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The importance of crayfish in the breakdown of rhododendron leaf litter

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SUMMARY

1. Rhododendron (*Rhododendron maximum*) is a common evergreen shrub in riparian areas of the southern Appalachians, where its leaves can comprise a large proportion of leaf litter in streams. However, they are relatively refractory and generally considered a low quality food resource for detritivores.
2. Our objective was to assess whether macroconsumers [primarily crayfish (*Cambarus bartonii*)] influence rhododendron leaf breakdown in a forested southern Appalachian stream in both summer (when leaves other than rhododendron are relatively scarce) and autumn (when other leaves are relatively abundant). We conducted two leaf decay experiments, one in summer and one in autumn, using pre-conditioned leaves. Macroconsumers were excluded from the benthos of a fourth-order stream using electric 'fences'; we predicted that excluding macroconsumers would reduce the decay rate of rhododendron leaves in both summer and autumn.
3. In both experiments, breakdown rate was lower in exclusion treatments. Macroconsumers accounted for approximately 33 and 54% of rhododendron decay in summer and autumn, respectively. We attribute this effect to direct shredding of rhododendron by crayfish. Biomass of insect shredders, insect predators and fungi did not differ between control and exclusion treatments, indicating that insectivorous sculpins (*Cottus bairdi*) had no effect on rhododendron decay and that omnivorous crayfish did not exert an indirect effect via alteration of insect or fungal biomass.
4. The influence of shredding insects varied between summer and autumn. In summer, when other, more palatable leaf types were not available, rhododendron leaf packs appeared to provide 'resource islands' for insect shredders. There was a significant inverse relationship between insect shredders and leaf pack mass in the summer exclusion treatment: insects were the only organisms eating leaves in this treatment and, as shredder biomass increased, remaining leaf pack mass decreased. In the control treatment, however, we did not see this relationship; here, the effect of insect shredders was presumably swamped by the impact of crayfish. In autumn, when other leaves were abundant, insect shredder biomass in rhododendron leaf packs was less than one-third of summer values.
5. Even at low density (approximately 2 m^{-2}) crayfish were able to influence an ecosystem process such as leaf decay in both summer and autumn. Given the threatened status of many crayfish species in the United States, this finding is especially relevant. Even small alterations in crayfish assemblages, whether via loss of native species and/or introduction of exotic species, may have significant repercussions for ecosystem function.

Keywords: crayfish, fungi, leaf decay, rhododendron, stream

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Introduction

The importance of macroconsumers (fish, shrimp, crayfish) in structuring stream communities has been documented by many researchers (e.g. Gelwick & Matthews, 1992; Pringle *et al.* 1993; Charlebois & Lamberti, 1996; Flecker, 1996). These relatively large organisms can influence numerous aspects of the stream environment, including sediment accumulation (e.g. Power, 1990a; Pringle & Blake, 1994), algal and invertebrate assemblages (e.g. Power, Matthews & Stewart, 1985; Power, 1990b; Flecker, 1992; Charlebois & Lamberti, 1996; Pringle & Hamazaki, 1998), and ecosystem processes such as leaf breakdown (e.g. Parkyn, Rabeni & Collier, 1997).

In many temperate streams, crayfish are a common component of the macrofaunal assemblage. Because crayfish are omnivorous, relatively long-lived and large-bodied (Momot, 1995), they can have significant impacts on in-stream resources, including algae, other invertebrates and detritus (e.g. Creed, 1994; Charlebois & Lamberti, 1996; Parkyn *et al.*, 1997; Keller & Ruman, 1998). In addition, crayfish are one of the most threatened faunal groups, with 65% of species in the United States considered vulnerable, threatened or extinct (Richter *et al.*, 1997). Determining the role of crayfish in structuring benthic communities and influencing energy flow through stream ecosystems is of growing importance, given their endangered status.

Crayfish are thought to feed primarily on detritus, especially as adults (Momot, 1995; Rabeni, Gossett & McClendon, 1995; Whitledge & Rabeni, 1997). Because they assimilate detritus inefficiently (typically ≤ 30%; Rabeni *et al.*, 1995; Whitledge & Rabeni, 1997) crayfish may consume large quantities of this resource, thereby greatly accelerating leaf breakdown rates (e.g. Parkyn *et al.*, 1997; Usio, 2000). Many leaf breakdown studies have been conducted at the Coweeta Hydrologic Laboratory, a US Forest Service (USFS) research facility in the southern Appalachian Mountains, U.S.A. [see Webster *et al.* (1999) for an overview]. Most of these studies have focused on the role of aquatic insects (e.g. Webster & Waide, 1982; Wallace, Webster & Cuffney, 1982) and microbes (e.g. Paul & Meyer, 1996) in leaf breakdown; only one has explicitly addressed the influence of crayfish.

Huryn & Wallace (1987) conducted laboratory feeding trials which showed that leaf processing by *Cambarus bartonii* (Fabricius), a common crayfish at Coweeta, was positively correlated with water temperature. They predicted that peak litter consumption by crayfish would occur from June to September, when temperature was high, other shredding invertebrates were less active and litter standing crops were low. Consequently, they postulated that *C. bartonii* may play a significant role in the breakdown of rhododendron [*Rhododendron maximum* (L.)] leaves in summer. Rhododendron is an evergreen shrub that loses its leaves primarily in autumn, dropping approximately 9% of its leaf standing crop each year (Monk, McGinty & Day, 1985). It is one of the most refractory leaf species at Coweeta (Whiles, Wallace & Chung, 1993), so it may persist in stream channels for long periods. By mid-summer, when other leaf types are relatively scarce, rhododendron leaves can be well-conditioned and available for crayfish consumption (Huryn & Wallace, 1987).

Our objective was to assess whether macroconsumers (primarily crayfish) influence rhododendron leaf breakdown in a forested southern Appalachian stream in both summer (when leaves other than rhododendron are relatively scarce) and autumn (when other leaves are relatively abundant). To answer this question, we conducted two rhododendron decay studies, one in summer and one in autumn, using pre-conditioned leaves. Macroconsumers were excluded from the benthos of a fourth-order stream using electric 'fences'; we hypothesized that macroconsumer exclusion would lead to a decreased rate of rhododendron breakdown in both summer and autumn.

