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Consumer presence and resource diversity independently induce stability of ecosystem function in a Piedmont stream

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Abstract. With the acceleration of species loss across multiple ecosystems, the mechanisms explaining subsequent changes in ecosystem processes are under continuing investigation. In detritus-based ecosystems, such as soils, small streams, and wetlands, one consequence of tree species loss is the shift in the species composition of leaf litter resources to consumers. Given substantial variation in resource quality among senesced leaf species, organic matter processing rates are known to change with litter species loss as both microbial and invertebrate consumers respond to loss of resource diversity. While the effects on processing rates are now well documented, the implications for such species loss on the stability of organic matter processing have not been explicitly tested. In a field experiment, leaf litter diversity was manipulated as single- and mixed-species treatments in a full-factorial design with the presence/absence of a functionally important leaf-shredding consumer, the caddisfly *Pycnopsyche gentilis*. It was hypothesized that in the absence of the consumer, loss of leaf litter species would result in higher variability (i.e., lower stability) in organic matter processing rates, owing to the portfolio effect commonly observed in plant communities. However, compensatory feeding by the consumer should offset the effect of leaf litter species loss. The results showed higher variation in litter processing among single-species leaf treatments compared to diverse mixtures. When *P. gentilis* had access, variation among single-species litter treatments was significantly reduced (i.e., stability increased), and was statistically indistinguishable from high diversity litter treatments. In small streams, which comprise >70% of stream miles in river drainages and often rely on allochthonous resources from riparian vegetation, how loss of stream-side forest species influences stability of in-stream organic matter processing can be independent of important detritivorous consumers.

Key words: biodiversity; compensatory feeding; *Cornus florida*; *Fagus grandifolia*; *Fraxinus pennsylvanica*; *Hamamelis virginiana*; headwater stream; leaf litter breakdown; *Liriodendron tulipifera*; *Pycnopsyche gentilis*; *Quercus prinus*; stability.

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INTRODUCTION

The consequences for changes in ecosystem function with species loss have received immense attention. A recent meta-analysis revealed that numerous mechanisms drive changes in the magnitude of various ecosystem processes, such

as primary production, nutrient cycling and rates of organic matter breakdown and decomposition (Srivastava et al. 2009). In detritus-based ecosystems, such as soils and streams that receive regular, pulsed inputs of leaf litter from deciduous vegetation, diversity of leaf litter resources can drive rates of organic matter breakdown

(Lecerf et al. 2007, Swan et al. 2009), owing largely to interspecific variation in substrate quality (e.g., C:N content, concentration of secondary compounds; Schindler and Gessner 2009). The mechanisms that induce non-additive effects of litter species loss on breakdown differ from that invoked for plants and consumers (e.g., competition, facilitation). Since leaf litter species do not interact directly via competition, preferential and compensatory feeding behavior by consumers are known to play a large role in mediating how loss of tree species can translate into changes in rates of organic matter breakdown (Hättenschwiler and Gasser 2005, Swan and Palmer 2006b). While the empirical evidence is mounting that loss of leaf litter species from the detrital pool can often result in a change in organic matter processing rate, there is less evidence to show implications for the variability, or stability, of this ecosystem process, as demonstrated for plant communities (Dovčiak and Halpern 2010). Furthermore, any independent or interactive effect of consumer presence on stability of organic matter processing is unknown in the context of leaf litter species loss in riverine ecosystems, even though detritivores exhibit flexible feeding behavior in response to variation in resource quality (Cummins and Klug 1979, Cuffney et al. 1990, Swan and Palmer 2006a).

Evidence in both soil and stream ecosystems that leaf litter diversity can lead to higher stability in organic matter processing is limited (Lecerf et al. 2007, Schädler and Brandl 2005). The results are thought to be largely due to the averaging of independent species effects on processing rate (e.g., the portfolio effect; Doak et al. 1998). This suggests that the consumer contribution to breakdown is independent of species richness of leaf litter, which is not always the case. For example, the presence of consumers in diverse leaf assemblages in a laboratory experiment led to the non-additive reduction in loss rate compared to single species breakdown (Swan and Palmer 2006b). This was attributed to accelerated consumer feeding activity on poor resources when given no alternate, higher quality leaf resources in single-species treatments. Consumers in general exhibit flexible feeding rates in response to resource quality (Cummins and Klug 1979, Rapport 1980, Bernays et al. 1994). How flexibility in feeding behavior interacts with

variation in resource quality, for example species rich leaf litter assemblages, to influence stability of breakdown is yet unknown. Understanding this interaction, or lack thereof, in the larger context of species loss from a community is important to understand because consumers could compound the effect of leaf litter species loss on processing of detritus.

