DDf	F value	Pr(F)	DDf	F value	Pr(F)
NULL	1	49			49			42		
Period	1	49	77.24	**0.0001**	49	5.20	**0.03**	NA	NA	NA
Mosq col	2	45	1.24	0.30	45	9.65	**0.0003**	42	0.44	0.65
Nat resource	1	45	0.23	0.64	45	2.32	0.13	42	1.12	0.30
Midge	1	45	10.93	**0.002**	45	0.001	0.98	42	1.31	0.26
Ant trt	2	45	0.01	0.98	45	0.089	0.91	42	3.15	**0.05**
Mosq trt	2	45	3.00	0.06	45	1.431	0.25	NA	NA	NA
Period ×Ant trt	2	49	0.25	0.78	49	2.349	0.11	NA	NA	NA
Period ×Mosq trt	2	49	2.75	0.07	49	0.047	0.95	NA	NA	NA
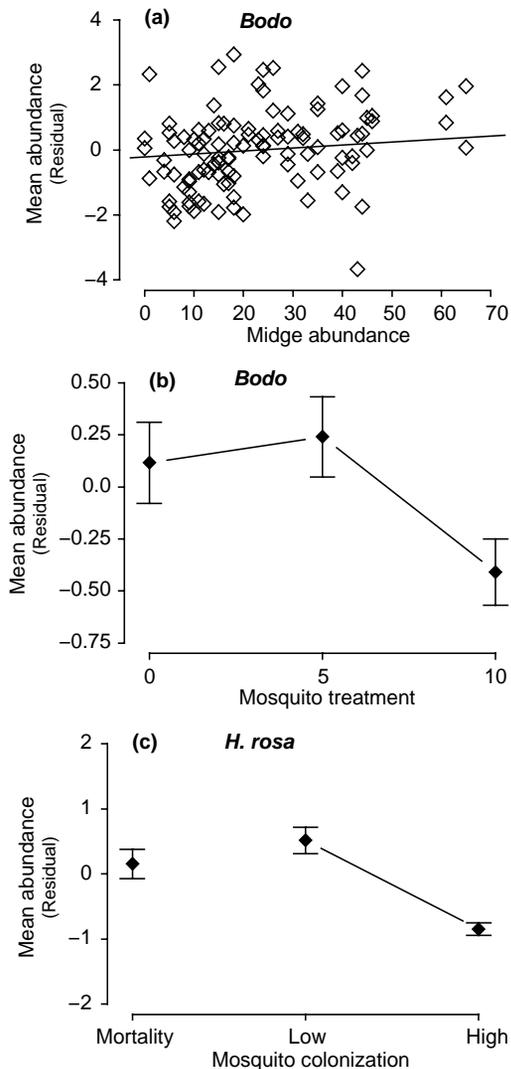
Fig. 3. Effects of midges and mosquitoes on abundance. *Bodo* abundance (a) increased with midges, and (b) was lower where mosquitoes were added. (c) *H. rosa* abundance was lower where mosquitoes had colonized. Residuals are plotted (mean effect ±SE after the other factors have been entered into the model, see Table 2). Mosquito manipulations were the addition of 0, 5, or 10 larvae.

partway through the experiment reduced bacterial density (P =0.03).

Effects on persistence and temporal variability

Enrichment was not destabilizing for *Bodo* populations; *Bodo* persisted longer in leaves with more midges (Table 3, Fig. 5a). Mosquitoes tended to decrease the persistence of *Bodo*, but effects were statistically marginal (mosquito colonization: P =0.09, and mosquitoes additions: P =0.08).
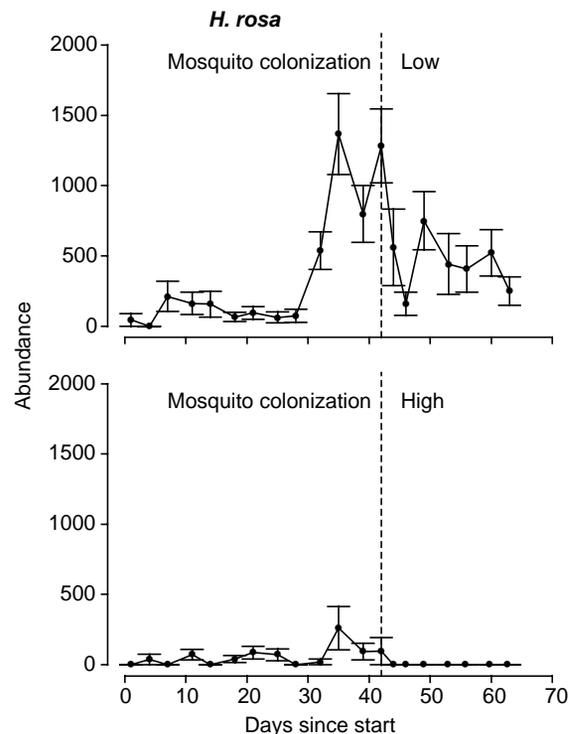

