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## Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown

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**Abstract** Leaf litter derived from riparian trees can control secondary production of detritivores in forested streams. Species-rich assemblages of leaf litter reflect riparian plant species richness and represent a heterogeneous resource for stream consumers. Such variation in resource quality may alter consumer growth and thus the feedback on leaf breakdown rate via changes in feeding activity. To assess the consequences of this type of resource heterogeneity on both consumer growth and subsequent litter breakdown, we performed a laboratory experiment where we offered a leaf-shredding stream detritivore (the stonefly *Tallaperla maria*, Peltoperlidae) ten treatments of either single- or mixed-species leaf litter. We measured consumer growth rate, breakdown rate and feeding activity both with and without consumers for each treatment and showed that all three variables responded to speciose leaf litter. However, the *number* of leaf species was not responsible for these results, but leaf species *composition* explained the apparent non-additive effects. *T. maria* growth responded both positively and negatively to litter composition, and growth on mixed-litter could not always be predicted by averaging estimates of growth in single-species treatments. Furthermore, breakdown and feeding rates in mixed litter treatments could not always be predicted from estimates of single-species rates. Given that species richness and composition of senesced leaves in streams reflects ripar-

ian plant species richness, *in-stream* secondary production of detritivores and organic matter dynamics may be related to species loss of trees in the riparian zone. Loss of key species may be more critical to maintaining such processes than species richness per se.

**Keywords** Mixed detritus · Non-additive effects · Plant species richness · Riparian · Stonefly

### Introduction

Allochthonous inputs of detritus and nutrients can influence both the structure and function of food webs (Hynes 1970; Polis and Hurd 1996; Anderson and Polis 1998). These inputs can increase the production of primary consumers, in turn, creating more prey for higher trophic levels (Strong 1992; Huxel and McCann 1998). For example, terrestrial food webs on desert islands are supported largely by arthropods that feed on ocean-derived shore detritus (Polis and Hurd 1996). Similarly, energy demands of many temperate stream ecosystems are met by terrestrially derived (e.g., riparian) leaf litter that enters the system during leaf fall (Fisher and Likens 1973; Cummins et al. 1989; Richardson 1991; Hall et al. 2001). Experimental exclusion of riparian leaf-fall to streams decreases consumer production and predator density (Wallace et al. 1999). While the effects of the presence of allochthonous resource inputs on consumers have received considerable study (e.g., Richardson 1991; Polis et al. 1997; Gende and Willson 2001; Hall et al. 2001; Power 2001; Murakami and Nakano 2002; Schindler and Scheuerell 2002; Takimoto et al. 2002), the extent to which *variation* in quality of these resources influences consumer growth and feeding in freshwater ecosystems remains largely unexplored.

Ecologists know that resource heterogeneity can affect trophic structure (Hilborn 1975) by altering inter-specific interactions and feeding rates (Hilborn 1975; Hanski 1981; Pacala and Roughgarden 1982; Naeem and Colwell 1991). For terrestrial herbivores, variability

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in plant nutritional quality can reduce temporal variability in feeding rates (Fox and Macauley 1977) and possibly affect consumer growth. There is evidence from both terrestrial and aquatic systems that the abundance (Blair et al. 1990; Kaneko and Salamanca 1999) and biomass (Leff and McArthur 1989; Swan and Palmer 2005) of detritivores may vary between mixed-versus single-leaf species litter. Taylor et al. (1989a) suggested that, in terrestrial systems, this results from enhanced consumer growth due to elevated nutrient cycling in mixed litter. However, it is also possible that changes in consumer growth are influenced by the length of the time when detritus is available to invertebrates (Golladay et al. 1983; Webster and Benfield 1986). Rapidly decomposing leaf species are palatable shortly after entering the detrital pool and may only be available for a brief period of time. Slower decomposing leaf species may not be immediately palatable but over time may become more digestible, providing an important resource for consumers. Given that there is temporal variation when leaf species are most palatable, litter that is made up of leaf mixtures—some rapidly decomposing and some more slowly decomposing—may be a more temporally stable resource base (e.g., over months) than single species-litter.

The relationship between resource species richness and consumer dynamics likely involves complex interactions between resource quality and the effects of consumer feeding on the rate of leaf breakdown. For example, litter consumption by invertebrates may fluctuate in response to litter availability (Cummins et al. 1989), leaf chemistry (Campbell and Fuchshuber 1995; Findlay et al. 1996) and microbial conditioning (Bärlocher and Kendrick 1975). Despite this complexity, the “quality” of the leaf as a resource for decomposers can be related to litter breakdown rate (Melillo et al. 1982; Taylor et al. 1989b; Ostrofsky 1997). Since the chemical attributes of a leaf (e.g., C:N or lignin:N) influence the rate of breakdown and leaf chemistry varies among leaf species (Webster and Benfield 1986; Ostrofsky, 1993, 1997; Haapala et al. 2001), the energy available to the invertebrate consumers can vary between leaf species (Iversen 1974; Herbst 1982; Irons et al. 1988; Sweeney 1993; Motomori et al. 2001). Therefore, variation in leaf litter resource quality, defined here as leaf species richness, may change consumer growth and resource use, with a subsequent feedback on the rate of leaf litter breakdown. We predicted changes in consumer growth and resource use on mixed litter, which would be associated with altered breakdown rates of mixed litter versus single-species litter. We tested these hypotheses using a common stream invertebrate detritivore and riparian leaf litter.

