

Differential consumption and assimilation of leaf litter by wetland herbivores: alternative pathways for decomposition and trophic transfer

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Abstract: The process of decomposition has received much attention in terrestrial and stream ecosystems, but our understanding of the factors that contribute to this process in wetlands remains relatively poor. Many macroconsumers in wetlands are classically labeled as herbivores, but increasing evidence suggests that they also contribute to the breakdown of dead plant litter depending on the nutritional quality (i.e., nutrient content, density, and toxicity) of the litter. We examined the relative contributions of 2 common North American temperate wetland consumers, the green frog tadpole (*Lithobates clamitans*) and the Ram's Horn snail (*Planorbella trivolvis*), to the decomposition of 5 chemically variable plant litter species. Based on anatomical differences (e.g., mouth parts, digestive structures), we hypothesized that snails would have higher consumption rates than tadpoles, but that tadpoles would have higher assimilation efficiency. We also predicted that consumption rates and assimilation efficiency would vary with litter nutritional quality. Overall, consumers exhibited substantial detritivory and caused up to 62% litter mass loss relative to treatments with only microbes. As hypothesized, snails consumed more than tadpoles, but this difference was largely explained by differences in consumer mass. Contrary to our hypothesis, snails and tadpoles exhibited similar assimilation efficiencies. Both litter mass loss and assimilation efficiency by consumers differed among litter species treatments. Litter mass loss tended to be negatively correlated with litter C : N and C : P, whereas assimilation efficiency had no detectable correlation with any measured litter characteristic. Our study demonstrates that studies of energy and nutrient budgets in wetlands should consider both consumer type and litter species to describe ecosystem function fully.

Key words: assimilation efficiency, detritivores, food web, litter breakdown, temperate forest, wetlands

Decomposition of primary production is an essential part of energy and nutrient cycling in ecosystems, particularly in temperate forests where decomposing plant material (i.e., litter) makes up as much as 99% of all organic matter (Facelli and Pickett 1991). In these forests, decomposition of plant litter provides a basal energy source to both terrestrial and aquatic systems (Fisher and Likens 1973, Swift et al. 1979) and is a major determinant of community interactions and productivity (Wallace et al. 1982). Decomposition rates are determined by rates of leaching, microbial conditioning (i.e., growth of microbes on litter), and fragmentation. Through a combination of these processes, plant litter directly fuels both primary and secondary productivity by releasing energy to decomposer communities and primary producers (Fisher and Likens 1973). Detritivores that ingest and fragment litter can accelerate such energy release (Wallace et al. 1982) by producing fragmented plant tissue, excretia, and feces that provide resources for other organisms (e.g., primary pro-

ducers) and are rapidly mineralized by microbes (Anderson and Sedell 1979).

Most knowledge of consumer-mediated litter decomposition stems from studies of terrestrial and stream communities, but appreciation for the contribution of pond and wetland communities to nutrient cycling is increasing (Taylor and Batzer 2010). These communities typically contain a diverse array of organisms including both invertebrates and vertebrates (Williams 2005). Several types of organisms, such as caddisflies and isopods, are thought to be specialist consumers of plant litter and other decomposing material (Batzer and Ruhí 2013). In contrast, other organisms, such as snails and tadpoles, have been categorized as herbivores (Brönmark et al. 1991, Altig et al. 2007). However, increasing evidence indicates that many wetland species have broader diets than previously considered. For example, snails are associated with increased rates of litter decomposition (Brady and Turner 2010), and stable isotope analysis has been

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used to show that several common tadpole species are non-selective feeders (Schiesari et al. 2009). Thus, much uncertainty exists regarding the contribution of many consumers to the process of decomposition. We explored the capacity of 2 common wetland consumers (snails and tadpoles) to influence litter decomposition and energy flow. To describe the functional roles of these consumers, we assessed their contributions to wetland nutrient cycling by measuring direct consumption of litter and assimilation efficiency.

The contribution of individual consumer species to litter decomposition and trophic energy transfer might depend only on the size of the consumer, or it might also depend on whether they possess traits for consuming and digesting relatively low-quality and recalcitrant food (Webster and Benfield 1986). Many species of snails and tadpoles have rigid mouthparts suitable for grazing detritus (i.e., chitinized radulae among snails, keratinized beaks among tadpoles). Chitin has greater tensile strength than keratin (Meyers et al. 2008), so one might predict that snails should graze and shred litter more rapidly than tadpoles. However, rates of animal movement and efficiencies of grazing action also are likely to influence consumption rate, and most tadpoles are far more active than any snail species. Tadpoles must accumulate resources and body mass in a relatively short period of time to achieve metamorphosis, but snails might need similar resources for reproductive efforts. Assimilation efficiency is equally difficult to predict among consumers. Differences in assimilation efficiencies typically are predicted by physiological factors, such as rates of peristalsis and intestine length (Sibly 1981), but snails and tadpoles have a dramatically different digestive morphology and physiology (e.g., rates of peristalsis, stomach structure; McDiarmid and Altig 1999, Castro and Huber 2003), so comparisons based solely on intestine length are potentially misleading.

