



Do macroconsumers affect insect responses to a natural stream phosphorus gradient?

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Abstract

We assessed the role of macroconsumers (e.g. fishes and shrimps) in affecting the response of insect assemblages to a natural phosphorus gradient formed by six streams with different phosphorus levels (range 12–350 $\mu\text{g/l}$). We hypothesized that insect responses to the phosphorus gradient would be strongest in the absence of macroconsumers. Within each stream, macroconsumers were allowed access to, or were excluded from, leaf packs using electric ‘fences’. Macroconsumers did not have significant effects on insects, but there was a significant phosphorus effect. Insect assemblages in high-phosphorus streams had 3–12-fold greater biomass and 3–11-fold greater abundance than assemblages in low-phosphorus streams. We also found that insect responses to phosphorus were more variable when assessed on the natural benthic substrate (e.g. mixed detritus) than in standardized leaf packs. In both substrates, the relationship between insects and phosphorus was not linear: abundance and biomass increased with phosphorus concentration to an asymptote. This suggests that insects were responding to a food resource gradient (e.g. fungi and bacteria). The Michaelis–Menten model provided a good fit for the relationship between insects and phosphorus concentrations, with half-saturation constants ranging from 12 to 60 $\mu\text{g SRP/l}$. The asymptotic relationship observed between phosphorus and insects suggests that phosphorus saturation occurred above a threshold of ca. 100 $\mu\text{g SRP/l}$. Our results provide support for the hypothesis that detritus-based food webs are mainly controlled by bottom-up forces.

Introduction

The relative importance of resources (bottom-up) versus predators (top-down) in controlling population dynamics has been the subject of much discussion in ecology (e.g. Hairston et al., 1960; Ehrlich & Birch, 1967). Ecologists now recognize that most populations are simultaneously influenced by both bottom-up and top-down controls (e.g. Carpenter et al., 1987; Hunter & Price, 1992; Belovsky & Joern, 1995; Osenberg & Mittelbach, 1996). This position is supported by studies on autotrophic-based food webs, in both terrestrial (e.g. Hunter et al., 1997; Stiling & Rossi, 1997; Forkner & Hunter, 2000) and aquatic ecosystems (e.g. McQueen et al., 1986; Leibold, 1989;

Hansson, 1992; Rosemond et al., 1993). In addition, food web theory predicts that the strength of top-down forces should increase as basal productivity in the ecosystem increases (Oksanen et al., 1981). Although this prediction remains to be thoroughly tested, there is supporting evidence from terrestrial ecosystems (Uriarte & Schmitz, 1998; Forkner & Hunter, 2000). While the relative roles of bottom-up and top-down forces in controlling populations of intermediate consumers has been extensively studied in autotrophic-based food webs, less is known about how they operate in detritus-based food webs (Polis, 1994; Polis & Strong, 1996). In detritus-based food webs, resources for basal trophic levels come from outside the ecosystem (e.g. plant litter), and their renewal is

not related to food web structure. Therefore, food web theory proposes that detritus-based ecosystems are mainly controlled by bottom-up forces and that predators should not strongly affect their prey (Hairton et al., 1960; Pimm, 1982; Bengtsson et al., 1995). In addition, changes in the productivity of the basal trophic level should not affect the effects of predators on their prey.

In streams, fishes and large-sized invertebrates (e.g. shrimps and crayfishes) are dominant macroconsumers (e.g. large-size consumers relative to other consumers, such as insects) at the top of the food web that consume a large proportion of insect production (Hynes, 1970; Hury, 1996). Studies assessing the role of macroconsumers in streams have shown that they can play important roles in controlling benthic insect assemblages, algal biomass, and sediment accumulation (e.g. Flecker, 1992; Power, 1992; Pringle & Hamazaki, 1997; Pringle & Hamazaki, 1998). However, most of these studies have been conducted in algal-based systems in relatively large streams that receive high light. The few studies that have been run in detritus-based ecosystems indicate that macroconsumers have weaker effects on benthic insects than they do in algal-based ecosystems (e.g. Flecker, 1984; Rosemond et al., 1998). Evidence also exists that the role of resources in controlling insect assemblages is more important than that of predators in detritus-based streams. In tropical streams, Rosemond et al. (2001) found that positive bottom-up effects of phosphorus on insect density were greater than negative top-down effects of macroconsumers.

