Functional Redundancy of Stream Detritivores: an Experimental Test

by

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We accept this thesis as conforming
to the required standard

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ABSTRACT

Relationships between species richness and ecosystem function may depend on the degree of functional differentiation vs. redundancy among coexisting species. Functional redundancy occurs when ecosystem function is maintained at nearly constant levels despite shifts in the populations driving that process. Detritivorous aquatic insect communities were experimentally manipulated by separately removing each of two dominant limnephilid caddisfly species to determine: (1) if species were functionally redundant, (2) if coexisting species interacted via inhibition or facilitation, and (3) if there were differential effects of intra- vs. interspecific density compensation. Per capita and per unit biomass effects of two response variables, leaf consumption (resource capture) and secondary production (insect growth) were compared. Density compensation was generally effective at maintaining leaf consumption after species loss, suggesting functional redundancy of the two caddisfly species. The two species, however, were not redundant for secondary production. *Psychoglypha prita* had significantly higher secondary production (during the experiment) than *Psychoglypha* sp. A. Treatments containing the two species in combination showed less leaf consumption and secondary production than predicted by 'null models' of no interaction, indicating inhibition (interspecific competition) between the two species. In monoculture, interference competition may have decreased individual growth. In summary, classifying these two species as redundant depends on the response variable considered.

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Introduction

Theoretical interest in the relationship between species diversity and the magnitude and stability of ecosystem processes has existed for decades (MacArthur 1955, Paine 1969, May 1972, Jones and Lawton 1995, Loreau 2000). Recently, accelerating extinction rates have stimulated empirical research on the relationships between species richness (number of species), species identity (community composition) and ecosystem processes (Schulze and Mooney 1993, Naeem et al. 1994, Tilman and Downing 1994, Tilman 1996, Aarsen 1997, Naeem and Li 1997, McGrady-Steed et al. 1997, Mikola and Setälä 1998, Symstad et al. 1998, Cardinale et al. 2000, Jonsson and Malmqvist 2000, Petchey 2000, Duffy et al. 2001, Jonsson et al. 2001, Ruesink and Srivastava 2001, Cardinale et al. 2002a, Jonsson et al. 2002, and others). Several studies have shown that as the number of species increases, ecological processes (e.g. decomposition, productivity, nutrient cycling etc.) increase in magnitude or stability (Naeem et al. 1994, Naeem and Li 1997, McGrady-Steed et al. 1997, Naeem 1998, Jonsson and Malmqvist 2000, Cardinale et al. 2002a). However, the contribution of number of species per se versus the effects of particular species on ecosystem functioning remains largely unexplored (but see Aarsen 1997, Symstad et al. 1998, Jonsson and Malmqvist 2000, Jonsson et al. 2002).

General models that predict an average relationship between the number of species and the magnitude of a response variable include the "rivet", "redundancy" and "idiosyncratic" hypotheses. The "rivet" hypothesis (Ehrlich and Walker 1998) maintains that all species contribute to ecosystem function in a small, but significant way, whereas the "redundancy" hypothesis (Walker 1992) suggests that certain species drive ecosystem functioning, while other so-called passenger species contribute less to function. The "idiosyncratic" hypothesis states that even if a change in function can be forecast, its size and direction may be impossible to predict, i.e., there is no consistent effect of species richness or identity on ecosystem processes (Lawton 1994). Untangling the mechanisms that drive the general relationships between species diversity and ecosystem function requires an understanding of how the characteristics of coexisting species influence ecosystem processes.

Mechanisms by which species diversity can influence ecosystem functioning include a 'selection effect', where a particular species is competitively dominant (Aarssen 1997), a 'complementarity effect' that occurs through either resource partitioning (Hooper and Vitousek 1997), phenological complementarity (Stevens and Carson 2001) or facilitative interactions between species (Soluk and Richardson 1997, Cardinale et al. 2002a), and a 'stability effect' where multiple, functionally similar species within an assemblage provide 'biological insurance' against changes in ecosystem function after species loss (Naeem and Li 1997, Naeem 1998, Fukame et al. 2001). Compensatory responses by species are another mechanism by which nearly constant levels of ecosystem processes can be maintained after species loss (Frost et al. 1995). A 'functional' response could maintain levels of ecosystem function if there is an increase in the per capita effects of individuals, while a 'numerical' response could maintain levels of function if there is density compensation by other species (Ruesink and Srivastava 2001).

Density compensation was equated to functional redundancy by Walker (1992), who suggested that complete functional redundancy could only occur if, following the removal of one species, there was density compensation by the remaining species. This definition of redundancy was also used by Frost et al. (1995), who suggested that redundancy be defined as the maintenance of ecosystem function at nearly constant levels despite changes in the composition of species driving that process. Mechanisms for the redundancy hypothesis were proposed by Mikola and Setälä (1998) using the concept of niche. One possible mechanism involves modification of a species' realized niche when biotic interactions change. In this scenario, the remaining species use the newly released resources and replace the biomass and production of the lost species. This mechanism is similar to the functional response suggested by Ruesink and Srivastava (2001). A second proposed mechanism does not involve niche modification, but rather, some sort of interspecific release, e.g. competitive release upon the loss of one species. In this scenario, the coexistence of species is not facilitated by resource partitioning, thus, species occupy similar niches all of the time (Mikola and Setälä 1998). Through either proposed mechanism, unchanged biomass and productivity within functional groups results in unchanged ecosystem functioning (Walker 1992; Lawton and Brown 1993).

The degree of functional redundancy among co-occurring species is critical to testing the effects of species richness on ecosystem processes (Lawton 1994). The majority of recent studies that have demonstrated a relationship between species richness and ecosystem function have focused on primary producers in grassland communities or aquatic microbial communities (reviewed by Schläpfer and Schmid 1999). In contrast, consumer effects on resources have rarely been examined in this context. Studies that have explicitly tested functional redundancy among consumer species are rare (Harris 1995, Morin 1995, Kurzava and Morin 1998, Duffy et al. 2001, Mermillod-Blondin 2001). Moreover, even fewer studies have investigated the mechanisms that mediate interactions between consumer species, and their effects on ecosystem level processes (Jonsson and Malmqvist 2000, Duffy et al. 2001, Ruesink and Srivastava 2001, Cardinale et al. 2002a, Jonsson et al. 2002). There is evidence of competition within stream invertebrate grazer communities (Hart 1985, Hawkins and Furnish 1987, Lamberti et al. 1987, Kohler 1992, Cross and Benke 2002) and facilitation between collector species (Cardinale et al. 2002a). However, competitive or facilitative interactions between detritivore species (those feeding on detritus > 1 mm^2) are understudied (Jonsson and Malmqvist 2000, Ruesink and Srivastava 2001, Jonsson et al. 2002).

Headwater streams are an ideal model system with which to investigate relationships between species diversity and ecosystem function. Headwater reaches of stream ecosystems receive the majority of their energy as allochthonous leaf litter input, and decomposition of this leaf litter is an important ecosystem process (Wallace et al. 1999). Changes in the magnitude or stability of leaf decomposition can affect local detritivore communities as well as the productivity of downstream consumers that rely on the conversion of coarse organic matter to fine organic matter performed by leaf shredding detritivores (Short and Maslin 1977, Heard and Richardson 1995). Additionally, this input of organic matter often occurs as a seasonal pulse, for example, during autumnal leaf fall, with subsequent mobilization and redistribution during spring freshet events. Leaf detritus can therefore become seasonally limiting in streams (Richardson 1991, Dobson and Hildrew 1992), which can lead to intense competition or niche complementarity between detritivorous species. Aggregations of species in the same guild that exploit ephemeral resource patches such as stream leaf packs (Finn 2001) provide an ideal opportunity to test for functional redundancy and mechanisms maintaining species coexistence.

I tested several hypotheses in this study. First, I tested the "redundancy" hypothesis by quantifying the effects of two detritivore species in monoculture on two ecosystem processes, leaf consumption (resource capture) and secondary production (growth). Second, I tested for interactions between species by comparing species performance in monoculture to the performance of species in combination. Finally, I tested for density dependence of leaf consumption and growth, and for differential effects of intraspecific vs. interspecific density compensation.

Materials and methods

Study site

Experiments were conducted in 2000 and 2001 near Cranbrook, British Columbia, Canada (49°19′ N, 115°42′ W; Fig. 1). Richard Creek is a small, second-order tributary (1:20,000 map scale) of Gold Creek, and is located approximately 1550 m above sea level. The study reach was located 2.6 km downstream of the source of Richard Creek. Richard Creek drains a catchment underlain with sedimentary and metamorphic rock including quartzite, argillites, siltstones, sandstones and conglomerates (Deverney Engineering Services Ltd. 2002). Managed conifer forests dominated by lodgepole pine (*Pinus contorta*) and western larch (*Larix occidentalis*) with minor components of Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*) cover almost all of the catchment area (C. Donaldson, Galloway Lumber Co., pers. comm.). The channel slope was ~4%, the width of the channel was 1-2 m (bankfull width), and the average water depth in riffles was ~ 5-10 cm at baseflow. The stream bottom

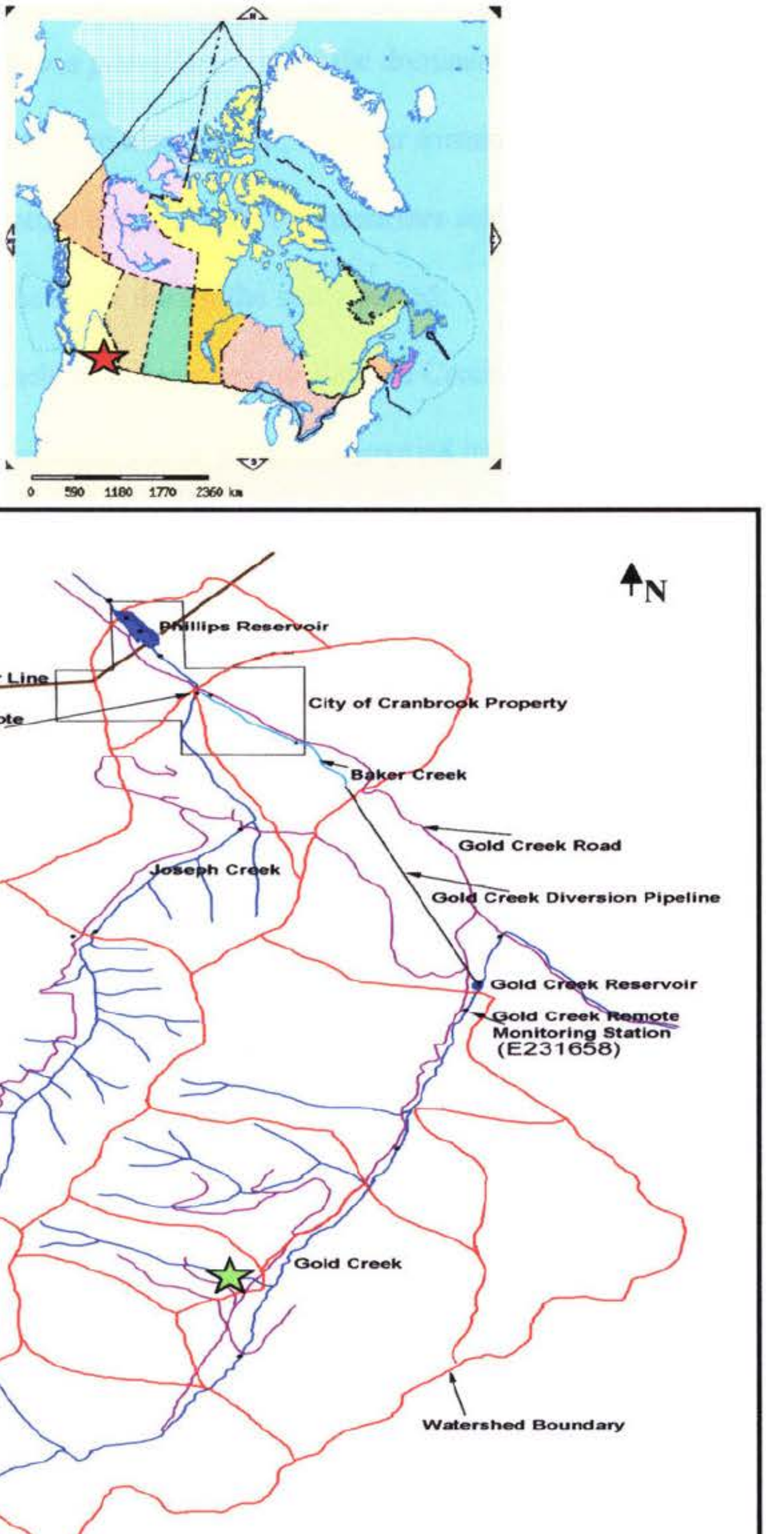

Figure 1. Location of study site near Cranbrook, British Columbia, Canada (denoted by star).

consisted primarily of cobble, gravel, and some moss-covered boulders. Sitka alder (*Alnus viridus*) and thimbleberry (*Rubus parviflorus*) were the dominant riparian species, but various other trees and shrubs were also present, together forming an almost closed canopy along most of the stream length. Table 1 summarizes selected physical and chemical characteristics of the creek during the study period.