Fig. 4. Temporal dynamics of *H. rosa* at Low (0–2 larvae) and High (>2 larvae) levels of mosquito colonization. Points are the average abundance (±SE) across leaves within each category. Dotted line indicates when mosquitoes were manipulated.

Table 3. Results of models testing for effects of resource and predator manipulation on the persistence (log transformed) of microfaunal populations. Covariates were mosquito colonization (Mosq col), natural resource level (Nat resource), and midge colonization (Midge). Significant values in bold.

			Bodo			*H. rosa*			*Cyclidium*	
	NDf	DDf	F value	Pr(F)	DDf	F value	Pr(F)	DDf	F value	Pr(F)
NULL	1	30			11			13		
Mean abundance	1	30	2.08	0.16	11	46.33	**0.0001**	13	6.11	**0.03**
Mosq col	2	30	2.63	0.09	11	12.30	**0.002**	13	0.25	0.78
Nat resource	1	30	0.06	0.81	11	0.06	0.81	13	0.41	0.53
Midge	1	30	8.41	**0.007**	11	2.84	0.12	13	0.00	0.99
Ant trt	2	30	3.16	0.06	11	4.63	**0.03**	13	2.02	0.17
Mosq trt	2	30	2.72	0.08	11	1.99	0.18	13	0.26	0.78
Midge ×mosq trt	2	30	1.24	0.31	11	3.03	0.09	13	NA	NA
Midge ×mosq col	2	30	0.45	0.64	11	6.07	**0.02**	13	NA	NA
Ant trt ×mosq trt	4	30	2.11	0.10	11	0.89	0.50	13	NA	NA
Ant trt ×mosq col	4	30	0.80	0.53	11	4.69	**0.02**	13	NA	NA

Enrichment and mosquitoes influenced the persistence of *H. rosa*, but there were interactions between resource-related factors and mosquitoes (Table 3). Persistence was lower where ants were added, but only in leaves where few mosquitoes had colonized (Fig. 5b). In leaves where mosquito colonization was high, adding resources increased persistence. Overall, mosquito colonization lowered persistence, but not in leaves with very few midges (Table 3). Mosquitoes also increased the temporal variability of *H. rosa* populations (Table 4, Fig. 5c).

Discussion

We found that variation in food web structure affected the stability (persistence) of microfaunal populations in pitcher plants leaves. There has been much debate over what constitutes a stable or regulated population (reviewed by Mueller and Joshi 2000, Murdoch et al. 2003, Turchin 2003), and current views of regulation include a stochastic stable equilibrium (with densities that form a stationary probability distribution) and stochastic boundedness (May 1973, Chesson 1978, 1982, Turchin 1995, 2003, Murdoch et al. 2003). We use persistence as a measure of stability, as persistence is implicit in both definitions; a regulated population is one that neither reaches zero nor shows unlimited growth. Persistence time has been used as a measure of stability by both theoreticians and empiricists (Ludwig 1975, 1976, Turelli 1978, Burkey 1997, Holyoak 2000, Mueller and Joshi 2000), and there are further links, as at least some factors influencing stability in simple dynamical models (e.g. growth rate, carrying capacity, dispersal) also influence persistence time (Ludwig 1996, Hill et al. 2002). The relationship between regulation and temporal variability is not a simple one (Nisbet and Gurney 1982), though it is often assumed that less regulated popula-

tions fluctuate more and thus are more prone to extinction (Inchausti and Halley 2003).