Variation in litter nutritional quality (i.e., the quantity and availability of nutrients, digestibility, and toxicity) is likely to play an equally important role in determining consumption rates and assimilation efficiency (Skelly and Golon 2003). Nutrient-rich litter species often support productive microbial communities outside and inside the consumer, and are consequently more palatable and nutritious for detritivores than are nutrient-poor litter species (Cummins and Klug 1979). In contrast, litter that is rich in structural and secondary compounds (e.g., lignin, cellulose, phenolic acids) can inhibit microbial growth and decrease the resource value of the litter for detritivores (Ardón and Pringle 2008). Differences in litter chemistry also might directly affect consumers that ingest fragments of litter. For example, phenolic acids in litter might bind to proteins in the digestive tract and decrease assimilation efficiency (Maerz et al. 2005). Given ongoing changes in plant diversity that often exist within and around wetlands (e.g., Saltonstall 2002), understanding how the chemical traits of plant litter influence wetland detritivory and nutrient/C cycling is important.

We sought to learn whether snails and tadpoles consume plant litter directly, thereby causing accelerated decomposition of the litter and allowing direct transfer of energy and biomass from detritus to these consumers. Which aspect of their functional morphologies direct feeding activity is not clear. Therefore, we hypothesized that snails would differ from tadpoles in terms of consumption rates and assimilation efficiency. We further hypothesized that consumption rates (measured as litter mass loss) and assimilation efficiency would be directly related to litter N and P content and indirectly related to density and phenolic acid content. We tested these hypotheses with a laboratory experiment in which we measured mass loss of 5 microbially conditioned plant litter species, with and without snail (*Planorbella* [*Helisoma*] *trivolis*) or tadpole (*Lithobates* [*Rana*] *clamitans*) consumers, and the assimilation efficiency of each consumer species fed each litter species.

METHODS

Our experimental design consisted of 3 consumer treatments (snail, tadpole, and microbe-only) crossed with 5 leaf-litter treatments. Each treatment was replicated 3 times for a total of 45 experimental units. Experimental units were 0.75-L plastic containers containing 0.19 ± 0.051 g dried litter of a single species, which is an ecologically relevant biomass (Rubbo et al. 2008).

We used 5 litter species including both tree and emergent species that are common to northeastern USA temperate regions. Tree species were green ash (*Fraxinus pennsylvanica*), red maple (*Acer rubrum*), and cottonwood (*Populus deltoides*). Emergent species were a nonnative strain of the common reed (*Phragmites australis*) and reed canary grass (*Phalaris arundinacea*). Green ash has relatively nutrient-rich leaves and is declining rapidly because of the spread of the invasive emerald ash borer (MacFarlane and Meyer 2005). In contrast, red maple is increasing in density because of loss of competitors (e.g., *Quercus* spp.), and has relatively nutrient-poor leaves with high concentrations of phenolic acids (Ostrofsky 1993, 1997). Cottonwood trees are associated with young, recently logged forests and have relatively nutrient-poor, lignin-rich leaves (Ostrofsky 1993, 1997, Abrams 2003). Both phragmites and reed canary grass are common invasive wetland macrophytes with nutrient-rich, but relatively tough and rigid tissues (Cohen et al. 2012).

We set aside samples of air-dried leaves for chemical analysis with procedures detailed by Graça et al. (2005). We measured nutrient quality as % N and % P in leaves (with wet-bench microKjedahl and ascorbic acid digestion assays, respectively). We measured toxicity as phenolic acid content, which we assayed spectrophotometrically after mixing leaf extract with Folin–Ciocalteu reagent. We estimated leaf digestibility as the ratio of leaf toughness to leaf thickness (hereafter, leaf density). We measured leaf

thickness as the mean width of a cross section of 4 leaf samples for each species, and we recorded the average mass required to penetrate leaves of each species with a 4-mm diameter penetrometer (Graça et al. 2005) after soaking the leaves in water for 24 h. A solid aluminum penetrating rod was attached to a funnel that was gradually filled with shot pellets until the rod penetrated a section of leaf firmly placed between 2 wooden boards. We avoided positioning the rod over large veins.