Artificial stream channels were built next to Richard Creek (Fig. 2). Water flowed from the creek into two underwater intake pipes and emptied into 4 holding tanks (header boxes), which delivered water to 24 experimental channels in total (Figs. 3 and 4). Each experimental channel was 17.5 cm wide, 13.85 cm high and 1.2 m long. I added coarse gravel substrate (~ 4 cm diameter natural round gravel) to each channel, and placed 1 mm nylon mesh screens over the inflow, outflow and top surface to prevent organisms and detritus from colonizing or escaping the channels.

Insects and leaves

I chose two congeneric limnephilid caddisflies (Trichoptera) that are abundant in late summer in Richard Creek as my study organisms - *Psychoglypha* sp. A and *Psychoglypha prita* (Milne). Larvae of both species feed on detritus and are common inhabitants of western North American montane streams (Wiggins 1996). No adult specimens of *Psychoglypha* sp. A were caught during the study period, therefore, this species was unidentifiable beyond genus level. *Psychoglypha* larvae occur in a wide range of cool water habitats, ranging from springs to larger streams and their marginal pools. Larval cases are typically constructed of small rock fragments and pieces of wood combined into a straight tube up to 43 mm in length (Wiggins 1996). The two species were distinguished

Table 1. Physical and chemical characteristics of Richard Creek, Cranbrook B.C. between May and September, 2001. Physical characteristics measured by P. Jordan, B.C. Ministry of Forests (Nelson), water sample collected by L. Shama (01/05/18), and chemical characteristics measured by S. Leahy, MB Labs, Sidney, B.C.

Watershed area (ha)	~696
Discharge (m^3/s)	range: 0.5 to 1.0
Water temperature (°C)	range: 2.5 to 9.5
Alkalinity (mg/L)	94.2
NH_3-N (µg/L)	3.5
Colour (TCU)	7.9
Conductivity (µS/cm)	128
TKN (mg/L)	0.2
NO_3-N (µg/L)	27.9
NO_2-N (µg/L)	0.7
Ortho phosphorus (µg/L)	3.5
pH	7.6
Total phosphorus (µg/L)	10.0
Dissolved phosphorus (µg/L)	5.9
TDS (mg/L)	71.4
TSS (mg/L)	15.0
Turbidity (NTU)	0.9

Note: TCU = total colour units; conductivity (µS/cm) = micro Siemens per cm; TKN = total Kjeldahl nitrogen (organic nitrogen); ortho phosphorus = ortho-phosphate (bioavailable P); total phosphorus = all particulate and dissolved P; TDS = total dissolved solids; TSS = total suspended solids; NTU = nephelometric turbidity units.

Figure 2. Artificial stream channels (front view) built beside Richard Creek, Cranbrook, B.C., Canada (photo by L. Shama).

Figure 3. Intake pipes in Richard Creek that delivered water to artificial stream channels, Cranbrook, B.C., Canada (photo by L. Shama).

Figure 4. Artificial stream channels (side view), showing header boxes, outflow pipes, mesh screens, and 24 experimental channels (photo by L. Shama).

in the field based on differences in larval case construction. *Psychoglypha* sp. A constructs a triangular shaped case of smooth, round bark disks, whereas *Psychoglypha prita* constructs a round tube embellished with twigs, rocks and roughly shaped pieces of bark. Wiggins (1996) states that *Psychoglypha* larvae burrow into bottom gravel in the autumn as time for pupation approaches, however, the phenology of *P. prita* and *Psychoglypha* sp. A are unknown. At least one species of *Psychoglypha* (*P. subborealis*) is believed to overwinter in the egg stage (Wiggins 1996), but adults of other species have been collected alive on snow in winter and early spring (Denning 1970). Natural densities of *Psychoglypha* spp. in Richard Creek ranged from ~20 - 50 larvae per square meter during spring and summer months (Shama unpubl.). I quantified natural densities using Surber samples (0.3 m^2) taken ~monthly between May and October in both 2000 and 2001.

Non-target species of stonefly and mayfly larvae were also included in the experimental communities. I included one species of stonefly, *Yoroperla* sp., and two species of mayfly, *Baetis* sp. and *Paraleptophlebia* sp. These three species are common in Richard Creek as revealed by my Surber samples (Table 2). Stoneflies (Plecoptera) are primarily associated with clean, cool running waters. *Yoroperla* is a shredder-detritivore genus of stonefly that is distributed throughout the West in mountain and intermountain streams (Merritt and Cummins 1996). Mayflies (Ephemeroptera) occur in a wide variety of lentic and lotic habitats, the greatest diversity being found in rocky-bottomed, low-order, headwater streams. *Baetis* is a widespread genus of mayfly that comprises collector-gatherers of detritus and diatoms. *Paraleptophlebia* is another genus of mayfly that is also widely distributed, and contains species of collector-gatherers and facultative shredder-detritivores (Merritt and Cummins 1996).

Table 2. Common invertebrate taxa found in Surber samples collected from Richard Creek during spring and summer months in 2000 and 2001.

- Order Trichoptera
    - Family Limnephilidae
        - *Psychoglypha* sp. A
        - *Psychoglypha prita*
        - *Cryptochia* sp.
        - *Dicosmoecus atripes*
        - *Ecclisomyia* sp.
        - *Chyranda centralis*
    - Family Rhyacophilidae
        - *Rhyacophila verrula*
    - Family Glossosomatidae
        - *Glossosoma* sp.
- Order Plecoptera
    - Family Pteronarcyidae
        - *Pteronarcys* sp.
    - Family Peltoperlidae
        - *Yoroperla* sp.
    - Family Perlidae
    - Family Chloroperlidae
- Order Ephemeroptera
    - Family Baetidae
        - *Baetis* sp.
    - Family Leptophlebiidae
        - *Paraleptophlebia* sp.

I used Sitka alder leaves (*Alnus viridus*) as a source of food for experimental insect communities. Alder leaves are processed rapidly in streams compared to other detritus such as wood and conifer needles (Petersen and Cummins 1974). Alder leaves were collected from trees just prior to abscission in September 2000, and kept frozen until August 2001. I added 26.0 g (air dried for 24 h) of alder leaves to each of the 24 experimental channels. My choice of 26.0 g as the initial weight of alder leaves was based on estimated leaf consumption rates of *Psychoglypha* sp. A and *P. prita* determined in a preliminary feeding trial (see below). Leaf conditioning time at which detritivore shredding is maximal may take between 1-4 weeks. Leaf conditioning is the enhancement of leaf palatability for detritivores by microbial and fungal colonization (Gessner et al. 1999). Richardson (1992) found maximum invertebrate biomass on red alder leaves (*Alnus rubra*) 30 days after their introduction as unconditioned leaves. In this study, insects were introduced into experimental channels after leaves had been conditioned for one week.

Feeding trial

I conducted a one-day feeding trial on July 17, 2001 in 'cages' within artificial stream channels to estimate daily leaf consumption rates of *Psychoglypha* sp. A and *P. prita*. Cages were constructed of 6-9" lengths of 2" diameter PVC pipe with 1 mm nylon mesh fastened over both ends. The feeding trial consisted of 10 treatments. Nine treatments were each replicated 2 times: 100% *Psychoglypha* sp. A (at 3 initial stocking densities: 2, 4 or 8 caddislarvae); 100% *P. prita* (2, 4 or 8 caddislarvae); 50/50% *Psychoglypha* sp. A/*P. prita* (2, 4 or 8 caddislarvae); and a no-insect control treatment was replicated 6 times. For each experimental insect, I added 6 leaf disks (conditioned alder disks cut out with a 6 mm diameter hole punch). Replicates containing 2, 4 and 8 insects had 12, 24 and 48 leaf disks, respectively, at the start of the feeding trial. A subsample of leaf disks was dried for 72h at 50°C to estimate initial dry weight. At the end of the feeding trial, all insects were counted, dried (48 h at 50°C) and weighed, and all leaf material dried (72h at 50°C) and weighed.

In the 100% *Psychoglypha* sp. A treatment, individuals consumed 2.22 (± 0.30) mg of leaf per day (mean consumption ± SE of 6 replicates, averaged across all density treatments). In the 100% *Psychoglypha prita* treatment, individuals consumed 3.4 (± 0.30) mg of leaf per day (again averaged across all density treatments). Daily per capita leaf consumption rates differed between the two species because *P. prita* (mean biomass 3.22 ± 0.74 mg; n=27) was 9.9% larger than *Psychoglypha* sp. A (mean biomass 2.93 ± 0.16 mg; n=28). To account for differences in biomass among treatments and replicates, daily leaf consumption rates per unit biomass were calculated as: leaf consumption (initial - final leaf mass)/ [insect biomass (final dry weight)]*days. *Psychoglypha* sp. A consumed 0.82 (± 0.17) mg of leaf per mg of insect biomass per day (mean consumption ± SE of 6 replicates; all densities combined). *Psychoglypha prita* consumed 1.40 (± 0.16) mg/mg*day, and the two species in combination consumed 1.24 (± 0.10) mg/mg*day. Using the highest daily consumption rate (1.40 ± 0.16 mg/mg*day), I estimated how much leaf matter could potentially be consumed by 10, 20 or 40 caddislarvae over a period of 30 days. For example, if the average dry weight of an individual insect was 10 mg, 10 individuals would total 100 mg of insect biomass that could consume 1.40 mg of leaf per mg of insect/day * 30 days, equaling 4.2 g of leaf consumption (dry weight). Forty individuals (10 mg each) at the same daily consumption rate per unit biomass could consume 16.8 g of leaf matter over 30 days.

Experimental design

The experiment consisted of 10 treatments. Nine treatments were each replicated 2 times: 100% *Psychoglypha* sp. A (at 3 initial stocking densities: 10, 20 or 40 caddislarvae); 100% *P. prita* (10, 20 or 40 caddislarvae); 50/50% *Psychoglypha* sp. A/*P. prita* (10, 20 or 40 caddislarvae); and a no-insect control treatment was replicated 6 times (Table 3). Treatment densities were comparable to natural densities found in Richard Creek. The lowest density treatment (10 individuals) represented 'maximum potential per capita resource capture and growth', 20 individuals represented 'ambient density', and 40 individuals represented 'high density' of larvae. I measured case length of each caddislarvae individual prior to introduction, to estimate initial caddisfly biomass per experimental channel (using case length-biomass regressions, see below), and to estimate secondary production (i.e., growth) over the duration of the experiment.

Experimental communities were also established with a fixed number and sizes of non-target species of stoneflies and mayflies. Each experimental insect community contained 10 stoneflies (*Yoroperla* sp.) at ~1.12 mg each, and 20 mayflies (10 *Baetis* sp. and 10 *Paraleptophlebia* sp.) at ~1.0 mg each, resulting in approximately 31.2 mg (dry weight) of additional insect biomass. The experiment was conducted from August 1 through August 29, 2001, after which all insects were counted, dried (48 h at 50°C) and weighed, and all leaf material dried (for several days at 50°C) and weighed.

Table 3. Density treatments for *Psychoglypha* sp. A (A), *P. prita* (B), and the two species in combination (A/B).

