

Article

Effects of Leaf Species and Conditioning State of Fresh Leaves on Colonization by Stream and Pond Macroinvertebrates

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Abstract: Fresh, green leaves are increasing as resources in aquatic ecosystems due to more frequent severe spring and summer storms, but research on allochthonous resources typically uses senescent leaves. We examined macroinvertebrate colonization of green leaves of three native deciduous trees (red maple, red oak, and tulip poplar) over two weeks within both a stream and fishless pond. Leaf colonization varied depending on the taxa of leaves and colonizers, submersion time, and the ecosystem examined. Within the stream, the densities of isopods (*Lirceus* sp.) and snails (mostly the invasive *Potamopyrgus antipodarum*) did not vary significantly across leaf species. In contrast, mayflies (*Tricorythodes* sp.) in the stream colonized tulip poplar in greater numbers than red oak leaves, while higher densities of planarians (order Tricladida) occurred within red oak leaves. The numbers of mayflies and snails decreased significantly by the second week, but the densities of isopods and planaria within stream leaf packs were consistent. In contrast, within the pond, significantly more isopods (*Caecidotea communis*) were collected after the first than after the second week of submersion and in tulip poplar leaves. Clams (Sphaeriidae) in the pond, on the other hand, were more prevalent in the second week but did not discriminate among leaf species. While the number of leeches (mostly *Helobdella stagnalis*) was consistent across weeks, significantly fewer leeches resided within tulip poplar leaves than within red oak leaves. Our results suggest that there are no consistent colonization-preference rankings of species of fresh leaves across freshwater benthic macroinvertebrate taxa. Even within a functional feeding group (e.g., the two types of isopods and snails, all detritivore-herbivores), there were differences in colonization patterns. Therefore, increased allochthonous inputs of fresh leaf litter due to severe spring- and summer-time storms are likely to promote the populations of various taxa to different extents.

Keywords: leaf litter; detritivores; riparian; nutrient cycling; shelter; food web



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1. Introduction

Benthic macroinvertebrate detritivores are typically essential to the function of freshwater ecosystems, often dominating the biomass of lower trophic levels [1] and boosting local primary production through their feeding activities [2–4]. Leaves and branches from riparian trees dominate the carbon budgets of most streams and ponds, but interspecies differences in chemical and mechanical properties can affect how and even when consumers use these resources [5]. A large portion of allochthonous coarse particulate organic matter (CPOM) is introduced to freshwater ecosystems in temperate regions via the drop of autumnal leaves from nearby deciduous trees [6–8]. In temperate streams and ponds, these autumn-shed leaves are often absent from the ecosystem by late springtime due to the activity of detritivores, spring rain, and snowmelt floods [9]. The main food resource in spring and summer in lotic systems is typically fine detritus with low nutritional and energy value [10]. However, the frequency of intense summer storms has increased [11]. These storms can promote pulses of allochthonous material into nearby freshwater ecosystems as high winds strip fresh, green leaves from branches individually or *en masse* via

broken branches. These fresh leaves may provide an important augmentation to food and refuge resources.

Comparatively few investigations have used green leaf litter when studying detritivore colonization and the degradation of leaves in aquatic ecosystems (see [12,13], and other references provided in Appendix B Table A1), as most studies to date have examined senescent leaves (e.g., [14,15]). However, various tree species resorb chemical and structural compounds from their leaves to different extents prior to abscission [16–18], which may dramatically alter the palatability and nutritional values compared with green leaves of the same species. Some aquatic invertebrates consume more fresh than conditioned leaves (e.g., [19]), and fresh leaves support higher taxa richness, numbers of individuals, and biomass [20]. Studies that use recently growing green leaves may not yield the same preferential rankings of colonizing invertebrates as studies of autumn-shed leaves. Thus, investigations of the relative use by different aquatic taxa of various species of green leaves may yield important insight into the response of freshwater systems to increasing influxes of a previously less-available resource.

Typically, aquatic animals cannot consume much senescent leaf litter until they attain a certain amount of conditioning, including both the rapid leaching of nutrients and lengthier microbial colonization [21,22]. The population densities of macroinvertebrates within leaf packs are often positively correlated with the amount of microbial colonization (e.g., [21,23,24]). However, leaf conditioning proceeds at different rates across leaf species, and the taxa of detritivores may vary in the amount of conditioning required (including consuming unleached more than conditioned leaves; [25]). Furthermore, leaves provide not only food but also shelter for a variety of aquatic invertebrate taxa. Stoneflies, mayflies, caddisflies, craneflies, isopods, and amphipods completely shred conditioned CPOM [26,27], removing the shelter value. In contrast, snails consume CPOM more selectively, leaving leaf veins intact [28], which may allow continued sheltering benefits for them and any co-inhabitants from the skeletonized leaves. Therefore, between the alterations incurred by microbial leaf conditioning, skeletonization, and the relative needs of detritivores for shelter that would hide them from predators, the relative proportions of the taxa present on green leaves may change over time.

Additionally, these dynamics may manifest differently in lotic and lentic ecosystems. While the macroinvertebrates of streams and ponds often overlap at the level of taxonomic order, the specific species and even genera typically do not and may possess distinct nutritional and sheltering needs and preferences. Furthermore, the turbulent flow in lotic systems can elevate rates of nutrient leaching and breakdown of allochthonous materials [29] and export leaves from the system. In contrast to the dense, continuous benthic layer of leaves in many forest ponds, leaves in streams are often aggregated in isolated packs. These contrasts may result in large differences in the relative use of, and rate of degradation of, leaf packs in lentic and lotic systems. Therefore, we examined the colonization of leaf packs by local benthic macroinvertebrates in both a stream and a pond.