We raised green frog tadpoles from egg masses shipped from Tennessee (Charles Sullivan Company, Nashville, Tennessee). Snails were progeny from a *Planorbella trivolvis* population originating from Pinchot Lake, Pennsylvania. Litter species used in our study are present in both of these regions. *Planorbella trivolvis* is present in freshwater ecosystems from Canada to Florida and shreds leaf litter (Brady and Turner 2010). Green frogs are common in freshwater ponds that might be subsidized by leaf litter (Conant and Collins 1998). Both consumers are found together frequently, but green frog tadpoles are present in moderate-to-open canopy wetlands, whereas Ram's Horn snails are restricted to open-canopy systems (Werner et al. 2007, Hoverman et al. 2011).

All consumers used in the study were hatched outdoors in 100-L plastic pools and fed conditioned green ash leaf litter ad libitum for 3 wk, after which we transported organisms to the laboratory and maintained them in aerated artificial spring water (ASW; Cohen et al. 1980) at room temperature (~20°C) for 2 wk. We conducted half-water changes every 3 d and fed both consumers a combination of TetraMin® Fish Flakes (Tetra Werke, Melle, Germany) and frozen spinach ad libitum until the start of the experiment. We did not feed consumers for 2 d prior to the experiment to allow clearance of their digestive tracts.

Before adding consumers to experimental containers in the laboratory, we conditioned dried litter in the containers for 7 d in 200 mL of pond water collected from a nearby wetland. This wetland receives all litter types used in our study, so it probably harbored microbes capable of colonizing all 5 litter types. We filtered pond water through a 53-µm Nytex® filter to remove zooplankton. We kept the containers in the laboratory at 21°C with a 12:12 light:dark cycle. We did not want leaf leachate to influence consumer growth or serve as a potential resource, so we discarded all water in the containers after 1 wk and immediately added 500 mL of ASW. More material might have leached from the leaves after this water change, but previous research suggests that most soluble material is leached from leaves after 3 or 4 d of inundation (Moore et al. 2004).

We set up 3 additional containers for each litter species to serve as leachate controls to correct for mass loss from leaching during the 7-d conditioning period. These containers had similar masses of leaf litter and were maintained for the same duration as the conditioning period,

but the leaves were placed in 500 mL of sterilized ASW instead of pond water to minimize microbial growth. At the end of the conditioning period, we measured the dry mass of this litter (see below).

After conditioning litter, we added consumers to the appropriate containers (day 0). We pooled all individuals of each consumer species and haphazardly selected groups of 3 individuals. We placed 1 group in each plastic container after measuring total wet mass of the group. Mean tadpole mass was 0.487 ± 0.136 g, and mean snail mass was 1.011 ± 0.160 g. We allowed consumers to feed without interruption for 10 d. During the 10-d feeding period, we collected animal feces every 3 d with plastic Pasteur pipettes. In other studies, researchers collected feces daily to prevent fecal decay (e.g., Mason 1970, Skelly and Golon 2003), but the feces remained solid and showed little sign of decay during our study. After the 2nd round of feces collection, we replenished water levels in all containers with ASW water. We stored feces at 4°C until the end of the experiment, when they were dried (65°C for 24 h) to obtain dry mass.

On day 10, we removed all animals and remaining leaf litter. We euthanized animals with a lethal dose of benzocaine (Vanable 1985). We dried leaves, snails, and tadpoles at 65°C for 24 h to obtain dry mass. We included shell mass of snails. We calculated % mass loss of leaf litter resulting from microbes or consumers as

$$\% \text{ litter mass loss} = \frac{\text{Initial litter mass} - \text{final litter mass}}{\text{Initial litter mass}} \times 100. \quad (\text{Eq. 1})$$

To correct for mass loss from leaching, we adjusted this value by subtracting the mean % mass loss for each litter species as measured in the leachate controls.

For consumer treatments, we calculated the litter mass consumed as the adjusted % litter mass loss multiplied by the initial litter mass. We then calculated assimilation efficiency as

$$\text{Assimilation efficiency} = \frac{\text{Litter mass consumed} - \text{feces mass}}{\text{Litter mass consumed}} \times 100. \quad (\text{Eq. 2})$$

We measured the blot-dry mass of animals before and after our study, but we did not incorporate consumer growth in the formula for assimilation efficiency because very little growth occurred over the short duration of our study and measurement error in the mass of small aquatic consumers is substantial.