In this paper, we build on results from our previous studies, which have shown that streams draining a volcanic landscape in Costa Rica vary in their natural phosphorus concentrations (Pringle, 1991; Pringle, unpublished data). Studies along phosphorus gradients, formed by different streams, showed that microbial respiration rates, detritus decay rates, and insect densities are positively affected by phosphorus (Ramírez, 2001; Rosemond et al., 2002; Ramírez et al., 2003). Here, we assess whether the presence of macroconsumers affect the response of benthic insect assemblages to a phosphorus gradient formed by streams with different phosphorus concentrations. We predict that insect abundance and biomass will increase along the gradient in the presence of macroconsumers, as previously found (Rosemond et al., 2002). However, we expect the magnitude of the response to be stronger in the absence of macroconsumers. Secondly, we also measure the response of

insect assemblages on the natural substrate of mixed leaf detritus, as opposed to a standard leaf substrate in the macroconsumer manipulation, to the phosphorus gradient. Previous studies have shown weaker and more variable biotic responses to phosphorus when using the natural benthic substrate (Ramírez, 2001; Ramírez et al., 2003) *versus* a standard substrate. Therefore, we hypothesize that insects in the natural benthic substrate will show weak responses to phosphorus concentrations, as substrate heterogeneity could potentially introduce enough variability in insect density to swamp any effects of phosphorus.

Methods

This study was conducted at La Selva Biological Station, owned and operated by the Organization for Tropical Studies. La Selva is located on the Caribbean slope of Costa Rica (10° 26' N, 84° 01' W) and protects 1536-ha of lowland tropical wet forest. The station receives almost 4000 mm of rainfall a year, with a wet season (>400 mm/mo) occurring from May to November (Sanford et al., 1994). Depending on their location in the landscape, some streams at La Selva receive inputs of geothermally modified groundwater that alter stream chemical characteristics (Pringle, 1991). Groundwater is modified by volcanic activity at high elevations, cools and is diluted as it moves downhill, and finally enters lowland streams as geothermally modified groundwater. One of the main signatures of modified groundwater is high concentration of solutes (e.g. phosphorus, sodium, and chloride; Pringle et al., 1993). For microbial communities colonizing detritus, phosphorus appears to be a key solute provided by geothermally modified groundwater (Rosemond et al., 2002; Ramírez et al., 2003). The dense riparian vegetation along streams results in light-limited algal communities (Pringle et al., 1986) and detritus-based food webs.

For the present study, we chose six streams with different inputs of geothermally modified groundwater that ranged in soluble reactive phosphorus (SRP) from 12 to 350 $\mu\text{g/l}$ and differed in water conductivity (Table 1). All streams were of low order (~2nd–3rd), located in close proximity to each other, and surrounded by primary forest. The dominant stream substrates were detritus and fine sediments, with boulders present at some sites. In addition, while large-order streams at La Selva support a diverse assemblage of fishes and shrimps, the low-order streams we focus on in

Table 1. Characteristics of the study streams at La Selva Biological Station, ordered by decreasing levels of soluble reactive phosphorus (SRP). All variables were determined at the beginning of the experiment. GMG = geothermally modified groundwater, calculated following Genereux & Pringle (1997)

	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper
Elevation (m)	30	30	60	60	60	30
Discharge (l/s)	160	760	110	520	250	30
Mean temperature (°C)	26	26	26	26	25	26
SRP ($\mu\text{g/l}$)	352	227	126	42	22	12
NO ₃ ($\mu\text{g/l}$)	211	202	164	263	225	183
Conductivity ($\mu\text{S/s}$)	297	158	88	28	23	23
pH	6	6	6	5	6	5
%GMG	32	14	8	0	0	0

this study are characterized by a subset of those assemblages. For example, of the more than 40 species of fishes recorded at La Selva (Bussing, 1994), approximately 10 can be found in each of our study streams (e.g. Burcham, 1988). In addition, low-order streams support lower fish densities (Burcham, 1988).

We assessed effects of macroconsumers (i.e. fishes and shrimps) on benthic insect assemblages along a gradient in phosphorus concentrations by excluding macroconsumers from small areas of the stream bottom. We used a modification of the electric exclusion technique described by Pringle & Blake (1994). Previous studies at La Selva showed that, when using a 12-volt electric source, this technique successfully excludes organisms larger than 1 cm in length without affecting insects and other small invertebrates (Pringle & Hamazaki, 1997; Pringle & Hamazaki, 1998; Rosemond et al., 1998). A complete description of the modified technique can be found in Pringle & Hamazaki (1997).

Since water conductivity can alter the efficacy of the electric exclusion, we tested the technique in the stream with the highest (Arboleda, conductivity: 297 $\mu\text{S/s}$) and lowest conductivity (Piper, conductivity: 23 $\mu\text{S/s}$). The test consisted of attaching pieces of fruit to a rock in the middle of the exclusion and control treatments, counting the number of fishes foraging on the fruit over a 10-min interval, and then repeating the process three times.

During July 1998, we set up one electric (fish and shrimp exclusion treatment) and one control treatment in each of the six streams along a phosphorus gradient. In this study, we sacrificed subsampling within one stream (e.g. setting up more than one electric and control device at each stream) to be able to include several

streams (e.g. replicates) in the analyses and obtain a landscape perspective. Treatments consisted of quadrats that were set up in areas of slow flow (flow range: 0 to 0.1 m/s; depth range: 40–50 cm), where leaves were the dominant benthic substratum. The quadrats were constructed with 2-cm diameter poly-vinyl chloride (PVC) pipe in the shape of a square (0.25 m²). A 12-volt solar electric fence charger (Parker-McCrory®) powered the electric treatment. Because of the closed canopy, batteries were recharged in the laboratory and replaced every three days. Control and exclusion treatments were identical, but controls were not connected to a fence charger.