	Experimental treatment									
	1	2	3	4	5	6	7	8	9	10
Psychoglypha sp. A	10A	20A	40A	5A	10A	20A	-	-	-	-
P. prita	-	-	-	5B	10B	20B	10B	20B	40B	-

Response variables

Net loss of leaf mass (g dry weight) was calculated as initial leaf mass - final leaf mass. Non-insect-caused leaf mass loss, i.e., microbial and fungal processing, leaching, and physical abrasion (Hieber and Gessner 2002), was estimated using the no-insect control treatment. Insect-caused leaf consumption (dry mg) was then calculated as: initial leaf mass (corrected for the mean net loss of leaf mass in the 6 no-insect control replicates) - final leaf mass.

I also measured shredder secondary production. As the approximate initial biomass of shredders in each replicate was known (via case length - biomass regression), and no known predators were present, shredder net secondary production can be estimated as the difference between initial and final biomasses (mg dry weight; Duffy et al. 2001). I estimated initial dry weight of experimental caddislarvae individuals from species-specific case length to dry weight regressions, based on caddislarvae collected from Richard Creek throughout the summer of 2001. Based on measurements of 39 larvae, initial weights of *Psychoglypha* sp. A individuals were estimated using the power function $Y=0.001(X)^{3.06}$, where X=case length (mm) and Y=initial dry weight (mg). Initial weights of *P. prita* individuals were estimated using $Y=0.002(X)^{2.91}$ (n=48). Additionally, I calculated the average daily growth rate of each species using: [*ln* (final weight/initial weight)]/days.

I calculated per capita and per unit biomass effects of the two response variables, leaf consumption and secondary production. Per capita effects were calculated as the change in consumption or production with increasing shredder abundance, i.e., the slope of leaf consumption (Y) vs. shredder abundance (X). Per unit biomass effects were calculated as the change in consumption or production with increasing shredder biomass, i.e., the slope of leaf consumption (Y) vs. shredder biomass (X). For experimental channels with missing caddislarvae, it was assumed that mortality occurred at the midpoint of the experiment. I also assumed that mortality followed a negative exponential function (Type III survivorship curve) over time. Hence, average shredder abundance over time was calculated as the geometric mean of initial and final abundance. Shredder biomass (average biomass at the midpoint of the experiment) was also calculated as the geometric mean of initial and final biomass.

Statistical analyses

Hypothesis 1: functional redundancy

I used one-way ANOVA to test for differences in net loss of leaf mass and secondary production among the experimental treatments. Significantly different treatments were identified using Tukey's post-hoc analyses. Within each insect treatment, there were three different initial densities, thus, by using one-way ANOVA, the within-treatment mean square (i.e., the residual variance) was inflated by differences in density. Hence, a more powerful model such as ANCOVA would incorporate differences in density and adjust for it, thereby increasing the probability of detecting differences among insect treatments.

I used ANCOVA models to test for differences in leaf consumption and secondary production (growth) among the three insect treatments using shredder abundance and shredder biomass as covariates. In the full ANCOVA model, I tested the homogeneity of slopes using the insect treatment*covariate interaction term. If the interaction term was not significant, i.e., the slopes were parallel, I tested the homogeneity of intercepts. Testing the homogeneity of intercepts tested for significant differences in elevation among insect treatments. Prior to statistical analysis, data were visually assessed for normality using quantile-quantile plots, and homogeneity of variances were assessed using Levene's test. All analyses were performed using SPSS (version 6.1.3). All means reported with ± 1 standard error unless otherwise stated, and I rejected the null hypothesis if the significance of p was ≤ 0.05.

Hypothesis 2: species interactions

I used three separate regressions to determine the per capita and per unit biomass effects of the two shredder species alone and in combination on the two response variables (leaf consumption and secondary production). Under the assumption of no non-additive effects (i.e., no inhibition or facilitation), I generated 'null models' for the expected impacts of the two species in combination. 'Null models' were calculated as the mean of the slopes and intercepts of the two species in monoculture. If there is inhibition, the impacts of the two species in combination should be less than that predicted by the 'null model' (suggesting that the interaction between the two species decreases overall consumption or secondary production). If there is facilitation, the impacts of the two species in combination should exceed that of the 'null model'. I tested for significant species interactions by comparing the mean slope of the two species in monoculture (i.e., the slope of the 'null model') to the slope of the two species in combination using Student's *t*-tests.

Hypothesis 3a: density dependence

I used separate ANCOVA models to test for density dependence of per capita leaf consumption and secondary production (per capita growth), and leaf consumption and growth per unit biomass. I predict that at higher densities, per capita and per unit biomass leaf consumption and growth would be less than that at lower densities due to resource limitation.

Hypothesis 3b: intra- and interspecific density compensation

I tested for differential effects of intra- and interspecific density compensation on per capita and per unit biomass resource capture and growth by comparing the slope of the 'null model' to the slope of the two species in combination using Student's *t*-tests. The slope of the 'null model' represented intraspecific density compensation, and the slope of the two species in combination represented interspecific density compensation. As above, I used three separate regressions to determine the per capita and per unit biomass effects of the three insect treatments on the two response variables (leaf consumption and secondary production) as a function of density. 'Null models' were then calculated as the mean of the two monocultures.

Results

Survivorship

Survivorship among caddislarvae was high for the experiment. Mean survivorship of caddislarvae for 16 of the 18 replicates that contained insects was 94.7 (± 2.89)%. There was low survivorship in two of the 100% *Psychoglypha* sp. A replicates (12.5% and 45.0%). These two replicates were excluded from the analyses of secondary production, as they had negative values for growth. Leaf consumption in these two replicates, however, was within the range of values for other replicates in that treatment, and were therefore included in the analyses of leaf consumption.

For each replicate, I calculated average shredder abundance using a linear and an exponential mortality model (Type II and Type III survivorship curves, respectively). For the linear mortality model, I calculated average shredder abundance as the arithmetic mean of initial and final abundance. For the exponential mortality model, I calculated average shredder abundance as the geometric mean of initial and final abundance. In each model, average shredder abundance occurs at the midpoint of the experiment (day 14). Average shredder abundance differed only slightly between the two mortality models, thus my use of the geometric mean of shredder abundance in the analyses was valid.

Survivorship was low among non-target stoneflies and mayflies for the experiment. Mean survivorship of stoneflies and mayflies for the 18 replicates that contained insects was ~13%, therefore, non-target insect biomass was excluded from all analyses. Possible sources of mortality for stoneflies and mayflies included starvation via interference from caddislarvae, stress resulting from non-optimal flow regimes, i.e., stream channel flow was faster than encountered in natural stream pools, and loss of individuals through adult emergence.

Leaf consumption

Net loss of leaf mass was 19.1% higher in insect treatments than in the no-insect control. One-way ANOVA showed that leaf mass loss was significantly higher in insect treatments than in the no-insect control ($F_{3,20}$=6.28; p=0.004; Fig. 5). There was, however, no significant difference in insect-caused leaf consumption among the three insect treatments. Although mean leaf consumption (i.e., for 23.33 insects over 28 days) of the 100% *P. prita* treatment was 81.1% higher than mean leaf consumption of the 100% *Psychoglypha* sp. A treatment, an ANOVA showed no significant difference among the three insect treatments ($F_{2,15}$=1.38; p=0.281; Table 4 and Fig. 5). Mean leaf consumption of the 100% *P. prita* treatment was 2050.41 (± 447.99) mg, 1132.09 (± 372.57) mg for the 100% *Psychoglypha* sp. A treatment, and 1714.78 (± 359.21) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment.

Per capita leaf consumption

Psychoglypha sp. A had higher per capita leaf consumption than *P. prita*, i.e., the slope of the leaf consumption vs. shredder abundance regression was steeper for *P.* sp. A than *P.prita*, but the difference in slopes was not significant. In the full ANCOVA model, the interaction of insect treatment and shredder abundance was not statistically significant. After removing the treatment*shredder abundance interaction term, the main effect of shredder abundance was statistically significant ($F_{1,14}$=88.76; $p < 0.001$) but treatment was not ($F_{2,14}$=1.88; p=0.190; Fig. 6 and Table 5). More insects ate more leaves, but there was no apparent effect of species composition on per capita leaf consumption.

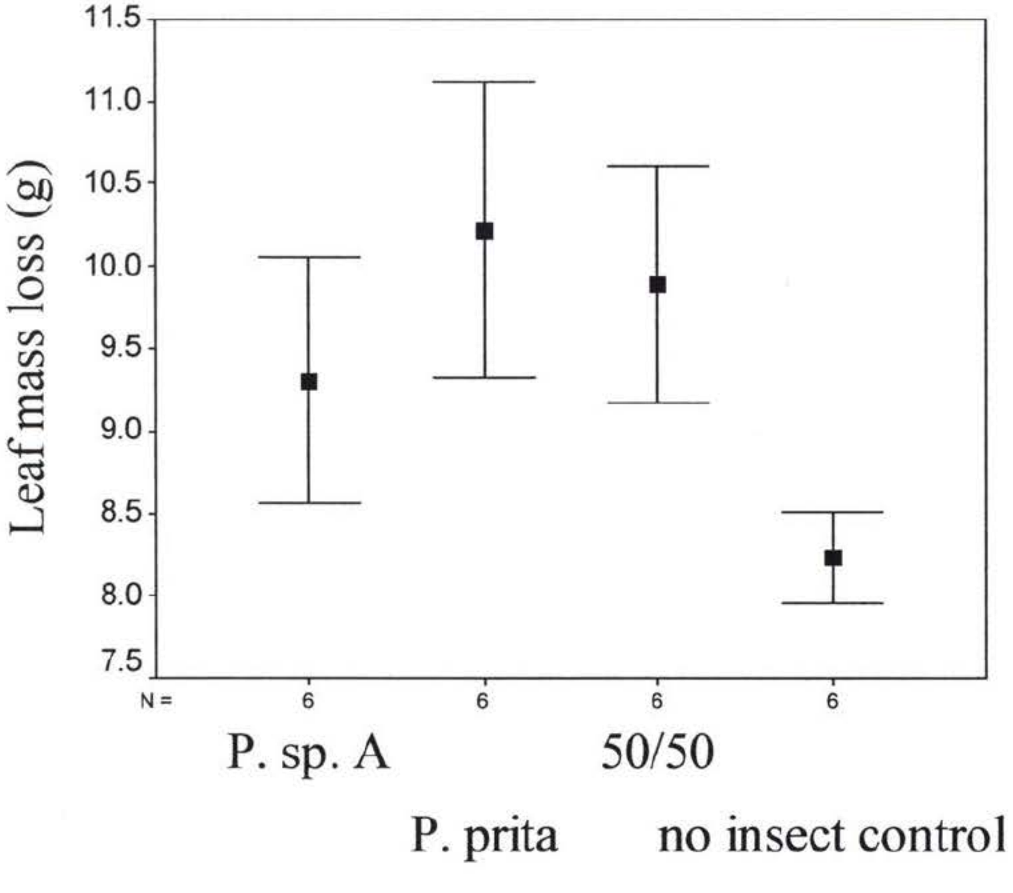

Figure 5. Mean (± SE, n=6) loss of leaf mass (dry g) over 28 days for the four experimental treatments (all densities combined).

Table 4. Analysis of variance of leaf consumption among the three insect experimental treatments (all densities combined).

