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Consumer responses to resource patch size and architecture: leaf packs in streams

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With 3 figures

Abstract: Accumulations of leaf litter in freshwaters can vary from individual leaves to large leaf packs. Past studies have demonstrated that decomposition rates decrease as leaf pack size increases. We considered a set of hypotheses that lower breakdown in larger leaf packs occurs as a consequence of diffusion gradients of oxygen and nutrients, or lower accessibility to larger detritivores to leaf tissue in the middle of these leaf packs. We manipulated leaf pack size in a stream to quantify decomposition rates and the abundances of consumers relative to the amount of detrital mass available. Mass loss rates of beech leaves were lower as leaf pack size increased. We found no differences in fungal biomass across our treatment gradients, or when comparing leaves in the middle of the leaf pack versus those on the outside. The lower decomposition of larger leaf packs would thus not result from a lower quality of the resource based on fungal biomass. Invertebrates per unit mass of leaf packs declined exponentially with size of leaf pack. Smaller invertebrates were less abundant per unit of resource as leaf pack size increased, but abundances of larger invertebrates declined even more dramatically than that of smaller ones. The results are consistent with accessibility within leaf packs decreasing as leaf pack size increases, a factor that is important for the estimation of consumer-resource functions for this patchy resource.

Keywords: decomposition; detritivores; detritus; invertebrates; microbial; refuge

Introduction

The size and shape of resource patches can determine resource use functions and predator prey interactions (e.g. Kareiva 1987; Fattebert et al. 2015), along with other biological processes. Locating resource patches may be a function of size against the matrix of non-resource areas. A great deal of theory has considered the role of competition in consumer-resource dynamics, and body size is one factor that can affect use of resources (e.g. Pess et al. 2011). Predator prey relations may also be influenced by physical structure of the en-

vironment, such as accumulations of leaves (e.g. Hildrew & Townsend 1982; Richardson 1992).

In streams, leaf packs form a critical resource for a large number of consumers (e.g. Wallace et al. 1999; Richardson & Sato 2015). Accumulations of leaves also provide habitat where they can find refuge from predators, from hydraulic forces and also collect fine particles that may serve as food (e.g. Richardson 1992). Leaf packs are patches of food resources against a matrix of physical habitats, and consumers aggregate on those patches (Webster & Waide 1982; Dobson & Hildrew 1992; Gjerløv & Richardson 2004). The spatial

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configuration of leaf patches in streams has important influences on consumer densities and species composition (e.g. Palmer et al. 2000). Moreover, consumers respond dynamically to short-term changes in resource abundances (e.g., Rowe & Richardson 2001). However, there are many questions about how resource patch size (leaf packs) influence consumer abundance and composition.

Rates of leaf litter breakdown vary with the amount of leaf litter in leaf packs, but are higher with size of leaf packs in some studies (e.g. Pozo et al. 2002) and lower in others (e.g. Reice 1974). However, most authors have found that decomposition is faster in smaller leaf packs (Reice 1974, Benfield et al. 1979, Campbell et al. 1994, Tsai et al. 2018), but the mechanisms for why decomposition rates vary with leaf pack size have not been tested. Reice (1974) speculated that accessibility to leaves in leaf packs diminished with increased pack size, but did not have data to test that. Nor has the slope of the relationship been estimated in many instances, and some of these studies might predict decomposition rates to reach zero as leaf pack size increases based on their empirical results (e.g., Campbell et al. 1994; Tsai et al. 2018).

In this study we sought to test the hypothesis that increasing leaf pack size would lead to increasing densities of consumers, but with a slope less than one relative to leaf abundance, and with a diminishing slope as other processes became limiting (e.g., Richardson 1993). We considered fungal biomass as a measure of the key decomposer on these leaf packs to determine if fungi could be limited by possible diffusion or position gradients within leaf packs of different sizes. We assessed the densities and types of detritivorous invertebrates on leaf packs of different sizes. Based on the literature we predicted a reduced decomposition rate and lower consumer densities per unit resource as leaf pack size increased.

Methods

The study site was in the Ruisseau de Peyreblanque (Alzeau River catchment; 43° 25' 41.5" N, 2° 13' 13.3" E) in southwest France. The stream is 1.5 to 2.0 m wide on average, with a gradient of about 3 %, at about 740 m elevation. Temperatures recorded from temperature data loggers ranged from 2 to 11 °C over the course of the study (17th January to 13th April 2007).