To provide a standard substrate for insect colonization, we tethered one leaf pack (30 g) in each treatment with binder clips and monofilament line. Leaf packs were made with leaves of *Ficus insipida* Willd. (= *glabrata* HBK), which is a dominant riparian tree in lowland Central America (Hartshorn, 1983). Newly abscised leaves were collected from the ground, dried at room temperature, and stored in an air-conditioned room for 1 month before the beginning of the experiment.

The experiment was run for 15 d to allow insects time to colonize leaf packs (Rosemond et al., 1998). Leaves were retrieved using a 250- μm mesh net to capture insects detached from the leaves. At the same time, three core samples (0.006 m² each) were collected from the vicinity of the experimental area to assess insect assemblages in the natural benthic substrate (e.g. mixed detritus). Samples were preserved in formalin (ca. 5%) and insects were removed from organic material using a dissecting microscope, under 10 \times . Insects were identified to the lowest taxonomic level possible (genus for most orders, except Diptera which were identified to family or sub-family). Biomass was estimated by measuring the length of each individual to the closest 0.5 mm and by applying length - mass relationships (Benke et al., 1999) derived from insects of similar morphology and typically from the same family.

Insect abundance and biomass were analyzed by dividing total densities into two categories: Chironomidae (Diptera) and remaining insects (non-chironomids). We analyzed the family Chironomidae independently because it was a major component of insect assemblages in all study streams and, in contrast to other insect larvae, chironomids live within leaf tissue as well as outside it by building retreats (Ramírez & Pringle, 1998; Rosemond et al., 1998). Taxon rich-

ness was determined as the total number of different taxonomic groups found (e.g. family or genus).

Nutrient concentrations were measured in two water samples collected from each stream at the beginning of the experiment. Samples were filtered (0.45 μm Millipore filters) and maintained frozen until analyzed at the University of Georgia, U.S.A. Nitrate ($\text{NO}_3\text{-N}$) and phosphorus (as soluble reactive phosphorus, SRP) concentrations were measured using continuous flow colorimetry and an Alpkem RFA 300 Colorimetric analyzer. The cadmium reduction and the ascorbic acid methods were used for nitrate and SRP, respectively (APHA, 1992).

Macroconsumer abundance at all study streams was assessed at the end of the experiment. Macroconsumers were collected from a 10 to 15 m reach that included the area where the experiment was located. Each reach was blocked upstream and downstream using seine nets (0.5 cm mesh) and the area was electroshocked three times. Fishes and shrimps were identified, counted, and released at each stream. Abundance was calculated as the total number of fishes after the three passes per stream area. Each fish species was assigned to a feeding group based on food preferences reported by Burcham (1988) and Bussing (1993, 1994).

Macroconsumer impacts on insects in each stream were assessed using a predator impact index ($\text{PI} = \text{Ln}(\text{insect density in control}/\text{insect density in exclusion})$, Cooper et al., 1990), which accounts for difference in predation pressure among streams. We anticipated a lack of correlation between macroconsumer density and PI due to the similarity in fish densities among streams. If that proved to be the case, then data were analyzed using treatment (i.e. macroconsumer exclusion and control) as the test variable, phosphorus as a covariable, and streams as replicates ($n = 6$). We used the generalized linear model procedure in SAS (proc genmod, log link function, poisson probability distribution, type 3 analysis; SAS Institute, Cary, North Carolina, U.S.A.) because we did not expect a linear response between insects and phosphorus (Rosemond et al., 2002). We run the analyses twice, first including an interaction factor between treatment and phosphorus and then without including this interaction. If the interaction was not significant we based our interpretation of the results on the second analysis (i.e. without the interaction), as it generally has a better log-likelihood (Agresti, 1984).

The relationship between insects and SRP was expected to be non-linear (e.g. Rosemond et al., 2002);

therefore, these parameters were fitted to a Michaelis–Menten model of enzyme-catalyzed reactions (Stryer, 1981). The model has the following form:

$$V = V_{\text{max}}([S]/([S] + K_m)),$$

where, for our purposes, V represents insect abundance or biomass, $[S]$ is the phosphorus concentration, V_{max} is the maximum rate of insect abundance or biomass accumulation, and K_m is the phosphorus concentration at which we obtain half the maximum value for insect abundance or biomass. The model was fitted to untransformed data using the iterative, least-squares non-linear fitting function in JMP (Version 4.0.4, SAS Institute, Cary, North Carolina, U.S.A.).