Statistical analysis

We tested the interactive effects of leaf species and consumer on % litter mass loss and assimilation efficiency with 2-way analysis of variance (ANOVA) using Type 2 sums of

squares. We first tested for the effects of leaf species, consumers, and the leaf \times consumer interaction on leaf mass loss with a factorial ANOVA. We detected a significant leaf species \times consumer interaction, so we conducted separate ANOVAs for each of the 3 consumer treatments (microbe-only, snail, and tadpole). To explore whether the consumer species effect on % litter mass loss might be driven primarily by differences in consumer mass (as a biological null hypothesis), we conducted an ANOVA including leaf species (5 treatments), consumer treatment (snail vs tadpole), and their interaction, with and without consumer mass as a covariate. If the effect of consumer species was significant without consumer mass as a covariate but nonsignificant with consumer mass as a covariate, we concluded that consumer mass explained most of the difference between these consumer species.

We tested for the effect of treatments on consumer assimilation efficiency with an ANOVA including leaf species (5 treatments), consumer (snail and tadpole treatments), and their interaction. We did not include the microbial consumer treatment in this analysis because we did not measure microbial assimilation efficiency. For all 1-way ANOVAs with significant effects, we conducted Tukey's Honestly Significant Difference post hoc comparisons to identify consumer-specific differences in consumption or assimilation rates among leaf species.

We used mixed-effect general linear models to test for effects of leaf structure and chemistry on assimilation efficiency and % litter mass loss of each consumer species. Preliminary evaluation of data indicated that they met the assumptions of linear regression. We included leaf species in each model as a random-effects variable to ensure that leaf species was treated as the unit of replication in testing for effects of leaf characteristics. Leaf density, C:N, C:P, and phenolic concentration of each leaf species were included in each model as fixed-effect predictors with a forward-stepwise-regression procedure in which variables with significant contributions to each model were retained ($p < 0.05$). We fit mixed-effects models with function *lme* in R package *nlme* (Pinheiro et al. 2013) and used a maximum log-likelihood estimator to ensure Akaike Information Criterion (AIC) values would be comparable among models with different fixed effects.

We arcsin $\sqrt{(x)}$ -transformed assimilation efficiency and % leaf mass loss prior to analyses to improve normality (Gotelli and Ellison 2004). We conducted all analyses in R (version 2.15.1; R Project for Statistical Computing, Vienna, Austria). R^2 values were calculated based on the Wald's statistic using *lmmR2W* from package *lmmfit* (Maj 2011), and F -statistics were calculated using *anova* (Fox and Weisberg 2010). Preliminary analysis indicated a correlation between litter C:P and C:N. We included both in our regression analyses to explore potential differences in nutrient limitation among treatments.

RESULTS

Litter mass loss

We detected significant main and interactive effects of litter species and consumer species on % litter mass loss (2-way ANOVA including all 3 consumer treatments; Table 1, Fig. 1). Snails generated 14.4% and 30.3% greater litter mass loss than tadpoles and microbes, respectively, and tadpoles generated 15.9% greater litter mass loss than microbes. Percent mass loss differed significantly among litter species in microbe-only and snail treatments and marginally in the tadpole treatment (separate 1-way ANOVA for each consumer treatment; Table 1). In the microbe-only treatment, maple litter lost 9.6 to 19.1% less mass than reed canary grass, cottonwood, and phragmites and 4.9% less than ash, but the difference in % mass loss between maple and ash was not significant ($p = 0.056$). Ash litter lost 12.7 and 14.1% less mass than reed canary grass and phragmites, respectively. In the snail treatment, ash litter had the highest % mass loss. Ash litter % mass lost was 33.5% and 36.0% greater than cottonwood and phragmites % mass lost, and reed canary grass lost 18.7% more than cottonwood, but the difference in mass lost between cottonwood and reed canary grass was not significant ($p = 0.087$). In the tadpole treatment, reed canary grass lost 22.0% more mass than maple, and ash lost 20.1% more mass than maple, but neither difference was significant ($p \leq 0.091$). See Fig. S1 for representative before-and-after images of each litter species in each consumer treatment.

Litter species and consumer species significantly affected % litter mass loss and the litter \times consumer species interaction was marginally significant in the model including only the 2 macroconsumer species (tadpoles and snails; Table 2). However, when consumer mass was used as a covariate in this model, the effects of consumer species and the litter \times consumer species interaction were not significant. After accounting for consumer mass, ash lost significantly more

Table 1. Results of analyses of variance examining the effects of litter and consumer species on % litter mass loss and assimilation efficiency and the effect of litter species on % litter mass loss within each consumer treatment.