Senesced beech leaves (*Fagus sylvatica* L.) were collected in the Montagne Noire region east of Toulouse, France in the autumn and dried at ambient temperature in the laboratory. These leaves were used to construct leaf packs of different sizes as noted below. These leaf packs were placed into 10-mm mesh bags of approximately 15 × 10 cm fastened into a tetrahedron shape to avoid compressing leaves by the bag itself. Leaf

packs of 0.5, 1, 2, 3, 4 and 5 g dry mass were prepared, with 8 replicates of each.

Leaves were placed in riffles in the stream on 17th January 2007 using a complete block design, with subsequent collections on 6th March (48 days after placement) and 13th April (86 days after placement). Some bags had a substantial cover of sand, but most (~80 %) were uncovered and on the streambed surface. Some litter bags had some external litter on them, which was brushed off, and any material not cleared off was clearly distinguishable from the leaves in the treatments.

Laboratory procedures

Leaves were washed gently in the laboratory to remove invertebrates, which were saved on a sieve (250 µm mesh) and preserved in ethanol for later enumeration. Leaves for fungal assessments had 15 leaf disks of 12-mm diameter removed using a corer and frozen for later ergosterol determination following the method of Gessner (2005). For leaf packs with 4 or 5 g (> 30 leaves per pack), leaves were divided into "outside" and "inside" leaves. Outside leaves were those that were clearly on the outside or had moved along the leaf pack so they were more-or-less by themselves in the nets. The "outside" or "inside" leaves were treated separately so that each set would have 15–12-mm disks, which were processed for ergosterol determination.

Additional leaf disks (12-mm diameter) were taken from leaves to estimate the dry mass of each leaf disk, which was subsequently added back to obtain the overall mass of the leaves, accounting for those disks taken for ergosterol determination. Leaves were dried to constant mass at 60 °C in a drying oven before weighing, ashing (at 500 °C for at least 2 h), and determination of ash-free dry mass.

Invertebrates were sorted from debris under 10× magnification. Identification of invertebrates was based on the keys in Tachet et al. (2000), generally determined to genus or subfamily (chironomids). All invertebrates were enumerated. Trophic group was determined based on information in Tachet et al. (2000).

Statistics were run in SAS (version 9.1, SAS Inc, Cary, NC) or R using generalised mixed models. We analysed fungal biomass as a function of leaf position (inside [centre] or outside) from larger leaf packs and its interaction by date in a two-way ANOVA. Analyses for mass loss and fungal biomass were conducted using ANCOVA with size of the initial leaf pack or remaining ash-free dry mass (AFDM) used as covariates. Percentage data were arcsin \sqrt{x} – transformed. We found no significant effect of block in our analyses for mass loss, and since there was no associated hypothesis for that term, we dropped it from subsequent analyses for simplicity. Numbers of invertebrates per mass of leaves were fitted using SigmaPlot's curve-fitting procedures (SigmaPlot ver. 14).

Results

Leaf packs

There was a positive, but not significant relation between initial leaf pack mass and amount remaining (ANCOVA), i.e. lower loss rates as leaf pack size increased. There was a significant effect of date ($p < 0.0001$), but no interaction of collection date with