Source of Variation	SS	DF	MS	F	p
Treatment	2590950.20	2	1295475.1	1.38	0.281
Error	14056158.66	15	937077.24		

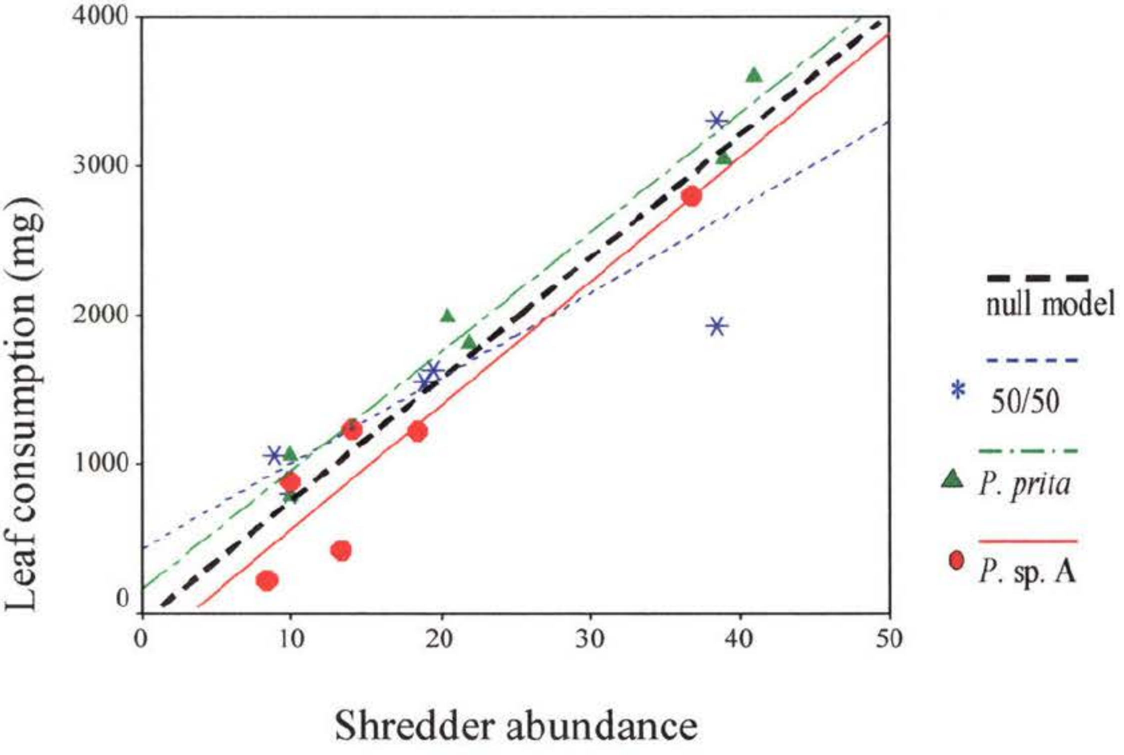

Figure 6. Per capita impacts on leaf consumption (dry mg) by shredder species alone, in combination, and in relation to a null model that predicts no facilitation or inhibition between species.

Table 5. Analysis of covariance of differences in leaf consumption among the three insect treatments using shredder abundance as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder abundance	12141230.04	1	12141230	88.76	<0.001
Treatment	513140.13	2	256570.07	1.88	0.190
Error	1914928.62	14	136780.62		

As expected, shredder abundance accounted for a large portion of the total variation in leaf consumption in each insect treatment. In the *P. prita*, *Psychoglypha* sp. A, and 50/50 treatment, abundance accounted for 97.2%, 89.7%, and 74.0% of the variation in leaf consumption, respectively (Fig. 6).

Leaf consumption per unit biomass

Psychoglypha sp. A had higher leaf consumption per unit biomass than *P. prita*, but the difference between the two species was not significant. In the full ANCOVA model, the interaction of treatment and shredder biomass was not statistically significant. After removing the treatment*shredder biomass interaction term, the main effect of shredder biomass was significant ($F_{1,14}=78.22$; $p< 0.001$) but treatment was not ($F_{2,14}=0.33$; $p=0.723$; Fig. 7 and Table 6). This shows that a higher insect biomass consumed more leaves, but again, there was no apparent effect of species composition on leaf consumption per unit biomass.

For each insect treatment, shredder biomass accounted for a large portion of the total variation in leaf consumption. In the *P. prita*, *Psychoglypha* sp. A, and 50/50 treatment, shredder biomass accounted for 87.7%, 87.2%, and 86.3% of the variation in leaf consumption, respectively (Fig. 7).

'null models': leaf consumption

I tested for interactions between the two species by comparing the observed species performance in combination (the 50/50 treatment) to 'null models' of the expected

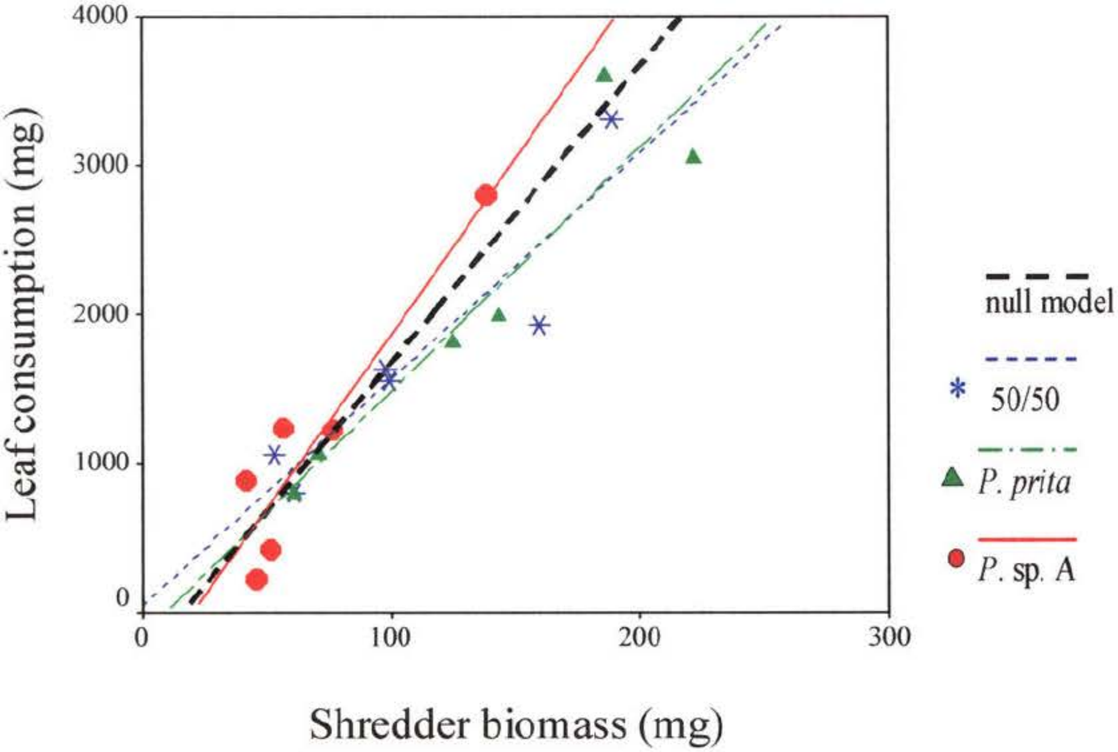

Figure 7. Per unit biomass (dry mg) impacts on leaf consumption (dry mg) of shredder species alone, in combination, and in relation to a null model.

Table 6. Analysis of covariance of differences in leaf consumption among the three insect treatments using shredder biomass as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder biomass	11922223.08	1	11922223	78.22	<0.001
Treatment	101326.48	2	50663.24	0.33	0.723
Error	2133935.58	14	152423.97		

performance of species in combination when there were no non-additive effects, i.e., no inhibition or facilitation. The interaction term in the full ANCOVA model used in previous analyses does not address non-additive effects, as the interaction term tests for differences among the three treatment slopes, not for differences between the 'null model' and the 50/50 treatment.

As indicated by the slopes, per capita impacts of the two species in combination (slope= 57.32 ± 17.0) was less than that predicted by the 'null model' (slope= 81.37 ± 7.75; Table 7 and Fig. 6). This suggested inhibition (interspecific competition) of per capita leaf consumption between the two species, although the difference in slopes was not statistically significant (two-tailed *t*-test: t=1.41, df=4; p=0.231). Similarly, the slope of leaf consumption per unit biomass of the two species in combination (slope= 15.17 ± 3.02) was less than that predicted by the 'null model' (slope= 19.91 ± 2.06; Table 7 and Fig. 7). Again, however, this difference was not statistically significant (two-tailed *t*-test: t=1.57, df=4, p=0.192).

Secondary production (insect growth)

Psychoglypha prita grew 118.3% more than *Psychoglypha* sp. A. One-way ANOVA showed that net secondary production (final - initial insect biomass) was significantly different among the three insect treatments ($F_{2,13}$=4.23; p=0.039; Fig. 8 and Table 8), and Tukey's post-hoc analysis showed that *P. prita* was significantly different from *P.* sp. A. Mean net secondary production (i.e., for 23.33 insects over 28 days) of the 100% *P. prita* treatment was 141.5 (± 20.91) mg , 64.82 (± 15.81) mg for the 100% *Psychoglypha* sp. A treatment, and 95.35 (± 15.23) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment

Table 7. Separate regressions of abundance and biomass effects on leaf consumption by two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	83.05	14.06	-269.22	272.31	34.88	0.004
#B	79.68	6.79	159.52	181.9	137.53	0.0003
#A/B	57.32	17.0	431.35	432.4	11.36	0.028
'null model'	81.37	7.75	-55.0	181.11	121.91	<0.001
A mg	23.48	4.49	-481.57	342.81	27.31	0.0064
B mg	16.34	3.05	-152.96	447.77	28.6	0.0059
A/B mg	15.17	3.02	44.95	364.04	25.24	0.0074
'null model'	19.91	2.06	-317.0	240.97	65.70	<0.001

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 biomass; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

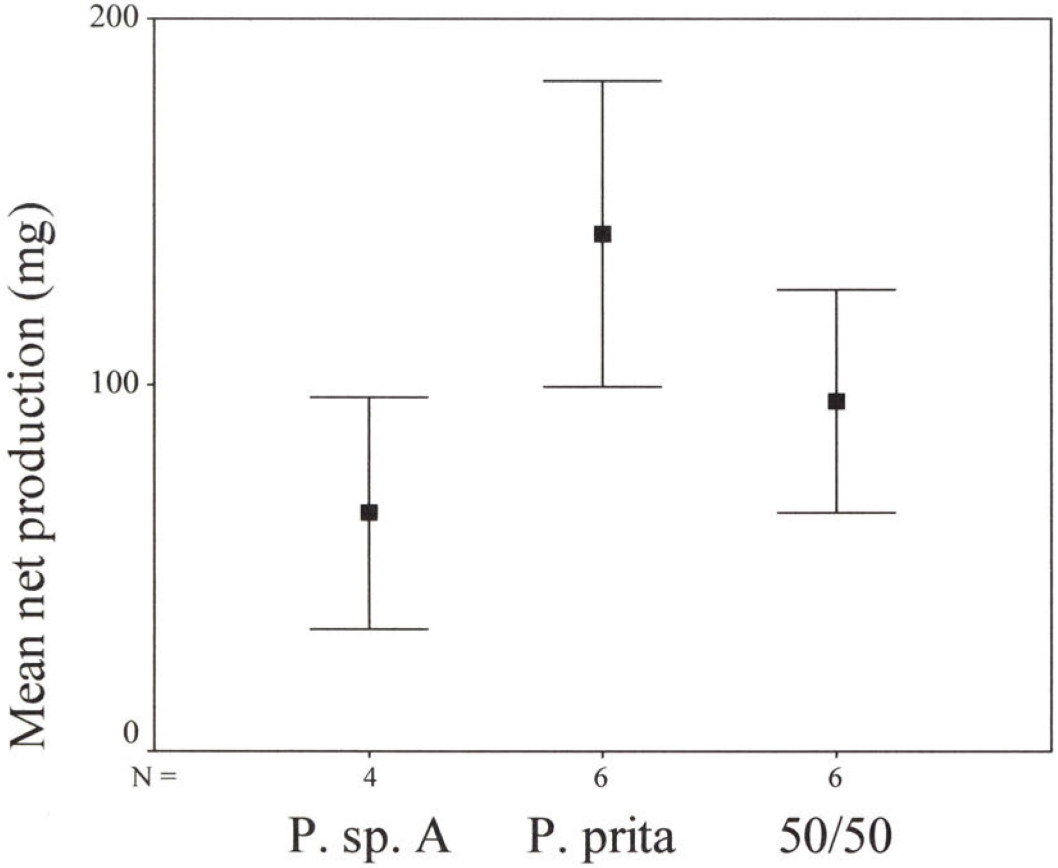

Figure 8. Mean secondary production (dry mg) over 28 days of the three insect treatments (all densities combined). Error bars indicate ± SE of the mean calculated from six replicate leaf bags (four replicates for 100% *Psychoglypha* sp. A treatment).

Table 8. Analysis of variance of secondary production among the three insect experimental treatments (all densities combined).