Model/source	Litter % mass loss		Assimilation efficiency	
	F	p	F	p
2-way factorial				
Litter species	10.36 _{4,30}	<0.001	7.30 _{4,20}	<0.001
Consumer species	72.20 _{2,30}	<0.001	5.56 _{1,20}	0.029
Litter \times consumer	6.34 _{8,30}	<0.001	0.71 _{4,20}	0.598
Microbe-only	17.63 _{4,10}	<0.001		
Snail only	8.09 _{4,10}	0.004		
Tadpole only	3.25 _{4,10}	0.059		

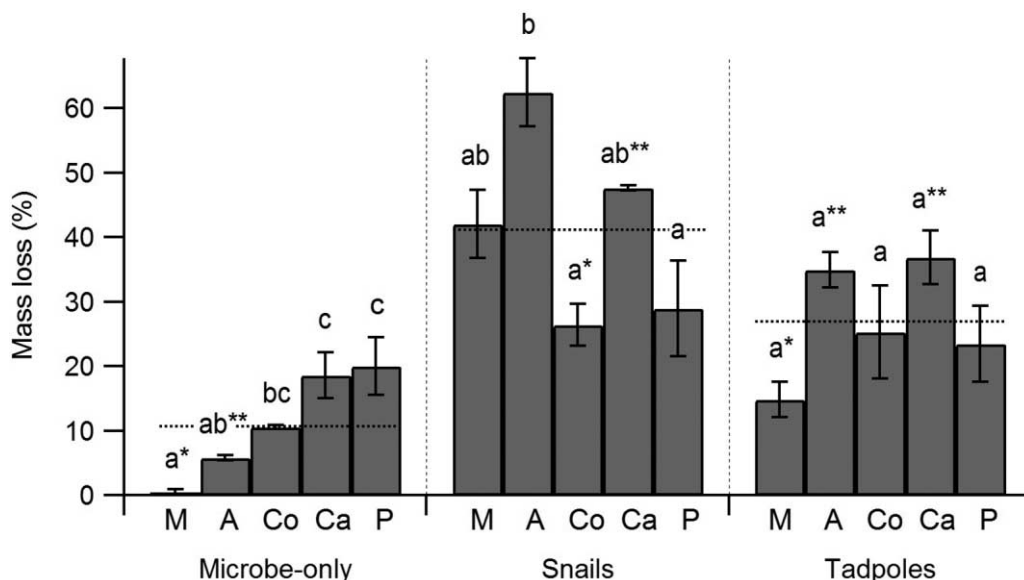


Figure 1. Mean (± 1 SE) % litter mass loss corrected for loss from leaching of the 5 litter species with only microbial conditioning (microbe-only) and with either snail or tadpole consumers. Horizontal dashed lines denote mean % litter mass loss for each consumer across litter species. Different letters above bars indicate significant differences ($p \leq 0.05$). Single and double asterisks indicate marginal differences ($0.05 < p < 0.10$) between treatments with different numbers of asterisks. M = red maple, A = green ash, Co = cottonwood, Ca = reed canary grass, P = phragmites.

litter mass than phragmites and cottonwood, and maple and reed canary grass % litter mass losses were intermediate.

Assimilation efficiency

Litter species and consumer species significantly affected assimilation efficiency, but their interaction did not (Table 1, Fig. 2). Tadpoles had 8.2% higher assimilation efficiency than snails. Assimilation efficiency was 18.3 to 25.7% higher for cottonwood and phragmites litter than maple litter, and 22.5% higher for phragmites litter than ash litter.

Effects of litter species characteristics on litter mass loss and assimilation

Litter traits (Table 3) explained variation in % litter mass loss but not assimilation efficiency. In tadpole treatments, % litter mass loss was significantly related to litter C:P and C:N, but the model with C:P provided the best fit to the data (Fig. 3A, B, Table 4). In microbe-only and tadpole treatments, litter % mass loss and phenolic concentration tended to be negatively related ($p < 0.100$) (Table 4).