Our present study used freshly removed leaves of three native species of broad-leaved hardwood deciduous trees: red maple (*Acer rubrum*), red oak (*Quercus rubra*), and tulip poplar (*Liriodendron tulipifera*). These three species commonly occur together in local forests as well as in local suburban backyards, but their natural relative-abundance ratios are shifting. Red oaks and (especially) red maples are increasing their local abundance; red maples now dominate many northern forests [30,31]. The potential impact on resident taxa from the current pattern of an increasing shift towards red maple leaves and an elevated influx of green leaves during summer (which may correspond with reduced amounts of senescent leaves in winter) is unknown.

Our current studies attempt to reduce the dearth of investigations examining aquatic invertebrate colonizers of packs of green leaves in streams and ponds in the summer. Red oak leaves have higher levels of nitrogen and tannins and decompose more slowly than leaves of red maple and a species confamilial with tulip poplar [32–34]. Lotic isopods are thought to consume senescent maple more than senescent red oak leaves [35]. There-

fore, we predicted that (1) over two-week colonization studies, population densities of macroinvertebrates would be highest in leaf packs containing freshly removed leaves of red maple, followed by tulip poplar, with the lowest numbers in red oak. Furthermore, we predicted that (2) in the second week's collection, invertebrates sheltering from visually oriented predators would be present in the smallest numbers within the highly skeletonized leaves, which were predicted to be maple leaves due to prior consumption by detritivores. We predicted that concomitant with increased microbial colonization, (3) the densities of detritivores would increase between the first and second week of deployment. However, we also predicted that (4) the number of herbivores would decrease over time because fresh leaves would better mirror their typical foods (live plants and algae) immediately after submersion.

2. Materials and Methods

2.1. Experimental Design

In July 2019, we conducted studies in Cedar Creek, a second-order stream in Allentown, PA (40.6° N, 75.5° W), and in Scout Pond, a small, shaded, fishless pond in Graver Arboretum in Bath, PA (40.8° N, 75.4° W). Both sites contained little submerged leaf litter at this time of year. Cedar Creek is an urban stream with anthropogenic influence (channelization, proximate impervious pavement, frequent flooding), although this reach is designated a "Class 2" waterbody by the Pennsylvania Department of Environmental Protection [36] and supports mayflies, caddisflies, and brown trout. Trees and bushes in proximity to the stream and pond provided patchy shade. The temperature varied more for the stream than the pond: the stream temperature was 11.5 °C on 15 July 2019 and 15 °C on 24 July 2019, while the pond was 25 °C on 17 July 2019 and 24 °C on 25 July 2019.

We collected intact, fully-expanded leaves from northern red maple (*Acer rubrum*), red oak (*Quercus rubra*), and tulip poplar (*Liriodendron tulipifera*) trees on the same day. The leaves were kept at 20 °C for 48 h before deployment. This delay until submersion likely parallels the natural delay experienced by many leaves that are blown from trees during summer storms. A qualitative attempt was made to ensure that each leaf pack started with a similar leaf mass; therefore, 12 to 13 red maple leaves, 8 to 9 red oak leaves, or 7 to 8 tulip poplar leaves were placed within each pack. Each leaf pack (15 × 15 cm) was a plastic mesh pouch (Vexar hardware cloth; 1.27 × 1.27 cm pore size) filled with the leaves of one species. This pore size was small enough to reduce leaf attrition through factors other than consumption but large enough to enable easy access/egress for all local invertebrates but crayfish in the streams and larger predators in the pond (large diving beetles, belostomatids, and water scorpions).

Nine leaf packs were arranged in a Latin square block design, attached at the corners using plastic cable ties (this unit is hereafter referred to as a "mat", N = 3 packs per mat for each species of leaf). To control for positional effects within a mat, the leaf species in the uppermost right-hand corner was rotated among the treatments, with leaf species at every other position within the mat then shifted accordingly. The mats were affixed tightly against the benthos to ensure continuity with the pre-existing leaf litter.

In mid-July, five mats were deployed at each site (N = 15 total packs per leaf species per site), with at least three meters between each pair of mats. Stream deployments were all within riffles and situated away from walking paths to reduce the potential for public disturbance. Three mats were in the stream's thalweg and rested on a submerged gravel bed. The other two mats lay near the bank, experienced slightly slower water flow, and rested on sediment that was predominantly silt. Mats in the pond were widely spaced apart in the shallows around the circumference, with an attempt to match similar water depths and levels of overhead shade.

A week after deployment, leaf mats were carefully removed from the ecosystem and disassembled at the site, with each leaf pack placed individually within a plastic bag for transportation to the laboratory. In the laboratory, on the same day as retrieval, the leaves were removed, and all of the benthic macroinvertebrates contained within were collected

and preserved in 70% ethanol. Specimens were identified to the lowest taxonomic level possible: genus or species for arthropods, leeches, and snails, family level for bivalves, and order level for planaria. Planaria (in stream samples) and leeches (in pond samples) were counted but not preserved due to their tendency to exude copious mucus that might impact other preserved specimens. Any planktonic species and those smaller than 0.5 mm (e.g., water mites) were not considered, as they were either collected incidentally (in the former case) or we could not be confident that our observed numbers were robust (in the latter case).