How interspecific variation can influence stability of breakdown rate in single- versus mixed-species assemblages centers on how the various factors known to contribute to breakdown rate respond to leaf litter quality. Breakdown rates in aquatic ecosystems are driven by abiotic (e.g., temperature, flow regime, pH, dissolved nutrients) and biotic (microbial enzymatic activity, consumer feeding, substrate quality) factors, with substrate quality defined by nutrient content, structural integrity and concentration of secondary compounds (Webster and Benfield 1986). In general, microbial and invertebrate consumers respond strongly to substrate quality, which is known to vary substantially among leaf species (Ostrofsky 1997, Swan et al. 2009). It is well documented that leaf litter species with high nutrient content and low concentrations of secondary and structural compounds support higher biomass and/or abundance of microbial and invertebrate consumers, and can often result in higher rates of microbial degradation and invertebrate feeding rates (Goladay et al. 1983, Campbell and Fuchshuber 1995). When exposed to different leaf litter species in isolation, and while holding the aforementioned abiotic variables relatively constant, it is straightforward to predict that high interspecific variation in leaf litter quality results in high variation in breakdown rate. However, in diverse litter mixtures, variation among different mixed-species assemblages is predicted to be low, owing to mathematical averaging of single-species effects (Doak et al. 1998). These two predictions assume, however, that the consumer contribution to breakdown of an individual leaf species remains the same whether presented alone, or in a mixture comprised of leaf species with different qualities.

Flexible feeding behavior by detritivorous consumers has the potential to alter how leaf species diversity affects stability of breakdown. Consumers in general are known to exploit

mixed resources, often to either dilute toxic compounds, or benefit from different nutrients available only through complementary resources (Bernays et al. 1994, Hägele and Rowell-Rahier 1999). This has been explored extensively for many trophic guilds (e.g., omnivores, Bjorndal 1991; predators, Evans and Stevenson 1999), but to a lesser extent in the detritivores (Swan and Palmer 2006b). Indeed, some effects of leaf litter species richness on organic matter decomposition manifest only in the presence of macro-detritivores (Hättenschwiler and Gasser 2005). The influence of flexible feeding on how loss of litter species influences the stability of organic matter processing is likely due to how consumers respond to single-species litter. As described above, consumer feeding rate, and thus influence on breakdown, might be positively correlated with resource quality. The result is high inter-specific variation in breakdown. However, compensatory behavior is predicted to result in the opposite effect on variation in breakdown. Consumers can accelerate feeding behavior on poor resources in an attempt to acquire nutrients in low concentrations (Cummins and Klug 1979, Swan and Palmer 2006b). Such adjustments in feeding behavior can then reduce variation in the influence of feeding on breakdown among single-species leaf litter resources. With increasing leaf litter diversity, however, compensatory feeding would be less necessary, as the species-rich litter assemblage is more likely to accommodate consumer resource requirements (Swan and Palmer 2006b). Under this set of predictions, the presence of a consumer exhibiting flexible feeding behavior results in no effect of leaf litter species diversity on variability in ecosystem processing of detritus.

In a field experiment, the presence of a macro-detritivore common to small headwater streams, larvae of the leaf shredding caddisfly *Pycnopsyche gentilis* (Trichoptera: Limnephilidae) and leaf litter diversity were manipulated in a full factorial design. The goal of the experiment was to test the following hypotheses: (1) in the absence of a strong consumer, leaf litter diversity should lead to lower variation in total organic matter breakdown rate, and (2) that consumer presence would stabilize organic matter breakdown independent of leaf litter species richness.

MATERIALS AND METHODS

Study site

The survey work and field experiment were carried out in an unnamed, headwater stream draining to the Patapsco River in Maryland, USA (lat. 39.23° N, long 76.74° E, elevation 97 m asl). The environmental characteristics have been described in detail elsewhere (Swan et al. 2009). This nutrient-poor, forested stream is dominated by an oak-tulip poplar overstory. The study reach was approximately 100 m long, averaging 1.0 m wide (SE = 0.08, $n = 25$) and 5.8 cm deep (SE = 0.53, $n = 15$). Temperature at the end of the study (April 2008) averaged 14.6°C (SE = 0.06, $n = 5$) and dissolved oxygen levels were typical of small, Piedmont streams in the region (9.0 mg l⁻¹, SE = 0.12, $n = 5$).

Litter input and consumer survey

To manipulate species composition of leaf litter assemblages for the field experiment, litter input rates of all riparian tree species were first surveyed over a 56 d period during autumnal leaf fall (28 Sept 2007–2 Nov 2007). A total of $n = 6$, 0.16-m² litter baskets were placed streamside, approximately 10 m apart, and visited four times at approximate 14-d intervals to collect all leaf material from each basket. Samples were returned to the laboratory, separated into the 6 dominant leaf species (comprising 93% of total inputs), dried for 24 h at 60°C, then AFDM determined after combustion at 550°C for 45 min (Swan et al. 2009). Species-specific daily input rates were calculated as g AFDM m⁻² d⁻¹.