Methods

Study site

Experiments were conducted in Lower Ball Creek, a fourth-order stream at the USFS Coweeta Hydrologic Laboratory in western North Carolina, USA (35°N, 83°30'W). Coweeta is a 2185-ha facility located in the Blue Ridge physiographic province of the southern Appalachians. Mean monthly air temperature ranges from 3 to 22 °C, and annual precipitation ranges from 180 cm at low altitude to 250 cm at high altitude (Swank & Crossley, 1988). During our experiments, continuous discharge data were collected at Lower Ball Creek by USFS researchers; continuous temperature

data were collected by Dr J.B. Wallace (University of Georgia, U.S.A.).

The Lower Ball Creek catchment is forested (approximately 100%) by mixed hardwood species such as red maple [*Acer rubrum* (L.)] and tulip-poplar [*Liriodendron tulipifera* (L.)]. Riparian areas are densely vegetated by rhododendron (*R. maximum*), mountain laurel [*Kalmia latifola* (L.)] and dogwood [*Cornus florida* (L.)]. Altitude at our study site is about 700 m, with a stream gradient of approximately 4 cm m^{-1}. Boulder, cobble and gravel comprise the stream substratum. Macroconsumer assemblages in Lower Ball Creek are dominated by crayfish (*C. bartonii*) and mottled sculpin [*Cottus bairdi* (Girard)], but longnose dace [*Rhinichthys cataractae* (Valienciennes)] and rosyside dace [*Clinostomus funduloides* (Girard)] are also present.

Experimental design

Rhododendron decay experiments were conducted in summer and autumn 1999. Freshly fallen rhododendron leaves (i.e. brown but not buried or decomposed) were collected near Lower Ball Creek on 17 March and 18 June for summer and autumn experiments, respectively. Previous research indicated that initial rhododendron decay is very slow (e.g. Webster & Waide, 1982; Benfield *et al*., 1991). Because we wanted to be able to detect a change in leaf mass over a limited experimental period, we used pre-conditioned leaves to accelerate the decay process. Leaves were placed in plastic mesh (5 mm) bags and secured in the stream with aluminium gutter nails for pre-conditioning. Summer leaves remained in the stream from 17 March to 15 July, for a pre-conditioning period of 1574 degree days (mean daily water temperature, 12.9 °C). Autumn leaves remained in the stream from 18 June to 25 August (mean daily water temperature, 17.2 °C). On 25 August, leaves were removed from the stream and rinsed to remove macro-invertebrates; they were then refrigerated at 4 °C from 26 August to 2 October to slow decomposition and compensate for higher pre-conditioning temperatures (i.e. relative to summer leaves). Pre-conditioning period for the autumn leaves was 1302 degree days.

On 7 July, 10 intact leaves were removed from summer pre-conditioning bags to determine a wet/dry mass conversion factor. Each leaf was weighed immediately upon removal from the stream to obtain a wet mass, then dried at 70 °C for 24 h and reweighed to obtain a dry mass. The wet/dry mass ratio (mean ± 1 SE) was 5.25 ± 0.08; thus, we used 26.2 g wet mass per pack for approximately 5 g dry mass leaf packs. The same ratio was used for autumn leaf packs, and initial dry mass was similar between summer and autumn experiments (mean ± 1 SE, 4.49 ± 0.08 g in summer versus 4.88 ± 0.21 in autumn). All macro-invertebrates were rinsed from leaves prior to leaf pack assembly. Rinsed leaves were distributed into packs of appropriate mass, which were held together by two plastic fasteners placed near leaf midribs. Because the pre-conditioned leaves were relatively fragile, packs also were wrapped in plastic mesh (2 cm) to minimize the loss of large leaf fragments; this mesh was large enough to allow access by macro-invertebrates, including crayfish.

Leaf packs were attached with nylon monofilament to polyvinylchloride frames (0.25 m^2) lined with copper wire. Each pack was weighted with a lead weight (85 g) to keep it flush with the substratum. In the summer experiment five leaf packs were secured in each frame. In the autumn experiment fewer intact leaves were available, so four packs were used per frame. During both summer and autumn, 10 frames (five pairs) were placed in run habitats of Lower Ball Creek, along an approximately 0.5 km stream reach. Placement of pairs was determined by preliminary shear stress measurements using calibrated hemispheres (Statzner & Müller, 1989); only sites which provided a suitable area (e.g. without large boulders) with similar shear stresses were used. Water velocity and depth were measured at the four corners of each frame using a Marsh McBirney (Frederick, MD, U.S.A.) current meter and a metre stick. Canopy cover was measured over the centre of each frame using a spherical densitometer (Forest Densiometers, Bartlesville, OK, U.S.A.).

To exclude macroconsumers, one frame in each pair was chosen by coin toss to be the exclusion treatment. This frame was connected to a 6-V solar-powered fence charger (Parmak Model DF-SP-SS, Parker McCrory Manufacturing, Kansas City, MD, U.S.A.) that delivered repeated pulses of electricity to the 0.25 m^2 frame area. These electric pulses prevented the entry of crayfish and fish, but did not adversely affect smaller organisms such as aquatic insect larvae. Many other studies have used this electric exclusion

technique (e.g. Pringle & Blake, 1994; Pringle & Hamazaki, 1997), which avoids some artefacts associated with traditional cage enclosure experiments (e.g. reduced water flow and increased sedimentation). The other frame in each pair served as a control area to which macroconsumers had access. Frames were placed approximately 0.5 m apart to minimize the impact of exclusion treatments on controls; given that macroconsumers were frequently found immediately outside electrified frames, this distance appeared to be more than adequate. Throughout the experiment, fence charger batteries were replaced every 5 days to ensure a consistent 6 V charge. Frames also were cleared of accumulated leaves every 5 days to minimize flow alterations and prevent loss of frames during spates.