After all animals were removed, the leaves were replaced within the same leaf pack and maintained overnight at 20 °C in water from their respective ecosystem to maintain the existing microbial community. The following morning, mats were re-assembled as before and each was redeployed in the same within-site location from which it had been removed the previous day. Two weeks after the initial deployment, the retrieval process was repeated. After the second census of macroinvertebrates, the degree of skeletonization of the gross aggregate of leaves within each leaf pack was assessed on a 1 to 5 scale (1 = no skeletonization to 5 = heavy skeletonization; see Figure 1 for examples). Because some leaf packs in Scout Pond had an extremely high degree of skeletonization, but the remaining web of leaf veins could still provide ample shelter, while other leaves were totally degraded with no remaining surface area, the percent of the surface area still covered by leaves was also estimated, and one of five categories was recorded (0%, 25%, 50%, 75%, 100%) for each leaf pack. Such differentiation was not warranted for the stream samples due to a consistently smaller degree of decay.

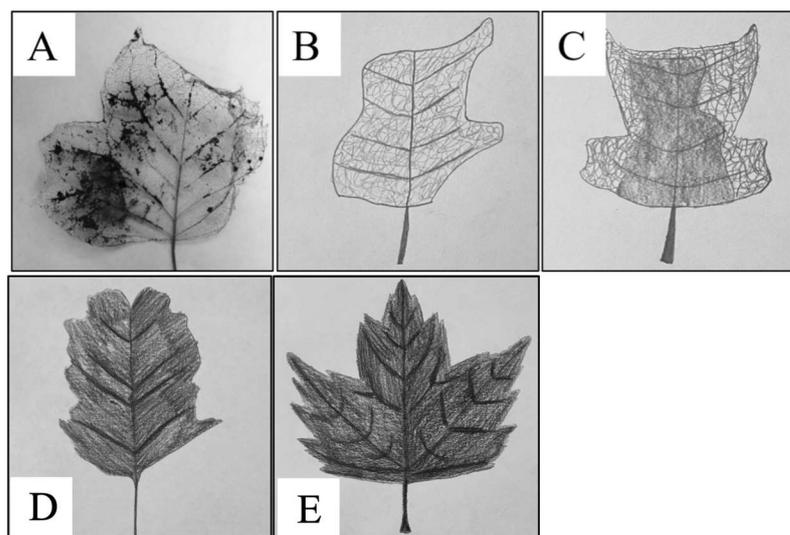


Figure 1. Visual depictions of representative leaves within different skeletonization categories and surface area quantiles. (A) a photograph of a real tulip poplar leaf of skeletonization category (SkC) 5, and surface area quantile (SAQ) 50%; (B) a sketch of a tulip poplar leaf of SkC 5 and SAQ 25%; (C) a sketch of a tulip poplar leaf of SkC 3 and SAQ 75%; (D) a sketch of a red oak leaf of SkC 1 and SAQ 50%; (E) a sketch of a red maple leaf of SkC 1 and SAQ 100%.

Water depth was recorded upon initial deployment for every mat location at the two sites. Additionally, after the final collection of the stream leaf packs, the surface sediment underlying each mat was removed and brought into the laboratory. There, for each sediment collection, a random-point grid was used to subsample 21 to 23 sediments, and the length of the intermediate axis of each particle (neither the longest nor shortest of the three mutually perpendicular sides of each particle; [37]) was measured. Measurements of water depth and sediment size are provided in Table 1. We did not measure mid-stream flow rates because boundary layers within the leaf packs and sediment substantially reduce the flow experienced by the benthic animals. The sediment sizes are provided as a

qualitative indicator of the typical local flow rates. While the stream sediment ranged in size from small to large gravel, the sediment in the pond was uniformly fine silt (<2 mm in length), reflecting the continual slow rate of water movement in this pond, and so individual pieces were not measured. Collections from the benthos where we deployed mats within the pond yielded red oak and red maple leaves, and less widely distributed tulip poplar and beech leaves. Aggregations of leaves were much less common in the stream, and there were none observed within the specific area in which we conducted our experiments.

Table 1. Habitat attributes of each location in Cedar Creek (CC) and Scout Pond (SP). Averages and ranges were calculated using 21 to 23 sediments that were randomly subsampled from all of the surface sediment underlying each mat. Sediment size is the intermediate axis measurement.

Site	Mat Location	Water Depth (cm)	Stream Width (m)	Sediment Average Size (mm)	Sediment Size Range (mm)
CC	1	29	5.4	9.71	1 to 39
	2	10	3.6	2.95	1 to 8
	3	9	3.6	6.33	1 to 19
	4	15	7.5	4.29	1 to 8
	5	15	7.5	6.00	1 to 25
SP	1	20			
	2	21			
	3	30			
	4	25			
	5	33			

2.2. Data Analysis

Data from each ecosystem (pond and stream) and from each commonly found taxon were analyzed separately using two-way ANOVAs (DataDesk; version 8.3). The number of individuals of each taxon was used as the dependent variable, leaf species (red maple, tulip poplar, or red oak) and leaf conditioning time (one or two weeks) as the independent variables, mat as a random blocking factor, and the interactions term was included. Compliance with the assumptions inherent in parametric ANOVA was tested using the Kolmogorov test for normality and Levene's test for equal variance. If required to meet the ANOVA assumptions, data were transformed using either $\ln(y + 1)$, which was needed for the mayflies, or $\ln(y + 0.1)$, which was needed for the snails, clams, and pond isopods. For fixed factors that were significant and contained more than two levels, post hoc linear contrasts were performed using a Bonferroni correction factor to obtain an overall $p < 0.05$ threshold to determine significance.