DISCUSSION

Our results extend our understanding of the functional roles of snails and tadpoles, which have classically been defined as herbivores. Inputs of leaf litter can either benefit or harm the survival and growth of snails and tadpoles (Brady and Turner 2010, Cohen et al. 2012, Earl et al. 2014). Our

study provides a potential mechanism underlying these associations, challenges long-standing assumptions of snail and tadpole herbivory, and expands the range of ecologically important detritivores (Batzer and Ruhí 2013). We demonstrated differential rates of detritivory on litter inputs of varying quality. Thus, our study adds to an increasing body of evidence suggesting that the quality of resource subsidies to freshwater systems is of equal importance to the quantity of those subsidies (Stoler and Relyea 2011, 2013, Cohen et al. 2012, Stephens et al. 2013, Cothran et al. 2014, Earl et al. 2014).

In the absence of large consumers, litter mass loss resulting from microbial conditioning varied substantially across litter species. Red maple and ash lost the least mass, and the 2 grass species lost the most mass. This pattern dif-

Table 2. Results of the analyses of variance examining the effects of litter species and the 2 macroconsumer species (i.e., snails and tadpoles) on % litter mass loss with and without consumer mass as a covariate.

Source	Without consumer mass		With consumer mass	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Litter species	8.13 _{4,20}	<0.001	8.57 _{4,19}	<0.001
Consumer species	19.33 _{1,20}	<0.001	0.55 _{1,19}	0.467
Litter × consumer	2.75 _{4,20}	0.057	2.69 _{4,19}	0.063
Consumer mass			1.23 _{1,19}	0.280

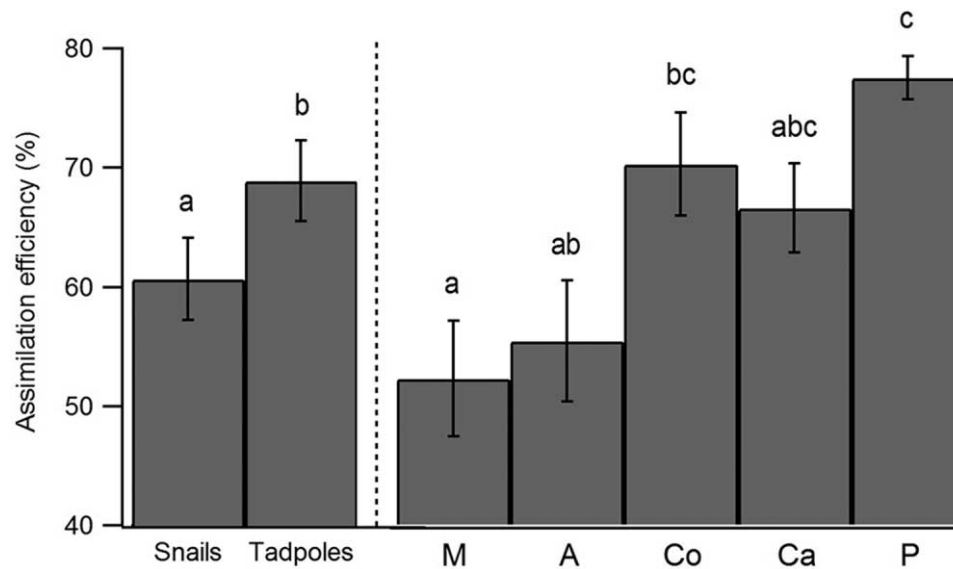


Figure 2. Mean (± 1 SE) assimilation efficiency by tadpoles and snails for the 5 litter species. Values to the right of the dashed line are mean assimilation efficiencies across all litter species for each consumer. Different letters above bars indicate significant differences ($p \leq 0.05$). M = red maple, A = green ash, Co = cottonwood, Ca = reed canary grass, P = phragmites.

fers from previously reported decay rates (Ostrofsky 1997, Bedford 2005, Gingerich and Anderson 2011), which indicated that cottonwood should exhibit the fastest rate of mass loss. However, many of our measured litter attributes also differed from previously reported values. The differences are not surprising, given the tremendous amount of intraspecific variation in litter chemistry (Martin and Blossey 2013). However, none of the leaf-litter attributes measured in our study could account for among-species differences in microbially mediated mass loss, and this result was surprising because variation in chemical and physical litter traits is known to influence rates of litter mass loss (Ostrofsky 1997). One possible explanation for this inconsistency is that our estimate of mass loss did not include a correction for the biomass of microbial growth on the litter surface. The biomass of microbial colonizers can reach up to 3% of total litter biomass in streams (Hieber and Gessner 2002), and this value is likely to be much higher in standing water. Thus, mass loss from some litter species (e.g., ash) might have been substantial, but microbial growth on the litter surface could have masked this effect. If this explanation is

correct, then addition of microbe-grazing consumers should reduce microbial biomass and substantially alter observed species-specific patterns of litter mass loss.