Food web structure in this study varied in two important respects: number of mosquitoes (omnivorous predators) and degree of enrichment, determined partly by the number of captured insects and partly by the activity of colonizing midges (Fig. 1). Omnivore effects were generally destabilizing (decreasing persistence and sometimes increasing variability), but enrichment could be stabilizing or destabilizing depending on the number of mosquitoes. Thus, what we have shown in this study is that one consequence of variation in food web structure in pitcher plant communities (caused by variable colonization and capture rates) is variation in the stability of local microfaunal populations.

Bottom-up (enrichment) effects on dynamics

Theory suggests that in simple consumer–victim interactions, enrichment should be destabilizing (Rosenzweig 1971). Many models, however, predict a reversal in the effect of enrichment on stability, depending on aspects of community structure (Arditi and Ginzburg 1989, Ruxton et al. 1992, Jansen 1995, Abrams and Walters 1996, Huxel and McCann 1998, Fussman and Heber 2002), and there is mounting empirical evidence for some of these predictions (McCauley and Murdoch 1990, Murdoch et al. 1998, Morin 1999).

We found the paradox of enrichment emerging in one case: increasing resources by adding ants lowered average persistence time (without affecting mean abundance) for the rotifer, *H. rosa* in communities with few or no colonizing mosquitoes. For communities with significant levels of mosquito colonization, however, adding ants increased persistence of *H. rosa*. Thus, as suggested recently (Kaunzinger and Morin 1998), omnivory can eliminate the paradox of enrichment.
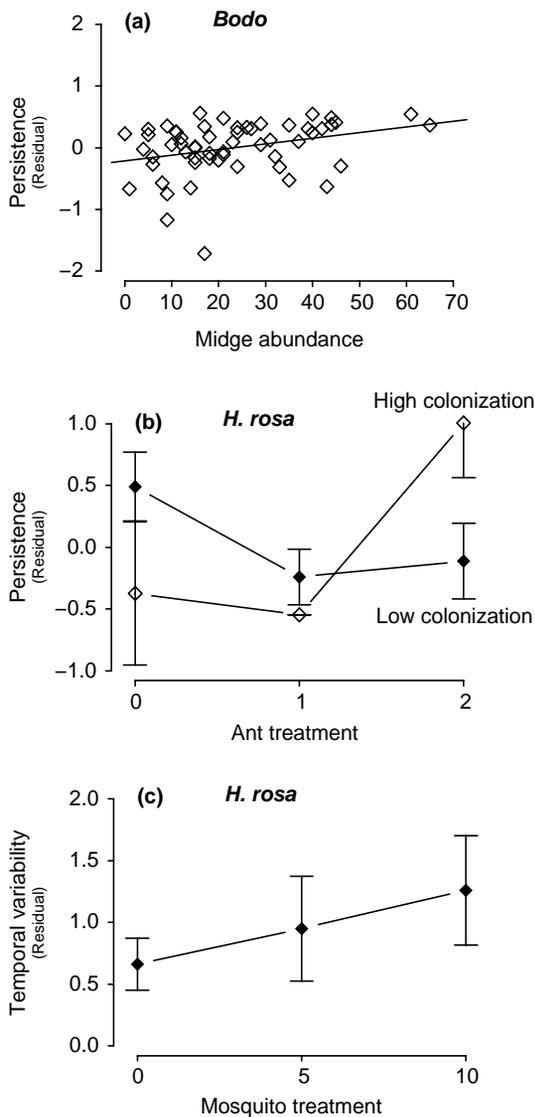
Fig. 5. Food-web effects on the persistence and temporal variability of *Bodo* and *H. rosa* populations. (a) The effect of midges on the persistence of *Bodo* populations. Residuals are plotted (effect after the other factors have been entered into the model, see Table 3). (a) Resource additions reduced persistence when colonization by mosquitoes was low, but increased persistence when mosquitoes were abundant. Ants were added 0, 1 and 2 bi-weekly. (b) Adding mosquitoes increased the temporal variability of *H. rosa* populations. Mosquito manipulations were the addition of 0, 5, or 10 larvae.

No paradox of enrichment was found for *Bodo* or *Cyclidium*. Enrichment had no effect on the persistence of *Cyclidium*. Persistence of *Bodo* was positively correlated with midge abundance, however, which was, in turn positively correlated with bacterial density. In pitcher plants, resource availability depends not only on the number of captured insects within the leaves, but also on the shredding activity of midges (Heard 1994, Fig. 2a).