Source of Variation	SS	DF	MS	F	p
Treatment	15009.66	2	7504.83	4.23	0.039
Error	23076.35	13	1775.10		

Per capita growth

Psychoglypha prita had significantly higher per capita growth than *Psychoglypha* sp. A. Mean initial weights (based on case length-biomass regressions) of *P.* sp. A and *P. prita* individuals were 2.49 (± 0.07) mg and 3.52 (± 0.11) mg, respectively. Mean final weights of *P.* sp. A and *P. prita* individuals were 5.93 (± 0.33) mg and 8.54 (± 0.37) mg, respectively. Average daily growth rate (calculated using: [*ln* (final weight/initial weight)]/days) was higher for *P. prita* (0.037 mg/mg*day^{-1}) than *P.* sp. A (0.027 mg/mg*day^{-1}).

In the full ANCOVA model, the interaction of insect treatment and shredder abundance was not statistically significant. After removing the treatment*shredder abundance interaction term, the main effect of shredder abundance was statistically significant ($F_{1,14}$=12.95; p=0.004), as was treatment ($F_{2,14}$=5.88; p=0.017; Fig. 9 and Table 9). This result shows that although the slopes of the three insect treatments were homogeneous, i.e., no difference among slopes, there was a significant difference among intercepts. Therefore, there was an effect of species composition on per capita growth. Stated another way, although the slopes of the growth vs. abundance regressions were not significantly different between the two species, *P. prita* was larger than *P.* sp. A at the start of the experiment, and maintained this difference in size throughout the course of the experiment.

For each insect treatment, shredder abundance accounted for a large portion of the total variation in growth. In the *Psychoglypha* sp. A, *P. prita* , and 50/50 treatment, abundance accounted for 92.4%, 60.7%, and 30.3% of the variation in growth,

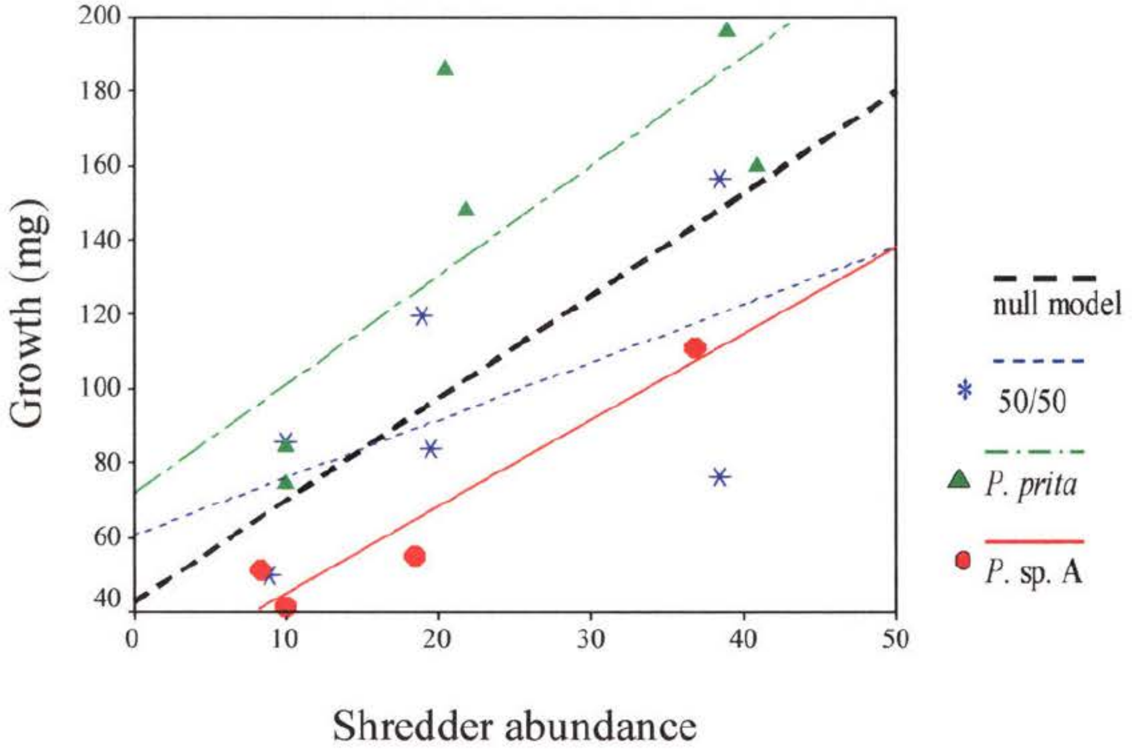

Figure 9. Per capita impacts on growth (dry mg) by shredder species alone, in combination, and in relation to a null model that predicts no facilitation or inhibition between species.

Table 9. Analysis of covariance of differences in secondary production (growth) among the three insect treatments using shredder abundance as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder abundance	11979.39	1	11979.39	12.95	0.004
Treatment	10876.50	2	5438.25	5.88	0.017
Error	11096.96	12	924.75		

respectively (Fig. 9).

Growth per unit biomass

Psychoglypha prita had higher growth per unit biomass than *Psychoglypha* sp. A, but the difference between the two species was not significant. In the full model, the interaction of insect treatment and shredder biomass was not statistically significant. After removing the treatment*shredder biomass interaction term, the main effect of shredder biomass was statistically significant ($F_{1,14}$=27.98; p<0.001), but treatment was not ($F_{2,14}$=3.36; p=0.070; Fig. 10 and Table 10). This result suggests that there was no apparent effect of species composition on growth per unit biomass.

For each insect treatment, shredder biomass accounted for a large portion of the total variation in growth. In the *Psychoglypha* sp. A, *P. prita* , and 50/50 treatment, shredder biomass accounted for 94.1%, 82.0%, and 45.9% of the variation in growth, respectively (Fig. 10).

'null models': growth

I tested for interactions between the two species by comparing the observed species growth in combination (the 50/50 treatment) to 'null models' of the expected growth of species in combination when there were no non-additive effects. As indicated by the slopes, per capita growth of the two species in combination (slope= 1.56 ± 1.18) was less than that predicted by the 'null model' (slope= 2.64 ± 1.09; Table 11 and Fig. 9). This suggested inhibition (interspecific competition) of per capita growth between the two

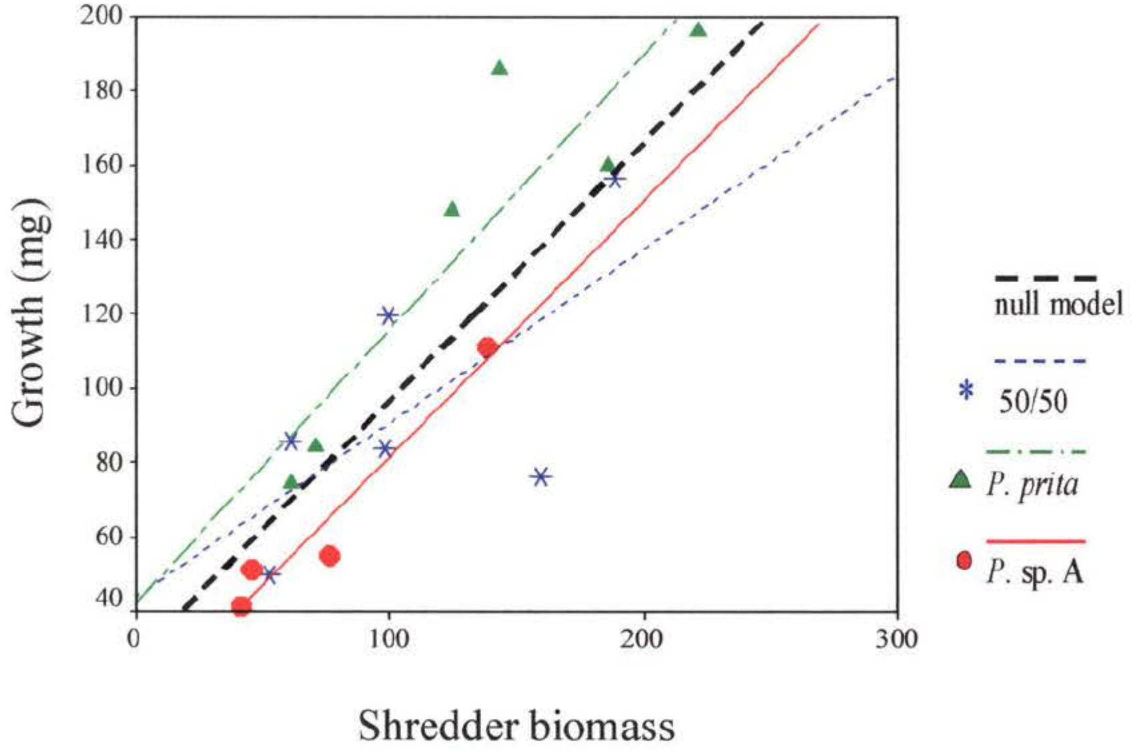

Figure 10. Per unit biomass (dry mg) impacts on growth (dry mg) of shredder species alone, in combination, and in relation to a null model.

Table 10. Analysis of covariance of differences in secondary production (growth) among the three insect treatments using shredder biomass as a covariate.

Source of Variation	SS	DF	MS	F	p
Shredder biomass	16149.89	1	16149.89	27.98	<0.001
Treatment	3875.38	2	1937.69	3.36	0.070
Error	6926.46	12	577.20		

Table 11. Separate regressions of per capita and per unit biomass effects on insect growth of two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	2.33	0.47	21.99	10.22	24.2	0.039
#B	2.94	1.18	71.79	31.68	6.17	0.068
#A/B	1.56	1.18	60.51	30.0	1.74	0.258
'null model'	2.64	1.09	46.89	27.19	8.80	0.018
A mg	0.69	0.12	12.59	10.35	32.09	0.030
B mg	0.74	0.17	42.06	25.28	18.28	0.013
A/B mg	0.47	0.25	43.75	30.72	3.39	0.140
'null model'	0.72	0.13	27.33	16.36	44.33	<0.001

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 abundance; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

species, although the difference in slopes was not statistically significant (two-tailed t-test: t=0.915, df=4; p=0.412). Similarly, the slope of growth per unit biomass of the two species in combination (slope= 0.47 ± 0.25) was less than that predicted by the 'null model' (slope= 0.72 ± 0.13; Table 11 and Fig. 10). Again, however, this difference was not statistically significant (two-tailed t-test: t=1.00, df=4, p=0.374).

Density dependence

Per capita consumption vs. density

Psychoglypha prita had 40.9% higher mean per capita leaf consumption (averaged across all density treatments) than *Psychoglypha* sp. A, and per capita leaf consumption was not density dependent. Mean per capita leaf consumption (averaged across all density treatments) in the 100% *P. prita* treatment was 88.5 (± 4.59) mg of leaf, 62.8 (± 11.09) mg for the 100% *Psychoglypha* sp. A treatment, and 83.45 (± 8.92) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 11). In the full ANCOVA model, the interaction of insect treatment and density was not statistically significant. After removing the treatment*density interaction term, the main effect of density was not statistically significant (ANCOVA $F_{1,14}$=0.58; p=0.460) nor was insect treatment (ANCOVA $F_{2,14}$=2.69; p=0.103; Table 12). This suggests that species composition and differences in density had no apparent effect on per capita leaf consumption (resource capture). Stated another way, resources did not seem to be limited at high density.