Sampling

The summer experiment began on 16 July and ended on 29 August. One leaf pack was removed from each frame on days 5, 10, 20, 32 and 44. In addition, six packs were brought back to the lab on day 0 to determine initial leaf weights and fungal biomass. The autumn experiment began on 3 October and ended on 28 November. Leaf packs were sampled on days 8, 20, 35 and 56, and nine packs were used for day 0 assessments. Fence chargers at exclusion treatments were turned off briefly (5–10 min) for sampling. A 210-μm mesh hand net was held downstream of each leaf pack as it was removed from the stream to retrieve any dislodged invertebrates. Leaf packs were placed in plastic bags, put on ice and returned to the laboratory (2 h away) for processing. Prior to removing the leaf packs, all replicates were examined using a clear plastic viewing box to determine whether any macroconsumers were present. In previous experiments we observed replicates for 5 min, but limited visibility in the current study made these prolonged observations inefficient. Instead, we recorded presence or absence of macroconsumers during spot checks of all replicates on all sampling dates, as well as every 5 days when fence charger batteries were changed ($n = 80$ spot checks in summer, 100 in autumn). In addition, any macroconsumers seen during leaf pack removal (i.e. that were hiding under leaf packs or cobbles during spot checks but were disturbed during sampling) were noted, and we conducted four spot checks of all replicates at night.

Leaf packs were processed within 24 h of sampling. Leaves were rinsed to remove invertebrates and sediment. Invertebrates were live-picked from the rinsed material and preserved in 70% ethanol. We chose to focus on insect shredders and predators because they were the functional feeding groups most likely to affect rhododendron decomposition (shredders directly through leaf consumption, predators indirectly through consumption of shredders). Insects classified as shredders or predators by Merritt & Cummins (1996) were later identified to the lowest practical level (usually family or genus) using a dissecting microscope (10× magnification), and measured to the nearest 0.5 mm using 1 mm grid paper. Shredder and predator biomasses were calculated using family-specific length-mass regressions from Benke *et al*. (1999). Organisms < 1.5 mm were identified to order and were not included in shredder or predator biomass values (typically they contributed < 0.01% of total invertebrate biomass). Shredders and predators from days 20, 32 and 44 (summer experiment) and days 20, 35 and 56 (autumn experiment) samples were identified.

After invertebrates were rinsed from leaf packs, 100 leaf discs were randomly removed from each pack using a hole punch (6 mm diameter). Fifty discs were preserved in methanol for fungal biomass analysis via ergosterol extraction (Newell, Arsuffi & Fallon, 1988; with slight modifications after Paul & Meyer, 1996). Ergosterol was extracted from day 0, 10, 20 and 32 (summer) and day 0, 8, 20 and 35 (autumn) samples. By day 44 of the summer experiment, only two control and two exclusion treatments had enough leaf material remaining for ergosterol analysis; by day 56 of the autumn experiment, no packs had enough leaf material remaining. Fungal biomass was estimated from ergosterol concentration using a conversion factor of 5 μg ergosterol (mg mycelial dry mass)$^{-1}$ (Gessner & Chauvet, 1993; Paul & Meyer, 1996). The remaining 50 discs from each pack underwent the same drying and ashing process as the leaf packs. Packs were dried at 70 °C for 3 days, weighed, then burned at 500 °C for 6 h and reweighed. Total ash-free dry mass (AFDM) remaining was calculated by summing AFDM of each leaf pack and 2 × AFDM of the 50 leaf discs.

To quantify the availability of rhododendron and non-rhododendron leaves at the end of each experiment, we randomly selected 10 cross-stream transects

(two near each treatment pair, each 1 m wide) and collected all leaves within each transect. These leaf collections were returned to the laboratory, rinsed free of macro-invertebrates, and sorted into rhododendron and non-rhododendron leaves. Leaves were dried at 70 °C for approximately 1 week, then weighed to determine dry weight (g m^{-2}) for the two leaf types.

To assess crayfish density, we sampled a 50-m transect within the experimental reach on 7 August and again on 4 November (no treatments were located inside the 50 m transect). On each date, 15 randomly located samples were taken using a quadrat sampler, which blocked off 1 m^2 of the stream bottom (i.e. total area sampled, 15 m^2). Crayfish from each sample were counted, identified and measured before being returned to the stream.

Statistical analysis

Initial physical parameters for each replicate were compared using a two-factor MANOVA (treatment and season), with water velocity, water depth, % canopy cover and shear stress as response variables. If MANOVA showed a significant effect, separate univariate two-factor ANOVAs were run for each physical parameter. Availability of rhododendron and non-rhododendron leaves was compared using a two-factor ANOVA (leaf type and season); if ANOVA showed a significant interaction between factors, separate paired *t*-tests were run for each season. To calculate leaf breakdown rate (k), we regressed the natural log of % AFDM remaining against day or degree day (where k is the slope of the regression). Breakdown rate was calculated for each replicate, then compared using two-factor ANOVA (treatment and season); separate ANOVAs were run for day and degree day calculations. A two-factor MANOVA (treatment and season), with predator and shredder biomass (average over three sample dates) as response variables, was run to test for any season or treatment differences in insect biomass. If significant effects were detected with MANOVA, univariate two-factor ANOVAs were run for each response variable. To examine whether insect shredders were affecting leaf pack mass, we regressed AFDM remaining against shredder biomass for the summer and autumn experiments. Fungal biomass (average over three sample dates) was compared using a two-factor ANOVA (treatment and season). Prior to all statistical analyses, Levene's test was used to determine whether variances were equal; where necessary, data were transformed using a natural log or inverse transformation. For all analyses, $\alpha = 0.05$, and all were conducted in SAS® System for Windows™, Release 6.12 (SAS Institute, Cary, NC, U.S.A.).

Results

Mean daily water temperature during the summer experiment was 17.9 °C (range 16.9–19.2 °C) and 11.2 °C (range 6.4–14.9 °C) during the autumn experiment. Peak daily discharge was greater and more variable in autumn (mean ± SE, 217.5 L s^{-1}± 54.7) than in summer (99.1 L s^{-1}± 5.2), largely because of

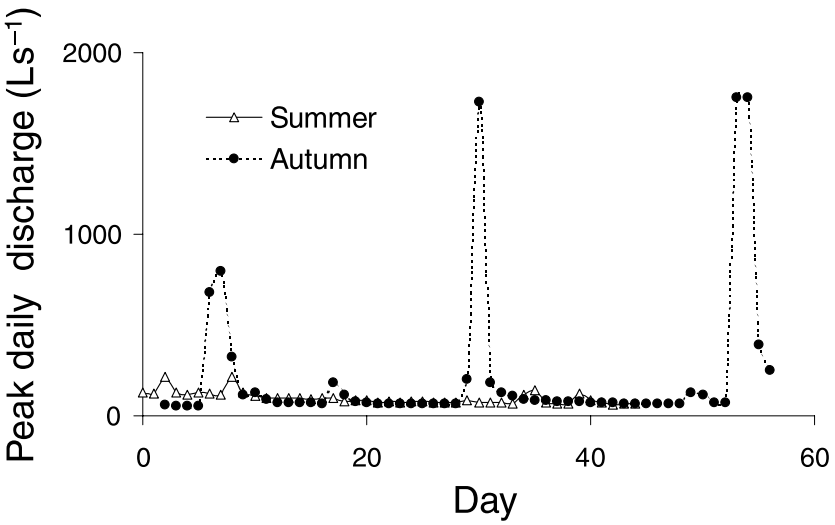

Fig. 1 Peak daily discharge (L s^{-1}) during summer and autumn experiments.