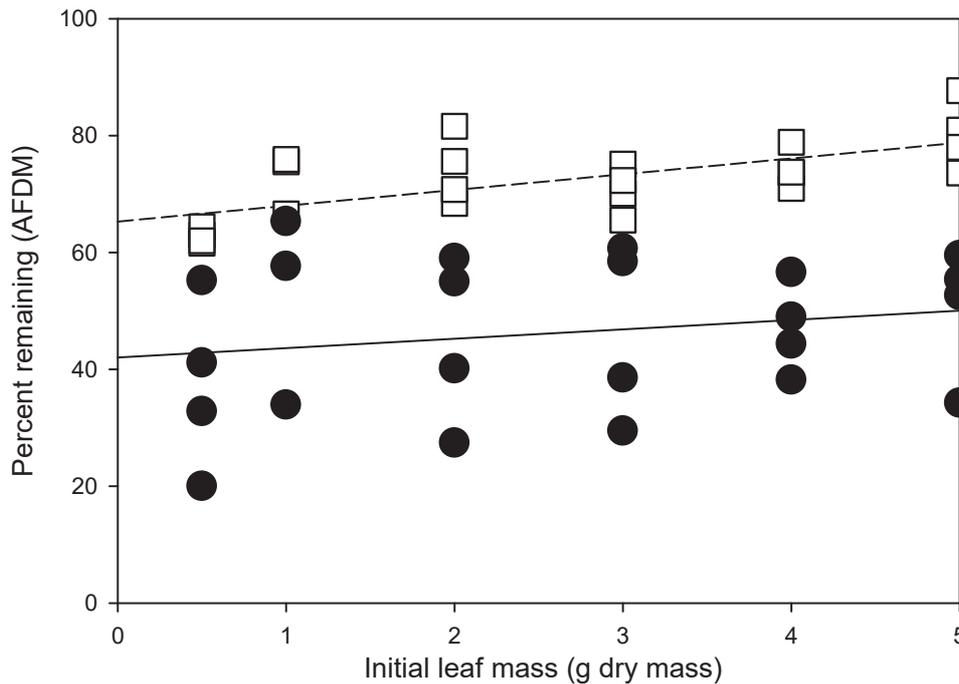


Fig. 1. AFDM remaining of beech leaves after exposure of 48 (open squares and dashed lines) or 86 days (filled circles and solid lines) in the stream as a function of initial leaf pack mass.

the initial mass of leaf packs. When the first date of sampling (day 48) was analysed alone, there was a significant positive relation between initial leaf pack size and amount remaining (slope = 0.137, $p < 0.0001$, Fig. 1A). Decomposition coefficients ($-k$) for our beech leaves (at 48 d) ranged from 0.0048 d^{-1} for the 5 g leaf packs to 0.0101 d^{-1} for the 0.5 g leaf packs.

Fungal biomass

There was no significant effect of leaf pack size on ergosterol content ($R^2 = 0.0053$, $p = 0.66$). Nor was there a significant effect of date ($p = 0.25$) or its interaction ($p = 0.52$, ANCOVA) (Fig. 2A). Comparison of fungal biomass (ergosterol) in the inside *versus* outside of 4 and 5 g leaf packs also showed no significant effect of position in the leaf pack (ANOVA, $F_{1,27} = 0.39$, $p = 0.54$) (Fig. 2B).

Invertebrates

The total numbers of invertebrates increased with leaf pack size, but numbers of invertebrates per g of remaining leaf litter AFDM fit a strong and negative function ($p < 0.0001$, $R^2 = 0.78$, Fig. 3A). Total numbers of invertebrates dropped off dramatically as leaf amount remaining exceeded ~ 1 g. As with total numbers of invertebrates, the relation between total num-

bers of detritivorous invertebrates of all types and leaf pack size was positive, but as a function of numbers per g of leaf AFDM the relation was negative ($R^2 = 0.51$, $p < 0.0001$, Fig. 3B). In addition to the caddisflies and stoneflies mentioned below, detritivores here included *Brillia* sp. (Chironomidae) and *Gammarus* sp.

For shredding caddisflies only (mostly Limnephilidae [*Potamophylax*, *Drusus*] and Lepidostomatidae) there was a significant negative exponential fit per g of leaf litter AFDM as leaf pack size increased ($R^2 = 0.67$, $p < 0.0001$, Fig. 3C), with very low levels reached even at moderate leaf pack size.

Detritivorous stoneflies (mostly Nemouridae [*Nemoura*, *Amphinemura*, *Protonemura*] and Leuctridae) declined as with other detritivores ($R^2 = 0.16$, $p = 0.0084$, Fig. 3D). However, the percentage of shredders that were stoneflies increased from 36.6% when there was < 1 g (AFDM) to 47.3% of total shredders for leaf remaining of > 1 g. Numbers per g leaf AFDM were also highly variable between leaf packs (Fig. 3D).