Results

Community composition

Abundance of macroconsumers that consumed aquatic insects (i.e. omnivores and predators of aquatic insects) ranged from 0.09 m^{-2} in Arboleda to 1.10 m^{-2} in Piper, whereas total abundance of all macroconsumers ranged from 0.22 to 1.50 m^{-2} (Table 2). Abundance of macroconsumers was not correlated with phosphorus concentrations ($r = -0.24$, $P > 0.10$). Fish assemblages were composed of 4–7 species in each stream (Table 2). Shrimps were represented by only one species, *Macrobrachium carcinus* (omnivore), which was found in all streams except Arboleda and Sura-30 (Table 2). However, it is likely that this species also occurs in those streams, but in relatively low densities.

Insects were the dominant group of invertebrates and insect assemblage composition was similar among study streams (Table 3). The family Chironomidae (Diptera) comprised the largest proportion of all insect taxa in terms of abundance. Ceratopogonidae (Diptera) and the genera *Caenis*, *Farrodes*, and *Leptohyphes* (Ephemeroptera) were also common in all streams (Table 3). Insect composition was also similar among substrate types, except for Trichoptera and Coleoptera that represented a larger proportion of the insect abundance in the natural benthic substrate relative to *Ficus* leaves (Table 3).

Efficacy of exclosures

Observations of fish behavior in control and exclusion treatments indicated that the electric exclusion

Table 2. Abundance of macroconsumers (i.e., fishes and shrimps; No. m⁻²) at all study sites. Feeding groups were assigned based on Burcham (1988) and Bussing (1994). Insectivorous macroconsumers were divided in those that eat mainly terrestrial insects (T) and those that eat mainly aquatic insects (A).

Family/Species	Arboleda	Sura-30	Saltito	Salto	Sura-60	Piper	Feeding group
Characidae							
<i>Astyanax fasciatus</i>	0.03	0.13	0.02	0.06	0.05	0.20	Omnivorous
<i>Brycon guatemalensis</i>				0.01			Frugivorous
Poeciliidae							
<i>Alfaro cultratus</i>	0.43	0.13	0.29	0.03	0.04	0.40	Insectivorous (T)
<i>Neoheterandria umbratilis</i>		0.01	0.02				Omnivorous
<i>Phallichthys amates</i>	0.01						Omnivorous
<i>Poecilia gillii</i>	0.01						Algivorous
<i>Priapichthys annectens</i>	0.01	0.01	0.10		0.05	0.60	Insectivorous (A)
Cichlidae							
<i>Cichlasoma alfari</i>	0.01		0.08		0.02	0.05	Insectivorous (A)
<i>Cichlasoma dovii</i>			0.08	0.01	0.01	0.05	Insectivorous (A)
Shrimps/Decapoda							
<i>Macrobrachium carcinus</i>			0.06	0.11	0.07	0.15	Omnivorous
Totals							
Macroconsumers	0.52	0.31	0.67	0.22	0.25	1.50	
Aquatic feeding macroconsumers	0.09	0.19	0.38	0.18	0.21	1.10	

Table 3. Percent of the total insect taxa at the study sites that composed >1% of the total abundance in *Ficus* leaves samples (F) in the control treatment and in mixed litter in benthic samples (M) (i.e. both with macroconsumers present).

Taxa	Arboleda		Sura-30		Saltito		Salto		Sura-60		Piper	
	F	M	F	M	F	M	F	M	F	M	F	M
Ephemeroptera												
<i>Caenis</i>	0	10	13	3	4	0	0	3				
<i>Farrodes</i>			1	3			1	0				
<i>Leptohyphes</i>	1	0	9	15	6	4	10	3	3	0		
<i>Tricorythodes</i>			0	3							2	0
Odonata												
<i>Argia</i>	1	0	1	0	1	4	1	0	3	0	1	0
Coleoptera												
Elmidae larvae	0	1	1	9	1	4	1	3	1	0	1	45
Trichoptera												
Leptoceridae	0	0	0	21	0	0	0	0	0	4	0	0
Diptera												
Chironomidae												
Tanytopodinae	37	32	9	15	7	38	38	31	13	4	12	9
Others	59	54	62	21	76	44	45	57	74	82	56	36
Ceratopogonidae	0	3	1	3	3	6	2	3	1	7	12	0

technique was effective in excluding macroconsumers from foraging within the electric treatment. In addition, the efficacy was not affected by water conductivity. During our three observation periods in both high (Arboleda) and low conductivity (Piper) streams, several fishes entered the control (mean 0.3/ min, range 0–2/min) while none entered the exclusion treatment in either stream.

Macroconsumer and phosphorus effects on insects colonizing Ficus leaves

Macroconsumer PI on insects was variable among streams and strong effects were observed only on non-chironomid taxa in Arboleda and Piper, as indicated by the large negative values (Table 4). In addition, PI was not correlated to fish abundance (r ranged from -0.19 to 0.60 for different insect groups, $P > 0.10$).