Table 1 Initial physical parameters for control and macroconsumer exclusion treatments, summer and autumn experiments. Values are mean of five (summer) or four (autumn) replicates, ± 1 SE

	Summer		Autumn	
	Control	Exclusion	Control	Exclusion
Water velocity (m s^{-1})	0.20 ± 0.01	0.18 ± 0.02	0.07 ± 0.02	0.11 ± 0.02
Water depth (cm)	16.8 ± 0.1	15.5 ± 0.1	12.1 ± 3.5	11.0 ± 1.1
Canopy cover (%)	88.3 ± 0.9	87.6 ± 1.1	97.7 ± 0.3	98.6 ± 0.3
Shear stress (dyn cm^{-2})	160 ± 26	160 ± 26	145 ± 28	145 ± 28

the occurrence of three distinct discharge peaks during the autumn experiment (Fig. 1). Water conductivity was similar in summer and autumn (mean ± SE, 12.5 μS cm^{-1} ± 0.26 in summer, 12.0 μS cm^{-1} ± 0.25 in autumn). Nutrient concentrations were relatively low in both summer and autumn, although concentrations were higher in summer: mean NO_3–N, NH_4–N, and soluble reactive phosphorus concentrations were 0.057, 0.004 and 0.009 mg L^{-1}, respectively, during the summer experiment, versus 0.004, 0.003 and 0.003 mg L^{-1} during the autumn experiment.

Initial physical parameters for treatment replicates are presented in Table 1. In the autumn experiment, one treatment pair differed significantly from the remaining four pairs in terms of these physical parameters. This pair was excluded from all analyses, leaving four replicate pairs for the autumn experiment and five replicate pairs for the summer experiment. Control and exclusion treatments did not differ in the measured parameters (MANOVA: Pillai's trace = 0.045, $F_{4,11} = 0.131$, $P = 0.968$), but there were significant seasonal (i.e. summer versus autumn) differences (MANOVA: Pillai's trace = 0.953, $F_{4,11} = 55.8$, $P < 0.0001$). Univariate analyses for each parameter indicated that water velocity (ANOVA: $F_{1,14} = 21.5$, $P = 0.0004$), water depth (ANOVA: $F_{1,14} = 6.25$, $P = 0.0254$), and percentage canopy cover (ANOVA: $F_{1,14} = 145$, $P < 0.0001$) contributed to this significant season effect: initial water velocities and depths were lower in autumn than in summer, while percentage canopy cover was greater (Table 1).

No macroconsumers were observed in the electrified frames, indicating that the exclusion technique was effective. Crayfish and sculpins occasionally entered the exclusion treatment while fence chargers were turned off briefly for sampling, but they left immediately when chargers were reactivated. During the summer experiment, a total of 11 crayfish were observed in control replicates (40 spot checks). During the autumn experiment large accumulations of leaves obscured spot checks, and only one crayfish and two sculpins were observed in control replicates (50 spot checks). Crayfish densities within the experimental reach were slightly higher in summer (mean ± SE, 2.33 m^{-2} ± 0.69) than in autumn (1.87 m^{-2} ± 0.50), although this difference was not significant.

Rhododendron leaves comprised more than 50% of the leaf material found in Lower Ball Creek at the end of the summer experiment (Table 2). Standing crop of rhododendron was similar in summer and autumn, while standing crop of non-rhododendron leaves (e.g. maple, birch, sycamore, dogwood) was nearly four times greater in autumn than in summer (Table 2). The ANOVA showed a significant leaf type–season interaction (ANOVA: $F_{1,36} = 13.8$, $P = 0.0007$); subsequent paired *t*-tests indicated that there were significantly more non-rhododendron than rhododendron leaves in autumn (*t*-test: $t_9 = -5.13$, $P = 0.0003$), but no significant difference in summer (*t*-test: $t_9 = 1.34$, $P = 0.106$).

Leaf breakdown

During both summer and autumn, exclusion of macroconsumers led to a decrease in rhododendron breakdown rate (Fig. 2). We estimated the amount of decay attributable to macroconsumers in each experiment by dividing the difference between breakdown rates in control and exclusion treatments by the breakdown rate in the control treatment. Macroconsumers were responsible for approximately 33% of

Table 2 Dry weight of rhododendron and non-rhododendron leaves (g m^{-2}) collected from in-stream transects at the end of summer and autumn experiments. Values represent mean of 10 transects, ± 1 SE

	Summer	Autumn
Rhododendron	3.17 ± 0.49	2.43 ± 0.59
Non-rhododendron	2.27 ± 0.69	9.78 ± 1.97