Discussion

We found a significant negative effect of leaf pack size on breakdown rate, although the slope of the relation-

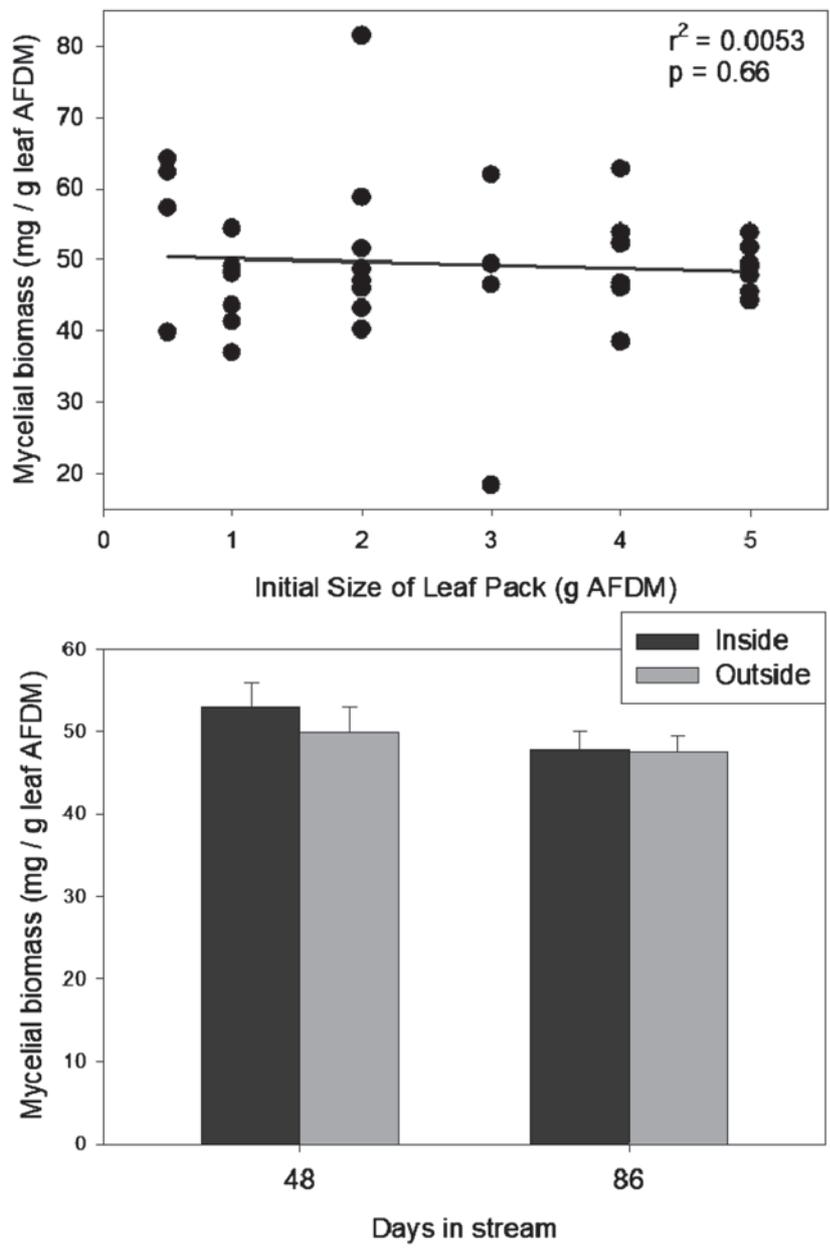


Fig. 2. Leaf-associated fungal biomass based on ergosterol determinations. Fungal biomass per g leaf AFDM across the gradient of initial leaf pack mass (A), and fungal biomass based on samples from the inside or outside of the leaf pack at days 48 and 86 (B).

ship was very low, and only for the first collection date. This pattern of lower decomposition rate as leaf pack size increases has been demonstrated previously (Reice 1974; Campbell et al. 1994; Ruetz et al. 2006; Tsai et al. 2018). In Reice (1974), decomposition rates declined with a slope of between -0.33 and -0.64 (depending on season) across a range of pack sizes from 1 to 40 g dry mass. Tsai et al. (2018) found that decomposition rates declined with a slope approaching -1 across a range from 1 to 8 g dry mass, which would result in rates close to zero in packs slightly larger than 8 g. Likewise, Campbell et al.'s (1994) relation would

have predicted zero decomposition at leaf pack sizes of 8.12 g. Reice (1974) found high rates of decomposition of *Fraxinus americanus* leaves during summer (breakdown range from smallest to largest packs: $k = 0.024$ to 0.011 d^{-1}) even at 40 g (the largest). Even though the effect of leaf pack size on loss rate in our study was small, we used a small gradient compared to the authors noted above. The processes involved in reducing these rates with increasing leaf pack size are not clear, but it could involve oxygen gradients if diffusion is constrained within leaf packs or some other influence on consumers, such as accessibility.