Leaf litter species richness was manipulated as a food resource for a stream detritivore, larvae of the stonefly *Tallaperla maria*. We created ten leaf litter treatments: five single-species leaf litter resources, and five mixture treatments comprised of all four-species combinations. We measured breakdown rate in the presence/absence of consumers, and growth and feeding activity in treatments

containing consumers. We asked: (1) How much does consumer growth rate, leaf breakdown rate, and/or feeding rate change on mixtures of leaf litter compared with single-species leaf litter? (2) Is species composition of leaf litter important in explaining patterns of consumer growth rate, leaf breakdown rate, and/or consumer feeding rate? and (3) If species composition is important, can consumer growth rate, breakdown rate, and/or consumer feeding rate on mixed resources be predicted by averaging the estimates from single-species diets?

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## Materials and methods

As larvae, the stonefly *T. maria* (Needham and Smith; Plecoptera, Peltoperlidae) feeds mainly on leaf detritus (i.e., shredder *sensu* Cummins and Klug 1979) gaining the majority of its energy demands from leaf tissue rather than resident microbial flora (Findlay et al. 1986). This species is found in cold, Piedmont streams in both the mid-Atlantic and northeastern United States (Stewart and Harper 1996). In November 2000, we collected larvae from a second-order Piedmont stream (Fishing Creek) located within the Frederick County Wildlife Management area of Maryland, USA (lat 39°31'N, long 77°28'E; elevation 375 m asl). The tree species employed were chosen because they represent the dominant species in local riparian habitats and vary in C:N content (analyzed with an automated CHN analyzer, University of Maryland Soils Testing Laboratory, College Park, MD, USA): Boxelder (*Acer negundo* L., C:N=21.1), American Sycamore (*Platanus occidentalis* L., C:N=47.5), Black Willow (*Salix nigra* Marsh., C:N=47.2), Black Walnut (*Juglans nigra* L., C:N=37.8) and Slippery Elm (*Ulmus rubra* Muhl., C:N=41.1). The leaf litter was dried at 60°C, and allocated to ten leaf species treatments: five single-species treatments, and five four-species treatments (hereafter, “mixed” treatments). We held total initial dry mass of the leaf treatments constant at 200 mg (e.g., 50 mg per species in the “mixed” treatments) and examined single-species versus mixed-species treatments. Additional treatment combinations (e.g., two- and three-species) were difficult to manage in the laboratory with adequate replication and thus were not used in the present study.

Chambers to raise individual shredders were constructed out of plastic containers (64 mm H × 65 mm dia.). Two lateral windows (27 mm dia.) and a single top window were cut into each chamber, covered with fiberglass screening (1.6 mm mesh), and secured with silicone cement. Each chamber received 200 mg of leaf material as coarsely broken fragments and ten standard aquarium rocks (~5 mm dia.). The chambers were randomly assigned to plastics bins (55 cm L × 37 cm W × 15 cm D), 30 chambers per bin, with each bin filled to ~4.5 cm with deionized water. Each bin was inoculated with 500 ml of stream water, filtered twice at 45 µm to remove invertebrates, while still adding microbial biomass. There were eight bins in total, four placed in each

of two environmental units set to 8°C with 12 h:12 h light:dark regime. The water in each bin was aerated with aquarium pumps and refreshed periodically.

The experiment began on 2 December 2000. The experimental design was a two-way factorial [(two shredder treatments (present/absent), ten litter treatments)], randomized block design (bin was designated as the blocking effect). Litter treatments were fully crossed with the presence and absence of the shredder with a total of  $n = 12$  chambers per litter  $\times$  shredder combination. Chambers of each treatment were divided evenly between the two environmental units, and randomly assigned to bins. After being wet-massed (mg), a single shredder (average wet mass 16.7 mg, SD = 5.2,  $n = 100$ ) was introduced to each of the chambers designated to be shredder-present treatments on day 5 after a complete water change to remove leached organic matter. Two chambers per treatment combination (one from each environmental unit) were sampled on days 5, 11, 19, 27, 47 and 67. Sampling involved emptying the contents of each chamber onto a 500  $\mu\text{m}$  sieve, and rinsing the contents with tap water. The shredder was removed, blotted dry and wet-massed (mg). The leaves were placed in pre-weighed aluminum tins, dried, then combusted at 550°C to determine ash-free dry mass (AFDM). If a shredder was lost from a chamber that replicate was dropped from the study. Water temperature was recorded for each bin on each date for use as a potential covariate.