A survey of the density of the leaf-shredding consumer, *Pycnopsyche gentilis*, was carried out on 12 April 2008 to confirm that manipulated densities in the field experiment were realistic. A total of $n = 19$ transects were randomly chosen perpendicular to channel flow along the study reach. Wetted width was measured, and the total coverage of leaf litter estimated by the fraction intersecting each transect. The leaf litter was then searched by hand and all *P. gentilis* counted within 0.1 m upstream and downstream of the transect. Transects were sampled in the upstream direction to reduce disturbance to downstream locations. *P. gentilis* abundance was standardized to number per m² of leaf cover.

Table 1. Summary of the relative allocation of each leaf litter species to mixture treatments based on the litter input survey. *Hamamelis virginiana* and *Cornus florida* are understory species.

Mixture treatment	Overstory species removed	Relative abundance
FP + HV + FG + CF + QP	<i>Liriodendron tulipifera</i>	26:25:25:16:8
LT + HV + FG + CF + QP	<i>Fraxinus pennsylvanica</i>	58:14:14:9:5
LT + FP + HV + CF + QP	<i>Fagus grandifolia</i>	58:14:14:9:5
LT + FP + HV + FG + CF	<i>Quercus prinus</i>	53:13:13:13:8
LT + FP + HV + FG + CF + QP	...	51:13:12:12:8:4

Notes: Species abbreviations are: LT, *Liriodendron tulipifera*; FP, *Fraxinus pennsylvanica*; HV, *Hamamelis virginiana*; FG, *Fagus grandifolia*; CF, *Cornus florida*; QP, *Quercus prinus*. Species in mixtures are presented in decreasing order of relative abundance.

Experimental manipulation of consumer presence and litter diversity

The goal of this study was to learn if the presence of a key consumer interacts with resource diversity to promote stability of ecosystem function. The presence of *P. gentilis* was manipulated in a full factorial design with 11 leaf litter treatments (6 single-species, 4 five-species mixtures, and a mixture of all six species; Table 1). Diversity was reduced by removing in four mixture treatments each of the dominant overstory species as they each represent targets of realistic losses to forest communities (e.g., logging, invasive pests) and can overwhelmingly contribute to changes in breakdown dynamics (Kominoski et al. 2007, Swan et al. 2009, Lecerf et al. 2011). A cage design was employed whereby a fixed mass of leaf litter was enclosed in a plastic cage with or without four individual *P. gentilis* larvae and allowed to break down for 39–40 days. Mass remaining was measured to estimate litter processing rate at the end of the study.

Leaf litter treatments were created following Swan et al. (2009). Proportional composition of the mixture treatments was based on the input rates ($\text{g AFDM m}^{-2} \text{d}^{-1}$) estimated from the input survey. A fresh mass to AFDM conversion was estimated for each of the six species (Table 1) by measuring AFDM on $n = 5$ fresh samples per species. Litter for each species was then weighed out accordingly into each mixture to the nearest 0.01 g. The target total mass for each cage was 2 g AFDM.

Cages were 13 L \times 13 W \times 2.5 H cm clear plastic containers fitted with plastic mesh (3 \times 3.5 mm) windows on the top, bottom and sides. Top and bottom windows were 10 \times 8 cm, and side windows 1 \times 5 cm. One cage per treatment

combination (2 consumer \times 11 litter treatments = 22 cages total) were arranged randomly within a block, with $n = 5$ blocks along the study reach. A total of 110 cages were anchored in the stream. Two blocks were deployed on 29 Feb 2008, two on 1 Mar 2008, and the final block on 2 Mar 2008. The leaf litter was allowed to condition for 2 weeks and then 4 late-instar *P. gentilis* individuals added to half the cages, corresponding to a density of 236.7 ind m^{-2} . The larvae were collected the day prior to addition and kept in stream water next to the study reach. The insects were added to blocks adhering to the initial deployment schedule (i.e., blocks 1 and 2 first, 3 and 4 the next day, and 5 the third day).

Cages were inspected every 3–5 days to observe breakdown, and sampling commenced on days 39–40 when $>50\%$ mass was lost. The entire cage was placed into a plastic bag and returned to the laboratory in a cooler. All contents were rinsed into a 500- μm sieve, individual *P. gentilis* removed and counted to determine survival, and leaf litter AFDM estimated as above. Loss rate of the entire leaf litter assemblage for each cage was taken as the fraction of initial AFDM lost per day ($\text{g g}^{-1} \text{d}^{-1}$).

Data analysis

Litter breakdown was analyzed two ways. Total litter mass loss rate was analyzed in a 2×11 factorial ANOVA, with two consumer treatments (presence, absence) and 11 litter treatments that included all six litter species alone, four mixture treatments comprising all litter species less one of the overstory species, and a mixture of all six species (Table 1). Planned pairwise comparisons were made between all six single-species treatments, separately for each consumer treatment.

Table 2. Relative contribution of species-specific leaf litter inputs from 28 Sept 2007 to 2 Nov 2007.