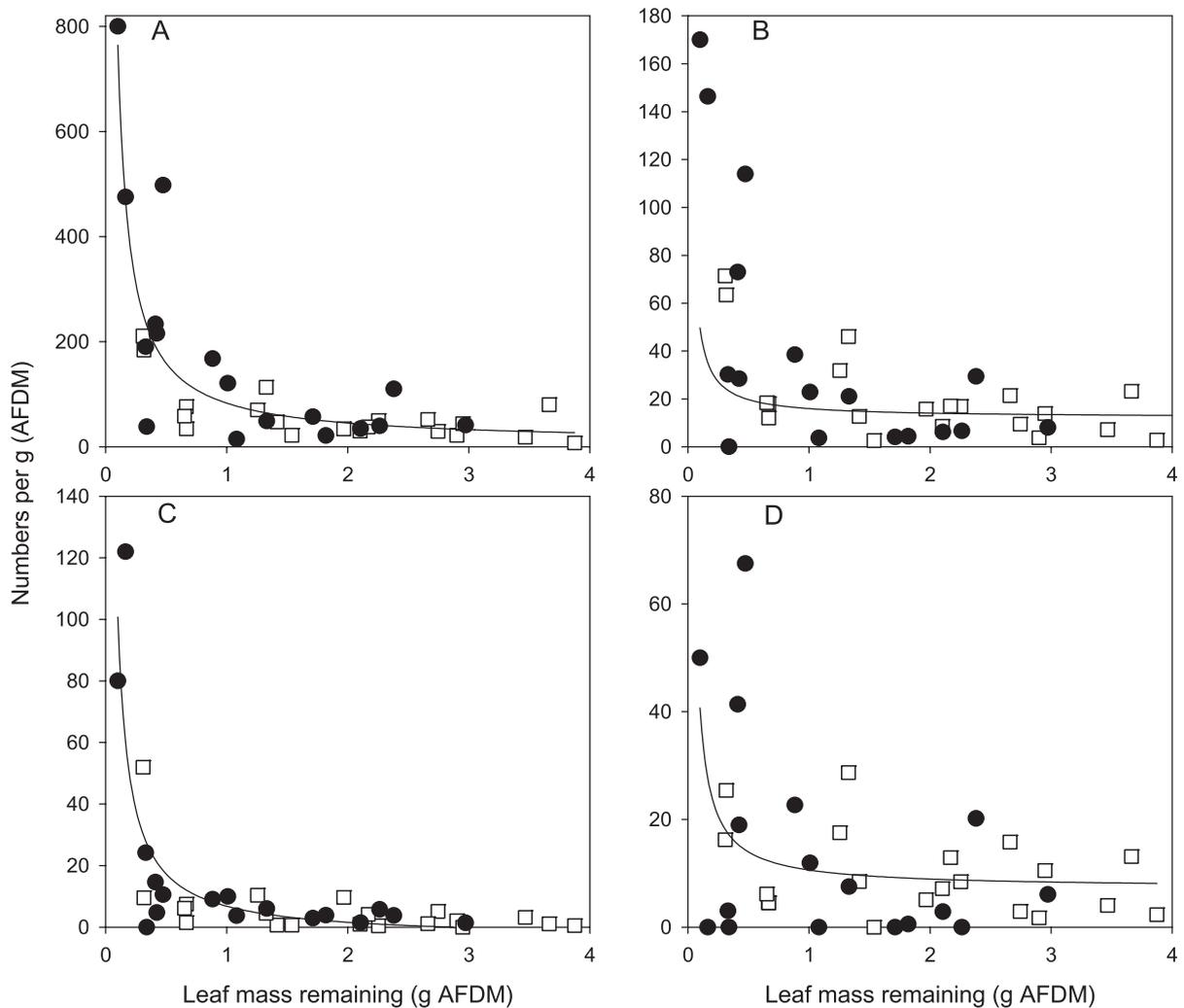


Fig. 3. Numbers of invertebrates per g AFDM of beech leaf litter for total invertebrates (A), total shredders (B), cased caddisflies (C) and stoneflies only (D). Note differences in y-axis scales. Squares are for day 48 and circles for day 86.