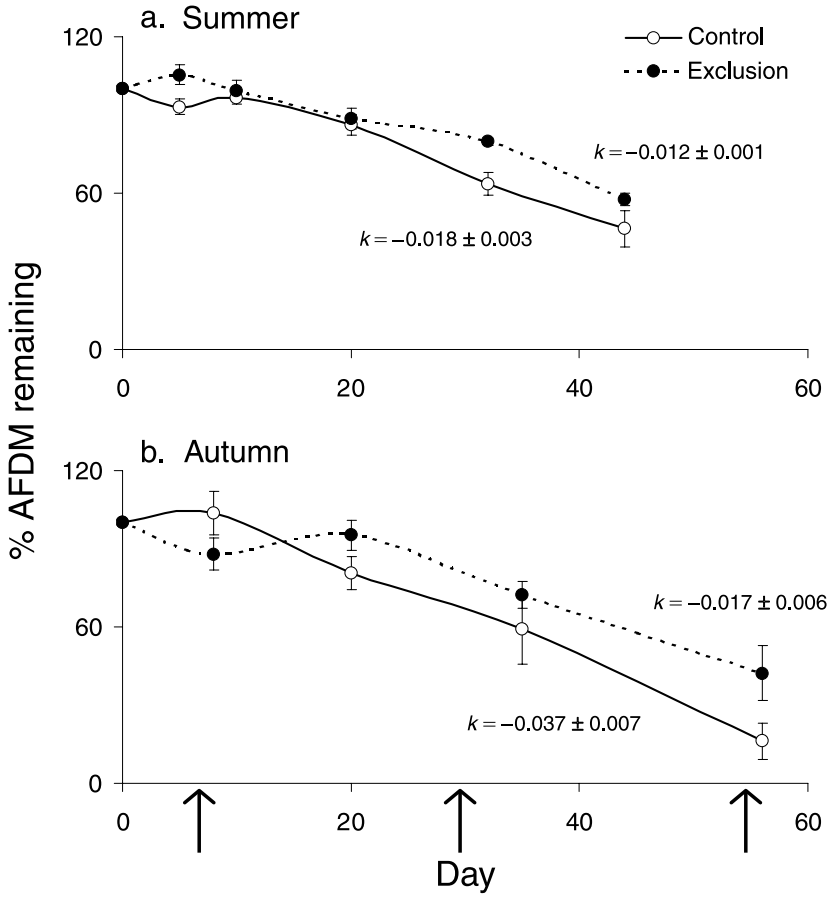

Fig. 2 Percentage AFDM remaining versus day in control and macroconsumer exclusion treatments for (a) summer and (b) autumn experiments. Points represent mean of five (summer) or four (autumn) replicates, ± 1 SE. Breakdown rates (k, day^{-1}) are given for control and exclusion treatments; these values represent mean of individual replicate breakdown rates, ± 1 SE. Arrows indicate occurrence of high discharge events during the autumn experiment (see Fig. 1).

rhododendron decay during the summer experiment, while this percentage increased to 54% in the autumn experiment. Comparison of individual replicate breakdown rates (k, day^{-1}) by ANOVA showed that there were significant treatment ($P = 0.011$) and season ($P = 0.016$, Table 3) effects: rhododendron breakdown was more rapid in autumn than in summer, and more rapid in control than in exclusion treatments (Fig. 2). No significant treatment–season interaction was found ($P = 0.136$, Table 3), although the difference between control and exclusion breakdown rates was much greater in autumn than in summer (Fig. 2).

To account for the shorter duration of the summer experiment (44 versus 56 days) we examined breakdown rates in two additional ways. When rates were calculated through day 32 (summer experiment) and day 35 (autumn experiment) no significant treatment or season effects were detected ($P \geq 0.121$, Table 3), indicating that treatment and season differences became pronounced only after more than a month of exclusion. We also calculated breakdown rates based

Table 3 Results of two-factor ANOVAs for leaf breakdown rates calculated by day. Breakdown rates were also calculated through day 32 (summer) and day 35 (autumn) for comparison; these data were transformed (1/X) prior to analysis to correct for unequal variances. Each factor had two levels (control and macroconsumer exclusion for treatment, summer and autumn for season)

	Source	d.f.	Sum of squares	F	P
k (day^{-1})	Treatment	1	7.38×10^{-4}	8.47	0.011
	Season	1	6.48×10^{-4}	7.44	0.016
	Treatment × season	1	2.19×10^{-4}	2.51	0.136
	Error	14	1.22×10^{-3}		
k (day^{-1}) through day 32 or day 35	Treatment	1	13652	2.73	0.121
	Season	1	4026	0.80	0.385
	Treatment × season	1	308	0.06	0.808
	Error	14	70071		

on degree days. Although the autumn experiment lasted longer than the summer experiment, water temperatures were significantly lower. As a result, leaf packs in the summer experiment experienced more degree days during both pre-conditioning (1574 versus 1302 degree days) and the experimental period (786 versus 621 degree days), although the summer experiment was of shorter duration. Comparison of individual replicate breakdown rates showed similar results whether k was calculated by day or by degree day (i.e. significant treatment and season effects, with no significant treatment–season interaction).

Insect shredder and predator biomass

In each season, four taxa dominated the assemblage of insect shredders (> 90% biomass), although these taxa differed between seasons. The stoneflies *Tallaperla* and *Pteronarcys* were among the dominant taxa in both summer and autumn; in addition, the stonefly *Leuctra* and the caddisfly *Lepidostoma* contributed to summer shredder biomass, while the stonefly *Taeniopteryx* and the cranefly *Leptotarsus* contributed to autumn shredder biomass. Similar predator taxa contributed the greatest biomass in both summer and autumn (i.e. perlid and perlodid stoneflies, dipteran predators such as *Atherix*, ceratopogonids and tanypodids).

Because *Pteronarcys* stoneflies can attain sizes comparable with small crayfish, it is possible that they could have been adversely affected by the exclusion treatment. Comparison of *Pteronarcys* biomass in control and exclusion treatments, however, showed no significant differences in either summer or autumn; in fact, the largest *Pteronarcys* individual obtained (length, 27 mm) was found in the exclusion treatment.

The MANOVA (using total predator and shredder biomass per pack as response variables) showed no significant difference between control and exclusion treatments ($P = 0.332$, Table 4). However, there was a significant effect of season ($P = 0.005$), with greater predator and shredder biomass found in summer versus autumn (Fig. 3). Univariate ANOVAs indicated that both insect shredders ($F_{1,14} = 10.9$, $P = 0.005$) and predators ($F_{1,14} = 7.70$, $P = 0.015$) demonstrated a significant seasonal effect. Similar results were obtained when biomass was expressed in terms of mg g^{-1} AFDM rather than mg $pack^{-1}$. Although no significant treatment differences were detected, there was a tendency toward greater insect predator biomass in control versus exclusion treatments in the autumn experiment (Fig. 3). Higher predator biomass was not accompanied by a significant decrease in shredder biomass in the control treatment.