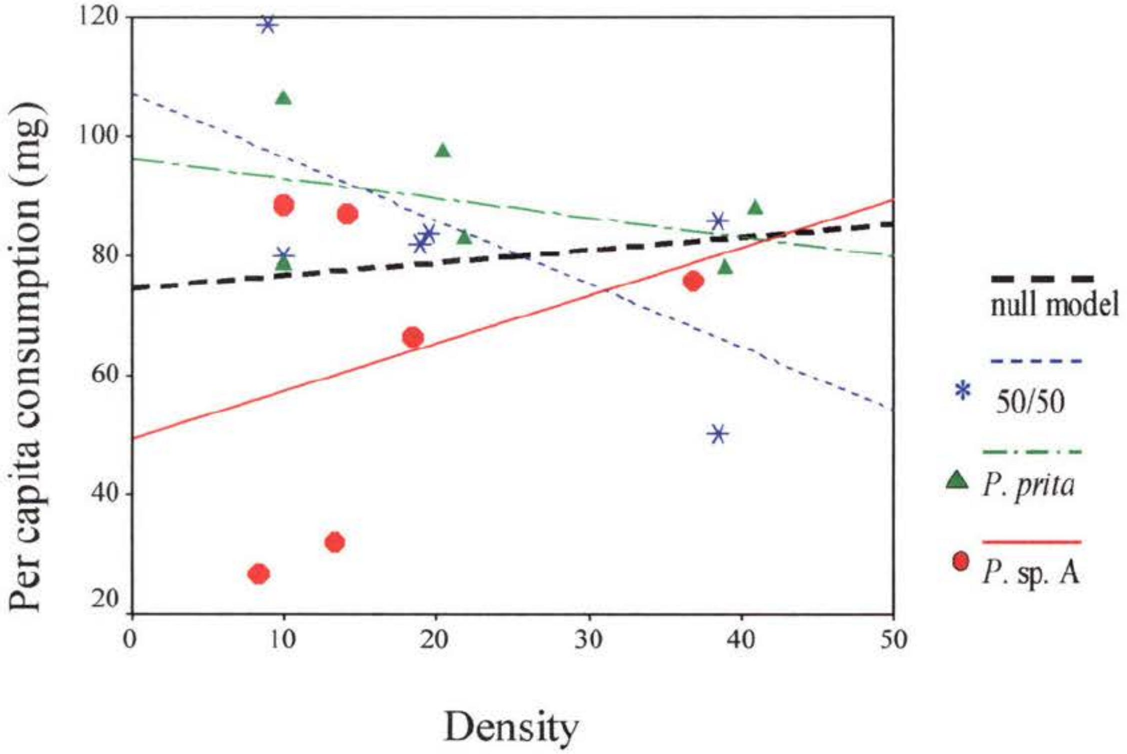

Figure 11. Per capita leaf consumption (mg) at increasing densities for the two shredder species alone, in combination, and in relation to a null model that predicts no interaction among species.

Table 12. Analysis of covariance of per capita impacts on leaf consumption of the three insect experimental treatments as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	265.29	1	265.29	0.58	0.460
Treatment	2474.84	2	1237.42	2.69	0.103
Error	6443.78	14	460.27		

Leaf consumption per unit biomass vs. density

Psychoglypha sp. A had 3% higher mean leaf consumption per unit biomass (averaged across all density treatments) than *P. prita,* and leaf consumption per unit biomass was not density dependent. Mean leaf consumption per unit of insect biomass (averaged across all density treatments) in the 100% *Psychoglypha* sp. A treatment was 15.32 (± 2.92) mg of leaf consumed per mg of insect biomass, 14.87 (± 0.94) mg leaf/mg insect for the 100% *P. prita* treatment, and 15.82 (± 1.20) mg leaf/mg insect for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 12). In the full model, the interaction of insect treatment and density was not significant. After removing the treatment*density interaction term, the main effect of density was not significant (ANCOVA $F_{1,14}=0.69$; $p=0.420$) nor was insect treatment (ANCOVA $F_{2,14}=0.10$; $p=0.910$; Table 13). Again, this suggests that species composition and differences in density had no apparent effect on resource capture per unit biomass.

Per capita growth vs. density

Psychoglypha prita had 66.3% higher mean per capita growth (averaged across all density treatments) than *Psychoglypha* sp. A., and per capita growth declined with density. Mean per capita growth (averaged across all density treatments) of the 100% *P. prita* treatment was 6.77 (± 0.81) mg, 4.07 (± 0.74) mg for the 100% *Psychoglypha* sp. A treatment, and 5.14 (± 0.92) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 13). In the full ANCOVA model, the interaction of insect treatment and density was not statistically

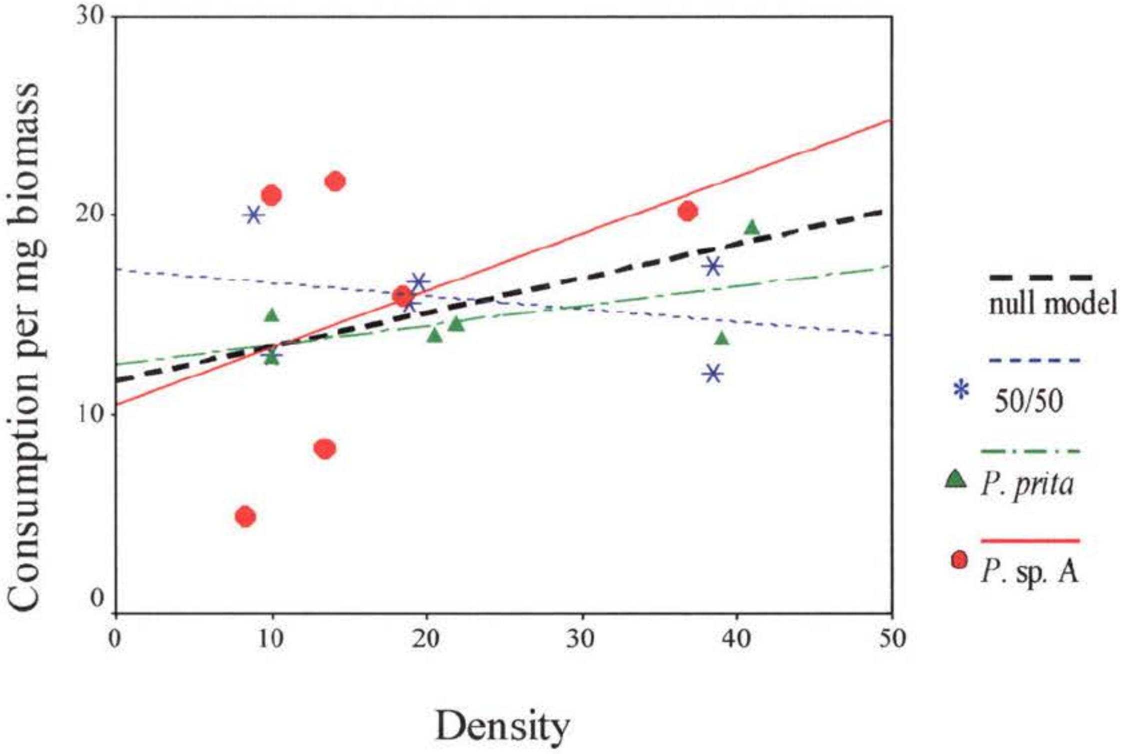

Figure 12. Leaf consumption per mg of insect biomass at increasing densities for the two shredder species alone, in combination, and in relation to a null model.

Table 13. Analysis of covariance of per unit biomass impacts on leaf consumption of the three insect experimental treatments as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	15.29	1	15.29	0.69	0.420
Treatment	4.23	2	2.11	0.10	0.910
Error	310.39	14	22.17		

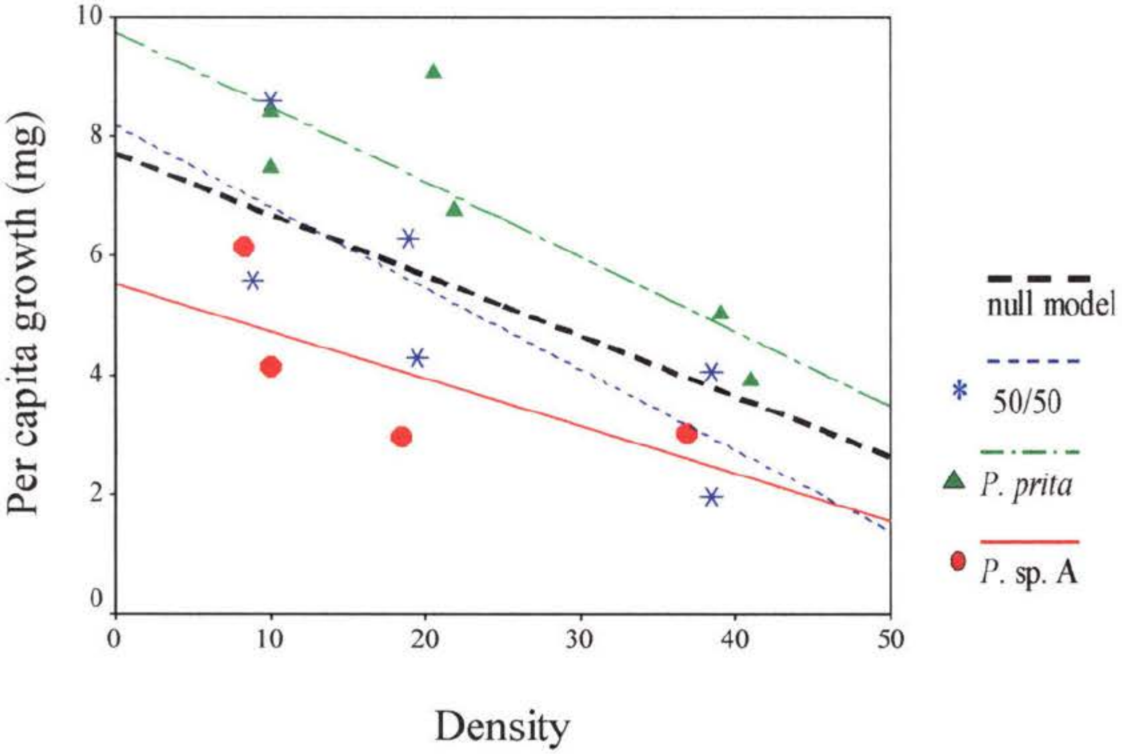

Figure 13. Density dependence of per capita growth (dry mg) of two shredder species alone, in combination, and in relation to a null model.

significant. After removing the treatment*density interaction term, the main effect of density was significant (ANCOVA $F_{1,12}$=20.83, p=0.001) as was insect treatment (ANCOVA $F_{2,12}$=8.52, p=0.005; Table 14). This suggests that species composition had a significant effect on per capita growth, and that growth decreased significantly at higher density.

Growth per unit biomass vs. density

Mean growth per unit biomass (mean weight gain per mg of insect, averaged across all density treatments) was 20.9% higher for *P. prita* than *Psychoglypha* sp. A, and growth per unit biomass declined with density. Mean growth per unit biomass (averaged across all density treatments) of the 100% *P. prita* treatment was 1.10 (± 0.07) mg, 0.91 (± 0.09) mg for the 100% *Psychoglypha* sp. A treatment, and 0.95 (± 0.13) mg for the 50/50% *Psychoglypha* sp. A/*P. prita* treatment (Fig. 14). In the full model, the interaction of insect treatment and density was not significant. After removing the treatment*density interaction term, the main effect of density was significant (ANCOVA $F_{1,12}$=14.21, p=0.003), but insect treatment was not (ANCOVA $F_{2,12}$=3.13, p=0.081; Table 15). This suggests that species composition had no apparent effect on growth per unit biomass, but that growth decreased significantly at high density.

Intra- and interspecific density compensation

I tested for differential effects of intra- and interspecific density compensation on per capita and per unit biomass leaf consumption and growth by comparing the slope of the

Table 14. Analysis of covariance of per capita impacts on insect growth as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	32.70	1	32.70	20.83	0.001
Treatment	26.74	2	13.37	8.52	0.005
Error	18.84	12	1.57		

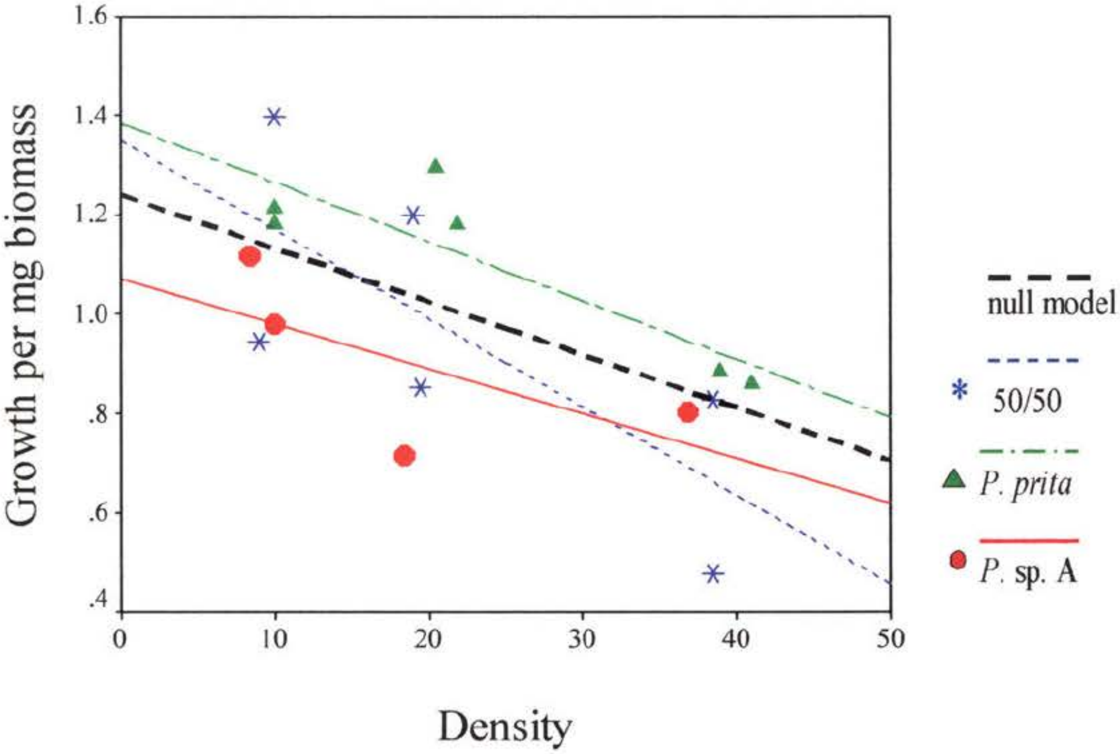

Figure 14. Density dependence of growth per unit biomass (dry mg) of two shredder species alone, in combination, and in relation to a null model.