## Data analysis

### Shredder growth

To analyze the growth of *T. maria*, individual wet mass (WM, mg) was converted to dry mass ( $\text{DM} = -0.7014 + 0.2582 \times \text{WM}$ ,  $n = 18$ ,  $r^2 = 0.764$ ). Shredder growth at time  $t$  was calculated as:

$$\text{Growth}_t = \frac{\text{SM}_t - \text{SM}_i}{\text{SM}_i} \quad (1)$$

where  $\text{SM}_i$  is initial dry mass and  $\text{SM}_t$  is the dry mass of the shredder at time  $t$ .  $\text{Growth}_t$  was analyzed as a function of day and the litter treatment (ten leaf species treatments)  $\times$  day interaction with an ANCOVA. No intercept was fitted since the fraction of mass accumulated initially was zero for all treatments. Growth rate was taken as the slope between percentage of initial shredder mass and day ( $\% \text{ days}^{-1}$ ) for each litter treatment  $\times$  day effect.

The output from the ANCOVA was used to make three sets of comparisons: (1) comparisons between one and four species treatments, (2) comparisons among single-species treatments and (3) comparisons between observed growth rates on each mixed-treatment and what would be expected if growth rate on each mixture was the average of the growth rates on each leaf species individually. For the first comparison, we used a linear

contrast to test for the difference between the mean growth of the shredder on one versus four species diets. For the second set of comparisons among single-species leaf treatments,  $P$  values were adjusted using Hommel's correction for multiple-comparisons (Westfall et al. 1999). For the third set of comparisons, we used linear contrasts to test for differences between the mean growth of the shredder across single-species litter treatments and the growth of the shredder under the corresponding mixed treatment. For example, a significant difference between the mean of the growth rates recorded on the Boxelder, American Sycamore, Black Willow and Black Walnut treatments and growth on the mixed treatment of these four species would indicate that growth rate on the mixed treatment was non-additive. To maintain Type I error rate and orthogonality, a multiple-linear contrast procedure was first conducted for all five mixed treatments, and upon obtaining a significant  $F$ -test, we proceeded with individual contrasts (Sokal and Rohlf 1981).

### Litter breakdown

To determine if leaf species composition influenced litter breakdown rate, we calculated a two-factor ANCOVA to determine how much the breakdown rates differed between various litter combinations both in the presence and absence of the shredder. Breakdown rate is routinely assessed by estimating  $k$  in the exponential decay model:

$$\frac{M_t}{M_i} = e^{-kt} \quad (2)$$

where  $M_i$  is initial mass and  $M_t$  is the mass of the litter at time  $t$  (Petersen and Cummins 1974). Therefore, the fraction of the initial litter mass remaining ( $\ln M_t M_i^{-1}$ ) was analyzed as a function of litter treatment  $\times$  shredder treatment  $\times$  day. No intercept was fitted since the fraction of initial litter mass remaining at the beginning of the study was known to be identical for all treatments. Three sets of post hoc comparisons were made using linear contrasts: (1) between one versus four species leaf treatments and the interaction with the shredder treatments, (2) between single-species treatments, and between observed versus predicted breakdown of mixtures in the presence of the shredder, and (3) between single-species treatments, and between observed versus predicted breakdown of mixtures in the absence of the shredder. Methods for detecting differences between observed and predicted values were the same as above.

### Feeding Rate

Consumption was calculated as

$$\text{Consumption}_t = \frac{(M_t - M_i)_S - (M_t - M_i)_{NS}}{\text{SM}_t} \quad (3)$$

where  $M_i$  and  $M_t$  are as in Eq. 2,  $SM_t$  as in Eq. 1, and the subscripts “S” and “NS” indicate shredder and no shredder treatments, respectively. This calculation corrected consumption for losses due to microbial processes, and assumed feeding activity by the consumer does not change the mass lost to microbial activity. The ANCOVA and post hoc comparisons were performed identically to growth rate, where feeding rate was estimated for each leaf treatment from the slope relating Eq. 3 to day  $t$ .

All analyses were completed using SAS (version 8.2, SAS Institute, Cary, NC, USA), and the results evaluated at  $\alpha=0.05$ . Denominator degrees of freedom for all models were adjusted to include the random block effect by selecting the Kenward–Roger method in SAS (based on calculations in Kenward and Roger 1997).