Tree species	Contribution to total (%)
<i>Liriodendron tulipifera</i> †	47.5
<i>Fraxinus pennsylvanica</i> †	11.8
<i>Fagus grandifolia</i> †	11.3
<i>Quercus prinus</i> †	3.9
<i>Hamamelis virginiana</i>	11.5
<i>Cornus florida</i>	7.1
Other	6.9

† Overstory species.

The P-values associated with each comparison were adjusted for inflation of error using the sequential Bonferroni procedure with $\alpha = 0.05$ (Rice 1989). To analyze stability of breakdown rate, the coefficient of variation was calculated for each consumer \times leaf litter treatment (i.e., 11 treatments total) for each of the five blocks separately. To test the independent and interactive effect of consumer presence and leaf litter diversity on stability of breakdown, the CV was analyzed with a 2×2 factorial ANOVA, with two consumer treatments (presence, absence) and two diversity treatments (single species, mixed species). All analyses were carried out using SAS version 9.2 (SAS Institute, Cary, NC). Denominator degrees of freedom were calculated using the Satterthwaite method (SAS Institute 2009). The assumptions of normality and homogeneity of residual variances were checked with the Shapiro-Wilk's test and by using rank correlation between absolute residuals and predicted values using PROC UNIVARIATE (SAS Institute, Cary, NC).

RESULTS

Litter input and consumer survey

Nearly 75% of litter input to the stream was comprised of four overstory species, dominated largely by *L. tulipifera*, which contributed almost half of the total input over the course of leaf fall (Table 2). The two understory species, *H. virginiana* and *C. florida*, together contributed ~19% (Table 2). Coverage of leaf litter on the streambed was estimated at 65.0% (SE = 7.1%, $n = 19$), with 100% cover in 5 of the 19 transects. Density of *P. gentilis* ranged from 0.0 to 250.0 ind m^{-2} , averaging 92.4 ind m^{-2} (SE = 20.7, $n = 18$) of leaf litter. One transect was excluded from this estimate because it had no litter coverage. Mean

Table 3. Factorial ANOVA results testing the main and interactive effects of leaf litter treatment and consumer presence on leaf litter breakdown rate.

Source	df	F	P
Leaf litter	10, 36.3	6.6	<0.001
Consumer	1, 50.4	81.9	<0.001
Leaf litter \times Consumer	10, 36.3	0.3	0.972

density is expressed per m^2 of litter cover since *P. gentilis* did not occur outside of litter cover during the survey (*personal observation*).

Leaf litter breakdown

There was a significant main effect of leaf litter treatment on breakdown rate (Table 3). In the absence of the consumer, breakdown ranged from negligible for *Q. prinus*, to highest for *L. tulipifera* (Fig. 1, open bars). However, this was the only significant difference found. In the presence of the consumer, the two slowest decomposing species were *F. grandifolia* and *Q. prinus*, and both were significantly slower to lose mass than any of the other species. The remaining species were statistically indistinguishable (Fig. 1, closed bars). *H. virginiana* was the fastest decomposing species, losing mass $2.2\times$ faster than *F. grandifolia*, the slowest (Fig. 1). While there was a strong main effect of the consumer treatment on breakdown rate (Table 3), with rates on average $3\times$ higher in the presence of *P. gentilis*, no significant difference among litter mixtures within each consumer treatment was detected (Fig. 2). *P. gentilis* induced significantly faster rates of breakdown independent of leaf litter treatment, but significant variation in breakdown was relegated to single-species treatments.

Stability of ecosystem processing

Stability of leaf litter processing was taken as the within-block coefficient of variation of the single-species litter treatments and the five-species mixtures. The results of the factorial ANOVA revealed significant main effects of leaf litter diversity (single-species vs. mixtures) and consumer presence (Table 4). Diversity of leaf litter alone resulted in a ~34% decrease in variability in breakdown. The reduction in variability was strongest in the absence of *P. gentilis*, but this did not result in a significant interaction term in the ANOVA ($P = 0.113$, Table