Although fish densities were variable, streams were considered as replicates in this analysis, due to the lack of correlation between PI and fish abundance. Insect abundance and biomass did not differ significantly between control and exclusion treatments (Fig. 1). Generalized linear models showed that macroconsumers did not have significant effects on the abundance or biomass of Chironomidae or non-chironomid insects colonizing *Ficus* leaves. There were also no macroconsumer effects on mean insect size (Table 5). In contrast, phosphorus had a significant effect on Chironomidae abundance and biomass and on non-chironomid insect biomass (Table 5). The interaction factor between macroconsumers and phosphorus was not significant and exclusion of this factor from the analysis improved the log-likelihood of all analyses; however, it did not change the results with respect to macroconsumers (Table 5).

Insect assemblages and phosphorus effects

As expected, the relationship between phosphorus concentration and insects was asymptotic (Fig. 2), supporting the use of the Michaelis–Menten model of enzyme–substrate kinetics to describe the relationships. For insects colonizing *Ficus* leaves, the mean abundance and biomass in control and exclusion treatments was used in the models. The Michaelis–Menten model described the relationships fairly well for insects colonizing *Ficus* leaves, except for abundance of non-chironomidae (Fig. 2b). Insects in the natural benthic substrate showed more variation (Fig. 2), and the Michaelis–Menten model fitted well only

the abundance of non-chironomidae (Fig. 2f). Half-saturation constants (K_m) were around 35 and 45 $\mu\text{g SRP/l}$ for insect abundance and biomass in *Ficus* leaves, respectively (Table 6). Half-saturation constants (K_m) were more variable for insects in the natural benthic substrate, ranging from 13 to 61 $\mu\text{g SRP/l}$ for Chironomidae and non-chironomidae abundance and biomass (Table 6). Examination of the plots indicate that phosphorus saturation occurred around 100 $\mu\text{g SRP/l}$ (Fig. 2).

Discussion

Contrary to our hypothesis, macroconsumers did not significantly decrease insect abundance or biomass in the study streams. These results contrast to those reported previously in larger streams at La Selva Biological Station (Pringle & Hamazaki, 1997, 1998) and other tropical streams (Flecker, 1992, 1996), which have reported strong top-down control of fishes over insect assemblages. Although most studies on the role of macroconsumers in tropical streams comes from open canopy streams that are algal-based (Flecker, 1992, 1996; Pringle & Hamazaki, 1997, 1998), it is becoming clear that in detritus-based ecosystems macroconsumers may have weaker effects on insects than they do in algal-based systems. Rosemond et al. (1998) summarized data on macroconsumer effects on insects in detritus- and algal-based ecosystems, concluding that the strongest impacts occur in algal-based ecosystems. Moreover, a previous study at La Selva that experimentally manipulated phosphorus and macroconsumers in a large (e.g. 4th–5th order) stream indicated that phosphorus had a larger effect in controlling insect assemblages on leaves than did predators (Rosemond et al., 2001). A potential reason for weaker macroconsumer effects on insects in detrital systems is the higher availability of refuges in detrital areas (e.g. leaf litter) than on hard substrates where algae commonly grow. While our results support the above studies by showing that macroconsumer control on insects is negligible in detritus-based streams, it contrasts with findings of Rosemond et al. (2001) in that we found an almost complete lack of macroconsumer effects instead of weak effects. We hypothesize that the lower and more variable abundance of fishes and shrimps in our small interior forest streams, in comparison with mid-order streams in Rosemond et al. (2001), and the lack of subsampling within each

Table 4. Predator impact index (PI) of macroconsumer effects on Chironomidae and non-chironomid insects colonizing *Ficus* leaves in each stream.

	Chironomidae		Non-chironomid insects		Taxon richness
	Abundance	Biomass	Abundance	Biomass	
Arboleda	-0.23	-0.44	-0.84	-0.64	-0.64
Sura-30	0.39	0.14	-0.02	-0.02	-0.11
Saltito	0.30	0.27	-0.34	-0.14	-0.07
Salto	0.30	0.20	0.11	-0.46	-0.15
Sura-60	0.00	-0.33	0.05	0.32	-0.22
Piper	-0.03	0.66	-0.47	-0.97	-0.31

Table 5. Generalized linear models with and without the interaction term of the effects of macroconsumers on Chironomidae and non-chironomid abundance and biomass on *Ficus* leaves.

Treatment	Chironomidae				Non-chironomid insects				Mean size	
	Abundance		Biomass		Abundance		Biomass		X^2	p
	X^2	p	X^2	p	X^2	p	X^2	p		
Log-likelihood	178.3		75.3		174		83.5		203	
Macroconsumer	0.28	ns	0.14	ns	0.12	ns	4E-04	ns	0.08	ns
Phosphorus	3.52	ns	6.94	0.008	2.76	ns	4.19	0.04	4.21	0.04
Interaction	0.09	ns	0.25	ns	0.06	ns	0.09	ns	0.33	ns
Log-likelihood	198.2		82.3		194.7		93.1		219	
Macroconsumer	0.24	ns	0.004	ns	0.08	ns	0.21	ns	0.05	ns
Phosphorus	3.84	0.05	7.68	0.005	3.06	ns	4.84	0.03	4.57	0.03

stream in our study were all potential reasons for the difference among studies.