## Results

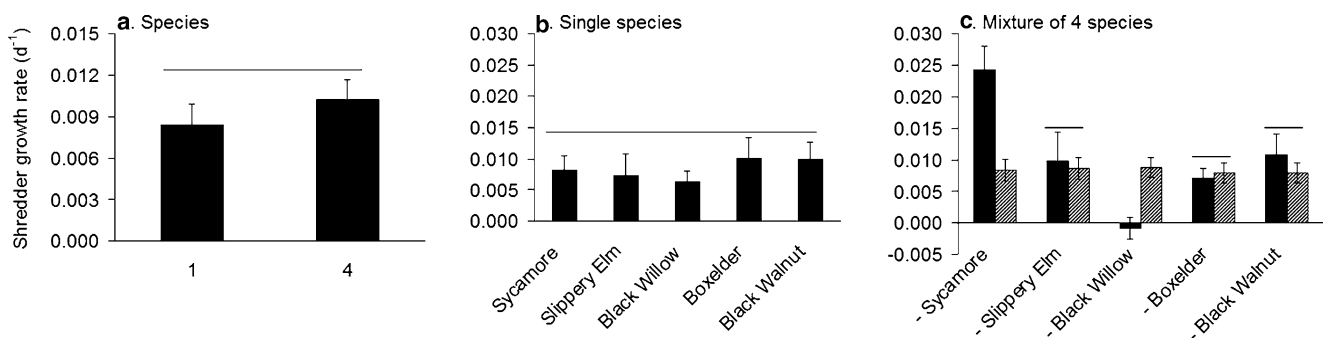
### Shredder growth rate

While resource species richness alone (i.e., one versus four species of leaves) failed to explain any difference in growth of *T. maria* (Fig. 1b, c), there was a significant effect of leaf litter treatment on shredder growth (ANCOVA; day:  $F_{1,31.9} = 71.95$ ,  $P < 0.0001$ ; day  $\times$  leaf treatment:  $F_{9,36} = 2.94$ ,  $P < 0.05$ ; Fig. 1c). Closer examination of litter treatments (Fig. 1a) revealed that shredder growth was similar across single-species leaf treatments. However, the growth rates on leaf mixtures showed strikingly different patterns than what would be predicted by averaging single-species estimates. The multiple contrast procedure to test for non-additive effects of mixing litter on shredder growth was highly significant ( $F_{5,34.7} = 4.88$ ,  $P < 0.01$ ). The mixture lacking Sycamore (-Sycamore) resulted in higher than predicted growth, while the mixture lacking Black Willow (-Black Willow) had slower than predicted growth (Fig. 1c). The magnitude of these responses was substantial; growth on the -Sycamore mixture exceeded what we expected by  $0.016 \text{ mg day}^{-1}$  and was nearly  $1.9\times$  the growth rate

observed on any of the single-species treatments. Growth on the -Black Willow treatment was not significantly different from zero, and thus slower than expected by  $0.009 \text{ mg day}^{-1}$  (Fig. 1c). Estimates of growth rates for all single-species leaf treatments together was  $0.008 \text{ mg day}^{-1}$ , suggesting that the degree to which mixtures deviated from expected growth pattern were large enough to be biologically significant (i.e., deviations of mixtures from single-species predictions were  $\geq$  the growth rates estimated for single-species alone).

### Leaf breakdown rate

The effect of litter treatment on breakdown rate was significant, and interacted with the presence of *T. maria* (significant day  $\times$  shredder effect, Table 1). On average, *T. maria* elevated breakdown rates by  $k = 0.0027 \text{ days}^{-1}$ , but did not interact with the level of species richness (Table 1; Fig. 2a). In contrast to the results for consumer growth rate, overall breakdown did differ among single-species treatments both when the shredder was present and absent. The litter species could be divided into two groups based on their rate of breakdown: the faster decomposing species were Boxelder and Black Walnut, which decomposed  $\sim 3.6\text{--}4.4\times$  faster than the slower decomposing species, Sycamore, Slippery Elm and Black Willow (Fig. 2b, d). With respect to non-additive effects of mixed litter on breakdown, when the shredder was present, two of the five mixed treatments deviated significantly from what would be predicted by averaging the estimates of single-species breakdown rates ( $F_{5,175} = 3.48$ ,  $P < 0.01$ ; Fig. 2c). The -Boxelder mixture decomposed more slowly than predicted, while the -Slippery Elm mixture was much faster than predicted. These differences were not trivial: -Boxelder was slower than predicted by  $k = 0.0029 \text{ days}^{-1}$ , while the -Slippery Elm mixture was faster than expected by  $k = 0.0025 \text{ days}^{-1}$ . American Sycamore was the slowest decomposing litter species, with the highest C:N, and had a breakdown rate of  $k = 0.0008 \text{ days}^{-1}$  (Fig. 2b) in the presence of *T. maria*. So, the magnitude of the



**Fig. 1** The effect of leaf litter (a) species richness and (b) single or (c) mixed treatments on shredder (*T. maria*) growth rate (defined in Eq. 1). For leaf mixtures of four species (c), solid bars indicate the observed growth rate and the patterned bars represent the

predicted growth rate calculated as the average of the growth on the four single species (given in b). Bars connected by a horizontal line are not significantly different. Each bar represents the mean  $\pm$  1 SE

**Table 1** ANCOVA results for litter breakdown. Bin water temperature on each sample day was a significant covariate in the final analysis of litter species effects

Effect	NDF	DDF	F	P value
Day	1	183	11.06	0.0011
Day × temperature	1	182	32.96	< 0.0001
Day × litter	9	175	4.97	< 0.0001
Day × temperature × litter	9	175	2.62	0.0073
Day × shredder	1	174	83.98	< 0.0001
Day × litter × shredder	9	175	3.15	0.0015

non-additivity exceeded the estimated breakdown rate of the slowest leaf species in this study. Furthermore, this effect was only revealed in the presence of the detritivore; breakdown of mixed-litter due to microbial activity alone did not deviate from additivity.