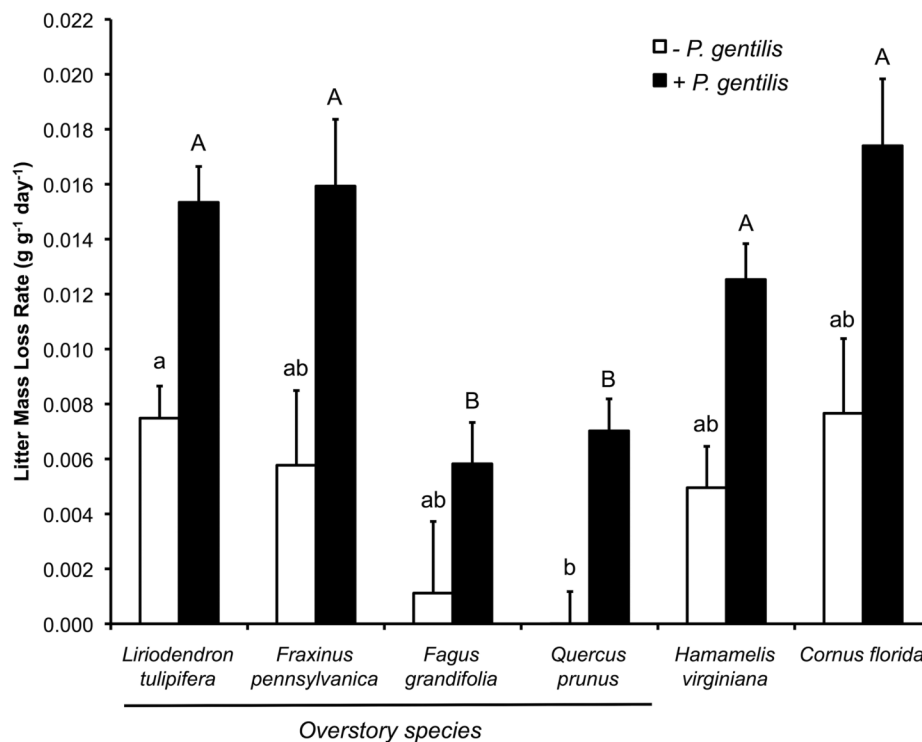


Fig. 1. Breakdown of single species leaf litter in the presence (dark bars) and absence (open bars) of *Pycnopsyche gentilis*. Comparisons among leaf litter treatments are restricted to within each consumer treatment. Bars with the same lowercase letters indicate statistically insignificant differences in the absence of *P. gentilis*, and uppercase letters for leaf litter treatments in the presence of the consumer. Statistical significance was evaluated at $\alpha = 0.05$ following a sequential Bonferroni adjustment for non-independent comparisons. Bars represent the mean + 1 SE.

4). Comparisons between consumer treatments within single-species resulted in a significant reduction in variability (by 47%) with *P. gentilis*, but this difference was lacking with an increase in leaf litter diversity. In fact, levels of variability in breakdown in the presence of the consumer for both diversity treatments were statistically indistinguishable from that estimated for the full, six-species mixture (solid and dashed lines, Fig. 3). This suggests diversity and consumer presence both induce stability of ecosystem processing of detritus in this stream.

DISCUSSION

While there has been substantial effort to understand the ecological conditions under which species loss can influence ecosystem processes, work in detrital-based ecosystems comprises a relatively smaller fraction of the

effort compared to other systems. Tree species loss from riparian forests translates to loss of resource heterogeneity, in the form of senesced leaf litter, owing to interspecific variation in leaf litter quality (Ostrowsky 1997, Gessner et al. 2010). Given that the vast majority of primary production enters the detrital pool in temperate ecosystems (Cebrian 1999), consumption of senesced leaf litter is a major energetic pathway in detritus-based food webs (Wallace et al. 1999). The consumer response to changes in resource heterogeneity is therefore an important factor to consider when studying any aspect of leaf litter species loss on processing of detritus (Hättenschwiler and Gasser 2005). Here, an in situ factorial manipulation of leaf litter species diversity and the presence of a macro-detritivore was performed to understand the independent and interactive effects of these factors on the stability of organic matter processing. Increasing