As hypothesized, the addition of consumers increased the rate of litter mass loss relative to the treatments with only microbes. Consumers actively grazed litter without producing leftover fragments, indicating that the increase in mass loss in the presence of macroconsumers was a consequence of direct consumption of litter rather than consumption of microbes on the surface of the litter. Tadpoles can engulf small fragments of litter (ABS, personal observation), and it is likely that the rasping action of the snail radula can bring small litter fragments into the digestive tract. Snails consumed more litter than tadpoles, but when consumer mass was added as a covariate to our model, differences between consumers became nonsignificant. Thus, rates of litter consumption probably were a simple, positive function of consumer biomass as predicted by metabolic theory (Brown et al. 2004). This result suggests that interspecific differences in anatomy and physiology were not major drivers of differences in consumption rates. Different detri-

Table 3. Results of chemical and structural assays for the 5 litter species in our study, including C:N, C:P, % phenolics, and leaf density. Leaf density is measured as the ratio of leaf toughness to leaf thickness.

Leaf species	C:N	C:P	Phenolics (%)	Leaf density	Mass loss from leaching (%)
Red maple	75.0	737.7	3.4	1.7	17.9
Green ash	19.6	215.9	0.0	2.3	18.4
Cottonwood	42.0	481.1	0.4	1.2	5.2
Reed canary grass	20.7	137.9	0.1	5.0	17.9
Phragmites	27.2	351.3	0.1	5.2	13.0

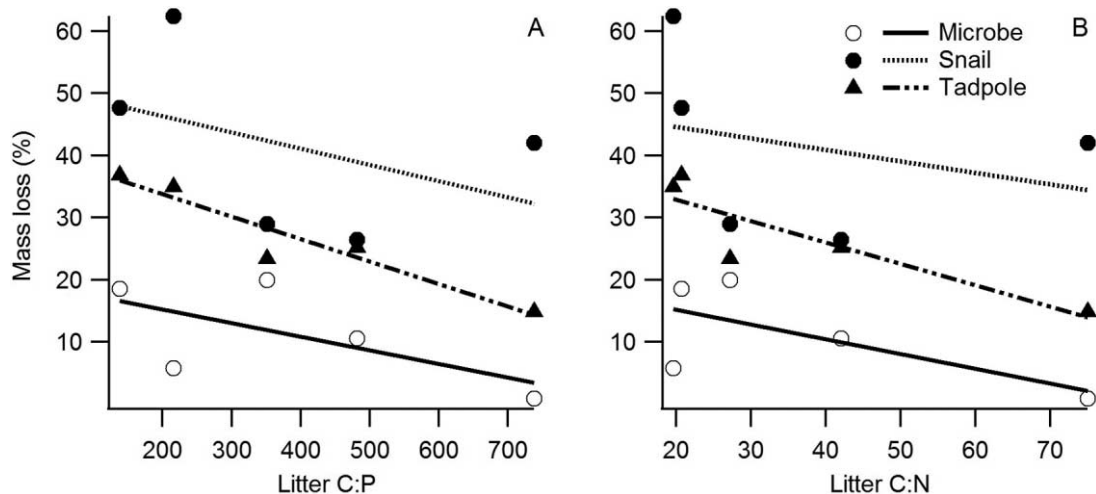


Figure 3. Percent litter mass loss vs litter C:P (A) and C:N (B) for microbe-only, snail, and tadpole treatments. Only the relationships between % litter mass loss and litter C:P and C:N for tadpole treatments were significant.

tivores certainly have subtle differences in feeding rates (Moore et al. 2004), but our results suggest that ecosystem function might be generally robust to changes in species composition so long as consumer biomass remains unchanged. Similar results have been found in streams (e.g., McKie and Malmqvist 2009), and more research is needed to assess whether if this pattern is a general trend across aquatic ecosystems.

As predicted, the actual amount of litter consumed by either consumer depended on the species of litter. Ash and reed canary grass litter lost the most mass in both consumer treatments, probably because of their relatively high nutritional quality (C:N and C:P). The relative magnitude of mass loss among litter species in our study is generally consistent with mass-loss values reported for the same litter species in a study by Stephens et al. (2013), who measured rates of litter mass loss in mesocosms containing foraging tadpoles. Overall mass loss was ~ 1.2 to $1.7\times$ greater across litter species in the study by Stephens et al. (2013) than in our study. The exception was red maple, which lost $3\times$ more mass in the study by Stephens et al. (2013) than in ours. However, Stephens et al. (2013) did not exclude mass loss from leaching from estimates of mass loss, and maple has a substantial amount of soluble C. This comparison suggests that consumptive mass loss can occur rapidly after consumers access the litter and that leachate is a significant component of total mass loss. Future investigators should consider potential implications of litter leaching for C cycling in ponds.