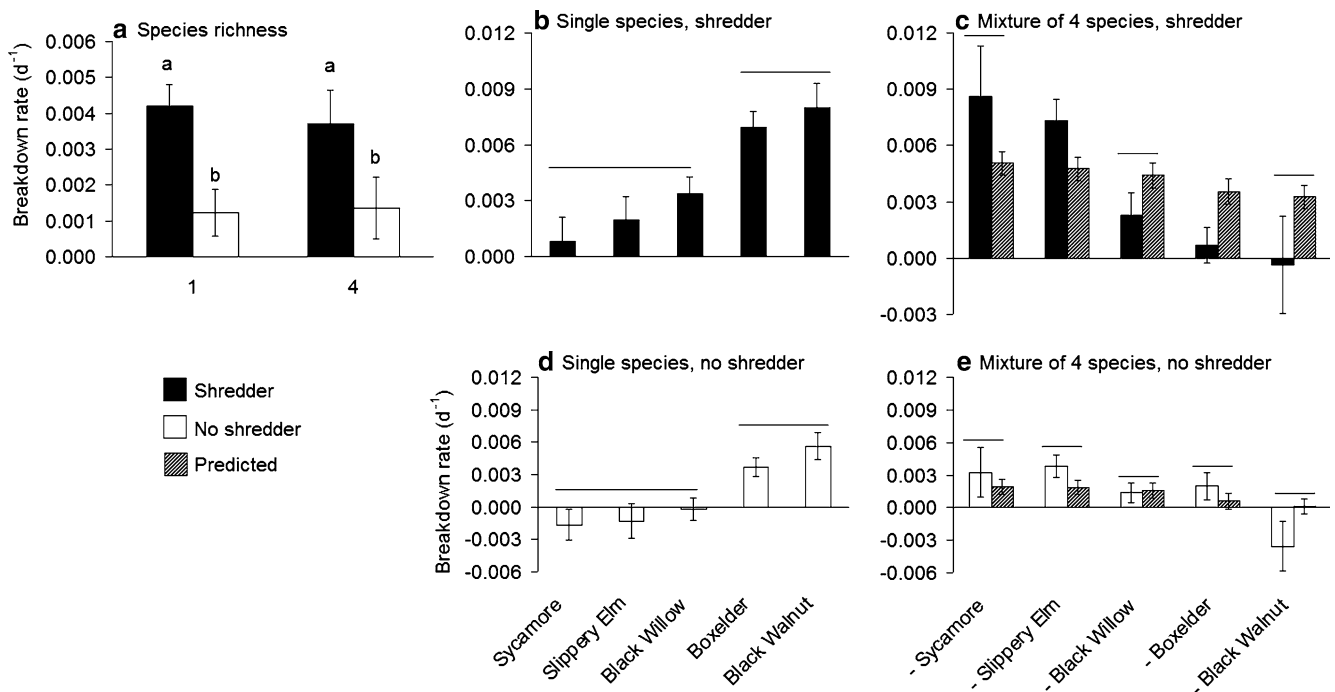
### Feeding rate

Feeding rate was different among litter treatments (ANCOVA; day:  $F_{1,53.6} = 89.83$ ,  $P < 0.0001$ ; day × leaf treatment:  $F_{9,56.5} = 8.09$ ,  $P < 0.05$ ; Fig. 3c, bottom panel), but was not different between high- and low levels of resource species richness (Fig. 3a, top panel). *T. maria* fed similarly among single-species litter treatments, but significantly faster on Boxelder compared with Black Walnut. On mixed litter, feeding rates differed from predicted values for both the -Boxelder and -Black Walnut mixtures ( $F_{5,56.5} = 6.75$ ,  $P < 0.0001$ ; Fig. 3b, c, bottom panel). Absence of Boxelder from the mixture resulted in drastically reduced feeding; variability in the

estimate was so high that feeding did not differ significantly from zero. However, with Black Walnut missing, feeding rate on the mixture was ~37% faster than that predicted from single-species estimates.