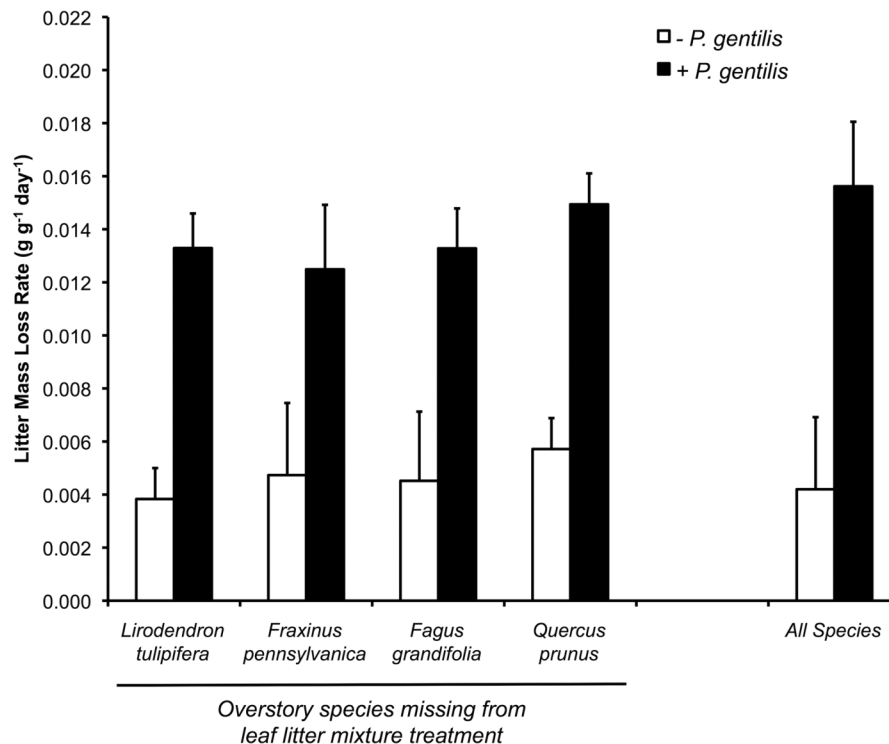


Fig. 2. Breakdown of litter mixture treatments in the presence (dark bars) and absence (open bars) of *Pycnopsyche gentilis*. Five species mixtures are labeled by indicating which overstory species was removed to create that particular mixture treatment. Bars represent the mean + 1 SE.

leaf litter diversity led to a significant increase in the stability of processing rates. However, the effect of the consumer on reducing variation in organic matter processing was nearly identical to that of leaf litter diversity alone.

Many biotic and abiotic variables control leaf litter breakdown (Webster and Benfield 1986). Here, abiotic conditions were held constant across treatment combinations by nature of carrying out the study in a single stream, and maintaining a consistent cage design across consumer treatments (i.e., this was an enclosure/exclosure study). Of the biotic components, substrate quality, as species composition of leaf litter, and consumer presence were manipulated. The remaining biotic contribution to litter breakdown was degradation by the microbial community, which was not manipulated. Indeed, microbial consumers can contribute substantially to organic matter processing (Gulis et al. 2004) and, in streams without an abundance of leaf chewing invertebrates, are the only source of

biological decomposers. Generally, though, microbial degradation comprises a smaller fraction of total breakdown in oligotrophic streams compared with flow and invertebrate feeding activity (Hieber and Gessner 2002). Therefore, it was assumed that microbial decomposers contributed minimally in a compensatory manner to single-species leaf resources relative to *P. gentilis*. In the absence of the consumer, variability in breakdown rate among single-species leaf litter treatments was significantly higher than in the presence of *P. gentilis*. However, this difference

Table 4. Factorial ANOVA results testing the main and interactive effects of litter diversity (single-, five-species mixtures) and consumer presence on the coefficient of variation in leaf litter breakdown rate.

Source	df	F	P
Litter diversity	1, 15	6.8	0.020
Consumer	1, 15	5.5	0.033
Litter diversity × Consumer	1, 15	2.8	0.113

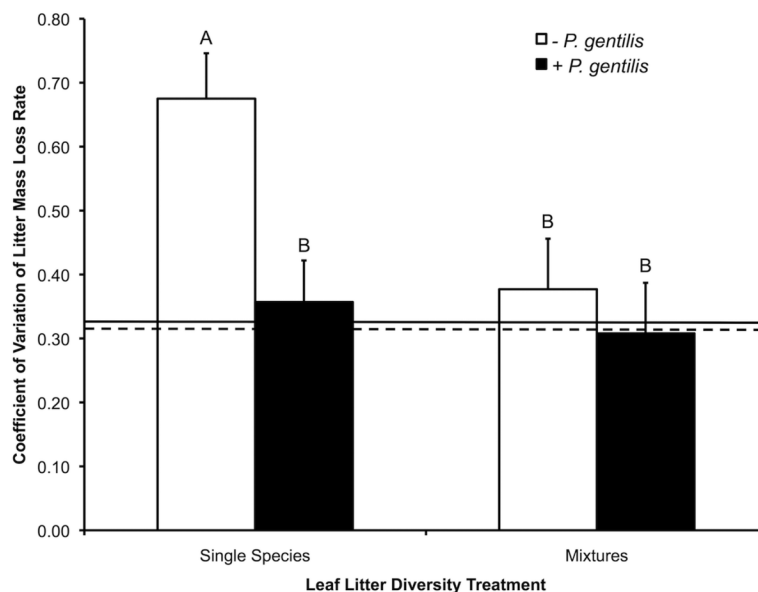


Fig. 3. Stability of breakdown, measured as the within block coefficient of variation, of single-species versus mixed litter in the presence (dark bars) and absence (open bars) of *Pycnopsyche gentilis*. Bars with the same letters indicate statistically insignificant differences. Statistical significance was evaluated at $\alpha = 0.05$ following a sequential Bonferroni adjustment for non-independent comparisons. Bars represent the mean + 1 SE. The solid and dashed horizontal lines indicate the CV of the six-species leaf litter treatment in the presence and absence of *P. gentilis*, respectively.

went away under high levels of leaf litter species diversity. It cannot be ruled out that there existed some complex interaction between litter diversity, microbes, and invertebrate consumers that could be driving the results. It is conceivable that invertebrate consumers could alter the degradative ability of microbes on leaf surfaces, either negatively via direct consumption, or positively via maintaining populations in log-phase growth (Ribblett et al. 2005). Were such interactions important here, they could only be revealed with both a detailed analysis of microbial community structure and estimates of total microbial degradative ability.