Table 4 Results of two-factor MANOVA for insect predator and shredder biomass (mg $pack^{-1}$). Values used in analysis were average biomass over 3 days (days 20, 32 and 44 in summer; days 20, 35 and 56 in autumn). Each factor had two levels (control and macroconsumer exclusion for treatment, summer and autumn for season)

Source	d.f. (num, den)	Pillai's trace	F	P
Treatment	2,13	0.156	1.20	0.332
Season	2,13	0.563	8.38	0.005
Treatment × season	2,13	0.039	0.26	0.773

When AFDM remaining was regressed against insect shredder biomass on each date, a significant relationship ($r^2 = 0.482$, $P = 0.006$) was found in the exclusion treatment during the summer experiment: as shredder biomass increased, AFDM remaining decreased (Fig. 4). This pattern was not observed in the control treatment during the summer ($r^2 = 0.041$, $P = 0.467$), nor was it observed in either control or exclusion treatments in the autumn experiment ($r^2 \leq 0.083$, $P \geq 0.364$).

Fungal biomass

No fungal biomass was detected on day 0 samples in either the summer or the autumn experiment. Fungal biomass increased throughout each experiment but, by the end of both summer and autumn, most leaf packs did not contain enough material for ergosterol extraction. Therefore, days 44 (summer) and 56 (autumn) were excluded from analyses. Comparison by ANOVA indicated that there was a significant effect of season (ANOVA: $F_{1,14} = 78.2$, $P < 0.0001$), with greater fungal biomass in summer than autumn (Table 5). In both seasons, however, fungal biomass remained relatively low. There was not a significant effect of treatment (ANOVA: $F_{1,14} = 0.04$, $P = 0.844$), although there was a significant treatment–season interaction (ANOVA: $F_{1,14} = 12.2$, $P = 0.004$). In summer, fungal biomass tended to be greater in control than exclusion treatments; in autumn, this trend was reversed (i.e. there was greater biomass in exclusion

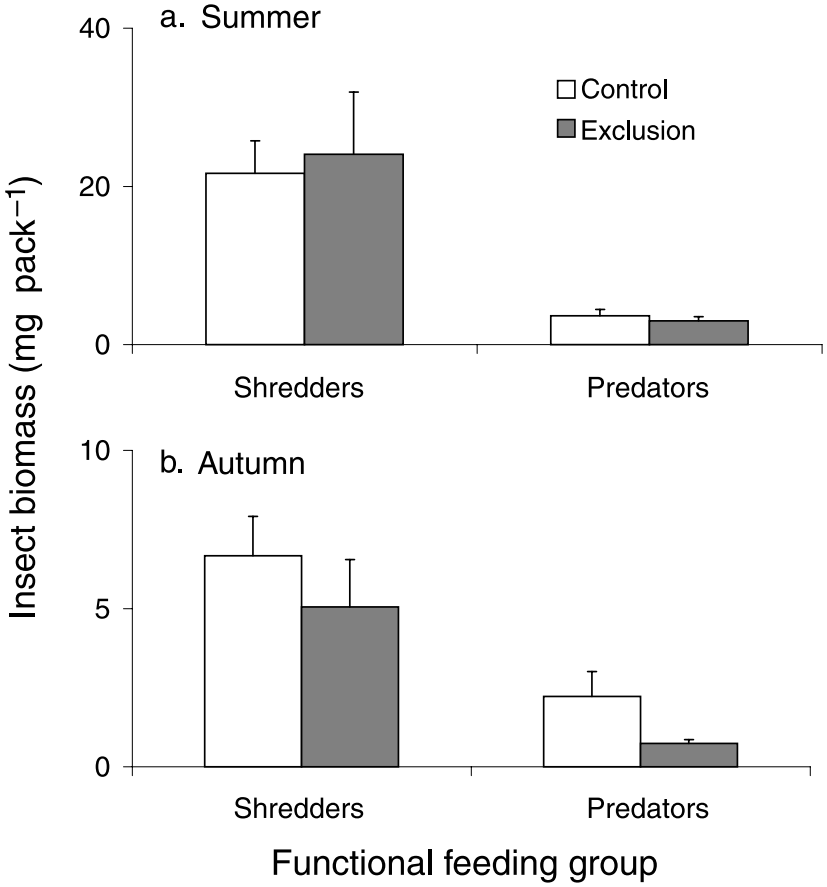

Fig. 3 Biomass (mg pack^{-1}) of insect shredders and predators in control and exclusion treatments for (a) summer and (b) autumn experiments. Values represent average biomass over 3 days (days 20, 32 and 44 in summer; days 20, 35 and 56 in autumn), + 1 SE. Note the difference in scale between summer and autumn graphs. Similar patterns were obtained for biomass in terms of g^{-1} AFDM remaining.

versus control treatments), and the difference between treatments was more pronounced (Table 5).

Discussion

Do macroconsumers influence rhododendron breakdown in both summer and autumn?

In both summer and autumn, breakdown rates (day^{-1} or degree day^{-1}) were slower when macroconsumers were excluded (Fig. 2), indicating that macroconsumers contribute to rhododendron breakdown. We attribute this macroconsumer effect to shredding by crayfish. In summer, when visibility was suitable for observations, crayfish were the only macroconsumers detected in control replicates. Although mottled sculpin are common in Lower Ball Creek, they are insectivorous, feeding primarily on aquatic insect larvae. In the study area, mottled sculpin feed predominantly on chironomids, heptageniid mayflies and hydropsychid caddisflies (i.e. taxa that are not shredders or predators); many of the dominant shredders found in rhododendron leaf packs (e.g. peltoperlid and taeniopterygid stoneflies, *Lepidostoma* caddisflies) make up < 5% of mottled sculpin diets (Stouder, 1990).

While sculpins (as well as crayfish) could have indirectly affected rhododendron breakdown via effects on insect shredders or predators (Short & Holomuzki, 1992; Malmqvist, 1993), there were no significant differences in insect biomass (mg pack^{-1} or mg g^{-1} AFDM) between control and exclusion treatments. Crayfish, however, have been shown to consume large quantities of detritus and to increase leaf breakdown (e.g. Huryn & Wallace, 1987; Parkyn *et al.*, 1997; Whitledge & Rabeni, 1997; Usio, 2000). Crayfish density is relatively low in Lower Ball Creek (approximately 2 m^{-2}), but even so they are able to influence an ecosystem process such as leaf decay.