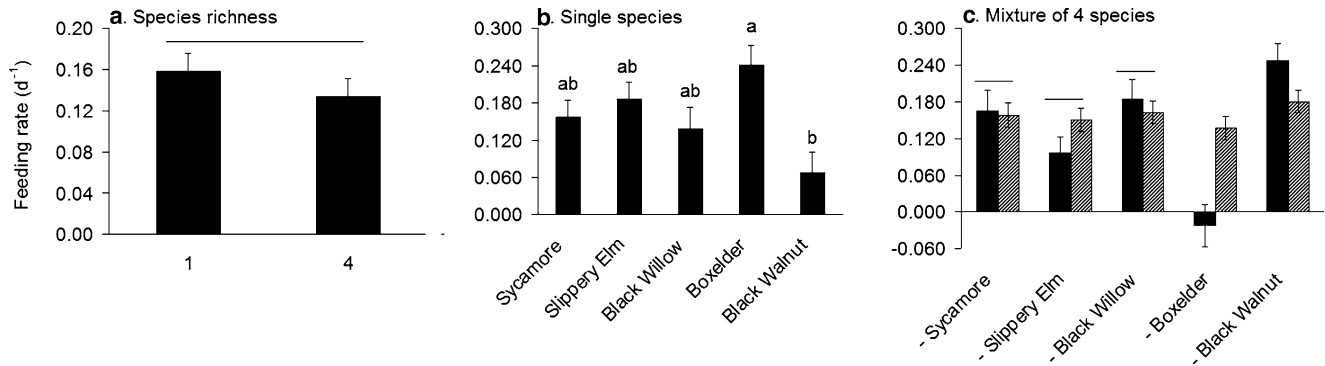
### Effects of species composition

With the exception of growth rate, the results for mixtures were explained by leaf species composition. Our experimental design was such that every combination of four leaf species were examined, allowing us to elucidate the role the absent species may have led in that treatment. Linear regressions of both leaf breakdown and feeding rate for mixtures on the same variable of the corresponding single-species treatment absent from that mixture were highly significant (Fig. 4b, c). For both variables, the faster the breakdown/feeding rate for the single-species, the slower the rate for the mixture lacking that species. These regressions were highly significant, and single-species loss explained  $\geq 88\%$  of the



**Fig. 2** The effect of leaf litter (a) species richness and single or mixed treatments on leaf litter breakdown rate ( $k$ , see Eq. 2) in the (b, c) presence (solid bars) and (d, e) absence (open bars) of the shredder, *T. maria*. Patterned bars (c, e) represent the predicted

breakdown rate calculated as the average of the breakdown rate of the four single species (given in b, d). Bars connected by a horizontal line are not significantly different. Each bar represents the mean  $\pm$  1SE



**Fig. 3** The effect of leaf litter (a) species richness and (b) single or (c) mixed treatments on shredder (*T. maria*) feeding rate (defined in Eq. 3). For leaf mixtures of four species (c), solid bars indicate the observed feeding rate and the patterned bars represent the

predicted feeding rate calculated as the average of the feeding rate on the four single species (given in b). Bars connected by a horizontal line or labeled with the same letter are not significantly different. Each bar represents the mean  $\pm$  1SE

variation for both measures. This was in stark contrast to the results for growth rate where single-species identity did not explain variation in growth on speciose leaf litter treatments.

## Discussion

The energy demands of food webs in many forested temperate streams are met by the input of leaf litter to the stream, and less by in situ primary production (Fisher and Likens 1973; Wallace et al. 1997, 1999; Hall et al. 2001). However, the extent to which variability in quality of these litter inputs influences consumer-resource dynamics remains a relatively open question. We expected resource species richness (in the form of speciose leaf litter) would change consumer growth rate, feeding rate and accelerate breakdown rates. The responses were very complicated—particular leaf species combinations had significant impacts, but these impacts were not always predictable based on averaging single-species effects.

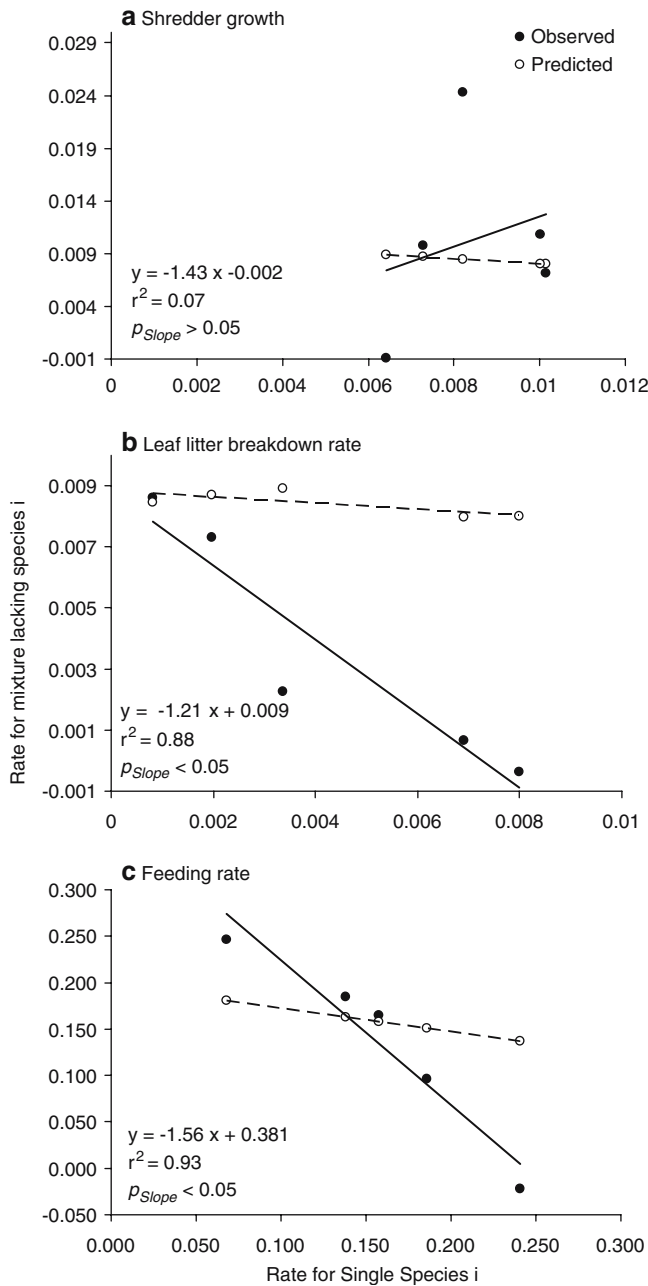
### Detritivore response to speciose leaf litter