One criticism of this study might be that comparing diverse litter assemblages to single-species assemblages is unrealistic. That is, one might not very often see patches of a single-species leaf litter in the stream. There was only one study found documenting the relative abundance of leaf litter species in accumulations on the streambed. In a survey of 50 litter assemblages in a eastern Piedmont stream, Swan and Palmer (2004) found that nearly half

contained only one species, with a range from 1–11 leaf species. This, in combination with the observation that many streams now drain monospecific forests and plantations (e.g., *Eucalyptus* sp., Graça et al. 2002), supports that the findings here are relevant to the patterns of riparian forest species richness occurring on the landscape. While the present approach was to compare very low to quite high levels of species diversity, an expanded investigation including intermediate levels from 2–4 species would help us understand where stability ceases to increase along the litter diversity gradient.

The detritivore density employed here was high, but not unrealistic. Consumer density ranged from 0–250 ind m^{-2} of leaf litter, and the density in the cages was set at 236.7 in m^{-2} . Indeed, there may have been some interference competition for resources. However, any such effects were unlikely to influence the results because (1) interference competition would drive feeding rates down (Jonsson and Malmqvist 2003), reducing any compensatory feeding behavior concluded to explain the observed pat-

terns, and (2) the study was stopped before all resources were consumed. While competition can occur among detritivores (Creed et al. 2009), it is generally not common because donor-controlled resources are not limited by consumers (Wallace et al. 1999; but see Richardson 1991), which motivated terminating the study prior to resource depletion. In small, forested streams, organic matter is rarely limiting, arriving to the channel via direct leaf and/or windfall, or from upstream reaches (Wallace et al. 1999).

The identity of the consumer employed in the study warrants some discussion. In general, the leaf-chewing caddisflies exhibit very high feeding rates compared to other stream-dwelling detritivores (Cummins and Klug 1979). Members of the Plecoptera (e.g., *Amphinemura* sp.), Diptera (*Tipula* sp.) and Amphipoda (*Gammarus* sp.) occur in the stream studied here, but in lower abundance and/or biomass (*personal observation*). For example, the leaf-chewing crane fly, *Tipula* sp., is quite large, and was also surveyed with *P. gentilis*. Its abundance, however, was nearly 10% of *P. gentilis*, averaging 10.8 per m² of litter ($n = 18$, SE = 4.0). This is likely the largest detritivore in this stream, yet *P. gentilis* was far more abundant. Nevertheless, interspecific variation in feeding rate and potential for compensatory feeding behavior among consumers will likely influence the patterns seen here (Cummins and Klug 1979). Consumers with a smaller influence on total breakdown rate, or those not exhibiting compensatory feeding at all, would not necessarily invoke the response observed. Furthermore, evidence from studies of multi-species consumer assemblages suggests niche complementarity among detritivores in streams (Jonsson and Malmqvist 2000, McKie et al. 2008), which may result in a different effect on breakdown of litter mixtures. In this system, as is the case in many small, forested Piedmont streams (e.g., Creed et al. 2009), detritivorous caddisflies were very abundant, and therefore a dominant contributor to organic matter processing among the invertebrate community.

Many factors contribute to the decline of tree species from deciduous forest communities, including selective logging (Chamberlin et al. 1991), herbivory by specialist pests (e.g., Emerald Ash Borer; Poland and McCullough 2006), and disease (e.g., sudden oak death; McPherson et al.

2005). One consequence is the loss of a specific leaf species from the detrital pool. Given there can exist substantial interspecific variation in litter resource quality (Ostrowsky 1997, Swan et al. 2009), loss of leaf species diversity on organic matter processing is being increasingly studied (e.g., Kominoski et al. 2007, Lecerf et al. 2007, 2011, Schindler and Gessner 2009, Swan et al. 2009). To date, there has been no explicit test of what the implications of litter species loss are for stability of ecosystem processing of detritus, nor the potential mechanisms. Here, the presence of a highly abundant leaf-chewing consumer, the caddisfly *P. gentilis*, appears to adjust its feeding rate in a compensatory manner to accommodate variation in leaf litter resource quality. This result was independent of the portfolio effect observed of highly diverse leaf litter assemblages. In this system, the presence of the consumer invoked stability of organic matter processing independently of leaf litter species diversity. This suggests that how this ecosystem process is maintained under scenarios of tree species loss can depend on the feeding behavior of adjacent trophic levels.

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LITERATURE CITED

- Bernays, E., K. Bright, N. Gonzalez, and J. Angel. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75:1997–2006.
- Bjorndal, K. 1991. Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. *Ecology* 72:1234–1241.
- Campbell, I. C., and L. Fuchshuber. 1995. Polyphenols, condensed tannins, and processing rates of tropical and temperate leaves in an Australian stream. *Journal of the North American Benthological Society* 14:174–182.
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American Naturalist* 154:449–468.
- Chamberlin, T., R. Harr, and F. Everest. 1991. Timber harvesting, silviculture, and watershed processes.