We found significant relationships between litter mass loss and nutrient content in tadpole treatments, but not in snail treatments. This pattern might indicate that tadpoles are slightly more nutrient limited than snails or that snails are limited by different nutrients than the ones we measured. Broad stoichiometric analyses of body nutrient composition in streams and wetlands indicate that *Lithobates*

[*Rana*] species are likely to have a more nutrient-rich body composition than snails (Vanni et al. 2002, Liess and Hillebrand 2005). Tadpoles also are in a phase of rapid growth relative to the adult snails used in our study and are likely to have higher nutrient demands for cell division (growth rate hypothesis; Sterner and Elser 2002) and bone deposition. Snails might be more limited by Ca which is needed for shell mass (Madsen 1987).

Snails and tadpoles assimilated leaf biomass and had similar assimilation efficiencies (52–78%). This result implies that direct consumption of litter by these species could be an important mechanism of energy transfer in wetland ecosystems. Tadpoles tended to have higher assimilation efficiencies than snails. This difference might reflect differences in digestive anatomy (e.g., longer gut length) between the consumers or higher energy and nutrient demands of tadpoles (Kemp and Hoyt 1969). Indeed, assimilation efficiency is likely to be highly consumer species-specific. Assimilation efficiency among tadpoles can range from 38 to 86% on a range of diets (Altig and McDearman 1975, Skelly and Golon 2003). More work is needed to identify potential physiological mechanisms underlying variation

Table 4. Results of linear mixed-effects regression analyses examining potential univariate fixed effects of litter attributes on litter mass loss for different consumer treatments. Only models with significant or nearly significant ($p < 0.1$) predictors are shown. AIC = Akaike's Information Criterion.

Consumer	Predictor variable	R^2	AIC	$F_{1,3}$	p
Tadpole	C:N	0.456	-20.43	10.92	0.046
	C:P	0.519	-22.25	14.01	0.033
	Phenolics	0.376	-18.34	7.82	0.068
Microbe-only	Phenolics	0.423	-23.64	9.52	0.054

in assimilation efficiency to understand the contribution of tadpoles and snails to litter decomposition.

The pattern of assimilation efficiencies for litter species did not necessarily mirror patterns of litter mass loss. In particular, assimilation efficiency of cottonwood and phragmites litter was relatively high, whereas the litter mass loss of these species was relatively low. These results concur with optimal digestion theory, which suggests that consuming more and assimilating less of a high-quality (i.e., high-nutrient content and easily digestible) resource can be energetically more favorable than expending energy to digest the more recalcitrant elements of that resource (Sibly 1981). Cottonwood and phragmites are both relatively low-quality litter species and had low mass loss but high assimilation efficiency. However, red maple litter mass loss and assimilation efficiency of litter were both relatively low, contradicting the prediction of optimal digestion theory. One possible explanation for this pattern is that the high phenolic content of red maple litter deterred consumer grazing and rendered ingested material relatively indigestible. These results indicate that multiple chemical attributes of the litter might interact to determine both litter mass loss and assimilation efficiency.

Implications for changes in wetland vegetation

Our study was conducted in simplified mesocosms, but our results suggest possible changes in decomposition and nutrient cycling that might occur in natural wetlands following shifts in the composition of forest plant communities. For example, ash populations are rapidly declining because of invasion by the emerald ash borer (MacFarlane and Meyer 2005). In contrast, maple populations are increasing in areas once dominated by oaks, which have been decimated by deer browsing, fire-suppression, and logging (Abrams 2003). Populations of nonnative phragmites strains also are increasing in North America, displacing native strains and other native wetland plants (Saltonstall 2002). These changes will directly affect litter species composition and chemistry of wetlands. Our results suggest that changes in litter chemistry will affect rates of litter mass loss and cycling of energy and nutrients in wetlands and that these changes might be mediated by consumer activity, density, and species composition. Further work will be required to understand the functional role of such consumers in a more natural context. For example, we need to understand the effects of litter leachates, which often contain chemicals that can both benefit and harm consumers (Earl et al. 2012). In addition, rates of litter consumption may be nonlinearly related to consumer density (Klemmer et al. 2012), and consumer interactions may facilitate litter decomposition by altering litter chemistry (Iwai et al. 2009). Future work should explore how litter consumption and assimilation drive this process.

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