Based on the predictions of Huryn & Wallace (1987), we expected that the effect of macroconsumer exclusion on rhododendron breakdown would be greater during periods of low (i.e. summer) versus high (i.e. autumn) general leaf availability. Contrary

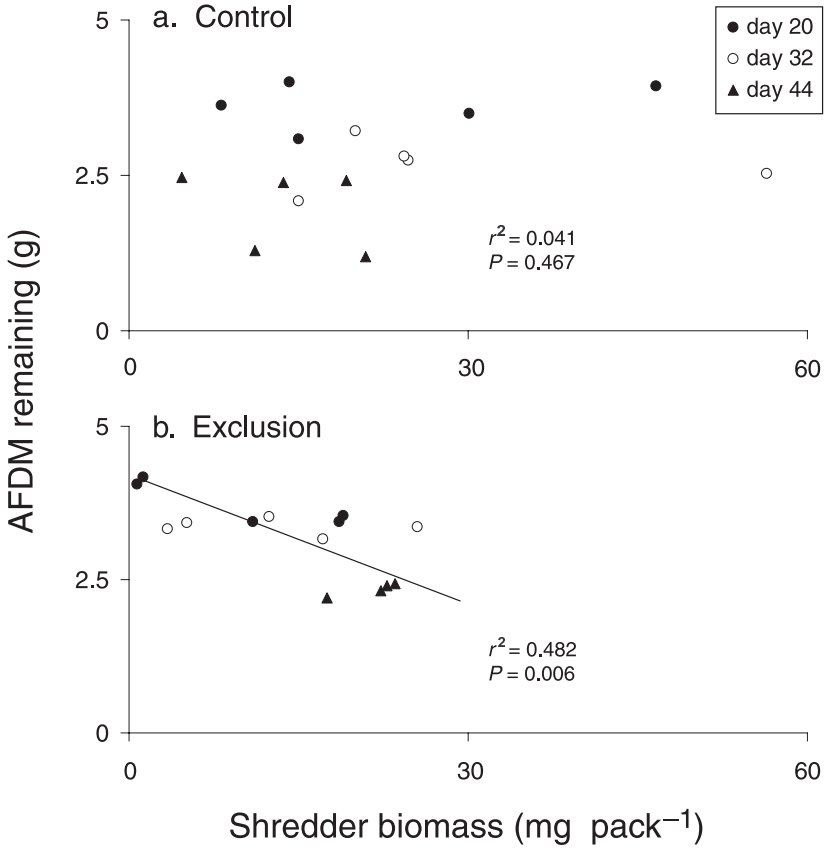

Fig. 4 AFDM remaining (g) versus shredder biomass (mg pack^{-1}) in (a) control and (b) macroconsumer exclusion treatments during the summer experiment. Each point represents one replicate on a given day; one day 44 exclusion replicate was omitted from the regression because it was considered an outlier (it contained a single 156 mg *Pteronarcys*).

Table 5 Fungal biomass (mg DM g^{-1} AFDM) in control and macroconsumer exclusion treatments during summer and autumn experiments. Values represent average biomass over 3 days (days 10, 20 and 32 in summer; days 8, 20 and 35 in autumn), ± 1 SE

	Summer	Autumn
Control	3.85 ± 0.16	0.90 ± 0.17
Exclusion	3.06 ± 0.32	1.78 ± 0.23

to expectations, we found no significant season–treatment interaction in breakdown rates. Crayfish accounted for about 33% of rhododendron breakdown in summer versus 54% in autumn. Given that we observed fewer crayfish in the control treatment during autumn than summer, this finding was especially surprising. However, we probably underestimated crayfish visits to the autumn control treatment, due to large accumulations of leaves obscuring our view (this was not a problem during spot checks in summer). Summer and autumn crayfish sampling did not yield significantly different densities, supporting this contention.

Direct comparison of summer and autumn rhododendron decay is difficult, and the lesser effect of macroconsumer exclusion during summer may have been an artefact of our experimental design. Because summer and autumn leaf packs were collected at different times and subjected to different pre-conditioning regimes, it is possible that initial leaf quality varied between our summer and autumn experiments, despite the fact that initial fungal biomass did not differ. Summer treatments experienced more degree days than autumn treatments, and average fungal biomass was higher. This difference could have influenced crayfish shredding, although this seems unlikely given that fungal biomass was extremely low in both summer and autumn. For example, Paul & Meyer (1996) conducted leaf decay experiments in Lower Ball Creek using three leaf species and found that fungal biomass averaged > 40 mg DM g^{-1} AFDM on tulip-poplar, compared with the ≤ 3 mg DM g^{-1} AFDM we obtained on rhododendron (they reported similarly low values for rhododendron). Finally, summer and autumn experiments were run for different lengths of time (44 versus 56 days), and

effects of macroconsumer exclusion became pronounced only after 32–35 days. It is possible that, had we extended our summer experiment for an additional 12 days, we would have observed greater treatment differences.

Total biomass of insect shredders and predators was more than fourfold greater in summer than in autumn leaf packs (Fig. 3), probably because summer leaf packs served as 'resource islands' in a relatively leaf-poor environment (Table 2). This phenomenon has been noted in several other studies (e.g. Webster & Waide, 1982; Benfield & Webster, 1985; Benfield *et al*., 1991). When natural leaf litter is unavailable (e.g. because of season, disturbance, etc.), even leaf species that were previously ignored may be colonized (Webster & Waide, 1982). Thus, rhododendron may be an especially important resource during summer, when other leaves are relatively unavailable. Rhododendron has refractory leaves that can persist for long periods in streams (Monk *et al*., 1985; Huryn & Wallace, 1987; Whiles *et al*., 1993) and can comprise a large proportion of the leaves available in forested southern Appalachian streams (Stout, Benfield & Webster, 1993). Shredders that are active in spring and summer (e.g. *Lepidostoma*) may be especially reliant on slow-decaying leaf species such as rhododendron (Cummins *et al*., 1989).

This 'resource island' effect and subsequent concentration of insects on summer leaf packs may have led to the significant relationship observed between insect shredder biomass and AFDM remaining. There was a significant inverse relationship between shredders and leaf pack mass in the summer macroconsumer exclusion treatment (Fig. 4). Insects were the only macro-organisms eating leaves in this treatment and, as shredder biomass increased, AFDM remaining decreased. In the control treatment, however, we did not see this relationship, and we speculate that the effect of insect shredders was swamped by crayfish impacts.