The categorical scores of the degree of skeletonization (for the stream and pond samples) and remaining leaf surface area quantile (only for the pond samples) were analyzed separately using separate chi-square tests of independence with leaf species as the independent variable. A threshold decision level of $p < 0.05$ was used for all analyses.

3. Results

Four invertebrate taxa frequently occurred within stream leaf packs (present in at least 20 of the 45 leaf packs per week, listed in order of decreasing frequency): isopods (*Lirceus* sp.), planarians (order Tricladida), snails (predominantly the invasive species *Potamopyrgus antipodarum*), and mayflies (order Ephemeroptera; *Tricorythodes* sp.). These taxa comprised 95.57% of the total 3024 specimens collected in week 1 and 96.17% of the 2323 collected in week 2.

The number of isopods inhabiting the leaf packs in the streams (Figure 2A) was not significantly affected by either the leaf species ($F_{2,80} = 0.893$, $p = 0.414$) or the length of conditioning time ($F_{1,80} = 0.70$, $p = 0.407$). There was a significant effect of the individual mat ($F_{4,80} = 18.93$, $p < 0.0001$), and while there was also a significant interaction term

between week and leaf species in this analysis ($F_{2,80} = 3.23, p = 0.045$), none of the post-hoc pairwise comparisons were statistically significant ($p > 0.05$ for each comparison).

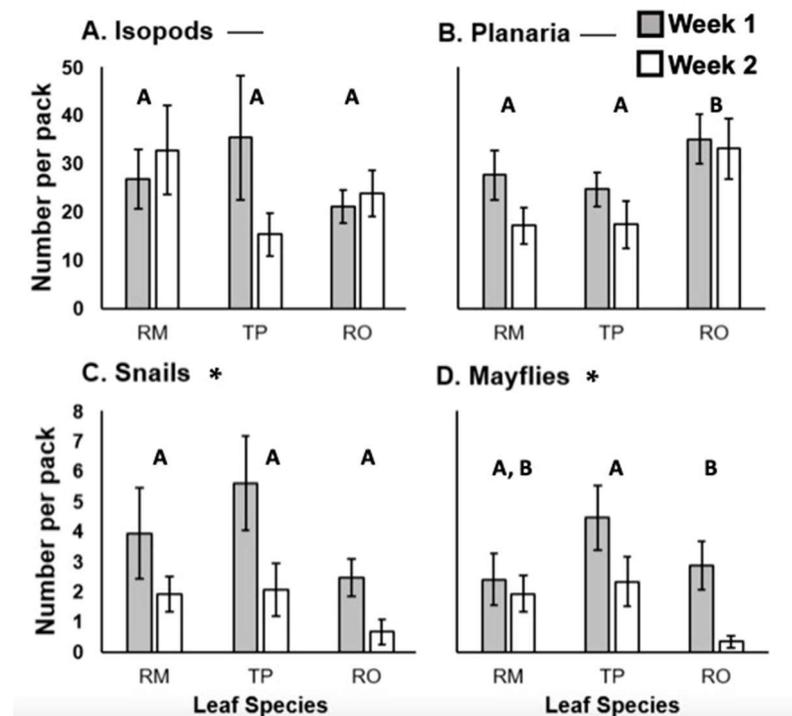


Figure 2. The effect of type of leaf and length of time in Cedar Creek on the average ($\pm 1SE$) density of (A) isopods (*Lirceus* sp.; ffg = detritivores/grazers), (B) planaria (Tricladida; ffg = carnivores), (C) snails (predominantly *Potamopyrgus antipodarum*; ffg = detritivores/grazers), and (D) mayflies (*Tricorythodes* sp.; ffg = collectors). Leaf species are arranged in order of descending predicted colonization densities. RM = red maple; TP = tulip poplar; RO = red oak. Note the different y-axis values in A and B versus in C and D. N = 15 for all bars. ffg = functional feeding group. Different letters above the bars indicate statistically significant differences among types of leaves. After the name of the taxon, — indicates no significant difference between collection dates, while * indicates significantly more animals present in the first week.

Leaf species had a significant effect on the number of planaria within leaf packs in the stream (Figure 2B; $F_{2,80} = 6.092, p = 0.0034$), with more planaria among red oak leaves than either of the other two leaves, but no significant difference in the number of planaria colonizing the red maple and tulip poplar leaves. Neither conditioning time ($F_{1,80} = 3.876, p = 0.052$) nor the interaction term ($F_{2,80} = 0.547, p = 0.581$) was significant, but there was a significant effect of the mat ($F_{4,80} = 9.348, p < 0.0001$) on the number of planaria.

The number of snails within stream leaf packs (Figure 2C) was not significantly determined by the species of leaf ($F_{2,80} = 2.635, p = 0.078$), and the interaction term was not significant ($F_{2,80} = 1.680, p = 0.193$). However, there were significantly more snails in the first week ($F_{1,80} = 19.667, p < 0.0001$), and there was a significant effect of the mat ($F_{4,80} = 3.868, p = 0.006$).

The number of mayflies in the stream (Figure 2D) was significantly impacted by both the leaf species ($F_{2,80} = 3.683, p = 0.030$) and the time of conditioning ($F_{1,80} = 9.569, p = 0.003$), while the interaction term was not significant ($F_{2,80} = 2.620, p = 0.079$). There were significantly more mayflies collected in the first week and in leaf packs composed of tulip poplar than in those of red oak, but all other pairwise post hoc comparisons were not significant.