Table 15. Analysis of covariance of per unit biomass impacts on insect growth as a function of density.

Source of Variation	SS	DF	MS	F	p
Density	0.42	1	0.42	14.21	0.003
Treatment	0.19	2	0.09	3.13	0.081
Error	0.36	12	0.03		

'null model' to the slope of the two species in combination. The slope of the 'null model' represents an average effect of intraspecific density compensation, and the slope of the two species in combination represents interspecific density compensation. In the previous ANCOVA models of density dependence, a significant main effect of density represents significant competition among individuals. However, to assess the relative strengths of intra- vs. interspecific competition, it was necessary to perform separate analyses between the 'null models' and the 50/50 treatments.

Leaf consumption

There were no differential effects of intra- and interspecific density compensation on per capita leaf consumption and leaf consumption per unit biomass. The slope of the 50/50 treatment (interspecific density compensation; slope= -1.06 ± 0.64) did not differ significantly from the slope of the 'null model' (intraspecific density compensation; slope= 0.24 ± 0.61; Table 16) for per capita leaf consumption (two-tailed *t*-test: t=2.05, df=4; p=0.110). Similarly, the slope of the 50/50 treatment (slope= -0.06 ± 0.11) did not differ significantly from the slope of the 'null model' (slope= 0.19 ± 0.12; Table 16) for leaf consumption per unit biomass (two-tailed *t*-test: t=2.41, df=4; p=0.074). As shown in the previous ANCOVA models of density dependence of leaf consumption, the main effect of density was not significant (Tables 12 and 13), therefore, individuals did not compete for leaf consumption. As expected, there was no detectable difference between the relative strengths of intra- vs. interspecific competition for leaf consumption.

Table 16. Separate regressions of per capita and per unit biomass effects on leaf consumption as a function of density of two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	0.80	1.24	49.27	24.06	0.42	0.554
#B	-0.32	0.38	96.17	10.21	0.72	0.444
#A/B	-1.06	0.64	107.18	16.15	2.78	0.171
'null model'	0.24	0.61	72.72	14.32	0.46	0.514
A mg	0.29	0.31	10.50	6.05	0.83	0.413
B mg	0.10	0.07	12.52	1.85	2.04	0.227
A/B mg	-0.06	0.11	17.28	2.71	0.37	0.575
'null model'	0.19	0.12	11.51	2.91	1.40	0.264

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 abundance; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

Secondary production (insect growth)

There were no differential effects of intra- and interspecific density compensation on per capita insect growth and growth per unit biomass. The slope of the 50/50 treatment (slope= -0.14 ± 0.05) did not differ significantly from the slope of the 'null model' (slope= -0.10 ± 0.05; Table 17) for per capita growth (two-tailed *t*-test: t=0.650, df=4; p=0.551). Similarly, the slope of the 50/50 treatment (slope= -0.02 ± 0.01) did not differ significantly from the slope of the 'null model' (slope= -0.01 ± 0.005; Table 17) for growth per unit biomass (two-tailed *t*-test: t=0.938, df=4; p=0.401). As shown in the previous ANCOVA models of density dependence of growth, the main effect of density was significant (Tables 14 and 15), therefore, individuals competed for growth. Indeed, *P. prita* experienced significant intraspecific competition, and the two species in combination experienced strong interspecific competition for growth (Table 17). However, there was no detectable difference between the relative strengths of intra- vs. interspecific competition for growth.

Discussion

Functional redundancy of stream detritivores

Communities may contain species that perform very similar ecological roles (Walker 1992, Lawton and Brown 1993). If species are functionally redundant, then ecosystem processes can be maintained at nearly constant levels despite changes in species composition (Frost et al. 1995). My experiment used the simplest and least ambiguous experimental design to test this hypothesis. Ecosystem responses of two species were measured in isolation and

Table 17. Separate regressions of per capita and per unit biomass effects on growth as a function of density of two shredder species alone, in combination, and in relation to a 'null model' of no interaction between species.

variable	slope	(SE)	intercept	(SE)	F	p
#A	-0.08	0.06	5.54	1.24	1.92	0.300
#B	-0.13	0.04	9.75	1.01	11.10	0.029
#A/B	-0.14	0.05	8.18	1.30	7.00	0.057
'null model'	-0.10	0.05	7.65	1.32	2.34	0.165
A mg	-0.01	0.01	1.07	0.16	1.52	0.343
B mg	-0.01	0.003	1.38	0.09	13.14	0.022
A/B mg	-0.02	0.01	1.35	0.21	4.82	0.093
'null model'	-0.01	0.005	1.23	0.11	3.67	0.092

(#A = *Psychoglypha* sp. A abundance; #B = *P. prita* abundance; #A/B = 50/50 abundance; A mg = *Psychoglypha* sp. A biomass; B mg = *P. prita* biomass; A/B mg = 50/50 abundance; 'null model' = mean of the slopes and intercepts of the two species in monoculture)

compared to the response of a mixture of those species (Inouye 2001). The two species were expected, a priori, to function similarly, as they were congeners that occurred simultaneously on the same resource (stream leaf packs). I found that the two detritivore species were functionally redundant for one ecosystem process, leaf consumption (resource capture), but not redundant for a second response variable, secondary production (growth). These results were consistent with Duffy et al. (2001), who found that three species of grazing amphipods were functionally redundant for impacts on epiphyte accumulation, but were functionally different in impacts on eelgrass biomass and on grazer secondary production. Thus, the demonstration of functional redundancy in my study and Duffy et al.'s (2001) study depends on the response variable considered. These findings are corroborated by many analogous tests of plant diversity effects (reviewed in Schläpfer and Schmid 1999), and studies of vertebrate predator redundancy (Morin 1995, Kurzava and Morin 1998).

Psychoglypha sp. A and *P. prita* had similar overall effects on leaf consumption. However, per capita and per unit biomass impacts of the two species differed. Although no differences were statistically significant, *P. prita* had higher per capita leaf consumption, and *Psychoglypha* sp. A had higher leaf consumption per unit biomass. These results may be explained by small differences in body size of the two species. Species of similar body size exert similar per capita effects (Peters 1983), which was consistent with my overall result of effects on leaf consumption. However, larger individuals are predicted to have higher per capita effects than smaller individuals. Estimated initial weights of experimental insects (based on case length-biomass regressions) and final weights were higher for *P. prita*, which resulted in higher per capita impacts. Additionally, larger individuals have lower per unit biomass food requirements than smaller individuals, i.e., a shrew has to eat its body weight in food each day, an elephant does not (Peters 1983). Although the differences in body size of *P*. sp. A and *P. prita* were relatively small, *P*. sp. A individuals may have required more food per unit biomass to maintain their smaller body size. Accordingly, leaf consumption per unit biomass was higher for *P*. sp. A than *P. prita*.

Several recent studies have found significant differences among species for per capita impacts on some ecosystem level process, and have used this as evidence for diversity effects on ecosystem functioning (Jonsson and Malmqvist 2000, and others). However, in many cases, impacts per unit biomass were not measured (Cardinale et al. 2002a), or the authors included a short statement such as, "although, when biomass was used as a covariate in the analysis, there was no difference among treatments" (Jonsson and Malmqvist 2000). I maintain that species impacts per unit biomass should not be treated as caveats, as they more accurately reflect the metabolic capacity of the assemblage, and thus, their potential impacts on ecosystem processes (Ruesink and Srivastava 2001). This idea is supported by Morin (1995) who maintains that while per capita effects may change with species composition, effects standardized by biomass might be more robust to changes in species composition.

Psychoglypha sp. A and *P. prita* were not redundant for one response variable, secondary production. Secondary production refers to the formation of animal biomass over time, and is the product of growth rate and biomass (Huryn and Wallace 2000). Insect detritivores are responsible for a major fraction of total secondary production in many stream ecosystems, and they are critical links in the food web to higher trophic levels

(Wallace et al. 1999). Furthermore, secondary production may be the most important response to consider when investigating mechanisms of population or community regulation (Benke 1984). Since production has simultaneous effects on multiple trophic levels, the potential for strong biotic control of production clearly exists. However, few studies have addressed the effects of competition, predation etc. in controlling energy flows through food webs in stream ecosystems (Huryn and Wallace 2000).

In this experiment, *P. prita* produced more biomass on both a per capita and per unit biomass basis than *Psychoglypha* sp. A. Differences in production may be due to differences in growth rate and size of the two species. Average daily growth rate was higher for *P. prita* than *Psychoglypha* sp. A. Additionally, *P. prita* was larger than *Psychoglypha* sp. A throughout the experiment. More biomass and a higher growth rate resulted in higher production for *P. prita* over the course of the experiment. However, it is unlikely that a one month 'snapshot' of the two species' growth reflects what occurs throughout the year. Quantifying the intrinsic rate of growth for both species over the course of one full year (including winter months) could reveal temporal segregation of maximum growth between these two species.

Phenological complementarity (asynchrony of species' growth rates) has been found in several studies (Grafius and Anderson 1980, Duffy et al. 2001, Stevens and Carson 2001, but see Richardson 2001). Phenological complementarity may enhance ecosystem function when resources are ephemeral and different species peak at different times throughout the growing season (Stevens and Carson 2001). Such seasonal complementarity likely results in more constant levels of ecosystem processes on an annual basis due to an averaging of the effects of several independently varying species (Duffy et al. 2001). Among closely related taxa, however, phylogenetic constraint may result in overlapping phenology. In this case, temporal separation of resource use may not occur since major growth periods for congeners would overlap to some extent (Richardson 2001). However, Grafius and Anderson (1980) found an approximately three month separation of maximum growth rate between congeners of *Lepidostoma* (Trichoptera).

Kurzava and Morin (1998) state that any assessment of functional redundancy will depend on the measure used to assess the impacts of species on ecosystem processes. If this is a truism, how do we define functional redundancy? Walker (1992) maintains that complete redundancy only occurs when there is density compensation among remaining species. However, Lawton and Brown (1993) state that redundancy occurs when biomass or productivity levels are maintained despite changes in species composition. My results suggest that density compensation may not necessarily return biomass or productivity levels to antecedent conditions. Differences in body size, and thus, per capita impacts of species can result in different levels of ecosystem functioning. Similarly, return to antecedent total biomass may not maintain levels of ecosystem processes if that biomass is divided among more individuals of smaller body size. Many small individuals will not have the same metabolic capacity as fewer large individuals, as metabolic rate scales nonlinearly with body size (Peters 1983). Finally, many small individuals may compete for resources at high density, and thus inhibit one another and overall productivity (see below). These things considered together, in conjunction with my experimental results confirm the difficulty of defining functional redundancy.