The relationship between insects and phosphorus suggests that insect assemblages are affected by phosphorus limitation over the natural phosphorus gradient. Insects collected on both substrates, *Ficus* leaves and mixed leaves, showed relationships with phosphorus concentrations. Several lines of evidence support the hypothesis that stream insects were responding to a gradient in food resources resulting from phosphorus in the La Selva landscape. First, previous studies at La Selva along a similar phosphorus gradient showed that microbial communities responded positively to increasing stream phosphorus concentrations. For example, fungal biomass on leaves and the decomposition rate of leaf litter increased along the natural phosphorus gradient (Rosemond et al., 2002), and microbial respiration, a measure of microbial activity, also increased along the gradient (Ramírez et al., 2003). Second, growth rates of insect collectors (i.e. Chironomidae) feeding on leaf litter were significantly higher under high phosphorus

conditions in the laboratory (Rosemond et al., 2001). Chironomids were also the dominant insect in our study streams. Finally, the relationship that we found between insects and phosphorus concentrations was an asymptotic curve similar to that found in studies assessing biotic responses to resource/productivity gradients (Tilman, 1982; Rosemond et al., 2002).

Previous studies at La Selva also found asymptotic responses of several biotic variables to the phosphorus gradient (Rosemond et al., 2002; Ramírez et al., 2003). Half-saturation constants in previous studies ranged from 3 to 12 $\mu\text{g SRP/l}$ for variables like ergosterol concentrations (an indicator of fungal biomass), decomposition rates of detritus, and microbial respiration (Rosemond et al., 2002; Ramírez et al., 2003). The half-saturation constants for insect assemblages that we found (range 12–60 $\mu\text{g SRP/l}$) are higher than those reported by Rosemond et al. (2002) for the biomass of insects colonizing *Ficus* leaves (7.26 $\mu\text{g SRP/l}$). A potential factor contributing to this difference is the larger number of streams used in Rosemond's study, which allowed for more

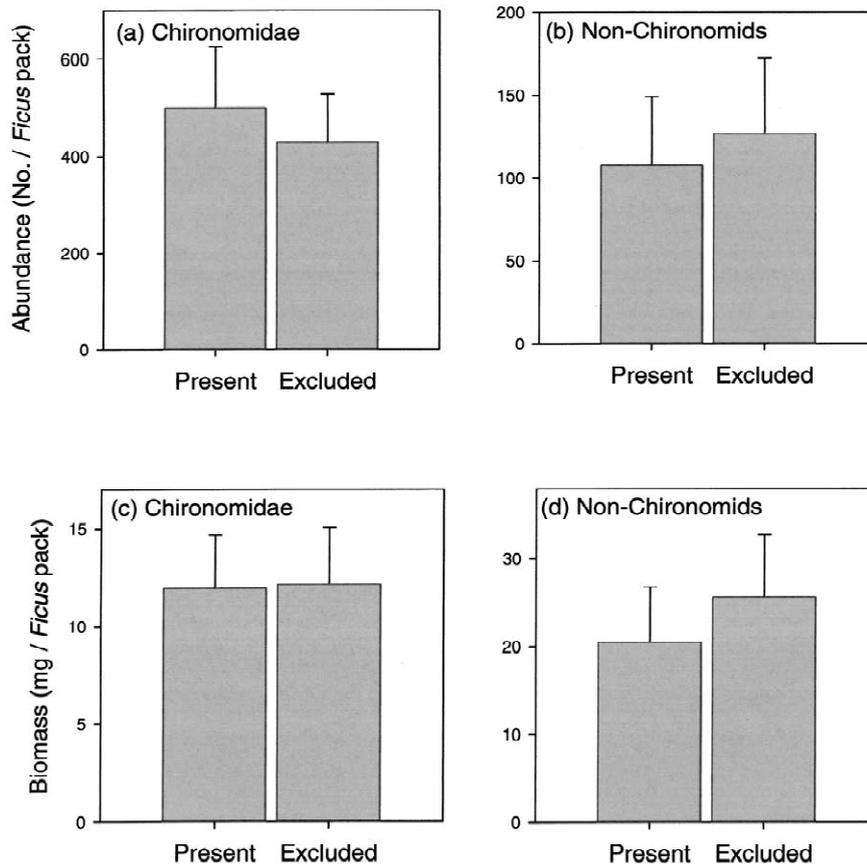


Figure 1. Abundance (a–b) and biomass (c–d) of Chironomidae and non-chironomid insects per leaf pack in control (present) and macroconsumer exclusion (excluded) treatments. Bars represent means ($n = 6$) \pm 1 S.E.

precise calculation of half saturation constants. In accordance with previous studies, results indicate that in the landscape of La Selva phosphorus saturation occurs above a threshold that ranges from 15 to 100 μg SRP/l depending on the variable measured.