During autumn, natural leaf litter availability was much higher (Table 2), and rhododendron leaf packs were relatively less important. Despite the fact that the biomass of insect shredders was much less on autumn leaf packs, the decay rate of rhododendron was faster. Physical fragmentation may have played a larger role in autumn, given that peak daily discharges were much greater. Paul & Meyer (1996) found that rhododendron decay was greatly enhanced following a flood. It seems likely that abiotic fragmentation (both in control and exclusion treatments) and crayfish effects (in the control treatment) were responsible for the majority of rhododendron breakdown in the autumn experiment. Thus, no significant relationships between insect shredder biomass and leaf pack mass were found in control or exclusion treatments in the autumn.

How do these results compare with other rhododendron breakdown experiments?

Many studies have examined rhododendron breakdown in southern Appalachian streams (Table 6). Our breakdown rates were similar to those reported in Hutchens (2000) and Paul & Meyer (1996), whether calculated by day or by degree day. For example, when the data in Hutchens (2000) are recalculated to obtain breakdown rates by degree day, a value of 0.003 is obtained (J.J. Hutchens, personal communication), while the data in Paul & Meyer (1996) yield a decay rate of 0.002. In comparison, our rhododendron decay rates calculated by degree day ranged from 0.001 to 0.003.

Most other studies, however, found much slower rhododendron breakdown rates (Table 6). With one exception (Paul & Meyer, 1996), previous studies were conducted in much smaller streams (first- and second- rather than fourth-order). Physical fragmentation by high flow may have been reduced in these headwater streams. In addition, *Pteronarcys* stoneflies are frequently absent from these headwater reaches (e.g. Grubaugh, Wallace & Houston, 1996). These large-bodied shredders are present in Lower Ball Creek, and their presence may have contributed to the faster breakdown rates we observed. Most previous studies also used leaf packs made from 5 mm or smaller mesh. This may have limited access by larger crayfish, which are thought to be more detritivorous than smaller individuals (Momot, 1995; Whitledge & Rabeni, 1997). Webster & Waide (1982) compared rhododendron breakdown at Coweeta between leaf bags (3 mm mesh) and packs (loosely tied with fishing line), and found that decay rates more than doubled when packs were used. Finally, our breakdown rates were accelerated by using pre-conditioned rhododendron leaves. We attempted to account for this by comparing our decay rates

Table 6 Summary of other rhododendron breakdown studies conducted at or near Coweeta. All studies were conducted in first- or second-order streams unless otherwise noted. Treatment refers to any manipulation or disturbance of the study stream

Mesh size (mm)	Initial dry weight (g)	Duration	Treatment	Breakdown rate (day^{-1})	Reference
20	5	July–Aug	None	0.018	This study
20	5	Oct–Nov	None	0.037	This study
20	5	July–Aug	Electric exclusion	0.012	This study
20	5	Oct–Nov	Electric exclusion	0.017	This study
5	8	Dec–Aug	None	0.019	Hutchens (2000)
5	8	Dec–Aug	None	0.010	Hutchens (2000)
12	15	Oct–June	None	0.007	Paul & Meyer (1996)
12	15	Oct–June	None	0.017*	Paul & Meyer (1996)
5	15	Dec–Dec	None	0.005†	Chung, Wallace & Grubaugh (1993)
5	15	Dec–Dec	Insecticide	0.002	Chung *et al.* (1993)
5	15	Dec–Dec	Insecticide recovery	0.006	Chung *et al.* (1993)
5	10	Nov–June	None	0.002	Benfield *et al.* (1991)
5	10	Nov–June	Forest disturbance	0.006‡	Benfield *et al.* (1991)
5	15	Dec–Dec	None	0.004§	Cuffney, Wallace & Luthgart (1990)
5	15	Dec–Dec	Insecticide	0.002	Cuffney *et al.* (1990)
5	15	Dec–Dec	Insecticide recovery	0.003§	Cuffney *et al.* (1990)
5	15	Feb–Feb	None	0.006	Wallace, Vogel & Cuffney (1986)
5	15	Feb–Feb	Insecticide recovery	0.009	Wallace *et al.* (1986)
3	2–4	Oct–Oct	None	0.004¶	Webster & Waide (1982)
3	2–4	Oct–May	Logging	0.001	Webster & Waide (1982)
3	2–4	Oct–May	Logging recovery	0.011¶	Webster & Waide (1982)
5	15	Feb–Nov	None	0.005	Wallace, Webster & Cuffney (1982)
5	15	Feb–Nov	Insecticide	0.001	Wallace *et al.* (1982)

*study conducted in a fourth-order stream; †4-year (1985, 1988–1990) average in reference stream; ‡average from three streams draining disturbed catchments; §3-year (1984–1987) average in reference stream; ¶average from three sites within 800 m reach.

with those obtained by Hutchens (2000) and Paul & Meyer (1996) for similar degree day periods (i.e. after their leaves had experienced 1300 degree days). In both studies, however, < 35% of rhododendron AFDM remained by the time 1300 degree days accumulated.

It is interesting to compare our results with other experimental manipulations. For example, Wallace *et al*. (1982) and Cuffney, Wallace & Lugthart (1990) found that rhododendron breakdown rates decreased by 62–78% in a headwater stream when shredders were greatly reduced by insecticide (Table 6). Our findings were similar, although the magnitude of change was not so great: when crayfish were excluded (here, by electricity), rhododendron breakdown was slowed by 33% in summer and by 54% in autumn. Whereas Wallace *et al*. (1982) and Cuffney *et al*. (1990) eliminated both insects and crayfish, our manipulation excluded only crayfish. Thus, our results suggest that a significant portion of decay rate decreases may be attributable to reductions in crayfish density.

In conclusion, crayfish play a significant role in the breakdown of rhododendron leaves during both summer and autumn, even though rhododendron is considered a low quality food. The influence of other factors (e.g. shredding insects, abiotic fragmentation) varies between seasons. Crayfish exert a direct impact, increasing rhododendron decay via shredding rather than by altering biomass of insect shredders and/or predators. Even at the relatively low density found in Lower Ball Creek (2 m^{-2}), crayfish are able to affect an ecosystem process such as leaf decay. Given the threatened status of many crayfish species in the U.S.A., this finding is especially relevant. Even small alterations in crayfish assemblages, whether via loss of native species and/or introduction of exotic species, may have significant repercussions for ecosystem function.

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