Species interactions

The importance of species interactions in structuring stream communities has been demonstrated in a number of studies (Hawkins and Furnish 1987, Malmqvist 1993, Hill 1992, Kohler 1992, Kohler and Wiley 1997, Soluk and Richardson 1997, Cardinale et al. 2002a, Cross and Benke 2002, and others). The focus on abiotic factors in affecting the distribution and abundance of species has been re-evaluated in light of these recent studies. Harsh environmental conditions of streams, e.g. variable flow regimes, were thought to maintain population sizes at levels where resource limitation was unlikely and the impact of predators were negligible relative to abiotic factors (Hynes 1970). However, streams differ in the magnitude of discharge variation, and resource limitation and biotic interactions can be strong even during periods of relatively stable flow (Kohler 1992). In relatively stable habitats, interactions among individuals may increase as a result of the release of physical constraints on their distribution and growth (Cross and Benke 2002).

Leaf detritus represents a limiting resource that can result in intense competition or complementarity among stream detritivores (Richardson 1991, Dobson and Hildrew 1992, Finn 2001). In this experiment, I tested for species interactions using 'null models'. 'Null models' represented expected responses of the two species in combination if there were no non-additive interactions between them (Emmerson and Raffaelli 2000). If *Psychoglypha* sp. A and *P. prita* inhibited or facilitated one another, the response of the 50/50 treatments would deviate from the 'null model'. Although not statistically significant, both leaf consumption and secondary production (on a per capita and a per unit biomass basis) revealed inhibition (interspecific competition) between the two species. In all cases, the two species in combination performed worse than the 'null models'. Interspecific competition has been found in several studies that investigated taxonomically distant pairs of stream invertebrates (Hart 1985, Hawkins and Furnish 1987, Lamberti et al. 1987, Hill 1992, Kohler 1992, Kohler and Wiley 1997). For example, Kohler (1992) found significant interspecific competition between caddislarvae (*Glossosoma* sp.; Trichoptera) and mayfly larvae (*Baetis* sp.; Ephemeroptera). However, few experiments have tested congeneric species (Cross and Benke 2002). Congeneric pairs, through their similar resource requirements, are good study organisms for competition experiments because they are likely to compete.

Mechanisms of competition include exploitative (or consumptive) competition and interference competition. In exploitative competition, the interaction between individuals is mediated by a limiting food resource. Interference competition involves aggressive or non-aggressive encounters between individuals (Lamberti et al. 1987). In communities dominated by mobile taxa, at least two forms of non-aggressive encounters can occur. By contacting other individuals while moving, individuals can affect the ability of others to remain in habitats and the amount of time individuals are able to feed (Kohler 1992).

My results suggest that both exploitative and interference competition may have occurred between *Psychoglypha* sp. A and *P. prita*. Although not statistically significant, reduced per capita leaf consumption at high density for the two species in combination suggests that individuals ate less when neighboured with congeners, and deviation of the 50/50 treatments from the 'null models' was evidence of interspecific competition for food. Evidence for interference competition was revealed by analyses of density dependence. Per capita leaf consumption and consumption per unit biomass were not density dependent, whereas per capita growth and growth per unit biomass were density dependent. This suggests that at high density, individuals were capturing similar amounts of leaf matter as at lower densities, but were not converting it to biomass. In monoculture particularly, resources did not seem to be limited, yet individuals still experienced a decline in growth. Individuals may have experienced non-aggressive encounters with one another at high density, for example, and may have been 'knocked off' of food patches by mobile neighbours before food could be consumed. Several other studies have found evidence of both exploitative and interference competition (Lamberti et al. 1987, Hawkins and Furnish 1987, Kohler 1992), thus these two mechanisms may be common mediators of interactions between stream invertebrates.

Intra- and interspecific density compensation

By varying intra- and interspecific density compensation among treatments, the experimental design used in this study addressed two questions simultaneously for each species. First, did competition occur, and second, what were the relative strengths of intra- and interspecific competition for each species (Underwood 1986, Inouye 2001). Determining the relative strengths of intra- and interspecific competition allows for assessment of whether or not interspecific interactions affect the distribution and abundance of populations. If intraspecific competition is stronger, conspecifics may regulate populations to levels below those where interspecific interactions will be realized (Lawton and Hassell 1981, Underwood 1986, Lamberti et al. 1987, Cross and Benke 2002).

There were no differential effects of intra- and interspecific density compensation among *Psychoglypha* sp. A and *P. prita*. Neither intra- nor interspecific density compensation resulted in detectable competition for per capita leaf consumption and leaf consumption per unit biomass. However, I found significant intraspecific competition within *P. prita*, and strong interspecific competition between *P.* sp. A and *P. prita* for both per capita growth and growth per unit biomass. In all cases, however, the relative strengths of intra- and interspecific competition did not differ significantly from one another, which potentially allows these two strong competitors to coexist.

Competition experiments and issues of species coexistence are coupled with one another. Despite strong interspecific competition for the same limiting resource, *Psychoglypha* sp. A and *P. prita* continue to coexist. Competition theory predicts that stable coexistence should occur if the effects of intraspecific competition are stronger than the effects of interspecific competition for both species (Connell 1983). Although I found no statistical difference between intra- and interspecific competition, my results are consistent with this theory and the results of Cross and Benke (2002), in that coexistence among these two species may be mediated by slightly stronger competition among conspecifics than congeners.

Coexistence of competitors may also be mediated by spatial segregation (e.g. non-overlapping distributions), disturbance (e.g. changes in flow regime that can reduce population densities and 'reset' the system) and predation (Cross and Benke 2002). None of these three possibilities was investigated in this study, as experiments were conducted within mesocosms (artificial stream channels) that imposed spatial aggregation, experienced stable flow regimes throughout the study, and excluded predators within the experimental communities. It is unlikely, however, that spatial segregation mediates the coexistence of *Psychoglypha* sp. A and *P. prita*, as they co-occur on leaf packs in Richard

Creek. Disturbance is also an unlikely mediator of coexistence in this system, although rare flash floods may occur in Richard Creek, which can reduce population densities. However, I have shown that competition can be strong during periods of relatively stable flow conditions. Predation may prevent competitive exclusion through direct consumption of prey or indirectly by changing prey life history or feeding behaviour (Paine 1969, Peckarsky et al. 2002). Predation may mediate species coexistence in this system as trout and insect predators were both present in Richard Creek. However, this possibility remains untested.

Context dependency of functional redundancy

Species may appear functionally redundant under a restricted set of conditions, yet their functional roles may vary with environmental context (Cardinale et al. 2000, Duffy et al. 2001, Mulder et al. 2001, Wellnitz and Poff 2001, Cardinale et al. 2002b, Rosenfeld 2002). Environmentally mediated shifts in species function may be temporal or spatial. Phenological complementarity (as previously discussed) can result in relatively constant levels of ecosystem processes on an annual basis due to an averaging of the effects of several independently varying species (Duffy et al. 2001). Spatial environmental heterogeneity can also influence species' performances. The contributions made by individual species to overall ecosystem function can be shaped by differences in ecological performance across natural gradients. For example, a species may appear redundant at one point along an environmental gradient, but out-perform guild members at another (Wellnitz and Poff 2001).

Context dependency of functional redundancy has been illustrated theoretically and empirically. Wellnitz and Poff (2001) provide a theoretical example of how functional redundancy of stream grazers can depend on environmental context (low, medium and high current velocity). In their example, three species of stream grazers (A, B and C) are functionally equivalent in terms of their ability to remove attached algae from rocks at low current velocity. Similarly, if algal removal is averaged over all velocities, the three species have redundant mean effects. However, at medium velocity, species C outperforms other guild members, and at high current velocity, species B performs best. This example illustrates the importance of examining species function at multiple points along environmental gradients, yet few studies of functional redundancy have incorporated environmental heterogeneity (but see Mulder et al. 2001, Cardinale et al. 2002b).

Two recent studies provide empirical evidence of context dependency of species' function. Mulder et al. (2001) used species of mosses and liverworts to demonstrate that under constant conditions, species appeared functionally redundant, whereas under drought conditions, biomass increased with species richness through facilitative interactions among species. Cardinale et al. (2002b) demonstrated that primary productivity of stream algae and respiration of benthic biofilm increased in high-heterogeneity treatments more so than in low-heterogeneity treatments. The mechanisms responsible for the observed differences were physically mediated (alterations in near-bed velocity and turbulence intensity), and illustrate the influence of environmental context on species' function.

Detectable differences

Experiments of species' functional roles performed in homogeneous environments may bias results toward finding redundancy. In most experiments that examine species' functional roles and their interactions, environmental 'noise' is treated as a variable to control (Wellnitz and Poff 2001). In particular, mesocosm experiments (e.g. artificial stream channels) attempt to design as uniform an environment as possible. While uniform environments provide controlled, replicatable habitats in which to conduct experiments, they may not promote niche partitioning which would likely occur under natural conditions, and thus may bias results toward finding redundancy (Duffy et al 2001). Mesocosm experiments are still useful, however, as they can be used to test predictions at the scale of individual organisms, populations and communities, and permit quantification of mechanisms that mediate species interactions (Huston 1999).

Experiments that test for functional redundancy performed in uniform environments promote similarity of species' functional roles, and may fail to detect a difference between species when it actually exists if experimental power is low (Osler 2002). Power analysis allows for post hoc estimation of experimental power and the *a priori* estimation of sample sizes required to test hypotheses at set levels of power. Statistical power is defined as $(1-\beta)$, where β is the probability of failing to reject the null hypothesis (no difference among treatments) when it is false. Four things affect power: (1) choice of α level, (2) sample size, (3) effect size, and (4) residual variance (Underwood 1997).

Experiments can be constrained by many factors that limit the maximization of power. My experiment failed to detect a significant difference between *Psychoglypha* sp. A and *P. prita* for several response variables. In this particular case, the experiment was constrained by all four variables that affect power. Most importantly, however, power was constrained by low sample size, which was fixed at 24 artificial stream channels. For example, to detect a significant difference between the slope of the 50/50% *Psychoglypha* sp. A/*P. prita* treatment and the 'null' slope for per capita leaf consumption and leaf consumption per unit biomass, I would have needed to double the number of replicates from six (e.g. per capita consumption: two-tailed *t*-test: t=1.41, df=4; p=0.231) to twelve (two-tailed *t*-test: t=2.33, df=10; p=0.042). Similarly, to detect a significant difference between the 50/50 slope and the 'null' slope for per capita growth and growth per unit biomass, I would have needed to quadruple the number of replicates from six (e.g. per capita growth: two-tailed *t*-test: t=0.915, df=4; p=0.412) to twenty four (two-tailed *t*-test: t=2.20, df=22; p=0.039). These examples illustrate the need for power analyses in tests of species' roles in ecosystem function to determine variables such as minimum sample sizes necessary to detect differences among treatments. However, few studies in this area of research report any estimates related to experimental power (Osler 2002).

Conclusions

Classifying species as functionally redundant depends on the response variable considered. Species may have similar functional effects for one response variable, but not another. In this experiment, *Psychoglypha* sp. A and *P. prita* were functionally redundant for leaf consumption, but differed for another response variable, secondary production. Thus, in terms of assessing the functional redundancy of individual species, the fewer response variables measured, the more likely it is that species will be classified as functionally redundant (Rosenfeld 2002).

Psychoglypha sp. A and *P. prita* were competitors in this experiment. Interspecific competition reduced performance in species-combination treatments compared to the performance of monocultures. Walker (1992) and Lawton and Brown (1993) consider such competition strong evidence of functional redundancy among species. Interspecific release of resources (Mikola and Setälä 1998) and compensatory growth (Frost et al. 1995) were likely mechanisms by which levels of ecosystem processes could be maintained at nearly constant levels. Coexistence of these two strong competitors may be mediated by nearly identical relative strengths of intra- and interspecific competition.

Finally, intense interest in the ecosystem consequences of declining diversity has prompted numerous studies searching for general relationships between species diversity and process rates. At a mechanistic level, however, it is the characteristics of coexisting species that are fundamental to explaining the form of these general relationships. Future studies in this area of research need to investigate mechanisms that mediate species coexistence. Furthermore, studies should be conducted under environmentally heterogeneous conditions to simulate natural conditions. This experimental approach should increase the detectability of differences among species when they exist. This is not a trivial issue, as failing to detect differences among species when they exist is potentially dangerous from a conservation perspective.

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Author [redacted]

Lisa Nadine Saba Shama

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