Three taxa frequently appeared within the leaf packs of the fishless pond (i.e., present in at least 20 of the 45 packs per week, listed in order of decreasing frequency): isopods (*Caecidotea communis*), predatory leeches (*Helobdella stagnalis*), and fingernail clams (*Sphaeri-*

idae). These taxa comprised 99.79% of the total 5758 specimens collected in week 1 and 99.67% of the 3634 collected in week 2.

Both leaf species and conditioning time were significant predictors of the number of pond isopods (Figure 3A; $F_{2,80} = 13.714$, $p < 0.0001$, and $F_{1,80} = 4.733$, $p = 0.033$, respectively), with greater numbers of isopods collected the first week and in tulip poplar leaves, but no significant difference in isopod numbers within red oak and red maple leaves, and the interaction term was not significant ($F_{2,80} = 1.402$, $p = 0.252$) but mat had a significant predictive value ($F_{4,80} = 13.93$, $p < 0.001$).

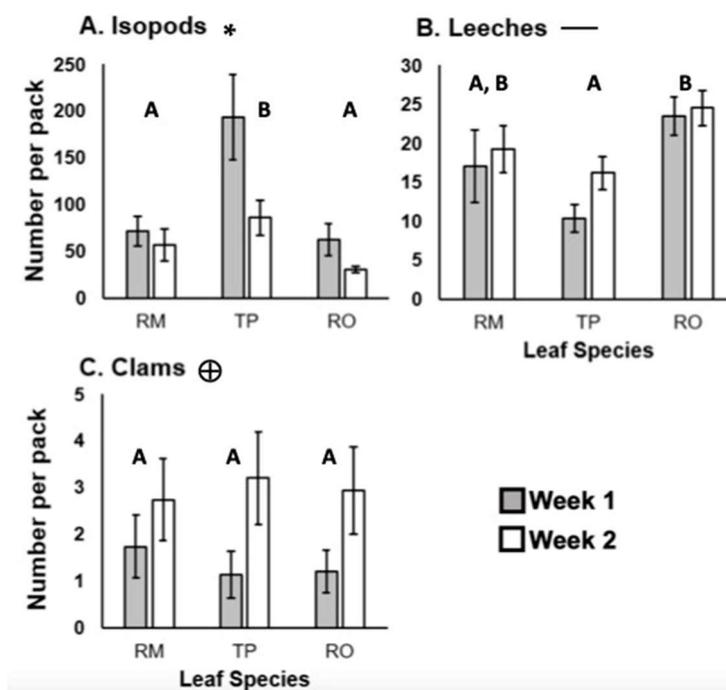


Figure 3. The effect of type of leaf and length of time in Scout Pond on the average (± 1 SE) density of (A) isopods (*Caecidotea communis*; ffg = detritivores/grazers), (B) leeches (predominantly *Helobdella stagnalis*; ffg = carnivores), (C) clams (*Sphaeriidae*; ffg = collectors). Leaf species are arranged in order of descending predicted colonization densities. RM = red maple; TP = tulip poplar; RO = red oak. Note the different y-axis values. $N = 15$ for all bars. ffg = functional feeding group. Different letters above the bars indicate statistically significant differences among types of leaves. After the name of the taxon, — indicates no significant difference between collection dates, * indicates significantly more animals present in the first week, and \oplus indicates significantly more animals in the second week.

While the number of leeches within the leaf packs (Figure 3B) did not differ significantly between weeks ($F_{1,80} = 1.831$, $p = 0.180$), and there was no significant interaction term ($F_{2,80} = 0.408$, $p = 0.666$), there was a significant effect of the mat ($F_{4,80} = 2.964$, $p = 0.025$) and of leaf species ($F_{1,80} = 7.673$, $p = 0.0009$), with fewer leeches within tulip poplar than red oak leaves, but the other post hoc pairwise comparisons among leaf types were not significant.

There was no significant effect of leaf species or the interaction term on clams (Figure 3C; $F_{1,80} = 0.012$, $p = 0.988$ and $F_{2,80} = 0.989$, $p = 0.377$, respectively), but there was a significant effect of mat ($F_{4,80} = 3.00$, $p = 0.023$) and significantly more clams in the second week ($F_{1,80} = 5.734$, $p = 0.019$).

We also examined (Appendix A Figures A1 and A2) the average proportional representation of each taxon present within the leaf packs. The relative presence of the various dominant taxa remained largely the same across sampling dates and species of leaves (Appendix A, Figure A1), as certain taxa (isopods, leeches) consistently maintained a dramatic numerical dominance within the community. Therefore, our ensuing discussion of

the implications of our data will discuss patterns of the within-pack count of each taxon rather than proportional representation.

The red oak leaves displayed significantly less skeletonization than the other two leaf species (Table 2; $df = 8$, $\chi^2 = 44.95$, $p < 0.001$ for Cedar Creek and $df = 8$, $\chi^2 = 45.4$, $p < 0.001$ for Scout Pond), which did not differ significantly from each other ($df = 4$, $\chi^2 = 2.5$, $p > 0.5$ for Cedar Creek and $df = 4$, $\chi^2 = 0.27$, $p > 0.5$ for Scout Pond). Red oak leaves in the pond also had a significantly higher remaining leaf surface area quantile than did the other species (Table 2; $df = 8$, $\chi^2 = 29.8$, $p < 0.001$), which were not significantly different from each other ($df = 4$, $\chi^2 = 1.53$, $p > 0.5$). The remaining leaf surface area quantiles were not collected for leaves conditioned within the stream due to almost uniformly high levels. Furthermore, the red maple leaves in both ecosystems developed a slippery surface film during the course of the experiment, while the red oak leaves did not noticeably alter their surface texture (Hoffman, personal observations).