Contrary to the evidence that fast decomposing leaves are better resources than more slowly decomposing leaves (e.g., Smock and MacGregor 1988; Sweeney 1993), *T. maria* exhibited similar growth rates on all single-species leaf treatments. Such results are conceivable as many consumers adjust their feeding rates to maintain growth rates (i.e., exhibit compensatory feeding; Iversen 1974; Simpson and Simpson 1990; Lindroth et al. 1993). However, *T. maria*'s growth rate was not the same on mixed litter—it grew at different rates depending on mixture type. Thus, while there was no uniform effect of increasing species richness of the plant litter on the consumers or on breakdown, the functional identity of leaf mixture treatments was quite important. This has interesting implications for stream ecosystems

because loss of individual riparian tree species is common (e.g., due to disease: American Chestnut blight, American Elm disease, Smock and MacGregor 1988; due to invasive herbivores: gypsy moth, hemlock woolly adelgid; Sweeney 1993; Snyder et al. 2002) and our results suggest that this may influence consumer production and material processing.

The lack of agreement between breakdown rate, feeding rate and shredder growth among single-species treatments suggests that leaf breakdown was not a good index of resource quality for this consumer. However, since differences were not evident until the leaf species were included in mixtures underlies the importance of examining the role detritivores play in stream ecosystems under natural resource conditions (i.e., speciose leaf litter; Swan and Palmer 2004). We know that shredders are important to the rate of leaf decay in streams (Sponseller and Benfield 2001), the rate at which fine-particulate organic matter is delivered to downstream consumers (Short and Maslin 1977), and the extent to which higher trophic levels are supported (Wallace et al. 1997; Johnson and Wallace 2005). The results from this study suggest that the magnitude of these factors may be controlled in part by the leaf-species mixtures available to shredders. For example, shredder growth differed from predicted growth patterns on two of the mixtures; it appears that the slowest decomposing species (American Sycamore) was an inhibitor of growth in mixtures since the treatment that lacked this species nearly doubled the rate at which *T. maria* grew. Increases in growth rates of stream insects can lead to larger individuals at emergence, resulting in enhanced fecundity among females (Anderson and Cummins 1979), perhaps increasing system secondary production. To interpret this another way, if American Sycamore was lost from a riparian zone dominated by the tree species used in this study, in-stream consumer secondary production could change.

Knowledge of how consumers respond to mixed diets may explain why leaf species composition, not species richness, may be driving the results of this study. Plant



**Fig. 4** a Shredder growth rate, b leaf litter breakdown, and c leaf litter feeding rate as affected by leaf litter species composition. Predicted values of mixtures lacking species *i* and species *i* alone (open circle) are shown for reference only. The equation for the linear regression is given for the observed data only (filled circle)

species can differ in nutrient content and respond differently to herbivores by producing secondary compounds (e.g., Campbell and Fuchshuber 1995; Wold and Marquis 1997). When leaf litter is delivered to the detrital pool, both nutrient content and secondary compounds can remain in the leaf tissue, and detritivores in both terrestrial and aquatic ecosystems respond to these “after-life” effects (Findlay et al. 1991, 1996). There exists evidence that herbivores can choose a mixed diet in order to consume complementary nutrients (both

macro- and micronutrients), or to dilute the toxicity of secondary compounds (Freeland and Janzen 1974; Pennings et al. 1993; Bernays et al. 1994). Mixtures, then, can present a suite of both positive (i.e., nutrient) and negative (i.e., secondary defense compounds) factors that drive consumer feeding preference and performance. If evidence from herbivore responses to mixed resources can be used as a basis to hypothesize detritivore response to mixed litter, competing influences of nutrients and toxins in the diet may act synergistically or antagonistically depending on the species of the consumer being studied. So, while *T. maria* may exhibit similar growth rates across single-species leaf resources, mixtures may present a suite of nutrients not completely available in single-species leaves, and result in very high growth rates, as was observed in the mixture lacking American Sycamore. Conversely, a mixture might have a stronger suite of toxic compounds, resulting in reduced growth, as was observed in the mixture lacking Boxelder. Therefore, species identity in a mixture may be more important than species richness per se for detritivore performance.