Similar effects of shredding invertebrates (increased bacteria due to increased surface area of smaller particles) occur in other aquatic systems (Merritt et al. 1984). A pattern of increased stability with enrichment is not often demonstrated, but is consistent with some empirical results from aquatic systems where enrichment failed to destabilize dynamics (McCauley and Murdoch 1990, Murdoch et al. 1998). No relationship (Morin 1999) and a non-linear relationship between enrichment and persistence (Diehl and Feißel 2000) have also been observed. Clearly, empirical results indicate that the effect of enrichment on stability is variable, and depends on the specifics of the food web interactions. Theory concurs, indicating that the paradox of enrichment may disappear with the inclusion of heterogeneity in edibility or vulnerability to predators, competitive interactions among consumer species, or spatial refuges (Abrams 1993, Grover 1995, Scheffer and de Boer 1995, Leibold 1996, McCann et al. 1998, Murdoch et al. 1998, Morin 1999). While we can only speculate as to which explanation might be most relevant to the pitcher plant fauna of this study, the microfaunal consumer level is clearly heterogeneous (different growth rates and food preferences), as is the basal level (various bacterial types: Cochran-Stafira and von Ende 1998, Fox 2002), and the activity of midges may further alter the composition of the bacterial guild. In addition, there is likely competition among some microfauna (e.g. *Bodo*, *Cyclidium*, Cochran-Stafira and von Ende 1998).

Top-down (predator) effects on dynamics

The top predator in pitcher plant communities is the omnivorous mosquito, which feeds on microfauna and bacteria. Its effects were strongest on the rotifer, *H. rosa*, where colonizing mosquitoes decreased persistence times, and mosquito additions increased temporal variability. Our results are thus consistent with simple models predicting a destabilizing effect of omnivory (Pimm and Lawton 1978), and with laboratory experiments that showed omnivores increasing the temporal variability of protist populations (Lawler and Morin 1993). In addition, *Cyclidium* disappeared at or just after the peak oviposition period for mosquitoes. We do not know if predation was the cause, but mosquitoes are capable of causing extinctions in ciliate and other protist populations (Maguire et al. 1968, Addicott 1974). Mosquitoes (both colonizing and manipulated) also tended to decrease persistence times for *Bodo* populations. Instability and local extinctions may, in fact, be common for prey of generalist predators in aquatic systems (Murdoch and Bence 1987, Blaustein et al. 1995), particularly where predator generation times are much longer than those of their prey.

Table 4. Results of models testing for effects of resource and predator manipulations on the temporal variability (CV) of microfauna. A period effect indicates a difference between pre- and post-mosquito manipulation periods. The effects of sampling variability were removed prior to analysis. Covariates were mosquito colonization (Mosq col), natural resource level (Nat resource) and midge colonization (Midge). Significant values in bold.

		Bodo			*H. rosa*			*Cyclidium*		
	NDf	DDf	F value	Pr(F)	DDf	F value	Pr(F)	DDf	F value	Pr(F)
NULL	1	48			25					
Period	1	48	14.46	**0.0004**	15	2.73	0.12	NA	NA	NA
Mosq col	2	45	1.24	0.30	25	0.13	0.88	12	0.20	0.82
Nat resource	1	45	0.03	0.86	25	0.20	0.66	12	0.20	0.66
Midge	1	45	0.45	0.51	25	0.27	0.61	12	0.11	0.75
Ant trt	2	45	0.76	0.47	25	1.11	0.35	12	1.08	0.37
Mosq trt	2	45	0.07	0.94	25	0.55	0.58	NA	NA	NA
Period × ant trt	2	48	0.95	0.39	15	0.29	0.75	NA	NA	NA
Period × mosq trt	2	48	0.18	0.83	15	3.83	**0.05**	NA	NA	NA

Conclusions

Both top-down and bottom-up factors influence the stability of pitcher plant microfaunal populations. Top-down (omnivorous mosquito) effects are strong and destabilizing for *H. rosa* and perhaps *Bodo* populations. Bottom-up (enrichment) effects are more variable. Indirect effects of midges on bacterial densities stabilize *Bodo* dynamics. Increasing resources either stabilizes or destabilizes *H. rosa* populations, depending on the predator regime. These results are broadly consistent with food web theory that suggests that omnivory and other food web complexities can eliminate the paradox of enrichment seen in simpler food webs.

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