Table 2. (A) Skeletonization scores and (B) remaining surface area quantile of leaf pack contents. CC was not scored in (B) due to such a consistently small amount of leaf decay.

A.		Skeletonization Rating (Low to High)				
Field Site	Leaf Species	Level 1	Level 2	Level 3	Level 4	Level 5
Cedar Creek	red maple	0	3	5	6	1
	tulip poplar	0	2	3	6	4
	red oak	14	1	0	0	0
Scout Pond	red maple	0	0	3	5	7
	tulip poplar	0	0	2	5	8
	red oak	15	0	0	0	0

B.		Remaining Surface Area Quantile				
Field Site	Leaf Species	0%	25%	50%	75%	100%
Scout Pond	red maple	0	3	10	2	0
	tulip poplar	0	6	7	2	0
	red oak	0	0	1	11	3

4. Discussion

4.1. Effect of Leaf Species

We predicted that the CPOM detritivores/grazers (isopods, snails) that use the leaves for food [38–42] would particularly colonize red maple leaves. These leaves have the lowest toughness and C:nutrient ratio of the three leaf species we used [43] and lack the high levels of condensed tannins present in red oak [44,45]. We even expected the FPOM collectors (mayflies, clams) and the predators/scavengers (planarians, leeches) to avoid the lower pH induced by oak tannins. However, our predictions were not supported; no taxon showed a significant preference for the red maple leaf packs. There was no consistent pattern across taxa as to which species of summer fresh leaves nor the amount of conditioning time would lead to a greater density of inhabitants. Indeed, contrary to our predictions, multiple taxa did not significantly discriminate among leaf packs based on either leaf species or collection period.

Snails, clams, and stream isopods did not discriminate among the three species of leaves. Perhaps these animals are not nitrogen- or phosphorus-limited, and so the lower concentrations of these nutrients in red oak leaves (versus tulip poplar or red maple leaves; [43]) were not deterrent. Red maple and red oak leaves were also colonized by comparable numbers of pond isopods but more inhabited tulip poplar leaves. High concentrations of tannins in red oaks and tough lignins [45] may explain fewer pond isopods within these leaf packs than within tulip poplar, but the parity of colonization by isopods within red oak and red maple leaves is not consistent with that explanation. More

mayflies moved into tulip poplar than red oak leaves, perhaps because of the relatively higher tannins and lower phosphorus:carbon ratio in the oaks [46], as mayfly growth is heavily correlated with their acquisition of phosphorus [47].

In contrast to the mayflies, more stream planaria colonized red oak than either tulip poplar or red maple leaves, while pond leech densities were higher in red oak than tulip poplar leaves. We were unable to find research on the relationship between planaria or leeches and leaf litter. Because neither taxon is reported as herbivorous (both are carnivores, feeding as predators or scavengers; [48–50]), leaves are likely background substratum for these worms, which move slowly and typically are darkly colored. High levels of skeletonization in tulip poplar and red maple leaves may have complicated planarian gliding compared with the relatively intact red oak leaves. However, because the colonization difference manifested by the first week's collection, before much skeletonization occurred, that cannot be the only causative factor. While all the leaves were a light green when initially picked, red oak leaves darkened substantially by the end of the experiment and may have provided better camouflage for these worms.

The lack of a predictable ranking of leaf colonization cannot be ascribed to inadequate leaf conditioning. Peak abundance of macroinvertebrates within packs of dried green leaves occurred fourteen days after submergence in another stream [51]. Also, the degradation of tulip poplar and red maple leaves in our experiments was so great after two weeks of submersion in either ecosystem that we stopped the experiment prematurely to avoid collecting empty packs after three weeks total. The relative abundances of our macroinvertebrates within the leaf packs were congruent with those in the sediments. While we do not have quantitative data on the densities of benthic animals at the precise locations of experimental deployments, multiple collections during the past decade at both sites have yielded similar relative abundances of the benthic taxa collected in our leaf packs (Iyengar, personal observations). No common invertebrates small enough to enter through the mesh were notably absent from the leaf packs. Thus, all of the abundant benthic local taxa seem likely to readily enter leaf aggregations.

Due to the low numbers of stream snails, mayflies, and pond clams, patterns for these taxa should be viewed conservatively. But colonization patterns also varied within the detritivores, even between the two types of isopods, suggesting that either all three of these green leaf species were equally desirable (similar palatability, nutrition, etc.), or none of them were directly used for food, or that green leaves represent an unusual resource within the stream that not even the detritivores/herbivores are adapted to detecting fresh-leaf cues. Alternatively, our method of connecting single-species leaf packs into a single, multi-species mat to facilitate deployment and standardize abiotic parameters across replicates may have impacted the data. Mixed-leaf-species diets can promote faster growth than single-species diets [9,34,52,53], and invertebrates may have followed the scent of a mixed assemblage. Once at the mat, an individual may have moved from one leaf species to the next, to gain a diversified diet, but we did not monitor within-stream movements and so can only know the single leaf pack any animal was in during collections. Future experiments examining the attraction to single- versus multi-species leaf packs would be of interest.