Stream enrichment studies have shown the importance of phosphorus and nitrogen in enhancing the flow of carbon among trophic levels in food webs. In autotrophic-based food webs, phosphorus addition increases algal biomass and the amount of primary production available to insect herbivores, which results in higher herbivore biomass (e.g. Hart & Robinson, 1990; Peterson et al., 1993). Moreover, increases in fish biomass have also been related to phosphorus enrichment, via higher prey availability for fishes (Peterson et al., 1993; Harvey et al., 1998). Similarly, it has been hypothesized for detritus-based ecosystems that phosphorus is a critical element in enhancing the flow of carbon from detritus to detritivores and to higher trophic levels (Rosemond et al.,

2001). Our study supports this hypothesis by showing that insect assemblages in high phosphorus streams had 3–12-fold (benthos and *Ficus* leaves, respectively) greater insect biomass and 3–11-fold greater insect abundance than assemblages in low phosphorus streams. Observed changes in abundance and biomass are larger than those reported by most previous studies. For example, short-term enrichment experiments that increased phosphorus concentration above 85 $\mu\text{g}/\text{l}$ measured increases in insect abundance or biomass in the range of 2–4-fold (Elwood et al., 1981; Hart & Robinson, 1990; Rosemond et al., 2001). In contrast, long-term phosphorus enrichments report wider ranges in insect abundance (e.g. 0–40-fold) using lower concentrations of phosphorus (<50 $\mu\text{g}/\text{l}$; Peterson et al., 1993; Deegan et al., 1997; Harvey et al., 1998). Duration of the experimental manipulation seems to be an important factor determining the magnitude of insect responses to phosphorus enrichments. In comparison to our results, only long-term artificial