- Pages 181–205 in W. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitat. American Fisheries Society, Bethesda, Maryland, USA.
- Creed, R., R. Cherry, J. Pflaum, and C. Wood. 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. *Oikos* 118:723–732.
- Cuffney, T. F., J. B. Wallace, and G. J. Lugthart. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshwater Biology* 23:281–299.
- Cummins, K., and M. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10:147–172.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist* 151:264–276.
- Dovčiak, M., and C. B. Halpern. 2010. Positive diversity-stability relationships in forest herb populations during four decades of community assembly. *Ecology Letters* 13:1300–1309.
- Evans, E., and A. Stevenson. 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia* 121:107–112.
- Gessner, M., C. Swan, C. Dang, B. McKie, R. Bardgett, D. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. *Trends in Ecology & Evolution* 25:372–380.
- Golladay, S., J. Webster, and E. Benfield. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. *Holarctic Ecology* 6:157–162.
- Graça, M. A. S., J. Pozo, C. Canhoto, and A. Eloise. 2002. Effects of *Eucalyptus* plantations on detritus, decomposers, and detritivores in streams. *The Scientific World Journal* 2:1173–1185.
- Gulis, V., A. D. Rosemond, K. Suberkropp, H. S. Weyers, and J. P. Benstead. 2004. Effects of nutrient enrichment on the decomposition of wood and associated microbial activity in streams. *Freshwater Biology* 49:1437–1447.
- Hägele, B. F., and M. Rowell-Rahier. 1999. Dietary mixing in three generalist herbivores: nutrient complementation or toxin dilution? *Oecologia* 119:521–533.
- Hättenschwiler, S., and P. Gasser. 2005. Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences of the United States of America* 102:1519–1524.
- Hieber, M., and M. Gessner. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83:1026–1038.
- Jonsson, M., and B. Malmqvist. 2000. Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos* 89:519–523.
- Jonsson, M., and B. Malmqvist. 2003. Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia* 134:554–559.
- Kominoski, J. S., C. M. Pringle, B. A. Ball, M. A. Bradford, D. C. Coleman, D. B. Hall, and M. D. Hunter. 2007. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology* 88:1167–1176.
- Lecerf, A., G. Risnoveanu, C. Popescu, M. O. Gessner, and E. Chauvet. 2007. Decomposition of diverse litter mixtures in streams. *Ecology* 88:219–227.
- Lecerf, A., G. Marie, J. Kominoski, C. LeRoy, C. Bernadet, and C. Swan. 2011. Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. *Ecology* 92:160–169.
- McKie, B. G., G. Woodward, S. Hladysz, M. Nistorescu, E. Preda, C. Popescu, P. S. Giller, and B. Malmqvist. 2008. Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivore richness, evenness and density. *Journal of Animal Ecology* 77:495–504.
- McPherson, B., S. Mori, and D. Wood. 2005. Sudden oak death in California: disease progression in oaks and tanoaks. *Forest Ecology and Management* 213:71–89.
- Ostrofsky, M. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *Journal of the North American Benthological Society* 16:750–759.
- Poland, T., and D. McCullough. 2006. Emerald Ash Borer: Invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* April/May:118–124.
- Rapport, D. J. 1980. Optimal foraging for complementary resources. *The American Naturalist* 116:324–346.
- Ribblett, S. G., M. A. Palmer, and D. W. Coats. 2005. The importance of bacterivorous protists in the decomposition of stream leaf litter. *Freshwater Biology* 50:516–526.
- Rice, W. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Richardson, J. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 72:873–887.
- SAS Institute. 2009. SAS/STAT 9.2 user's guide. Second edition. SAS Institute, Cary, North Carolina, USA.
- Schädler, M., and R. Brandl. 2005. Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biology and Biochemistry* 37:329–337.

- Schindler, M. H., and M. O. Gessner. 2009. Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology* 90:1641–1649.
- Srivastava, D. S., B. J. Cardinale, A. L. Downing, J. E. Duffy, C. Jouseau, M. Sankaran, and J. P. Wright. 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90:1073–1083.
- Swan, C., M. Gluth, and C. Horne. 2009. Leaf litter species evenness influences nonadditive breakdown in a headwater stream. *Ecology* 90:1650–1658.
- Swan, C. M., and M. A. Palmer. 2006a. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. *Oecologia* 147:469–478.
- Swan, C. M., and M. A. Palmer. 2006b. Preferential feeding by an aquatic consumer mediates non-additive decomposition of speciose leaf litter. *Oecologia* 149:107–114.
- Swan, C., and M. Palmer. 2004. Leaf diversity alters litter breakdown in a Piedmont stream. *Journal of the North American Benthological Society* 23:15–28.
- Wallace, J., S. Eggert, J. Meyer, and J. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69:409–442.
- Webster, J., and E. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567–594.