4.2. No Impact of Leaf Skeletonization

Highly skeletonized leaves that do not hide macroinvertebrates from visually-oriented predators were not significantly avoided by any of the animals in either habitat. The only taxa to inhabit red oak substantially more than red maple or tulip poplar leaves (planaria and leeches; Figures 2 and 3) did not significantly increase their numbers in the later week, when skeletonization differences manifested. Indeed, mayflies preferred tulip poplar to red oak leaves and had even higher numbers in the second week (Figure 2), when the degree of skeletonization was markedly pronounced (Table 2).

This lack of preference in the second week for the mostly intact red oak leaves suggests that the main role of leaf litter selection is not concealment. Perhaps simple sight-obstructing shelters, as provided by leaves, do not provide sufficient protection. Indeed, stream isopods

exposed to fish moved to shelter within three-dimensional tufts of algae more than into leaf packs [54].

Across both ecosystems, of the seven taxa under consideration, four showed significant differences in colonizing numbers across weeks: pond clams, stream mayflies, stream snails, and pond isopods. More pond clams were collected in the second than in the first week's collection (Figure 3). As non-selective filter feeders ingest fine particulate organic material (FPOM; [55]) that likely also feeds as collectors ([56], the density increase of clams over time was expected. As leaf degradation increased due to the macroinvertebrate detritivores, microbes, and abiotic processes, likely the local FPOM levels increased, and the clams moved into the leaf packs to take advantage of the newly available resource.

The colonization pattern of stream snails (Figure 2C), stream mayflies (Figure 2D), and pond isopods (Figure 3A) was the opposite of the pattern of clam colonization: higher numbers of these first three taxa occurred in the first week of deployment. While *P. antipodarum* mudsnails and *Tricorythodes* mayflies often feed as FPOM detritivores, they also graze on algae [38,40–42]. Green leaves that have recently entered the stream (the first week of our experiment) are likely more similar to autochthonous photosynthetic material than heavily microbe-infested leaves (as after two weeks in our experiment). Furthermore, after two weeks, a mesh of intact veins typically remained in the skeletonized areas of the red maple and tulip poplar leaves, which may be evidence of snail grazing [28] rather than of shredders. While decreased leaf surface area by the second week may have reduced the numbers of grazers, the still-intact red oak leaves also contained lower numbers of snails and mayflies in the later collection. Therefore, rather than merely lower CPOM availability over time, perhaps a more attractive food resource than leaves, such as an ephemeral alga, appeared during our experiment and enticed the snails and mayflies from the leaves.

Despite the previously documented preference of isopods for fungal-colonized, rather than unconditioned, senescent leaf litter ([23,57], and even studies in this same stream reach in [58]), neither of the types of isopods in our study increased their colonization densities over time. The pond isopods had greater colonization numbers in the first week, and the stream isopods did not alter their densities between weeks (Figure 2A). Microbial conditioning of fresh green leaves may not be necessary for sufficient nutrition. Styron [59] noted that successful laboratory rearing of isopods required fresh leaves for the young to mature. Indeed, microbial communities may reduce the value of fresh leaves over time (this can even occur in senescent leaves; [25]).

Lirceus sp. (the stream isopods) may be more generalist feeders than *Caecidotea communis* (the pond isopods), as the stream isopod densities were not affected by leaf type or length of deployment (Figure 2A), whereas pond isopods were significantly impacted by both factors (Figure 3A). Future research will examine a broader range of green leaf species and attempt to determine whether this pattern (if it continues) is due to taxonomy (different genera) or habitat (the stream isopods may ingest proportionately more periphyton; [60]). The leaves may provide refuge, more than nutrition, for the stream isopods, and these three species of fresh leaves may provide similar levels of refuge from streamflow drag forces and attacking predators, even if they differ in nutritional value and degree of skeletonization (the overlying mesh structure still provides defense).

4.3. Importance of These Studies

The increasing frequency of intense summer storms [11] is elevating the biomass of fresh (green) leaves in aquatic ecosystems, largely through event-pulse additions. Furthermore, as red maple and red oak are increasing in abundance in the forests of the northeastern United States [30,31], these species are likely to provide a proportionally greater amount of allochthonous material to local streams and ponds. Invertebrates may discriminate among species of these sometimes-abundant fresh material resources differently than the autumn senescent leaf drop of the same species. Studies of macroinvertebrate colonization and the durability of these green leaves in the system are key to understanding the relative performance of sympatric taxa in these changing ecosystems.

Unfortunately, albeit perhaps not surprisingly, given the range of functional feeding groups and taxa we examined, there is a lack of a clear, consistent pattern of use of fresh leaf litter resources by stream and pond benthic macroinvertebrates. Similar to our findings, previous authors also reported variability in the impact of green leaves across invertebrate species [9,61], that relative amounts of consumption may be unrelated to nutritional and toughness differences among leaf species [19], and that exposure time, rather than leaf species, can be the main predictor of the degree of invertebrate colonization (e.g., [58,62]). Our current data suggest that allochthonous inputs of fresh summer leaves are often rapidly disintegrated (in little more than two weeks) in both lentic and lotic ecosystems, although some species (e.g., red oaks) retain their integrity substantially longer. An ideal future experiment would be to use green and senescent leaves concurrently, in single-species and mixed-species aggregations, to directly determine whether there was an impact of senescence on macroinvertebrate choice. Red oak and other slow-decaying fresh leaves may be important as long-term in-stream/in-pond leaf resources during summer.