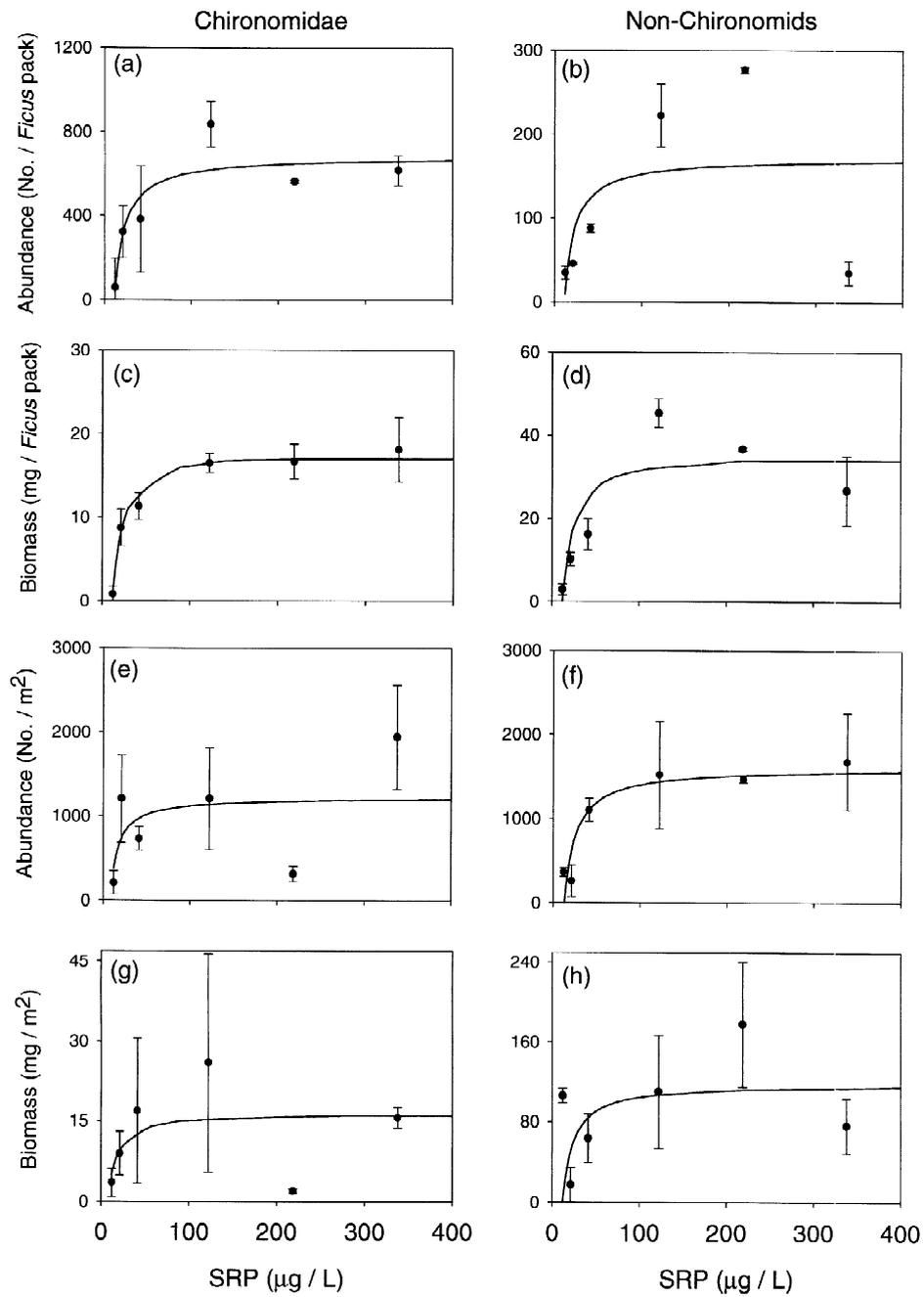


Figure 2. Relationship between phosphorus ($\mu\text{g SRP/l}$) concentrations and abundance and biomass of insects in *Ficus* leaves (a–d) and in natural mixed leaf substrate (e–h). Fitted curves are based on the Michaelis–Menten model of enzyme kinetics.

Table 6. V_{\max} and k_m resulting from fitting a Michaelis–Menten model to the relationship between insects abundance and biomass and phosphorus concentrations. V_{\max} is insects per *Ficus* leaf pack or insects per m² of stream bottom and K_m are in $\mu\text{g SRP per L}$.

	<i>Ficus</i> leaves				Mixed benthic substrate			
	V_{\max}	SE	K_m	SE	V_{\max}	SE	K_m	SE
Abundance								
Chironomidae	766.98	156.47	35.74	26.18	1275.9	509.29	17.52	30.55
Non-chironomids	193.38	97.79	34.8	63.57	2026.3	342.01	61.26	32.19
Biomass								
Chironomidae	20.74	2.51	41.4	17.35	15.8	6.82	12.89	27.1
Non-chironomids	42.44	11.7	48.83	44.66	150.49	53.97	56.68	64.74

enrichments reported increases in insect abundance and biomass within the range of those we measured in naturally phosphorus-rich and -poor streams.

A major control of insect assemblages in our study streams is the geomorphology of the La Selva landscape. Insects responded to stream phosphorus concentrations, which result from inputs of geothermally modified groundwater. The geomorphic setting of the landscape controls where this phosphorus-rich groundwater emerges in the landscape (Pringle et al., 1993). At La Selva, upwelling of geothermally modified groundwater occurs at a gradient break at 50 m.a.s.l., which is near the terminus of Pleistocene lava flows (Pringle, 1991). Thus, stream reaches receive inputs of phosphorus-rich groundwater depending on their location in the landscape, with most phosphorus-rich streams located at, or below, 50 m.a.s.l. Although geothermally modified groundwater also has high concentrations of other solutes (e.g. calcium, chloride, and magnesium), our previous research shows that phosphorus is the main element in the modified groundwater that is related to microbial activity (Ramírez et al., 2003).

Donor control in detritus-based stream food webs

Our study provides supporting evidence for the hypothesis that detritus-based ecosystems are donor-controlled by showing that insects are regulated by food resources more than predation. Although there are several definitions, donor-controlled ecosystems are those in which resource renewal rates are independent of consumption, thus all trophic levels are food-limited (Pimm, 1982; Bengtsson et al., 1995). Detritus-based ecosystems have been described as donor-controlled because inputs of detritus are inde-

pendent of food web structure, at least over short time scales. In addition, detritus may provide refuges from large-size predators, such as macroconsumers. As a result, only a small proportion of prey is available and predators have a limited controlling effect (Persson et al., 1996).

Donor-controlled systems are in direct contradiction to the view that both resources and predators alternate in their control of trophic levels depending on the length of the food chain, as proposed by Hairston et al. (1960) and later modified by Oksanen et al. (1981). In our study streams, we can readily identify three trophic levels: microbes, insects, and macroconsumers. The results of this study in combination with previous studies at La Selva (Rosemond et al., 2001; Ramírez et al., 2003) and elsewhere in the tropics (Pearson & Connolly, 2000) demonstrate that both microbial communities and insect assemblages are resource-limited. Although we still do not know whether macroconsumers are food-limited in these headwater streams, our results indicate that they do not control insect assemblages. Resource control has been found in other small stream food webs in temperate regions. Wallace et al. (1997, 1999) demonstrated that reduction of basal resources (i.e. detritus) in a first-order stream resulted in reductions in the biomass and production of all trophic levels associated with detritus in the food web. In addition, the assessment of secondary production of insect predators and their prey suggested that predators were food limited (Wallace et al., 1999).

In conclusion, our results show that food resources control detritus-based headwater streams in lowland Costa Rica (i.e. bottom-up control), with predators having little controlling effect on their prey. This supports the over-arching ecological hy-

pothesis that detritus-based stream ecosystems are donor-controlled.

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