#### Consumer mediation of speciose leaf litter decay

The in-stream processing of detritus delivered to the channel from deciduous riparian trees may depend on both the species composition of the tree community (e.g., Swan and Palmer 2004) and the extent to which aquatic detritivores impact leaf litter breakdown. Our experimental design allowed us to elucidate whether any one single species was driving the dynamics of the mixtures as a whole. While there does not seem to be a monotonic relationship between leaf-litter species richness and any of the variables studied, species identity explained a substantial amount of variation in mixture effects on both feeding rate and total leaf breakdown. For example, if a fast decomposing species was missing from a mixture, then that mixture would likely decompose at a slower rate. The interesting result from this study was the overwhelming strength of this relationship. Breakdown in two of the five mixtures was non-additive, likely due to the relatively slow decomposing Slippery Elm and the relatively fast decomposing Boxelder. If these results hold in the field, then loss of these species from the riparian zone could dramatically alter organic matter dynamics in streams.

In streams where shredders are important for leaf breakdown (e.g., Crowl et al. 2001; Sponseller and Benfield 2001), mixtures of leaf species could change the effect shredders have on organic matter dynamics. Our results show that in mixtures, loss of extremely fast (e.g., Boxelder) and extremely slow (e.g., Slippery Elm) decomposing leaf species had an impact on how leaf mixtures as a whole decompose. This was only evident in the presence of the shredder; microbial decay of mixtures did not deviate from additivity. Often, C:N content is used as an indicator of food quality; high concentra-

tions of carbon generally reduce palatability, while nitrogen is a valuable nutrient that increases palatability. Among the leaf species used in this study, Boxelder had the lowest C:N, and therefore it is not surprising that mixtures containing all other species generally resulted in both reduced leaf breakdown and feeding rate (but not growth). However, resource C:N could not explain why *T. maria* grew so differently in two of the five mixtures, when it grew so uniformly on single-leaf species diets. Despite such difference between growth and feeding, it is important to note that the non-additive effects of mixtures on total leaf breakdown did not occur unless the shredder was present.

How could the mixture *lacking* Black Walnut (Sycamore + Elm + Willow + Boxelder) result in such a variable breakdown rate (i.e., not significantly different from zero), even *gaining* mass in some replicates. Furthermore, how can this be if the single-species leaves in that mixture all supported positive, or a least not as negative, responses alone? In the treatments lacking the shredder, the microbial community could have developed substantial biomass by incorporating nutrients and dissolved substances from the water column, resulting in a slight mass gain. However, the rate at which mass was gained by this mixture was not as high as when the shredder was absent. This could mean that *T. maria* was harvesting biofilm over leaf tissue, despite it being a detritivore reported to subsist more leaf tissue than microbial biofilms (Findlay et al. 1986). Since feeding rate was calculated by taking the difference between mass lost with the shredder from that lost without, feeding rate on this mixture was positive, and significantly faster than predicted. Taken together, this result suggests that despite variability in total litter breakdown, feeding rate by this consumer was altered by both the nature of the mixed leaf species *and* potential interactions with the microbial community. The assumption that shredder feeding activity does not alter microbial degradative ability, as was the case in calculating feeding rate (Eq. 3), may not be appropriate.

Why did feeding rate and breakdown rates not parallel the pattern found in growth? Consumers can exhibit preferential feeding (Iversen 1974; Golladay et al. 1983; Herbst 1982; Irons et al. 1988) or compensatory feeding (Simpson and Simpson 1990) when foraging on resources of varying palatabilities. Given that leaf palatability changes with microbial conditioning over time (Bärlocher and Kendrick 1975; Bärlocher 1985), feeding preference by shredders may change with time on mixtures. Compensatory feeding may have been more common among single species treatments, explaining why growth rate was maintained across single-species, but feeding rate was altered. On mixtures, however, the scenario may have involved both preferential and compensatory feeding effects. By providing leaf species of different initial palatabilities, both temporal and spatial variation in resource quality was presented to the consumer. The consumer, in an effort to maintain its bioenergetic requirements, could have adjusted its feeding

to accommodate both competing quality factors (e.g., variation in nutrient/toxin concentration) and changes in palatability through time as bacteria and fungi facilitate the release of nutrition from the leaf material. Key improvements to future studies would be a detailed analysis of both macro- and micronutrients and key secondary compounds, in addition to studies of the feeding behavior of many detritivore taxa.

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## Conclusion

In sum, this work suggests that mixed resources result in (1) altered consumer growth, (2) different rates of leaf breakdown and resource consumption, and (3) that characteristics of individual resources may control how mixtures decompose. Detritivore-litter systems are interesting because the detritivores are using resources that were once living plants, and the quality of leaf tissue is closely related to tree species identity. This is accentuated by knowledge that detritivores can alter their feeding rates, via preferential and compensatory behavior, to maintain their bioenergetic processes. Given the current interest in how species diversity can alter ecosystem processes (e.g., breakdown), the effects of variability in leaf quality on consumer–resource interactions are critical to understand. The results from this work show that plant species richness can have effects on breakdown, the contribution invertebrates make to breakdown, and detritivore performance in the aquatic setting.

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