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Appendix A

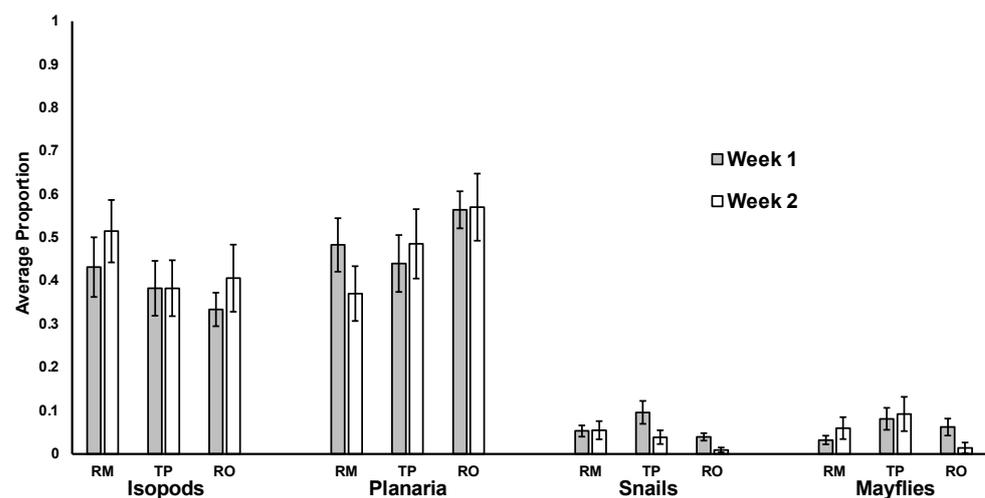


Figure A1. The effect of leaf species and length of deployment time in Cedar Creek on the average ($\pm 1SE$) proportional representation of the sum of numbers of individuals of dominant taxa within each leaf pack. RM = red maple; TP = tulip poplar; RO = red oak. N=15 for all bars.

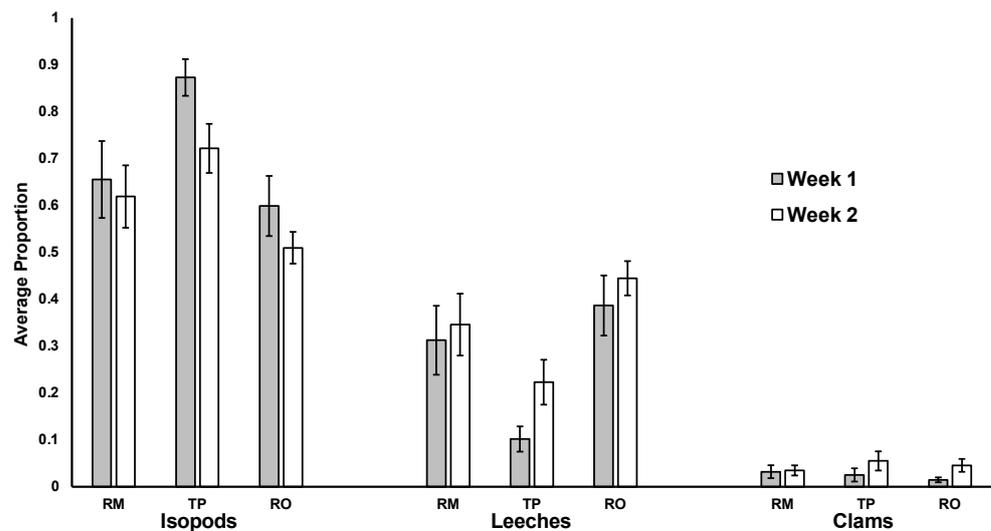


Figure A2. The effect of leaf species and length of deployment time in Scout Pond on the average ($\pm 1SE$) proportional representation of the sum of numbers of individuals of dominant taxa within each leaf pack. RM = red maple; TP = tulip poplar; RO = red oak. N=15 for all bars.

Appendix B

Table A1. Previous aquatic studies utilizing fresh, green leaf litter in studies of decomposition, degradation, and macroinvertebrate colonization. N/A indicates that the study examined leaf-specific processes, not macroinvertebrate colonization. 'Ecosystem' lists the source habitat of the experimental leaves and animals. The experiments were conducted in situ, unless the habitat listed is within parentheses, which indicates that the experiments were conducted in the laboratory.

Reference	Ecosystem	Invertebrates Studied	Leaves Are Congeners of the Current Study?
[16]	lotic	N/A	no
[19]	(lotic)	Amphipoda, Trichoptera	no
[63]	lotic	N/A	no
[13]	lotic	N/A	no
[9]	(lotic)	Trichoptera	Yes, maple and oak
[64]	lotic	Amphipoda, Trichoptera	Yes, maple
[12]	lotic	Amphipoda, Trichoptera	Yes, maple
[52]	lotic	N/A	Yes, maple and oak
[65]	lotic	wide variety of shredders	no
[66]	lotic	aggregated functional feeding groups	Yes, red maple
[67]	lotic	N/A	Yes, oak
[51]	lotic	Amphipoda, Coleoptera, Diptera, Ephemeroptera, Plecoptera, Trichoptera	Yes, maple
[68]	lotic	aggregated functional feeding groups	Yes, red maple
[20]	lotic	Diptera, Ephemeroptera, Plecoptera, Trichoptera	no
[61]	(lotic)	Gastropoda, Ephemeroptera, Trichoptera	no

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