In our results we found no significant effects of leaf pack size on fungal biomass, even though one of our sampling dates likely coincided with the maximum mycelial accumulation on beech (Gessner & Chauvet 1994), thus optimizing the chance to detect an effect if one was present. Moreover, we found no difference between fungal biomass on leaves on the outside of a leaf pack *versus* those within. This would suggest that there was no diffusion gradient of oxygen or nutrients that limited fungal biomass in the middle of these leaf packs. When leaves get buried within the hyporheic zone of a stream, there can be a restriction in the rates of colonisation of leaves by fungal spores, and also in the types of fungi (Cornut et al. 2014). However, in our well-oxygenated stream, it is likely that fungal spores were able to colonize all leaf surfaces without

impediment, and they were apparently not limited by diffusion of oxygen and nutrients (at least up to the size of our leaf packs).

Abundances of all invertebrates declined as a function of the size of the resource patch (leaf pack) in our experiment. Likewise, Tsai et al. (2018) found that invertebrate numbers per gram of leaf litter decreased as pack size increased (all with slope < 1.0 in their figure). We observed that large, cased caddisfly larvae declined most strongly in abundance per unit resource, presumably because they do not have access to the inner leaves in larger leaf packs, whereas smaller shredders do. This would mean that with increasing leaf pack size, a larger proportion of the pack is unavailable for these larger consumers. Reice (1974) had speculated that accessibility might be one hypoth-

esis to support his observation of lower decomposition rates as leaf pack size increased. On the other hand, other consumers, including fungi and small-bodied detritivores, have access to leaves throughout the leaf pack. Tsai et al. (2018) found that the effect of leaf pack size was most pronounced for the cased caddisfly *Anisocentropus*, less strong for Nemouridae, and least for the leaf-boring chironomid *Stenochironomus*. However, Ruetz et al. (2006) found no consistent difference in biomass of detritivores across a gradient of leaf pack sizes similar to ours. Their most common shredder was *Gammarus pseudolimnaeus* (~81% of invertebrates) which may have been able to get into the leaf packs more easily than cased caddisflies (Ruetz et al. 2006).

We found no evidence that small-bodied shredders exhibited any compensation in density because of fewer larger-bodied species, and in fact, the slope of small-bodied invertebrate numbers *versus* leaf pack mass was negative and weak, although not significant. A smaller number of large-bodied detritivores per unit mass of leaves could have led to reduced facilitation of growth by smaller-bodied species, as demonstrated by Tonin et al. (2018).

Another hypothesis that could explain lower densities of invertebrate consumers as leaf pack size increases is diminished concentrations of oxygen inside larger packs as microbes use up available oxygen. Leaf packs that are buried beneath the surface of a stream have lower oxygen concentrations, which apparently lead to lower fungal biomass and lower decomposition rates (Cornut et al. 2010). It is also possible there could be a diffusion gradient of nutrients, but the biomass of fungi per biomass of leaf showed no decrease with leaf pack size, which would have been evidence for such a possibility. Thus, we do not see indication that any gradient in oxygen or nutrients could have been responsible for the lack of differences in fungal biomass throughout the leaf packs. Fragmentation of leaves at the outside of leaf packs through abrasion can be a possible source of variation, but we saw no visual evidence of that, and that would be inconsistent with the relationships with invertebrate densities. Moreover, the absence of evidence for variation in resource quality further supports accessibility of the interior of leaf packs as the explanation for lower densities per unit leaf mass of detritivores with increasing leaf size. The steeper slope of that diminishing curve of density per unit leaf mass for large-bodied detritivores is also consistent with reduced accessibility to resources deep within a larger leaf pack.

The quality of leaves in leaf packs varies considerably across species of leaf litter. Our leaf litter packs might have been avoided in preference to higher quality litter. However, in the stream we used, most litter was beech leaves, and thus the leaf packs we prepared would represent the natural leaf resource, or even a high-quality resource against the alternative, which was pine and spruce needles. Given that the leaves were of the same quality as most of the background detritus, leaf quality would not account for differential consumer use of differently sized leaf packs.

Leaf pack size and the architecture of these microhabitats clearly affect the kinds of consumers that have access to these resource patches. We may need to consider leaf pack size as another variable affecting decomposition rates. This is an added detail for consumer-resource dynamics consideration, and another reason measures of resource abundance or density per mass of resources should be included in studies of populations and community ecology of detrital-based streams.

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